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Optimal Harvesting Theory for Predator-Prey Metapopulations

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Declaration

This work contains no material which has been accepted for the award of any other degree in any university or other tertiary institution. To the best of my knowledge and belief, it contains no material previously written or published by any other person, except where due reference has been made in the text.

I give consent to this copy of my thesis, where deposited in the University Library, being available for loan and photocopying.

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1. Supriatna, A.K. and H.P. Possingham. Optimal harvesting for a predator-prey metapopulation. *Bulletin of Mathematical Biology* **60**(1): 49-65, 1998.
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5. Supriatna, A.K., G.N. Tuck and H.P. Possingham. Optimal harvesting strategies for metapopulations with delayed juvenile recruitment (in preparation).

Abstract

In this thesis I develop mathematical models of commercially exploited populations. I address the question of how to harvest a predator-prey metapopulation. Optimal harvesting strategies are found using dynamic programming and Lagrange multipliers. Rules about harvesting source/sink subpopulations, more/less vulnerable prey subpopulations and more/less efficient predator subpopulations are explored.

The results suggest that if one of the prey subpopulations is a relative source and exporter subpopulation then we should protect the relative source prey subpopulation in two ways: directly, with a higher escapement for the prey, and indirectly, with a lower escapement of the predator living in the same patch with this prey subpopulation. On the other hand, if there is no exporter/importer and source/sink hierarchy, and there is no biological variability except the vulnerability of the prey, then we should harvest the less vulnerable prey subpopulation more conservatively than the other prey subpopulation which is more vulnerable to predation. This is intuitive and agrees with a belief held by many fishery biologists that we should be more protective in dealing with critical subpopulations, such as those act as source subpopulations and those living in spawning and refugial areas. Furthermore, if the prey vulnerabilities of the two prey subpopulations are exactly the same, but the predator efficiencies differ between the two predator subpopulations, then we should harvest the prey living in the same patch with the relatively more efficient predator more conservatively than the other prey subpopulation. This result suggests that if the predator has a high biological efficiency, then we should leave enough prey to sustain the predator population. This rule is more apparent when the predator species more valuable than the prey species. In this case, a 'negative' harvest of the prey species might be optimal. A negative harvest might be considered a seeding or feeding strategy. This is not surprising considering the "bioeconomic role" of the prey population which can be converted into a more economically valuable species through the predator-prey interaction. I also discuss the costs of not harvesting the population properly, that is, if we did not realise that the population was a metapopulation.

Contents

Erratum[*]

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p. iv, l. 15:
Replace … those act …
with … those which act …

p. iv, l. 22:
Replace …species more valuable …
with …species is more valuable …

p. iv, l. 24:
Replace …might be considered a seeding …
with …might be considered as a seeding …

p. 1, ls. 24-25:
Replace …One of these factors is predator-prey interactions, …
with …One such factor is predator-prey interaction, …

p. 1, l. 30:
Replace …preyed on …
with …preyed upon …

p. 1, l. 31:
Replace …Getz and Haigh, 1989).
with …Getz and Haight, 1989).

p. 2, l. 33:
Replace …For example, …
with …An example is provided by …

p. 2, l. 45:
Replace …, that is, …
with …, namely, …

p. 4, ls. 11-12:
Replace … metapopulation models, the rationale is …
with … metapopulation models. The rationale for this is …

p. 4, l. 22:
Replace … is related to the patch where the juveniles come from.
with … is related to the patch where the juveniles originate.

p. 4, l. 25:
Replace … (Chapter 8) concludes the main results in this thesis, …
with … (Chapter 8) summarizes the main results in this thesis, …

p. 5, 7 ls. from bottom:
Replace … prey
with … prey population

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[*] This erratum follows errors brought to the attention of the candidate by the external examiners of the thesis.

p. 6, l. 9:
Replace … prey which is consumed by the predator …
with … prey consumed by the predator …

p. 6, 15 ls. from bottom:
Add Lotka (1925) also investigated a predator-prey model of the same form as in equations (2.1) and (2.2) independently and found similar results to that in Volterra (1926). For this reason, equations (2.1) and (2.2) are more known as Lotka-Volterra model.
after the last sentence in that paragraph.

p. 6, last line:
Replace … without the presence …
with … in the absence …

p. 8, l. 8:
Insert The dynamic behaviour and stability of a predator-prey system can be different in a discrete-time model. If there is a density dependence in both prey and predator populations then the stability condition is determined by the product of the predator coefficient (analogous to α in equation (2.1)) and conversion coefficient (analogous to β in equation (2.2)). Co-existence of the species is guaranteed if the instantaneous rates of growth of the prey (analogous to a in equation (2.1)) is positive (Basson and Fogarty, 1997).
between (Colling, 1995; Kohlmeier and Ebenhoh, 1995).
and The following section discusses …

p. 13, l. 19:
Replace … Krebs (1985) told us not to use …
with … Krebs (1985) recommended eschewing …

p. 13, 9 ls. from bottom:
Replace … among them are the instability of the population dynamics, it ignores all social and economics aspects …
with … among them are the instability of the population dynamics; the fact that it ignores all social and economic aspects …

p. 13, 6 ls. from bottom:
Replace Similarly, Wooster (1988) argued that the management …
with Similarly, Wooster (1988) argued that management …

p. 14, l. 5:
Replace …, to be under sole-ownership.
with …, to be under sole-ownership or its surrogate.

p. 14, ls. 26-27:
Replace …, was caused by the present value maximisation policy …
with …, might be caused by the present value maximisation policy …

p. 18, 10 ls. and 14 ls. from bottom:
Replace … Lotka-Volterra …
with … modified Lotka-Volterra …

p. 20, 10 ls. from bottom:

Replace … regenerates annually, like salmon.
with … regenerates seasonally, like salmon.

p. 22, l. 7:

Replace … Reed and Heras (1992) …
with … Reed and Echavarria (1992) …

p. 33, ls. 16-17:

Replace … the system reflects a Lotka-Volterra predator-prey interaction.
with … the system reflects a predator-prey interaction.

p. 33, 3 ls. from bottom:

Replace … is a discounting factor, …
with … is *per annum* discount factor, …

p. 34, ls. 6-7:

Replace … to remove H_x amount from …
with … to remove amount H_x from …

p. 37, l. 18:

Replace In some cases we only need to harvest either the prey or the predator population.
with In some cases only the prey population or only the predator population may be harvested.

p. 37, l. 23:

Replace Using present value maximisation, now the objective is …
with Using present value maximisation, the objective is …

p. 39, l. 10:

Replace Note that, predation is behaving like discounting.
with Note that, predation behaves like discounting.

p. 46, 18 ls. from bottom:

Replace The differences are due to the rounding error using integer numbers in dynamic programming while in the analytical method I use real numbers as the population sizes.
with The differences are due to using integer values for the numerical dynamic programming solution, and real numbers for the analytic method.

p. 83, ls. 20-21:

Replace How and to what extent does this prey population affect … predator.
with How and to what extent does this prey population affect … predator?

p. 240, l. 8:

Replace Reed, W. J. and H. E. Heras (1992) …
with Reed, W. J. and H. Echavarria H. (1992) …

p. 225, 6 ls. from bottom:

Add In regards to these rules, one could notice the potential effect of selective patch harvesting on genetic diversity. This will lead to a new avenue of research in the future.
after …source/sink, more/less vulnerable or more/less efficient.

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Chapter 1

Introduction

Human demands on resources have depleted world fish stocks. An example is the depletion of Antarctic blue whales, *Balaenoptera musculus*, to the edge of extinction, until the International Whaling Commission (IWC) banned the blue whale fishery in 1965 (Clark, 1990). The depletion of the Antarctic blue whale is an example of a negative effect of human exploitation on a renewable resource. To avoid unwanted impacts of the exploitation of natural resources, we need to guide their utilisation. In the case of fish and marine mammal exploitation, prudent fisheries management is needed.

Substantial efforts have been invested in science and research to obtain better management of the fishery industry (Parma *et al.*, 1998). However, mismanagement, over-fishing, and even stock collapse, have occurred in the industry (Danielson, 1997; Symes, 1997; Botsford *et al.*, 1997). Some fishery scientists believe that the major factors in the collapse of the fisheries industries are economic and political factors (Ludwig *et al.*, 1993; Holmes, 1994; Healey and Hennessey, 1998). Other scientists argue that other factors, such as unsound biological recommendations given by scientists, might equally have driven the fisheries to these undesirable situations (Danielson, 1997). For this reason, a much broader appreciation of general environmental and ecological conditions need to be acknowledged and accounted for in the process of management formulation (Frank and Leggett, 1994; Symes, 1997; Botsford *et al.*, 1997; Roughgarden, 1998).

Parma *et al.* (1998) pointed out that we may fail to recognise all possible factors that regulate the nature of biological resources, let alone include all of them in the process of management formulation. However, major factors that have significant effects on the dynamics and distributions of the resources have to be included. One of these factors is predator-prey interactions, which is increasingly credited as a factor which must not be excluded in understanding and managing biological populations. This is because of its role in regulating the nature of the populations (Jansen, 1994; Reynolds and Tapper, 1996; Christensen, 1996; Agnew, 1997). This is obvious for marine populations, since most exploited marine populations are part of a predator-prey interaction. Many fish prey on other fish and most species are preyed on, especially in their juvenile stage (Larkin, 1979; Getz and Haigh, 1989). Furthermore, many fishing industries target more than one species so that both species of predator-prey interaction may be harvested.

The exploitation of multi-species fisheries, such as fisheries with predator-prey interactions between species, is not well understood (Clark, 1976a; Stroud and Clepper, 1979; Goh, 1980; Pauly and Murphy, 1982; May, 1984; Hilborn and Walters, 1992).

Many scientists point out that appropriate policies for fisheries management are only possible if we have a comprehensive understanding of the underlying systems which are exploited (Yodzis, 1994; Botsford *et al.*, 1997). They also argue that management practices could be improved if we include interactions between species in developing multi-species models (Hall, 1998). For this reason, a number of scientists have tackled problems on predator-prey interactions in fisheries management (Larkin, 1966; Brauer and Sanchez, 1975; Brauer *et al.*, 1976; Clark, 1976a; Brauer and Soudack, 1978; Beddington and Cooke, 1982; Beddington *et al.*, 1985; Mesterton-Gibbons, 1988, 1996; Ströbele and Wacker, 1991; Murphy, 1995; Azar *et al.*, 1995; Degee and Grasman, 1998).

To improve our understanding of the exploitation of multi-species fisheries, including those having predator-prey interactions, we need to delineate all factors that may affect the decision on how we should manage those fisheries, and include these factors into models of the fisheries. Spatial heterogeneity is recognised as a factor that needs to be taken into account in population modelling in general (Rosen, 1977; Shukla and Das, 1982; Allen, 1983; Takeuchi, 1986; Wilson *et al.*, 1995; Cantrell and Cosner, 1998) and in fisheries modelling in particular (Beverton and Holt, 1957; May *et al.*, 1979; Clark, 1984, 1985c; Brown and Murray, 1992; Frank, 1992; Frank and Leggett, 1994). The inclusion of spatial heterogeneity in fisheries modelling may improve decisions in the management of those fisheries (Tuck and Possingham, 1994; Pelletier and Magal, 1996; Brown and Roughgarden, 1997; Botsford *et al.*, 1997).

The two most common frameworks for understanding the effects of spatial heterogeneity in ecological modelling are metapopulation theory and diffusion theory (Allen, 1983; Taylor, 1991; Nisbet *et al.*, 1993). Metapopulation theory assumes that suitable habitat exists in discrete patches while diffusion theory assumes spatially continuous habitat (Crowley, 1981). A population can be called a metapopulation if it has local populations (subpopulations) that are connected by dispersal of individuals. Hanski and Gilpin (1991) defined a local population as a group of individuals living in the same patch (habitat) and these individuals are different from the rest of the population. Metapopulation models can include variation between patch characteristics, e.g. patch size and patch quality, and between properties of local populations, e.g. fecundity and mortality (Day and Possingham, 1995).

All marine populations show some degree of spatial heterogeneity. For example, benthic marine invertebrate populations in which the species occurs in several isolated subpopulations of sessile adults that are connected by movement of their pelagic larvae. Sometimes this spatial heterogeneity means that modelling the species as one single population is not adequate. For example, abalone, *Haliotis rubra*, has a metapopulation structure with local populations connected by the dispersal of their larvae (Prince *et al.*, 1987, Prince, 1992). Brown and Murray (1992) and Shepherd and Brown (1993) argued that management for abalone should depend on the characteristics of local populations. Frank (1992) provided another example of metapopulation structure. He pointed out that fish stocks like the cod of Iceland and West Greenland which are separated by a large distance, and the two haddock stocks of the Scotian Shelf, are strongly coupled by the dispersal of individuals. He also suggested that those stocks possess the property described by Sinclair (1988) and Pulliam (1988), that is, persistence of the population in a sink habitat can be maintained by the migration from a source habitat (sink and source habitat are defined precisely in the next chapter). Furthermore, Frank and Leggett (1994) argued that the collapse of major fisheries such as North Atlantic cod and Atlantic and Pacific salmon, may due to the over-exploitation of the source population. If there is more than one subpopulation, a catch at a fixed rate can maintain the size of one subpopulation at a certain sustainable level, but, at the same time it may cause the size of the other subpopulation, for example the population with a lower larval production, to decline (Policansky and Magnuson, 1998).

Despite the importance of spatial heterogeneity, increasing the complexity of a population model by adding spatial heterogeneity is rarely done in fishery management modelling, even for single-species (Clark, 1984). Exceptions are Clark (1976a) and Tuck and Possingham (1994) for a single-species, and Hilborn and Walters (1987), Leung (1995), and Murphy (1995) for multi-species. Hilborn and Walters (1987) and Leung (1995) are the only authors who simultaneously considered spatial structure, ecological interactions and harvesting in their model.

In this thesis I present some models for spatially-structured predator-prey populations. I address the issues of spatial structure and predator-prey interactions, and study optimal harvesting for the populations. These issues are very important in the development of prudent management for the exploitations of natural resources. The work in this thesis explores two common features of biological populations simultaneously: biological interactions and spatial structure. It includes relevant features that occur in most fish populations, that is, predator-prey interactions, and takes into account the existence of the exchange of individuals between subpopulations, which is a common phenomenon in nature (Parma *et al.*, 1998). To illustrate the need for this kind of work, Parma *et al.* (1998) emphasised two of the ways in which a population model can be incorrect, that is, it either ignores the biological interactions between species, or ignores the spatial structure of the species.

I use a metapopulation approach to describe the spatial structure of the predator-prey system. The metapopulation approach is a framework within which we can study the movement of individuals between local populations and the consequences of this movement for the metapopulation, in this case for the optimal harvesting strategies of the metapopulation (Burke *et al.*, 1995). Using this approach, differences in the characteristics of local populations, like fecundity, mortality, vulnerability to predation etc, can be modelled explicitly. I obtain the optimal harvest for each local population which tells us how we should harvest a population if the management can be different for local populations. I use the same methods used by Tuck (1994) and Tuck and Possingham (1994) to build a single-species population model using coupled difference equations. They found the optimal harvesting strategies for the system using dynamic programming and the method of Lagrange multipliers, and they developed some rules of thumb on how to deal with source/sink and exporter/importer local populations. A similar approach is used in this thesis to find the optimal harvesting strategies for predator-prey metapopulations. Their rules of thumb for harvesting a single-species metapopulation are examined when predators are added to the system.

Thesis summary

Chapter 2 reviews the literature on predator-prey theory and harvesting theory. The chapter is intended to give some background about the concepts and definitions that are used in the subsequent chapters in this thesis. Results for the single-species population and the single-species metapopulation harvesting theory are discussed in detail to enable me to compare the results in this thesis with those previous results for single-species populations and single-species metapopulations. I derive optimal escapements for a discrete-time one-patch predator-prey population and discuss these escapements in details in Chapter 3.

In most of the thesis the model in Chapter 3 is extended to include spatial-heterogeneity in a variety of ways. Chapter 4 considers a model for a two-patch predator-prey metapopulation where the predator-prey interactions occur in the juvenile life-stages of the populations and the two patches are connected by the dispersal of juveniles. I then determine the optimal harvesting strategies for this predator-prey metapopulation. The strategies are compared to strategies where spatial structures are ignored, such as strategies from an unconnected two-patch predator-prey population and a well-mixed predator-prey population.

I also investigate optimal harvesting strategies for other predator-prey metapopulation models, the rationale is that I want to know how different, or how robust, the results presented in Chapter 4 are to the kind of interactions between the populations. Chapter 5 considers two-patch predator-prey metapopulations where the predator-prey interaction occurs in the adult life-stages of the populations and Chapter 7 considers two-patch predator-prey metapopulation where the adults migrate between patches.

In nature the juveniles of many exploited populations experience a delay in joining the adult class. In Chapter 6 I extend the predator-prey model in Chapter 5 by including a recruitment delay in juvenile recruitment to the adult class. Two different models of delay-recruitment predator-prey metapopulations are discussed. The first model assumes that the delay is related to the patch where the juveniles migrate and the second model assumes that the delay is related to the patch where the juveniles come from. Furthermore, in Chapter 7 I generalise the predator-prey model in Chapter 5 by including adult migration with M subpopulations. The last chapter in this thesis (Chapter 8) concludes the main results in this thesis, discusses how they relate to the previous results in harvesting theory, and suggests future directions for research.

Chapter 2

Review

In this chapter I review the literature on predator-prey and renewable resource exploitation, emphasising a modelling perspective. I introduce the concepts, definitions and notations that are used in the subsequent chapters, then I define the concept of a "metapopulation". In general, this chapter shows that optimal harvesting strategies for spatially-structured predator-prey populations have not been addressed explicitly. I begin the review with the following discussion on predator-prey theory followed by the review of the contribution of the concept of metapopulation to the development of the theory.

2.1 Predator-prey theory

Before I proceed further with the review of predator-prey population theory, I will define the following terms: population and predator-prey interaction. A population is a group of conspecific organisms living in the same place at the same time (Krebs, 1985; Smith, 1986). A predator-prey interaction is an interaction involving two or more species in which one or more species acts as predator and the other acts as prey. A predator is an animal that survives and reproduces by killing and eating other animals, while a prey is an animal that is killed and eaten by the predator. A more general definition of a predator-prey interaction is given by May (1976), who defined a predator-prey interaction as an interaction in which the number of one species becomes smaller due to the increasing number of the other species. Some predator-prey models are reviewed in the next section followed by the discussion of the role of spatial heterogeneity in the development of predator-prey theory.

2.1.1 Early development of predator-prey population theory

Early studies on predator-prey systems can be traced back to the work of Lotka (1925), Volterra (1926) and Gause (1934). Classic questions in predator-prey systems concern long-term behaviour of the interaction. For example, how many predators and how many prey will exist in the future if the initial conditions are known? Will the prey become extinct or will it survive? Is there a co-existence condition? If there is, what happens if predator or prey are added into the system? Is the system dynamically stable? (Luckinbill, 1973; Maly, 1975).

Gause (1934) studied the interaction between *Paramecium* and *Didinium* and showed that there are three different kinds of population dynamics arising from three different treatments of his laboratory experiment using one predator and one prey. In the first experiment the predator became extinct. In the second experiment both species became extinct, and the third experiment showed that the number of each species oscillates. In fact, before Gause (1934) showed that the number of individual prey and its predator oscillate, Volterra (1926) predicted this behaviour using a mathematical model.

Volterra's (1926) predator-prey model is deterministic. It assumes that the growth of prey without the presence of predators is exponential, and the growth of predators in the absence of prey is exponential decay. Furthermore, the number of prey which is consumed by the predator is assumed to be proportional to the product of the number of prey and predators, and the birth rate of the predators is also assumed to be proportional to the number of the prey which are consumed. The model takes form as a system of two differential equations

$$\frac{dN}{dt} = (a - \alpha P)N, \tag{2.1}$$

$$\frac{dP}{dt} = (-b + \beta N)P, \tag{2.2}$$

where N is the number of prey, P is the number of predators, a is the per-capita rate of increase of the prey in the absence of the predators, αN describes the number of prey which is consumed per predator per unit time, b is the per capita rate of the predator decay due to the dependency on the prey, and βN describes the per capita rate of predator production. Nicholson and Bailey (1935) proposed a discrete-time analog for host-parasitoid interaction similar to the Volterra's model. Becker (1973) provided some examples of stochastic predator-prey models and also explained some comparisons between these models and their analogous deterministic models.

Volterra's predator-prey differential equation system has a family of closed loops as its solutions which means that the number of individuals of both species fluctuates periodically. Different initial conditions may produce a different loop. In other words, its equilibrium exhibits neutrally stable cycles, and its solution depends on the initial value (see Figure 2.1.a). Volterra (1926) was able to use his model to explain why the selachians in the Adriatic Sea, which feed on some commercial fishes, have increased during the Word War I. During this time, fishing on commercial fish species almost completely closed. The closure of the fishery provided an abundance of food for the selachians, and caused a dramatic increase in their population size.

Although the Lotka-Volterra model can be regarded as an advance in ecological modelling, it does not satisfy many ecologists. Maynard-Smith and Slatkin (1973) pointed out three reasons why it is not satisfactory. First, in the Lotka-Volterra equations there is an assumption of continuous breeding for both predators and prey which is dependent on the rate of food intake, hence, there is no delay time between consumption and reproduction. Second, the assumption that the rate at which prey are consumed is proportional to the product of the density of prey and predators is too simple. Third, the absence of some upper limit to the number of prey in the absence of predators.

The Lotka-Volterra model has been revised by modifying equations (2.1) and (2.2). In the original Lotka-Volterra model the growth of the prey in the absence of the predator is assumed to be exponential, while the predator, in the absence of prey, experiences exponential decay. If it is assumed that there is a carrying capacity, K, in the growth of the prey without the presence of the predator, then the model is more

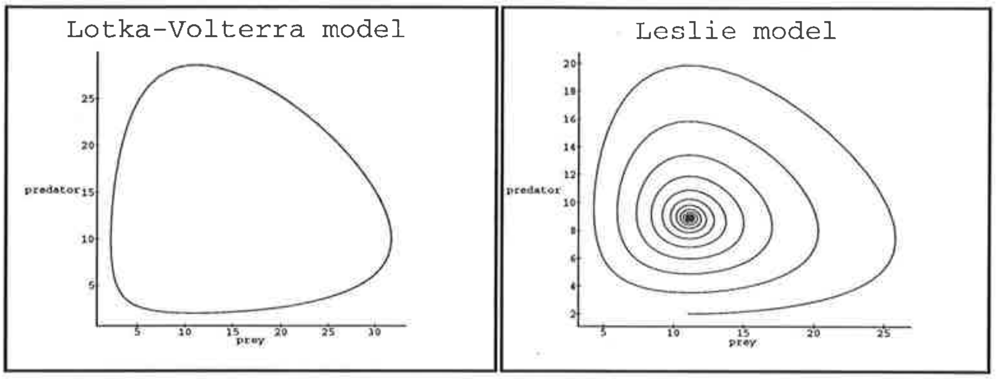
(a) (b)

Figure 2.1: The phase diagram for Lotka-Volterra predator-prey model with parameters $a = 1$, $b = 1$, $\alpha = 0.1$, and $\beta = 0.09$ with certain initial values (Figure 2.1.a). Figure 2.1.b is the phase diagram for a Leslie predator-prey model with prey carrying capacity $K = 100$ with all other parameters as in Lotka-Volterra model.

realistic; now the growth of the prey can be written as

$$\frac{dN}{dt} = r_1(1 - \frac{N}{K})N - \alpha_1 PN. \tag{2.3}$$

The solution for this model will be different from the solution in the original Lotka-Volterra model. With this modification the Lotka-Volterra system of equations (2.2) and (2.3) has a stable equilibrium. Another modification of the predator equation, suggested by Leslie (1948), has the form

$$\frac{dP}{dt} = s_1 P(1 - \beta_1 \frac{P}{N}). \tag{2.4}$$

The system of equations (2.3) and (2.4) still has a stable equilibrium point (Berryman, 1992; see also Figure 2.1.b).

A predator-prey system can be described in a general form

$$\frac{dN}{dt} = f(N)N - g(N,P)P, \tag{2.5}$$

$$\frac{dP}{dt} = \epsilon g(N,P)P - \mu P \tag{2.6}$$

(Ginzburg and Akçakaya, 1992; see Freedman (1980) for other forms of the general predator-prey model). In the Lotka-Volterra equation, $g(N,P) = \alpha N$ only depends on the number of prey population. In some cases it may depend on the number of the predators and other parameters. The function g is called the "functional response" or "trophic function" while ϵg is a "numerical response" (with trophic efficiency ϵ) which describes the per capita rate of prey attacked by and the per capita rate of birth of the predator as a result of eating the prey, respectively (May, 1976; Ehrlich and Roughgarden, 1987).

Some generalisations of the Lotka-Volterra equation have been carried out using various functional and numerical responses. This work was pioneered by Holling (1959,

1965) and Ivlev (1961) who showed the significance of these responses to predator-prey dynamics. A realistic model of a predator-prey system becomes more complex when the functional and numerical responses are non-linear functions of prey density. In extended models, the functional response can be a function of prey density, rate of searching, time during which the prey are exposed to the predator, and time spent for the predator to handle each prey (Glen, 1975). Other assumptions are introduced in further studies of predator-prey systems, for example prey refuges and cannibalism (Colling, 1995; Kohlmeier and Ebenhoh, 1995). The following section discusses the effects of spatial heterogeneity on the qualitative dynamics of predator-prey systems.

2.1.2 The role of spatial heterogeneity in predator-prey dynamics

The Lotka-Volterra equations assume that the population distribution of predator and prey are spatially homogeneous. This leads to an oscillatory solution of the system. The solution predicts the periodic fluctuation of the population and agrees with many experimental results (Taylor, 1991). Comins and Blatt (1974) showed that results from a spatially homogeneous predator-prey system may be different to results from a spatially heterogeneous system. For example, they studied the effect of predator and prey movements due to habitat variations and they found that the solution of the system is no longer cyclical as in the original Lotka-Volterra model.

Despite the importance of spatial heterogeneity in predator-prey systems, Caswell and Etter (1993) found that few authors have considered this. Some of the authors who have tackled the problem of spatial heterogeneity in a predator-prey system are McMurtrie (1978), Voller (1990), Timm and Okubo (1992), Casal *et al.* (1994) and Jansen (1994). Their work was able to explain the stabilisation effect observed in Huffaker's (1958) experiment, which is otherwise difficult to explained using a spatially homogeneous predator-prey model. Most of the authors studied spatially-structured predator-prey populations using diffusion theory, on a one dimensional axis. However, Sabelis *et al.* (1991) pointed out that there might be patchy patterns in predator-prey systems, in which the spatial structure occurs discretely. For this reason, diffusion theory may be less appealing in describing such a system. A common approach to modelling a discrete spatial structure for a population is to use the idea of a metapopulation. I discuss the background of metapopulation theory as it applies to predator-prey systems in the following section.

2.1.3 What is a predator-prey metapopulation?

In nature many populations are spatially-structured and are made up of smaller populations inhabiting different patches of habitat known as local populations or subpopulations. These subpopulations are often connected by movement of individuals (e.g. dispersal of juveniles, see Figure 2.2). Hanski and Gilpin (1991) used the term *metapopulation* to refer to a population which has a patchy spatial structure, and defined it as a population of populations. A metapopulation falls between two extremes of possible population structures: a well-mixed population and an unconnected collection of populations (Harrison, 1991; Day, 1995; McCulough, 1996). In a metapopulation, the interaction between individuals within a patch ("intra-patch interaction") should occur more frequently than interactions between individuals from different patches ("inter-patch interaction"). If there is no migration between patches, then the population is a

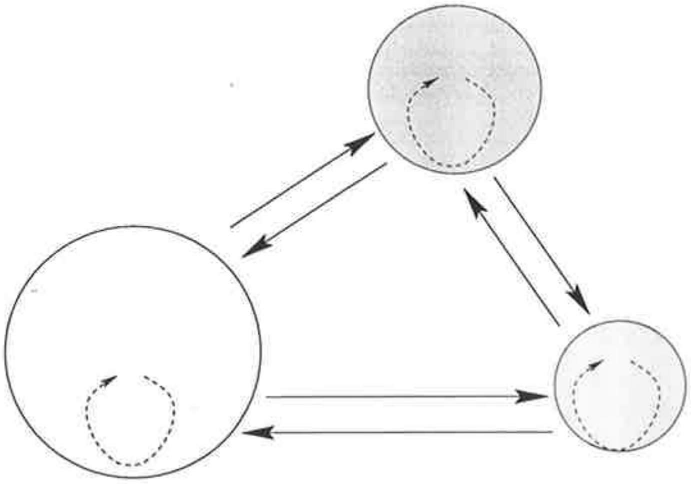

Figure 2.2: A metapopulation made up of three subpopulations. Lines indicate migration of individuals between patches. Dashes indicate movement of individuals within a patch. The different sizes indicate that subpopulations may vary in size and characteristics.

collection of unconnected populations. However, the population is better considered as a single well-mixed population if migration between patches is very common (Hanski and Thomas, 1994; Day, 1995).

Early studies of metapopulation dynamics concentrated on the dynamics of patch-occupancy, that is, the study of extinction and recolonisation of patches or habitats by the populations, like the study of Levins (1969). Levins (1969) made a clear distinction between the dynamics of a (regular) population, which deals with the number of individuals, from the dynamics of a set of populations, which deals with the number of extant subpopulations. Levins (1969) proposed the model

$$\frac{dp}{dt} = mp(1-p) - ep, \tag{2.7}$$

where p denotes the proportion of population sites which is inhabited by a certain species. This proportion is a function of time t, that is, $p = p(t)$. The rate of local extinction and colonisation of empty patches is given by e and m respectively. The model assumes that the whole population has a discrete spatial structure, that is, each subpopulation inhabits a patch with discrete boundaries, every patch is identical, and the population within each patch is assumed to be homogeneous and well-mixed (Day, 1995). Although in nature there is no real metapopulation which perfectly meets all these assumptions (Hanski and Gilpin, 1997), many populations are known to form a metapopulation structure, to some extent, for example they have several subpopulations and these subpopulations are connected by the dispersal of individuals. Examples of metapopulations of commercial fisheries are documented in Tuck (1994), some of them are occupying positions either as prey or predator in complex food-webs as described by Jones (1982), Estes and Van Blaricom (1985), Tegner *et al.* (1989), and Kojima (1990) [see Table 2.1].

Hanski and Gilpin (1991) noted that Levins' model is analogous to the logistic model for population growth, that is, equation (2.7) can be written in the form

$$\frac{dp}{dt} = (m-e)p(1 - \frac{p}{(1-\frac{e}{m})}). \tag{2.8}$$

Organism:	Reference:
Sea urchin	Karlson and Levitan, 1990
Sea hare	Pennings, 1991
Scallop	Orensanz *et al.*, 1991
Copepod	Kurdziel and Bell, 1992
Scotian Shelf haddock	Frank, 1992
Iceland and West Greenland cod	Frank, 1992
Abalone	Shepherd and Brown, 1993
Red sea urchin	Quinn *et al.*, 1993
North Atlantic cod	Frank and Leggett, 1994
Slider turtles	Burke *et al.*, 1995
Sturgeon fish	Planes *et al.*, 1996
Barnacles	Brown and Roughgarden, 1997
Pacific salmon	Policansky and Magnuson, 1998

Table 2.1: Some known metapopulations of commercial fish.

While Levins' model deals with a single-species, in nature it is possible that one site or one habitat is occupied by two or more different species which in turn may depend on each other. A metapopulation which describes this interaction is often called a *metacommunity*. I review some models of metacommunities in the following section. A complete review of single-species metapopulation theory can be found in Gilpin and Hanski (1991) and Hanski and Gilpin (1997).

Some examples of works attempting to understand metacommunities for predator-prey interaction have been done by Sabelis *et al.* (1991), Nachman (1991), and Taylor (1991). Following Levins (1969), Sabelis *et al.* (1991) studied the extension of Lotka-Volterra models for predator-prey systems using the number of resource patches occupied by predators and prey instead of the numbers of the predators and the prey themselves as state variables. Their equations to describe predator-prey systems in a patchy environment are

$$\frac{dN}{dt} = aN - bNM - cN, \tag{2.9}$$

$$\frac{dM}{dt} = bNM - dN, \tag{2.10}$$

where N and M denotes the number of patches occupied by prey and predator respectively, a denotes the rate of successful colonisation of dispersing prey from prey population into empty patches. The rate of predator invasion to patches occupied by prey is bM, where b is a "reaction coefficient", and c and d respectively represent the rate of prey and predator population extinction.

Sabelis *et al.*'s (1991) model is analytically tractable and it has a neutrally stable equilibrium point. This is not surprising because this system of equations is equivalent to a Lotka-Volterra predator-prey system which also has a neutrally stable equilibrium (Sabelis *et al.*, 1991). Furthermore, they concluded that the stabilising effect on the global predator-prey interaction may be caused by "a prey dispersal phase of non-negligible duration" (p. 272). The same result is also suggested by Diekmann (1993). These two results indicate the significant influence of individual movement between patches on the dynamics of the whole system.

Levins' model focuses on the dynamics of subpopulations. Several authors also consider the abundance of individuals in each subpopulation (St. Amant, 1970; Nisbet *et al.*, 1993). St. Amant (1970) developed a predator-prey system, to model the relationship between mussel clumps and starfish, using the system of equations

$$\frac{dN_i}{dt} = a_i N_i - \alpha_i N_i P_i + p_{ji} N_j, \tag{2.11}$$

$$\frac{dP_i}{dt} = -b_i P_i + \beta_i N_i P_i + q_{ji} P_j, \tag{2.12}$$

where N_i and P_i denote the number of prey and predators in patch i, respectively, and p_{ji} and q_{ji} denote the rate of prey and predator migration from patch j to patch i, respectively. Assuming the model has a positive equilibrium value, St. Amant (1970) proved that the hypothetical equilibrium value is stable (Murdoch and Stewart-Oaten, 1975). This result is different from the result of the original Lotka-Volterra model, which has a neutrally stable equilibrium point (Figure 2.1.a). Therefore, the migration introduced by St. Amant stabilises the Lotka-Volterra predator-prey system. St. Amant's model assumes that immigrants only affect the number of animals in the destination patch and do not interact with the local population in the destination patch. However, if the interaction between the immigrants and the local population is taken into account, then migration does not always stabilise the system (Allen, 1975).

Allen (1975) suggested a spatially-structured predator-prey model in which it is assumed that immigrating predators interact with local prey and local predators interact with immigrating prey. The model is

$$\begin{aligned} \frac{dN_i}{dt} &= -\alpha_i(p_{ii}N_i q_{ii}P_i + p_{ii}N_i q_{ji}P_j + p_{ji}N_j q_{ii}P_i + p_{ji}N_j q_{ji}P_j) \\ &\quad + a_i(p_{ii}N_i + p_{ji}N_j), \end{aligned} \tag{2.13}$$

$$\frac{dP_i}{dt} = \beta_i(p_{ii}N_i q_{ii}P_i + p_{ii}N_i q_{ji}P_j + p_{ji}N_j q_{ii}P_i + p_{ji}N_j q_{ji}P_j), \tag{2.14}$$

where p_{ij} and q_{ij} denotes the probability of prey and predator moving from patch i to patch j, respectively, and $i = 1, 2$. Unlike St. Amant (1970), in which the equilibrium point is hypothetical, Allen (1975) found the equilibrium population size of the system. In some cases this equilibrium population size might be unstable, however, Allen (1975) believed that this instability is temporary and the orbit eventually will be trapped by a stable limit cycle (May, 1972).

St. Amant (1970) and Allen (1975) assumed that emigration is lumped together with other parameters. Chewning (1975) introduced emigration explicitly and assumed that the populations may be distributed unevenly, that is, each subpopulation has different dynamics. However, unlike Allen (1975), in Chewning's (1975) model immigrating predators do not interact with local prey and local predators do not interact with immigrating prey. Chewning's model for a two-patch predator-prey system is

$$\frac{dN_i}{dt} = k(N_i - N_i P_i) + p_{ji} N_j - p_{ij} N_i, \tag{2.15}$$

$$\frac{dP_i}{dt} = k(-P_i + N_i P_i) + q_{ji} P_j - q_{ij} P_i, \tag{2.16}$$

where p_{ij} and q_{ij} respectively denotes the instantaneous migration rate of the prey and the predator from patch i to patch j, $i = 1, 2$, $j = 1, 2$. The k ($k = i$) on the right hand side of equations (2.15) and (2.16) is indicating that the populations are distributed unevenly.

Chewning (1975) found that for a small migration rate between patches, a stabilising effect exists if at least one species migrates from patch one and at least one species migrates from patch two, that is, $p_{ij} + q_{ij} > 0$ for $i = 1, 2$ and $j = 1, 2$. Furthermore, if both patches are identical, that is, $p_{ij} = p_{ji}$ and $q_{ij} = q_{ji}$, then the stabilising effects on the equilibrium no longer exist, but the populations oscillate. Chewning (1975) also provided some conditions under which the more general k-patch predator-prey metapopulation is stabilised by low migration rates. Zeigler (1977) modified Chewning's model to include logistic growth of the prey population, similar to Leslie's predator-prey model.

Other metapopulation models of predator-prey interactions can be found in Auger and Faivre (1993) and Pogialle *et al.* (1995), in which they investigated the effects of migration if it is assumed that animals move from one patch to another patch several times in certain periods. They explored the system of equations

$$\frac{dN_i}{dt} = a_i N_i + (p_{ji} N_j - p_{ij} N_i) - (p_{ii} P_i + p_{ji} P_j) N_i, \tag{2.17}$$

$$\frac{dP_i}{dt} = -b_i P_i + (q_{ji} P_j - q_{ij} P_i) + (q_{ii} N_i + q_{ji} N_j) P_i, \tag{2.18}$$

which has quasi-periodic trajectories as the solution.

The original Lotka-Volterra model and all the predator-prey metapopulation models derived from the Lotka-Volterra model discussed above are continuous-time population models. In many cases, population systems are more conveniently modelled by difference equations, especially when biological or non-biological mechanisms take place periodically, such as seasonal recruitment and periodic exploitation (Basson and Fogarty, 1996). Many predator-prey interactions have been explored in discrete-time populations models (Maynard-Smith and Slatkin, 1973; Beddington *et al.*, 1975; Beddington and Free, 1976; Hasting, 1984; Neubert and Kot, 1992; Basson and Fogarty, 1996). Some of them focus on the effects of exploitation on the dynamics of predator-prey systems (Basson and Fogarty, 1996). However, the important question of how to harvest a predator-prey metapopulation has received less attention.

In this thesis I study predator-prey metapopulations, in discrete-time deterministic models, emphasising the optimal harvesting strategies of the metapopulations. The predator-prey metapopulations are extensions of Tuck and Possingham's (1994) single-species metapopulation

$$N_{i(k+1)} = a_i N_{ik} + p_{ii} F_i(N_{ik}) + p_{ji} F_j(N_{jk}), \tag{2.19}$$

to include Lotka-Volterra's predation terms, like those in equations (2.1) and (2.2). In the following section I review the literature on optimal harvesting and define some concepts and symbols that I use in the subsequent chapters.

2.2 Bioeconomics modelling in fisheries management

What is fisheries management? Royce (1984) defined fishery management as an action which uses scientific knowledge for human benefits in connection with the exploitation of the living resources of the water. This includes marine, estuarine and freshwater habitats. In this context, fisheries management science is defined as the body of knowledge which relates to the management of living resources in the water. It is an interdisciplinary field that includes biologists, economists, politicians and mathematicians (Cunningham, 1981). This collaboration among scientists from different disciplines has lead to the emergence of a relatively new body of scientific research – *bioeconomics*, the science that "deals with the economics of the utilisation of biological resources" (Clark, 1990; Reed, 1991). In this case, biological resources means resources which have a capability for regeneration (Conrad, 1980), which is the nature of all living resources.

There are two different approaches to understanding the phenomena of nature. Van Dyne (1969) recognised them as conceptual or methodological tools and mathematical or analytical tools. The methodological approach should follow the sequence: real world problem recognition, hypothesis designing, physical experiment execution, data analysis, interpretation of the results, and conclusion. While the second approach, a mathematical approach, needs a model from the abstraction of the real problem, model analysis using available mathematical arguments, and interpretation of the resulting mathematical solution into the original problem (Van Dyne, 1969). There are advantages and disadvantages in the use of mathematical models as a tool in resource management, to the extent that Krebs (1985) told us not to use any mathematical models to understand the paradigms of population regulation, or at least be very cautious in believing results from mathematical models (Soulé, 1987). On the other hand, many influential works in resource management researches use mathematical models (Hotelling, 1931; Gordon, 1954; Ricker, 1954; Schaefer, 1954; Clark, 1976a; Reed, 1979). One of the strengths of mathematical modelling is that we can predict the influence of a change in an external variable, e.g. exploitation intensity, on the ecological systems which are observed, in this case the resource, without doing a large scale experiment (Jørgensen, 1983). This prediction may give a better insight into how we should perform the management of the resource. In this thesis I discuss fishery management using mathematical models.

What are the precise objectives of fishery management? Cunningham (1981) reviewed the evolution of fishery management objectives from classic maximum sustainable yield, which is extensively criticised but still very popular in practice, to modern active-adaptive control management. At least until two decades ago, the practice of renewable resource management was based on the concept of Maximum Sustainable Yield (MSY). This concept was first proposed by Graham (1935), the idea being to obtain the maximum steady state harvest. Ricker (1946) called this harvest a maximum sustainable yield and Schaefer (1954, 1957) formalised the concept mathematically. Despite the common practices of MSY as an objective in managing renewable resources, the concept of MSY itself received many critics for numerous reasons (Roedel, 1975; Clark, 1976a; Larkin, 1977; May *et al.*, 1979; Cunningham, 1981; Eltringham, 1984). Conrad and Clark (1987) listed some of the problems with the concept of MSY, among them are the instability of the population dynamics, it ignores all social and economics aspects and does not make logical sense in harvesting ecologically and economically interdependent multi-species fisheries. Similarly, Wooster (1988) argued that the management should try to maximise benefits to society not fish, hence it should incorporate economic considerations.

Gordon (1954) was the first to add economic considerations into the analysis of renewable resource exploitation. He argued that in open-access or common-property stock exploitation there is a stable "bionomic equilibrium" E_∞ at which total revenue from the resource exactly equals total cost to harvest the resource. In this situation, fishers join the open-access fishery if they are making profit until no one is making a profit. This situation is known as "the tragedy of the commons" (Hardin, 1968). For this reason, Gordon (1954) suggested that it is important for resources, or sections of a resource, to be under sole-ownership.

In the presence of sole-ownership, using the concept of maximum economic yield (MEY) proposed by Gordon (1954), there would be a level of harvesting effort at which the marginal rate of net revenue from the resource is maximised. Gordon's (1954) work provides a solution for over-fishing and it is also able to differentiate economic over-fishing, which occurs in any open-access fishery, from biological over-fishing, which occurs if the ratio of price to cost is high enough (Clark, 1985a). However, the model is not adequate due to its static formulation. It overlooks the important of inter-temporal economic benefits and the biological processes of the resource (Clark, 1976a). Other authors who have attempted to describe policies that will prevent over-fishing are Clark (1980) with restricted access policy and Gatto and Ghezzi (1992) with their tax regulation policy.

Smith (1969) proposed a dynamic version of the Gordon and Schaefer model for an open-access fishery, however, an optimal solution for managing renewable resources was not established until Clark (1971, 1973) devised an optimal harvesting strategy for a single-species population almost four decades after the same idea was proposed for non-renewable resource exploitation by Hotelling (1931). Clark's approach to renewable resource exploitation is known as "present value maximisation" (PVM). Clark (1973) demonstrated that if the growth rate of the resource is less than the discounting rate, then a rational sole-owner of the resource would exploit the resource to extinction. Extinction of the exploited population is only optimal when present value maximisation is used. The depletion of the Antarctic blue whale, *Balaenoptera musculus*, was caused by the present value maximisation policy (Clark, 1973). Depletion as a result of a high discounting rate is also known in the exploitation of any other stocks (Heal, 1985).

Clark's (1973) paper has been very influential in the development of the economic theory of renewable resource exploitation and disproved the belief of some economists, like Turvey (1964), who said that dynamic consideration of resource management only complicates matters and does not give any new significant result (Munro, 1992). The paper has pioneered a new era of fishery management within a capital investment framework (Clark and Munro, 1975; Clark *et al.*, 1979; Clark, 1985b; Conrad and Clark, 1987) and has been extended to include various economic and biological complexities (Reed, 1979, 1982; Agnew, 1982; Gatto *et al.*, 1982; Clark and Tait, 1982; Ludwig and Walters, 1982; Charles, 1983; Chaudhuri, 1986; Mesterton-Gibbons, 1987, 1988, 1996; Lovejoy, 1988; Clark, 1990; Reed and Heras, 1992; Botsford, 1992; Tuck and Possingham, 1994; Ganguly and Chaudhuri, 1995).

In the following section, the development of mathematical models of renewable resource exploitation are described in detail. This includes the three most common objectives in fishery management, maximum sustainable yield (MSY), maximum economic yield (MEY) and maximum present value (MPV). I discuss different types of model formulation such as continuous-time and discrete-time models, single-species and multi-species models, and spatially homogeneous and spatially heterogeneous models.

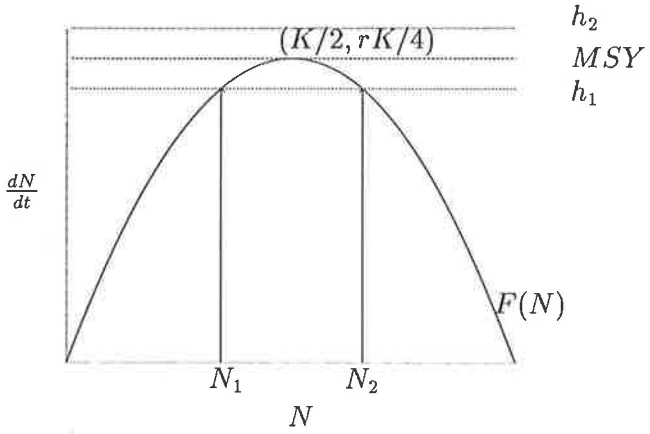

Figure 2.3: Maximum sustainable yield (MSY).

2.2.1 Single-species fisheries continuous-time models

In this section, I review the development of bioeconomic models. The material in this section can be found in more detail in Clark (1976a) which is the classic book on the theory of renewable resource management.

Schaefer (1954) proposed a model of fish population dynamics and assumed that the growth of the fish population is logistic. If N denotes the number of fish, the Schaefer model is

$$\frac{dN}{dt} = F(N) = rN\left(1 - \frac{N}{K}\right), \tag{2.20}$$

where r is the per capita intrinsic growth rate of the fish and K is the natural or environmental carrying capacity. $F(N)$ is known as the surplus production function. Schaefer's (1954) surplus production function is a special case of a more general form proposed by Pella and Tomlinson (1969). Fishing is introduced to the model using a harvesting rate $h(E, N)$, that is the harvest rate is a function of fish population N and fishing effort E. The dynamics of the fished population is

$$\frac{dN}{dt} = F(N) - h(E, N). \tag{2.21}$$

According to Schaefer (also Russell (1931) and Graham (1935)), a stable harvesting strategy will ensure

$$\frac{dN}{dt} = 0, \tag{2.22}$$

that is, we should harvest the fish population to a point at which the size of the population is neither increasing nor decreasing. Schaefer called the catch satisfying this condition the "maximum equilibrium catch", however the popular name is "maximum sustainable yield" (first coined by Ricker (1946)).

Some features of MSY are illustrated in Figure 2.3. Assume that the harvesting rate is constant, that is, $h(E, N) = h \equiv \textit{constant}$. At equilibrium we obtain

$$h = F(N) = rN\left(1 - \frac{N}{K}\right). \tag{2.23}$$

To find the MSY choose N that maximises h, say N^*. Substitute N^* back to equation (2.23) to produce h^* which is the MSY. With this procedure, we find $N^* = K/2$ and $h^* = rK/4$. If the MSY of the population can be determined exactly, then harvesting at the level MSY, that is, $h = h^*$, does not change the size of the population in the long-term, because the natural growth is zero, if the population is in its equilibrium $N^* = K/2$. If the population size is more than the equilibrium, long-term harvesting at MSY level drives the population to this equilibrium. However, if the population size is less than the equilibrium, harvesting drives the population to extinction. Hence, this equilibrium is "semi-stable". Furthermore, in practice, the exact value of the MSY is difficult to determine. We only can estimate it roughly. Let us assume we have estimated h^* as the MSY. If we are harvesting at a slightly lower rate, h_1, than the MSY, then we would drive the population to a stable equilibrium size N_2 if the initial population size is higher than N_1 and drive the population to extinction if the initial population size is less than N_1. If, however, we are harvesting at a slightly higher rate, h_2, than the MSY, then we would drive the population to extinction regardless of the initial population size before harvesting begins. Harvesting the population at the level of its MSY, theoretically, is the best strategy, from the point of producing food in the long-term, but due to the difficulty in finding its exact value and its instability, harvesting at the level of MSY is risky. This is one of the limitations of the MSY harvesting strategy (Clark, 1976a; Larkin, 1977; May *et al.* 1979; Cunningham, 1981; Caddy and Mahon, 1995). Other limitations are that MSY ignores economic considerations and the fact most fisheries are multi-species (Clark, 1984, 1985a).

Now assume that the rate of harvesting is not constant but is a function of effort, that is, $h(E, N) = qEN$ where q is catchability coefficient. This is more likely for most species where effort tends to be fixed by the number of ships. For simplicity assume $q = 1$. Equation (2.21) now becomes

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - EN. \tag{2.24}$$

The equilibrium population size is found when $\dot{N} = 0$, that is,

$$N^* = K\left(1 - \frac{E^*}{r}\right) \tag{2.25}$$

for a fixed effort $E = E^*$, with another equilibrium at $N^* = 0$ which means extinction of the population. As before, this equilibrium is stable (see Figure 2.4). Assume $r < E^*$, the equilibrium harvest is

$$h = E^*N^* = E^*K\left(1 - \frac{E^*}{r}\right). \tag{2.26}$$

This harvest is a "sustainable yield" and its graph is called a "yield-effort curve" (Clark, 1976a). It can be seen in Figure 2.4 that increasing the level of effort from E' to E'' increases the yield h' to h'' until it reaches the maximum harvest MSY$= maxF(N) = rK/4$ at

$$N_{MSY} = K/2, \tag{2.27}$$

or equivalently

$$E_{MSY} = r/2. \tag{2.28}$$

Increasing or decreasing the level of effort beyond the threshold level $E = r/2$ decreases the yield.

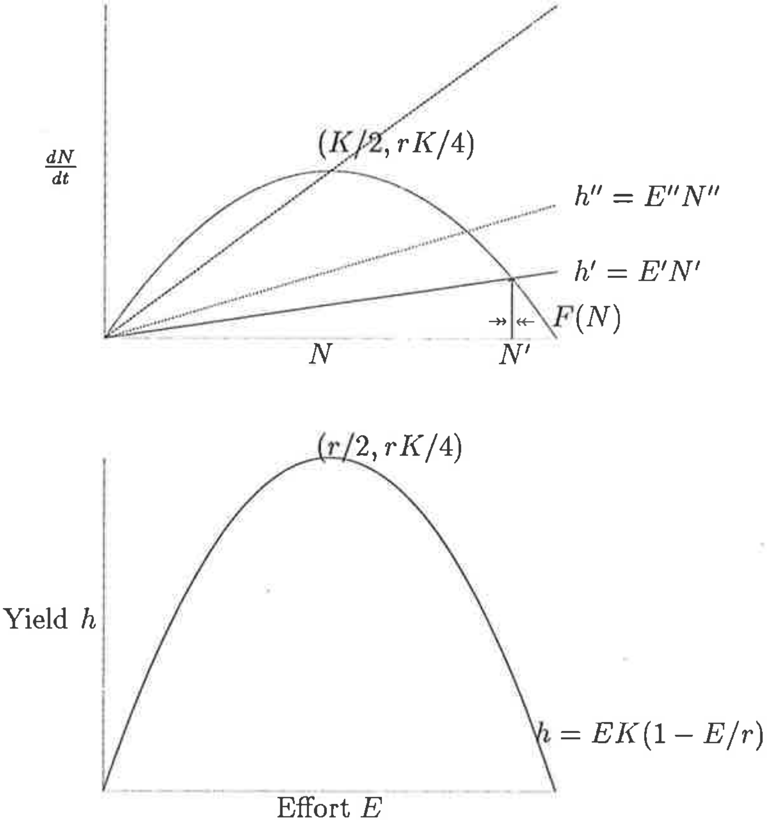

Figure 2.4: Yield as a function of population size and effort (upper figure) and "yield-effort curve" (lower figure). Details are in text.

Gordon (1954) analysed the effect of effort on the resulting yield, if economics is incorporated, based on Schaefer's yield-effort curve. Gordon (1954) assumed the price per unit harvested fish is constant and the cost to harvest the fish is proportional to the amount of effort that is spent. So revenue is

$$R = ph(E) = pEN \tag{2.29}$$

and cost is

$$C = cE. \tag{2.30}$$

The graph of the revenue is similar to the graph of yield effort, that is, quadratic with linear cost, with respect to effort (see Figure 2.5).

Maximum economic yield (MEY) is the yield that maximises the difference between revenue and cost. Let E_{MEY} be the effort that generates MEY. To find E_{MEY}, solve the equations $\frac{\partial(R(E)-C(E))}{\partial E} = 0$ and $\frac{\partial(R(E)-C(E))}{\partial N} = 0$ to give

$$E_{MEY} = \frac{Kp - cr}{2Kp} \tag{2.31}$$

and

$$N_{MEY} = \frac{Kp + c}{2p}. \tag{2.32}$$

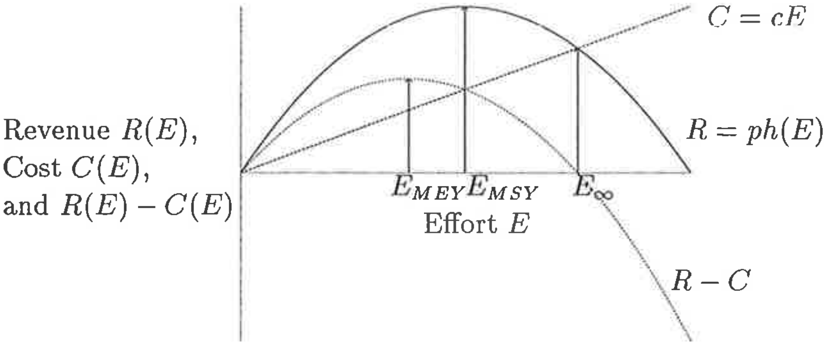

Figure 2.5: Relationship among E_{MSY}, E_{MEY} and bionomic equilibrium E_∞.

This yield is a suitable objective of a sole-owner. However, in an open-access fishery, Gordon (1954) argued that "bionomic equilibrium" E_∞ occurs (see Figure 2.5). This is because, if $C(E) < R(E)$ then more fishers will join the fishery. This is a stable equilibrium effort which maintains the level of revenue exactly the same as the level of cost in a long-term unregulated fishery. At this point, the marginal revenue equals the marginal value of cost. By solving equation $R(E) - C(E) = 0$, a bionomic equilibrium is found at the effort

$$E_\infty = \frac{Kp - cr}{Kp} \tag{2.33}$$

and bionomic equilibrium population size

$$N_\infty = \frac{c}{p}. \tag{2.34}$$

Figure 2.5 shows that E_{MEY} is always lower than E_{MSY} and E_∞. As a result, a harvesting policy based on MEY is more conservative than that derived from MSY.

Both MSY and MEY are static. They do not consider harvesting over time. Schaefer (1954) looked at the effect of fishing effort on the dynamics of exploited fish populations. Schaefer used Lotka-Volterra predator-prey interactions to describe the dynamics of fish populations (prey) and fishing effort (predator). The model is able to explain the relationship between fishing intensity and the mean population of Californian sardine. A spiral trajectory to a stable equilibrium for that population is observed as predicted by the solution of the Lotka-Volterra predator-prey system (Schaefer, 1954; see also McGarvey, 1994, 1995). Smith (1969) developed a similar model applied to open-access fishery and the model is able to describe oscillations in the North Pacific fur seal fishery (Clark, 1985). Schaefer's (1954) and Smith's (1969) predator-prey models can describe the growth and the decline of a fishery. Schaefer's (1954) and Gordon's (1954) models predict that extinction of an exploited population is never optimal. However, Clark (1971, 1973) showed that this belief can be misleading. He argued that a rational sole-owner, in certain circumstances, may drive the population deliberately to extinction, if we maximise the economic rent from the fishery over time (dynamically). In a dynamic context, the total present value or economic rent from the fishery over time is

$$PV = \int_0^{\infty} e^{-\delta t}(p(t) - c)E(t)dt, \tag{2.35}$$

where δ is a discounting rate and c is a decreasing function of the population. Assuming $\delta = 10\%$, the inclusion of the discounting rate means one dollar now is worth about two dollars in seven years time.

Clark (1971, 1976a) found an implicit expression for the optimal population level, N^*, that maximises net present value PV in the form

$$\delta = F'(N^*) + \frac{c'(N^*)F(N^*)}{p - c(N^*)}, \tag{2.36}$$

known as the "modified golden rule" of resource accumulation (Clark and Munro, 1975). If F is a logistic function such as in the Gordon and Schaefer model, Clark (1976a, 1985a) found an explicit form for the optimal population size

$$N^* = \frac{1}{4}\left[\bar{N} + K\left(1 - \frac{\delta}{r}\right) + \sqrt{\left(\bar{N} + K\left(1 - \frac{\delta}{r}\right)\right)^2 + \frac{8K\bar{N}\delta}{r}}\right] \tag{2.37}$$

with $\bar{N} = \frac{c}{p}$. Four special cases occur. First, if there is no discounting ($\delta = 0$), then equation (2.37) reduces to

$$N^* = \frac{1}{4}2(\bar{N} + K) = \frac{Kp + c}{2p} = N_{MEY}. \tag{2.38}$$

Second, if in addition the cost of harvesting is also zero, then

$$N^* = \frac{K}{2} = N_{MSY}. \tag{2.39}$$

Third, if there is discounting ($\delta \neq 0$) and the cost of harvesting is zero, then

$$N^* = \frac{1}{4}\left[K\left(1 - \frac{\delta}{r}\right) + \sqrt{\left(K\left(1 - \frac{\delta}{r}\right)\right)^2}\right]. \tag{2.40}$$

Therefore, in this case, it is economically optimal for the harvester to exploit the fish down to extinction when the discounting is higher than the growth rate of the population ($\delta > r$). Fourth, if $c(N) = \frac{c}{N}$ then bionomic equilibrium N_{∞}, which is found from solving $R - C = 0$, is the limiting case if δ tends to infinity. This can be regarded as an open-access exploitation, because open-access only cares about profit this year, same as $\delta = \infty$. In this case equation (2.36) becomes

$$\delta = r\left(1 - \frac{2N}{K}\right) + \frac{cr(1 - N/K)}{c - pN}, \tag{2.41}$$

which if $\delta \longrightarrow \infty$ then $N^* \longrightarrow \frac{c}{p} = N_{\infty}$.

What is the optimal policy for harvesting a single-species population? If the modified golden rule, equation (2.36), has a unique optimal escapement $N = N^*$ that determines the optimal size of stock to leave for the next period, Munro (1992) argued that keeping the stock at any level above N^* would be over-investment. On the other

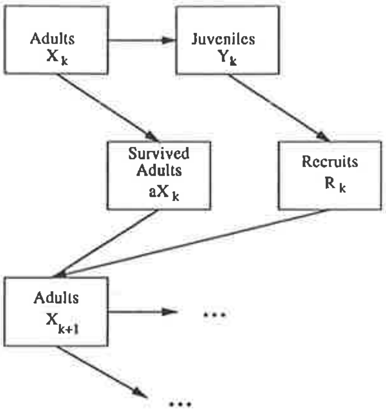

Figure 2.6: Life cycle of parental survival population. Modified from Clark (1976a).

hand, any stock below the level N^* is also not optimal, for example to harvest at that level is expensive if we assume cost is a decreasing function of the stock. Therefore, the optimal strategy is to drive the stock to N^* as rapidly as possible. Mathematically, this can be written as a function

$$h^*(t) = \begin{cases} h_{max} & \text{if } N(t) > N^* \\ F(N) & \text{if } N(t) = N^* \\ 0 & \text{if } N(t) < N^*. \end{cases} \tag{2.42}$$

This strategy is called the "most-rapid-approach" path strategy. It assumes an upper bound of the harvest rate $h = h_{max}$. If the stock level is above N^* than we harvest the stock at maximum harvest rate, if the stock is exactly at the level of optimal escapement then it should be kept at that level, and if the stock is below the optimal escapement then close the fishery completely until it reaches the level of optimal escapement. Other authors who investigated harvesting policies under net present value maximisation are Quirk and Smith (1969), Plourde (1970), Brown (1974) and Herfindahl and Kneese (1974). Other models, such as discrete-time, delay-recruitment and cohort models and some extensions of Clark's models are discussed in sections to follow.

2.2.2 Single-species fisheries discrete-time models

Schaefer's (1954) surplus production function discussed in the previous section is a continuous-time population model. In some circumstances, discrete-time models seem to be more realistic, for example in modelling a population which regenerates annually, like salmon. In general, discrete-time models use a "stock-recruitment function" (see Figure 2.6). A stock-recruitment function is a relation between the number of spawning adults and the subsequent recruitment that enters the adult class, usually known as a harvestable class. A fairly general stock-recruitment function is presented by Deriso (1980) and Schnute (1985) as a generalisation of the Schaefer surplus production function.

The discrete-time model is able to differentiate between two types of adult survivorship. The first one, the model with no adult survival for the next period ($a = 0$ in Figure 2.6), is called a non-overlapping growth model. This model is best to describe the growth of some species of salmon, where all adult die after the reproductive process. This model is considered as a discrete-time analog of the continuous model (Clark, 1976a). The second one, the model which is called an overlapping growth discrete-time model. Clark (1971, 1973, 1976a) investigated optimal harvesting strategies for these discrete-time population models. The results are presented in this section briefly and the method is used to obtain optimal harvesting strategy in a more complex system, that is a predator-prey system, in Chapter 3 .

The general model represents a discrete-time population dynamic that can be written in the form

$$N_{k+1} = aN_k + R_k, \tag{2.43}$$

where $R_k = F(N_k)$, see Figure 2.6. If we assume the generations of the population are not overlapping ($a = 0$) and there is harvesting with the rate H_k, then the equation becomes

$$N_{k+1} = R_k - H_k, \tag{2.44}$$

hence $R_{k+1} = F(R_k - H_k)$ with harvest H_k satisfies $0 \leq H_k \leq R_k$. Clark (1976a) defined economic rent from the fishery in period k as

$$\Pi(R_k, S_k) = \int_{S_k}^{R_k} (p - c(\xi))d\xi, \tag{2.45}$$

where $S_k = R_k - H_k$ is defined as escapement in period k. The expression above assumes that the price of the fish is constant and the cost of harvesting is a function of the fish abundance (see Appendix 4A for the formal derivation of the cost function).

The maximisation is carried out with respect to escapement S_k over T periods with present value

$$PV = \sum_{k=0}^{T} \rho^k \Pi(R_k, S_k), \tag{2.46}$$

where $\rho = \frac{1}{1+\delta}$ is a discounting factor with a discounting rate δ. Using dynamic programming, Clark found implicit expression for the optimal escapement S^* satisfying

$$1 + \delta = F'(S^*)\frac{p - c(F(S^*))}{p - c(S^*)}, \tag{2.47}$$

which he called the "fundamental equation of renewable resources".

The optimal approach to this optimal escapement is the most-rapid-approach path, exactly as before. Hence if the initial population is below the level of optimal escapement then do not harvest the population, while if the stock level is above the level of the optimal escapement then harvest the population down to this optimal escapement. Clark (1971) and Reed (1979) showed that if the recruitment function is concave and deterministic then the population will never fall below this optimal escapement once it exceeds the optimal escapement. Equation (2.47) is also known as a discrete-time analog of the modified golden rule equation [equation (2.36)].

An explicit expression of the optimal escapement can be obtained for special cases, for example, if the cost of harvesting is negligible (clupeid fisheries, e.g. herring, pilchard and sardine fisheries, may be considered costless to some extent (Munro, 1992)) and the recruitment function is assumed to be fitted with a Schaefer recruitment function, that is, $F(N) = rN(1 - N/K)$. In this case the optimal escapement is

$$S^* = \frac{K}{2} - \frac{K}{2r}(1 + \delta). \tag{2.48}$$

From this equation, we can conclude that it is optimal to drive the population to extinction if the natural growth of the population is less than the inverse of the discounting factor. This is consistent with the result for the continuous case discussed previously. Both Clark's (1976a) continuous- and discrete-time single-species models are extended by other authors. For example Reed (1978, 1979) and Charles (1983) included stochasticity and uncertainty, Reed (1982) included sex-selective harvesting, Charles (1988, 1989) included bio-socio-economic aspects, Reed and Heras (1992) included resource vulnerability to extinction and Jørgensen and Kort (1997) included perfectly reversible investment, etc. (see also Clark *et al.*, 1979; Agnew, 1982; Gatto *et al.*, 1982; Clark and Tait, 1982; Ludwig and Walters, 1982; Chaudhuri, 1986, 1988; Mesterton-Gibbons, 1987, 1988, 1996; Tuck and Possingham, 1994; Ganguly and Chaudhuri, 1995). In the following section I move from single-species harvesting to review harvesting theory for multi-species fisheries.

2.2.3 Multi-species fisheries models

This section reviews the models and qualitative results in multi-species harvesting theory. I address questions such as: when does a multi-species strategy differ from a single-species strategy? and is extinction of one or both species economically optimal? I begin with the definition of a multi-species fisheries.

There are two types of multi-species fisheries: "technologically interdependent" and "biologically interdependent" multi-species fisheries. The first type occurs when the gear to harvest a species also affects mortality of another species while the second type occurs when the exploited species in the fisheries have a biological relationship, like competition, predation, etc., with the other species. Anderson (1975) addressed the issue of maximum economic yield and open-access equilibrium for these two types of multi-species fishery. Clark (1976a) solved the general problem of technologically interdependent multi-species fisheries and left a conjecture for biologically interdependent multi-species fisheries, that is, the optimal control of the fisheries is attainable. There is also another type of fishery closely related to a multi-species fishery, that is, a multi-purpose fleet which harvests a certain fish at one season and then another fish at another season (Huppert, 1979; Anderson, 1982) which I will not discuss further.

Gatto *et al.* (1982) extended Clark's technologically interdependent multi-species model to include the effects of a limited total effort on the exploitation. The main differences between their model and Clark's (1976a) model is that in their model total effort is constrained by a constant maximum effort, that is, $0 \leq E_1(t) + E_2(t) \leq E_{max}$ for each time period t. If a constraint like this is not present, then the analysis can be done by assuming the system consists of two separate single-species fisheries. They found that if total maximum effort E_{max} is very low, it is optimal to exploit only one of the fisheries, if they are totally regulated. In contrast, if the fisheries are totally unregulated, the discounting rate δ is not zero and total maximum effort E_{max} sufficiently large, then the fisheries reach bionomic equilibrium. They proposed a compromise between a totally unregulated and a totally regulated fishery, a "regulated competition" fishery. In this regulated competition fishery, the stock with a lower net return per unit effort should be exploited less.

In many situations a multi-species fishery of the second type may exhibit complex interactions. The effect of exploitation on the population may not be straight forward. The indirect effect of one species on the other species can be very complex. For example, in the North Sea fisheries, demersal species such as cod, haddock and plaice feed on pelagic species like herring and mackerel. On the other hand, adults of these pelagic species also feed on early larval stages of the demersal species (Gulland, 1977). Gulland (1977) argued that increasing catches of cod reduces predation by cod on herring and generating larger catches of herring. Larger catches of herring means the declining of food supply for the cod, which finally reduces cod stock. Furthermore, Gulland (1977) suggested that extensive fishing of herring increases the number of surviving cod juveniles recruited into the adult class of the cod. This is because extensive fishing of herring also reduces predation on the larvae of cod. These complex interactions have made the management of multi-species fisheries difficult. Despite complex biological interactions in the underlying systems of multi-species fisheries, concepts for harvesting multi-species fisheries are similar to concepts for single-species fisheries (May *et al.*, 1979).

Larkin (1963, 1966) was among the first to study harvesting of multi-species fisheries. He studied multi-species fisheries in which the species are ecologically interconnected, that is, competition (Larkin, 1963) and predation (Larkin, 1966). In both cases Larkin (1966) found equilibrium abundances of the interacting species in the presence of harvesting as explicit functions of the fishing rate. Therefore, the effect of exploitation on the population and the profit from fishing can be easily determined. Jensen (1994) applied Larkin's predation model to study the dynamic of lake trout, *Salvelinus namaycush*, and sea lamprey, *Petromyzon marinus*, and found that in certain circumstances extinction of one species is possible in the presence of harvesting.

Ströbele and Wacker (1991) studied the yield per unit effort curve from harvesting an ecologically-interconnected multi-species fishery and compared the curve to the yield per unit effort curve from harvesting a single-species fishery. They showed that, either under a selective or combined harvesting strategy, yield from a mutualistic system is higher and yield from a competitive system is lower, compared to yield from a single-species system. Furthermore, they argued that selective harvesting of the prey in a predator-prey system is comparable to harvesting the competitive system, because the yields from both systems are lower than the yield from a single-species population. On the other hand, selective harvesting of the predator is comparable to the mutualistic system, because the yields from both systems are higher than the yield from a single-species population. However, they derived no general rule for optimal harvesting of a predator-prey system.

Parrish and Saila (1970) modified Larkin's models to include three species, one predator and two competing prey. The dynamics of their model with the inclusion of predator exploitation are explored by Azar *et al.* (1995). The effects of two different harvesting strategies, namely constant harvest quota and constant harvest effort, on the dynamics of the populations, are investigated. Azar *et al.* (1995) showed that the system is stable when a constant harvest effort is used as a harvesting strategy, while a constant harvest quota on the predator may destabilise the system. This result agrees with the finding of Brauer and Sanchez (1975) for a single-species and Brauer *et al.* (1976) for a predator-prey system with only one prey and one predator, who showed that if exploitation is introduced into a predator-prey system using a constant harvest quota and the rate of exploitation is above some critical threshold, then extinction of the predator may occur. For this reason, Brauer and Soudack (1978) argued that exploitation using proportional harvesting is safer than constant rate harvesting if the extinction of the predator is undesirable.

In a multi-species fisheries, the determination of the level of effort that maximises yield is only possible if the level of effort in the other fishery is known. MSY for both fisheries occurs when the total yields from both fisheries is maximised. Furthermore, combined MEY has a different combination of effort than those associated with the individual MEYs. For this reason, multi-species fisheries should be managed as a whole (Anderson, 1975). Silvert and Smith (1977) pointed out that, as in the case of harvesting a single-species fishery, MEY and MSY are the special cases of the more general objective, that is, dynamic MEY or MPV. Silvert and Smith (1977) studied the multi-species system previously proposed by Larkin (1963, 1966) in a dynamic framework, with the inclusion of an interest rate. They found that a species that might be heavily harvested in a single-species fishery, could be conserved better in multi-species fisheries if it enhances the present value through its bioeconomic role. For example, if the prey in a predator-prey system grows slowly then it would be better not to harvest it and use it as food for the predator.

Extinction of species in a harvested multi-species system may be the optimal strategy to obtain a higher harvest (Flaaten, 1988, 1989). For example, May *et al.* (1979) investigated the effect of the harvesting rate of one species on the yield of the other species in the predator-prey population previously proposed by Leslie (1948). Their model applied to the exploitation of the Antarctic krill, *Euphausia superba*, which is also food for baleen whales. The model is

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - aNP, \tag{2.49}$$

$$\frac{dP}{dt} = sP\left(1 - \frac{P}{\alpha N}\right). \tag{2.50}$$

They assumed that the prey and predator are harvested under constant efforts at rate rE_N and sE_P, respectively. Both efforts are rescaled so that $E_N = E_P = 1$ corresponds to a fishing rate equal to the intrinsic growth rates r and s respectively. The yield for the prey is $Y_N = rE_N N$ and the yield for the predator is $Y_P = sE_P P$. Introducing $X_N = N/K$ and $X_P = P/(\alpha K)$ as new scaled variables, the dynamic of the exploited populations are

$$\frac{dX_N}{dt} = rX_N\left(1 - E_N - X_N - \nu X_P\right) \tag{2.51}$$

and

$$\frac{dX_P}{dt} = sX_P\left(1 - E_P - \frac{X_P}{X_N}\right) \tag{2.52}$$

for the prey and predator, respectively, with $\nu = a\alpha K/r$. May *et al.* (1979) found the equilibrium population sizes X_N^* and X_P^*, and yields Y_N^* and Y_P^*,

$$X_N^* = \frac{1 - E_N}{1 + \nu(1 - E_P)}, \tag{2.53}$$

$$X_P^* = \frac{(1 - E_N)(1 - E_P)}{1 + \nu(1 - E_P)}, \tag{2.54}$$

$$Y_N^* = \frac{(rK)E_N(1 - E_N)}{1 + \nu(1 - E_P)}, \tag{2.55}$$

$$Y_P^* = \frac{(\alpha sK)(1 - E_N)E_P(1 - E_P)}{1 + \nu(1 - E_P)}. \tag{2.56}$$

It is easy to see that if there is no predation ($\nu = 0$), yield from the prey is maximised by applying a harvest rate at the level of the prey MSY, because the system reduces to a single-species population. If $\nu \neq 0$ then the yield for the prey is maximised by the depletion of the predator, while the yield for the predator is maximised by not harvesting the prey at all. They argued that the appropriate MSY is one that maximises the yield from a weighted sum of both yields. For this reason, they propose a possible management objective by maximising the total weighted yields $Y = Y_N^* + \gamma Y_P^*$, where γ is the intrinsic relative value of the predator relative to the prey. Rewrite Y to give

$$Y = \frac{C(1 - E_N)(E_N + \beta E_P(1 - E_P))}{1 + \nu(1 - E_P)}, \tag{2.57}$$

where C is constant and $\beta = \gamma\alpha(s/r)$. They interpret β as the intrinsic relative value (γ) discounted by the ratio of predator's intrinsic growth and prey's intrinsic growth (s/r) and by the biological conversion (α). This discounted intrinsic relative value determines the optimal yield combination for the prey and predator. If this value is small, for example if the biological conversion is small and the intrinsic growth of the predator is also small compared to the intrinsic growth of the prey, then it is optimal to harvest the less valuable predator heavily. In some circumstances it is optimal to harvest the predator down to extinction and harvest the prey sustainably (Figure 2.7.a). On the other hand, if the discounted intrinsic relative value is large, it is optimal to harvest only the predator and the prey is more valuable as the food of the predator (Figure 2.7.b). Figure 2.7.c illustrates the case where both species have similar values and it is optimal to keep both species. Clark (1985c) modified May *et al.*'s (1979) model to include a concentration effect. He assumed that the intrinsic growth of the predator depends on the density of the prey and found that excessive exploitation of the prey may cause the predator to go extinct even though we left them unharvested.

Beddington and Cooke (1982) investigated harvesting strategies for the same system (equation (2.49) and (2.50)). They assumed the prey is harvested with constant yield while the predator is harvested with constant effort. In dimensionless form the system becomes

$$\frac{dX_N}{dt} = r\left(X_N\left(1 - X_N - \nu X_P\right) - Y_N\right) \tag{2.58}$$

and

$$\frac{dX_P}{dt} = sX_P\left(1 - E_P - \frac{X_P}{X_N}\right). \tag{2.59}$$

They found that, for fixed effort E_P, to obtain an equilibrium prey yield, Y_N needs to satisfy $Y_N < 1/4(1 + \nu(1 - E_P))$. Because it is scaled to r, then the "absolute" MSY is $r/4(1 + \nu(1 - E_P))$. Now let $E_P = 0$, that is, only the prey is harvested. They showed that different from harvesting a single-species, in which harvesting the population below MSY drives the population to a locally stable equilibrium, here harvesting only the prey from a predator-prey system may not produce a stable equilibrium. A stable equilibrium is attained only if

$$Y_N = \frac{1 - ((1 - s/r)2(1 + \nu)/(2 + \nu) - 1)^2}{4(1 + \nu)}. \tag{2.60}$$

They referred to this yield as the "stable" MSY which is smaller than the "absolute" MSY. They argued that this "stable" MSY is more useful than if we modify the concept of MSY for a single-species system to apply to harvesting prey population from a predator-prey system. Furthermore, they found that whether we harvest only the prey or harvest both populations the difference between the "absolute" MSY and the

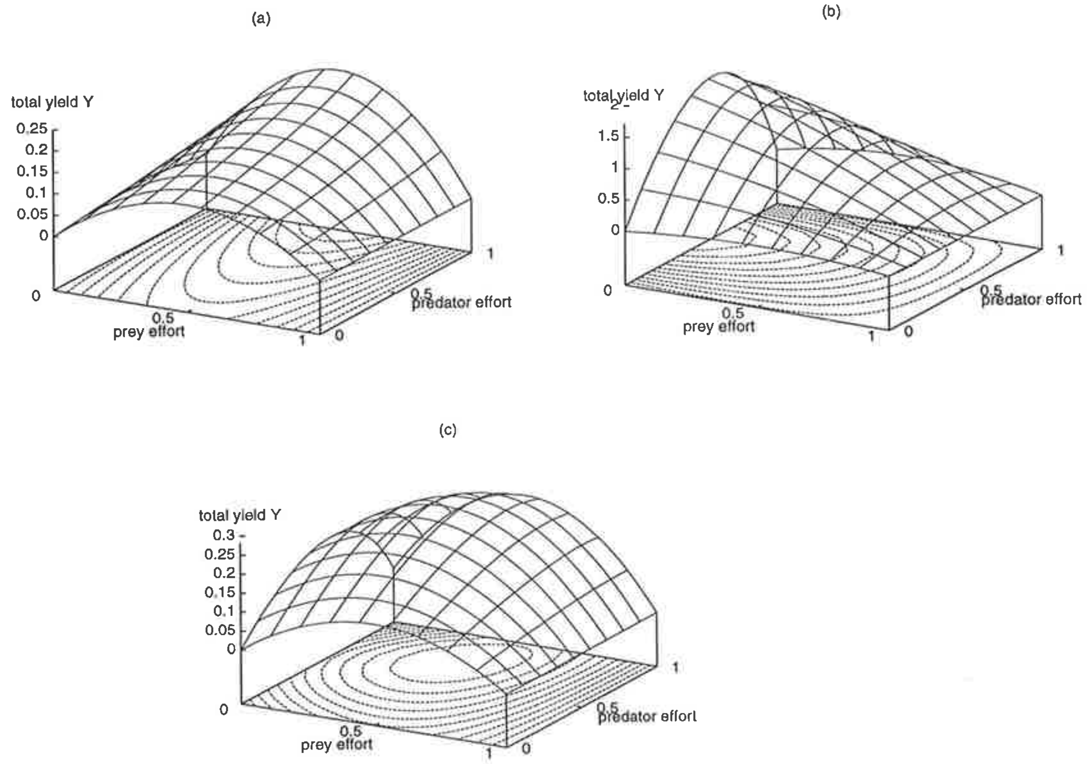

Figure 2.7: Total sustainable yield, Y, is graphed as a function of prey and predator efforts, E_N and E_P. The parameters are chosen as in May *et al.* (1979) with $\beta = 0.1$ (Figure 2.7.a), $\beta = 10$ (Figure 2.7.b) and $\beta = 1$ (Figure 2.7.c).

"stable" MSY is greatest when the ratio of the intrinsic growth of the predator to the intrinsic growth of the prey, s/r, is small. They proposed that if the predator is harvested at a constant effort then it is better to harvest the prey at a level of about 90% of the "stable" maximum sustainable yield, because the domain of attraction to the stable equilibrium is larger than at a higher level, for example 99% of the "stable" MSY. Harvesting at the "stable" MSY, to some extent, is also risky; fluctuations of the population from natural disturbances may lead to the collapse of the system.

In harvesting a multi-species fisheries, Beddington and May (1980) pointed out that the most common outcome of using weighted total sustainable yield, is to harvest one species and either ignore or drive the other species to extinction. This makes the weighted total sustainable yield approach contentious. In theory and in practice controversies emerge in harvesting predator-prey systems. For example, Flaaten (1988) concluded that in the Barents Sea fishery one should deliberately deplete sea mammals to increase fish production from the fishery. The similar controversies of conservation significance occur almost in all fisheries in which the stocks are also food for higher trophic species, like sea mammals and birds (Beddington *et al.* 1985; Yodzis, 1994; Greenstreet and Tasker, 1996). The increasing surplus of Antarctic krill is assumed to be a direct effect of baleen whales depletion (May *et al.*, 1979; Nicol and de la Mare, 1993), which in turn ends in the conclusion that marine mammals are detrimental to fisheries, hence their numbers should be kept as low as possible (Flaaten, 1988). To reach this conclusion, Flaaten used Leslie's predator-prey model, as described in

May *et al.* (1979). Yodzis (1994) argued that the use of this predator-prey model in mammal-fish interactions is misleading and so the conclusion derived from this model is biased. Leslie (1948) used a "laissez-faire" functional response (see equation (2.49)). In this case we assume that predators do not interfere with each other in their activities, feeding for example, but, there is also predator interference which is linked with the food availability (the numerical response in equation (2.50)). This is not appropriate in mammal-fish interactions, for example a recent paper reveals that predation of the Antarctic cod, *Gadus morhua*, by grey seals, *Halichoerus grypus*, is not a major factor in the collapse of the cod population (Mohn and Bowen, 1996).

The harvesting theory for multi-species fisheries discussed above assumes the system is at equilibrium and there is no economic discounting. The following part of this section reviews multi-species harvesting theory for a more general model in a dynamic time setting.

A multi-species fisheries model for n-species can be written in the form

$$\frac{dN_i}{dt} = F_i(N_1, ..., N_n) - h_i(t). \tag{2.61}$$

Here we assume harvesting can be done selectively. If the cost of harvesting is a function of the population size, that is, $c_i(N_i)$, then using a similar framework to the present value maximisation for a single-species fishery, the present value of the net revenue or economic rent from the fisheries over time is

$$PV = \int_0^\infty \left(\sum_{i=1}^n (p_i - c_i(N_i))(F_i(N_1, ..., N_n) - \frac{dN_i}{dt})\right) e^{-\delta t} dt. \tag{2.62}$$

Maximisation of this present value with respect to N_i subject to $0 \leq N_i \leq N_i^{max}$ must satisfy the Euler equation (Clark, 1976a: p. 39-40). Hence we have

$$\delta(p_i - c_i) = -\frac{dc_i}{dN_i}F_i + \sum_{j=1}^n (p_j - c_j)\frac{\partial F_j}{\partial N_i}. \tag{2.63}$$

Using this general implicit equation of optimal escapement, Hannesson (1983) investigated the effects of discounting rate on the standing stock of biomass for a predator-prey system previously studied by Larkin (1966). Hannesson (1983) found that if predator efficiency is relatively high then both optimal escapements, for the prey and predator, decrease. In the other case, that is, in a partial predator-prey system in which the predator has other foods besides the prey, the increasing of the discounting rate may increase optimal escapement of one species while it also decreases optimal escapement of the other species. This seems contrary to the single-species harvesting theory in which increasing discounting rate always decreases the level of optimal escapement. Hannesson (1983) also confirmed the need of predator extermination in the presence of discounting if the growth of the predator is slower than the prey.

Clark (1976a) applied the same theory to obtain an optimal harvesting strategy for a Lotka-Volterra predator-prey system

$$\frac{dN}{dt} = F_N(N, P) - h_N(t), \tag{2.64}$$

$$\frac{dP}{dt} = F_P(N, P) - h_P(t), \tag{2.65}$$

where $F_X(N,P) = r_X X(1-X/K_X)+\alpha_X NP$, $X = N, P$, $\alpha_N < 0$ and $\alpha_P > 0$. Optimal escapements S_N^* and S_P^* are found implicitly and satisfy equations

$$(p_N - c_N(S_N))\frac{\partial F_N}{\partial S_N} + (p_P - c_P(S_P))\frac{\partial F_P}{\partial S_N} - C_N' F_N = \delta(p_N - c_N(S_N)) \tag{2.66}$$

and

$$(p_N - c_N(S_N))\frac{\partial F_N}{\partial S_P} + (p_P - c_P(S_P))\frac{\partial F_P}{\partial S_P} - C_P' F_P = \delta(p_P - c_P(S_P)). \tag{2.67}$$

These equations are generalisations of the modified golden rule for a predator-prey optimal escapement. Clark (1976a) interpreted $(p_N-c_N(S_N))\frac{\partial F_N}{\partial S_P}$ and $(p_P-c_P(S_P))\frac{\partial F_P}{\partial S_N}$ as an addition to the marginal value product of the prey and predator populations with the increase in predator and prey population respectively. He argued that the optimal approach path to the optimal escapement (S_N^*, S_P^*) is difficult to obtain, but it is possible to obtain a unique optimal trajectory passing through these optimal escapements. He also conjectured that the optimal path from any population size (S_N, S_P) can be attained by constructing a straight line from the initial population size to the optimal trajectory, and then follow the optimal trajectory up to the optimal escapement (S_N^*, S_P^*). For practical uses, he suggested a suboptimal approach

$$h_X = \begin{cases} h_{max} & \text{if } X(t) > S_X^* \\ 0 & \text{if } X(t) < S_X^*, \end{cases} \tag{2.68}$$

similar to the most-rapid-approach-path.

Clark's (1976a) analysis for optimal harvesting discussed above applies to a predator-prey system with selective harvesting. Mesterton-Gibbons (1988, 1996) obtained an analogous optimal policy to harvest a predator-prey system using a combined harvest from the prey and predator. His work generalises the result for combined harvesting of independent populations (Clark, 1976a; Mesterton-Gibbons, 1987), combined harvesting of competing populations (Clark, 1976a; Chaudhury, 1986) and harvesting a predator-prey system with prey has no economic value (Ragozin and Brown, 1985).

A significant difference between strategies to harvest a single-species fishery and strategies to harvest a multi-species fishery becomes apparent when we cannot harvest the biologically interacting species selectively. For example, if a proportion of prey is caught for effort expended to harvest the predator, then the "fundamental principle of renewable resource economics" (Clark, 1985a), that is, that the increasing of the discounting rate δ usually decreases the optimal escapement of the fish stock, may not hold. In this case, extinction may be optimal as the discounting rate decreases (Sieveking and Semmler, 1997).

2.2.4 Spatially-structured fisheries models

As explained in the previous section, all marine populations display some degree of spatial heterogeneity. This spatial heterogeneity has been recognised since the early development of fishery management (e.g. Beverton and Holt, 1957), but fisheries bioeconomic models are largely based on a single homogeneous stock. Much recent research in fisheries shows that this spatial heterogeneity means that modelling the species as one single population is not adequate (Caddy, 1975; Hilborn, 1976; Frank, 1992; Frank and Leggett, 1994). This is true especially for stocks in which dispersal of individuals is relatively high, like some species of cod and haddock in West Greenland and Iceland (Frank and Leggett, 1994).

Early investigation of the effect of spatial heterogeneity on optimal escapement goes back to the work of Paulik *et al.* (1967), Clark (1976a), Hilborn (1976), Clark and Mangel (1979), and Hilborn and Walters (1987). Paulik *et al.* (1967) studied a harvesting strategy for multiple stocks where the fishery effort is uncontrolled – "open-access". They assumed that each substock is governed by Ricker's reproduction function for a single-species population. Each substock is allowed to be different from other substocks, for example they may have different productivities. They calculated the MSY from the fishery and found the rate of harvesting that maximises the total sustainable yield for the population. However, Hilborn (1976) argued that the rate of harvesting in Paulik *et al.* (1967) is computed when the population is in its equilibrium state, which rarely occurs in real fish population. Furthermore, Hilborn (1976) pointed out that a fixed escapement is more often used as a policy than a fixed harvest. In the case of harvesting a population consists of different stocks, he concluded that harvesting with a fixed escapement policy may not be optimal when the population is not at equilibrium.

Further development of harvesting theory for spatially-structured populations allowed individual movement between substocks. In his inshore-offshore fishery model Clark (1976a) assumed that diffusion occurs from the substock which has a higher abundance to the substock with less abundance. If κ is the proportional constant of diffusion, N_i and $F_i(N_i)$ denote the abundance and the natural growth rate of the substock i, and E_i is fishing effort applied to harvest the substock i, then the model is

$$\frac{dN_1}{dt} = F_1(N_1) + \kappa(N_2 - N_1) - E_1 N_1, \tag{2.69}$$

$$\frac{dN_2}{dt} = F_2(N_2) + \kappa(N_1 - N_2) - E_2 N_2. \tag{2.70}$$

Using similar optimisation tools to those he developed for single-species harvesting, Clark (1976a) found optimal harvesting strategies for both populations. If there is no diffusion, $\kappa = 0$, then an implicit equation for the optimal escapement is exactly the same as the equation for a single-species. Furthermore, Clark (1976a) suggested that if, in the absence of diffusion, the marginal cost of harvesting the inshore substock is less than the marginal cost of the offshore substock, then it is optimal to reserve the offshore stock. The offshore stock productivity is harvested when it comes to the economically less expensive inshore fishery.

Clark and Mangel (1979) constructed a model of harvesting a surface population which exchanges individuals with a subsurface school. Harvesting only targets the surface population, while the subsurface population remains unharvested. They found that if the rate of migration from subsurface population ("intrinsic schooling rate") is less than its intrinsic growth rate, then for any fishing effort the surface fishery is sustainable. On the other hand, if this migration rate is higher than the intrinsic growth rate, then a high level of harvesting effort may cause extinction of the population. This model is applied to the Skipjack tuna fishery, *Euthynnus pelamis*, by Hilborn (1989a) and extended to allow harvesting the subsurface population (Hilborn, 1989b). Further analysis of Clark and Mangel's model can be found in Mangel (1982).

Using the difference model of Deriso (1980) and Schnute (1985), Hilborn and Walters (1987) simulated stock and fleet dynamics of the six major stocks of abalone in Australia. If there is spatial movement among the stocks, they suggested that this movement can be inserted into the model using a spatial transition matrix $P = [p_{ij}]$ in form

$$B_k = PB^* \tag{2.71}$$

and

$$R_k = PR^*, \tag{2.72}$$

where p_{ij} is the probability of successful migration from stock i to stock j, B^* and R^* are biomass calculated before the movement, where B_k and R_k denotes the Deriso-Schnute biomass model and the recruitment function, respectively.

Using a model analogous to Hilborn and Walters (1987), Tuck and Possingham (1994) developed a model, assuming that the spatial movement takes place at the juvenile or larval life stage of the stocks and that some proportion of adults survive to the next period. Their model can be written

$$\begin{pmatrix} B_{1(k+1)} \\ B_{2(k+1)} \end{pmatrix} = \begin{pmatrix} a_1 B_{1k} \\ a_2 B_{2k} \end{pmatrix} + \begin{pmatrix} p_{11} & p_{21} \\ p_{12} & p_{22} \end{pmatrix} \begin{pmatrix} R_{1k} \\ R_{2k} \end{pmatrix}. \tag{2.73}$$

They investigated optimal harvesting strategies for the system and found the following rules of thumb for harvesting a single-species metapopulation:

TP 1 If we use a single-species metapopulation harvesting theory, a relative source subpopulation would be harvested more conservatively than a relative sink subpopulation.

TP 2 If we use a single-species metapopulation harvesting theory, a relative exporter subpopulation would be harvested more conservatively than if we use an unconnected single-species population theory, while a relative importer subpopulation would be harvested more heavily.

TP 3 If we use a single-species metapopulation harvesting theory, a relative source subpopulation would be harvested more conservatively than if we use a well-mixed single-species population theory, while a relative sink subpopulation would be harvested more heavily.

Source/sink and exporter/importer subpopulations are defined precisely in Chapter 4.

Other models that deal with exploited metapopulations are Quinn *et al.* (1993) and Brown and Roughgarden (1997). The former analyses the effects of harvest on the metapopulation with an Allee effect, illustrated by the red sea urchin, *Strongylocentrotus franciscanus*, and the latter investigates optimal harvesting policies for marine species with a two part life-cycle, illustrated by the barnacle, *Balanus glandula.* Quinn *et al.* (1993) found that excessive exploitation may lead to the extinction of a metapopulation, unless some of its subpopulations are excluded from the exploitation. Their finding is consistent with those of Roughgarden and Iwasa (1986) and Pulliam (1988) who argued that persistence of sink subpopulations can be maintained by spatial movement from source subpopulations. Brown and Roughgarden (1997) discovered an explicit rule which states that harvesting a metapopulation described by their model should be carried out on no more than one site. This is consistent with that of McCullough (1996) who argued that a metapopulation can be exploited only for a limited harvest and in general it does not have a high potential harvest. In contrast, harvesting strategies proposed by Tuck and Possingham (1994), e.g. TP 1 above, allow a relatively high harvest compared to two other known harvesting strategies, namely unconnected single-species and well-mixed single-species. This is because their strategies recognise the importance of source subpopulations, and hence these subpopulations are harvested conservatively. On the other hand, we can harvest sink subpopulations heavily. In this case, protecting the source subpopulation is also means protecting the replenishment of the other subpopulation (Mangel *et al.*, 1997; Gary *et al.*, 1998). Tuck and Possingham (1994) also showed that these strategies could improve the economic gain from the exploitation.

2.3 Concluding remarks

In this chapter I have reviewed the development of harvesting theory using several dichotomies: continuous-time and discrete-time models, static and dynamic models, single-species and multi-species models, spatial and non-spatial models, etc. One question of interest to resource managers that still needs further investigation is that of optimal harvesting of spatially-structured predator-prey populations. Addressing this question is very important in obtaining adequate management for commercially exploited marine biological populations, since all the populations are part of predator-prey interactions and they are spatially heterogeneous. Many scientists believe that a model which does this could improve the management practices of multi-species fisheries (Hall, 1998). However, this issue has not been addressed explicitly in the literature (Semmler and Sieveking, 1994).

In this thesis I develop models of spatially-structured predator-prey populations and investigate optimal harvesting strategies for the populations. The models are deterministic and take the form of coupled difference equations. In Chapter 3 I discuss optimal harvesting theory for a spatially homogeneous discrete-time predator-prey population. That chapter contains the work of other authors. I redo and review their work to ensure that I have a base which is internally-consistent to compare the optimal harvesting strategies for spatially heterogeneous predator-prey populations in the subsequent chapters. In the subsequent chapters I extend the model from Chapter 3 to include spatial structure of the populations.

Chapter 3

Spatially-homogeneous predator-prey population

Most of the harvesting theory for predator-prey populations discussed in Chapter 2 deals with the continuous-time case. In this chapter, I review and redo the work of other authors on a deterministic, discrete-time predator-prey harvesting model. The chapter is intended to give a background for comparing the optimal harvesting strategies for spatially heterogeneous predator-prey populations in the subsequent chapters. Although the model in this chapter is not new, nor are the results, I discuss an interpretation of a negative harvest as a feeding strategy which has not been addressed explicitly by other authors.

The model in this chapter follows the structure and assumptions in Clark (1976a), Walters and Hilborn (1976) and Tuck and Possingham (1994). I use dynamic programming and the method of Lagrange multipliers to find optimal harvesting strategies for the system considering two different types of fishing. First, I assume both species, the prey and the predator, are harvested. Examples of fisheries with this type of exploitation are the whale and krill fishery, the cod and capelin fishery, the salmon and pilchard fishery, and the Pacific herring and Pacific hake fishery (Laws, 1977; Gulland, 1977; Cappo, 1987; Spencer and Collie, 1996). Second, I assume that harvesting only targets the prey population. For example, the sandeel, *Ammodytes marinus*, fishery. In this fishery, the sandeel is harvested while it also provides food for many seabirds, like Arctic tern (*Sterna paradisae*), kittiwakes (*Rissa tridactyla*) and the puffin (*Fratercula arctica*) (Wright, 1996). Another example is the Australasian pilchard fishery, where the pilchards (*Sardinops pilchardus*) are also a major prey for the little penguins (*Eudyptula minor*) of Western Australia (Klomp and Wooler, 1988).

3.1 The model

There are two ways to incorporate predator-prey interactions into the single-species discrete-time model discussed in the previous chapter. In the first way it is assumed that predation occurs in the adult stage. In this case, a predation term $-cN_kP_k$ is added into the right hand side of equation (2.43) in the absence of exploitation to form $N_{k+1} = aN_k + F(N_k) - cN_kP_k$. The second way is to assume that predation occurs in the juvenile stage. In this case, the predation term is added into the recruitment production function $F(N_k)$ in equation (2.43) to form $N_{k+1} = aN_k + F(N_k)$, where $F(N_k) = rN_k(1 - N_k/K - cP_k)$ (Walter and Hilborn, 1992).

I assume that some proportion of adults in one period survive to the next period, hence the model reflects an overlapping population. All adults have the same mortality rate and their fecundity for all ages is the same. If the population size of the prey and predator at the beginning of period k are denoted by N_k and P_k respectively, then the growth of prey and predator is given by equations

$$N_{(k+1)} = aN_k + F(N_k) + \alpha N_k P_k, \tag{3.1}$$

$$P_{(k+1)} = bP_k + G(P_k) + \beta N_k P_k, \tag{3.2}$$

where a and b denote the survival rate of adult prey and adult predator. The functions $F(N_k)$ and $G(P_k)$ are the recruit production functions of the prey and predator in time period k. I will assume that the recruit production functions are logistic for the remainder of this chapter, that is,

$$F(N_k) = rN_k\left(1 - N_k/K\right), \tag{3.3}$$

and

$$G(P_k) = sP_k\left(1 - P_k/L\right), \tag{3.4}$$

where r (s) and K (L) respectively denote the intrinsic growth of the prey (predator) and prey (predator) carrying capacity. In this case $\alpha < 0$ and $\beta > 0$ ensure that the system reflects a Lotka-Volterra predator-prey interaction. In this model I assume that the predator can survive in the absence of the prey. Many predators do not depend on only one species. For example, Clers and Prime (1996) pointed out that harbour seals from Lower Loch Fyne, Scotland, eat about seventeen species of fish.

To explore harvesting we need to introduce exploitation into the system. I assume that the only possible exploitation is through a selective harvesting policy, for example using a certain type of net and certain size of mesh, we can harvest a pelagic predator and leave a benthic prey unharvested, and vice-versa. If the amount of harvest taken from the prey and predator stocks at the beginning of period k are H_{Nk} and H_{Pk}, then $S_{Nk} = N_k - H_{Nk}$ and $S_{Pk} = P_k - H_{Pk}$ can be defined as prey and predator escapements at the end of that period. These escapements determine the growth of the population after exploitation. Hence, if these survivors of harvesting are substituted into equations (3.1) and (3.2), then the model for an exploited predator-prey system is

$$N_{(k+1)} = aS_{N_k} + F(S_{N_k}) + \alpha S_{N_k} S_{P_k}, \tag{3.5}$$

$$P_{(k+1)} = bS_{P_k} + G(S_{P_k}) + \beta S_{N_k} S_{P_k}. \tag{3.6}$$

To consider an optimal economic strategy, we need to make an assumption about the ownership of the fishery. I assume there is sole-ownership of the fishery where the owner uses maximum present value as the objective in managing the fishery. Using present value maximisation, the objective of the sole-owner is to maximise the net revenue resulting from harvesting each subpopulation of the prey and the predator up to time horizon $t = T$. If Π_X represents the present value of net revenue resulting from harvesting population X, $X \in \{N, P\}$, and ρ is a discounting factor, then the sole-owner should maximise

$$PV = \sum_{k=0}^{T} \rho^k \sum_{X \in \{N,P\}} \Pi_X(X_k, S_{X_k}) \tag{3.7}$$

subject to equations (3.5) and (3.6), and $0 \leq S_{X_k} \leq X_k$. I will assume $\rho = 1/(1+\delta)$ for the reminder of the thesis, where δ is the annual discounting rate. The net revenue Π_x is given by

$$\Pi_X(X_k, S_{X_k}) = \int_{S_{X_k}}^{X_k} (p_X - c_X(\xi))d\xi, \tag{3.8}$$

which reflects the net revenue from the harvest H_{X_k} in period k. Hence, it is assumed that the price of the harvested stock X is fixed. The cost of effort to remove H_X amount from the stock X is assumed to be a decreasing function of X.

3.2 Optimal escapements for prey and predator

To obtain the optimal harvesting strategy I use dynamic programming (Appendix 3A). The escapement method described by Clark (1976a) and Tuck and Possingham (1994) is used. Let

$$J_T(N_0, P_0) = \max_{0 \leq S_{X_0} \leq X_0} \left(\sum_{k=0}^{T} \rho^k \sum_{X \in \{N,P\}} \Pi_X(X_k, S_{X_k}) \right) \tag{3.9}$$

be a value function which is the sum of the discounted net revenue resulting from harvesting both populations in both patches up to period $t = T$. We need to maximise this function by choosing optimal escapements S_{X_k}. Equation (3.9) is then used recursively to obtain the value function at time $T+1$, $J_{T+1}(N_0, P_0)$, which is

$$\begin{aligned} J_{T+1}(N_0, P_0) &= \max_{0 \leq S_{X_0} \leq X_{i0}} \Bigg(\rho J_T(N_1, P_1) \\ &\quad + \sum_{X \in \{N,P\}} \Pi_X(X_0, S_{X_0}) \Bigg) . \end{aligned} \tag{3.10}$$

This equation implies that the optimal revenue over $T+1$ periods can be achieved using appropriate escapements, $S^*_{N_0}$ and $S^*_{P_0}$, that maximise the immediate revenue in the first period, together with appropriate escapements that maximise the revenue taken from future harvests if the population sizes change from N_0 and P_0 to $N_1(S^*_{N_0}, S^*_{P_0})$ and $P_1(S^*_{N_0}, S^*_{P_0})$.

To find optimal escapements, a gradual step with respect to the time horizon is carried out. First consider $T = 0$. In this case, the sole-owner would maximise the immediate net revenue taken from immediate harvests without considering the future value of the immediate harvested stock, in other words no discounting factor is applied. The immediate net revenue is given by

$$J_0(N_0, P_0) = \max_{0 \leq S_{X_0} \leq X_0} \left(\sum_{X \in \{N,P\}} \Pi_X(X_0, S_{X_0}) \right) . \tag{3.11}$$

To satisfy this maximisation, we need $\frac{\partial \Pi_X}{\partial S_X} = 0$. Let us assume that the optimal escapement is $S_{X\infty}$, then $p_X - c_X(S_{X\infty}) = 0$. Hence the maximum revenue is given by

$$J_0(N_0, P_0) = \sum_{X \in \{N,P\}} \Pi_X(X_0, S_{X\infty}). \tag{3.12}$$

Two cases can occur. If the recommended escapement is greater than the actual population size, than the sole-owner should not harvest the stock at all. While if it is smaller than the population size then a harvest, as much as the difference between these two quantities, can be removed from the stock. This is the optimal strategy for the sole-owner to exploit the resource.

Next, consider the next time horizon, $T = 1$. Recall that, from equation (3.10), $J_{T+1}(N_0, P_0)$ is given by

$$\begin{aligned} J_1(N_0, P_0) &= \max_{0 \le S_{X_0} \le X_0} \Bigg(\rho J_0(N_1, P_1) \\ &\qquad + \sum_{X \in \{N,P\}} \Pi_X(X_0, S_{X_0}) \Bigg) . \end{aligned} \tag{3.13}$$

Rewrite it using equation (3.12) to obtain

$$\begin{aligned} J_1(N_0, P_0) &= \max_{0 \le S_{X_0} \le X_0} \Bigg(\rho \sum_{X \in \{N,P\}} \Pi_X(X_1, S_{X\infty}) \\ &\qquad + \sum_{X \in \{N,P\}} \Pi_X(X_0, S_{X_0}) \Bigg) . \end{aligned} \tag{3.14}$$

The optimum value will be given by the condition

$$\frac{\partial J_1(N_0, P_0)}{\partial S_{X_0}} = 0 \tag{3.15}$$

To find the partial derivatives, let

$$V(N_k, P_k) = \sum_{X \in \{N,P\}} \Pi_X(X_k, S_{X\infty}). \tag{3.16}$$

Using equation (3.8) for $k = 1$ we obtain

$$\begin{aligned} \frac{\partial V(N_1, P_1)}{\partial S_{Y_0}} &= \sum_{X \in \{N,P\}} \frac{\partial \left(\int_{S_{X\infty}}^{X_1} (p_X - c_X(\xi)) d\xi \right)}{\partial S_{Y_0}} \\ &= \sum_{X \in \{N,P\}} \frac{\partial \left(\int_{S_{X\infty}}^{X_1} (p_X - c_X(\xi)) d\xi \right)}{\partial \varphi(S_{X_0})} \cdot \frac{\partial \varphi(S_{X_0})}{\partial S_{Y_0}}, \end{aligned} \tag{3.17}$$

where $Y = N, P$ and $\varphi(S_{X_0}) = X_1$ as in equations (3.5) and (3.6). Solving the partial derivative of the integral in equation (3.8) gives

$$\frac{\partial \Pi_X(X_0, S_{X_0})}{\partial S_{X_0}} = -(p_X - c_X(S_{X_0})). \tag{3.18}$$

Substitute this result into the partial derivatives $\frac{\partial V(N_1, P_1)}{\partial S_{X_0}}$ to obtain the following solution for equation (3.15)

$$\frac{p_N - c_N(S_{N_0})}{\rho} = (a + F'(S_{N_0}) + \alpha S_{P_0})(p_N - c_N(N_1)) + \beta S_{P_0}(p_P - c_P(P_1)), \tag{3.19}$$

$$\frac{p_P - c_P(S_{P_0})}{\rho} = (b + G'(S_{P_0}) + \beta S_{N_0})(p_P - c_P(P_1)) + \alpha S_{N_0}(p_N - c_N(N_1)). \tag{3.20}$$

These equations are the general form of the optimal harvesting equation for a predator-prey population governed by equations (3.5) and (3.6). The escapements obtained by solving these equations, that is, $S^*_{N_0}$ and $S^*_{P_0}$, are the optimum escapements of the prey and the predator that maximise revenue provided the Hessian matrix of $J_1(S_{N_0}, S_{P_0})$, that is, $J_1''(S_{N_0}, S_{P_0})$, satisfies

$$[J_1''(S^*_X)(S_X - S^*_X)] \cdot [S_X - S^*_X] < 0 \tag{3.21}$$

where $S_X = (S_{N_0}, S_{P_0})$ and $S^*_X = (S^*_{N_0}, S^*_{P_0})$. Another alternative is using the second derivative test where we need

1. $\frac{\partial^2 J_1}{(\partial S_{N_0})^2} < 0$,
2. $\frac{\partial^2 J_1}{(\partial S_{P_0})^2} < 0$,
3. $\frac{\partial^2 J_1}{(\partial S_{N_0})^2} \frac{\partial^2 J_1}{(\partial S_{P_0})^2} - (\frac{\partial^2 J_1}{\partial S_{N_0} \partial S_{P_0}})^2 > 0$.

The detailed conditions are given in Appendix 3B. As in Clark (1976a), these optimal escapements hold for all time horizon $T \geq 1$. The proof will be given in the next chapter in a more complex predator-prey system (Appendix 4B).

If the costs of harvesting is negligible, then equations (3.19) and (3.20) become

$$\frac{p_N}{\rho} = (a + F'(S_{N_0}))p_N + \alpha S_{P_0} p_N + \beta S_{P_0} p_P, \tag{3.22}$$

$$\frac{p_P}{\rho} = (b + G'(S_{P_0}))p_P + \alpha S_{N_0} p_N + \beta S_{N_0} p_P. \tag{3.23}$$

Furthermore, if $p_N = p_P$ then the optimal escapements are given by

$$S^*_N = \frac{A\frac{2s}{L} + CB}{\Delta} \tag{3.24}$$

and

$$S^*_P = \frac{B\frac{2r}{K} + CA}{\Delta}, \tag{3.25}$$

provided $\Delta = C^2 - \frac{2r}{K}\frac{2s}{L} \neq 0$, where $A = \frac{1}{\rho} - r - a$, $B = \frac{1}{\rho} - s - b$, and $C = \alpha + \beta \leq 0$. It can be proved that if A and B are negative, and C is non-positive with $C > max\{\frac{2B}{K}, \frac{2A}{L}\}$, then:

1. Δ is negative,
2. S^*_N and S^*_P are positive,
3. $S^*_N < S^*_{N_s}$ and $S^*_P < S^*_{P_s}$, where $S^*_{N_s}$ and $S^*_{P_s}$ are the optimal escapements for single species, and
4. the second derivative test for maximum is satisfied.

The condition $A < 0$ means that the escapements are positive if the reciprocal of the discounting factor, $1/\rho$, is lower than the sum of the proportion of surviving adults of prey, a, and the intrinsic growth rate, r. The condition $B < 0$ is interpreted similarly for predators. If S_{N_1} is an escapement if we use a discounting rate δ_1 and S_{N_2}

is an escapement if we use a discounting rate δ_2, where $\delta_1 \neq \delta_2$, $A < 0$ and $B < 0$, and in addition $C > -\frac{2s}{L}$, then, by considering the sign of $S_{N_1} - S_{N_2}$, it can be proved that higher discounting rates imply lower escapements. This is known as the "fundamental principle of renewable resource economics" (Clark, 1976a, 1985a) and considered as a normal situation in single-species harvesting theory, otherwise it is best to harvest the populations down to zero escapements (Schmitt and Wissel, 1985; Daly and Cobb, 1989; Ackerman, 1994; Dawid and Kopel, 1997). Appendix 3C shows that this rule is also true if there are price differences between the prey and the predator. In this case the optimal escapement for each species is affected by the "economic efficiency" of the predator, $\frac{m\beta}{|\alpha|}$. A similar result is also found for continuous-time predator-prey models (Ströbele and Wacker, 1995). The "fundamental principle of renewable resource economics" for a single-species population generalises to the multi-species population. This is because we assume that harvesting can be carried out selectively. This is not always the case in harvesting a multi-species system. Sieveking and Semmler (1997) showed that a lower discounting rate may also cause a lower escapement in harvesting a predator-prey population, if we harvest the population non-selectively.

3.3 Harvesting only the prey species

In some cases we only need to harvest either the prey or the predator population. In this section, optimal escapements for harvesting only the prey population are derived using similar method to harvesting both prey and predator. Optimal escapements for harvesting only the predator population can also be obtained using the same method (see Section 4.3.3 for a more complex predator-prey system).

Using present value maximisation, now the objective is to maximise the net revenue from harvesting prey population up to time horizon $t = T$. As before, Π_N represents the present value of net revenue from harvesting prey population N, then we need to maximise

$$PV = \sum_{k=0}^{T} \rho^k \Pi_N(N_k, S_{N_k}) \tag{3.26}$$

subject to

$$N_{k+1} = aS_{N_k} + F(S_{N_k}) + \alpha S_{N_k} P_k, \tag{3.27}$$

$$P_{k+1} = bP_k + G(P_k) + \beta S_{N_k} P_k, \tag{3.28}$$

and $0 \leq S_{N_k} \leq N_k$. Let

$$J_T(N_0, P_0) = \max_{0 \leq S_{N_0} \leq N_0} \left(\sum_{k=0}^{T} \rho^k \Pi_N(N_k, S_{N_k}) \right) \tag{3.29}$$

be a value function from harvesting only the prey population up to period $t = T$. The value function at time $T + 1$ can be written recursively as

$$J_{T+1}(N_0, P_0) = \max_{0 \leq S_{N_0} \leq N_0} \left(\rho J_T(N_1, P_1) + \Pi_X(X_0, S_{X_0}) \right). \tag{3.30}$$

A step by step process with respects to time remaining t is carried out to obtain the optimal escapements for the system. First let us consider $T = 0$.

$$\begin{aligned} J_0(N_0, P_0) &= \max_{0 \leq S_{N_0} \leq N_0} \left(\Pi_N(N_0, S_{N_0}) \right) \\ &= \Pi_N(N_0, S_{N\infty}). \end{aligned} \tag{3.31}$$

Next let us consider the next time horizon, $T = 1$,

$$\begin{aligned} J_1(N_0, P_0) &= \max_{0 \leq S_{N_0} \leq N_0} [\Pi_N(N_0, S_{N_0}) + \rho J_0(N_1, P_1)] \\ &= \max_{0 \leq S_{N_0} \leq N_0} [\Pi_N(N_0, S_{N_0}) + \rho \Pi_N(N_1, S_{N\infty})] . \end{aligned} \tag{3.32}$$

A necessary condition for an optimum is $\frac{\partial J_1(N_0,P_0)}{\partial S_{N_0}} = 0$, hence the optimal escapement is given by the equation

$$\frac{p_N - c_N(S_{N_0})}{\rho} = (a + F'(S_{N_0}) + \alpha P_0)(p_N - c_N(N_1)) . \tag{3.33}$$

This equation is the implicit equation of the optimal escapement for one period to go. The optimal escapement for one period to go is denoted by $S_N^{1*}(P_0)$ which is a function of predator population size P_0. In harvesting both the prey and predator populations, the optimal escapement is independent of the time horizon considered. But here this is no longer true. Appendix 3D derives an equilibrium prey optimal escapement as a function of predator equilibrium population size, P, using dynamic programming. The appendix shows that if

$$|\rho(b + G'(P) + \beta S_N^*)| < 1 \tag{3.34}$$

then the implicit expression of the equilibrium prey optimal escapement is given by

$$\begin{aligned} \frac{(p_N - c_N(S_N^*))}{\rho} &= (a + F'(S_N^*) + \alpha P)(p_N - c_N(N)) \\ &\quad + \rho \left[\frac{\alpha \beta P S_N^*}{1 - \rho(b + G'(P) + \beta S_N^*)} \right] (p_N - c_N(N)). \end{aligned} \tag{3.35}$$

This implicit optimal escapement equation is similar to the implicit form of optimal escapement for a partially reserved metapopulation discussed in the work of Tuck (1994). The difference is that the occurrence of a nonlinear term $\alpha\beta P S_N^*$, which makes the interpretation of the equation more difficult. To find the optimal escapement we need to satisfy condition (3.34). However, using the method of Lagrange multipliers (Appendix 3E), the same equation can be derived without requiring the fulfilment of this condition. Hence, to obtain the optimal escapement S_N^* we only need to solve equation (3.35) together with the predator dynamic

$$P = bP + G(P) + \beta S_N^* P. \tag{3.36}$$

Next, I will interpret equation (3.35) for some special cases.

The case of $\alpha = 0$. In this case, equation (3.35) reduces to

$$0 = -(p_N - c_N(S_N^*)) + \rho[(p_N - c_N(N))(a + F'(S_N^*))]. \tag{3.37}$$

This is the optimal escapement equation for a single-species population (Clark, 1976a).

The case of $\beta = 0$ *and* $\alpha \neq 0$. In this case, the interaction only affects prey population and does not give an influence to the growth of the predator and equation (3.35) becomes

$$0 = -(p_N - c_N(S_N^*)) + \rho[(p_N - c_N(N))(a + F'(S_N^*) + \alpha P)], \tag{3.38}$$

which is the implicit equation of prey escapement for one period to go (equation (3.33)).

The case of $\alpha \neq 0$*,* $\beta \neq 0$ *and* $|\rho(b + G'(P) + \beta S_N^*)| < 1$. In this more general case, equation (3.35) is equivalent to

$$-(p_N - c_N(S_N^*)) + \rho[(p_N - c_N(N))(a + F'(S_N^*) + \alpha P)] > 0, \qquad (3.39)$$

since S_N^* is a root of equation (3.35). Furthermore, if the cost of harvesting is negligible (or independent of the population size) and F is a logistic recruitment function then we obtain

$$\begin{aligned} F'(S_N^*) &> \frac{1}{\rho} - a - \alpha P \\ r - \frac{2r}{K} S_N^* &> \frac{1}{\rho} - a - \alpha P \\ S_N^* &< \frac{K}{2} + \frac{K}{2r}\left(a - \frac{1}{\rho} + \alpha P\right). \end{aligned} \qquad (3.40)$$

Note that, predation is behaving like discounting. Hence, as far as economically optimal harvesting strategies are concerned, an increase in the discounting rate is equivalent to an increase in predation rate or to an increase in the number of predators, which means a decreasing prey escapement. It can also be interpreted that, for the same predator population size, the equilibrium optimal escapement is always less than the optimal escapement for one period to go. Next, since α is negative then

$$S_N^* < \frac{K}{2} + \frac{K}{2r}\left(a - \frac{1}{\rho}\right). \qquad (3.41)$$

By comparing this with equation (2.48), the right hand side in (3.41) is the optimal escapement for a single-species population. This suggests that in the presence of an unexploited predator, assuming logistic recruitment, the stock recruitment is lower than in the absence of the predator. This situation is intuitive and can be observed in many fisheries that exploit only the prey population. For example, Harwood (1987) and Harwood and Croxall (1988) observed the declining of inshore commercial fisheries with the increase of the grey seal, *Halichoerus grypus*, population in the British Isles water. Next further interpretation is obtained by recalling that $(1 - \frac{K}{2}\alpha\beta P) > 0$ and substituting predator equilibrium equation (3.36) into inequality (3.40) to produce

$$\begin{aligned} S_N^* &< \frac{K}{2}\left(1 + \frac{1}{r}\left(a - \frac{1}{\rho} + \alpha P\left[b + s\left(1 - \frac{P_0}{L}\right) + \beta S_N^*\right]\right)\right) \\ S_N^*\left(1 - \frac{K}{2r}\alpha\beta P\right) &< \frac{K}{2}\left(1 + \frac{1}{r}\left(a - \frac{1}{\rho} + \alpha P\left[b + s\left(1 - \frac{P}{L}\right)\right]\right)\right) \\ S_N^* &< \frac{\frac{K}{2}\left(1 + \frac{1}{r}\left(a - \frac{1}{\rho} + \alpha P b\right)\right) + \frac{s}{r}\frac{K}{2}\alpha P\left(1 - \frac{P}{L}\right)}{\left(1 - \frac{K}{2r}\alpha\beta P\right)}. \end{aligned} \qquad (3.42)$$

The last inequality suggests that, for a fixed prey intrinsic growth, if the resulting predator equilibrium is less than the predator carrying capacity, then increasing the ratio of predator intrinsic growth to the prey intrinsic growth causes the right hand side of the inequality to decrease. In other words, it causes the upper bound of the optimal escapement S_N^* to decrease. Numerical examples in the section that follows show that it may also decrease the optimal escapement itself.

3.4 Numerical examples: Harvesting one or both species

In this section some numerical examples are given to illustrate optimal escapements for the predator-prey population in the previous section. I consider two types of harvesting: harvesting both species and harvesting only the prey species. These escapements are compared to escapements if we manage the stock as a single-species population. I use a relatively small number for the carrying capacity of each species to facilitate comparisons between escapements derived analytically [equations (3.22) and (3.23)] and escapements obtained by iterating Bellman's equation (3.10).

3.4.1 Harvesting both species

Let the prey population have a carrying capacity $K = 2000$, with intrinsic growth rate $r = 2$ and adult survival per period $a = 0.1$, while the predator has carrying capacity $L = 40$, intrinsic growth rate $s = 2$, and adult survival rate $b = 0.1$. Let the coefficients of predator-prey interaction be $\alpha = -0.001$ and $\beta = 0.001$. To find the optimal harvesting strategy, assume: the initial population size of the prey and predator are at their equilibrium population size, an economic discounting rate $\delta = 10\%$, the cost associated with harvesting is negligible and there is no difference between prey and predator prices.

Solving equations (3.1) and (3.2), the equilibrium population size for the prey and predator are found, that is, $\bar{N} = 1057$ and $\bar{P} = 43$. Furthermore, solving equations (3.24) and (3.25) gives optimal escapements for the prey and predator $S_N^* = 500$ and $S_P^* = 10$, respectively, with equilibrium optimal harvests $H_N^* = 295$ and $H_P^* = 11$. These optimal escapements and their equilibrium optimal harvests can be observed in Figure 3.1. The optimal escapement for the predator is slightly different to the result from iterating Bellman's equation (3.10), that is, $S_N^* = 500$ and $S_P^* = 11$, as shown in Table 3.1. This difference is due to the rounding error involved in solving the dynamic programming problem and using a discrete state space.

The optimal escapements for the prey and predator are the same as the optimal escapements if we assumed the species were independent, that is, no predator-prey interaction between the species. In this case, initial population sizes $N_{s0} = 1100$ and $P_{s0} = 22$, optimal equilibrium escapements $S_{N_s}^* = 500$ and $S_{P_s}^* = 10$, and equilibrium optimal harvests $H_{N_s}^* = 300$ and $H_{P_s}^* = 6$ are obtained. This is because we assume the predator is very efficient, that is, $|\alpha| = \beta$. In the next chapter, it will be shown that this rule is also true for a spatially-structured predator-prey population.

In this example the prey's optimal harvest from the predator-prey population escapements is lower than optimal harvest from the single-species population model. On the other hand the predator's optimal harvest from the predator-prey population escapements is higher than the optimal harvest from the single-species population model. This is not surprising because in predator-prey populations the fishers are competing with the predator, so that the numbers of the prey decreases while the numbers of the predators may increase. In this case, it is best to harvest the predator below its MEY.

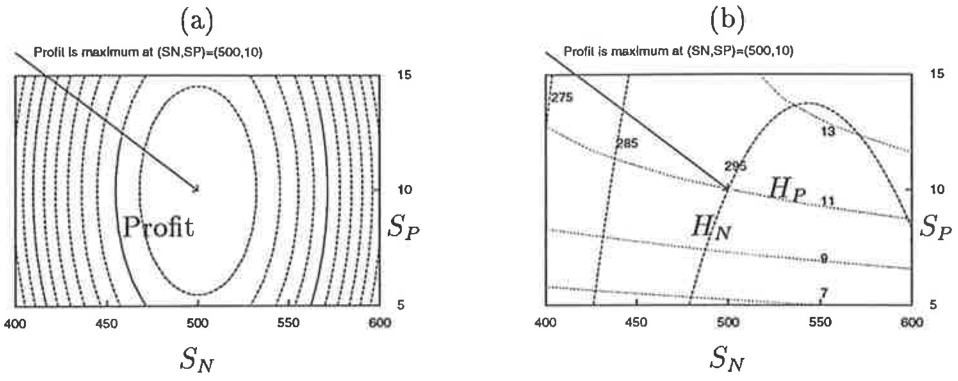

Figure 3.1: Contour plot of the profit function PV (Figure 3.1.a) and the optimal equilibrium harvests (Figure 3.1.b) as functions of prey and predator escapement S_N and S_P. The dashes in Figure 3.1.b are the contour plots of the prey equilibrium harvests, H_N, and the dots are the contour plots of the predator equilibrium harvests, H_P. The optimal escapements are found to be $S_N^* = 500$ and $S_P^* = 10$ with equilibrium harvests $H_N^* = 295$ and $H_P^* = 11$.

3.4.2 Variation of parameters

Impact on harvesting strategy of the variation in the prey vulnerability parameters

In this section I discuss the effect of prey vulnerability on optimal escapements. Rewrite the optimal escapements in equations (3.24) and (3.25) as $S_N^* = \frac{D}{\Delta}$ and $S_P^* = \frac{E}{\Delta}$, where $D = \frac{2sA}{L} + CB$, $E = \frac{2rB}{K} + CA$. Using this notation, the first derivative of the optimal escapements with respect to α are

$$\frac{\partial S_N^*}{\partial \alpha} = \frac{D'\Delta - \Delta' D}{\Delta^2} \tag{3.43}$$

and

$$\frac{\partial S_P^*}{\partial \alpha} = \frac{E'\Delta - \Delta' E}{\Delta^2}. \tag{3.44}$$

In our example these reduce to

$$\frac{\partial S_N^*}{\partial \alpha} = \frac{-1}{C^2 - \frac{1}{5000}} + 2\frac{(0.1 + C)C}{(C^2 - \frac{1}{5000})^2} \tag{3.45}$$

and

$$\frac{\partial S_P^*}{\partial \alpha} = \frac{-1}{C^2 - \frac{1}{5000}} + 2\frac{(0.002 + C)C}{(C^2 - \frac{1}{5000})^2}. \tag{3.46}$$

Using these derivatives I investigate the effect of prey vulnerability on the optimal escapements. For simplicity, let us fix $\beta = 0.001$. With increment $\Delta\alpha = 0.0005$ we expect the change in escapement $\Delta S_N = -10718(0.0005) = -5.36$ at $\alpha = -0.004$. The exact value of the prey escapement S_N^* at $\alpha = -0.004$ is 508, and at $\alpha = -0.0035$ is 503. With the same increment we expect the change in escapement $\Delta S_N = 5000(0.0005) = 2.5$ at $\alpha = -0.001$. The exact value of the prey escapement S_N^* at $\alpha = -0.001$ is 500,

t	N	P	S_N^*	S_P^*	H_N^*	H_P^*
0	1057	43	500	11	557	32
1	795	23	500	11	295	12
2	795	23	500	11	295	12
3	795	23	500	11	295	12
4	795	23	500	11	295	12
5	795	23	0	0	795	23

Table 3.1: Optimal escapements for predator-prey population derived by iterating Bellman's equation (3.10). Optimal escapement for the prey and predator are S_N^* and S_P^*, respectively, while H_N^* and H_P^* denote their optimal harvests for each species. The t^{th} row indicates the value for $5-t$ periods to go.

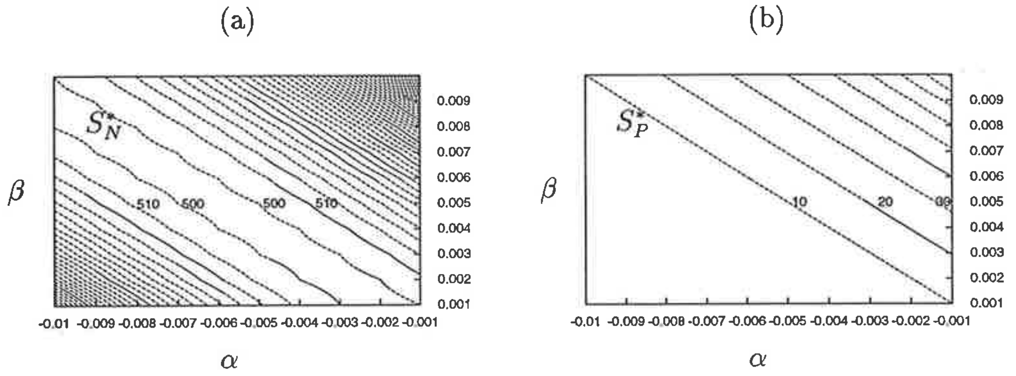

Figure 3.2: Contour plots of optimal escapements S_N^* (Figure 3.2.a) and S_P^* (Figure 3.2.b) as the functions of prey vulnerability α and predator biological conversion parameter β.

and at $\alpha = -0.0005$ is 503. This result is illustrated in Figure 3.2.a. A similar result is also obtained for the predator optimal escapement S_P^*. With increment $\Delta\alpha = 0.0005$ we expect the change in escapement $\Delta S_P = 5000(0.0005) = 2.5$ at $\alpha = -0.001$. The exact value of $S_P^* = 10$ is at $\alpha = -0.001$ and $S_P^* = 12.52$ is at $\alpha = -0.0005$. With the same increment we expect the change in escapement $\Delta S_N = 5400(0.0005) = 2.7$ at $\alpha = -0.004$ (see Figure 3.2.b). Hence, the difference in escapements from the same increment is lower for a higher predator efficiency, that is, $C = \alpha + \beta = 0$. This suggests that a decision to adopt optimal escapements for a predator-prey population should not be affected by the uncertainty about the exact value of the prey vulnerability if the predator efficiency is high.

Now let us look at the effect of prey vulnerability α and predator efficiency C on the equilibrium optimal harvests H_N^* and H_P^*. Recall that equilibrium optimal harvests are given by equations

$$H_N^* = (aS_N^* + rF(S_N^*) + \alpha S_N^* S_P^*) - S_N^* \tag{3.47}$$

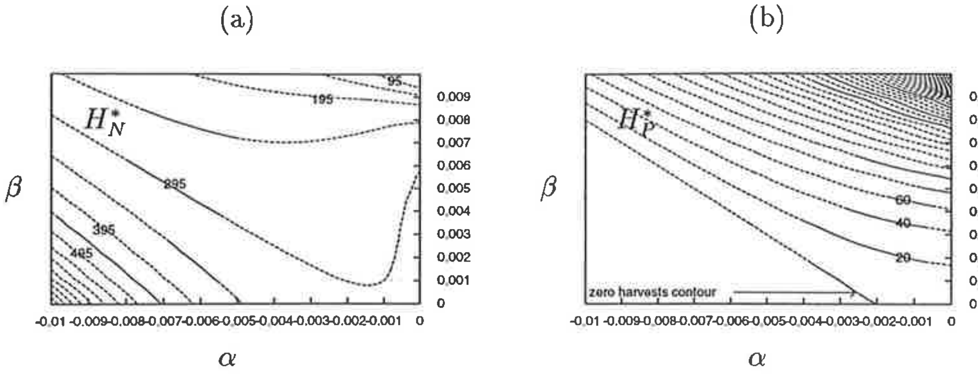

Figure 3.3: Contour plot of equilibrium optimal harvests H_N^* (Figure 3.3.a) and H_P^* (Figure 3.3.b) as the functions of prey vulnerability α and predator biological conversion parameter β.

and similarly

$$H_P^* = (bS_P^* + sG(S_P^*) + \beta S_N^* S_P^*) - S_P^*. \tag{3.48}$$

Using a similar method to the previous analysis on the effects of variations of prey vulnerability α and predator parameter β on optimal escapements, the following result is obtained. At a fixed value of $\beta = 0.001$, the increment of 0.0005 in α at the point $\alpha = -0.002$ decreases the optimal harvest by as much as two individuals from $H_N^* = 295$ to $H_N^* = 293$. The same increment decreases the optimal harvest by as much as six individuals at the point $\alpha = -0.004$ from $H_N^* = 311$ to $H_N^* = 305$. This can be observed graphically in Figure 3.3.a. As for the optimal escapements, the effect of the variation of prey vulnerability on the equilibrium optimal harvests is less intense when $C = \alpha + \beta$ close to zero (Figure 3.3).

Impact on harvesting strategies of the variation in the predator efficiency and relative market price parameters

In this section I discuss the effects of the predator efficiency, $\beta/|\alpha|$, and the relative predator market value, m, on the optimal escapements and harvests S_N^*, S_P^*, H_N^*, and H_P^*. If the ratio of the predator market price to the prey market price is $p_P/p_N = m$, then, using the same procedure to the previous analysis in which there is no differences between the two market prices, the optimal escapements are

$$S_N^* = \frac{A\frac{2ms}{L} + mCB}{\Delta} \tag{3.49}$$

and

$$S_P^* = \frac{B\frac{2mr}{K} + CA}{\Delta}, \tag{3.50}$$

where $\Delta = C^2 - m\frac{2r}{K}\frac{2s}{L} \neq 0$, $C = \alpha + m\beta$, A and B as in (3.24) and (3.25), respectively. Partial derivatives of these escapements with respect to the relative predator market price are

$$\frac{\partial S_N^*}{\partial m} = \frac{KL\left[2sAK(\alpha^2 - m^2\beta^2) + m\alpha\beta BKL(2\alpha + m\beta)\right]}{\Delta^2}$$

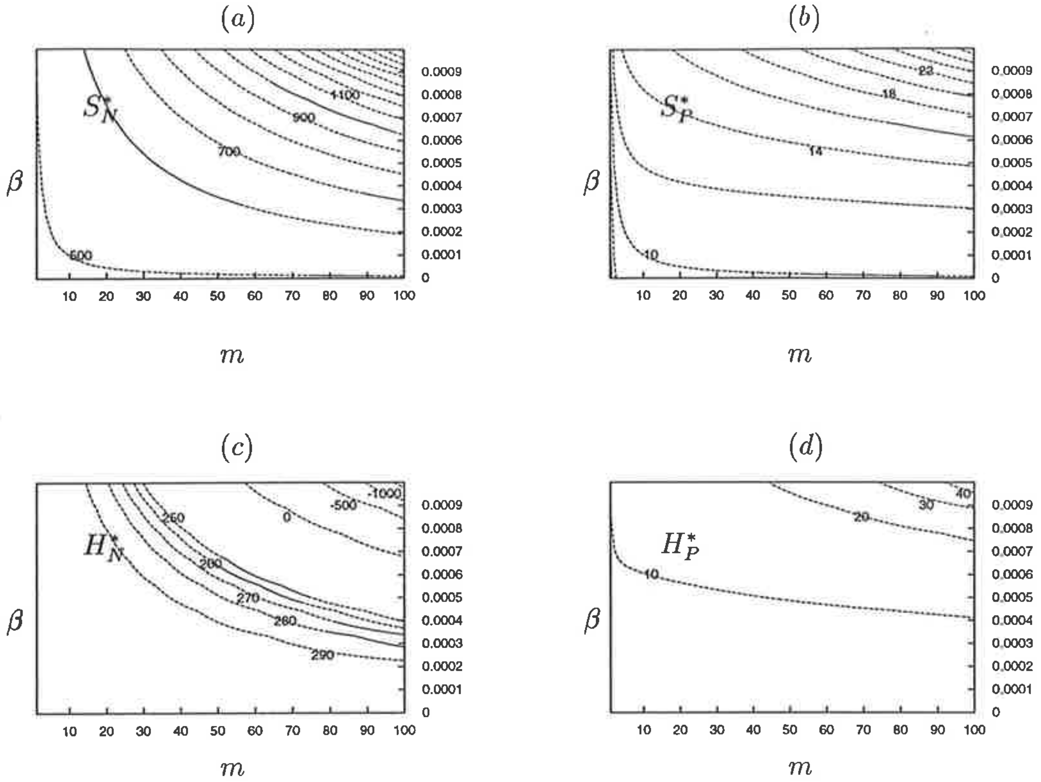

Figure 3.4: Optimal escapements S_N^* and S_P^* (Figure 3.4.a and Figure 3.4.b) and equilibrium harvests H_N^* and H_P^* (Figure 3.4.c and Figure 3.4.d) as the functions of predator conversion coefficient β and the relative predator market price m, for a fixed prey vulnerability $\alpha = -0.001$. Figure 3.4.c reveals that if the predator efficiency is very high and the relative predator market price is also very high, it is optimal to feed the predator population, indicated by the negative harvest for the prey population.

$$-\frac{KL\left[m\beta BKL\left(\frac{4msr}{KL}-\frac{\alpha^3}{m\beta}\right)\right]}{\Delta^2} \tag{3.51}$$

and

$$\begin{aligned}\frac{\partial S_P^*}{\partial m} &= \frac{-KL\left[\beta AKL(\alpha^2+m\beta(2\alpha+m\beta))\right]}{\Delta^2}\\ &\quad+\frac{KL\left[2rBL(\alpha^2-m^2\beta^2)+4A\alpha sr\right]}{\Delta^2}.\end{aligned} \tag{3.52}$$

If the predator has a high biological efficiency such that this efficiency is greater than twice the inverse of the relative predator market price, that is, $\beta/|\alpha| > \frac{2}{m}$, then both partial derivatives are positive. Hence in this case, the increase in the relative predator market price increases both the prey and the predator escapement. The prey escapement increases because it is important as food for the predator, which is an efficient biomass converter and has a better economic value than the prey. The predator escapement increases because of the increasing escapement of the prey.

Note that a large difference in the relative prices of the species, where the relative price for the predator higher than the relative price for the prey, drives the less valuable

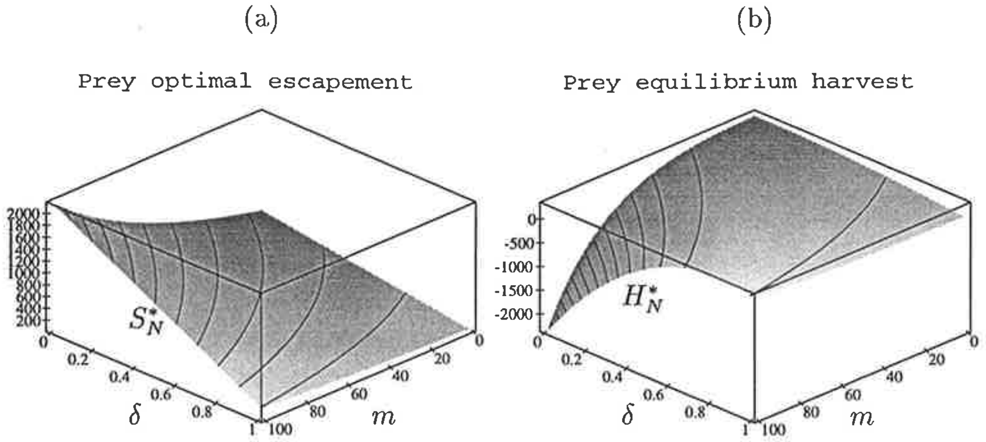

Figure 3.5: Figure 3.5.a is the graph of prey escapement, S_N^*, as a function of predator's relative price, m, and the discounting rate, δ. Figure 3.5.b is the graph of its equilibrium harvest, H_N^*. Consistent to harvesting a single-species population, high discounting rate is likely causing the manager of the resource to deplete the resource. This is indicated by the declining of optimal escapement for prey population (Figure 3.5.a) as the discounting increases. Seeding strategy into prey population which occurs for discounting rate $\delta = 10\%$ ($m = 10$ and $\beta = 0.001$ in Figure 3.4) is not optimal for larger discounting rates (Figure 3.5.b).

prey species to a high level of escapement. [For comparison, Agnew (1982) shows that a large difference in the relative prices of each species in a competitive system decreases the optimal escapement level of the less valuable species. This is because, in a competitive system, the less valuable species does not contribute anything to the growth of the more valuable species positively. While in a predator-prey system, the less valuable species (the prey) is converted into the more valuable species (the predator) with respect to a certain biological efficiency].

Hence, if predators are more valuable than prey species, it can be concluded that it is better to leave the prey species to be consumed by its predator than to harvest the prey which only has a low market price compared to the predator. The consumed prey are converted into a predator, and in turn we harvest the predator which is m times more valuable than the prey. However, this strategy only works when predator efficiency is high (see Figure 3.4.a). Therefore, if the predator efficiency is relatively high and the harvest from the predator is profitable (indicated by large m) then the harvest from the prey could be very low, due to the importance of the prey as food for the predator. In a real fishery, capelin off eastern Canada is only harvested at the rate of no more than ten per cent of its spawning biomass. This is because the capelin is very important as food for other commercial fish, like cod (Caddy and Mahon, 1995). Furthermore, Shelton *et al.* (1993) showed that production of the cod could be negatively affected by the excessive harvesting of the capelin.

Figure 3.4.c shows that if m and β are even larger, for a fixed α, our equations show that the optimal prey harvest is negative. In this case a seeding strategy for the prey population is an optimal strategy. This strategy can also be regarded as a feeding strategy, where we put prey into the system to feed the predator. This strategy

t	N	P	S_N^*	P^*	H_N^*	H_P^*
0	1057	43	476	43	580	0
1	753	18	528	18	225	0
2	820	31	463	31	357	0
3	744	31	463	31	281	0
4	744	31	463	31	281	0
5	744	31	0	31	744	0

Table 3.2: Optimal escapements and their harvests derived by iterating Bellman's equation (3.10) with $s = 2$, if we harvest only the prey species. All notations are identical to those in Table 3.1.

is economically optimal because the economic efficiency of the predator, $m\beta/|\alpha|$, is relatively large compared to the discounting rate, δ. However, when the discounting rate is high, investment through increasing the predator population by feeding them prey, is not likely to be profitable. As a result, a negative harvest or seeding strategy is no longer optimal for a high discounting rate (see Figure 3.5 for $m = 10$ and $\delta = 100\%$; see also Appendix 3C).

3.4.3 Harvesting only the prey species

Suppose that we are only harvesting the prey population. The optimal escapement from iterating Bellman's equation is shown in Table 3.2. Different optimal escapements are found for different periods to go and they rapidly approach an equilibrium optimal escapement, that is, $S_N^* = 463$ with a predator equilibrium population size $P^* = 31$. This numerically calculated equilibrium optimal escapement is different from the analytical result found by solving equations (3.35) and (3.36). The analytical method gives a result of $S_N^* = 480$ and $P^* = 32$. Hence the numerical procedure gives an error of about 3.5% of the analytical result. The differences are due to the rounding error using integer numbers in dynamic programming while in the analytical method I use real numbers as the populations sizes. The first year escapement from the numerical result ($S_N^* = 476$) is also lower than the first year escapement from the graphical illustration of the analytical method (Figure 3.6).

Inequality (3.42) suggests that, for a fixed prey intrinsic growth rate, if the resulting predator equilibrium is less than the predator carrying capacity, then the increase in the ratio of predator intrinsic growth to prey intrinsic growth decreases the upper bound of the optimal escapements S_N^*. Iteration of Bellman's equation for the previous example ($K = 2000$, $|\alpha| = \beta = 0.001$ and $s = 2$) with the changing of the predator intrinsic growth s to $s = 3$ gives an equilibrium prey optimal escapement of $S_N^* = 389$ (Table 3.3). The equilibrium prey optimal escapement for $s = 2$ is $S_N^* = 463$ (Table 3.2) which is higher than the equilibrium optimal escapement for $s = 3$. Hence, in this example, if the resulting predator equilibrium is less than the predator carrying capacity, then the increase of the ratio of predator intrinsic growth to prey intrinsic growth not only decreases the upper bound of the optimal escapements S_N^*, but also decreases the resulting optimal escapements S_N^* itself, for a fixed prey intrinsic growth (see inequality (3.42)).

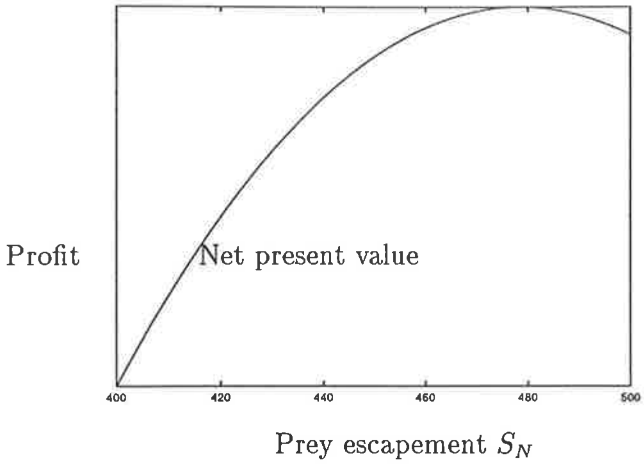

Figure 3.6: Profit function as a function of prey escapement with time period $T = 1$. The optimal escapement lies between 476-480.

Time to go	30	29	28	...	5	4	3	2	1	0
S_N^*	481	530	468	...	403	389	389	389	389	0
P	42	18	41	...	13	33	33	33	33	33

Table 3.3: Optimal escapements for the prey population, S_N^*, and their equilibrium predator population size, P, if we harvest only the prey species.These escapements are derived by iterating Bellman's equation (3.10) with $s = 3$.

3.5 Concluding remarks

In this chapter I have modelled a deterministic, discrete-time predator-prey system using coupled difference equations as a generalisation of Clark's (1976a) discrete-time single-species population model with overlapping generations. I use dynamic programming and the method of Lagrange multipliers to find optimal harvesting strategies for the system considering two different types of exploitation: harvesting both species and harvesting only the prey species.

In some circumstances, for example when costs are negligible, a multi-species fishery exploiting a predator-prey population should concentrate the exploitation on the predator species if the predator is an efficient biomass converter and more valuable in the market than the prey. This is intuitively logical and consistent with the results of May *et al.* (1979), Hannesson (1983), Ragozin and Brown (1985), and Degee and Grasman (1998). They pointed out that if the prey has a very low value then it is better to leave the prey as food for the predator rather than as exploited stock. In this case, if we assume that the cost (or effort) of harvesting is the same for the prey and predator then harvesting the predator gives a higher net return per unit effort than harvesting the prey. This is known for other types of multi-species fisheries, for example Gatto *et al.* (1982) suggested that, in a multi-species fishery with non-interacting species, stock with lower net return per unit effort should be less exploited than the other stock. Caddy (1975), Hilborn and Ledbetter (1979) and Hilborn and Kennedy (1992) have also discussed multi-species fisheries with spatially different stocks and their results conform to the results presented here.

Most of the conclusions in this chapter are not new. The main purpose is to present a baseline result with which I can compare the spatially-structured optimal harvesting strategies. One conclusion that has not been discussed in other work is the interpretation of a negative harvest as a feeding strategy. A numerical example for harvesting both species shows that if the predator has an extremely high biological efficiency and high market value, increasing the prey species through seeding may be optimal. This is indicated by a negative harvest $H_N = X_N - S_N$ where $X_N < S_N$. In this case increasing the prey species can be regarded as feeding the predator. In many situations a seeding or feeding strategy is logistically and economically unlikely, for example in a trans-boundary fishery in which the exploited fish stock is not governed by a single authority or country. In this case, the benefit of seeding or feeding strategy implemented by one authority can accrue to another authority. Another limitation of this seeding or feeding strategy is that I assume that seeding has a cost (negative harvest profit) equal to the price of prey. This might not be true and the seeding cost is likely to be higher. In this case an optimal harvesting strategy is to apply a zero harvest until the prey abundance is higher than the prey optimal escapement. Another alternative for dealing with negative harvests is proposed by Tuck and Possingham (1994) and discussed in Chapter 5 for a more complex predator-prey population.

If we harvest the prey population, it can be concluded that an optimal harvesting strategy is less conservative than either an optimal harvesting strategy derived from single-species theory or a harvesting strategy derived by considering maximum economic yield as the objective of harvesting management [see inequality (3.40)]. This is because we compete with the predator, while we are also maximising the net revenue. The right hand side of inequality (3.40) is an upper bound on the prey optimal escapement. The inequality suggests that more predators implies a lower upper bound for the prey optimal escapement. A numerical example shows that it may also cause a lower prey optimal escapement, which can be observed in many fisheries. For example, Harwood (1987) and Harwood and Croxall (1988) have observed the declining of inshore commercial fisheries with the increasing of grey seal, *Halichoerus grypus*, populations in the British Isles.

The right hand side of inequality (3.40) can be considered an escapement associated with maximum economic yield if $\delta = 0$. It suggests that, assuming the number of predators is in a steady state, this escapement decreases with increasing prey vulnerability. In general the number of predators would change if the number of prey changes. However, in the model in this chapter, I assume the predator has another main food, and if the biological conversion rate β is relatively small, then the number of predators would not change substantially.

In the next chapter I add spatial structure into the model in this chapter. I derive optimal harvesting strategies and compare them to harvesting strategies if we incorrectly ignore the spatial structure of the population.

3.6 Appendices

Appendix 3A: "Bellman's principle of optimality"

Dynamic programming is a technique to solve an optimisation problem. It was developed by Richard Bellman four decades ago. The core of dynamic programming is the following "principle of optimality".

> "An optimal policy has the property that whatever the initial state and initial decision are, the remaining decisions must constitute an optimal policy with regard to the state resulting from the first decision" (Bellman, 1957).

This principle is obvious to Bellman (1957) who stated that "a proof by contradiction is immediate". Other authors, e.g. Sniedovich (1992) proved the principle in a more precise mathematical formulation.

In general, a dynamic programming problem involves a multi-stage decision process or an n-dimensional optimisation problem. Among many advantages of the dynamic programming approach in solving this n-dimensional optimisation problem is that using this approach we can obtain n one-dimensional optimisation problems and produces the global maxima or minima as the solution of the problem. Cooper and Cooper (1981) pointed out that a dynamic programming problem as a multi-stage decision process has the following elements:

Stage , i.e., a variable reference of when the process is taking place. For example, in a discrete multi-stage decision processes, stages are usually associated or represented by the numbers in $k = \{1, 2, 3, ...\}$ (see Figure 3.7). In resource management the stage is usually time, and often the time interval is a year.

State , i.e., a variable that describes the condition of the system at a certain stage (figure 3.7).

Decision , i.e., an action available when the system is in a certain stage and certain state (see Figure 3.7). An ordered set of decisions is usually referred to as a ***policy***.

Transformation , i.e., an action that makes a process move from one stage to another stage after choosing a certain decision. This transformation relates the state in one stage to the state occurring in the previous stage. For example, $f(X_k, S_k(X_k), k)$ in Figure 3.7 determines the movement of the process from stage k and state X_k to the next stage by choosing a decision $S_k(X_k)$.

Furthermore, because a dynamic programming problem is an optimisation problem, then there is an objective function that generates the overall return from the implementation of any policy.

Let us consider the following dynamic programming example, taken from Conrad and Clark (1987).

$$\max_{\{S_k\}} \sum_{k=0}^{T} \Pi(X_k, S_k, k) \tag{3.53}$$

subject to

$$X_{k+1} = f(X_k, S_k, k),\ k = 0, 1, \cdots, T-1 \tag{3.54}$$

$$S_k \in \mathcal{S},\ k = 0, 1, \cdots, T \tag{3.55}$$

with $X_0 = a$ is given. If X is the state variable at a stage when only n periods remains, define $J_n(X)$ as the maximum total value up to that stage, hence

$$J_n(X) = \max \sum_{k=T-(n-1)}^{T} \Pi(X_k, S_k, k) \tag{3.56}$$

$$\text{with } X_{T-(n-1)} = X \tag{3.57}$$

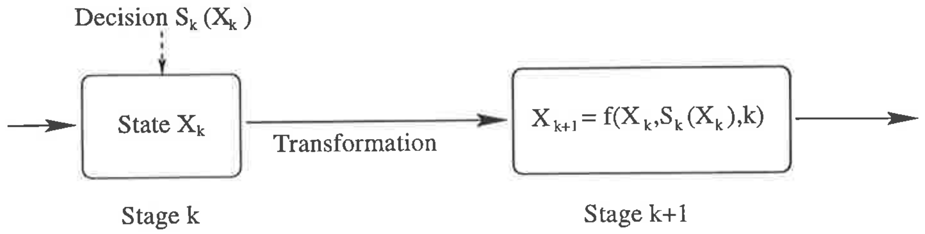

Figure 3.7: The dynamics of the decision process at the stage k (modified from Sniedovich (1992)).

subject to (3.54) and (3.55) but for $k \geq T-(n-1)$.

For $n=1$ and $n=2$ the problem above reduces to

$$\begin{aligned} J_1(X) &= \max_{S_T \in \mathcal{S}} \Pi(X_T, S_T, T) && (3.58) \\ &\quad \text{with } X_T = X, && (3.59) \end{aligned}$$

$$\begin{aligned} J_2(X) &= \max_{S_{T-1} \in \mathcal{S}} \sum_{k=T-1}^{T} \Pi(X_k, S_k, k) && (3.60) \\ &\quad \text{with } X_{T-1} = X, && (3.61) \end{aligned}$$

respectively. By substituting (3.58) into (3.60), the maximum total value in (3.60) can be written as

$$\begin{aligned} J_2(X) &= \max_{S_{T-1} \in \mathcal{S}} [\Pi(X_{T-1}, S_{T-1}, T-1) \\ &\qquad + J_1(f(X_{T-1}, S_{T-1}, T-1))] && (3.62) \\ &\quad \text{with } X_{T-1} = X. && (3.63) \end{aligned}$$

If we use a decision S_{T-1} at the stage $T-1$, the first term on the right hand side of (3.62) is the immediate return resulting from the implementation of the decision. Now, having made a decision at the stage $T-1$, we still have one period to go, in which the state now is $X_T = f(X_{T-1}, S_{T-1}, T-1)$. Let us rewrite Bellman's principle of optimality in the following way.

> An optimal policy (in this case $\{S_{T-1}, S_T\}$) has the property that whatever the initial state (in this case X_{T-1}) and initial decision (in this case S_{T-1}) are, the remaining decisions (in this case S_T) must constitute an optimal policy for the process starting in the state $X_T = f(X_{T-1}, S_{T-1}, T-1)$ as a result of the adoption of the decision S_{T-1} (see also Cooper and Cooper (1981)).

Hence if we want the policy S_{T-1} and S_T to be optimal for the last two period process, then the final decision S_T for the terminal period should also be chosen optimally. The iteration of equation (3.62) can be used to determined the entire policy if the final decision is known. The general "n periods to go" decision is given by

$$J_n(X) = \max_{S_{T-(n-1)} \in \mathcal{S}} \Big[\Pi(X_{T-(n-1)}, S_{T-(n-1)}, T-(n-1))$$

$$+ J_{n-1}(f(X_{T-(n-1)}, S_{T-(n-1)}, T-(n-1)))] \tag{3.64}$$

$$\text{with } X_{T-(n-1)} = X, \tag{3.65}$$

which is known as "Bellman's equation". Stockey and Lucas (1989) defined dynamic programming as a study of dynamic optimisation problems through the analysis of Bellman's equation.

Appendix 3B: The second derivative test for a maximum net present value

Escapements $S^*_{N_0}$ and $S^*_{P_0}$ obtained by solving equations (3.19) and (3.20) give a maximum net present value if they satisfy the second derivative test: $\frac{\partial^2 J_1}{(\partial S_{N_0})^2} < 0$, $\frac{\partial^2 J_1}{(\partial S_{P_0})^2} < 0$ and $\frac{\partial^2 J_1}{(\partial S_{N_0})^2}\frac{\partial^2 J_1}{(\partial S_{P_0})^2} - (\frac{\partial^2 J_1}{\partial S_{N_0}\partial S_{P_0}})^2 > 0$. Recalling that

$$\begin{aligned} J_1(N_0, P_0) &= \int_{S_{N_0}}^{N_0} (p_N - c_N(\xi))d\xi + \int_{S_{P_0}}^{P_0} (p_P - c_P(\xi))d\xi \\ &\quad + \rho\left[\int_{S_{N\infty}}^{N_1} (p_N - c_N(\xi))d\xi + \int_{S_{P\infty}}^{P_1} (p_P - c_P(\xi))d\xi\right], \end{aligned} \tag{3.66}$$

$$\begin{aligned} \frac{\partial J_1}{\partial S_{N_0}} &= -(p_N - c_N(S_{N_0})) \\ &\quad + \rho\left[(p_N - c_N(N_1))(a + F'(S_{N_0}) + \alpha S_{P_0}) + (p_P - c_P(P_1))(\beta S_{P_0})\right], \end{aligned} \tag{3.67}$$

$$\begin{aligned} \frac{\partial J_1}{\partial S_{P_0}} &= -(p_P - c_P(S_{P_0})) \\ &\quad + \rho\left[(p_P - c_P(P_1))(b + G'(S_{P_0}) + \beta S_{N_0}) + (p_N - c_N(N_1))(\alpha S_{N_0})\right], \end{aligned} \tag{3.68}$$

then the conditions in the second derivative test equivalent to

$$\begin{aligned} \frac{\partial^2 J_1}{(\partial S_{N_0})^2} &= c'_N(S_{N_0}) + \rho\left[-c'_N(N_1)(a + F'(S_{N_0}) + \alpha S_{P_0})^2\right. \\ &\quad \left. + F''(S_{N_0})(p_N - c_N(N_1)) - c'_P(P_1)(\beta S_{P_0})^2\right] < 0, \end{aligned} \tag{3.69}$$

$$\begin{aligned} \frac{\partial^2 J_1}{(\partial S_{P_0})^2} &= c'_P(S_{P_0}) + \rho\left[-c'_P(P_1)(b + G'(S_{P_0}) + \beta S_{N_0})^2\right. \\ &\quad \left. + G''(S_{P_0})(p_P - c_P(P_1)) - c'_N(N_1)(\alpha S_{N_0})^2\right] < 0 \end{aligned} \tag{3.70}$$

and

$$\frac{\partial^2 J_1}{(\partial S_{N_0})^2}\frac{\partial^2 J_1}{(\partial S_{P_0})^2} - (\frac{\partial^2 J_1}{\partial S_{N_0}\partial S_{P_0}})^2 > 0, \tag{3.71}$$

where

$$\begin{aligned} \frac{\partial^2 J_1}{\partial S_{N_0}\partial S_{P_0}} &= \rho\left[-c'_N(N_1)(a + F'(S_{N_0}) + \alpha S_{P_0})(\alpha S_{N_0}) + \alpha(p_N - c_N(N_1))\right. \\ &\quad \left. - c'_P(P_1)(b + G'(S_{P_0}) + \beta S_{N_0})(\beta S_{P_0}) + \beta(p_P - c_P(P_1))\right]. \end{aligned} \tag{3.72}$$

Appendix 3C: "Fundamental principle of renewable resource economics" for a predator-prey population.

In single-species harvesting theory a higher discounting rate usually causes a lower escapement (Clark, 1985a). I show here that it is also true in selective harvesting of a predator-prey population.

Let the economic efficiency of the predator be $\frac{m\beta}{|\alpha|} > 1$ and also

$$\frac{m\beta}{|\alpha|} < min\left\{\frac{2r}{|\alpha|K}+1, \frac{2s}{|\alpha|L}+1\right\}, \tag{3.73}$$

where m denotes the relative value of predator to the prey. If the costs of harvesting are negligible then optimal escapements for prey and the predator are given by

$$S_N^* = \frac{A\frac{2ms}{L}+mCB}{\Delta}, \tag{3.74}$$

$$S_P^* = \frac{B\frac{2mr}{K}+CA}{\Delta}, \tag{3.75}$$

where $\Delta = C^2 - m\frac{2r}{K}\frac{2s}{L} \neq 0$ and $C = \alpha + m\beta$. Partial derivatives of the prey and predator escapements with respect to the discounting rate are

$$\frac{\partial S_N}{\partial \delta} = \frac{\frac{2ms}{L}+Cm}{\Delta}, \tag{3.76}$$

$$\frac{\partial S_P}{\partial \delta} = \frac{\frac{2mr}{K}+C}{\Delta}. \tag{3.77}$$

Furthermore, from (3.73) we can obtain $C < \frac{2r}{K}$ and $C < \frac{2s}{L}$. Since the economic efficiency $\frac{m\beta}{|\alpha|} > 1$ is equivalent to $C > 0$, this proves $\Delta < 0$. Finally, we conclude from (3.76) and (3.77) that increasing the discounting rate δ decreases optimal escapements for both the prey and predator. This is consistent with harvesting a single-species population, that is, a high discounting rate causes the manager of the resource to avoid high investment by leaving a lower escapement of the resource (Sieveking and Semmler (1997) showed that this principle may fail for non-selective harvesting of a predator-prey population).

Appendix 3D: "Prey equilibrium optimal escapement"

An equilibrium prey optimal escapement, when we only harvest the prey species, can be written as a function of predator's equilibrium population size. To show this let $S_N^{k*} = S_N^{k*}(P_0)$ denotes the optimal escapement for k periods to go. First let us consider $T = 2$ and recall that

$$\begin{aligned} J_1(N_0, P_0) &= \max_{0 \leq S_{N_0} \leq N_0} [\Pi_N(N_0, S_{N_0}) + \rho\Pi_N(N_1, S_{N\infty})] \\ &= \Pi_N(N_0, S_N^{1*}) + \rho\Pi_N(N_1, S_{N\infty}), \end{aligned} \tag{3.78}$$

where

$$N_1(S_N^{1*}, P_0) = aS_N^{1*} + F(S_N^{1*}) + \alpha S_N^{1*}P_0.$$

Let

$$V(N_k) = \int_{S_{N\infty}}^{N_k} (p - c_N(\xi))d\xi = \Pi_N(N_k, S_N\infty), \tag{3.79}$$

then

$$\begin{aligned}\Pi_N(N_0, S_{N_0}) &= \int_{S_{N_0}}^{S_{N\infty}} (p - c_N(\xi))d\xi + \int_{S_{N\infty}}^{N_0} (p - c_N(\xi))d\xi \\ &= V(N_0) - V(S_{N_0}).\end{aligned} \tag{3.80}$$

Using this notation $J_i(N_0, P_0)$ for $i = 1, 2$ can be written as

$$J_1(N_0, P_0) = V(N_0) - V(S_N^{1*}) + \rho V(N_1) \tag{3.81}$$

and

$$\begin{aligned}J_2(N_0, P_0) &= \max_{0 \le S_{N_0} \le N_0} [\Pi_N(N_0, S_{N_0}) + \rho J_1(N_1, P_1)] \\ &= \max_{0 \le S_{N_0} \le N_0} [V(N_0) - V(S_{N_0}) \\ &\quad + \rho[V(N_1) - V(S_N^{1*}) + \rho V(N_2)]],\end{aligned} \tag{3.82}$$

where

1. $N_1(S_{N_0}, P_0) = aS_{N_0} + F(S_{N_0}) + \alpha S_{N_0} P_0$,
2. $N_2(S_N^{1*}, P_1) = aS_N^{1*} + F(S_N^{1*}) + \alpha S_N^{1*} P_1$,
3. $P_1(S_{N_0}, P_0) = bP_0 + G(P_0) + \beta S_{N_0} P_0$.

A necessary condition for an optimum is $\frac{\partial J_2(N_0,P_0)}{\partial S_{N_0}} = 0$, hence

$$\begin{aligned}0 &= -(p - c_N(S_{N_0})) + \rho(p - c_N(N_1))\frac{\partial N_1}{\partial S_{N_0}} + \rho^2(p - c_N(N_2))\frac{\partial N_2}{\partial P_1}\frac{\partial P_1}{\partial S_{N_0}} \\ &= -(p - c_N(S_{N_0})) + \rho(p - c_N(N_1))(a + F'(S_{N_0}) + \alpha P_0) \\ &\quad + \rho^2(p - c_N(N_2))\alpha S_N^{1*}\beta P_0.\end{aligned} \tag{3.83}$$

The optimal escapement for $T = 2$, that is, S_N^{2*}, can be obtained from equation (3.83).

Next, let us consider the next time horizon, $T = 3$. Substitute the optimal escapement S_N^{2*} into J_2 in equation (3.82) to produce J_3 as follows

$$\begin{aligned}J_2(N_0, P_0) &= \max_{0 \le S_{N_0} \le N_0} [V(N_0) - V(S_N^{2*}) \\ &\quad + \rho[V(N_1) - V(S_N^{1*}) + \rho V(N_2)]],\end{aligned} \tag{3.84}$$

$$\begin{aligned}J_3(N_0, P_0) &= \max_{0 \le S_{N_0} \le N_0} [\Pi_N(N_0, S_{N_0}) + \rho J_2(N_1, P_1)] \\ &= \max_{0 \le S_{N_0} \le N_0} [V(N_0) - V(S_{N_0}) + \rho[V(N_1) - V(S_N^{2*}) \\ &\quad + \rho[V(N_2) - V(S_N^{1*}) + \rho V(N_3)]]],\end{aligned} \tag{3.85}$$

where

1. $N_1(S_{N_0}, P_0) = aS_{N_0} + F(S_{N_0}) + \alpha S_{N_0} P_0$,
2. $N_2(S_N^{2*}, P_1) = aS_N^{2*} + F(S_N^{2*}) + \alpha S_N^{2*} P_1$,
3. $N_3(S_N^{1*}, P_2) = aS_N^{1*} + F(S_N^{1*}) + \alpha S_N^{1*} P_2$,

4. $P_1(S_{N_0}, P_0) = bP_0 + G(P_0) + \beta S_{N_0} P_0$,
5. $P_2(S_N^{2*}, P_1) = bP_1 + G(P_1) + \beta S_N^{2*} P_1$

A necessary condition for an optimum is $\frac{\partial J_3(N_0,P_0)}{\partial S_{N_0}} = 0$, hence

$$\begin{aligned} 0 &= -(p - c_N(S_{N_0})) + \rho[(p - c_N(N_1))(a + F'(S_{N_0}) + \alpha P_0)] \\ &\quad +\rho^2[(p - c_N(N_2))\alpha S_N^{2*} \beta P_0] \\ &\quad +\rho^3[(p - c_N(N_3))\alpha S_N^{1*}(b + G'(P_1) + \beta S_N^{2*})\beta P_0]. \end{aligned} \tag{3.86}$$

The optimal escapement for $T = 3$, that is, S_N^{3*}, can be found from equation (3.86).

The next further step let us consider $T = 4$ by substituting the optimal escapement S_N^{3*} into J_3 in equation (3.85) to produce J_4 as follows

$$\begin{aligned} J_3(N_0, P_0) &= \max_{0 \le S_{N_0} \le N_0} [V(N_0) - V(S_N^{3*}) \\ &\quad \rho[V(N_1) - V(S_N^{2*}) \\ &\quad +\rho[V(N_2) - V(S_N^{1*}) + \rho V(N_3)]]], \end{aligned} \tag{3.87}$$

$$\begin{aligned} J_4(N_0, P_0) &= \max_{0 \le S_{N_0} \le N_0} \Pi_N(N_0, S_{N_0}) + \rho J_3(N_1, P_1) \\ &\quad \max_{0 \le S_{N_0} \le N_0} \Pi_N(N_0, S_{N_0}) + \rho[V(N_1) - V(S_N^{3*}) \\ &\quad \rho[V(N_2) - V(S_N^{2*}) \\ &\quad \rho[V(N_3) - V(S_N^{1*}) + \rho[v(N_4)]]]], \end{aligned} \tag{3.88}$$

where

1. $N_1(S_{N_0}, P_0) = aS_{N_0} + F(S_{N_0}) + \alpha S_{N_0} P_0$,
2. $N_2(S_N^{3*}, P_1) = aS_N^{3*} + F(S_N^{3*}) + \alpha S_N^{3*} P_1$,
3. $N_3(S_N^{2*}, P_2) = aS_N^{2*} + F(S_N^{2*}) + \alpha S_N^{2*} P_2$,
4. $N_4(S_N^{1*}, P_3) = aS_N^{1*} + F(S_N^{1*}) + \alpha S_N^{1*} P_3$,
5. $P_1(S_{N_0}, P_0) = bP_0 + G(P_0) + \beta S_{N_0} P_0$,
6. $P_2(S_N^{3*}, P_1) = bP_1 + G(P_1) + \beta S_N^{3*} P_1$,
7. $P_3(S_N^{2*}, P_2) = bP_2 + G(P_2) + \beta S_N^{2*} P_2$.

A necessary condition for an optimum is $\frac{\partial J_4(N_0,P_0)}{\partial S_{N_0}} = 0$, hence

$$\begin{aligned} 0 &= -(p - c_N(S_{N_0})) \\ &\quad +\rho[(p - c_N(N_1))(a + F'(S_{N_0}) + \alpha P_0)] \\ &\quad +\rho^2[(p - c_N(N_2))\alpha S_N^{3*} \beta P_0] \\ &\quad +\rho^3[(p - c_N(N_3))\alpha S_N^{2*}(b + G'(P_1) + \beta S_N^{3*})\beta P_0] \\ &\quad +\rho^4[(p - c_N(N_4))\alpha S_N^{1*}(b + G'(P_2) + \beta S_N^{2*})(b + G'(P_1) + \beta S_N^{3*})\beta P_0]. \end{aligned} \tag{3.89}$$

It can be proved by induction that for time horizon $T = n$ the necessary condition can be written as

$$\begin{aligned} 0 &= -(p - c_N(S_{N_0})) + \rho[(p - c_N(N_1))(a + F'(S_{N_0}) + \alpha P_0)] \\ &\quad + \sum_{k=2}^{n} \rho^k \left[(p - c_N(N_k))\alpha\beta P_0 S_N^{(n+1-k)*} \prod_{j=1,k>2}^{k-2} (b + G'(P_j) + \beta S_N^{(n-j)*}) \right]. \end{aligned} \tag{3.90}$$

It is difficult to interpret the optimal escapement in this case. To facilitate interpretation, I proceed further to obtain the equilibrium optimal escapement, S_N^*. By assigning $N_k = N_{k+1} = N$ for $k > 0$ and $P_k = P_{k+1} = P$ for $k \geq 0$, and the time horizon is infinity, the following equations are obtained:

$$\begin{aligned} 0 &= -(p - c_N(S_N^*)) + \rho[(p - c_N(N))(a + F'(S_N^*) + \alpha P)] \\ &\quad + \sum_{k=2}^{\infty} \rho^2 \rho^{k-2} (p - c_N(N))\alpha\beta P S_N^* (b + G'(P) + \beta S_N^*)^{k-2} \\ &= -(p - c_N(S_N^*)) + \rho[(p - c_N(N))(a + F'(S_N^*) + \alpha P)] \\ &\quad + \rho^2 (p - c_N(N))\alpha\beta P S_N^* \sum_{j=0}^{\infty} [\rho(b + G'(P) + \beta S_N^*)]^j. \end{aligned} \tag{3.91}$$

To simplify the last equation I assume

$$|\rho(b + G'(P) + \beta S_N^*)| < 1, \tag{3.92}$$

hence,

$$\begin{aligned} 0 &= -(p - c_N(S_N^*)) + \rho[(p - c_N(N))(a + F'(S_N^*) + \alpha P)] \\ &\quad + \rho^2 (p - c_N(N)) \left[\frac{\alpha\beta P S_N^*}{1 - \rho(b + G'(P) + \beta S_N^*} \right]. \end{aligned} \tag{3.93}$$

Appendix 3D: "Derivation of prey equilibrium optimal escapement using the method of Lagrange multipliers"

This appendix shows that, using the method of Lagrange multipliers, the implicit equation of equilibrium optimal escapement (3.35) can be obtain without requiring the fulfilment of the condition (3.34).

Assume that the time horizon in the maximisation is infinite, so that we need to maximise net present value

$$PV = \sum_{k=0}^{\infty} \rho^k \Pi_N(N_k, H_{N_k}) \tag{3.94}$$

subject to equations (3.27) and (3.28), and $0 \leq H_{N_k} \leq N_k$, where

$$\Pi_N(N_k, H_{N_k}) = \int_{N_k - H_{N_k}}^{N_k} (p - c_N(\xi))d\xi. \tag{3.95}$$

The Lagrangian for the maximisation is

$$\begin{aligned} \mathcal{L} &= \sum_{k=0}^{\infty} \{\rho^k \Pi_N(N_k, H_{N_k}) \\ &\quad -\lambda_{1k}[N_{k+1} - a(N_k - H_{N_k}) - F(N_k - H_{N_k}) - \alpha(N_k - H_{N_k})P_k] \\ &\quad -\lambda_{2k}[P_{k+1} - b(P_k) - G(P_k) - \beta(N_k - H_{N_k})P_k]\}, \end{aligned} \tag{3.96}$$

with necessary conditions for the value function PV to be maximum are:

1. $\frac{\partial \mathcal{L}}{\partial N_k} = 0$, $\frac{\partial \mathcal{L}}{\partial P_k} = 0$ for $k \geq 1$, and
2. $\frac{\partial \mathcal{L}}{\partial H_{N_k}} = 0$ for $k \geq 0$.

These conditions are equivalent to

$$0 = \rho^k \frac{\partial \Pi_N}{\partial N_k} - \lambda_{1(k-1)} + \lambda_{1k}(a + F'(N_k - H_{N_k}) + \alpha P_k) + \lambda_{2k}\beta P_k, \tag{3.97}$$

$$0 = \lambda_{1k}\alpha(N_k - H_{N_k}) - \lambda_{2(k-1)} + \lambda_{2k}(b + G'(P_k) + \beta(N_k - H_{N_k})), \tag{3.98}$$

$$0 = \rho^k \frac{\partial \Pi_N}{\partial H_{N_k}} - \lambda_{1k}(a + F'(N_k - H_{N_k}) + \alpha P_k) - \lambda_{2k}\beta P_k. \tag{3.99}$$

Eliminating λ_2 by substituting equation (3.99) into equation (3.97) produces

$$\lambda_{1(k-1)} = \rho^k \left(\frac{\partial \Pi_N}{\partial N_k} + \frac{\partial \Pi_N}{\partial H_{N_k}} \right). \tag{3.100}$$

Place back λ_{1k} into the equation (3.99) to obtain

$$\lambda_{2k} = \frac{\rho^k \frac{\partial \Pi_N}{\partial H_{N_k}} - \rho^{k+1} \left(\frac{\partial \Pi_N}{\partial N_k} + \frac{\partial \Pi_N}{\partial H_{N_k}} \right) (a + F'(N_k - H_{N_k}) + \alpha P_k)}{\beta P_k}. \tag{3.101}$$

Recall that $S_{N_k} = N_k - H_{N_k}$ and let $F_{N_k} = a + F'(N_k) + \alpha P_k$ and $G_{P_k} = b + G'(P_k) + \beta S_{N_k}$. Substitute λ_{1k}, λ_{2k}, and $\lambda_{2(k-1)}$ into equation (3.98) to produce

$$\begin{aligned} 0 \;=\; & \rho^{k+1} \left(\frac{\partial \Pi_N}{\partial N_{k+1}} + \frac{\partial \Pi_N}{\partial H_{N_{k+1}}} \right) \alpha S_{N_k} \\ & - \frac{\rho^{k-1} \frac{\partial \Pi_N}{\partial H_{N_{k-1}}} - \rho^k \left(\frac{\partial \Pi_N}{\partial N_{k-1}} + \frac{\partial \Pi_N}{\partial H_{N_{k-1}}} \right) \left(a + F'(S_{N_{k-1}}) + \alpha P_{k-1} \right)}{\beta P_{k-1}} \\ & + \frac{\rho^k \frac{\partial \Pi_N}{\partial H_{N_k}} - \rho^{k+1} \left(\frac{\partial \Pi_N}{\partial N_k} + \frac{\partial \Pi_N}{\partial H_{N_k}} \right) (a + F'(S_{N_k}) + \alpha P_k)}{\beta P_k} G_{P_k}. \end{aligned} \tag{3.102}$$

To reduce the complexity, I only consider equilibrium escapement $S_{N_{k+1}} = S_{N_k} = S^*_N$, and equilibrium harvest $H_{N_{k+1}} = H_{N_k}$ with equilibrium population size $P_{k+1} = P_k = P, k \geq 0$ and $N_{k+1} = N_k, k > 0$. Multiply both sides of equation (3.102) by $\frac{\beta P_k}{\rho^{k+1}}$ to produce

$$\begin{aligned} 0 \;=\; & \left(\frac{\partial \Pi_N}{\partial N_k} + \frac{\partial \Pi_N}{\partial H_{N_k}} \right) \alpha\beta S^*_N P - \frac{1}{\rho^2} \frac{\partial \Pi_N}{\partial H_{N_k}} + \frac{1}{\rho} \left(\frac{\partial \Pi_N}{\partial N_k} + \frac{\partial \Pi_N}{\partial H_{N_k}} \right) F_{N_K} \\ & + \left(\frac{1}{\rho} \frac{\partial \Pi_N}{\partial H_{N_k}} - \left(\frac{\partial \Pi_N}{\partial N_k} + \frac{\partial \Pi_N}{\partial H_{N_k}} \right) F_{N_k} \right) G_{P_k} \\ =\; & \left(\frac{\partial \Pi_N}{\partial N_k} + \frac{\partial \Pi_N}{\partial H_{N_k}} \right) \alpha\beta S^*_N P \\ & + \left[\frac{1}{\rho} - G_{P_k} \right] \left[\left(\frac{\partial \Pi_N}{\partial N_k} + \frac{\partial \Pi_N}{\partial H_{N_k}} \right) F_{N_K} - \left(\frac{1}{\rho} \frac{\partial \Pi_N}{\partial H_{N_k}} \right) \right] \end{aligned}$$

$$
\begin{aligned}
&= \rho\left(\frac{\partial\Pi_N}{\partial N_k}+\frac{\partial\Pi_N}{\partial H_{N_k}}\right)\alpha\beta S_N^* P \\
&\quad +[1-\rho G_{P_k}]\left[\left(\frac{\partial\Pi_N}{\partial N_k}+\frac{\partial\Pi_N}{\partial H_{N_k}}\right)F_{N_K}-\left(\frac{1}{\rho}\frac{\partial\Pi_N}{\partial H_{N_k}}\right)\right] \\
&= \rho\left(\frac{\partial\Pi_N}{\partial N_k}+\frac{\partial\Pi_N}{\partial H_{N_k}}\right)\alpha\beta S_N^* P \\
&\quad +[1-\rho G_{P_k}]\left(\frac{\partial\Pi_N}{\partial N_k}+\frac{\partial\Pi_N}{\partial H_{N_k}}\right)F_{N_k}-[1-\rho G_{P_k}]\left(\frac{1}{\rho}\frac{\partial\Pi_N}{\partial H_{N_k}}\right) \\
&= -\frac{\partial\Pi_N}{\partial H_{N_k}}+\rho\left(\frac{\partial\Pi_N}{\partial N_k}+\frac{\partial\Pi_N}{\partial H_{N_k}}\right)F_{N_k}+\rho^2\frac{\left(\frac{\partial\Pi_N}{\partial N_k}+\frac{\partial\Pi_N}{\partial H_{N_k}}\right)\alpha\beta S_N^* P}{1-\rho G_{P_k}} \\
&= -(p-c_N(S_N^*))+\rho[(p-c_N(N))(a+F'(S_N^*)+\alpha P)] \\
&\quad +\rho^2(p-c_N(N))\left[\frac{\alpha\beta P S_N^*}{1-\rho(b+G'(P)+\beta S_N^*)}\right].
\end{aligned}
\tag{3.103}
$$

Chapter 4

Predator-prey metapopulations with juvenile migration and juvenile interaction

This chapter describes a deterministic, discrete-time model for a spatially-structured predator-prey population. The model has similar structure and assumptions to the model described in Tuck and Possingham (1994), and generalises the model in Chapter 3 by including spatial structure. I use dynamic programming to find the optimal harvesting strategy for the populations. The model best describes a marine population with sessile adults and pelagic larvae in which recruitment occurs seasonally, such as with many species of mollusc. However, the model would also be useful for any fish species that have relatively sedentary adults – like reef fish. It assumes predation takes place in the early life stages of the prey. This is a common assumption in most of the literature, because in nature younger and inexperienced animals are likely to be more vulnerable to predation (Curio, 1976). For example, at least a quarter of juvenile Atlantic salmon are eaten by brook trout (Symons, 1974) and most prey consumed by silver hake are in post larval and immature life stages (Sessiwine, 1984).

In this chapter I will show that some of the rules of harvesting a single-species metapopulation generalise to predator-prey metapopulations. In single-species harvesting theory (Tuck and Possingham (1994)), a relative source subpopulation should be harvested more conservatively than a relative sink subpopulation (TP 1 in Chapter 2). It can be shown that if predator efficiency is relatively high then we still should harvest the relative prey subpopulation more conservatively than the relative sink subpopulation, with an addition that we should also harvest the predator living in the same patch with the relative source subpopulation more heavily than the predator living in the other patch. This result only applies when harvesting targets both species selectively. When harvesting only targets the prey species, in some circumstances, the rule is still true for one period optimal escapements, that is, optimal escapements with only one unit of time horizon.

I will also show that some rules for harvesting a predator-prey population when there is no spatial structure generalise to the case where the population is spatially-structured. For example, May *et al.* (1979) showed that, in harvesting a spatially homogeneous predator-prey population, if the predator biological conversion is very small and the predator intrinsic growth rate is also small compared to the prey intrinsic growth, then it may be optimal to harvest the predator to extinction. It can be shown that this rule is also true in harvesting a predator-prey metapopulation, especially for

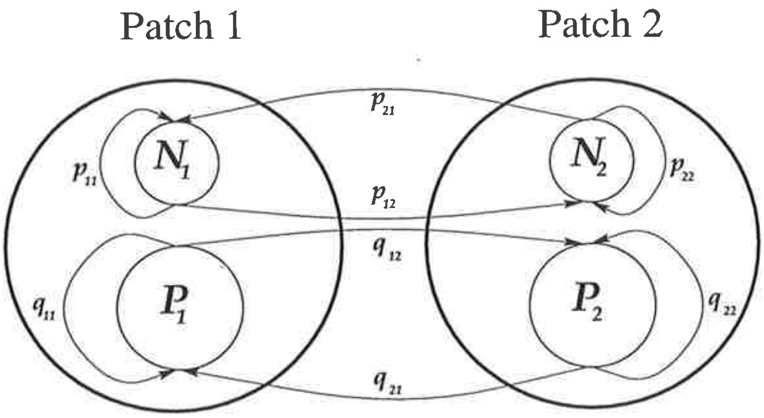

Figure 4.1: Predator-prey metapopulation diagram for a two-patch model. The numbers of predator and prey subpopulation i are respectively indicated by P_i and N_i, their juvenile migration rate are q_{ij} and p_{ij} respectively.

a relative sink/importer predator subpopulation or a predator living in the same patch with a relative source/exporter prey subpopulation. Other questions, such as how to harvest a relatively more vulnerable prey population and a relatively more efficient predator population, are also investigated in this chapter.

4.1 The model

Assume that there is a predator-prey population in each of two different patches, namely patch one and patch two. In the ocean, population patches may exist from scales of metres to thousands of kilometres and often occur in response to physical and biological processes, like advection, temperature and food quality (Haury *et al.*, 1978; Mackas *et al.*, 1985; Davies *et al.*, 1991; Maravelias *et al.*, 1996; Letcher and Rice, 1997). Let the movement of individuals between the local populations be caused by the dispersal of the juveniles. Adults are assumed to be sedentary, and they do not migrate from one patch to another patch. If the population size of the prey and predator on patch i at the beginning of period k are denoted by N_{ik} and P_{ik} respectively, then the growth of the prey and predator is given by the equations

$$N_{1(k+1)} = a_1 N_{1k} + p_{11} F_1(N_{1k}, P_{1k}) + p_{21} F_2(N_{2k}, P_{2k}), \tag{4.1}$$

$$N_{2(k+1)} = a_2 N_{2k} + p_{12} F_1(N_{1k}, P_{1k}) + p_{22} F_2(N_{2k}, P_{2k}), \tag{4.2}$$

$$P_{1(k+1)} = b_1 P_{1k} + q_{11} G_1(N_{1k}, P_{1k}) + q_{21} G_2(N_{2k}, P_{2k}), \tag{4.3}$$

$$P_{2(k+1)} = b_2 P_{2k} + q_{12} G_1(N_{1k}, P_{1k}) + q_{22} G_2(N_{2k}, P_{2k}), \tag{4.4}$$

where a_i and b_i denote the survival rate of adult prey and adult predator in patch i. Let the proportion of prey and predator juveniles from patch i that successfully migrate to patch j be p_{ij} and q_{ij} respectively. The functions $F_i(N_{ik})$ and $G_i(P_{ik})$ are the recruit production functions of the prey and the predator on patch i in time period k. I will assume that the recruit production functions are logistic plus an interaction term for the remainder of this chapter, that is,

$$F_i(N_{ik}, P_{ik}) = r_i N_{ik}\left(1 - \frac{N_{ik}}{K_i}\right) + \alpha_i N_{ik} P_{ik} \tag{4.5}$$

and

$$G_i(N_{ik}, P_{ik}) = s_i P_{ik}\left(1 - \frac{P_{ik}}{L_i}\right) + \beta_i N_{ik} P_{ik}, \tag{4.6}$$

where r_i (s_i) denotes the intrinsic growth of the prey (predator), and K_i (L_i) denotes the prey (predator) carrying capacity in the absence of the other species. In this case $\alpha_i < 0$ and $\beta_i > 0$ ensures that the system is a predator-prey interaction. It is important to note that predation is affecting recruitment for both prey and predator. The functions in (4.5) and (4.6) are consistent with predators eating juveniles. Furthermore, the function $G_i(N_{ik}, P_{ik})$ implies that the predator has another food resource.

To explore harvesting, we need to introduce exploitation into the system. I assume that the only possible exploitation is through a selective harvesting policy, for example using a particular fishing method (e.g. net type size) we can harvest a pelagic predator and leave a benthic prey unharvested, and vice-versa. If the amount of harvest taken from the prey and predator stocks in patch i at the beginning of period k are $H_{N_{ik}}$ and $H_{P_{ik}}$ respectively, let $S_{N_{ik}} = N_{ik} - H_{N_{ik}}$ and $S_{P_{ik}} = P_{ik} - H_{P_{ik}}$ be prey and predator escapements on patch i at the end of that period. These escapements are the only contributors to the growth of the population after exploitation. Hence, if the escapements are substituted into equations (4.1) - (4.4), then the model for an exploited two-patch predator-prey metapopulation is

$$\begin{aligned} N_{1(k+1)} &= a_1 S_{N_{1k}} + p_{11} F_1(S_{N_{1k}}, S_{P_{1k}}) + p_{21} F_2(S_{N_{2k}}, S_{P_{2k}}) \\ &= f_1(S_{N_{1k}}, S_{N_{2k}}, S_{P_{1k}}, S_{P_{2k}}), \end{aligned} \tag{4.7}$$

$$\begin{aligned} N_{2(k+1)} &= a_2 S_{N_{2k}} + p_{12} F_1(S_{N_{1k}}, S_{P_{1k}}) + p_{22} F_2(S_{N_{2k}}, S_{P_{2k}}) \\ &= f_2(S_{N_{1k}}, S_{N_{2k}}, S_{P_{1k}}, S_{P_{2k}}), \end{aligned} \tag{4.8}$$

$$\begin{aligned} P_{1(k+1)} &= b_1 S_{P_{1k}} + q_{11} G_1(S_{N_{1k}}, S_{P_{1k}}) + q_{21} G_2(S_{N_{2k}}, S_{P_{2k}}) \\ &= g_1(S_{N_{1k}}, S_{N_{2k}}, S_{P_{1k}}, S_{P_{2k}}), \end{aligned} \tag{4.9}$$

$$\begin{aligned} P_{2(k+1)} &= b_2 S_{P_{2k}} + q_{12} G_1(S_{N_{1k}}, S_{P_{1k}}) + q_{22} G_2(S_{N_{2k}}, S_{P_{2k}}) \\ &= g_2(S_{N_{1k}}, S_{N_{2k}}, S_{P_{1k}}, S_{P_{2k}}). \end{aligned} \tag{4.10}$$

Equations (4.7) - (4.10) together with equations (4.5) and (4.6) represent a model of a spatially-structured predator-prey population with recruitment controlled by the predation process. In many cases, the predator-prey interaction occurs between adults and hence predation affects prey adult survival (Shepherd and Breen, 1992; McQuaid, 1994). This adult-interaction predator-prey metapopulation will be discussed in the next chapter.

To find an optimal economic strategy, we need to make an assumption about the ownership of the fishery and we need to define an objective. I assume there is a sole-owner of the fishery and the objective is to maximise present value. This objective includes economic discounting which is critical for managing systems with a dynamic state variable (Clark, 1976a). The effect of the discounting rate on optimal harvesting strategies for a spatially-homogeneous predator-prey system is discussed by Silvert and Smith (1977), Mesterton-Gibbons (1988), and more recently by Sieveking and Semmler (1997).

With present value maximisation the objective of the sole-owner is to maximise the net revenue resulting from harvesting each subpopulation of the prey and the predator up to time horizon $t = T$. If Π_{Xi} represents the present value of net revenue resulting from harvesting population X in patch i, where $X \in \{N, P\}$ and $i \in \{1, 2\}$, and ρ is a discount factor, then the sole-owner should maximise

$$PV = \sum_{k=0}^{T} \rho^k \sum_{i=1}^{2} \sum_{X \in \{N,P\}} \Pi_{Xi}(X_{ik}, S_{X_{ik}}) \tag{4.11}$$

subject to the state variable equations (4.7) - (4.10), with non-negative escapement less than or equal to the population size. I will assume a discounting factor of

$$\rho = \frac{1}{(1+\delta)} \tag{4.12}$$

for the reminder of this chapter, where δ denotes a periodic discount rate (e.g. $\delta = 5\%$).

If there is no discount rate ($\delta = 0$) then the net revenue (4.11) in any period generated by escapements S_{N_i} and S_{P_i} has exactly the same value as the net revenue from the same escapements in any other period. Hence, we only need to find optimal escapements for one period (Agnew, 1982). The resulting revenue by applying this zero discount rate is often known as maximum economic yield (MEY). If the discount rate is extremely high ($\delta \longrightarrow \infty$) then the net revenue (4.11) approaches

$$PV_\infty = \sum_{i=1}^{2} \sum_{X \in \{N,P\}} \Pi_{Xi}(X_{i0}, S_{X_{i0}}), \tag{4.13}$$

which is the immediate net revenue without considering the future and is maximised by optimal escapements $S^*_{X_{i\infty}}$. I use the symbol "∞" to indicate that the exploiter only cares about profit this period, which is the same as applying a large discount rate – it is equivalent to open-access exploitation.

The net revenue for a two-patch predator-prey population is

$$\Pi_{Xi}(X_{ik}, S_{X_{ik}}) = \int_{S_{X_{ik}}}^{X_{ik}} (p_X - c_{Xi}(\xi))d\xi, \tag{4.14}$$

where p_X is the price of the harvested stock X which is assumed to be constant, and c_{Xi} is the unit cost of harvesting which is assumed to be a non-increasing function of X_i and may depend on which patch the stock is in. For example, in the case of inshore-offshore harvesting, when we treat the inshore fishery as one patch and the offshore fishery as the other patch, the cost to run the vessel to the patch depends on how far the vessel goes from the coastline. See Appendix 4A for a detailed derivation of the net revenue in equation (4.14).

4.2 Optimal escapements

To obtain the optimal harvesting strategies for a two-patch predator-prey population, the escapement method described by Tuck and Possingham (1994) needs to be generalised. First I will look at the optimal escapement when there is no discounting. Next I will look at the optimal escapement when there is only one time period to go and then the resulting escapement will be used to look at the optimal escapement for a higher time horizon. Let

$$J_T(N_{10}, N_{20}, P_{10}, P_{20}) = \max_{0 \le S_{Xi0} \le X_{i0}} \left(\sum_{k=0}^{T} \rho^k \sum_{i=1}^{2} \sum_{X \in \{N,P\}} \Pi_{Xi}(X_{ik}, S_{X_{ik}}) \right) \tag{4.15}$$

be a value function which is the sum of the discounted net revenue resulting from harvesting both populations in both patches up to period $t = T$. We need to maximise this function by choosing appropriate optimal escapements $S^*_{X_{ik}}$ for each patch and each time period. Equation (4.15) can be used recursively to obtain the value function at time $T+1$, that is,

$$\begin{aligned} J_{T+1}(N_{10}, N_{20}, P_{10}, P_{20}) &= \max_{0 \le S_{Xi0} \le X_{i0}} \Bigg(\rho J_T(N_{11}, N_{21}, P_{11}, P_{21}) \\ &\quad + \sum_{i=1}^{2} \sum_{X \in \{N,P\}} \Pi_{Xi}(X_{i0}, S_{X_{i0}}) \Bigg). \end{aligned} \tag{4.16}$$

Hence, the long-term optimal escapements $S^*_{N_{i0}}$ and $S^*_{P_{i0}}$ can be found by iterating this equation back from time T.

First let us consider $T = 0$. In this case, the sole-owner would maximise immediate net revenue taken from immediate harvests without considering the future value of the harvested stock. This means no discounting factor is applied, and hence the best strategy is the strategy that maximises PV_∞ in (4.13), that is,

$$J_0(N_{10}, N_{20}, P_{10}, P_{20}) = \max_{0 \le S_{Xi0} \le X_{i0}} \left(\sum_{i=1}^{2} \sum_{X \in \{N,P\}} \Pi_{Xi}(X_{i0}, S_{X_{i0}}) \right). \tag{4.17}$$

Let us assume that the optimal escapements are $S_{X_{i\infty}}$, then the maximum revenue is given by

$$J_0(N_{10}, N_{20}, P_{10}, P_{20}) = \sum_{i=1}^{2} \sum_{X \in \{N,P\}} \Pi_{Xi}(X_{i0}, S_{X_{i\infty}}). \tag{4.18}$$

Let us consider two cases, a constant and a non-constant unit cost of harvesting, and obtain optimal escapements $S_{X_{i\infty}}$ for each case.

Case one, a constant unit cost of harvesting, $c_{Xi}(X_i) = c_{Xi}$. In this case $p_X - c_{Xi}$ in (4.14) is constant. The integral in (4.14), and hence PV_∞ in (4.13), is maximised by $S^*_{X_{i\infty}}$ satisfying

$$S^*_{X_{i\infty}} = \begin{cases} X_i & \text{if } p_X \le c_{Xi} \\ 0 & \text{if } p_X > c_{Xi}. \end{cases} \tag{4.19}$$

Therefore, if the unit cost of harvesting is independent of the stock density and lower than the unit price of harvested stock then it is optimal to harvest the entire stock. On the other hand, if the unit cost of harvesting is constant and greater than or equal to unit price of harvested stock then we should not harvest the stock at all, which is what we would expect.

Case two, a non-constant unit cost of harvesting. In this case PV_∞ in (4.13) is maximised by $S^*_{N_{i\infty}}$ and $S^*_{P_{i\infty}}$ satisfying $\frac{\partial \Pi_{Xi}(X_{i0}, S_{Xi0})}{\partial S_{Xi0}}\Big|_{S_{Xi0} = S^*_{X_{i\infty}}} = 0$. Differentiate the integral in (4.14) with respect to $S^*_{X_{i0}}$ to obtain $p_N - c_N(S^*_{N_{i\infty}}) = 0$ and $p_P - c_P(S^*_{P_{i\infty}}) = 0$. The last two equations state that optimal escapements occur if the marginal revenue equals the marginal value of cost. This condition is known as "bionomic equilibrium" (Gordon, 1954). If the recommended escapement is greater than the actual population size, then the sole-owner should not harvest the stock at all. While if it is smaller than the population size then the sole-owner should harvest as much as the difference between these two quantities.

Next let us consider the next time horizon, $T = 1$. First, rewrite equation (4.16) for $T = 0$ and obtain $J_0(N_{11}, N_{21}, P_{11}, P_{21})$ in a similar way to J_0 in equation (4.18) to give

$$\begin{aligned} J_1(N_{10}, N_{20}, P_{10}, P_{20}) &= \max_{0 \le S_{X i0} \le X_{i0}} \left(\rho J_0(N_{11}, N_{21}, P_{11}, P_{21}) \right. \\ &\qquad \left. + \sum_{i=1}^{2} \sum_{X \in \{N,P\}} \Pi_{Xi}(X_{i0}, S_{X_{i0}}) \right) \\ &= \max_{0 \le S_{X i0} \le X_{i0}} \left(\rho \sum_{i=1}^{2} \sum_{X \in \{N,P\}} \Pi_{Xi}(X_{i1}, S_{X_{i\infty}}) \right. \\ &\qquad \left. + \sum_{i=1}^{2} \sum_{X \in \{N,P\}} \Pi_{Xi}(X_{i0}, S_{X_{i0}}) \right). \end{aligned} \tag{4.20}$$

The first term on the right hand side is the discounted net revenue from last year, and the last term is the revenue from the penultimate year. The optimum value will be given by the condition

$$\frac{\partial J_1(N_{10}, N_{20}, P_{10}, P_{20})}{\partial S_{X_{i0}}} = 0. \tag{4.21}$$

To find the partial derivatives, let

$$V(N_{1k}, N_{2k}, P_{1k}, P_{2k}) = \sum_{i=1}^{2} \sum_{X \in \{N,P\}} \Pi_{Xi}(X_{ik}, S_{X_{i\infty}}). \tag{4.22}$$

Substitute equation (4.14) into (4.22), for $k = 1$, to obtain

$$\begin{aligned} \frac{\partial V(N_{11}, N_{21}, P_{11}, P_{21})}{\partial S_{Y_{i0}}} &= \sum_{i=1}^{2} \sum_{X \in \{N,P\}} \frac{\partial \left(\int_{S_{X i\infty}}^{X_{i1}} (p_X - c_{Xi}(\xi)) d\xi \right)}{\partial S_{Y_{i0}}} \\ &= \sum_{i=1}^{2} \sum_{X \in \{N,P\}} \frac{\partial \left(\int_{S_{X i\infty}}^{X_{i1}} (p_X - c_{Xi}(\xi)) d\xi \right)}{\partial \varphi(S_{X_{i0}})} \cdot \frac{\partial \varphi(S_{X_{i0}})}{\partial S_{Y_{i0}}}. \end{aligned} \tag{4.23}$$

where $Y = N, P$ and $\varphi(S_{X_{i0}}) = X_{i1}$ as in equations (4.7) - (4.10). Solving the partial derivative of the integral in the form equation (4.14) yields

$$\frac{\partial \Pi_{Xi}(X_{i0}, S_{X_{i0}})}{\partial S_{X_{i0}}} = -(p_X - c_{Xi}(S_{X_{i0}})). \tag{4.24}$$

Substituting this result into the partial derivatives

$$\frac{\partial V(N_{11}, N_{21}, P_{11}, P_{21})}{\partial S_{X_{i0}}} \tag{4.25}$$

generates the following solution for equation (4.21) in terms of the optimal escapements $S^*_{X_{i0}}$:

$$\begin{aligned} \frac{p_N - c_{N1}(S^*_{N_{10}})}{\rho} &= \left(a_1 + p_{11} F_1^{(S^*_{N10})}(S^*_{N_{10}}, S^*_{P_{10}}) \right) (p_N - c_{N1}(N_{11})) \\ &+ \left(p_{12} F_1^{(S^*_{N10})}(S^*_{N_{10}}, S^*_{P_{10}}) \right) (p_N - c_{N2}(N_{21})) \\ &+ \left(q_{11} G_1^{(S^*_{N10})}(S^*_{N_{10}}, S^*_{P_{10}}) \right) (p_P - c_{P1}(P_{11})) \\ &+ \left(q_{12} G_1^{(S^*_{N10})}(S^*_{N_{10}}, S^*_{P_{10}}) \right) (p_P - c_{P2}(P_{21})), \end{aligned} \tag{4.26}$$

$$\begin{aligned}\frac{p_N - c_{N2}(S^*_{N_{20}})}{\rho} &= \left(a_2 + p_{22}F_2^{(S^*_{N20})}(S^*_{N_{20}}, S^*_{P_{20}})\right)(p_N - c_{N2}(N_{21})) \\ &\quad + \left(p_{21}F_2^{(S^*_{N20})}(S^*_{N_{20}}, S^*_{P_{20}})\right)(p_N - c_{N1}(N_{11})) \\ &\quad + \left(q_{22}G_2^{(S^*_{N20})}(S^*_{N_{20}}, S^*_{P_{20}})\right)(p_P - c_{P2}(P_{21})) \\ &\quad + \left(q_{21}G_2^{(S^*_{N20})}(S^*_{N_{20}}, S^*_{P_{20}})\right)(p_P - c_{P1}(P_{11}))\,, \end{aligned} \tag{4.27}$$

$$\begin{aligned}\frac{p_P - c_{P1}(S^*_{P_{10}})}{\rho} &= \left(b_1 + q_{11}G_1^{(S^*_{P10})}(S^*_{N_{10}}, S^*_{P_{10}})\right)(p_P - c_{P1}(P_{11})) \\ &\quad + \left(q_{12}G_1^{(S^*_{P10})}(S^*_{N_{10}}, S^*_{P_{10}})\right)(p_P - c_{P2}(P_{21})) \\ &\quad + \left(p_{11}F_1^{(S^*_{P10})}(S^*_{N_{10}}, S^*_{P_{10}})\right)(p_N - c_{N1}(N_{11})) \\ &\quad + \left(p_{12}F_1^{(S^*_{P10})}(S^*_{N_{10}}, S^*_{P_{10}})\right)(p_N - c_{N2}(N_{21}))\,, \end{aligned} \tag{4.28}$$

$$\begin{aligned}\frac{p_P - c_{P2}(S^*_{P_{20}})}{\rho} &= \left(b_2 + q_{22}G_2^{(S^*_{P20})}(S^*_{N_{20}}, S^*_{P_{20}})\right)(p_P - c_{P2}(P_{21})) \\ &\quad + \left(q_{21}G_2^{(S^*_{P20})}(S^*_{N_{20}}, S^*_{P_{20}})\right)(p_P - c_{P1}(P_{11})) \\ &\quad + \left(p_{22}F_2^{(S^*_{P20})}(S^*_{N_{20}}, S^*_{P_{20}})\right)(p_N - c_{N2}(N_{21})) \\ &\quad + \left(p_{21}F_2^{(S^*_{P20})}(S^*_{N_{20}}, S^*_{P_{20}})\right)(p_N - c_{N1}(N_{11}))\,. \end{aligned} \tag{4.29}$$

In these equations I use the symbols $F_i^{(S^*_{Xi0})}$ and $G_i^{(S^*_{Xi0})}$ to indicate $\frac{\partial F_i}{\partial S^*_{Xi0}}$ and $\frac{\partial G_i}{\partial S^*_{Xi0}}$, respectively. The equations are the general form of the optimal harvesting equation for a two-patch predator-prey population system. The equations are the fundamental result and much of the rest of this chapter will be exploring these equations. It can be seen that if we set $G_i(S_{N_{i0}}, S_{P_{i0}}) = 0$ and $F_i(S_{N_{i0}}, S_{P_{i0}}) = F_i(S_{N_{i0}})$, then Tuck and Possingham's (1994) optimal harvesting equation for a single-species metapopulation is obtained. Furthermore if there is no migration between patches, $p_{ij} = q_{ij} = 0$ for $i \neq j$ and $F'(S) = a_i + p_{ii}F_i^{(S_{Ni0})}(S_{N_{i0}}, S_{P_{i0}})$ together with $G_i(S_{N_{i0}}, S_{P_{i0}}) = 0$, then the equations reduce to the optimal harvesting equation for a single-species population (Clark, 1976a). Note these are implicit expressions for prey and predator escapements. The escapements S^*_{Xi0} found by solving these equations are the optimum escapements of the prey and the predator on each patch that maximise revenue provided the Hessian matrix $J_1''(S_{N_{10}}, S_{N_{20}}, S_{P_{10}}, S_{P_{20}})$ satisfies

$$[J_1''(S^*_X)(S_X - S^*_X)] \cdot [S_X - S^*_X] < 0, \tag{4.30}$$

where $S_X = (S_{N_{10}}, S_{N_{20}}, S_{P_{10}}, S_{P_{20}})$ and $S^*_X = (S^*_{N_{10}}, S^*_{N_{20}}, S^*_{P_{10}}, S^*_{P_{20}})$.

Clark's (1976a) optimal escapement for a single-species population and Tuck and Possingham's (1994) optimal escapement for a single-species metapopulation hold for all time horizons $T \geq 1$. It can be shown that the optimal escapements for the predator-prey metapopulation are independent of the time horizon considered. This is true because we harvest all species in all patches. Equations (4.26) - (4.29) show that optimal escapements when there is one period to go, S_{Ni}^{1*} and S_{Pi}^{1*}, are functions of prey and predator abundances N_{i0} and P_{i0}, $i = 1, 2$, from equations (4.1) - (4.4). But since we also have state dynamics equations, that is, equations (4.7) - (4.10), then the abundances are controlled by the exploitation, and hence optimal escapements are no longer dependent on the population abundances (Tuck, 1994). I prove this claim, in more detail, in Appendix 4B. I will show in the next chapter that if only one species is harvested then this independence no longer holds.

4.3 Results with negligible costs

In this section, the optimal escapements in equations (4.26) - (4.29) are compared to the strategies in which spatial structure is not recognised by the fisher managers, when costs are negligible. The rationale for this is that I want to know how important it is to use the theory presented here for choosing optimal escapements, that is, how important is spatial structure in determining harvesting strategies? I consider two ways in which spatial structure can be ignored. First, the whole system can be considered a well-mixed homogeneous population. Second, the existence of the patches might be recognised, but we mistakenly assume that there is no migration of individuals between patches. Our optimal escapements from the real two-patch connected predator-prey model are compared to those systems in which spatial structure is ignored.

I adopt the following definitions and ideas from Tuck and Possingham (1994) about the characteristics of local populations or subpopulations.

1. Prey subpopulation i is a *relative exporter* prey subpopulation if it exports more larvae to prey subpopulation j than it imports, that is, $r_1 p_{12} > r_2 p_{21}$. In this case, prey subpopulation j is called a *relative importer* prey subpopulation. Relative exporter and relative importer predator subpopulations are defined similarly.

2. Prey subpopulation i is a *relative source* prey subpopulation if its per capita larval production is greater than the per capita larval production of prey subpopulation j, that is, $r_i(p_{ii} + p_{ij}) > r_j(p_{jj} + p_{ji})$. In this case, prey subpopulation j is called a *relative sink* subpopulation. Relative source and relative sink predator subpopulations are defined similarly.

In addition, I define the following terms:

3 Prey subpopulation i is a *relatively more vulnerable* prey subpopulation to predation if $|\alpha_i| > |\alpha_j|$. Conversely, prey subpopulation j is called a *relatively less vulnerable* subpopulation.

4 Predator subpopulation i is a *relatively more efficient* predator subpopulation if $\frac{\beta_i}{|\alpha_i|} > \frac{\beta_j}{|\alpha_j|}$. Conversely, predator subpopulation j is called a *relatively less efficient* subpopulation. The quantity of $\frac{\beta_i}{|\alpha_i|}$ will be referred to as ϵ and called *regular predator efficiency* or *biological predator efficiency.* Besides this quantity, if $\alpha_i = \alpha_j$ or $\beta_i = \beta_j$, I also define other types of efficiency, depending whether it is measured before or after migration: *pre-dispersal predator efficiency* $C_{ib} = \alpha_i + \beta_i$ and *post-dispersal predator efficiency* $C_{ia} = r_i(p_{i1} + p_{i2})\alpha_i + s_i(q_{i1} + q_{i2})\beta_i$.

Regular predator efficiency is equivalent to pre-dispersal predator efficiency, since $\frac{\beta}{|\alpha|} = 1 + \frac{\alpha+\beta}{|\alpha|} = 1 + \frac{C}{|\alpha|}$.

To simplify the analysis, I assume that the costs of harvesting are negligible. Using this assumption, equations (4.26) - (4.29) for the optimal escapements become

$$\begin{aligned} \frac{p_N}{\rho} &= a_i p_N + (p_{i1} + p_{i2}) \left(F_i^{(S^*_{Ni0})}(S^*_{N_{i0}}, S^*_{P_{i0}}) p_N \right) \\ &\quad + (q_{i1} + q_{i2}) \left(G_i^{(S^*_{Ni0})}(S^*_{N_{i0}}, S^*_{P_{i0}}) p_P \right), \end{aligned} \tag{4.31}$$

$$\begin{aligned} \frac{p_P}{\rho} &= b_i p_P + (p_{i1} + p_{i2}) \left(F_i^{(S^*_{Pi0})}(S^*_{N_{i0}}, S^*_{P_{i0}}) p_N \right) \\ &\quad + (q_{i1} + q_{i2}) \left(G_i^{(S^*_{Pi0})}(S^*_{N_{i0}}, S^*_{P_{i0}}) p_P \right). \end{aligned} \tag{4.32}$$

Two cases are investigated in the following sections. The first case is exploitation in which both species are harvested (Section 4.3.1). The second case considers the case where only one species is harvested, either the prey (Section 4.3.2) or the predator (Section 4.3.3). For the two last cases, I only present analysis of optimal escapements for one period to go (time horizon = 1). Agnew (1982) pointed out that the optimal escapement for one period to go is equal to the optimal escapement for any period (greater than one) to go if there is no discounting. The analysis of optimal escapements with more than one period to go, when harvesting targets only one species, is presented in the next chapter for an adult-interaction predator-prey metapopulation.

4.3.1 Harvesting both species with equal prices

In this section I will explore the behaviour of the optimal escapements if both species are harvested. To simplify the problem let us assume that there is no difference between the prices of the harvested prey and predator, then equations (4.31) and (4.32) become

$$\begin{aligned} \frac{1}{\rho} &= a_i + (p_{i1} + p_{i2}) \left(F_i^{(S^*_{Ni0})}(S^*_{N_{i0}}, S^*_{P_{i0}}) \right) \\ &\quad + (q_{i1} + q_{i2}) \left(G_i^{(S^*_{Ni0})}(S^*_{N_{i0}}, S^*_{P_{i0}}) \right), \end{aligned} \tag{4.33}$$

$$\begin{aligned} \frac{1}{\rho} &= b_i + (p_{i1} + p_{i2}) \left(F_i^{(S^*_{Pi0})}(S^*_{N_{i0}}, S^*_{P_{i0}}) \right) \\ &\quad + (q_{i1} + q_{i2}) \left(G_i^{(S^*_{Pi0})}(S^*_{N_{i0}}, S^*_{P_{i0}}) \right). \end{aligned} \tag{4.34}$$

Recall that due to the time independence of the optimal escapements, there is a notational change for the remainder of the chapter, that is, we simply use $S^*_{X_i}$ to denote optimal escapement for subpopulation X in patch i. Next, using equations (4.5) and (4.6) for the recruitment functions, F_i and G_i, and substituting all of their first order partial derivatives, then the above equations become

$$\begin{aligned} \frac{1}{\rho} &= a_i + (p_{i1} + p_{i2}) \left(r_i - \frac{2r_i}{K_i} S^*_{N_i} + \alpha_i S^*_{P_i} \right) \\ &\quad + (q_{i1} + q_{i2}) \left(\beta_i S^*_{P_i} \right), \end{aligned} \tag{4.35}$$

$$
\begin{aligned}
\frac{1}{\rho} &= b_i + (p_{i1} + p_{i2})\left(\alpha_i S^*_{N_i}\right) \\
&\quad +(q_{i1} + q_{i2})\left(s_i - \frac{2s_i}{L_i} S^*_{P_i} + \beta_i S^*_{N_i}\right). \qquad (4.36)
\end{aligned}
$$

Rearrange these equations and let

$$A_i = \frac{1}{\rho} - (p_{i1} + p_{i2})r_i - a_i, \qquad (4.37)$$

$$B_i = \frac{1}{\rho} - (q_{i1} + q_{i2})s_i - b_i, \qquad (4.38)$$

and

$$C_i = C_{ia} = (p_{i1} + p_{i2})\alpha_i + (q_{i1} + q_{i2})\beta_i, \qquad (4.39)$$

then equations (4.35) and (4.36) become

$$
\begin{aligned}
-\quad (p_{i1} + p_{i2})\frac{2r_i}{K_i} S^*_{N_i} + C_i S^*_{P_i} &= A_i, \\
C_i S^*_{N_i} - (q_{i1} + q_{i2})\frac{2s_i}{L_i} S^*_{P_i} &= B_i,
\end{aligned}
\qquad (4.40)
$$

which has a unique and explicit solution for the optimal escapements

$$S^*_{N_i} = \frac{A_i(q_{i1} + q_{i2})\frac{2s_i}{L_i} + B_i C_i}{\Delta_i} \qquad (4.41)$$

and

$$S^*_{P_i} = \frac{B_i(p_{i1} + p_{i2})\frac{2r_i}{K_i} + A_i C_i}{\Delta_i}, \qquad (4.42)$$

provided

$$\Delta_i = \begin{vmatrix} C_i & -(p_{i1} + p_{i2})\frac{2r_i}{K_i} \\ -(q_{i1} + q_{i2})\frac{2s_i}{L_i} & C_i \end{vmatrix} \neq 0. \qquad (4.43)$$

Explicit expressions of the optimal escapements $S^*_{N_i}$ and $S^*_{P_i}$ can be obtained as long as Δ_i does not vanish. The chance of Δ_i vanishing is infinitesimally small. Considering $C_i < 0$, this condition occurs only if $\frac{\beta_i}{|\alpha_i|} = 1 + \frac{2}{\alpha}\sqrt{\left(\frac{r_i(p_{i1}+p_{i2})}{K_i}\right)\left(\frac{s_i(q_{i1}+q_{i2})}{L_i}\right)}$, which can be interpreted as the predator biological efficiency exactly equal to one plus twice the geometric mean of the ratio of the per capita larval productions to the carrying capacity of the two species divided by the prey vulnerability. When $C_i = 0$, that is, when the predator is extremely efficient, explicit expressions of the optimal escapements always exist.

Equations (4.41) and (4.42) are the generalisation of the optimal escapements for a single-species derived by Clark (1976a) and a single-species metapopulation derived by Tuck and Possingham (1994). By assigning $\alpha_i = \beta_i = 0$, the optimal harvesting for the single-species metapopulation is established. Furthermore, if in addition I remove ($p_{ij} = p_{ji} = q_{ij} = q_{ji} = 0$, and $p_{ii} = p_{jj} = q_{ii} = q_{jj} = 1$) then optimal escapements for the single-species model (Clark, 1976a) with adult survival rates a_i and b_i are obtained.

In the case of $\alpha_i = \beta_i = 0$, the system reduces to a single-species metapopulation system. Tuck and Possingham (1994) concluded some rules of thumb for harvesting a single-species metapopulation system, that is, TP 1, TP2 and TP 3 described in Chapter 2.

To see how important spatial structure is in determining harvesting strategies, I address two separate questions, that is, how do we treat different patches and how does the optimal strategy from the real two-patch predator-prey metapopulation compared to the two incorrect strategies. There are two trivial cases in which optimal escapements are easily investigated. The first case when $|\alpha_i| = \beta_i$, and the second case when $|\alpha_i| \neq \beta_i$ but $\frac{\beta_i}{|\alpha_i|} = \frac{p_{ii}+p_{ij}}{q_{ii}+q_{ij}}$.

The first case: $|\alpha_i| = \beta_i$. If $|\alpha_i| = \beta_i = 0$, then $C_i = 0$. The system reduces to a couple of independent metapopulations. Each subpopulations obeys all the properties described by Tuck and Possingham (1994) (TP 1, TP 2 and TP 3 described in Chapter 2). Furthermore, if $|\alpha_i| = \beta_i \neq 0$, then $C_i = (p_{i1} + p_{i2})\alpha_i + (q_{i1} + q_{i2})\beta_i = ((p_{i1}+p_{i2})-(q_{i1}+q_{i2}))\alpha_i$. In this subcase, if the predator is very efficient and both predator and prey have the same proportions of their juveniles lost from the system, then the connected two-patch predator-prey system can be managed as two separate metapopulation systems. Their interdependence does not affect the optimal escapements when harvesting both of them compared to the optimal escapements in a single-species metapopulation. Hence, the rules of thumb TP 1, TP 2 and TP 3 are preserved in the presence of predators.

The second case: $|\alpha_i| \neq \beta_i$ *but* $\frac{\beta_i}{|\alpha_i|} = \frac{p_{ii}+p_{ij}}{q_{ii}+q_{ij}}$. In this case the predator efficiency is given by the fraction of the proportion of prey juveniles and predator juveniles in the system, and hence C_i vanishes. In this case, a connected two-patch predator-prey system can be managed as a couple of single-species metapopulation systems. Again, the rules of thumb for harvesting a single-species metapopulation (TP 1, TP 2 and TP3) are preserved in this trivial case.

In general both cases above are unlikely. It is important to derive some more general results. The following results are the results for more general cases.

Result 1 *(Sufficient conditions for positive escapements) Let* $S^*_{N_i}$ *and* $S^*_{P_i}$ *denote the optimal escapement from predator-prey metapopulation given by the equations (4.41) and (4.42). If* A_i *and* B_i *are negative, and* $max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\} < C_i \leq 0$, *then:*

1. Δ_i *is negative,*

2. $S^*_{N_i}$ *and* $S^*_{P_i}$ *are positive.*

Proof

1. Let $S^*_{N_i} = \frac{D_i}{\Delta_i}$ and $S^*_{Pi} = \frac{E_i}{\Delta_i}$. Note that since $-(p_{i1} + p_{i2})r_i/A_i = [(p_{i1} + p_{i2})r_i]/[(p_{i1}+p_{i2})r_i + (a_i - (1+\delta))] \geq 1$, the condition $C_i > 2B_i/K_i$ implies $C_i > (-(p_{i1}+p_{i2})r_i/A_i)(2B_i/K_i)$, similarly we obtain $C_i > (-(q_{i1}+q_{i2})s_i/B_i)(2A_i/L_i)$. Hence $C_i > max\{-2B_i(p_{i1} + p_{i2})r_i/[A_iK_i], -2A_i(q_{i1} + q_{i2})s_i/[B_iL_i]\}$ or in other words $D_i < 0$ and $E_i < 0$. From $E_i < 0$ we obtain $B_i(p_{i1} + p_{i2})\frac{2r_i}{K_i} < -C_iA_i$ or alternatively $B_i < (-C_iA_i)/\left((p_{i1} + p_{i2})\frac{2r_i}{K_i}\right)$. Since $-C > 0$ then $-C_iB_i < -C_i\left[(-C_iA_i)/\left((p_{i1} + p_{i2})\frac{2r_i}{K_i}\right)\right]$. This means $A_i(q_{i1} + q_{i2})\frac{2s_i}{L_i} < -C_i\left[(-C_iA_i)/\left((p_{i1} + p_{i2})\frac{2r_i}{K_i}\right)\right]$, because we also have $A_i(q_{i1}+q_{i2})\frac{2s_i}{L_i} < -C_iB_i$. Finally, since A_i is negative, then we have $(q_{i1} + q_{i2})\frac{2s_i}{L_i}(p_{i1} + p_{i2})\frac{2r_i}{K_i} > C_i^2$ which means $\Delta_i < 0$. □

2. From equation (4.41) and (4.42), since D_i, E_i and Δ_i are all negative. □

An interpretation of the condition $A_i < 0$ is that the sum of the proportion of surviving adults a_i and the per capita larval production (product of intrinsic growth and the proportion of juveniles that remain in the system $(p_{ii} + p_{ij})r_i$) is higher than the reciprocal of the discounting factor, $1/\rho$. This is a normal situation in single-species harvesting theory, otherwise it is best to harvest the populations down to zero escapements (Clark, 1976a; Dawid and Kopel, 1997). The same thing is also known in single-species metapopulation harvesting theory (Tuck and Possingham, 1994). The condition $B_i < 0$ is interpreted similarly. To interpret the condition $C_i \leq 0$, let us rewrite this condition as $\alpha_i \frac{p_{i1}+p_{i2}}{q_{i1}+q_{i2}} + \beta_i \leq 0$. This condition is satisfied if $\frac{p_{i1}+p_{i2}}{q_{i1}+q_{i2}} \geq 1$, since $|\alpha_i| \geq \beta_i$. Hence if $C_i \leq 0$ the proportion of prey juveniles that remain in the system is higher compared to the proportion of predator juveniles that remain in the system.

Result 1 can be used to explore the relationship between escapements from the predator-prey metapopulation presented in this chapter and escapements from the single-species metapopulation discussed in the paper of Tuck and Possingham (1994). The relationship is summarised in the following corollary.

Corollary 1 *(Escapement comparison to a single-species metapopulation) Let* $S^*_{N_i}$ *and* $S^*_{P_i}$ *denote the optimal escapement from a predator-prey metapopulation given by equations (4.41) and (4.42), and let* $S^*_{N_{is}}$ *and* $S^*_{P_{is}}$ *denote the optimal escapement from a single-species metapopulation given by the same equations by assigning* $\alpha_i = \beta_i = 0$*. If* A_i *and* B_i *are negative and* $max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\} < C_i \leq 0$*, then:*

1. $S^*_{N_i} - S^*_{N_{is}} = \frac{C_i}{(p_{i1}+p_{i2})2r_i/K_i} S^*_{P_i} \leq 0,$
2. $S^*_{P_i} - S^*_{P_{is}} = \frac{C_i}{(q_{i1}+q_{i2})2s_i/L_i} S^*_{N_i} \leq 0.$

Proof

1. We need to determine the sign of $S^*_{N_i} - S^*_{N_{is}}$.

$$
\begin{aligned}
S^*_{N_i} - S^*_{N_{is}} &= \frac{A_i(q_{i1}+q_{i2})\frac{2s_i}{L_i} + C_iB_i}{\Delta_i} - \frac{A_i}{-(p_{i1}+p_{i2})\frac{2r_i}{K_i}} \\
&= \frac{C_iB_i(p_{i1}+p_{i2})\frac{2r_i}{K_i} + C_i^2A_i}{\Delta_i(p_{i1}+p_{i2})\frac{2r_i}{K_i}} \\
&= \frac{B_i(p_{i1}+p_{i2})\frac{2r_i}{K_i} + C_iA_i}{\left(\Delta_i(p_{i1}+p_{i2})\frac{2r_i}{K_i}\right)/C_i} \\
&= \frac{C_i}{(p_{i1}+p_{i2})2r_i/K_i} S^*_{P_i}.
\end{aligned}
$$

Because $S^*_{P_i} > 0$ and $C_i \leq 0$ then we have $S^*_{N_i} - S^*_{N_{is}} \leq 0$. The proof of the second part is analogous to this proof. □

Escapement comparisons between patches

Corollary 1 shows that the optimal escapement from a predator-prey metapopulation is always less than, or equal to, the optimal escapement from a single-species metapopulation depending on the sign of C_i. However, we can not draw any conclusion on whether we should harvest the relative source subpopulation more conservatively than the relative sink subpopulation, except for one case when $C_i = 0$. In this case, that is, when the predator efficiency in both patches equals the proportion of surviving prey juveniles and surviving predator juveniles, optimal escapement from a predator-prey metapopulation is equal to the optimal escapement if the population were managed as a single-species metapopulation. Hence, the rules of thumb TP 1, TP 2 and TP 3 in Chapter 2 are satisfied. The following Lemma enables us to investigate these rules of thumb for a more general case, that is if $C_i \leq 0$.

Lemma 1 *(Migration trade-off equations) Let* $S^*_{N_i}$ *and* $S^*_{P_i}$ *denote the optimal escapement from a predator-prey metapopulation given by equations (4.41) and (4.42). If* $a_i = a$, $b_i = b$, $K_i = K$, $L_i = L$, $C_i = C$, $R = \frac{1}{\rho} - a$, $S = \frac{1}{\rho} - b$, $r_{im} = (p_{ii} + p_{ij})r_i$ *and* $s_{im} = (q_{ii} + q_{ij})s_i$ *then:*

1. $$(S^*_{N_1} - S^*_{N_2})\Delta_1\Delta_2 = \left(C^2(s_{1m} - s_{2m}) - \frac{4s_{1m}s_{2m}}{KL}(r_{2m} - r_{1m})\right)\left(\frac{2R}{L} - C\right) - \frac{2C}{L}\left(C - \frac{2S}{K}\right)(r_{1m}s_{1m} - r_{2m}s_{2m}),$$

2. $$(S^*_{P_1} - S^*_{P_2})\Delta_1\Delta_2 = \left(C^2(r_{1m} - r_{2m}) - \frac{4r_{1m}r_{2m}}{KL}(s_{2m} - s_{1m})\right)\left(\frac{2S}{K} - C\right) - \frac{2C}{K}\left(C - \frac{2R}{L}\right)(r_{1m}s_{1m} - r_{2m}s_{2m}).$$

Proof

1.

$$\begin{aligned} S^*_{N_1} - S^*_{N_2} &= \frac{(R - r_{1m})\frac{2s_{1m}}{L} + C(S - s_{1m})}{\Delta_1} - \frac{(R - r_{2m})\frac{2s_{2m}}{L} + C(S - s_{2m})}{\Delta_2} \\ &= \frac{\left((R - r_{1m})\frac{2s_{1m}}{L} + C(S - s_{1m})\right)(C^2 - r_{2m}s_{2m}\frac{4}{KL})}{\Delta_1\Delta_2} \\ &\quad - \frac{\left((R - r_{2m})\frac{2s_{2m}}{L} + C(S - s_{2m})\right)(C^2 - r_{1m}s_{1m}\frac{4}{KL})}{\Delta_1\Delta_2} \end{aligned}$$

where $\Delta_i = C^2 - r_{im}s_{im}\frac{4}{KL}$, $i = 1, 2$. Completing and simplifying the numerator of the right hand side of the above equation will end up to the form of the right hand side of equation (1) in this lemma. The proof of the second part is analogous to this proof. □

In general it is difficult to give a simple interpretation of the relationship of optimal escapements between patches. Lemma 1 suggests that there is a trade-off between prey and predator juvenile migrations that determines the relationship between the escapements for the two patches. However, in some special cases, this relationship can be determined. For example, if $r_{1m} = s_{2m}$ and $r_{2m} = s_{1m}$, that is, if prey subpopulation i has the same per capita larval production with predator subpopulation j, then $(S^*_{N_1} - S^*_{N_2})\Delta_1\Delta_2 = \Delta_1(r_{2m} - r_{1m})(\frac{2R}{L} - C)$. If A_i and B_i are negative and $max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\} < C_i \leq 0$ then Δ_1 is negative and $\frac{2R}{L} - C$ is positive. Hence, the sign of the difference depends critically on the sign of $r_{2m} - r_{1m}$. If the per capita larval productions are equal for both prey subpopulations, that is, $r_{2m} = r_{1m}$, then we should harvest the prey in both patches equally. While if $r_{2m} > r_{1m}$, that is, if prey subpopulation two is a relative source subpopulation and predator subpopulation two is a relative sink subpopulation, then we should harvest prey subpopulation two more conservatively than prey subpopulation one. Similarly, we conclude that the predator living in the same patch with a relative source prey subpopulation should be harvested less conservatively than the predator living in the other patch. If we ignore the predator-prey interaction, then the same rule is clearly obtained from the single-species metapopulation's rule of thumb (TP 1).

The rules above are derived by assuming that prey subpopulation i has the same per capita larval production as predator subpopulation j, which is unlikely. The following result describes a similar rule to the result above for a fairly more general case. It will also show that unlike a single-species metapopulation, in a spatially-structured predator-prey population, subpopulations with symmetric migration may have different escapements. To gain a better insight into the effect of juvenile migration on the decision of how to exploit a spatially-structured predator-prey system, I assume the predator has symmetric migration, that is, $s_{1m} = s_{2m} = s_m$, in all the results that follow.

Result 2 *(Escapement comparison between subpopulations) Let one of the prey subpopulations be a relative source while all other parameters of the prey and the predator are identical for both subpopulations. Without loss of generality let us assume the prey subpopulation one is a relative source, that is,* $(p_{11} + p_{12})r_1 > (p_{22} + p_{21})r_2$. *If* $|\alpha| = \beta$, *or if* A_i *and* B_i *are negative and* $C > max\{\frac{2B_i}{K}, \frac{2A_i}{L}\}$, *then:*

1. $S^*_{N_1} > S^*_{N_2}$,
2. $S^*_{P_1} \leq S^*_{P_2}$.

Proof

1. Let $\Delta_{S_N} = (S^*_{N_1} - S^*_{N_2})\Delta_1\Delta_2$. Using Lemma 1 we obtain

$$\begin{aligned}
\Delta_{S_N} &= \left(-\frac{4s_m^2}{KL}(r_{2m} - r_{1m})\right)\left(\frac{2R}{L} - C\right) - \frac{2C}{L}\left(C - \frac{2S}{K}\right)s_m(r_{1m} - r_{2m}) \\
&= s_m\left[-\left(\frac{4s_m}{KL}\right)\left(\frac{2R}{L} - C\right) + \frac{2C}{L}\left(C - \frac{2S}{K}\right)\right](r_{2m} - r_{1m}) \\
&= s_m\left[\frac{2}{L}\left(C^2 - \frac{4s_mR}{KL} - C\left(\frac{2S}{K} - \frac{2s_m}{K}\right)\right)\right](r_{2m} - r_{1m}) \\
&= s_m\left[\frac{2}{L}\left(C^2 - \frac{4s_mR}{KL} - \frac{2C}{K}(S - s_m)\right)\right](r_{2m} - r_{1m}) \\
&= s_m\left[\frac{2}{L}\left(C\left(C - \frac{2B}{K}\right) - \frac{4s_mR}{KL}\right)\right](r_{2m} - r_{1m}).
\end{aligned}$$

Clearly $\Delta_{S_N} > 0$, since $\frac{2B}{K} < C \leq 0$. □

2. Let $\Delta_{S_P} = (S^*_{P_1} - S^*_{P_2})\Delta_1\Delta_2$. Using Lemma 1 we obtain

$$\begin{aligned}
\Delta_{S_P} &= C^2(r_{1m} - r_{2m})\left(\frac{2S}{K} - C\right) - \frac{2C}{K}\left(C - \frac{2R}{L}\right)s_m(r_{1m} - r_{2m}) \\
&= C(r_{1m} - r_{2m})\left[\left(\frac{2S}{K} - C\right)C - \frac{2}{K}\left(C - \frac{2R}{L}\right)s_m\right]
\end{aligned}$$

$$= C(r_{1m} - r_{2m}) \left[\left(\frac{2B}{K} - C \right) C + \frac{4Rs_m}{KL} \right].$$

Clearly $\Delta_{S_P} \leq 0$, since $\frac{2B}{K} < C \leq 0$. □

Result 2 shows that if the natural growth rates of the prey and predator are greater than the reciprocal of the discounting factor, $1/\rho$, so A_i and B_i are negative, and the predator efficiency C is relatively high, such that $C > max\{\frac{2B_i}{K}, \frac{2A_i}{L}\}$, then we should protect a relative source prey subpopulation more than a relative sink prey subpopulation in the sense that we should leave the relative source prey subpopulation with a higher escapement than the sink subpopulation. Similarly, by investigating the effect of prey migration (relative source/sink prey subpopulation) on the predator optimal escapements, it can be shown that we protect the relative source prey subpopulation in two different ways: directly, with a higher escapement of the relative source prey subpopulation, and indirectly, with a lower escapement of the predator living in the same patch with the relative source prey subpopulation. The importance of the relative source prey subpopulation is intuitively reasonable.

Furthermore, let us assume that one predator subpopulation is a relative source while all other parameters of the prey and the predator are identical for both subpopulations, and $|\alpha| = \beta$, or $C > \frac{2B_i}{K}$. Using predator-prey metapopulation optimal escapements as a policy to manage the exploitation of a predator-prey metapopulation system would harvest the relative source predator subpopulation more conservatively than the other predator subpopulation which is a relative sink subpopulation. On the other hand, it would harvest both prey equally, or would harvest the prey living in the same patch with the relative source predator more than the other prey subpopulation.

The analogous result for the predator is easier to interpret whenever both predator subpopulations have the same rates of non-migrating juveniles, that is, $q_{ii}s_i = q_{jj}s_j$. In this case, one of the predators is a relative exporter subpopulation. Let predator subpopulation one be a relative exporter, then we harvest this subpopulation conservatively while we also harvest the prey subpopulation on the other patch conservatively. The rationale for this result is as follows. Since the predator in patch one is a relative exporter, then the outflow of its juveniles to the other patch is greater than the inflow, consequently, we should leave the prey higher in the target patch of the exporter predator subpopulation.

Up to this point it has been shown that the rule of thumb on how to exploit a relative source/sink subpopulation in a single-species metapopulation generalises to a predator-prey metapopulation for some region of parameters in which the predator efficiency C_i is above a certain threshold. In addition, I have also established rules to harvest more/less vulnerable prey and more/less efficient predator subpopulations. These rules are summarised in the following result.

Lemma 2 *(Efficiency trade-off equations) Let $S^*_{N_i}$ and $S^*_{P_i}$ denote the optimal escapement from a predator-prey metapopulation given by equations (4.41) and (4.42). If $a_1 = a_2 = a$, $b_1 = b_2 = b$, $K_1 = K_2 = K$, $L_1 = L_2 = L$, $p_{11} = p_{22}$, $p_{12} = p_{21}$, $q_{11} = q_{22}$, $q_{12} = q_{21}$, $r_1 = r_2$, $s_1 = s_2$, $R = \frac{1}{\rho} - a$, $S = \frac{1}{\rho} - b$, $r_{1m} = r_{2m} = r_m = (p_{ii} + p_{ij})r_i$, and $s_{1m} = s_{2m} = s_m = (q_{ii} + q_{ij})s_i$, then:*

1. $(S^*_{N_1} - S^*_{N_2})\Delta_1\Delta_2 \;=\; (C_2 - C_1)\left[\frac{2As_m}{L}(C_2 + C_1) + \frac{4Br_ms_m}{KL} + B(C_1C_2)\right],$

2. $(S^*_{P_1} - S^*_{P_2})\Delta_1\Delta_2 \;=\; (C_2 - C_1)\left[\frac{2Br_m}{L}(C_2 + C_1) + \frac{4Ar_ms_m}{KL} + A(C_1C_2)\right].$

Proof

The proof is similar to the proof of Lemma 1. □

Result 3 *(Escapement comparison between subpopulations) Let one of the predator subpopulations be relatively more efficient while all other parameters of the prey and the predator are identical for both subpopulations. Without loss of generality let us assume the predator subpopulation one is relatively more efficient, that is,* $C_1 > C_2$*. If* $A_1 = A_2 = A$ *and* $B_1 = B_2 = B$ *are negative, and* C_i *is non-positive with* $C_i > max\{-\frac{r_{im}B}{AK}, -\frac{s_{im}A}{BL}\}$*, then*

$$S^*_{N_1} > S^*_{N_2} \textit{ and } S^*_{P_1} > S^*_{P_2}.$$

Proof

From lemma 2, we only need to show $\left[\frac{2As_m}{L}(C_2 + C_1) + \frac{4r_m s_m B}{KL} + B(C_1C_2)\right] < 0$, which is satisfied by $C_i > -\frac{r_m B}{AK}$. The second part can be proved analogously. □

The result shows that if the migration between subpopulations is symmetric and there is no biological variability between populations except the vulnerability of the prey, then we should harvest a relatively less vulnerable prey subpopulation more conservatively than the other prey subpopulation which is more vulnerable to predation. A special case occurs when there is no predation in one of the patches, say patch one. In this case, patch one is a refugial habitat for the prey. This rule ensures that we harvest the prey living in their refugial habitat more conservatively than the prey living in the habitat where predation occurs. Furthermore, if the prey vulnerability of the two prey subpopulations are the same, but the predator efficiency differs between patches, then we should harvest the prey living in the same patch with the relatively more efficient predator more conservatively than the other prey subpopulation. It suggests that if the predator has a high biological efficiency, then we should leave enough prey to sustain the predator population. In the chapter that follows, it will be shown that if the market value of the predator is large enough compared to the market value of the prey, then the optimal strategy can be a "seeding strategy" where prey are put into the system. This is similar to the conclusion in Chapter 3. The difference is that in the spatial model we may not need to seed all of the prey subpopulations. Seeding might be optimal in only one prey subpopulation.

Escapement comparisons between strategies

The previous results allow us to compare the predator-prey optimal escapements between different patches. The results show that if C, predator efficiency calculated after dispersal, is relatively high, then the rule of thumb TP 1 from single-species metapopulation harvesting theory is preserved. To see how important and how different is our predator-prey metapopulation escapement compared to the escapements if we incorrectly consider the population as a spatially-unstructured system, such as an unconnected two-patch predator-prey system or a well-mixed predator-prey system, I construct Results 4 and 6. These results are similar to the rules of thumb TP 2 and TP 3 for a single-species metapopulation in Chapter 2, but they are more restrictive.

The unconnected two-patch predator-prey system assumes that there is no migration between sub-populations, and the well-mixed predator-prey system assumes that there is only one 'big' homogeneous patch rather than two connected patches. Optimal harvesting equations for an unconnected and well-mixed predator-prey population can be obtained from equations (4.26) and (4.28) by assigning $p_{ij} = q_{ij} = 0$ for $i \neq j$, and $p_{ii} = q_{ii} = 1, i = 1, 2$. However, if we incorrectly assume that there is no connection between subpopulations, we would measure the growth rate for prey subpopulation i as

$$r_{iu} = r_i p_{ii} + r_j p_{ji} \tag{4.44}$$

if it was incorrectly believed to be an unconnected predator-prey system. If it is considered a well-mixed predator-prey system, then let us assume the per capita growth rate of the whole prey population is estimated by the averaged juvenile production across the system

$$r_w = [r_i(p_{ii} + p_{ij}) + r_j(p_{jj} + p_{ji})]/2. \tag{4.45}$$

The growth rate for the predator is measured similarly. Both growth rates in (4.44) and (4.45) are measured at the end of migration period, otherwise migration does not have any effect on the growth of the population. By comparing optimal escapements with different growth rate measurement, I obtain the following result.

Result 4 *(Comparison of strategy with an unconnected two-patch predator-prey system) Let $S^*_{N_i}$ and $S^*_{P_i}$ denote the optimal escapement from a predator-prey metapopulation given by equations (4.41) and (4.42), and let $S^*_{N_{iu}}$ and $S^*_{P_{iu}}$ denote the optimal escapement if we incorrectly consider the system as a system consisting of two unconnected predator-prey systems. Assume that one of the prey subpopulations is a relative exporter while all other parameters of the prey and the predator are identical for both subpopulations. Without lost of generality let subpopulation one be a relative exporter subpopulation, $p_{12}r_1 > p_{21}r_2$. If A_i and $B_1 = B_2 = B$ are negative and $min\{\alpha + \beta, C\} > max\{\frac{2B}{K}, \frac{2A}{L}\}$ then:*

1. $S^*_{N_1} > S^*_{N_{1u}}$,
2. $S^*_{P_2} > S^*_{P_{2u}}$,

whenever $\alpha + \beta < (p_{ii} + p_{ij})\alpha + (q_{ii} + q_{ij})\beta$. If, however, $\alpha + \beta > (p_{ii} + p_{ij})\alpha + (q_{ii} + q_{ij})\beta$ then:

3 $S^*_{N_2} < S^*_{N_{2u}}$,

4 $S^*_{P_1} < S^*_{P_{1u}}$.

Proof

1. All parameters are equal except $p_{12}r_1 > p_{21}r_2$. Recall that

$$S^*_{N_1} = \frac{(R - r_{1m})\frac{2s_{1m}}{L} + CB}{C^2 - \frac{4r_{1m}s_{1m}}{KL}},$$

and

$$S^*_{N_{1u}} = \frac{(R - r_{1u})\frac{2s_{1m}}{L} + C_u B}{C_u^2 - \frac{4r_{1u}s_{1m}}{KL}},$$

where $C = (p_{11} + p_{12})\alpha + (q_{11} + q_{12})\beta$ and $C_u = \alpha + \beta$. Let us define

$$S^*_{N_{1a}} = \frac{(R - r_{1u})\frac{2s_{1m}}{L} + CB}{C^2 - \frac{4r_{1u}s_{1m}}{KL}},$$

then from Lemma 2

$$(S^*_{N_{1u}} - S^*_{N_{1\bar{u}}})\Delta_1\Delta_2 = (C - C_u)\left[\frac{2A_{1u}s_{1m}}{L}(C + C_u) + \frac{4Br_{1u}s_{1m}}{KL} + B(CC_u)\right].$$

The condition $min\{C, C_u\} > \frac{2B}{K}$ implies $min\{C, C_u\} > -\frac{r_{1u}B}{A_{1u}K}$ which guarantees $\frac{2A_{1u}s_{1m}}{L}(C+C_u)+\frac{4Br_{1u}s_{1m}}{KL}+B(CC_u) < 0$. Since $C_u < C$, this means $S^*_{N_{1u}} < S^*_{N_{1\bar{u}}}$. Hence we only need to show $S^*_{N_{1\bar{u}}} < S^*_{N_1}$. We obtain

$S^*_{N_1} - S^*_{N_{1\bar{u}}} =$

$$\frac{\left((R - r_{1m})\frac{2s_{1m}}{L} + CB\right)\left(C^2 - \frac{4r_{1u}s_{1m}}{KL}\right) - \left((R - r_{1u})\frac{2s_{1m}}{L} + CB\right)\left(C^2 - \frac{4r_{1m}s_{1m}}{KL}\right)}{\left(C^2 - \frac{4r_{1u}s_{1m}}{KL}\right)\left(C^2 - \frac{4r_{1m}s_{1m}}{KL}\right)}.$$

Simplify the equation to obtain

$$(S^*_{N_1} - S^*_{N_{1\bar{u}}})\Delta_{1\bar{u}}\Delta_1 = (r_{1u} - r_{1m})\left(C(C - \frac{2B}{K}) - \frac{4Rs_{1m}}{KL}\right)\frac{2s_{1m}}{L},$$

where $\Delta_{1\bar{u}} = C^2 - \frac{4r_{1u}s_{1m}}{KL}$, and $\Delta_1 = C^2 - \frac{4r_{1m}s_{1m}}{KL} < 0$ (this also can be derived from Lemma 1). Since $p_{11}r_1 \geq p_{22}r_2$ and $\Delta_i < 0, i = 1, 2$, then $\Delta_{1\bar{u}} < 0$. Furthermore since $r_{1m} > r_{1u}$ and $0 > C > \frac{2B}{K}$, then we have $S^*_{N_1} - S^*_{N_{1\bar{u}}} > 0$. This completes the proof. □

2. Using a similar procedure we obtain

$$(S^*_{P_2} - S^*_{P_{2\bar{u}}})\Delta_{2\bar{u}}\Delta_2 = (r_{2u} - r_{2m})Y,$$

where $Y = \left(C(C - \frac{2B}{K}) - \frac{4Rs_{2m}}{KL}\right)C > 0$. Hence $S^*_{P_2} - S^*_{P_{2\bar{u}}} > 0$. Similarly, $S^*_{P_{2u}} < S^*_{P_{2\bar{u}}}$ can be obtained. This completes the proof. □

The proof for the case of $\alpha + \beta > (p_{ii} + p_{ij})\alpha + (q_{ii} + q_{ij})\beta$ is analogous.

The result suggests that if we use unconnected predator-prey theory to harvest a predator-prey metapopulation, and $C > C_u$, that is, predator efficiency after dispersal is higher than predator efficiency before dispersal, then we would harvest the source prey subpopulation and the predator living in the same patch as the sink prey subpopulation less conservatively [the condition $C > C_u$ can be achieved, for example, if the proportion of surviving predator $q_{ii}+q_{ij}$ is higher than the proportion of surviving prey $p_{ii}+p_{ij}$]. Unlike the rule of thumb TP 2, in a predator-prey metapopulation we cannot draw any conclusion for the sink prey subpopulation and the predator living in the same patch as the source prey subpopulation. However with an additional condition, that is, if we assume that the predator efficiency, ϵ, proportional to the ratio of the proportion of the lost of migrating prey from the system to the proportion of the lost of migrating predator from the system,

$$\epsilon_i = \frac{\beta}{|\alpha_i|} = \frac{1 - (p_{i1} + p_{i2})}{1 - (q_{i1} + q_{i2})}, \tag{4.46}$$

then predator efficiency before and after dispersal are equal, that is, $C_i = C_{iu}$. Consequently, following the proof in the previous result, we obtain $S^*_{N_1} > S^*_{N_{1u}}$, $S^*_{N_2} < S^*_{N_{2u}}$, $S^*_{P_1} < S^*_{P_{1u}}$ and $S^*_{P_2} > S^*_{P_{2u}}$. This is a generalisation of the rules of thumb TP 2 for a predator-prey metapopulation with juvenile-migration and juvenile-interaction. The detail proof for the last two identities is given in a similar result for the juvenile-migration and adult-interaction model in Chapter 5.

Other special cases are

$$p_{ii} + p_{ij} = q_{ii} + q_{ij} = 1 \tag{4.47}$$

and

$$\alpha + \beta = 0 \qquad and \qquad p_{ii} + p_{ij} = q_{ii} + q_{ij}. \tag{4.48}$$

If either condition (4.47) or (4.48) is satisfied, then $C = C_u$ and consequently the analogous rule of thumb TP 2 holds. Condition (4.47) is interpreted as both prey and predator having no mortality associated with the migration of their juveniles. While condition (4.48) is interpreted as high predator efficiency (measured before dispersal) together with the same proportion of prey and predator juveniles that successfully survive in the system. The following results compare equilibrium optimal harvests between patches and gives a sufficient condition for the predator-prey system in order $S^*_{X_i} < (>) S^*_{X_{iu}}$ implies $H^*_{X_i} > (<) H^*_{X_{iu}}$.

Result 5 *(Equilibrium harvest comparison between strategies) Let* $S^*_{N_i}$ *and* $S^*_{P_i}$ *denote the optimal escapement from the predator-prey metapopulation given by equations (4.41) and (4.42), and let* $S^*_{N_{iu}}$ *and* $S^*_{P_{iu}}$ *denote the optimal escapement if we incorrectly consider the system as a system consisting of two unconnected predator-prey systems. Let us assume that one of the prey subpopulations is a relative exporter while all other parameters of the prey and the predator are identical for both subpopulations. Without lost of generality let subpopulation two be a relative exporter subpopulation,* $p_{21}r_2 > p_{12}r_2$. *All other assumptions in result 4 are satisfied. In addition assume that there is no source/sink prey subpopulation with* $p_{11} = p_{21}$ *and* $p_{22} = p_{12}$. *If the resulting optimal escapements satisfy* $p_{11}(r + \alpha S^*_{P_1}) + (a-1) < 0 < r + \alpha S^*_{P_1}$ *and* $S^*_{N_i}, S^*_{P_i} < \frac{r+\alpha S^*_{P_i}}{2} K_i$ *then* $S^*_{N_{1u}} > S^*_{N_1} = S^*_{N_2} > S^*_{N_{2u}}$ *and also* $H^*_{N_{1u}} < H^*_{N_1}$ *and* $H^*_{N_{2u}} > H^*_{N_2}$.

Proof

From Results 2 and 4 we obtain $S^*_{N_{1u}} > S^*_{N_1} = S^*_{N_2} > S^*_{N_{2u}}$, hence part of the result is proved. Recall that

$$\begin{aligned} H^*_{N_1} - H^*_{N_{1u}} &= (a-1)(S^*_{N_1} - S^*_{N_{1u}}) \\ &\quad + p_{11}(F_1(S^*_{N_1}, S^*_{P_1}) - F_1(S^*_{N_{1u}}, S^*_{P_{1u}})) \\ &\quad + p_{21}(F_2(S^*_{N_2}, S^*_{P_2}) - F_2(S^*_{N_{2u}}, S^*_{P_{2u}})). \end{aligned}$$

Let us consider the sum of the first two terms

$$\begin{aligned} \Delta_{H1} &= (a-1)(S^*_{N_1} - S^*_{N_{1u}}) + p_{11}(F_1(S^*_{N_1}, S^*_{P_1}) - F_1(S^*_{N_{1u}}, S^*_{P_{1u}})) \\ &= p_{11}\left[\left(rS^*_{N_1}\left(1 - \frac{S^*_{N_1}}{K}\right) + \alpha S^*_{N_1} S^*_{P_1} + \frac{(a-1)}{p_{11}} S^*_{N_1}\right)\right. \\ &\quad \left. - \left(rS^*_{N_{1u}}\left(1 - \frac{S^*_{N_{1u}}}{K}\right) + \alpha S^*_{N_{1u}} S^*_{P_1} + \frac{(a-1)}{p_{11}} S^*_{N_{1u}}\right)\right] \\ &= Dp_{11}\left[S^*_{N_1}\left(1 - \frac{S^*_{N_1}}{DK}\right) - S^*_{N_{1u}}\left(1 - \frac{S^*_{N_{1u}}}{DK}\right)\right], \end{aligned}$$

where $D = \frac{p_{11}(r+\alpha S^*_{P_1})+(a-1)}{p_{11}}$. Let $F_D(x) = x\left(1 - \frac{x}{DK}\right)$. Since we assume $p_{11}(r + \alpha S^*_{P_1}) + (a-1) < 0$, then the function F_D crosses the x-axis at $x = 0$ and $DK < 0$. The extreme point is $\frac{DK}{2} < 0$, and since its second derivative $-\frac{2}{DK}$ is greater than zero then the function is a minimum at this extreme point. Since F_D is a logistic function, then it must be increasing along the positive x-axis. Therefore, $S^*_{N_1} < S^*_{N_{1u}}$ implies $F_D(S^*_{N_1}) < F_D(S^*_{N_{1u}})$, and consequently $Dp_{11}(F_D(S^*_{N_1}) - F_D(S^*_{N_{1u}})) > 0$. Now we investigate the last term

$$\begin{aligned}
\Delta_{H2} &= p_{21}(F_2(S^*_{N_2}, S^*_{P_2}) - F_2(S^*_{N_{2u}}, S^*_{P_2})) \\
&= p_{21}\left[\left(rS^*_{N_2}\left(1 - \frac{S^*_{N_2}}{K}\right) + \alpha S^*_{N_2} S^*_{P_2}\right)\right. \\
&\quad \left. - \left(rS^*_{N_{2u}}\left(1 - \frac{S^*_{N_{2u}}}{K}\right) + \alpha S^*_{N_{2u}} S^*_{P_2}\right)\right] \\
&= Ep_{21}\left[S^*_{N_2}\left(1 - \frac{S^*_{N_2}}{EK}\right) - S^*_{N_{2u}}\left(1 - \frac{S^*_{N_{2u}}}{EK}\right)\right],
\end{aligned}$$

where $E = r + \alpha S^*_{P_1}$. Let $F_E(x) = x\left(1 - \frac{x}{EK}\right)$. Since we assume $r + \alpha S^*_{P_1} > 0$, then the function F_E crosses the x-axis at $x = 0$ and $EK > 0$. The extreme point is $\frac{EK}{2} > 0$, and since its second derivative $-\frac{2}{EK}$ is less than zero then the function reaches a maximum at this extreme point. Since F_E is a logistic function and $S^*_{N_{2u}} < S^*_{N_2} < \frac{EK}{2}$ then $F_E(S^*_{N_2}) > F_E(S^*_{N_{2u}})$, and consequently $Ep_{21}(F_E(S^*_{N_2}) - F_E(S^*_{N_{2u}})) > 0$. □

Hence, in some circumstances, incorrectly using unconnected two-patch predator-prey harvesting theory to harvest a predator-prey metapopulation would under-harvest the relative importer prey subpopulation while it also would over-harvest the relative exporter prey subpopulation (in the previous result, I defined the terms over-harvest and under-harvest with respect to escapements but in the present result the terms are defined with respect to harvests). In this case, $S^*_{N_{1u}} > S^*_{N_1} = S^*_{N_2} > S^*_{N_{2u}}$ implies $H^*_{N_{1u}} < H^*_{N_1}$ and $H^*_{N_{2u}} > H^*_{N_2}$. Numerical examples in the next section show that this rule is robust to the inclusion of harvesting costs. Comparisons between optimal escapements from a predator-prey metapopulation and the optimal escapement if we incorrectly manage the metapopulation as a well-mixed predator-prey population is given in the following result.

Result 6 *(Comparison of strategy with a well-mixed predator-prey system) Let* $S^*_{N_i}$ *and* $S^*_{P_i}$ *denote the optimal escapement from predator-prey metapopulation given by equations (4.41) and (4.42), and let* $S^*_{N_w}$ *and* $S^*_{P_w}$ *denote the optimal escapement if the predator-prey metapopulation system is incorrectly considered as a well-mixed predator-prey system. Let us assume that prey subpopulation one is a relative source subpopulation. All hypotheses and assumptions of Result 4 are satisfied, and C is the non-positive root of equation* $-3(R-r_w)\frac{s_m C^2}{L} - BC^3 + \frac{Br_w 2 s_m C}{KL} = 0$. *If* $\alpha+\beta < (p_{ii}+p_{ij})\alpha + (q_{ii}+q_{ij})\beta$ *then:*

1. $S^*_{N_1} > \frac{1}{2}S^*_{N_w}$,
2. $S^*_{P_2} > \frac{1}{2}S^*_{P_w}$.

Similarly is If $\alpha + \beta > (p_{ii} + p_{ij})\alpha + (q_{ii} + q_{ij})\beta$ *then:*

3 $S^*_{N_2} < \frac{1}{2}S^*_{N_w}$,

4 $S^*_{P_1} < \frac{1}{2}S^*_{P_w}$.

Proof

1. Recall that

$$\begin{aligned} S^*_{N_w} &= \frac{(R_w - r_w)\frac{2s_w}{L_w} + C_w B_w}{C_w^2 - \frac{4Q_w r_w}{K_w L_w}} \\ &= \frac{(R - r_w)\frac{s_w}{L} + C_w B}{C_w^2 - \frac{s_w r_w}{KL}}. \end{aligned}$$

Hence

$$\frac{1}{2} S^*_{N_w} = \frac{(R - r_w)\frac{s_m}{L} + C_w B}{2C_w^2 - \frac{2s_m r_w}{KL}}.$$

Let us define

$$\frac{1}{2} S^*_{N_{\bar{w}}} = \frac{(R - r_w)\frac{s_m}{L} + CB}{2C^2 - \frac{2s_m r_w}{KL}},$$

then from the previous result

$$S^*_{N_1} = \frac{(R - r_{1m})\frac{2s_m}{L} + CB}{C^2 - \frac{4s_m r_{1m}}{KL}} > \frac{(R - r_w)\frac{2s_m}{L} + CB}{C^2 - \frac{4s_m r_w}{KL}} = S^0$$

if $r_{1m} > r_w$. Furthermore, If C is the root of $\left(\frac{1}{2}S^*_{N_{\bar{w}}} - S^0\right)\Delta_0\Delta_{\bar{w}} = -3(R - r_w)\frac{s_m C^2}{L} - BC^3 + \frac{Br_w 2s_m C}{KL} = 0$ then $S^*_{N_1} > \frac{1}{2}S^*_{N_{\bar{w}}}$ (one of the roots is the trivial case $C = 0$). Since $C_w < C$, then we have $\frac{1}{2}S^*_{N_w} < \frac{1}{2}S^*_{N_{\bar{w}}}$. This completes the proof. The other parts can be proved similarly. □

The result suggests that if we use a well-mixed predator-prey theory to harvest a predator-prey metapopulation, then we would harvest the source prey subpopulation and the predator living in the same patch with the sink prey subpopulation less conservatively. As for Result 4, if either condition (4.46) or (4.47) or (4.48) is satisfied then we can draw conclusions for the prey and predator in the other patch, that is $S^*_{N_1} > \frac{1}{2}S^*_{N_w}$, $S^*_{N_2} < \frac{1}{2}S^*_{N_w}$, $S^*_{P_1} < \frac{1}{2}S^*_{P_w}$, $S^*_{P_2} > \frac{1}{2}S^*_{P_w}$. The following section discusses harvesting only one species either the prey or predator

4.3.2 Harvesting only the prey species

In the previous section I assumed that harvesting targets both species. In this section I will look at harvesting strategies when only one species is harvested, for example when the predator does not have an economical value. This is the situation where birds are the predators eating commercially valuable sandeels and pilchards (Klomp and Wooler, 1988; Wright, 1996). Harvesting only the prey can also occur in a fishery involving predator-prey interactions between two commercial species. Many fisheries have shifted from exploiting a top predator to exploiting a lower trophic because the predator stock has collapsed. In the first case, where the predator does not have any commercial value, the optimal strategy may be a strategy that may drive the predator to a very low population level, while in the second case the best strategy might be to recover the predator population from depletion (Christensen, 1996; Reynolds and Tapper, 1996).

Why do we need to take into account the existence of predator-prey interactions when we only harvest the prey? The decline of prey species due to the extensive exploitation can lead to a decreasing abundance of its predator. For example, many predatory seabird species have experienced tremendous breeding failures as a result of the declining of sandeel population as their prey (Bailey *et al.*, 1991). The decline of marine mammals as a result of prey exploitation is also documented (Christensen, 1996). A recent study revealed that the reproductive success and adult survival of the Adelie penguin, *Pygoscelis adeliae*, has decreased due to a high catch of krill, *Euphausia superba*, in the krill fishery (Mangel and Switzer, 1998). This shows the need for multi-species considerations to be taken into account in obtaining more appropriate harvesting strategies, as suggested by Hall (1998). In this section I investigate harvesting strategies for prey exploitation while considering the role of the prey as food of another species.

In the previous section, where we harvest both the prey and the predator, optimal escapements are independent of the initial prey and predator population size. We would expect that the optimal escapement for the prey, when we harvest only the prey, is a function of predator population size, since in this case we cannot control the predator population size. To compare optimal harvesting strategies for the prey to single-species strategies, I simplify the resulting optimal escapements by only considering one period to go exploitation. If it is assumed that profit generated from these escapements in this period is the same as the profit generated from the same escapements in any periods, that is, the discount rate δ is zero, then we only need to optimise escapement for one period to go (Agnew, 1982). The long-term equilibrium case is discussed in the next chapter.

Using the same method as in the previous chapter, optimal escapements can be found by maximising the net revenue

$$J_T(N_{10}, N_{20}, P_{10}, P_{20}) = \max_{0 \leq S_{Ni0} \leq N_{i0}} \left(\sum_{k=0}^{T} \rho^k \sum_{i=1}^{2} \Pi_{Ni}(N_{ik}, S_{N_{ik}}) \right). \tag{4.49}$$

The escapements are similar to escapements $S_{N_{i0}}$ in equation (4.31) with $p_P = 0$ and $S_{P_{i0}} = P_{i0}$, that is,

$$\frac{1}{\rho} = a_i + (p_{i1} + p_{i2}) \left(F_i^{(S_{Ni0})}(S_{N_{i0}}, P_{i0}) \right), \tag{4.50}$$

where F_i is defined by equation (4.5). Equation (4.50) has a unique solution for the optimal escapement

$$S^*_{N_i} = \frac{K_i}{2} - \frac{K_i}{2r_i} \frac{(\delta + 1 - a_i)}{(p_{i1} + p_{i2})} + \frac{K_i}{2r_i}(\alpha_i P_i) \tag{4.51}$$

where P_i is the number of unharvested predator in patch i.

In the case of harvesting both species (Section 4.3.1), if prey subpopulation i is relatively more vulnerable than prey subpopulation j, that is, $|\alpha_i| > |\alpha_j|$, and all other parameters are the same for both subpopulations, then $S^*_{N_i} < S^*_{N_j}$. However, equation (4.51) suggests that, when harvesting only targets prey species, this rule is no longer necessarily true, unless $|\alpha_i| P_i > |\alpha_j| P_j$. Thus, if the size of predator subpopulation i is greater than, or equal to, the size of predator subpopulation j, that is, $P_i \geq P_j$, then it can be concluded that with the optimal strategy we should exploit the more vulnerable prey subpopulation more and the less vulnerable prey subpopulation should be conserved. This is because optimal escapements for both prey subpopulation are always lower than half a carrying capacity K, and hence a greater recruitment will be produced by a greater prey escapement with a low prey vulnerability, for a fixed level of predator escapement (see equation (4.5)).

Similarly, if $(p_{ii}+p_{ij})r_i > (p_{jj}+p_{ji})r_j$, that is, prey subpopulation i is a relative source subpopulation, while all other parameters are identical for both patches, then the result $S^*_{N_i} > S^*_{N_j}$ is true only if $P_i \leq P_j$. Hence, if the size of predator subpopulation i is less than, or equal to, the size of predator subpopulation j, that is, $P_i \leq P_j$, then the best strategy is to protect a relative source prey subpopulation more than a relative sink prey subpopulation as in the case of optimal escapements for a single-species metapopulation (TP 1).

Escapement comparisons

In this section I compare optimal escapements from the predator-prey metapopulation with three other systems: a single-species metapopulation, an unconnected two-patch predator-prey and a well-mixed predator-prey system. By comparing these escapements we can see how important it is to use the theory presented here for choosing optimal escapements of a predator-prey system.

First, I consider the case where the predator-prey metapopulation is incorrectly believed to be a single-species metapopulation system and exploited. The optimal escapements for the system are given by

$$S^*_{N_{is}} = \frac{K_i}{2} - \frac{K_i}{2r_i}\frac{(\delta+1-a_i)}{(p_{i1}+p_{i2})}. \tag{4.52}$$

The total optimal escapement, $S^*_{N_{1s}}+S^*_{N_{2s}}$, is higher than the total optimal escapements from the predator-prey metapopulation theory, since

$$(S^*_{N_1}+S^*_{N_2}) - (S^*_{N_{1s}}+S^*_{N_{2s}}) = \frac{K_1}{2r_1}\alpha_1 P_1 + \frac{K_2}{2r_2}\alpha_2 P_2 < 0. \tag{4.53}$$

Hence, the optimal escapements for a metapopulation produce a less conservative total harvest than escapements from a single-species metapopulation. This is not surprising because the fisher is competing with the predator.

Second, a connected two-patch predator-prey system can also be identified incorrectly as an unconnected two-patch predator-prey system. In this case we want to maximise

$$J_T(N_{i0}, P_{i0}) = \max_{0 \leq S_{Ni0} \leq N_{i0}} \left(\sum_{k=0}^{T} \rho^k \Pi_{Ni}(N_{ik}, S_{N_{ik}}) \right) \tag{4.54}$$

for each patch. The escapements are similar to escapements $S_{N_{i0}}$ given by equation (3.22) with $p_P = 0$ and $S_{P_{i0}} = P_{i0}$, that is,

$$\frac{1}{\rho} = a_i + \left(F_i^{(S_{Ni0})}(S_{N_{i0}}, S_{P_{i0}}) \right). \tag{4.55}$$

The equation above has a unique solution

$$S^*_{N_{iu}} = \frac{K_i}{2} - \frac{K_i}{2r_{iu}}(\delta+1-a_i) + \frac{K_i}{2r_{iu}}(\alpha_i P_i) \tag{4.56}$$

where P_i is the number of unharvested predators on patch i and $r_{iu} = r_i p_{ii} + r_j p_{ji}$ is measured after migration is completed at one period. If the prey on patch i is a relative exporter in comparison with that on patch j, that is, $r_i p_{ij} > r_j p_{ji}$, then $S^*_{N_i} > S^*_{N_{iu}}$. Hence, optimal escapements resulting from a connected two-patch predator-prey system protect the relative exporter prey subpopulation more than the escapements resulting from an unconnected two-patch predator-prey system, if the system is connected.

The converse, that is, optimal escapement for the relative importer prey subpopulation derived by the predator-prey metapopulation theory less than the escapement from unconnected two-patch predator-prey population, is true only if $r_i < r_{iu}$. If $r_1 = r_2$, this means $p_{11} + p_{21} > 1$ which rarely occurs. Furthermore, if $p_{11} = p_{22}$ then the condition $p_{11} + p_{21} > 1$ is impossible. As for the case of harvesting both species, it can be shown that in the case of adult-interaction (Chapter 5) this additional condition, $p_{11}+p_{21} > 1$, is not necessary.

In general the number of predators would change if the number of prey changes. However, in the model in this chapter, I assume the predator has another main food, and if the biological conversion rate β is relatively small, then the number of predators would not change substantially. Consequently, if both predator subpopulations are identical then the difference of the predator population sizes between subpopulations is negligible, that is, $P_{i0} = P_{j0} = P$. Although we can not draw any conclusion about escapement comparisons for a relative importer/sink prey subpopulation, we can compare total escapement from these different methods, if the difference of the predator population sizes is negligible. I will show that if one of the prey subpopulations is a relative exporter, $r_i = r_j$, $p_{ii} = p_{jj}$ and $P_{i0} = P_{j0} = P$, then the total escapement from a connected two-patch predator-prey system protects the prey population more than the total escapements from an unconnected two-patch predator-prey system, if the system is connected.

To prove this rule we need to show that

$$(S^*_{N_1} + S^*_{N_2}) - (S^*_{N_{1u}} + S^*_{N_{2u}}) > 0. \tag{4.57}$$

Let us recall that

$$S^*_{N_i} = \frac{K}{2} - \frac{K}{2r_i}\frac{(\delta + 1 - a)}{(p_{i1} + p_{i2})} + \frac{K}{2r_i}(\alpha P), \tag{4.58}$$

$$S^*_{N_{iu}} = \frac{K}{2} - \frac{K}{2r_{iu}}(\delta + 1 - a) + \frac{K}{2r_{iu}}(\alpha P), \tag{4.59}$$

where $r_{iu} = r_i p_{ii} + r_j p_{ji}$. Let $(S^*_{N_1} + S^*_{N_2}) - (S^*_{N_{1u}} + S^*_{N_{2u}}) = \Delta S_{N_u}$. Following Tuck and Possingham (1994), let $A_{ij} = r_i p_{ij}$ and $\bar{A} = A_{11} + A_{12} + A_{21} + A_{22} > 0$ then

$$\begin{aligned}\Delta S_{N_u} \;=\;& \frac{K}{2}(\delta + 1 - a)\left[\frac{1}{A_{11} + A_{21}} + \frac{1}{A_{22} + A_{12}} - \frac{1}{A_{11} + A_{12}} - \frac{1}{A_{21} + A_{22}}\right] \\ & + \frac{K}{2}(|\alpha|P)\left(\left[\frac{1}{A_{11} + A_{21}} + \frac{1}{A_{22} + A_{12}}\right] - \left[\frac{1}{r_1} + \frac{1}{r_2}\right]\right).\end{aligned} \tag{4.60}$$

Consider the numerator of first part of the sum.

$$\begin{aligned} & (A_{22} + A_{12})(A_{11} + A_{12})(A_{21} + A_{22}) + (A_{11} + A_{21})(A_{11} + A_{12})(A_{21} + A_{22}) \\ & -(A_{11} + A_{21})(A_{22} + A_{12})(A_{21} + A_{22}) - (A_{11} + A_{21})(A_{22} + A_{12})(A_{11} + A_{12}) \\ = \; & \left[\bar{A}(A_{11} + A_{12})(A_{22} + A_{21})\right] - \left[\bar{A}(A_{11} + A_{21})(A_{22} + A_{12})\right] \\ = \; & \bar{A}\left[A_{11}A_{21} + A_{22}A_{12} - A_{11}A_{12} - A_{22}A_{21}\right] \\ = \; & \bar{A}\left[r_1 p_{11} r_2 p_{21} + r_2 p_{22} r_1 p_{12} - r_1^2 p_{11} p_{12} - r_2^2 p_{22} p_{21}\right] \\ = \; & \bar{A}\left[(r_2 p_{21} - r_1 p_{12})(r_1 p_{11} - r_2 p_{22})\right] \\ = \; & 0. \end{aligned} \tag{4.61}$$

Since one of the prey subpopulation is a relative exporter, without loss of generality, let us assume $r_2 p_{22} + r_2 p_{21} = r_1 p_{11} + r_2 p_{21} < r_1 p_{11} + r_1 p_{12} < r_1$ and $r_2 p_{22} + r_1 p_{12} =$

$r_2p_{11} + r_2p_{12} < r_2$, and hence ΔS_{N_u} reduces to

$$\begin{aligned} \Delta S_{N_u} &= \frac{K}{2}(|\alpha|P)\left(\left[\frac{1}{A_{11}+A_{21}} + \frac{1}{A_{22}+A_{12}}\right] - \left[\frac{1}{r_1}+\frac{1}{r_2}\right]\right) \\ &> \frac{K}{2}(|\alpha|P)\left(\left[\frac{1}{r_1}+\frac{1}{r_2}\right] - \left[\frac{1}{r_1}+\frac{1}{r_2}\right]\right) \\ &= 0. \end{aligned} \tag{4.62}$$

This completes the proof that $(S^*_{N_1} + S^*_{N_2}) - (S^*_{N_{1u}} + S^*_{N_{2u}}) > 0$.

Third, another possibility of not harvesting a predator-prey metapopulation properly is by managing it as a well-mixed predator-prey system. In this case the existence of the two patches is not recognised at all. The total net revenue which should be maximised is similar to J_T in equation (4.54). This maximisation is satisfied by the escapement

$$S^*_{N_w} = \frac{K_w}{2} - \frac{K_w}{2r_w}(\delta + 1 - a_w) + \frac{K_w}{2r_w}(\alpha_w P_w) \tag{4.63}$$

where $K_w = K_i + K_j$, $r_w = [r_1(p_{11}+p_{12}) + r_2(p_{22}+p_{21})]/2$, $a_w = [a_1 + a_2]/2$, $\alpha_w = [\alpha_1 + \alpha_2]/2$ and $P_w = P_i + P_j$. Let all parameters on both patches be equal except $r_i(p_{ii} + p_{ij}) > r_j(p_{jj} + p_{ji})$, that is, the prey on patch i is a relative source. Then $S^*_{N_{iw}} = S^*_{N_w}/2 < S^*_{N_i}$, provided $2r_i > r_w$ (this condition is always guaranteed). This means that a prey subpopulation which is a relative source in a connected two-patch predator-prey system would be over-harvested if it is falsely considered to be a well-mixed predator-prey system. The converse, a relative sink prey subpopulation would be harvested too conservatively is not always true since it needs $2r_i < r_w$ which, if $r_1 = r_2$, it is impossible to obtain.

If there is no relative source subpopulation, the harvest from a single-species metapopulation and a well-mixed population are the same (Tuck and Possingham, 1994). However, optimal strategy for a two-patch predator-prey metapopulation gives a higher total escapement than escapement from a well-mixed predator-prey population. To show this, let us recall that

$$S^*_{N_i} = \frac{K}{2} - \frac{K}{2r_i}\frac{(\delta + 1 - a)}{(p_{i1} + p_{i2})} + \frac{K}{2r_i}(\alpha P), \tag{4.64}$$

$$S^*_{N_w} = K - \frac{2K(\delta + 1 - a - \alpha 2P)}{r_1(p_{11}+p_{12}) + r_2(p_{21}+p_{22})}. \tag{4.65}$$

Let $(S^*_{N_1} + S^*_{N_2}) - (S^*_{N_w}) = \Delta S_{N_w}$ and let $V_i = r_i(p_{ii} + p_{ij})$. Since $r_i > r_i(p_{ii} + p_{ij}) = V_i$ and following Tuck and Possingham (1994), then we have

$$\begin{aligned} \Delta S_{N_w} &> K - K\frac{(\delta + 1 - a - \alpha P)}{2}\left[\frac{1}{V_1} + \frac{1}{V_2}\right] \\ &\quad - \left(K - K(\delta + 1 - a - \alpha 2P)\left[\frac{2}{V_1 + V_2}\right]\right) \\ &= -K(\delta + 1 - a - \alpha P)\left[\left(\frac{1}{2V_1} + \frac{1}{2V_2}\right) - \frac{2}{V_1 + V_2}\right] \\ &\quad - K\alpha P\left[\frac{2}{V_1 + V_2}\right] \\ &= -K(\delta + 1 - a - \alpha P)\left[\frac{2V_2 + 2V_1}{4V_1V_2} - \frac{2}{V_1 + V_2}\right] \end{aligned}$$

$$
\begin{aligned}
& -K\alpha P\left[\frac{2}{V_1+V_2}\right] \\
= \quad & -K(\delta+1-a-\alpha P)\left[\frac{(V_1-V_2)^2}{2(V_1+V_2)V_1V_2}\right] \\
& -K\alpha P\left[\frac{2}{V_1+V_2}\right]. \qquad (4.66)
\end{aligned}
$$

Since $V_1 = V_2$ then $\Delta S_{N_w} > 0$. This completes the proof.

To conclude, in general, the escapement comparion rules between subpopulations and between strategies in harvesting both species do not necessarily hold if harvesting only targets the prey species. However, if the difference of predator population size between patches is negligible then rules of how to harvest relative source/sink, exporter/importer and more/less vulnerable prey subpopulations in Section 4.3.1 can be applied. The next section will discuss optimal harvesting strategies when harvesting only targets the predator species.

4.3.3 Harvesting only the predator species

In real fisheries, prey may not have any economic value, but its presence may have significant effects on the optimal profit from harvesting the predator. In a newly developed fishery, the top predators and other larger species are usually the initial targets of exploitation (Christensen, 1996). For example, whaling was developed in the early exploitation of the Arctic and only since the decline of the whale population has krill exploitation begun (Pauly, 1979). In this section I will look at how optimal escapement for a single-species would be different if we take the existence of its prey population into account. How and to what extent does this prey population affect the optimal escapement of the predator. As in the previous section I also compare this optimal escapement to escapements derived from other strategies.

Optimal escapements for the predator population can be obtained by maximising

$$
J_T(N_{10}, N_{20}, P_{10}, P_{20}) = \max_{0 \le S_{Pi0} \le P_{i0}} \left(\sum_{k=0}^{T} \rho^k \sum_{i=1}^{2} \Pi_{Pi}(P_{ik}, S_{P_{ik}}) \right). \qquad (4.67)
$$

The resulting escapements are similar to escapements $S_{P_{i0}}$ from equation (4.32) with $p_N = 0$ and $S_{N_{i0}} = N_{i0}$, that is,

$$
\frac{1}{\rho} = b_i + (q_{i1} + q_{i2}) \left(G_i^{(S_{Pi0})}(N_{i0}, S_{P_{i0}}) \right) \qquad (4.68)
$$

which has a unique solution

$$
S^*_{P_i} = \frac{L_i}{2} - \frac{L_i}{2s_i} \frac{(\delta + 1 - b_i)}{(q_{i1} + q_{i2})} + \frac{L_i}{2s_i}(\beta_i N_i) \qquad (4.69)
$$

where N_i is the number of unharvested prey on patch i.

In the case of harvesting both species (Section 4.3.1), if predator subpopulation i is relatively more efficient than predator subpopulation j, that is, $\beta_i > \beta_j$, with $\alpha_i = \alpha_j$, and all other parameters are the same for both subpopulations, then $S^*_{P_i} > S^*_{P_j}$. However, equation (4.69) suggests that, when harvesting only targets predator species, this rule may not true, unless $\beta_i N_i > \beta_j N_j$. Thus, if the size of prey subpopulation i is greater than, or equal to, the size of prey subpopulation j, that is, $N_i \ge N_j$, then it can be concluded that the more efficient the predator population, the more it should be conserved, the less efficient the predator population, the more it should be exploited. Similarly, if the predator juveniles in patch i have a higher survivorship than predator juveniles in patch j, that is, $q_{ii}+q_{ij} > q_{jj}+q_{ji}$, while all other parameters are identical for both patches, then $S^*_{P_i} > S^*_{P_j}$ is true only if $N_i \geq N_j$, which is different from the case when we harvest both species. Here, a relative source predator subpopulation is more protected than a relative sink predator population only if the prey living in the same patch with the relative source predator subpopulation is more abundance than the other prey subpopulation. This is reasonable since the model in this chapter assumes that predation takes place before the juveniles in a subpopulation migrate and recruit to another subpopulation.

As before, I compare the optimal escapements from the predator-prey metapopulation with escapements from three other systems, a single-species metapopulation, an unconnected two-patch predator-prey and a well-mixed predator-prey system, to see how important it is to use the theory presented here for choosing optimal escapements of a predator-prey system.

First, assume the predator-prey metapopulation is incorrectly believed to be a single-species metapopulation. If it is exploited under this incorrect assumption then the optimal escapements for a connected two-patch single-species exploitation is

$$S^*_{P_{is}} = \frac{L_i}{2} - \frac{L_i}{2s_i}\frac{(\delta+1-b_i)}{(q_{i1}+q_{i2})}. \tag{4.70}$$

The sum of escapements from a predator-prey metapopulation is always greater than the sum of escapements from the incorrect consideration, that is, when the presence of the prey is ignored, since

$$(S^*_{P_1}+S^*_{P_2}) - (S^*_{P_{1s}}+S^*_{P_{2s}}) = \frac{L_1}{2s_1}\beta_1 N_1 + \frac{L_2}{2s_2}\beta_2 N_2 > 0. \tag{4.71}$$

Hence, optimal escapements from a two-patch predator-prey metapopulation system produces a more conservative harvest than if we incorrectly manage the population as a single-species metapopulation.

Second, when a two-patch predator-prey metapopulation is identified incorrectly as an unconnected two-patch predator-prey population. In this case we want to maximise

$$J_T(N_{i0}, P_{i0}) = \max_{0 \leq S_{Pi0} \leq P_{i0}} \left(\sum_{k=0}^{T} \rho^k \Pi_{Pi}(P_{ik}, S_{P_{ik}}) \right) \tag{4.72}$$

for each patch. The escapement is similar to the escapement $S_{P_{i0}}$ in equation (3.23) with $p_N = 0$ and $S_{N_{i0}} = N_{i0}$, that is,

$$\frac{1}{\rho} = b_i + \left(G_i^{(S_{Pi0})}(N_{i0}, S_{P_{i0}}) \right). \tag{4.73}$$

This equation has a unique solution

$$S^*_{P_{iu}} = \frac{L_i}{2} - \frac{L_i}{2s_{iu}}(\delta+1-b_i) + \frac{L_i}{2s_{iu}}(\beta_i N_i) \tag{4.74}$$

where N_i is the number of unharvested prey on patch i and $s_{iu} = s_i q_{ii} + s_j q_{ji}$. Assuming that $N_i = N_j = N$, if the predator on patch i is a relative importer, that is, $s_i q_{ij} < s_j q_{ji}$, and $s_i > s_{iu}$, then $S^*_{P_i} < S^*_{P_{iu}}$. Hence, optimal escapements from a connected two-patch predator-prey system will harvest the relative importer predator population more than the escapements resulting from an unconnected two-patch predator-prey system, if the system is connected. The converse is true only if $s_i < s_{iu}$. Furthermore, if one of the predator subpopulations is a relative exporter, $s_i = s_j$ and $q_{ii} = q_{jj}$, then

$$(S^*_{P_1} + S^*_{P_2}) - (S^*_{P_{1u}} + S^*_{P_{2u}}) < 0. \tag{4.75}$$

To see this recall that

$$S^*_{P_i} = \frac{L}{2} - \frac{L}{2s_i}\frac{(\delta + 1 - b)}{(q_{i1} + q_{i2})} + \frac{L}{2s_i}(\beta N), \tag{4.76}$$

$$S^*_{P_{iu}} = \frac{L}{2} - \frac{L}{2s_{iu}}(\delta + 1 - b) + \frac{L}{2s_{iu}}(\beta N), \tag{4.77}$$

where $s_{iu} = s_i q_{ii} + s_j q_{ji}$. Let $(S^*_{P_1} + S^*_{P_2}) - (S^*_{P_{1u}} + S^*_{P_{2u}}) = \Delta S_{P_u}$. As in the case of harvesting only the prey species (Section 4.3.2), let $B_{ij} = s_i q_{ij}$ and $\bar{B} = B_{11} + B_{12} + B_{21} + B_{22} > 0$ then we have

$$\begin{aligned}\Delta S_{P_u} &= \frac{L}{2}(\delta + 1 - b)\left[\frac{1}{B_{11} + B_{21}} + \frac{1}{B_{22} + B_{12}} - \frac{1}{B_{11} + B_{12}} - \frac{1}{B_{21} + B_{22}}\right] \\ &\quad -\frac{L}{2}(\beta N)\left(\left[\frac{1}{B_{11} + B_{21}} + \frac{1}{B_{22} + B_{12}}\right] - \left[\frac{1}{s_1} + \frac{1}{s_2}\right]\right).\end{aligned} \tag{4.78}$$

The first part of this sum is zero. Since one of the predator subpopulations is a relative exporter, without loss of generality assume $s_2q_{22}+s_2q_{21} = s_1q_{11}+s_2q_{21} < s_1q_{11}+s_1q_{12} < s_1$ and $s_2q_{22} + s_1q_{12} = s_2q_{11} + s_2q_{12} < s_2$, and hence ΔS_{P_u} becomes

$$\begin{aligned}\Delta S_{P_u} &= -\frac{L}{2}(\beta N)\left(\left[\frac{1}{B_{11} + B_{21}} + \frac{1}{B_{22} + B_{12}}\right] - \left[\frac{1}{s_1} + \frac{1}{s_2}\right]\right) \\ &< -\frac{L}{2}(\beta N)\left(\left[\frac{1}{s_1} + \frac{1}{s_2}\right] - \left[\frac{1}{s_1} + \frac{1}{s_2}\right]\right) \\ &= 0.\end{aligned} \tag{4.79}$$

This completes the proof that $(S^*_{P_1} + S^*_{P_2}) - (S^*_{P_{1u}} + S^*_{P_{2u}}) < 0$. This means incorrectly managing a predator-prey metapopulation as an unconnected two-patch predator-prey population would under-harvest the predator population.

Third, the two-patch predator-prey metapopulation is incorrectly managed as a well-mixed predator-prey population. In this case the existence of two patches is not recognised at all. The total net revenue which should be maximised is similar to J_T in equation (4.72) with solution

$$S^*_{P_w} = \frac{L_w}{2} - \frac{L_w}{2s_w}(\delta + 1 - b_w) + \frac{L_w}{2s_w}(\beta_w N_w), \tag{4.80}$$

where $L_w = L_i + L_j$, $s_w = [s_1(q_{11} + q_{12}) + s_2(q_{22} + q_{21})]/2$, $b_w = [b_1 + b_2]/2$, $\beta_w = [\beta_1 + \beta_2]/2$, and $N_w = N_i + Nj$.

Let us assume that all parameters for both patches are equal except $s_i(q_{ii} + q_{ij}) > s_j(q_{jj} + q_{ji})$, that is, the predator on patch i is a relative source subpopulation. Then $S^*_{P_{iw}} = S^*_{P_w}/2 < S^*_{P_i}$, provided $2r_i < r_w$, which means that a source predator subpopulation in a connected two-patch predator-prey system would be over-harvested if it is wrongly believed to be a well-mixed predator-prey system. The converse is true, a relative sink prey subpopulation would be harvested too conservatively, only if $2r_i > r_w$. Furthermore, if there is no relative source subpopulation, the harvest from a single-species metapopulation and a well-mixed population are the same (Tuck and Possingham 1994). In contrast, in a two-patch predator-prey metapopulation, incorrectly managing the metapopulation as a well-mixed predator-prey population would under-harvest the predator population. To prove this we need to show $(S^*_{P_1} + S^*_{P_2}) - (S^*_{P_w}) < 0$. Recall that

$$S^*_{P_i} = \frac{L}{2} - \frac{L}{2s_i}\frac{(\delta + 1 - b)}{(q_{i1} + q_{i2})} + \frac{L}{2s_i}(\beta N), \tag{4.81}$$

$$S^*_{P_w} = L - \frac{2L(\delta + 1 - b - \beta 2N)}{s_1(q_{11} + q_{12}) + s_2(q_{21} + q_{22})}. \tag{4.82}$$

Let $(S^*_{P_1} + S^*_{P_2}) - (S^*_{P_w}) = \Delta S_{P_w}$ and let $W_i = s_i(q_{ii} + q_{ij})$. Since $s_i > s_i(q_{ii} + q_{ij}) = W_i$, as in the case of harvesting only the prey species, I obtain

$$\begin{aligned} \Delta S_{P_w} &< L - L\frac{(\delta + 1 - b - \beta N)}{2}\left[\frac{1}{W_1} + \frac{1}{W_2}\right] \\ &\quad - \left(L - L(\delta + 1 - b - \beta 2N)\left[\frac{2}{W_1 + W_2}\right]\right) \\ &= -L(\delta + 1 - b - \beta N)\left[\frac{(W_1 - W_2)^2}{2(W_1 + W_2)W_1 W_2}\right] \\ &\quad -L\beta N\left[\frac{2}{W_1 + W_2}\right]. \end{aligned} \tag{4.83}$$

Furthermore, since $W_1 = W_2$ then $\Delta S_{P_w} < 0$. This completes the proof.

In Section 4.3.1 I have discussed optimal escapements in equations (4.26) - (4.29) by comparing them to escapements derived from other models, such as the unconnected two-patch predator-prey and the well-mixed predator-prey models. In Sections 4.3.2 and 4.3.3 the results in Section 4.3.1, where harvesting targets both species, are compared to strategies where we only harvest one of the species – the prey or the predator. The results in Sections 4.3.2 and 4.3.3 showed that the escapement comparison rules between subpopulations, that is, rules of how to harvest relative source/sink, exporter/importer and more/less vulnerable prey subpopulations and relative source/sink, exporter/importer and more/less efficient predator subpopulations may no longer hold if harvesting only targets one species, except for a limited situation. Moreover, escapement comparison rules to other strategies only work if the population size differences between the unexploited species are negligible, which may not be true for many real populations. To support and illustrate the results presented in these sections, I give some numerical examples in the following section.

4.4 Numerical examples

In this section, I present some numerical examples to illustrate the properties of escapements from a predator-prey metapopulation. The examples support the analytical results in the previous section. Some examples also reveal the properties of the escapements that are not observed in the analytical results, such as the effect of parameters variations (migration, prey vulnerability and predator efficiency) on the optimal escapements. I use parameters for populations similar to those in Tuck and Possingham (1994) to facilitate the comparisons.

4.4.1 Harvesting both species

Example 1:One prey subpopulation is a relative exporter and there is no source/sink subpopulation

Comparison of optimal strategy to single-species metapopulation strategy

Assume that prey in both patches have carrying capacities $K_1 = K_2 = 400000$, with intrinsic growth rates $r_1 = r_2 = 1000$ and adult survival rates $a_1 = a_2 = 0.001$. Prey subpopulation two is a relative exporter population with juvenile migration coefficients $p_{11} = p_{21} = 0.001$ and $p_{12} = p_{22} = 0.0009$. Assume the discounting rate δ is 10%. Before the exploitation begins, it is assumed that the population is in the equilibrium state. In the absence of the predator, the unharvested population sizes for prey subpopulations one and two are $\bar{N}_1 = 199116$ and $\bar{N}_2 = 179204$. The optimal escapements for the prey subpopulations one and two are $S^*_{N_{1s}} = 84316$ and $S^*_{N_{2s}} = 84316$ (see equation (4.41) with $C_i = 0$). Both subpopulations are harvested equally (in terms of escapement) because it is assumed that there is no source or sink subpopulation. However, the optimal harvests are different, that is, the first period optimal harvests are $H^*_{N_{1s}} = 114800$ and $H^*_{N_{2s}} = 94889$ while the equilibrium optimal harvests are $H^*_{N_{1s}} = 48854$ and $H^*_{N_{2s}} = 35546$, hence the relative exporter prey subpopulation is harvested more conservatively.

Now suppose the predator is present. Let the intrinsic growth of the predator be $s_i = r_i = 1000$ with the carrying capacities $L_1 = L_2 = 40000$. Let us assume the adult survival per period of the predator are not different from the adult survival per period of the prey. Let us also assume that those survivals are not different between patches, hence $b_1 = b_2 = 0.001$. Furthermore, it is assumed that both predator subpopulations are identical, with migration parameters $q_{11} = q_{12} = q_{21} = q_{22} = 0.00095$. Let $|\alpha_i| = \beta_i = 0.001$, that is, the predator has a high conversion efficiency. Using NAG routine c05nbf, I obtain one of the positive equilibrium population sizes for this two-patch predator-prey metapopulation, that is, $(\bar{N}_1, \bar{N}_2, \bar{P}_1, \bar{P}_2) = (188149, 169334, 26118, 26118)$. Furthermore, using equations (4.41) and (4.42), I obtain the optimal escapements for the system, that is $S^*_{N_1} = S^*_{N_2} = 84316$ and $S^*_{P_1} = S^*_{P_2} = 8432$ (see Figure 4.2 and Table 4.1). As suggested by Corollary 1, these escapements are exactly the same as the escapements from a single-species metapopulation, because $C = (p_{i1} + p_{i2})\alpha + (q_{i1} + q_{i2})\beta = 0$. However, the equilibrium optimal harvest for the prey is less than the equilibrium optimal harvest for the prey from single-species metapopulation, that is, $H^*_{N_1} = 47433$, $H^*_{N_2} = 34266$ and for the predator $H^*_{P_1} = H^*_{P_2} = 5571$. The difference between equilibrium harvest from predator-prey metapopulation and single-species metapopulation is critically depend on prey vulnerability, α, for the prey, and depends on predator biological conversion, β, for the predator. In this example, in which there is no source/sink subpopulation for both prey and predator and $C = 0$, it can be shown that $H^*_{N_i} < H^*_{N_{is}}$ and $H^*_{P_i} > H^*_{P_{is}}$ (see Appendix 4C). Hence if these additional assumptions are satisfied, that is, prey subpopulation one is a relative exporter with $p_{11} = p_{21} > p_{12} = p_{22}$ (no relative source/sink prey subpopulation), then the prey equilibrium harvest from a predator-prey metapopulation is smaller than from a single-species metapopulation and the predator equilibrium harvest from a predator-prey metapopulation is larger than from a single-species metapopulation, provided $C = 0$. This means that if we incorrectly manage a predator-prey metapopulation as two independent species we would over-harvest the “prey” species and under-harvest the “predator” species.

t	N_1	N_2	$S^*_{N_1}$	$S^*_{N_2}$	$H^*_{N_1}$	$H^*_{N_2}$
0	188149	169334	84316	84316	103834	85019
1	131748	118582	84316	84316	47433	34266
2	131748	118582	84316	84316	47433	34266
3	131748	118582	84316	84316	47433	34266
4	131748	118582	84316	84316	47433	34266
5	131748	118582	0	0	131748	118582

t	P_1	P_2	$S^*_{P_1}$	$S^*_{P_2}$	$H^*_{P_1}$	$H^*_{P_2}$
0	26118	26118	8432	8432	17687	17687
1	14002	14002	8432	8432	5571	5571
2	14002	14002	8432	8432	5571	5571
3	14002	14002	8432	8432	5571	5571
4	14002	14002	8432	8432	5571	5571
5	14002	14002	0	0	14002	14002

Table 4.1: Optimal escapements and harvests for prey and predator populations derived from equations (4.41) and (4.42). Optimal escapements for the prey and predator subpopulations i are $S^*_{N_i}$ and $S^*_{P_i}$, respectively, while $H^*_{N_i}$ and $H^*_{P_i}$ denote their optimal harvests. The t^{th} row indicates the value for $5-t$ periods to go.

Note that although both prey optimal escapements from a predator-prey metapopulation are equal, their equilibrium optimal harvests are different, in this case we harvest the relative importer prey subpopulation (subpopulation one) with a higher harvest than prey subpopulation two (in other words less conservatively in terms of harvest), that is, $H^*_{N_1} = 47433 > H^*_{N_2} = 34266$. This is generally true in harvesting a predator-prey metapopulation when one prey subpopulation is a relative exporter with its prey migration rate is equal to the retention rate of the other prey subpopulation, there is no source/sink subpopulation, predator populations are indistinguisable, and prey recruitment is greater than the number of prey eaten by the predator (see Appendix 4D). If these additional assumptions are satisfied, then using escapements from predator-prey metapopulation theory would harvest a relative exporter prey subpopulation more conservatively in both senses, that is, higher escapement and lower harvest, than the other prey subpopulation. Furthermore, there are no harvest differences between both predator subpopulations (Table 4.1).

Comparison of optimal strategy to spatially-unstructured strategies

I compare optimal escapements and equilibrium harvests from a predator-prey metapopulation to optimal escapements and equilibrium harvests if spatial structure is ignored. I compare the two different systems, namely the unconnected two-patch and the well-mixed. First, if the predator-prey metapopulation system was incorrectly considered an unconnected two-patch predator-prey system, then the optimal escapements are found from equations (4.41) and (4.42) by replacing p_{ii}, p_{ij}, q_{ii} and q_{ij} with 1, 0, 1 and 0 respectively, and replacing $(p_{ii}+p_{ij})r_i$ and $(q_{ii}+q_{ij})s_i$ with r_{iu} given by equation (4.44), and $(q_{ii}+q_{ij})s_i$ is replaced by s_{iu} similarly. The resulting escapements are

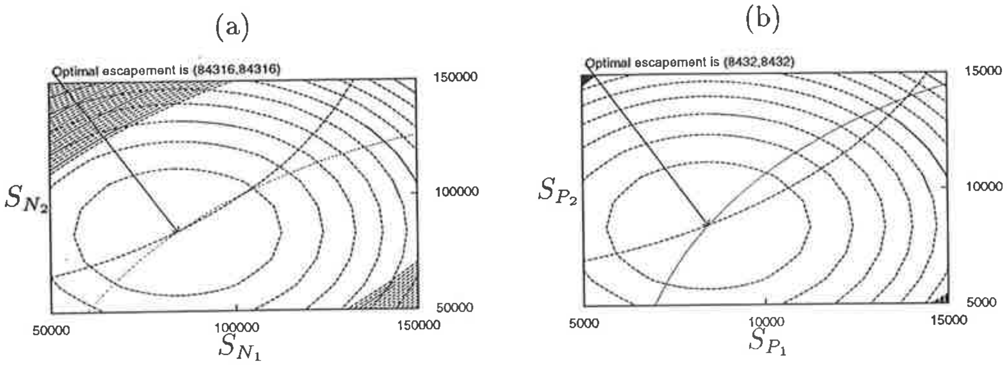

Figure 4.2: Using fixed escapements $S^*_{P_1} = S^*_{P_2} = 8432$, optimal escapements for the prey $S^*_{N_1} = S^*_{N_2} = 84316$ are found. The point (84316,84316) is the point where the contour plot $H^*_{N_1} = 47433$ intersects the contour plot $H^*_{N_2} = 34266$, hence optimal harvests from these escapements are $H^*_{N_1} = 47433$ and $H^*_{N_2} = 34266$. The shaded region in the upper-left corner is the region in which the combination of escapements produces a negative harvest for prey subpopulation two, $H^*_{N_2} < 0$, while the shaded region in the lower-right corner is the region in which the combination of escapements produces a negative harvest for prey subpopulation one, $H^*_{N_1} < 0$ (Figure 4.2.a). Similarly, Figure 4.2.b illustrates optimal escapements and optimal harvests for the predator.

$S^*_{N_{1u}} = 90100$, $S^*_{N_{2s}} = 77889$, $S^*_{P_{1u}} = S^*_{P_{2u}} = 8432$. The harvesting strategy from these escapements produces optimal equilibrium harvests $H^*_{N_{1u}} = 41101$, $H^*_{N_{2u}} = 40187$, $H^*_{P_1} = H^*_{P_2} = 5566$ with total harvest $H^*_u = H^*_{N_u} + H_{P_u} = 92422$. This total harvest is less than the total harvest which arises if we correctly use predator-prey metapopulation escapements, that is, $H^* = H^*_N + H^*_P = 92841$ (see Table 4.2). This is because if we use the unconnected predator-prey theory, we fail to recognise the exporter prey subpopulation which is important as a contributor to the other prey subpopulation. In this case, we exploit the relative exporter prey subpopulation less conservatively (in terms of escapement, with escapement $S^*_{N_{2u}} = 77889$ less than $S^*_{N_2} = 84316$) while the relative importer prey subpopulation is harvested too conservatively (in terms of escapement, with escapement $S^*_{N_{1u}} = 90100$ more than $S^*_{N_1} = 84316$).

In this example a lower escapement means a higher harvest, that is, $S^*_{N_{1u}} > S^*_{N_1}$ and $S^*_{N_{2u}} < S^*_{N_2}$ means $H^*_{N_{1u}} < H^*_{N_1}$ and $H^*_{N_{2u}} > H^*_{N_2}$. Note that in Table 4.2, $H^*_{N_{1u}} = 41101 < H^*_{N_1} = 47433$ and $H^*_{N_{2u}} = 40189 > H^*_{N_2} = 34266$. This is because the example satisfies all assumptions in Result 5. Hence, in this example, incorrectly using unconnected two-patch predator-prey harvesting theory to harvest a predator-prey metapopulation would under-harvest the relative importer prey subpopulation while it also would over-harvest the relative exporter prey subpopulation, in terms of harvest. Furthermore, $S^*_{N_{1u}} > S^*_{N_1} = S^*_{N_2} > S^*_{N_{2u}}$ implies $H^*_{N_{1u}} < H^*_{N_1}$ and $H^*_{N_{2u}} > H^*_{N_2}$. Numerical examples show that this rule may be true if the cost of harvesting is included. Table 4.3 shows the comparison between escapements and harvests from a predator-prey metapopulation and from other predator-prey systems (unconnected two-patch and well-mixed predator prey system). In this example, I assume that the cost function is in the form

$$c_X(X_i) = (m_{X_i} + c_i n_{X_i} X_i)/(n_{X_i} X_i) \tag{4.84}$$

which is a decreasing function with respect to X_i and has a non-zero limit ($c_i \neq 0$) as X_i approaches ∞. Hence, with this cost function I assume that there is a constant cost of harvesting whenever the stock size is high and the cost is lower than the cost of harvesting in a very small stock level. I assume that the predator-prey metapopulation has the same parameters as in the previous example (the example in the case of negligible costs) with additional parameters $m_{N_1} = m_{N_2} = m_{P_1} = m_{P_2} = 1000$, $n_{N_1} = n_{N_2} = n_{P_1} = n_{P_2} = 0.005$, $c_1 = c_2 = 10000$ and $p_N = p_P = 800$.

Second, if the predator-prey metapopulation system is incorrectly considered to be a well-mixed predator-prey system, then the optimal escapements found are exactly the same as the escapements from the predator-prey metapopulation from equations (4.41) and (4.42) by replacing p_{ii}, p_{ij}, q_{ii} and q_{ij} with 1, 0, 1 and 0 respectively, and replacing $(p_{ii} + p_{ij})r_i$ and $(q_{ii} + q_{ij})s_i$ with r_w given by equation (4.45), and $(q_{ii} + q_{ij})s_i$ is replaced by s_w. The resulting escapements are $S^*_{N_w} = 168632$ and $S^*_{P_w} = 16864$ (or $S^*_{N_w}/2 = 84316$ and $S^*_{P_w}/2 = 8432$ for the prey and predator in each patch). This is not surprising because there is no source or sink subpopulation for either the prey or the predator, hence $r_{iw} = r_i$ and $s_{iw} = s_i$.

Example 2. One prey subpopulation is a relative source and exporter

Assume that all parameters of the prey and predator are as in Example 1, except the migration parameters. In this example I will assume that $p_{12} = 0.002$ is twice the migration rate as all the others. Using these parameters, I compare the optimal harvesting strategy from predator-prey metapopulation escapements to the harvesting strategy from spatially-unstructured predator-prey escapements, that is, unconnected two-patch and well-mixed predator-prey escapements. The result is presented in Table 4.2 (the lower table).

From the table, it can be seen that the source prey subpopulation (prey subpopulation one) should be harvested more conservatively (with more escapement) than the other prey subpopulation. The equilibrium harvest from the source prey subpopulation is less than the equilibrium harvest from the sink prey subpopulation. On the other hand, we should harvest the predator living in the same patch with the relative source prey subpopulation with a lower escapement and a higher harvest than the other predator subpopulation.

Compared to the strategy using escapements from the unconnected two-patch predator-prey harvesting theory, the relative exporter prey subpopulation is harvested more conservatively in terms of its escapement ($S^*_{N_1} = 126217 > S^*_{N_{1u}} = 90100$) while the relative importer prey subpopulation is harvested less conservatively, in terms of its escapement ($S^*_{N_2} = 90100 < S^*_{N_{2u}} = 126733$). Similarly, compared to the strategy using escapements from the well-mixed predator-prey harvesting theory, the relative source prey subpopulation is harvested more conservatively both in terms of escapement ($S^*_{N_1} = 126217 > S^*_{N_w}/2 = 224160/2$) and in terms of harvest ($H^*_{N_1} = 28315 < S^*_{N_w}/2 = 174391/2$). The relative sink prey subpopulation is harvested less conservatively both in terms of escapement ($S^*_{N_2} = 90100 < S^*_{N_w}/2 = 224160/2$) and in terms of harvest ($H^*_{N_1} = 149808 > S^*_{N_w}/2 = 174391/2$).

PPM	$S^*_{N_1} = 84316$	$H^*_{N_1} = 47433$	$S^*_{P_1} = 8432$	$H^*_{P_1} = 5571$
	$S^*_{N_2} = 84316$	$H^*_{N_2} = 34266$	$S^*_{P_2} = 8432$	$H^*_{P_2} = 5571$
	$S^*_N = 168632$	$H^*_N = 81699$	$S^*_P = 16864$	$H^*_P = 11142$
UPP	$S^*_{N_{1u}}=90100$	$H^*_{N_{1u}}=41101$	$S^*_{P_{1u}}=8432$	$H^*_{P_{1u}}=5566$
	$S^*_{N_{2u}}=77889$	$H^*_{N_{2u}}=40189$	$S^*_{P_{2u}}=8432$	$H^*_{P_{2u}}=5566$
	$S^*_{N_u}=167989$	$H^*_{N_u}=81290$	$S^*_{P_u}=16864$	$H^*_{P_u}=11132$
WPP	$S^*_{N_w}=168632$	$H^*_{N_w}=81699$	$S^*_{P_w}=16864$	$H^*_{P_w}=11142$

PPM	$S^*_{N_1} = 126217$	$H^*_{N_1} = 28315$	$S^*_{P_1} = 7748$	$H^*_{P_1} = 7277$
	$S^*_{N_2} = 90100$	$H^*_{N_2} = 149808$	$S^*_{P_2} = 9010$	$H^*_{P_2} = 6016$
	$S^*_N = 216317$	$H^*_N = 178123$	$S^*_P = 16758$	$H^*_P = 13293$
UPP	$S^*_{N_{1u}} = 90100$	$H^*_{N_{1u}} = 64421$	$S^*_{P_{1u}} = 9010$	$H^*_{P_{1u}} = 6914$
	$S^*_{N_{2u}} = 126733$	$H^*_{N_{2u}} = 96818$	$S^*_{P_{2u}} = 9010$	$H^*_{P_{2u}} = 6914$
	$S^*_{N_u} = 216833$	$H^*_{N_u} = 161239$	$S^*_{P_u} = 18020$	$H^*_{P_u} = 13828$
WPP	$S^*_{N_w} = 224160$	$H^*_{N_w} = 174391$	$S^*_{P_w} = 18020$	$H^*_{P_w} = 13960$

Table 4.2: Escapement and harvest comparisons between correct and incorrect assumptions with $p_N = p_P$, costs are negligible, $p_{11} = p_{21} = 0.001$, $p_{12} = p_{22} = 0.0009$, and $q_{11} = q_{12} = q_{21} = q_{22} = 0.00095$ (upper table) and $p_{11} = p_{21} = p_{22} = q_{11} = q_{12} = q_{21} = q_{22} = 0.001$ and $p_{12} = 0.002$ (lower table). PPM, UPP and WPP denote predator-prey metapopulation, unconnected predator-prey population and well-mixed predator-prey population, respectively.

Parameter variations: migration, vulnerability and efficiency

In this section I discuss the behaviour of the predator-prey optimal escapement with respect to the change in migration rates, prey vulnerability and predator efficiency. In single-species metapopulation harvesting theory, the behaviour of the optimal escapements, as the migration parameters p_{ij} change, can be determined easily because of the simple form of the derivative of the optimal escapements. The main conclusion in single-species harvesting theory is that the uncertainty of the exact value of the migration parameters should not influence the decision in determining the optimal escapement as long as the individual's migration rate is relatively high (p_{ij} is large), that is, a relative source/exporter subpopulation should be harvested with more escapement than a relative sink/importer subpopulation (Tuck, 1994)

In the following discussion I investigate the behaviour of predator-prey metapopulation escapements as the prey migration $p_{ij}, i \neq j$ changes. I keep all parameters fixed, the values are given as in Example 1 except the prey migration p_{12} and p_{21}. Algebraic simplification gives the following result for the optimal escapements.

$$S_{N_1} = -10000\frac{-86841 + 0.94199 \times 10^9 p_{12}}{-47419 - 0.4768 \times 10^8 p_{12} + 0.1 \times 10^9 p_{12}^2},$$

$$S_{P_1} = 10000\frac{-39159 - 0.5004 \times 10^8 p_{12} + 0.1 \times 10^{11} p_{12}^2}{-47419 - 0.4768 \times 10^8 p_{12} + 0.1 \times 10^9 p_{12}^2},$$

$$S_{N_2} = -16000\frac{-2263 + 0.11774875 \times 10^8 p_{21}}{-853 - 954000 p_{21} + 0.2 \times 10^7 p_{21}^2},$$

PPM	$S^*_{N_1} = 84308$ $S^*_{N_2} = 84308$	$H^*_{N_1} = 47433$ $H^*_{N_2} = 34267$	$S^*_{P_1} = 8422$ $S^*_{P_2} = 8422$	$H^*_{P_1} = 5568$ $H^*_{P_2} = 5568$
	$S^*_N = 168616$	$H^*_N = 81700$	$S^*_P = 16844$	$H^*_P = 11136$
UPP	$S^*_{N_{1u}} = 90123$ $S^*_{N_{2u}} = 77918$	$H^*_{N_{1u}} = 41103$ $H^*_{N_{2u}} = 40182$	$S^*_{P_{1u}} = 8462$ $S^*_{P_{2u}} = 8461$	$H^*_{P_{1u}} = 5573$ $H^*_{P_{2u}} = 5574$
	$S^*_{N_u} = 168041$	$H^*_{N_u} = 81285$	$S^*_{P_u} = 16923$	$H^*_{P_u} = 11147$
WPP	$S^*_{N_w} = 180246$	$H^*_{N_w} = 82343$	$S^*_{P_w} = 16924$	$H^*_{P_w} = 11344$

Table 4.3: Escapement and harvest comparisons between correct and incorrect assumptions with $p_N = p_P = 800$, cost function is given by equation (4.84), $p_{11} = p_{21} = 0.001$, $p_{12} = p_{22} = 0.0009$, and $q_{11} = q_{12} = q_{21} = q_{22} = 0.00095$.

$$S_{P_2} = 1000 \frac{-6811 - 0.1048 \times 10^8 p_{21} + 0.2 \times 10^{10} p_{21}^2}{-853 - 954000 p_{21} + 0.2 \times 10^7 p_{21}^2}.$$

Hence all escapements from patch i are not affected by the changes in prey migration p_{ji}. The rate of change of the prey and predator escapements on patch one due to change in prey migration p_{12} are given by:

$$\frac{\partial S_{N_1}}{\partial p_{12}} = -0.94199 \times 10^{13} \frac{1}{-47419 - 0.4768 \times 10^8 p_{12} + 0.1 \times 10^9 p_{12}^2}$$
$$+10000 \frac{(-86841 + 0.94199 \times 10^9 p_{12})(-0.4768 \times 10^8 + 0.2 \times 10^9 p12)}{(-47419 - 0.4768 \times 10^8 p_{12} + 0.1 \times 10^9 p_{12}^2)^2},$$

$$\frac{\partial S_{P_1}}{\partial p_{12}} = 10000 \left(\frac{-0.5004 \times 10^8 + 0.2 \times 10^{11} p_{12}}{-47419 - 0.4768 \times 10^8 p_{12} + 0.1 \times 10^9 p_{12}^2} \right.$$
$$\left. - \frac{(-39159 - 0.5004 \times 10^8 p_{12} + 10^{10} p_{12}^2)(-0.4768 \times 10^8 + 0.2 \times 10^9 p_{12})}{(-47419 - 0.4768 \times 10^8 p_{12} + 0.1 \times 10^9 p_{12}^2)^2} \right).$$

The effect of a small increment in prey migration p_{12} to the prey optimal escapement S_{N1} and predator escapement S_{P1} can be found using these partial derivatives. For example, with increment $\Delta p_{12} = 0.000005$ at the point $p_{12} = 0.0001$ we expect the prey's optimal escapement will increase by 896. The same increment only gives an increment of 11 to the prey optimal escapement at $p_{12} = 0.01$. Similarly, a small increment in predator migration $\Delta q_{12} = 0.000005$ at the point $q_{12} = 0.0001$ will change the optimal escapements as much as 114, but a similar increment gives change in the predator optimal escapements as small as 1 at the point $q_{12} = 0.01$. Figures 4.3 and 4.4 give a graphical depiction of the changes in optimal escapements in both patches. As in single-species metapopulation harvesting theory (Tuck, 1994), the effects of a small change in the migration parameter of one sub-species to the optimal escapement of that sub-species is smaller at a higher migration parameter than at a lower migration parameter. This change does not affect any optimal escapements of the other sub-species in the other patch (Figure 4.3 and 4.4). However, the change in either the prey or predator migration parameters affect both sub-species in the same patch (Figure 4.3 and 4.4).

Figures 4.3 and 4.4 are interpreted as follows. If the migration rate of prey sub-population one is significantly smaller compared to the migration rate of the predator,

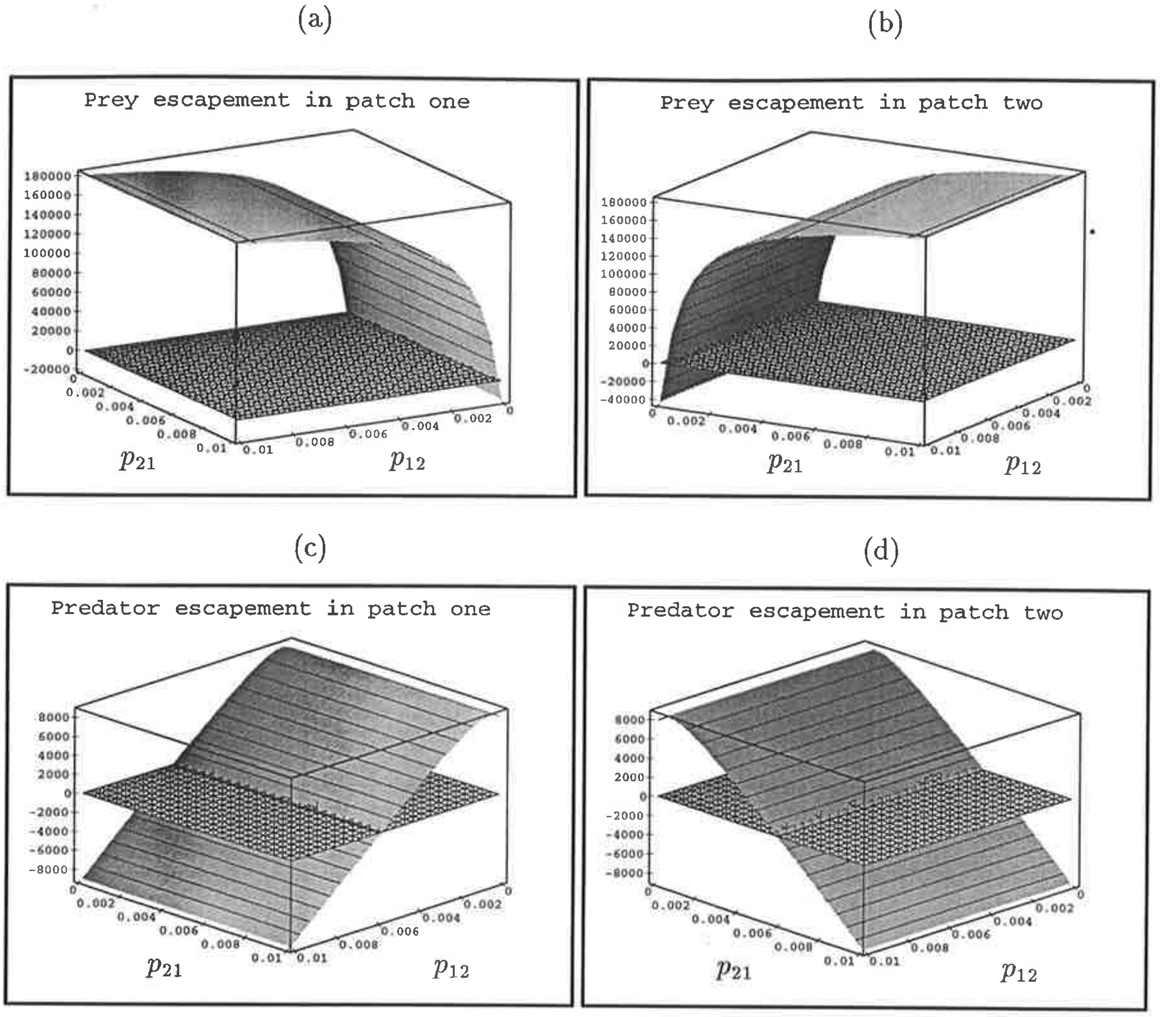

Figure 4.3: Optimal escapements $S^*_{N_1}$, $S^*_{N_2}$, $S^*_{P_1}$ and $S^*_{P_2}$ as functions of migration parameters p_{12} and p_{21}. A small variation in prey migration p_{12} causes a lower change in optimal escapement $S^*_{N_1}$ at a higher prey migration than at a lower prey migration (Figure 4.3.a). A small variation in prey migration p_{21} causes a lower change in optimal escapement $S^*_{N_2}$ at a higher prey migration than at a lower prey migration (Figure 4.3.b). See text for details.

$p_{12} \ll q_{12} = 0.00095$, then it is optimal to harvest all individuals of prey subpopulation one (upper-left part of Figure 4.3). On the other hand, if it is significantly larger, $p_{12} \gg q_{12} = 0.00095$, then it is optimal to harvest all individuals of predator subpopulation one (lower-left part of the same figure). Similarly, if the migration rate of predator subpopulation one is significantly smaller compared to the migration rate of the prey, $q_{12} \ll p_{12} = 0.0009$, then it is optimal to harvest all individuals of predator subpopulation one (lower-left part of Figure 4.4). On the other hand, if it is significantly larger, $q_{12} \gg p_{12} = 0.0009$, then it is optimal to harvest both prey and predator subpopulation one with more escapements. The effects of p_{21} and q_{21} are interpreted similarly. To some extent this result agrees with the result for a single-species population (May *et al.*, 1979).

Similarly, I investigate the effect of a small increment in prey vulnerability α_1 and predator efficiency β_1 to the prey optimal escapement S_{N1} and predator escapement S_{P1} using the partial derivative of these escapement with respect to α_1 and β_1. For

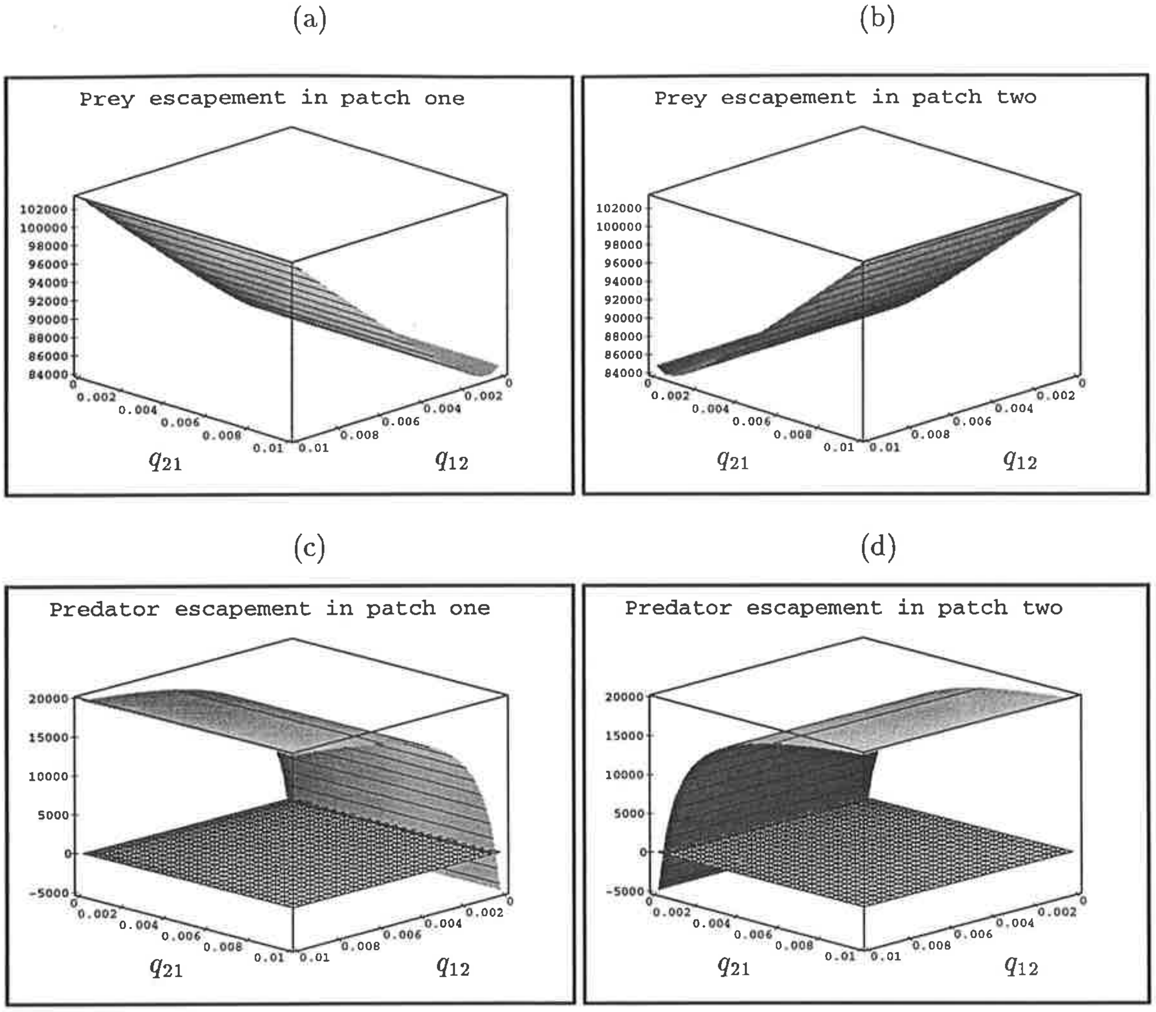

Figure 4.4: Optimal escapements $S^*_{N_1}$, $S^*_{N_2}$, $S^*_{P_1}$ and $S^*_{P_2}$ as functions of migration parameters q_{12} and q_{21}. A small variation in predator migration q_{12} causes a lower change in optimal escapement $S^*_{P_1}$ at a higher predator migration than at a lower predator migration (Figure 4.4.c). A small variation in predator migration q_{21} causes a lower change in optimal escapement $S^*_{P_2}$ at a higher predator migration than at a lower predator migration (Figure 4.4.d). See text for details.

example, with increment $\Delta\alpha_1 = 0.00001$ at the point $\alpha_1 = 0.001$ we find that the prey and predator optimal escapements will increase with the change as much as 17. A similar increment changes the prey and predator optimal escapement as much as 23 and 18, respectively, at $\alpha_1 = 0.0001$, and changes the prey and predator optimal escapements as much as -84 and 36, respectively, at $\alpha_1 = 0.01$. Figure 4.5 shows that the effect of a small variation in prey vulnerability to prey and predator optimal escapements is smaller around the line $|\alpha_1| = \beta_1$ than at any other region. This suggests that in the absence of the exact value of prey vulnerability, a small variation of predicted prey vulnerability should not alter the decision on how we harvest the prey and predator population, as long as the predator efficiency is high enough (C_1 is close to zero). As in the case of the migration parameter variation, the variation of prey vulnerability or predator efficiency of one sub-species does not affect the choice of optimal escapement for the sub-species in the other patch. This is clear from the escapement equations, that is, equations (4.41) and (4.42).

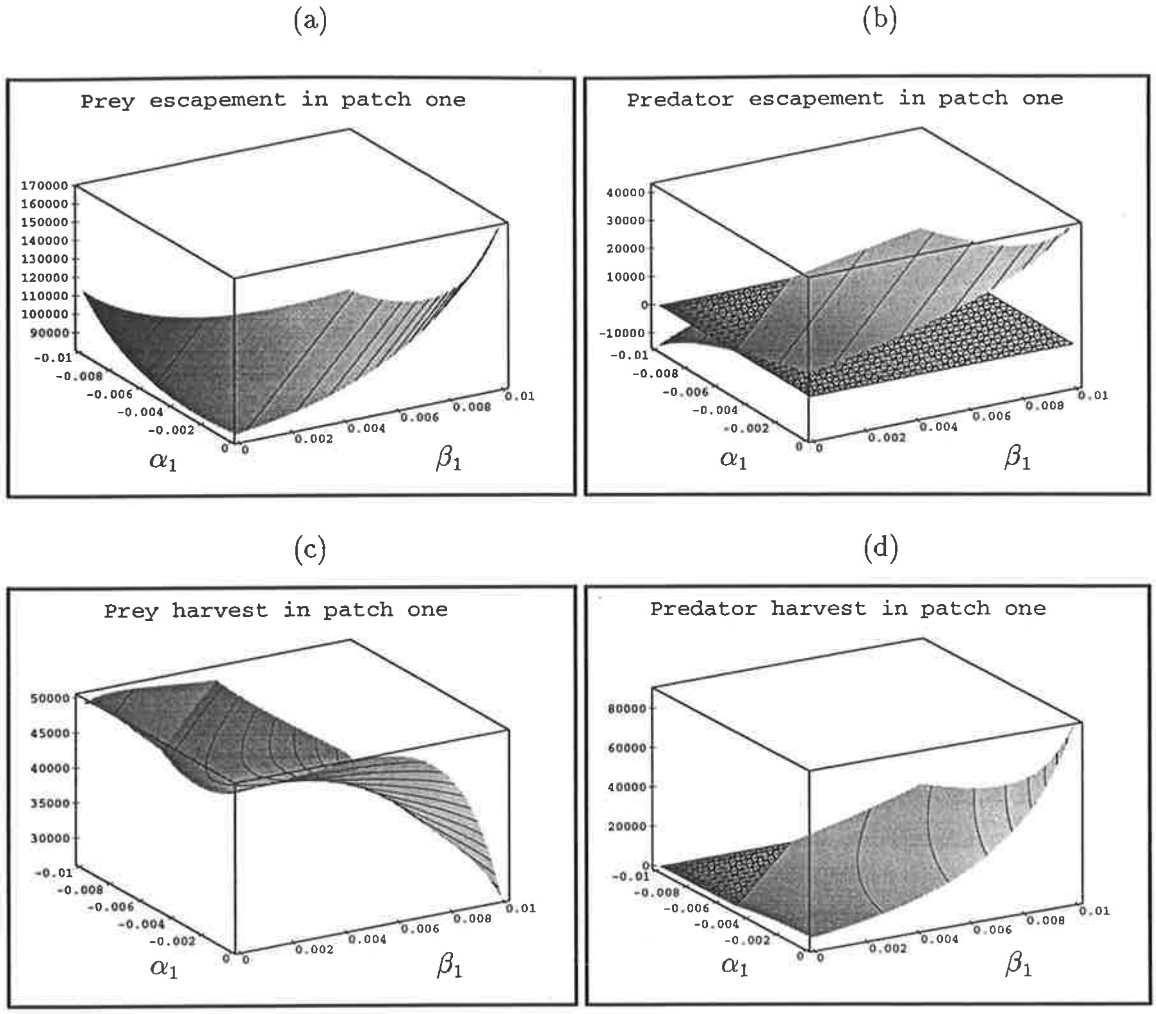

Figure 4.5: Optimal escapements $S^*_{N_1}$ and $S^*_{P_1}$ and equilibrium harvests H^*_{N1} and $H^*_{P_1}$ as functions of prey vulnerability α_1 and predator biological conversion β_1. See text for details.

Figure 4.5 show prey and predator escapements $S^*_{N_1}$ and $S^*_{P_1}$ and harvests $H^*_{N_1}$ and $H^*_{P_1}$ as functions of prey vulnerability α_1 and predator conversion β_1. When the prey is very vulnerable and the predator is less efficient, the optimal strategy is to harvest all the predator (Fig. 4.5.b) producing a relatively constant harvest of the prey for every choice of α_i less than approximately -0.008 (Fig. 4.5.c). We can expect that if predator subpopulation two is a relative exporter and source (for example, if q_{21} is greater than a certain threshold), then predator subpopulation two will have a non-zero escapement for any value of α_1 and β_1 in Figure 4.5 (see Result 2). This example shows that May *et al.*'s (1979) suggestion to harvest a predator population which has a low biological efficiency and intrinsic growth rate generalises to a predator-prey metapopulation. However, if there is predator migration variability between the two patches, extinction may not be optimal for the relative source predator subpopulation.

4.4.2 Harvesting only the prey species

In this section I provide two numerical examples to illustrate the behaviour of optimal escapements from predator-prey metapopulation theory. The prey population

t	N_1^*	N_2^*	S_{N1}^*	S_{N2}^*	H_{N1}^*	H_{N2}^*
0	132.73	105.02	55.00	64.00	77.73	41.02
1	110.65	89.79	55.00	64.00	55.65	25.79
2	110.65	89.79	55.00	64.00	55.65	25.79
3	110.65	89.79	55.00	64.00	55.65	25.79
4	110.65	89.79	55.00	64.00	55.65	25.79
5	110.65	89.79	0	0	110.65	89.79

Table 4.4: Escapements and harvests from a single-species metapopulation (Tuck and Possingham, 1994). The t^{th} row indicates the value for $5-t$ periods to go.

in the first example is taken from Tuck (1994), and in the second example I use the predator-prey metapopulation from the previous example in harvesting both species (Example 2).

Example 1:

Assume that prey populations in both patches have carrying capacities $K_1 = K_2 = 200$, with intrinsics growth rates $r_1 = r_2 = 10$ and adult survival per period $a_1 = a_2 = 0.1$. Prey subpopulation two is assumed to be a relative source and exporter subpopulation. The migration parameters are $p_{11} = p_{12} = p_{22} = 0.1$ and $p_{21} = 0.15$. It is assumed that there is no discounting, that is, $\delta = 0$. Before the exploitation commences, it is assumed that the population is in the equilibrium state. In the absence of the predator, the unharvested population sizes for prey subpopulations one and two are $\bar{N}_1 = 133$ and $\bar{N}_2 = 105$ respectively. Using equation (4.41) with $C_i = 0$, the optimal escapements for prey subpopulations one and two are obtained, that is, $S_{N1}^* = 55$ and $S_{Ni1}^* = 64$ with the equilibrium harvests $H_{N1}^* = 56$ and $H_{N2}^* = 26$, respectively. It is clear that the relative source prey subpopulation is more protected than the relative sink prey subpopulation.

Now, suppose that the predator is present. For simplicity I choose the intrinsic growth rates of the predator to be $s_i = r_j$, $i = 1, 2$. The predator carrying capacities are $L_1 = L_2 = 10$, and adult survival rate are $b_1 = b_2 = 0.1$. The juveniles migrate symmetrically, in this case I use the migration parameters $q_{11} = q_{12} = q_{21} = q_{22} = 0.1$. Assume that $\alpha_1 = \alpha_2 = -0.1$ and $\beta_1 = \beta_2 = 0.01$. As in the single-species metapopulation model, I assume the unharvested equilibrium population size as the initial population size before the exploitation begins.

The equilibrium population sizes for this predator-prey metapopulation are $\bar{N}_1 = 118$, $\bar{N}_2 = 94$, $\bar{P}_1 = 6.56$, and $\bar{P}_2 = 6.56$. Unlike the case of harvesting both species, here prey optimal escapements depend on the number of unexploited predator. However, as it can be seen in Table 4.5, the equilibrium escapements and harvests exist. Table 4.6 shows the numerical result from iterating Bellman's equation.

Optimal escapements from a predator-prey metapopulation are always less than the escapements from a single-species metapopulation. It does not mean that the harvests resulting from two-patch predator-prey escapements is higher than the harvests resulting from single-species metapopulation escapements (Table 4.4 and 4.5 give a clear example for this comparison). This is because the initial population size before

t	N_1^*	N_2^*	S_{N1}^*	S_{N2}^*	H_{N1}^*	H_{N2}^*
0	117.94	93.68	48.44	57.44	69.49	36.24
1	94.14	76.45	49.14	58.14	45.01	18.32
2	95.84	77.82	48.93	57.93	46.90	19.89
3	95.34	77.42	48.97	57.97	46.37	19.45
4	95.44	77.50	48.96	57.96	46.47	19.54
5	95.42	77.48	48.97	57.97	46.45	19.52
6	95.42	77.49	48.97	57.97	46.45	19.51
7	95.42	77.49	0	0	95.42	77.49

Table 4.5: Prey escapements and harvests from a predator-prey metapopulation [equation (4.51)]. The t^{th} row indicates the value for $7 - t$ periods to go.

t	S_{N1}^*	S_{N2}^*	H_{N1}^*	H_{N2}^*
0	41	58	77	36
1	49	58	41	15
2	49	58	46	19
3	0	0	95	77

Table 4.6: Prey escapements and harvests from iterating the dynamic programming equations. The t^{th} row indicates the value for $3 - t$ periods to go. These escapements are only slightly different from those derived analytically in Table 4.5.

the exploitation begins is the unharvested equilibrium population size. Meanwhile, in the presence of the predator, this equilibrium size for the prey is less than that in the absence of the predator. For this reason, if the actual system considered is indeed a predator-prey metapopulation, then incorrectly using the harvests derived from single-species metapopulation escapements may cause the prey stock to suffer from over-exploitation (see Figure 4.7). However, Figure 4.7 also shows that if we use optimal escapements from a single-species metapopulation to manage a predator-prey metapopulation, the equilibrium optimal harvests are not too different from the equilibrium optimal harvests using predator-prey metapopulation escapements.

Example 2:

Assume that all parameters of the prey and predator are as in Example 1 for harvesting both species except the migration parameters, that is, $p_{11} = p_{21} = p_{22} = 0.001$, $p_{12} = 0.002$, and $q_{11} = q_{12} = q_{21} = q_{22} = 0.001$ and $\alpha_i = -\beta_i = -0.00001$. Using these parameters, I compare the optimal harvesting strategy from predator-prey metapopulation escapements to the harvesting strategies from spatially-unstructured predator-prey escapements, that is, unconnected two-patch and well-mixed predator-prey escapements. In this example I assume that there is no discounting. The result is presented in Table 4.7.

As expected, Table 4.7 shows that using predator-prey metapopulation escape-

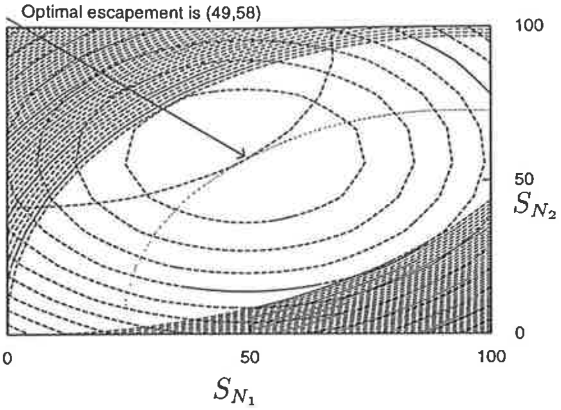

Figure 4.6: Graphical illustration for optimal escapements and optimal harvests in Example 1. Optimal escapements for the prey are $S^*_{N_1} = 49$ and $S^*_{N_2} = 58$. The point (49,58) is the point where the contour plot $H^*_{N_1} = 46.45$ intersects the contour plot $H^*_{N_2} = 19.51$, therefore, optimal harvests from these escapements are $H^*_{N_1} = 46.45$ and $H^*_{N_2} = 19.51$. The shaded region on the upper-left corner is the region in which the combination of the escapements produce a negative harvest for prey subpopulation two, $H^*_{N_2} < 0$, while the shaded region on the lower-right corner is the region in which the combination of the escapements produce a negative harvest for prey subpopulation one, $H^*_{N_1} < 0$.

ments we harvest a relative exporter/source prey subpopulation with more escapement ($S^*_{N_1} = 128440$) than if we use either an unconnected or a well-mixed predator-prey, with escapements $S^*_{N_{1u}} = 80040$ and $S^*_{N_{1w}} = 175984/2$ respectively. In this example, harvesting the relative exporter/source prey subpopulation more conservatively yields a higher total harvest, that is, $H^*_N = 168952 > H^*_{N_w} = 167281 > H^*_{N_u} = 160131$.

4.5 Concluding remarks

In this chapter harvesting strategies for a spatially-structured predator-prey system were established as a generalisation of harvesting strategies for a single-species metapopulation. Some properties of the escapements for a single-species metapopulation are preserved in the presence of predators, such as the strategies of how to harvest a relative source/sink and exporter/importer local population. I considered two situations. In the first situation both species are harvested. In this situation I obtained optimal escapements for the two species in both patches which are independent of the time horizon considered. In the second situation harvesting targets only one species, either the prey or the predator. In this situation I obtained optimal escapements for one period to go. If there is no discounting, then these escapements are as the same as the long-term escapements. This is because when there is no discounting, the profit in any period generated from escapements S_{X_i} has exactly the same value as profit from the same escapements in any other period. Hence we only need to find escapements for one period to go. Optimal escapements for the case where discounting is not zero are considered and examined in the next chapter for the model in which predator-prey

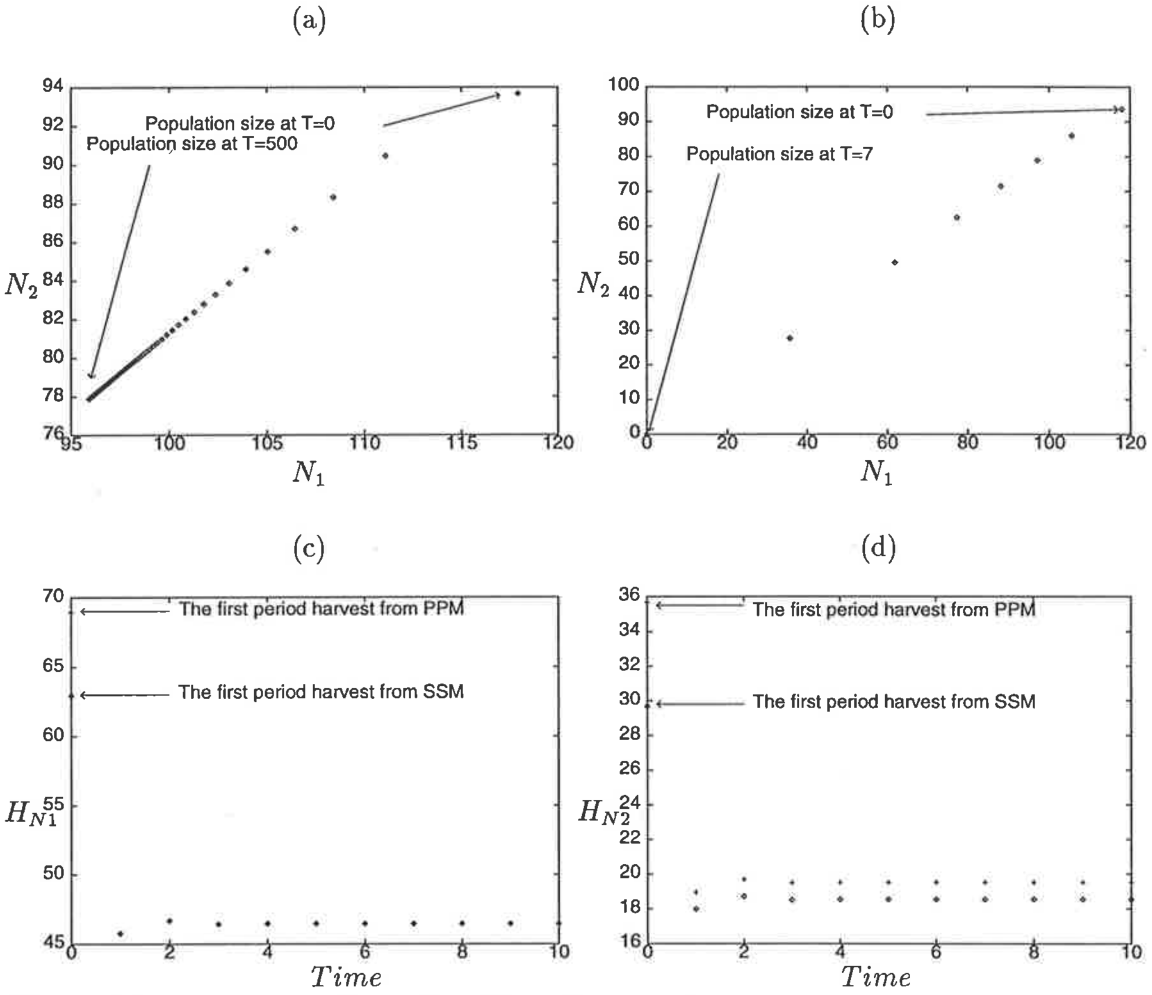

Figure 4.7: Figure 4.7.a shows that if fixed harvests from a predator-prey metapopulation are used as the policy to manage the metapopulation then the exploited metapopulation reaches an equilibrium ($N_1 = 95$ and $N_2 = 78$, see Table 4.5). However, Figure 4.7.b shows that if fixed harvests from a single-species metapopulation are used then the metapopulation is collapses after 5 periods of exploitation. Figures 4.7.c and 4.7.d show that equilibrium harvests, if we incorrectly assume a single-species metapopulation is always lower than, or at most as much as, equilibrium harvests from predator-prey metapopulation escapements.

PPM	$S^*_{N_1} = 128440$	$H^*_{N_1} = 25782$
	$S^*_{N_2} = 95107$	$H^*_{N_2} = 143170$
	$S^*_N = 223547$	$H^*_N = 168952$
UPP	$S^*_{N_{1u}} = 80040$	$H^*_{N_{1u}} = 68035$
	$S^*_{N_{2u}} = 120027$	$H^*_{N_{2u}} = 92096$
	$S^*_{N_u} = 200067$	$H^*_{N_u} = 160131$
WPP	$S^*_{N_w} = 175984$	$H^*_{N_w} = 167281$

Table 4.7: Equilibrium escapement and equilibrium harvest comparisons between correct and incorrect assumptions with $p_N = p_P$, costs are negligible, $p_{11} = p_{21} = p_{22} = q_{11} = q_{12} = q_{21} = q_{22} = 0.001$ and $p_{12} = 0.002$.

interactions take place in the adult stage.

If the following is true: harvesting targets both species, the only difference between populations is the prey migration rate, there is no market price differences between the two species, and the cost of harvesting is negligible or independent of the stock abundance, then the first rule of thumb for harvesting a single-species metapopulation (TP 1 in Chapter 2) can be used to manage a predator-prey metapopulation provided the post-dispersal predator efficiency (C_{ib}) is above a threshold. This first rule states that we should harvest the relative source prey subpopulation more conservatively than the relative sink prey subpopulation. We protect the relative source prey subpopulation directly with a higher escapement for the prey, and indirectly, with a lower escapement for the predator living in the same patch with this prey subpopulation.

On the other hand, if the migrations between subpopulations are symmetric, and there is no biological variability except the vulnerability of the prey, then we should harvest a relatively less vulnerable prey local population more conservatively than the other prey local population which is more vulnerable to predation. A special case occurs when there is no predation in one of the patches, say patch one. In this case, patch one is a refugial patch for the prey. This rule ensures that we harvest the prey living in the refugial patch more conservatively than the prey living in the habitat where predation occurs.

Furthermore, if the prey vulnerability of the two prey subpopulations are the same, but the predator efficiencies differ between patches, then we should harvest the prey living in the patch with the relatively more efficient predator more conservatively than the other prey subpopulation. This result suggests that if the predator has a high biological efficiency, then we should leave enough prey to sustain the predator population. In the chapter that follows, it will be shown that if the market value of the predator is large enough compared to the market value of the prey, then the optimal strategy can be a "seeding strategy" where prey are put into the system from another patch.

Unlike the results of optimal harvesting for a single-species metapopulation, the results generalised here are more restrictive. To establish the generalisation of the rule of thumb TP 2, that is Result 4 in this chapter, an extreme condition, that the predator efficiency before and after dispersal is the same, is needed. Otherwise only some parts of the rule are true, depending on whether the predator efficiency before dispersal is less, or more, than the predator efficiency after dispersal. In the case when the predator

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efficiency before dispersal is less than the predator efficiency after dispersal then we harvest the relative exporter prey subpopulation and the predator living in the same patch with the relative importer prey subpopulation more conservatively than if we use the strategy from unconnected two-patch predator-prey harvesting theory. Conversely, in the case when the predator efficiency before dispersal is more than the predator efficiency after dispersal then we harvest the relative importer prey subpopulation and the predator living in the same patch with the relative exporter prey subpopulation less conservatively than if we use the strategy from unconnected two-patch predator-prey harvesting theory. The same condition is also required to establish the rule that generalises rule of thumb TP 3.

If harvesting only targets one species then rules of how to manage a predator-prey metapopulation might be different from rules if harvesting targets both species. Escapement comparison rules with incorrect policies only work if the population size differences between the unexploited subpopulations are negligible, which is unlikely. However, escapement comparison rules between subpopulations hold in some reasonable circumstances. The rules include a conclusion that if harvesting only targets the prey (predator) species and if the only difference between populations is prey (predator) migration parameters, then optimal escapements for one period to go suggest that we should harvest the relative source prey (predator) subpopulation more conservatively than the other prey (predator) subpopulation regardless of the value of predator efficiency. Similarly, if the migrations between subpopulations are symmetric, and there is no biological differences between the subpopulations except for the prey vulnerability to predation (the predator efficiency) then we should harvest a relatively less vulnerable prey (a more efficient predator) subpopulation more conservatively than the other prey (predator) subpopulation regardless of the value of predator efficiency.

To establish the rules discussed in this chapter I assumed that the cost of harvesting is negligible or independent of the stock abundance and that the market values of both species are the same. In one section in the next chapter I will show how the inclusion of the cost of harvesting and market value differences may affect the results presented in this chapter.

4.6 Appendices

Appendix 4A: Derivation of net revenue function Π

This appendix derives the net revenue function in equation (4.14). Note that the cost function for two-patch predator-prey exploitation can be derived analogously to the cost function for single-species exploitation (Clark, 1990). Suppose that the instantaneous exploitation cost $C_{Xi}(X_i, H_{X_i})$ is linear in H_{X_i}, then

$$C_{Xi}(X_i, H_{X_i}) = C_{Xi}(X_i)H_{X_i}. \tag{4.85}$$

The total cost of the exploitation to harvest $H_{X_{ik}}$ taken from the available stock X_{ik} is $C_T(X_{ik}, H_{X_{ik}})$, which can be formulated as

$$C_{Xi}(X_{ik}) + C_{Xi}(X_{ik} - 1) + \cdots + C_{Xi}(X_{ik} - H_{X_{ik}} + 1). \tag{4.86}$$

Hence

$$C_T(X_{ik}, H_{X_{ik}}) \approx \int_{X_{ik}-H_{Xik}}^{X_{ik}} C_{Xi}(\xi)d\xi. \tag{4.87}$$

The net revenue is then given by

$$\begin{aligned}\Pi_{Xi}(X_{ik}, H_{X_{ik}}) &= p_{Xi}H_{X_{ik}} - C_T(X_{ik}, H_{X_{ik}}) \\ &= \int_{X_{ik}-H_{Xik}}^{X_{ik}} (p_X - c_{Xi}(\xi))d\xi \\ &= \int_{S_{Xik}}^{X_{ik}} (p_X - c_{Xi}(\xi))d\xi. \qquad (4.88)\end{aligned}$$

Appendix 4B: Independence of optimal escapements on time horizon

To prove the claim of time horizon independence, first consider the time horizon $T = 2$. Let us rewrite the net revenue with time horizon $T = 1$, $J_1(N_{10}, N_{20}, P_{10}, P_{20})$, in equation (4.20) above using equation (4.22) for $k = 1$ into the first term of equation (4.20) and using equation (4.22) for $k = 0$ together with equation (4.14) into the second term to obtain an expression for the net revenue with time horizon one

$$\begin{aligned}J_1(N_{10}, N_{20}, P_{10}, P_{20}) = \max_{0\leq S_{Xi0}\leq X_{i0}} (\rho V(N_{11}, N_{21}, P_{11}, P_{21}) \\ + V(N_{10}, N_{20}, P_{10}, P_{20}) - V(S_{N_{10}}, S_{N_{20}}, S_{P_{10}}, S_{P_{20}})). \qquad (4.89)\end{aligned}$$

If the optimal escapements S^*_{Xi0} can be obtained from equations (4.26) - (4.29) then the above equation becomes

$$\begin{aligned}J_1(N_{10}, N_{20}, P_{10}, P_{20}) &= \rho V(N^*_{11}, N^*_{21}, P^*_{11}, P^*_{21}) + V(N_{10}, N_{20}, P_{10}, P_{20}) \\ &\quad - V(S^*_{N_{10}}, S^*_{N_{20}}, S^*_{P_{10}}, S^*_{P_{20}}), \qquad (4.90)\end{aligned}$$

where each stock abundance X^*_{i1} is a function of the escapement S^*_{Xi0} of the previous period. To produce the net revenue for the next time horizon, $T = 2$, use the following procedure. Rewrite $J_2(N_{10}, N_{20}, P_{10}, P_{20})$ in equation (4.16) in the following form

$$\begin{aligned}J_2(N_{10}, N_{20}, P_{10}, P_{20}) &= \max_{0\leq S_{Xi0}\leq X_{i0}} \Bigg(\rho J_1(N_{11}, N_{21}, P_{11}, P_{21}) \\ &\quad + \sum_{i=1}^{2} \sum_{X\in\{N,P\}} \Pi_{Xi}(X_{i0}, S_{X_{i0}}) \Bigg). \qquad (4.91)\end{aligned}$$

This represent present value revenue as a function of prey and predator populations at the last time step. Rewrite $J_1(N_{11}, N_{21}, P_{11}, P_{21})$ in equation (4.16), in a similar way, as follows

$$\begin{aligned}J_1(N_{11}, N_{21}, P_{11}, P_{21}) &= \max_{0\leq S_{Xi0}\leq X_{i0}} \Bigg(\rho J_0(N_{12}, N_{22}, P_{12}, P_{22}) \\ &\quad + \sum_{i=1}^{2} \sum_{X\in\{N,P\}} \Pi_{Xi}(X_{i1}, S_{X_{i1}}) \Bigg) \\ &= \max_{0\leq S_{Xi0}\leq X_{i0}} \Bigg(\rho \sum_{i=1}^{2} \sum_{X\in\{N,P\}} \Pi_{Xi}(X_{i2}, S_{X_{i\infty}}) \\ &\quad + \sum_{i=1}^{2} \sum_{X\in\{N,P\}} \Pi_{Xi}(X_{i1}, S_{X_{i1}}) \Bigg)\end{aligned}$$

$$
\begin{aligned}
&= \max_{0\le S_{Xi0}\le X_{i0}} (\rho V(N_{12}, N_{22}, P_{12}, P_{22}) \\
&\quad + V(N_{11}, N_{21}, P_{11}, P_{21}) - V(S_{N_{11}}, S_{N_{21}}, S_{P_{11}}, S_{P_{21}})) \\
&= \rho V(N_{12}^*, N_{22}^*, P_{12}^*, P_{22}^*) + V(N_{11}, N_{21}, P_{11}, P_{21}) \\
&\quad - V(S_{N_{11}}^*, S_{N_{21}}^*, S_{P_{11}}^*, S_{P_{21}}^*).
\end{aligned} \tag{4.92}
$$

Substitute this result into equation (4.91) to produce

$$
\begin{aligned}
J_2(N_{10}, N_{20}, P_{10}, P_{20}) = \max_{0\le S_{Xi0}\le X_{i0}} &\rho(\rho V(N_{12}^*, N_{22}^*, P_{12}^*, P_{22}^*) \\
&+ V(N_{11}, N_{21}, P_{11}, P_{21}) - V(S_{N_{11}}^*, S_{N_{21}}^*, S_{P_{11}}^*, S_{P_{21}}^*)) \\
&+ V(N_{10}, N_{20}, P_{10}, P_{20}) - V(S_{N_{10}}, S_{N_{20}}, S_{P_{10}}, S_{P_{20}})).
\end{aligned} \tag{4.93}
$$

All terms with stars are constant with respect to S_{Xi0}, hence

$$
\begin{aligned}
J_2(N_{10}, N_{20}, P_{10}, P_{20}) = \max_{0\le S_{Xi0}\le X_{i0}} &\rho V(N_{11}, N_{21}, P_{11}, P_{21}) \\
&+ V(N_{10}, N_{20}, P_{10}, P_{20}) - V(S_{N_{10}}, S_{N_{20}}, S_{P_{10}}, S_{P_{20}}) + \rho C).
\end{aligned} \tag{4.94}
$$

Then equation (4.89) is used to obtain

$$
J_2(N_{10}, N_{20}, P_{10}, P_{20}) = J_1(N_{10}, N_{20}, P_{10}, P_{20}) + \rho C. \tag{4.95}
$$

Note that the maximisation of the discounted net revenue resulting from harvesting two periods from the end is given by the same first period escapements of the maximisation with only one period, that is given by $S_{X_{i0}}^*$ which result from solving equations (4.26) to (4.29). A similar method can be used to show that the expected net revenue three periods from the end is

$$
J_3(N_{10}, N_{20}, P_{10}, P_{20}) = J_2(N_{10}, N_{20}, P_{10}, P_{20}) + \rho^2 C \tag{4.96}
$$

and mathematical induction can be used to show that expected net revenue $T+1$ periods from the end is

$$
J_{T+1}(N_{10}, N_{20}, P_{10}, P_{20}) = J_T(N_{10}, N_{20}, P_{10}, P_{20}) + \rho^T C. \tag{4.97}
$$

To prove this claim let us recall that the optimal escapements for time horizon $t = T$ is given by solving the value function of the sum of the discounted net revenue from harvesting up to period $t = T$. This value function is $J_T(N_{10}, N_{20}, P_{10}, P_{20}) = J_{T-1}(N_{10}, N_{20}, P_{10}, P_{20}) + \rho^{T-1}C$. Using equations (4.16) the value function up to the next time horizon is given by

$$
\begin{aligned}
J_{T+1}(N_{10}, N_{20}, P_{10}, P_{20}) &= \max_{0\le S_{Xi0}\le X_{i0}} \Bigg(\rho J_T(N_{11}, N_{21}, P_{11}, P_{21}) \\
&\quad + \sum_{i=1}^{2} \sum_{X\in\{N,P\}} \Pi_{Xi}(X_{i0}, S_{X_{i0}}) \Bigg) \\
&= \max_{0\le S_{Xi0}\le X_{i0}} \Bigg(\rho[J_{T-1}(N_{11}, N_{21}, P_{11}, P_{21}) + \alpha^{T-1}C] \\
&\quad + \sum_{i=1}^{2} \sum_{X\in\{N,P\}} \Pi_{Xi}(X_{i0}, S_{X_{i0}}) \Bigg) \\
&= J_T(N_{10}, N_{20}, P_{10}, P_{20}) + \rho^T C.
\end{aligned} \tag{4.98}
$$

This proves that the optimal first-period escapements are independent on the choice of time horizon considered.

Appendix 4C: Optimal harvest comparisons between single-species and predator-prey metapopulations

If there is no source/sink and exporter/importer prey subpopulation and predator efficiency is extremely high ($C = 0$) then prey equilibrium harvest from a predator-prey metapopulation, $H^*_{N_i}$, is lower than the one from a single-species metapopulation. To prove this recall that

$$H^*_{N_i} = (aS^*_{N_i} + p_{ii}(rS^*_{N_i}(1 - \frac{S^*_{N_i}}{K}) + \alpha S^*_{N_i}S^*_{P_i}) + p_{ji}(rS^*_{N_j}(1 - \frac{S^*_{N_j}}{K}) + \alpha S^*_{N_j}S^*_{P_j})) - S^*_{N_i}.$$

If $H^*_{N_{is}}$ is prey equilibrium harvest from a single-species metapopulation then

$$\begin{aligned} H^*_{N_i} - H^*_{N_{is}} &= (a-1)(S^*_{N_i} - S^*_{N_{is}}) \\ &\quad + r\left[(p_{ii} - p_{ii})S^*_{N_i}\left(1 - \frac{S^*_{N_i}}{K}\right) + (p_{ji} - p_{ij})S^*_{N_j}\left(1 - \frac{S^*_{N_j}}{K}\right)\right] \\ &\quad + \alpha(p_{ii} + p_{ji})S^*_{N_i}S^*_{P_i} \\ &= \alpha(p_{ii} + p_{ji})S^*_{N_i}S^*_{P_i} < 0, \end{aligned} \tag{4.99}$$

since $S_{X_1} = S_{X_2}$ and $S_{X_i} = S_{X_{is}}$. Similarly, if $H^*_{P_i}$ and $H^*_{P_{is}}$ denote predator equilibrium harvest from predator-prey and single-species metapopulations,respectively, then

$$H^*_{P_i} - H^*_{P_{is}} = \beta(q_{ii} + q_{ji})S^*_{N_i}S^*_{P_i} > 0. \tag{4.100}$$

Appendix 4D: Optimal harvest comparisons between subpopulations

If prey subpopulation two is a relative exporter subpopulation with prey migration rate p_{21} is the same as the retention rate of prey subpopulation one p_{11}, there is no source/sink subpopulation, the predator populations are indistinguisable, and prey recruitment is greater than the number of prey eaten by the predator, that is, $rS^*_{N_i}(1 - S^*_{N_1}/K) > |\alpha|S^*_{N_i}S^*_{P_i}$, then the equilibium harvest for prey subpopulation one is greater than the equilibrium harvest for prey subpopulation two. This can be proved as follows.

$$\begin{aligned} H^*_{N_1} - H^*_{N_2} &= (a-1)(S^*_{N_1} - S^*_{N_2}) \\ &\quad + r((p_{11} - p_{12})S^*_{N_1}(1 - \frac{S^*_{N_1}}{K}) + (p_{21} - p_{22})S^*_{N_2}(1 - \frac{S^*_{N_2}}{K})) \\ &\quad + \alpha((p_{11} - p_{12})S^*_{N_1}S^*_{P_1} + (p_{21} - p_{22})S^*_{N_2}S^*_{P_2}). \\ &= 2(p_{11} - p_{12})(rS^*_{N_1}(1 - \frac{S^*_{N_1}}{K}) + \alpha S^*_{N_1}S^*_{P_1}) > 0. \end{aligned} \tag{4.101}$$

Similarly, it can be shown that $H^*_{P_1} - H^*_{P_2} = 2(q_{11} - q_{12})(sS^*_{P_1}(1 - \frac{S^*_{P_1}}{L}) + \beta S^*_{N_1}S^*_{P_1}) = 0$.

Chapter 5

Predator-prey metapopulations with juvenile migration and adult interaction

The model in the previous chapter assumes that the predator eats the juvenile phase of the prey. In this chapter I assume that the predator-prey interaction occurs in the adult stage of the prey and predator populations. More simply put, adults feed on adults. In nature, predation on adult life stages is not uncommon. Many marine species do not eat a particular prey species until they reach a certain age (Overholtz *et al.*, 1991).

Zaret (1980) divided predators in aquatic communities into two types: "gape-limited predators" and "size-dependent predators". The first type of predator eats prey by swallowing it whole. Hence the prey needs to be smaller than the predator's gape. There is no chance that a predator will eat prey larger than its gape. The second type of predator eats prey by piercing, crushing or sucking it, and hence can eat prey which is bigger than the predator's mouth diameter. Examples include sea lamprey, *Petromyzon marinus*, that prey on many species of fish, like lake trout, salmon, rainbow trout, whitefish, burbot, walleye and catfish, and octopus that prey on many species of crustaceans and gastrophods (Cortez *et al.*, 1998). However, some predators have preferential feeding habits. For example, several species of *Coregonus* and many planktivorous fish only eat the largest prey individuals (deBernardi and Giussani, 1975; Vanni, 1987; deBarros *et al.*, 1998). The maximum body size of the prey that is captured by the gape-limited predators is limited by the diameter of the predator's mouth, while the maximum body size of the prey that is captured by the size-dependent predators is only limited by the predator ability in capturing and handling the prey (Zaret, 1980). For example, large crabs can prey on large abalone, up to 200 mm (Shepherd and Breen, 1992) and large octopi eat large mussels by drilling through the shells (McQuaid, 1994). This evidence shows that predation on prey adult life stages is common in marine systems.

The model to describe this adult interaction predator-prey metapopulation has a similar structure and assumptions to the previous model, except for the details of the predator-prey interaction. Generally food suplies may affect predator reproduction and adult survival of the predator (Mangel and Switzer, 1998). For this reason, I investigate optimal escapements for two different models. The first model assumes that predation affects predator survival and the second model assumes that predation affects predator recruitment. I investigate both cases and compare how their optimal escapements differ and examine the robustness of the results in the previous chapter.

As in the previous chapter I use dynamic programming and the method of Lagrange multipliers to find the optimal harvesting strategies for the populations in both models. The results in this chapter show that the most significant rule, that we should harvest a relative source subpopulation more conservatively than a relative sink subpopulation, is robust regardless of the structure of the predator-prey interaction.

Unlike the previous chapter, in this chapter I present the optimal escapement for any period to go, when harvesting only targets one of the species. In the previous chapter, escapement analysis for one period to go shows that the most significant rule, that we should harvest a relative source subpopulation more conservatively than a relative sink subpopulation, is true for a limited situation when harvesting only targets one species. In this chapter, numerical examples show that this rule holds for any period to go. I also explore the situation where the optimal harvest for one of the populations is negative. While at first glance this appears unlikely, a negative harvest could be implemented in some cases by seeding stock.

5.1 The first model: Predator survival model

Assume that there are predator and prey populations in each of two different patches, namely patch one and patch two. Let the movement of individuals between the local populations be caused by the dispersal of juveniles. Adults are assumed to be sedentary, and they do not migrate from one patch to another. If the population size of the prey and predator on patch i at the beginning of period k are denoted by N_{ik} and P_{ik} respectively, then the dynamics of the prey and predator populations are

$$N_{i(k+1)} = a_i N_{ik} + \alpha_i N_{ik} P_{ik} + p_{ii} F_i(N_{ik}) + p_{ji} F_j(N_{jk}), \tag{5.1}$$

$$P_{i(k+1)} = b_i P_{ik} + \beta_i N_{ik} P_{ik} + q_{ii} G_i(P_{ik}) + q_{ji} G_j(P_{jk}), \tag{5.2}$$

where a_i and b_i denote the survival rate of adult prey and adult predator in patch i. Let the proportion of prey and predator juveniles from patch i that successfully migrate to patch j be p_{ij} and q_{ij} respectively, as illustrated by Figure 4.1. The functions $F_i(N_{ik})$ and $G_i(P_{ik})$ are the recruit production functions of the prey and the predator on patch i in time period k. Different from the model in Chapter 4, I assume that the recruit production functions are logistic and given by equations (3.3) and (3.4). To ensure that the system is a Lotka-Volterra predator-prey interaction, I assume $\alpha_i < 0$ and $\beta_i > 0$.

As in the previous chapter I introduce exploitation into the system and assume that the only possible exploitation is through a selective harvesting policy. If the amount of harvest taken from the prey and predator stocks in patch i at the beginning of period k are $H_{N_{ik}}$ and $H_{P_{ik}}$ respectively, let $S_{N_{ik}} = N_{ik} - H_{N_{ik}}$ and $S_{P_{ik}} = P_{ik} - H_{P_{ik}}$ be prey and predator escapements on patch i at the end of that period. Hence, if the escapements are substituted into equations (5.1) and (5.2), then the model for an exploited two-patch predator-prey metapopulation with adult interaction is

$$N_{i(k+1)} = a_i S_{N_{ik}} + \alpha_i S_{N_{ik}} S_{P_{ik}} + p_{ii} F_i(S_{N_{ik}}) + p_{ji} F_j(S_{N_{jk}}), \tag{5.3}$$

$$P_{i(k+1)} = b_i S_{P_{ik}} + \beta_i S_{N_{ik}} S_{P_{ik}} + q_{ii} G_i(S_{P_{ik}}) + q_{ji} G_j(S_{P_{jk}}). \tag{5.4}$$

Using present value maximisation, the objective of the resource owner is to maximise the net present value, PV, from harvesting each subpopulation of the prey and the predator up to time horizon $t = T$. If Π_{Xi} represents the present value of net revenue resulting from harvesting population X in patch i, and ρ is a discount factor, then the sole-owner should maximise PV in (4.11) subject to equations (5.3) and (5.4), with non-negative escapement less than or equal to the population size. As in the previous chapter, I assume $\rho = 1/(1+\delta)$, where δ denotes a periodic discounting rate. The net revenue $\Pi_{Xi}(X_{ik}, S_{X_{ik}})$ is given by (4.14), which is the net revenue from the harvest $H_{X_{ik}}$ of the local population X_i in period k. It is assumed that the price of the harvested stock is fixed. The cost of harvesting H_{X_i} from stock X_i is assumed to be a non-increasing function of X_i and may depend on the location of the stock.

To obtain optimal harvesting strategies for the system, I use the same procedure as in Chapter 4, and hence I do not provide the details here. This procedure yields optimal escapements $S^*_{N_{i0}}$ and $S^*_{P_{i0}}$, for the prey and the predator, respectively, which can be shown to be independent of the time horizon considered. The optimal escapements satisfy the implicit equations

$$\begin{aligned}\frac{p_N - c_{Ni}(S^*_{N_{i0}})}{\rho} &= \Big(a_i + \alpha_i S^*_{P_{i0}} + p_{ii}F_i'(S^*_{N_{i0}})\Big)\big(p_N - c_{Ni}(N_{i1})\big) \\ &\quad + \Big(p_{ij}F_i'(S^*_{N_{i0}})\Big)\big(p_N - c_{Nj}(N_{j1})\big) \\ &\quad + \beta_i S^*_{P_{i0}}\left(p_P - c_{Pi}(P_{i1})\right), \qquad (5.5)\end{aligned}$$

$$\begin{aligned}\frac{p_P - c_{Pi}(S^*_{P_{i0}})}{\rho} &= \Big(b_i + \beta_i S^*_{N_{i0}} + q_{ii}G_i'(S^*_{P_{i0}})\Big)\big(p_P - c_{Pi}(P_{i1})\big) \\ &\quad + \Big(q_{ij}G_i'(S^*_{P_{i0}})\Big)\big(p_P - c_{Pj}(P_{j1})\big) \\ &\quad + \alpha_i S^*_{N_{i0}}\left(p_N - c_{Ni}(N_{i1})\right). \qquad (5.6)\end{aligned}$$

These equations are the general form of the optimal harvesting equation for a two-patch predator-prey metapopulation with adult interaction. It can be seen that if we set $\alpha_i = \beta_i = 0$, then Tuck and Possingham's (1994) optimal harvesting equation for a single-species metapopulation is obtained. Furthermore if there is no migration between patches, $p_{ij} = q_{ij} = 0$ for $i \neq j$, and $F'(S) = a_i + p_{ii}F_i'(S_{N_{i0}})$ together with $\alpha_i = \beta_i = 0$, then the equation reduces to the optimal harvesting equation for a single population (Clark, 1976a). The escapements $S^*_{X_{i0}}$ found by solving these equations are the optimum escapements of the prey and the predator that maximise revenue provided the Hessian matrix $J_1''(S_{N_{10}}, S_{N_{20}}, S_{P_{10}}, S_{P_{20}})$ satisfies $[J_1''(S^*_X)(S_X - S^*_X)]\cdot[S_X - S^*_X] < 0$, where $S_X = (S_{N_{10}}, S_{N_{20}}, S_{P_{10}}, S_{P_{20}})$ and $S^*_X = (S^*_{N_{10}}, S^*_{N_{20}}, S^*_{P_{10}}, S^*_{P_{20}})$.

5.1.1 Optimal escapements

In this section, the optimal escapements in equations (5.5) and (5.6) are compared to the strategies in which spatial structure is not recognised. The comparison is carried out to see how important it is to use the theory presented here for choosing optimal escapements. As before, I consider two ways in which spatial structure can be ignored. First, the whole system can be considered a well-mixed homogeneous population. Second, the existence of the patches is recognised, but we assume that there is no migration of individuals between patches. The optimal escapements from a connected two-patch predator-prey model are compared to those systems in which spatial structure is ignored.

To facilitate comparisons, I use the concept of source/sink and exporter/importer subpopulation and more/less efficient predator subpopulation and more/less vulnerable prey subpopulation defined in Chapter 4. Optimal harvesting equations for an unconnected and well-mixed predator-prey population can be obtained from equations (5.5) and (5.6) by assigning $p_{ij} = q_{ij} = 0$ for $i \neq j$, and $p_{ii} = q_{ii} = 1, i = 1, 2$. However, if we incorrectly consider there is no connection between subpopulations, the growth rate for prey subpopulation i would be measured as $r_{iu} = r_i p_{ii} + r_j p_{ji}$ if it was incorrectly believed to be an unconnected predator-prey system, and $r_{iw} = [r_i(p_{ii} + p_{ij}) + r_j(p_{jj} + p_{ji})]/2$ if it was incorrectly believed to be a well-mixed predator-prey system, as in the previous chapter. The growth rate for the predator is measured similarly.

5.1.2 Results with negligible costs

To simplify the analysis, I assume the costs of harvesting are negligible and there is no difference between the prices of the prey and predator. Using these assumptions, and substituting all derivatives of the logistic recruitment functions, F_i and G_i, in equations (3.3) and (3.4), equations (5.5) and (5.6) become

$$\frac{1}{\rho} = a_i + (p_{i1} + p_{i2})\left(r_i - \frac{2r_i}{K_i} S_{N_i}\right) + (\alpha_i + \beta_i) S_{P_i}, \tag{5.7}$$

$$\frac{1}{\rho} = b_i + (q_{i1} + q_{i2})\left(s_i - \frac{2s_i}{L_i} S_{P_i}\right) + (\alpha_i + \beta_i) S_{N_i}. \tag{5.8}$$

Let $A_i = \frac{1}{\rho} - (p_{i1} + p_{i2}) r_i - a_i$, $B_i = \frac{1}{\rho} - (q_{i1} + q_{i2}) s_i - b_i$, and $C_i = \alpha_i + \beta_i$. Solving equations (5.7) and (5.8) produces optimal escapements for prey and predator populations $S^*_{N_i}$ and $S^*_{P_i}$,

$$S^*_{N_i} = \frac{A_i (q_{i1} + q_{i2}) \frac{2s_i}{L_i} + C_i B_i}{\Delta_i}, \tag{5.9}$$

$$S^*_{P_i} = \frac{B_i (p_{i1} + p_{i2}) \frac{2r_i}{K_i} + C_i A_i}{\Delta_i}, \tag{5.10}$$

provided $\Delta_i = C_i^2 - (p_{i1} + p_{i2}) \frac{2r_i}{K_i} (q_{i1} + q_{i2}) \frac{2s_i}{L_i} \neq 0$.

As expected, equations (5.9) and (5.10) are similar to equations (4.41) and (4.42) in Chapter 4, only now C_i takes the form of a pre-dispersal predator efficiency being a combination of the conversion efficiency β and the predator attack rate α. In the previous chapter the predator efficiency takes the form of a post-dispersal predator efficiency in which the value is affected by the migration parameters p_{ij} and q_{ij}. Equations (5.9) and (5.10) are generalisations of the optimal escapements for a single-species derived by Clark (1976a) and a single-species metapopulation derived by Tuck and Possingham (1994). By assigning $\alpha_i = \beta_i = 0$, the optimal harvesting strategy for the single-species metapopulation is established. Furthermore, if in addition we remove dispersal ($p_{ij} = p_{ji} = q_{ij} = q_{ji} = 0$, and $p_{ii} = p_{jj} = q_{ii} = q_{jj} = 1$) then Clark's (1976a) optimal escapements for the single-species model, with adult survival rates a_i and b_i, are obtained. In the case of $\alpha_i = \beta_i = 0$, the escapements reduce to escapements for a single-species metapopulation, which satisfy the rules of thumb TP 1 to TP 3 described in Chapter 2. In the presence of predator-prey interactions, I establish the following results as generalisations of the rules of thumb harvesting strategies for a single-species metapopulation.

Result 7 *(Sufficient conditions for positive escapements) Let* $S^*_{N_i}$ *and* $S^*_{P_i}$ *denote the optimal escapement from predator-prey metapopulation given by equations (5.9) and (5.10). If* A_i *and* B_i *are negative, and* C_i *is non-positive with* $C_i > max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}$, *then:*

1. Δ_i *is negative,*
2. $S^*_{N_i}$ *and* $S^*_{P_i}$ *are positive.*

Proof

1. Note that since $-(p_{i1}+p_{i2})r/A = [(p_{i1}+p_{i2})r]/[(p_{i1}+p_{i2})r + (a-(1+\delta))] \geq 1$, the condition $C > 2B/K$ implies $C > (-(p_{i1}+p_{i2})r/A)(2B/K)$. Hence $C_i > max\{-2B_i(p_{i1}+p_{i2})r_i/[A_iK_i], -2A_i(q_{i1}+q_{i2})s_i/[B_iL_i]\}$. We have $B_i(p_{i1}+p_{i2})\frac{2r_i}{K_i} < -C_iA_i$ or alternatively $B_i < \frac{-C_iA_i}{(p_{i1}+p_{i2})\frac{2r_i}{K_i}}$. Since $-C > 0$ then $-C_iB_i < -C_i\left(\frac{-C_iA_i}{(p_{i1}+p_{i2})\frac{2r_i}{K_i}}\right)$. Since we have $A_i(q_{i1}+q_{i2})\frac{2s_i}{L_i} < -C_iB_i$ then $A_i(q_{i1}+q_{i2})\frac{2s_i}{L_i} < -C_i\left(\frac{-C_iA_i}{(p_{i1}+p_{i2})\frac{2r_i}{K_i}}\right)$. Finally, since A_i negative, then we have $(q_{i1}+q_{i2})\frac{2s_i}{L_i}(p_{i1}+p_{i2})\frac{2r_i}{K_i} > C_i^2$ which means $\Delta_i < 0$. □
2. It is clear from equations (5.9) and (5.10). □

An analogous result can be obtained if A_i and B_i are positive and C_i is non-negative. However, $C_i > 0$ is biologically unacceptable since it means that the predator efficiency is more than 100%. As in the previous chapter, an interpretation of the condition $A_i < 0$ is that the natural growth rate of the prey, that is, the sum of the proportion of surviving adults and the per capita larval production, is higher than the reciprocal of the discounting factor $1/\rho$. The condition $B_i < 0$ for the predator is interpreted similarly, while C_i is non-positive with $C_i > max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}$ is interpreted as a high predator efficiency. Both conditions, $A_i < 0$ and $B_i < 0$, are fairly likely for typically fast growing fish populations. I use Result 7 to explore the relationship between escapements from a predator-prey metapopulation presented in this chapter and escapements from a single-species metapopulation discussed in the paper of Tuck and Possingham (1994). The relationship is summarised in the following Corollary.

Corollary 2 *(Escapement comparison to a single-species metapopulation) Let* $S^*_{N_i}$ *and* $S^*_{P_i}$ *denote the optimal escapement from a predator-prey metapopulation given by equations (5.9) and (5.10), and let* $S^*_{N_{is}}$ *and* $S^*_{P_{is}}$ *denote the optimal escapement from a single-species metapopulation given by the same equations by assigning* $\alpha_i = \beta_i = 0$. *If* A_i *and* B_i *are negative, and* C_i *is non-positive with* $C_i > max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}$, *then:*

1. $S^*_{N_i} - S^*_{N_{is}} = \frac{C_i}{(p_{i1}+p_{i2})2r_i/K_i} S^*_{P_i} < 0$,
2. $S^*_{P_i} - S^*_{P_{is}} = \frac{C_i}{(q_{i1}+q_{i2})2s_i/L_i} S^*_{N_i} < 0$.

Proof

1. The sign of $S^*_{N_i} - S^*_{N_{is}}$ needs to be determined.

$$\begin{aligned}
S^*_{N_i} - S^*_{N_{is}} &= \frac{A_i(q_{i1}+q_{i2})\frac{2s_i}{L_i} + C_iB_i}{\Delta_i} - \frac{A_i}{-(p_{i1}+p_{i2})\frac{2r_i}{K_i}} \\
&= \frac{C_iB_i(p_{i1}+p_{i2})\frac{2r_i}{K_i} + C_i^2A_i}{\Delta_i(p_{i1}+p_{i2})\frac{2r_i}{K_i}} \\
&= \frac{B_i(p_{i1}+p_{i2})\frac{2r_i}{K_i} + C_iA_i}{\left(\Delta_i(p_{i1}+p_{i2})\frac{2r_i}{K_i}\right)/C_i}
\end{aligned}$$

Because the denominator is positive and $B_i(p_{i1}+p_{i2})\frac{2r_i}{K_i} < -C_iA_i$, then $S^*_{N_i} - S^*_{N_{is}} < 0$. The proof of the second part is analogous to this proof. □

Corollary 2 suggests that the optimal escapement from a predator-prey metapopulation is always greater than, or equal to, the optimal escapement from a single-species metapopulation depending on the efficiency of the predator, C_i. However, we can not draw any conclusion on whether we should harvest the relative source subpopulation more conservatively than the relative sink subpopulation, except for one case when the predator is perfectly efficient, $C_i = 0$. In this case, the optimal escapement from a predator-prey metapopulation is equal to the optimal escapement if the population were managed as a single-species metapopulation. Hence, all rules of thumb described by Tuck and Possingham (1994), i.e. TP 1, TP 2 and TP 3 in Chapter 2, are satisfied.

In many cases, the predator efficiency C_i falls somewhere between α_i and zero. In this case, Corollary 2 does not give us a clear insight on how the predator-prey metapopulation optimal escapements differ from spatially-unstructured predator-prey optimal escapements. The following Lemma enables us to explore these differences.

Lemma 3 *(Migrations trade-off equations) Let* $S^*_{N_i}$ *and* $S^*_{P_i}$ *denote the optimal escapement from a predator-prey metapopulation given by equations (5.9) and (5.10). If* $a_i = a$, $b_i = b$, $K_i = K$, $L_i = L$, $C_i = C$, $R = \frac{1}{\rho} - a$, $S = \frac{1}{\rho} - b$, $r_{im} = (p_{ii} + p_{ij})r_i$ *and* $s_{im} = (q_{ii} + q_{ij})s_i$, *for* $i = 1, 2$, *then:*

1. $$\begin{aligned}(S^*_{N_1} - S^*_{N_2})\Delta_1\Delta_2 &= \left(C^2(s_{1m} - s_{2m}) - \frac{4s_{1m}s_{2m}}{KL}(r_{2m} - r_{1m})\right)\left(\frac{2R}{L} - C\right) \\ &\quad - \frac{2C}{L}\left(C - \frac{2S}{K}\right)(r_{1m}s_{1m} - r_{2m}s_{2m}),\end{aligned}$$

2. $$\begin{aligned}(S^*_{P_1} - S^*_{P_2})\Delta_1\Delta_2 &= \left(C^2(r_{1m} - r_{2m}) - \frac{4r_{1m}r_{2m}}{KL}(s_{2m} - s_{1m})\right)\left(\frac{2S}{K} - C\right) \\ &\quad - \frac{2C}{K}\left(C - \frac{2R}{L}\right)(r_{1m}s_{1m} - r_{2m}s_{2m}).\end{aligned}$$

Proof

1.

$$S^*_{N_1} - S^*_{N_2} = \frac{(R - r_{1m})\frac{2s_{1m}}{L} + C(S - s_{1m})}{\Delta_1} - \frac{(R - r_{2m})\frac{2s_{2m}}{L} + C(S - s_{2m})}{\Delta_2}$$

$$= \frac{\left((R - r_{1m})\frac{2s_{1m}}{L} + C(S - s_{1m})\right)(C^2 - r_{2m}s_{2m}\frac{4}{KL})}{\Delta_1\Delta_2} - \frac{\left((R - r_{2m})\frac{2s_{2m}}{L} + C(S - s_{2m})\right)(C^2 - r_{1m}s_{1m}\frac{4}{KL})}{\Delta_1\Delta_2}$$

where $\Delta_i = C^2 - r_{im}s_{im}\frac{4}{KL}$, $i = 1, 2$. Completing and simplifying the numerator of the right hand side of the above equation will end up to the form of the right hand side of equation 1 in this lemma. The second part can be proved analogously. □

In general it is difficult to compare the optimal escapements between patches. Lemma 3 suggests that there is a trade-off between prey and predator juvenile migrations to determine which patch has a higher escapement. In some special cases, we can determine it easily. For example, if $r_{1m} = s_{2m}$ and $r_{2m} = s_{1m}$, that is, if prey subpopulation i has the same per capita larval production with predator subpopulation j, then $(S^*_{N_1} - S^*_{N_2})\Delta_1\Delta_2 = \Delta_1(r_{2m} - r_{1m})(\frac{2R}{L} - C)$. If A_i and B_i are negative and $max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\} < C_i \leq 0$ then Δ_1 is negative and $\frac{2R}{L} - C$ is positive. Hence, the sign of the difference depends critically on the sign of $r_{2m} - r_{1m}$. In this case, if $r_{2m} = r_{1m}$, clearly we should harvest the prey equally in both patches. While if $r_{2m} > r_{1m}$, that is if prey subpopulation two is a relative source subpopulation and predator subpopulation two is a relative sink subpopulation, then we should harvest prey subpopulation two more conservatively than prey subpopulation one. Similarly, it can be concluded that the predator living in the same patch with a relative source prey subpopulation should be harvested less conservatively than the predator living in the other patch. If we ignore the predator-prey interaction, then the same rule is obtained from the single-species metapopulation's rule of thumb (TP 1).

However, the rules above are derived by assuming $r_{im} = s_{jm}$, which is unlikely. The following result describes a similar rule to the results above for a more general case. It will also show that, unlike the single-species metapopulation case, in a spatially-structured predator-prey population subpopulations with symmetric migration may have different escapements. To gain a better insight into the effect of juvenile migration on the decision of how the exploitation of a spatially-structured predator-prey system should be done, most parts of the following discussion will assume that there is no difference in juvenile migration for the predator, that is, $s_{1m} = s_{2m} = s_m$. In other words, the predator has symmetric migration. To enable comparisons to escapements if we ignore spatial-structure, I define r_{iu} as the growth of prey subpopulation i if it is considered an unconnected population, and has a value as given in equation (4.44). Furthermore I define r_w as the growth of the prey population if it is considered a well-mixed population, which has a value given by equation (4.45).

Result 8 *(Escapement comparison between subpopulations) Let one of the prey subpopulations be a relative source while all other parameters of the prey and the predator are identical for both subpopulations, without loss of generality let us assume that prey subpopulation one is a relative source, that is,* $(p_{11} + p_{12})r_1 > (p_{22} + p_{21})r_2$. *If* $|\alpha| = \beta$, *or if* A_i *and* B_i *are negative, and* C_i *is non-positive with* $C_i > max\{\frac{2B}{K}, \frac{2A}{L}\}$, *then:*

1. $S^*_{N_1} > S^*_{N_2}$,
2. $S^*_{P_1} \leq S^*_{P_2}$.

Proof

1. Let $\Delta_{S_N} = (S^*_{N_1} - S^*_{N_2})\Delta_1\Delta_2$, then using Lemma 3 Δ_{S_N} can be written as

$$
\begin{aligned}
\Delta_{S_N} &= \left(-\frac{4s_m^2}{KL}(r_{2m} - r_{1m})\right)\left(\frac{2R}{L} - C\right) - \frac{2C}{L}\left(C - \frac{2S}{K}\right)s_m(r_{1m} - r_{2m}) \\
&= s_m\left[-\left(\frac{4s_m}{KL}\right)\left(\frac{2R}{L} - C\right) + \frac{2C}{L}\left(C - \frac{2S}{K}\right)\right](r_{2m} - r_{1m}) \\
&= s_m\left[\frac{2}{L}\left(C^2 - \frac{4s_mR}{KL} - C\left(\frac{2S}{K} - \frac{2s_m}{K}\right)\right)\right](r_{2m} - r_{1m}) \\
&= s_m\left[\frac{2}{L}\left(C^2 - \frac{4s_mR}{KL} - \frac{2C}{K}(S - s_m)\right)\right](r_{2m} - r_{1m}) \\
&= s_m\left[\frac{2}{L}\left(C\left(C - \frac{2B}{K}\right) - \frac{4s_mR}{KL}\right)\right](r_{2m} - r_{1m}).
\end{aligned}
$$

Since $\frac{2B}{K} \leq C \leq 0$ then $\Delta_{S_N} > 0$. □

2. Let $\Delta_{S_P} = (S^*_{P_1} - S^*_{P_2})\Delta_1\Delta_2$, then using Lemma 3 Δ_{S_P} can be written as

$$
\begin{aligned}
\Delta_{S_P} &= C^2(r_{1m} - r_{2m})\left(\frac{2S}{K} - C\right) - \frac{2C}{K}\left(C - \frac{2R}{L}\right)s_m(r_{1m} - r_{2m}) \\
&= C(r_{1m} - r_{2m})\left[\left(\frac{2S}{K} - C\right)C - \frac{2}{K}\left(C - \frac{2R}{L}\right)s_m\right] \\
&= C(r_{1m} - r_{2m})\left[\left(\frac{2B}{K} - C\right)C + \frac{4Rs_m}{KL}\right].
\end{aligned}
$$

Clearly $\Delta_{S_P} \leq 0$, since $\frac{2B}{K} \leq C \leq 0$. □

Result 8 shows that there is a region of parameter space where we protect a relative source prey subpopulation more than a relative sink prey subpopulation in the sense that we leave the relative source prey subpopulation with a higher escapement than the sink subpopulation. Similarly, by investigating the effect of prey migration (relative source/sink prey subpopulation) to the predator's optimal escapements, it can be concluded that we protect the relative source prey subpopulation in two different ways: directly, with a higher escapement of the relative source prey subpopulation, and indirectly, with a lower escapement of the predator living in the same patch with the relative source prey subpopulation. The importance of the relative source prey subpopulation is intuitively reasonable.

Similarly, let us assume that one predator subpopulation is a relative source while all other parameters of the prey and the predator are identical for both subpopulations, and $|\alpha| = \beta$, or $C > \frac{2B}{K}$. Using predator-prey metapopulation optimal escapements as a policy to manage the exploitation of a predator-prey metapopulation system we would harvest the relative source predator subpopulation more conservatively than the other predator subpopulation which is a relative sink subpopulation. On the other hand, we would harvest both prey equally, or would harvest the prey living in the same patch with the relative source predator more than the other prey subpopulation.

The analogous result for the predator is easier to interpret whenever $q_{ii}s_i = q_{jj}s_j$. In this case, one of the predators is a relative exporter subpopulation. Let predator subpopulation one be a relative exporter, then we harvest this subpopulation conservatively while we also harvest the prey subpopulation in the other patch conservatively. The rationale is as follows. Since the predator in patch one is a relative exporter, then the outflow of its juveniles to the other patch is greater than the inflow, consequently, we should leave the prey higher in the targeting patch of the exporter predator subpopulation.

The previous results allow us to compare our predator-prey optimal escapements between different patches. Up to this point, I have concluded that if predator efficiency is relatively high, then the rule of thumb TP 1 from single-species metapopulation harvesting theory is preserved. To see how important and how different the predator-prey metapopulation escapement is, compared to the escapements if we incorrectly consider the population as a spatially-unstructured system, I construct the following results. The results are the generalisations of the rules of thumb TP 2 and TP 3 for a single-species metapopulation.

Result 9 *(Comparison of strategy with an unconnected two-patch predator-prey system) Let* $S^*_{N_i}$ *and* $S^*_{P_i}$ *denote the optimal escapement from a predator-prey metapopulation given by equations (5.9) and (5.10), and let* $S^*_{N_{iu}}$ *and* $S^*_{P_{iu}}$ *denote the optimal escapement if we incorrectly consider the system as a system consisting of two unconnected predator-prey systems. Let us assume that one of the prey subpopulations is relative exporter and also a relative source while all other parameters of the prey and the predator are identical for both subpopulations. Without lost of generality let* $p_{12}r_1 > p_{21}r_2$ *and* $p_{11}r_1 \geq p_{22}r_2$. *If* $A_1 = A_2 = A$ *and* $B_1 = B_2 = B$ *are negative and* $C_1 = C_2 = C$ *with* $C > max\{\frac{2B}{K}, \frac{2A}{L}\}$ *then:*

1. $S^*_{N_1} > S^*_{N_{1u}}$,
2. $S^*_{N_2} < S^*_{N_{2u}}$,
3. $S^*_{P_1} < S^*_{P_{1u}}$,
4. $S^*_{P_2} > S^*_{P_{2u}}$,
5. $S^*_{N_1} + S^*_{N_2} \leq S^*_{N_{1u}} + S^*_{N_{2u}}$,
6. $S^*_{P_1} + S^*_{P_2} \geq S^*_{P_{1u}} + S^*_{P_{2u}}$.

Proof

1. All parameters are equal except $p_{12}r_1 > p_{21}r_2$. Recall that

$$S^*_{N_1} = \frac{(R - r_{1m})\frac{2s_{1m}}{L} + CB}{C^2 - \frac{4r_{1m}s_{1m}}{KL}},$$

and

$$S^*_{N_{1u}} = \frac{(R - r_{1u})\frac{2s_{1m}}{L} + CB}{C^2 - \frac{4r_{1u}s_{1m}}{KL}}.$$

Hence, equation 1 in Lemma 3 can be written as

$$(S^*_{N_1} - S^*_{N_{1u}})\Delta_{1u}\Delta_1 = (r_{1u} - r_{1m})\left(C(C - \frac{2B}{K}) - \frac{4Rs_{1m}}{KL}\right)\frac{2s_{1m}}{L},$$

where $\Delta_{1u} = C^2 - \frac{4r_{1u}s_{1m}}{KL}$, and $\Delta_1 = C^2 - \frac{4r_{1m}s_{1m}}{KL} < 0$. Since $p_{11}r_1 \geq p_{22}r_2$ and $\Delta_i < 0, i = 1, 2$, then $\Delta_{1u} < 0$. Furthermore since $r_{1m} > r_{1u}$ and $0 > C > \frac{2B}{K}$, then $S^*_{N_1} - S^*_{N_{1u}} > 0$. This completes the proof. □

2. The proof of this part is analogous to the proof above. □

3. Using a similar procedure we obtain

   $$(S^*_{P_1} - S^*_{P_{1u}})\Delta_{1u}\Delta_1 = (r_{1u} - r_{1m})Y,$$

   where $Y = \left(C(C - \frac{2B}{K}) - \frac{4Rs_{im}}{KL}\right) C > 0$. Hence $S^*_{P_1} - S^*_{P_{1u}} < 0$. □

4. This part can be proved analogously. □

5. Recall that from 1, we have

   $$(S^*_{N_1} - S^*_{N_{1u}}) = \frac{(r_{1u} - r_{1m})X}{\Delta_{1u}\Delta_1},$$

   and similarly

   $$(S^*_{N_2} - S^*_{N_{2u}}) = \frac{(r_{2u} - r_{2m})X}{\Delta_{2u}\Delta_2},$$

   where

   $$X = \left(C(C - 2B/K) - \frac{4Rs_{im}}{KL}\right)\frac{2s_{im}}{L} < 0$$

   with $s_{1m} = s_{2m}$. If

   $$\Delta S_{N_u} = (S^*_{N_1} + S^*_{N_2}) - (S^*_{N_{1u}} + S^*_{N_{2u}}),$$

   then

   $$\begin{aligned} & \Delta S_{N_u}\Delta_1\Delta_{1u}\Delta_2\Delta_{2u}/X \\ = & \ (r_{1u} - r_{1m})\left[C^4 - (r_{2m} + r_{2u})4s_{im}C^2/(KL) + r_{2m}r_{2u}16s^2_{im}/(K^2L^2)\right] \\ & +(r_{2u} - r_{2m})\left[C^4 - (r_{1m} + r_{1u})4s_{im}C^2/(KL) + r_{1m}r_{1u}16s^2_{im}/(K^2L^2)\right]. \\ = & \ (r_{1u} - r_{1m} + r_{2u} - r_{2m})C^4 - 2(r_{1u}r_{2u} - r_{1m}r_{2m})4s_{im}C^2/(KL) \\ & +(r_{1u}r_{2u}(r_{1m} + r_{2m}) - r_{1m}r_{2m}(r_{1u} + r_{2u}))16s^2_{im}/(K^2L^2). \end{aligned}$$

   Since $r_{1u} + r_{2u} = r_{1m} + r_{2m}$, then the first term is zero, and the third term is equal to $(r_{1u}r_{2u} - r_{1m}r_{2m})(r_{1m} + r_{2m})16s^2_{im}/(K^2L^2)$. Hence,

   $$\begin{aligned} \Delta S_{N_u} &= \frac{(-8s_{im}C^2/(KL) + (r_{1m} + r_{2m})16s^2_{im}/(K^2L^2))(r_{1u}r_{2u} - r_{1m}r_{2m})}{\Delta_1\Delta_{1u}\Delta_2\Delta_{2u}}X \\ &= \frac{(8s_{im}/(KL)(\frac{2(r_{1m}+r_{2m})s_{im}}{KL} - C^2))(r_{1u}r_{2u} - r_{1m}r_{2m})}{\Delta_1\Delta_{1u}\Delta_2\Delta_{2u}}X. \end{aligned}$$

   Since $\Delta_i < 0$ with $i = 1, 2$, then $C^2 - \frac{2(r_{1m}+r_{2m})s_{im}}{KL} < 0$. We can prove that if $p_{11}r_1 \geq p_{22}r_2$ then $(r_{1u}r_{2u} - r_{1m}r_{2m}) \geq 0$. This completes the proof that $\Delta S_{N_u} \leq 0$. □

6. Using a similar procedure we obtain

   $$\Delta S_{P_u} = \frac{(8s_{im}/(KL)(\frac{2(r_{1m}+r_{2m})s_{im}}{KL} - C^2))(r_{1u}r_{2u} - r_{1m}r_{2m})}{\Delta_1\Delta_{1u}\Delta_2\Delta_{2u}}Y > 0.$$

   hence $(S^*_{P_1} + S^*_{P_2}) > (=)(S^*_{P_{iu}} + S^*_{P_{ju}})$, whenever $p_{11}r_1 > (=)p_{22}r_2$. □

Result 10 *(Comparison of strategy with a well-mixed predator-prey system) Let* $S^*_{N_i}$ *and* $S^*_{P_i}$ *denote the optimal escapements from a predator-prey metapopulation given by equations (5.9) and (5.10), and let* $S^*_{N_w}$ *and* $S^*_{P_w}$ *denote the optimal escapements if the predator-prey metapopulation system is incorrectly considered to be a well-mixed predator-prey system. If all hypothesis and assumptions of the Result 9 are satisfied and in addition if* C *satisfies* $C(BC^2 + \frac{3(R-r_w)s_m}{L}C - \frac{2Br_ws_m}{KL}) = 0$, *then:*

1. $S^*_{N_1} > \frac{1}{2}S^*_{N_w}$,
2. $S^*_{N_2} < \frac{1}{2}S^*_{N_w}$,
3. $S^*_{P_1} < \frac{1}{2}S^*_{P_w}$,
4. $S^*_{P_2} > \frac{1}{2}S^*_{P_w}$,
5. $S^*_{N_1} + S^*_{N_2} < S^*_{N_w}$,
6. $S^*_{P_1} + S^*_{P_2} > S^*_{P_w}$.

Proof

1. Recall that

$$S^*_{N_w} = \frac{(R_w - r_w)\frac{2s_w}{L_w} + C_wB_w}{C_w^2 - \frac{4Q_wr_w}{K_wL_w}} = \frac{(R - r_w)\frac{s_w}{L} + CB}{C^2 - \frac{s_wr_w}{KL}}.$$

Hence

$$\frac{1}{2}S^*_{N_w} = \frac{(R - r_w)\frac{s_m}{L} + CB}{2C^2 - \frac{2s_mr_w}{KL}}.$$

Using Result 8 we obtain

$$S^*_{N_1} = \frac{(R - r_{1m})\frac{2s_m}{L} + CB}{C^2 - \frac{4s_mr_{1m}}{KL}} > \frac{(R - r_w)\frac{2s_m}{L} + CB}{C^2 - \frac{4s_mr_w}{KL}} = S^0$$

since $r_{1m} > r_w$. Furthermore, since C is the root of $\frac{1}{2}S^*_{N_{\bar{w}}} - S^0 = -3(R - r_w)\frac{s_mC^2}{L} - BC^3 + \frac{Br_w2s_mC}{KL} = 0$ then $S^*_{N_1} > \frac{1}{2}S^*_{N_w}$. □

Since the proof for 2, 4 and 5 are similar to 1, and for 6 is similar to 3, then we only need to prove 3.

3. $\Delta S_{N_w} = (S^*_{N_1} + S^*_{N_2}) - S^*_{N_w} = (S^*_{N_1} - S^0) + (S^*_{N_2} - S^0)$. Following the proof in Result 3, we obtain

$$\Delta S_{N_w} = \frac{(8s_m/KL(\frac{2(r_{1m}+r_{2m})s_m}{KL} - C^2))(r_wr_w - r_{1m}r_{2m})}{\Delta_1\Delta_1\Delta_0\Delta_0}X,$$

where $X < 0$ whenever $C \geq \frac{2B}{K}$. Since $\Delta_i < 0, i = 1, 2$, $\Delta_0 = C^2 - \frac{4s_mr_w}{KL} < 0$, and $(r_w^2 - r_{1m}r_{2m}) > 0$, then $\Delta S_{N_w} > 0$. □

Results 8, 9 and 10 are the generalisations of the rules of thumb in Tuck and Possingham (1994) for harvesting a single-species metapopulation. Numerical examples given in the section that follows show that a subpopulation with lower escapement may not give a higher harvest. In addition to the rules summarised in these results, I also establish rules to harvest more or less vulnerable prey and more or less efficient predator subpopulations. These rules are summarised in the following result.

Lemma 4 *(Efficiency trade-off equations) Let* $S^*_{N_i}$ *and* $S^*_{P_i}$ *denote the optimal escapement from predator-prey metapopulation given by equations (5.9) and (5.10). If* $a_1 = a_2 = a$, $b_1 = b_2 = b$, $K_1 = K_2 = K$, $L_1 = L_2 = L$, $p_{11} = p_{22}, p_{12} = p_{21}, q_{11} = q_{22}, q_{12} = q_{21}, r_1 = r_2, s_1 = s_2$, $r_{1m} = (p_{11} + p_{12})r_1 = r_{2m} = r_m$ *and* $s_{1m} = (q_{11} + q_{12})s_1 = s_{2m} = s_m$ *then:*

1. $$(S^*_{N_1} - S^*_{N_2})\Delta_1\Delta_2 = (C_2 - C_1)\left[\frac{2As_m}{L}(C_2 + C_1) + \frac{4r_m s_m B}{KL} + B(C_1C_2)\right],$$

2. $$(S^*_{P_1} - S^*_{P_2})\Delta_1\Delta_2 = (C_2 - C_1)\left[\frac{2Br_m}{K}(C_2 + C_1) + \frac{4r_m s_m A}{KL} + A(C_1C_2)\right].$$

Result 11 *(Escapement comparison between subpopulations) Let one of predator subpopulations be relatively more efficient while all other parameters of the prey and the predator are identical for both subpopulations, without loss of generality, let us assume that predator subpopulation one is relatively more efficient, that is,* $C_1 > C_2$. *If* $A_1 = A_2 = A$ *and* $B_1 = B_2 = B$ *are negative, and* C_i *is non-positive with* $C_i > max\{-\frac{r_{im}B}{AK}, -\frac{s_{im}A}{BL}\}$, *then*

$$S^*_{N_1} > S^*_{N_2} \text{ and } S^*_{P_1} > S^*_{P_2}.$$

Proof

From lemma 4, we only need to show that $\left[\frac{2As_m}{L}(C_2 + C_1) + \frac{4r_m s_m B}{KL} + B(C_1C_2)\right] < 0$ which is satisfied by $C_i > -\frac{r_m B}{AK}$. The second part can be proved analogously. □

Result 11 suggests that to harvest a predator-prey metapopulation optimally, we should leave both subpopulations living in the patch with a relatively more efficient predator with higher escapements than the other subpopulations. A special case is when $\beta_1 = \beta_2$ and $\alpha_1 \neq \alpha_2$. In this case, we should leave both subpopulations living in the patch with relatively less vulnerable prey with higher escapements than the other subpopulations. I illustrate these results and the previous results with some numerical examples in the following section.

5.1.3 Numerical examples with negligible costs

In this section, a numerical example is presented to illustrate and to compare the two-patch predator-prey optimal escapements to escapements from other methods. For the purpose of comparisons, parameters for the prey and predator population are the same as those in the previous chapters.

Comparison of optimal policy to a single-species metapopulation policy

Assume that the prey in both patches have carrying capacities $K_1 = K_2 = 400,000$, with intrinsic growth rates $r_1 = r_2 = 1000$ and adult survival rates per period $a_1 = a_2 = 0.001$. The juveniles migrate symmetrically, that is, $p_{11} = p_{22} = 0.001$ and $p_{12} = p_{21} = 0.003$, hence there is no relative source/sink and exporter/importer prey subpopulation. Let the discounting rate to be $\delta = 10\%$. Before exploitation begins, assume that the population is in the equilibrium state. In the absence of the predator, the unharvested population sizes for prey subpopulation one and two are $\bar{N}_1 = \bar{N}_2 =$

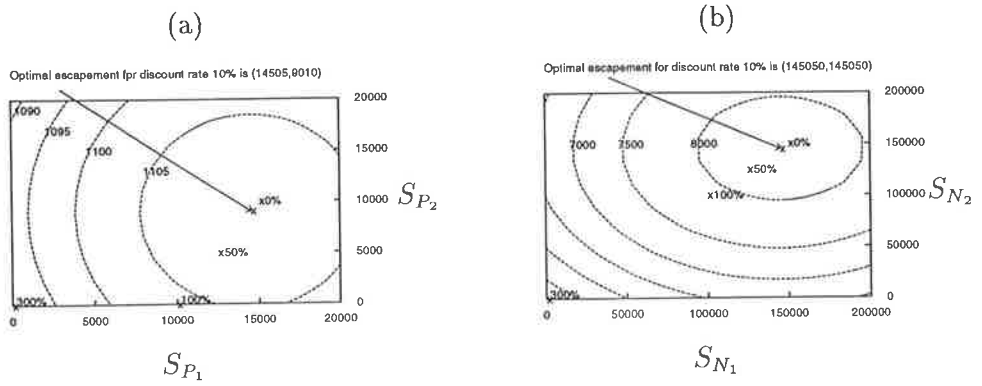


Figure 5.1: Contour plot for the profit in (4.11) as a function of predator escapements (Figure 5.1.a) and as a function of prey escapements (Figure 5.1.b), calculated in millions with a discounting rate 10%. Optimal escapements $S^*_{P_1} = 14505$ and $S^*_{P_2} = 9010$ are found as the predator optimal escapements (Figure 5.1.a) and escapements $S^*_{N_1} = S^*_{N_2} = 145050$ are found as the prey optimal escapements (Figure 5.1.b). The symbol "x" indicates the position of equilibrium escapements for various discounting rates, e.g. x0% indicates the position with no discounting rate.

300100. Using equation (5.9) with $C_i = 0$, I obtain the optimal escapements for prey subpopulations one and two which are $S^*_{N_{1s}} = S^*_{N_{2s}} = 145050$, hence both prey subpopulations are harvested equally with first period optimal harvests $H^*_{N_{1s}} = H^*_{N_{2s}} = 155050$ and equilibrium optimal harvests $H^*_{N_{1s}} = H^*_{N_{2s}} = 224900$.

Now suppose that the predator, P_i, is present. For simplicity I choose intrinsic growth rates of the predator $s_1 = s_2 = 1000$ with carrying capacities $L_1 = L_2 = 40000$. I assume that the predator's adult survival rates per unit time is not different from the prey's adult survival and is not different between patches, hence $b_1 = b_2 = 0.001$. The predator on patch one is assumed to be a relative source and exporter subpopulation, with the migration parameters $q_{11} = q_{21} = q_{22} = 0.001$, and $q_{12} = 0.003$. Let $|\alpha_i| = \beta_i = 0.00001$, that is, the predator has a high conversion efficiency. Using NAG routine c05nbf to solve equations (5.1) and (5.2), one of the positive equilibrium population sizes for this two-patch predator-prey system is obtained, that is, $(\bar{N}_1, \bar{N}_2, \bar{P}_1, \bar{P}_2) \doteq (270581, 205331, 43248, 76676)$.

Furthermore, using equations (5.9) and (5.10), the optimal escapements for the system, $S^*_{N_1} = S^*_{N_2} = 145050$, $S^*_{P_1} = 14505$ and $S^*_{P_2} = 9010$, are obtained. These escapements are similar to the escapements for a single-species metapopulation since we have $|\alpha_i| = \beta_i$ for each patch as is explained in the result. However, the optimal harvests are different. In this case, the first period optimal harvests $H^*_{N_1} = 125531$, $H^*_{N_2} = 60281$, $H^*_{P_1} = 28743$, $H^*_{P_2} = 6766$, and the equilibrium optimal harvests $H^*_{N_1} = 203861$, $H^*_{N_2} = 211831$, $H^*_{P_1} = 22775$, and $H^*_{P_2} = 38784$ are obtained.

If we use single-species metapopulation theory (Tuck and Possingham, 1994), we should harvest the prey equally in each patch. In contrast, if we use a two-patch predator-prey metapopulation, we harvest prey subpopulation two less than prey subpopulation one. This is because predator subpopulation one is a relative exporter subpopulation, and consequently there would be less prey in patch two as is indicated by the fact that the unharvested prey equilibrium population size in patch one is greater than the one in patch two, that is, $\bar{N}_1 > \bar{N}_2$. As expected, because there is no source/sink or exporter/importer prey subpopulation, using both methods we harvest predator subpopulation one more conservatively than predator subpopulation two, and in this case $H^*_{P_1} = 22775$, and $H^*_{P_2} = 38784$ from two-patch predator-prey escapements, and $H^*_{P_{1s}} = 1735$, and $H^*_{P_{2s}} = 25715$ from single-species metapopulation escapements. In conclusion, even though the degree of predator-prey interaction appears weak, that is, α and β are small, optimal harvests for a metapopulation are very different if a predator is included in the system. In general, if $C_i \leq 0$ the optimal escapement for a predator-prey metapopulation is less than, or equal to, optimal escapement for a single-species metapopulation. As a result, if we use optimal escapements for a single-species metapopulation as a policy to manage a predator-prey metapopulation system, then we might under-harvest the stock. On the other hand, if we use the optimal harvests from a single-species metapopulation, we might over-harvest the prey and under-harvest the predator.

Comparison of optimal policy to spatially homogeneous predator-prey policies

In this section, I compare the optimal escapements and equilibrium harvests from a predator-prey metapopulation to the optimal escapements and equilibrium harvests if spatial structure is ignored.

Firstly, if our predator-prey metapopulation system was incorrectly believed to be an unconnected two-patch predator-prey system, then the optimal escapements are found from equations (5.9) and (5.10) by replacing p_{ii}, p_{ij}, q_{ii} and q_{ij} with 1, 0, 1 and 0 respectively, and replacing $(p_{ii} + p_{ij})r_i$ and $(q_{ii} + q_{ij})s_i$ with r_{iu} given by equation (4.44), and $(q_{ii} + q_{ij})s_i$ is replaced by s_{iu} similarly. The resulting escapements are $S^*_{N_{1u}} = S^*_{N_{2s}} = 145050$, $S^*_{P_{1u}} = 9010$, and $S^*_{P_{2u}} = 14505$. The harvesting strategy from these escapements produces optimal equilibrium harvests $H^*_{N_{1u}} = 211831$, $H^*_{N_{2u}} = 203861$, $H^*_{P_1} = 20294$, and $H^*_{P_2} = 36736$ with total harvest $H^*_u = H^*_{N_u} + H_{P_u} = 472722$. This total harvest is less than the total harvest if we correctly use predator-prey metapopulation escapements, that is, $H^* = H^*_N + H^*_P = 477251$ (see Table 5.1). This is because if we use unconnected predator-prey theory, we fail to recognise the exporter predator subpopulation which is important as a contributor to the other predator subpopulation. In this case, we exploit the relative exporter predator too much, with an escapement of only 9010, while the relative importer predator is harvested too conservatively with an escapement of 14505.

Note that there is no difference in the total harvest of the prey, and that the difference is only in the harvest from each patch. If we use the harvesting strategy from unconnected two-patch predator-prey escapements, we would over-harvest the prey living in the same patch with the relative exporter predator, while the prey living in the same patch with the relative importer predator is under-harvested. In conclusion, in this example, comparing the strategy from unconnected two-patch predator-prey escapements, the harvesting strategy from a predator-prey metapopulation gives a higher total harvest while it also leaves the relative exporter predator a higher escapement.

Secondly, if our predator-prey metapopulation system was incorrectly considered to be a well-mixed predator-prey system, then the optimal escapements are found from equations (5.9) and (5.10) by replacing p_{ii}, p_{ij}, q_{ii} and q_{ij} with 1, 0, 1 and 0 respectively, and replacing $(p_{ii}+p_{ij})r_i$ and $(q_{ii}+q_{ij})s_i$ with r_w given by equation (4.45),

PPM	$S^*_{N_1} = 145050$	$H^*_{N_1} = 203861$	$S^*_{P_1} = 14505$	$H^*_{P_1} = 22775$
	$S^*_{N_2} = 145050$	$H^*_{N_2} = 211831$	$S^*_{P_2} = 9010$	$H^*_{P_2} = 38784$
	$S^*_N = 290100$	$H^*_N = 415692$	$S^*_P = 23515$	$H^*_P = 61559$
UPP	$S^*_{N_{1u}}$=145050	$H^*_{N_{1u}}$=211831	$S^*_{P_{1u}}$=9010	$H^*_{P_{1u}}$=20294
	$S^*_{N_{2u}}$=145050	$H^*_{N_{2u}}$=203861	$S^*_{P_{2u}}$=14505	$H^*_{P_{2u}}$=36736
	$S^*_{N_u}$ =290100	$H^*_{N_u}$ =415692	$S^*_{P_u}$=23515	$H^*_{P_u}$=57030
WPP	$S^*_{N_w}$ =290100	$H^*_{N_w}$ =413036	$S^*_{P_w}$ =25346	$H^*_{P_w}$ =63391

Table 5.1: Escapement and harvest comparisons between correct and incorrect assumptions, where $p_N = p_P$. PPM, UPP and WPP denote predator-prey metapopulation, unconnected predator-prey population and well-mixed predator-prey population, respectively.

and $(q_{ii} + q_{ij})s_i$ is replaced by s_w similarly. The resulting escapements are $S^*_{N_w} = 290100$, and $S^*_{P_w} = 25346$. The harvesting strategy from these escapements produces optimal equilibrium harvests $H^*_{N_w} = 413034$ and $H^*_{P_w} = 63392$ with total harvest $H^*_w = H^*_{N_w} + H_{P_w} = 476426$. This total harvest is less than the total harvest from the predator-prey metapopulation, that is, $H^* = 477251$ (see Table 5.1). As indicated by Result 10, using the escapement from a well-mixed predator-prey population would over-harvest the relative source predator subpopulation, P_1, and under-harvest the relative sink predator subpopulation, P_2, since $S^*_{P_1} = 14505 > S^*_{P_w}/2 = 12673 > S^*_{P_2} = 9010$.

5.1.4 Numerical examples with prey and predator differential prices

In the previous section, I assume the prey and predator have the same market value. In this section, I assume that there is a different market value for each species. I assume the price of a unit prey stock is $p_N = 8000$ while the price of a unit predator is five times the prey's price, that is, $p_P = 40000$. I obtain optimal escapements for the system from equations (5.5) and (5.6). These escapements are $S^*_{N_1} = 189196$, $S^*_{N_2} = 194131$, $S^*_{P_1} = 22073$ and $S^*_{P_2} = 24540$, with equilibrium optimal harvests $H^*_{N_1} = 168682$, $H^*_{N_2} = 157462$, $S^*_{P_1} = 39088$ and $S^*_{P_2} = 62287$. From Table 5.2, we see that the rule of source/sink exploitation no longer holds. However, from Table 5.5, the value of the total harvest from the predator-prey metapopulation escapements is higher than those from the unconnected two-patch predator-prey and well-mixed predator-prey escapements.

5.1.5 Numerical examples with costs included

In the previous example, costs of harvesting are considered to be negligible. The example illustrates the properties of the optimal escapements from a predator-prey metapopulation. Analytically the properties illustrated by the example are described in the previous results. However, the results ignore the costs of harvesting. In this section, optimal escapements from the same predator-prey metapopulation are compared to other escapements and the costs of harvesting are taken into account. To obtain optimal escapements, I use the cost function

$$c_X(X_i) = (m_{X_i} + c_i n_{X_i} X_i)/(n_{X_i} X_i) \tag{5.11}$$

PPM	$S^*_{N_1} = 189196$ $S^*_{N_2} = 194131$	$H^*_{N_1} = 168682$ $H^*_{N_2} = 157462$	$S^*_{P_1} = 22073$ $S^*_{P_2} = 24540$	$H^*_{P_1} = 39088$ $H^*_{P_2} = 62287$
	$S^*_N = 383327$	$H^*_N = 326144$	$S^*_P = 46613$	$H^*_P = 101375$
UPP	$S^*_{N_{1u}}=194131$ $S^*_{N_{2u}}=189196$	$H^*_{N_{1u}}=157462$ $H^*_{N_{2u}}=168682$	$S^*_{P_{1u}}=24540$ $S^*_{P_{2u}}=22073$	$H^*_{P_{1u}}=42502$ $H^*_{P_{2u}}=58057$
	$S^*_{N_u}=383327$	$H^*_{N_u}=326144$	$S^*_{P_u}=46613$	$H^*_{P_u}=100559$
WPP	$S^*_{N_w}=381486$	$H^*_{N_w}=330028$	$S^*_{P_w}=45692$	$H^*_{P_w}=100293$

Table 5.2: Escapement and harvest comparisons between correct and incorrect assumptions, where $p_N = \frac{1}{5}p_P$. PPM, UPP and WPP denote predator-prey metapopulation, unconnected predator-prey population and well-mixed predator-prey population, respectively.

which is a decreasing function with respect to X_i and has a non-zero limit ($c_i \neq 0$) as X_i approaches ∞. Hence, with this cost function I assume that there is a constant cost per unit stock whenever the stock size is high.

In this example, I use $m_{N_1} = m_{N_2} = m_{P_1} = m_{P_2} = 2000$, $n_{N_1} = n_{N_2} = 0.25$, $c_i = 1000$, and $n_{P_1} = n_{P_2} = 0.05$. Since $n_{P_i} < n_{N_i}$, I assume that the cost of harvesting per unit predator is higher than the cost of harvesting per unit prey. I investigate two cases, first when there is no difference between the price of a unit of prey and predator, I assume $p_N = p_P = 8000$. Second, I assume that there is difference between p_N and p_P; let $p_N = 8000$ and $p_P = 40000$. Using these parameters, I conclude that in the presence of a price difference between the prey and predator, the rule of thumb about source/sink exploitation may not hold. We harvest the relative source predator subpopulation less conservatively than the relative sink predator subpopulation.

In Result 12 I provide some conditions that must be satisfied under which we harvest the relative source predator subpopulation conservatively. One of the conditions is that the ratio of the predator adult survival in patch one to the predator adult survival in patch two must be equal to the ratio of the marginal net revenue from harvesting predator subpopulation two to the marginal net revenue from harvesting predator subpopulation one, that is, $b_1/b_2 = (p_P - c_{P2})/(p_P - c_{P1})$. This condition is not satisfied in this example. Figure 5.2 compares the predator optimal escapements for various combinations of market price and cost of harvesting and shows how robust the rule is in the presence of the costs of harvesting.

As in the case of negligible costs, profit from predator-prey metapopulation escapements is higher than from the other predator-prey escapements (Table 5.6). In the following section I discuss the effects of prey vulnerability variations on the optimal escapements, and in Section 5.1.7 I establish rules similar to the rules of thumb discussed above with the inclusion of harvesting costs in the analysis.

5.1.6 Variation in the prey vulnerability parameters

I consider a predator-prey metapopulation that is homogeneous, except for differences in the prey vulnerability, α_i. Assume that all parameters of the metapopulation are exactly the same as the previous example, except the migration parameters. In this example, prey migration parameters are $p_{11} = p_{22} = q_{11} = q_{22} = 0.001$ and $p_{12} = p_{21} = q_{12} = q_{21} = 0.003$. Assuming that costs are negligible and both the prey and predator have the same price, I vary the prey vulnerability, α_i, from -0.00001 to -0.00003. I

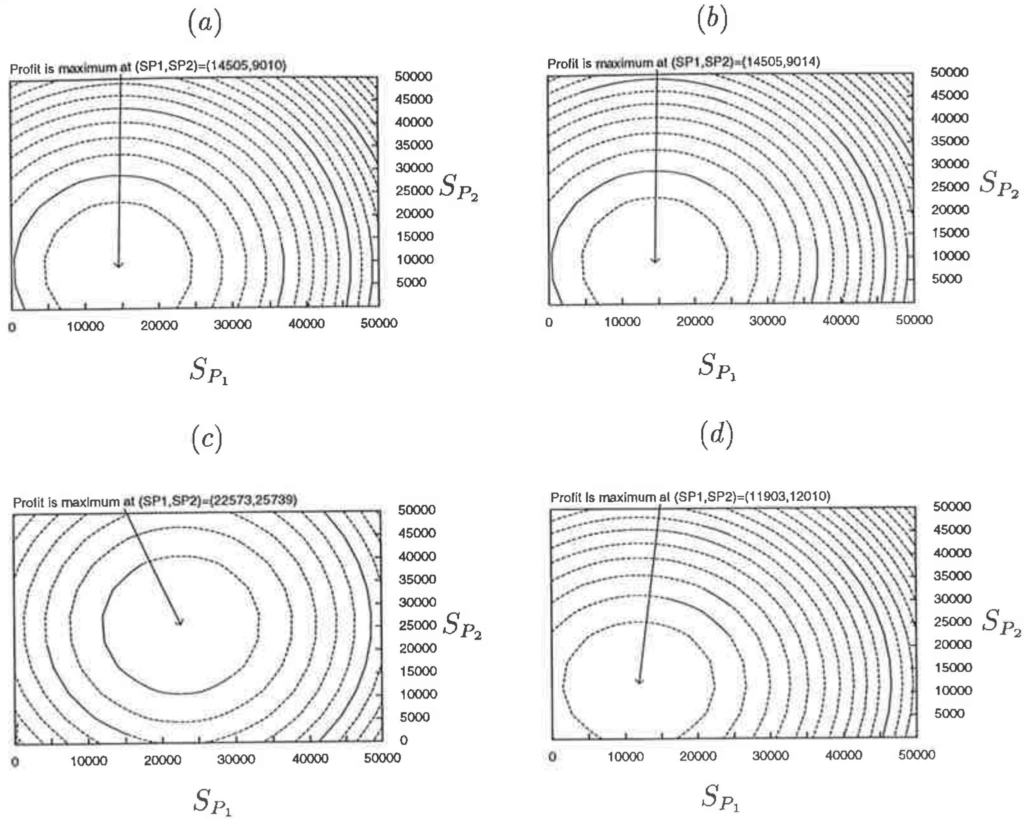


Figure 5.2: Optimal escapement comparisons for various prices and costs of harvesting. The Figure shows the optimal escapements for $p_N = p_P$ with negligible costs (Figure 5.2.a), the optimal escapements for $p_N = p_P$ with $c_1 = c_2$ (Figure 5.2.b), the optimal escapements for $p_N = \frac{1}{5}p_P$ with $c_1 = c_2$ (Figure 5.2.c), and the optimal escapement for $p_N = p_P$ with $c_1 = \frac{1}{4}c_2$ (Figure 5.2.d). Figure 5.2.c shows that the rule to harvest a relative source predator subpopulation more conservatively than a relative sink predator subpopulation may fail if $b_1/b_2 \neq (p_P - c_{P2})/(p_P - c_{P1})$, in this case $S^*_{P_1} < S^*_{P_2}$ (see Result 12).

plot the contours of the escapements and their equilibrium optimal harvests, both for the prey and predator, as functions of the prey vulnerability α_i, with a constant $\beta_i = 0.00001$ (Figure 5.3).

In Figure 5.3.a I plot the escapement of prey subpopulation one and the escapement of prey subpopulation two. As expected in Result 11, if $C_i > max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}$ (this is satisfied by $\alpha_i \geq -0.000025$ in Figure 5.3), the increase of prey vulnerability causes the decrease of the prey's optimal escapement. For example, with $\alpha_1 = \alpha_2 = -0.00001$ we obtain $S^*_{N_1} = S^*_{N_2} = 145050$, while with $\alpha_1 = \alpha_2 = -0.00002$ we obtain $S^*_{N_1} = S^*_{N_2} = 141331$. In this region, $\alpha_i \geq -0.00002$, the increase of prey vulnerability causes the increase of prey optimal harvests (Figure 5.3.b), hence we harvest the prey subpopulation more conservatively if it is less vulnerable to the predator.

In Figure 5.3.c I plot the escapement of predator subpopulation one and the escapement of the prey subpopulation two as functions of prey vulnerabilities, α_1 and α_2. We see that the increase of prey vulnerability causes the decrease of the predator's

PPM	$S^*_{N_1} = 145049$ $S^*_{N_2} = 145050$	$H^*_{N_1} = 203861$ $H^*_{N_2} = 211824$	$S^*_{P_1} = 14505$ $S^*_{P_2} = 9014$	$H^*_{P_1} = 22777$ $H^*_{P_2} = 38788$
	$S^*_N = 290099$	$H^*_N = 415685$	$S^*_P = 23519$	$H^*_P = 61565$
UPP	$S^*_{N_{1u}}=145049$ $S^*_{N_{2u}}=145050$	$H^*_{N_{1u}}=211829$ $H^*_{N_{2u}}=203858$	$S^*_{P_{1u}}=9012$ $S^*_{P_{2u}}=14506$	$H^*_{P_{1u}}=20296$ $H^*_{P_{2u}}=36740$
	$S^*_{N_u}=290099$	$H^*_{N_u}=415687$	$S^*_{P_u}=23518$	$H^*_{P_u}=57036$
WPP	$S^*_{N_w}=290098$	$H^*_{N_w}=413033$	$S^*_{P_w}=25348$	$H^*_{P_w}=63394$

Table 5.3: Escapement and harvest comparisons between correct and incorrect assumptions, where $p_N = p_P$ and costs are included.

PPM	$S^*_{N_1} = 196644$ $S^*_{N_2} = 203882$	$H^*_{N_1} = 159023$ $H^*_{N_2} = 143723$	$S^*_{P_1} = 22573$ $S^*_{P_2} = 25739$	$H^*_{P_1} = 40849$ $H^*_{P_2} = 65444$
	$S^*_N = 400526$	$H^*_N = 302746$	$S^*_P = 48312$	$H^*_P = 106293$
UPP	$S^*_{N_{1u}}=203881$ $S^*_{N_{2u}}=196644$	$H^*_{N_{1u}}=143724$ $H^*_{N_{2u}}=159023$	$S^*_{P_{1u}}=25739$ $S^*_{P_{2u}}=22573$	$H^*_{P_{1u}}=45775$ $H^*_{P_{2u}}=59202$
	$S^*_{N_u}=400525$	$H^*_{N_u}=302747$	$S^*_{P_u}=48312$	$H^*_{P_u}=104977$
WPP	$S^*_{N_w}=397768$	$H^*_{N_w}=308918$	$S^*_{P_w}=47106$	$H^*_{P_w}=104734$

Table 5.4: Escapement and harvest comparisons between correct and incorrect assumptions, where $p_N = \frac{1}{5}p_P$ and costs are included.

optimal escapement until finally it reaches zero at $\alpha_i = -0.00003$. For example, with $\alpha_1 = \alpha_2 = -0.00001$ we obtain $S^*_{P_1} = S^*_{P_2} = 14505$, while with $\alpha_1 = \alpha_2 = -0.00002$ we obtain $S^*_{P_1} = S^*_{P_2} = 7438$. The increase of prey vulnerability causes the decrease of the predator's optimal harvest (Figure 5.3.d). This is because I assume $\beta_i = 0.00001$ is constant, hence a higher prey vulnerability means a lower predator efficiency and from Result 11 we should harvest the prey subpopulation less conservatively if it is a less efficient predator subpopulation. At $\alpha_i = -0.00003$ we harvest both predator subpopulations down to extinction, because it is not optimal to waste the prey as food for the predator due to the low predator efficiency in converting prey captured into predator offspring. In this case, we only keep a high predator escapement if its efficiency is relatively high.

Furthermore, if a negative harvest is interpreted as a "seeding" strategy (Tuck, 1994), then for a low prey vulnerability in subpopulation one and a high prey vulnerability in subpopulation two, there is a small range (the range between contour lines $H_{P_1} = 0$ and $H_{P_2} = 0$ in the lower right part of Figure 5.4.c and 5.4.d) where we should seed the relatively more efficient predator subpopulation and then harvest all individuals of the relatively less efficient predator subpopulation two. This is because there is seasonal migration of predator juveniles from subpopulation one recruited by predator subpopulation two (see also Figure 5.5).

Figure 5.4 shows contour plots of escapements and harvests for prey and predator subpopulations if one of the predator subpopulations is a relative source and exporter subpopulation. I assume that all parameters are the same as in the previous example, except $q_{21} = 0.001$, that is, predator subpopulation one is a relative exporter subpopulation. Figure 5.4 is interpreted as in the symmetrical migration case (Figure 5.3).

PPM	$S^*_{N_1} = 119020$ $S^*_{N_2} = 164832$	$H^*_{N_1} = 241262$ $H^*_{N_2} = 163261$	$S^*_{P_1} = 11903$ $S^*_{P_2} = 12010$	$H^*_{P_1} = 19040$ $H^*_{P_2} = 41285$
	$S^*_N = 283852$	$H^*_N = 404523$	$S^*_P = 23913$	$H^*_P = 60325$
UPP	$S^*_{N_{1u}}=145049$ $S^*_{N_{2u}}=145049$	$H^*_{N_{1u}}=211828$ $H^*_{N_{2u}}=203858$	$S^*_{P_{1u}}=9012$ $S^*_{P_{2u}}=14507$	$H^*_{P_{1u}}=20296$ $H^*_{P_{2u}}=36740$
	$S^*_{N_u}=290098$	$H^*_{N_u}=415686$	$S^*_{P_u}=23519$	$H^*_{P_u}=57036$
WPP	$S^*_{N_w}=290098$	$H^*_{N_w}=413030$	$S^*_{P_w}=25350$	$H^*_{P_w}=63397$

Table 5.5: Escapement and harvest comparisons between correct and incorrect assumptions, where $p_N = p_P$ and costs between patches are different, that is, $c_1 = \frac{1}{4}c_2$.

Escapements used	**Without costs**		**With costs**		
	$p_N = p_P$	$p_N = \frac{1}{5}p_P$	$p_N = p_P$		$p_N = \frac{1}{5}p_P$
			$c_1 = c_2$	$c_1 = \frac{1}{4}c_2$	
PPM	38180	66642	33407	26402	62646
UPP	37818	66315	33090	25872	62132
WPP	38114	66520	33350	26203	62470

Table 5.6: Profit comparison between correct and incorrect assumptions. Numbers are in hundreds of thousands.

5.1.7 Analytical results with costs included

I assume that both unit costs of harvesting, C_{Xi}, and market prices, p_X, are constant, but the costs may differ between patches and the prices may differ between species. A relatively constant unit cost of harvesting is known, for example, in the clupeoids fishery (Munro, 1992). Furthermore, I assume that the marginal net revenue from harvesting, $p_X - c_{Xi}$, is always positive, so that the fishery is always profitable regardless of the density of the fish stock. Using these assumptions optimal escapements for both the prey and predator have exactly the same form as escapements where costs are negligible, that is,

$$S^*_{N_{ci}} = \frac{A_{ci}Q_{ci}\frac{2s_i}{L_i} + C_{ci}B_{ci}}{\Delta_{ci}}, \tag{5.12}$$

$$S^*_{P_{ci}} = \frac{B_{ci}P_{ci}\frac{2r_i}{K_i} + C_{ci}A_{ci}}{\Delta_{ci}}, \tag{5.13}$$

provided $\Delta_{ci} = C^2_{ci} - P_{ci}\frac{2r_i}{K_i}Q_{ci}\frac{2s_i}{L_i} \neq 0$ with

$$A_{ci} = \frac{(p_N - c_{Ni})}{\rho} - [p_{ii}(p_N - c_{Ni}) + p_{ij}(p_N - c_{Nj})]r_i - a_i(p_N - c_{Ni}), \tag{5.14}$$

$$B_{ci} = \frac{(p_P - c_{Pi})}{\rho} - [q_{ii}(p_P - c_{Pi}) + q_{ij}(p_P - c_{Pj})]s_i - b_i(p_P - c_{Pi}), \tag{5.15}$$

$$C_{ci} = \alpha_i(p_N - c_{Ni}) + \beta_i(p_P - c_{Pi}), \tag{5.16}$$

$$P_{ci} = p_{ii}(p_N - c_{Ni}) + p_{ij}(p_N - c_{Nj}), \tag{5.17}$$

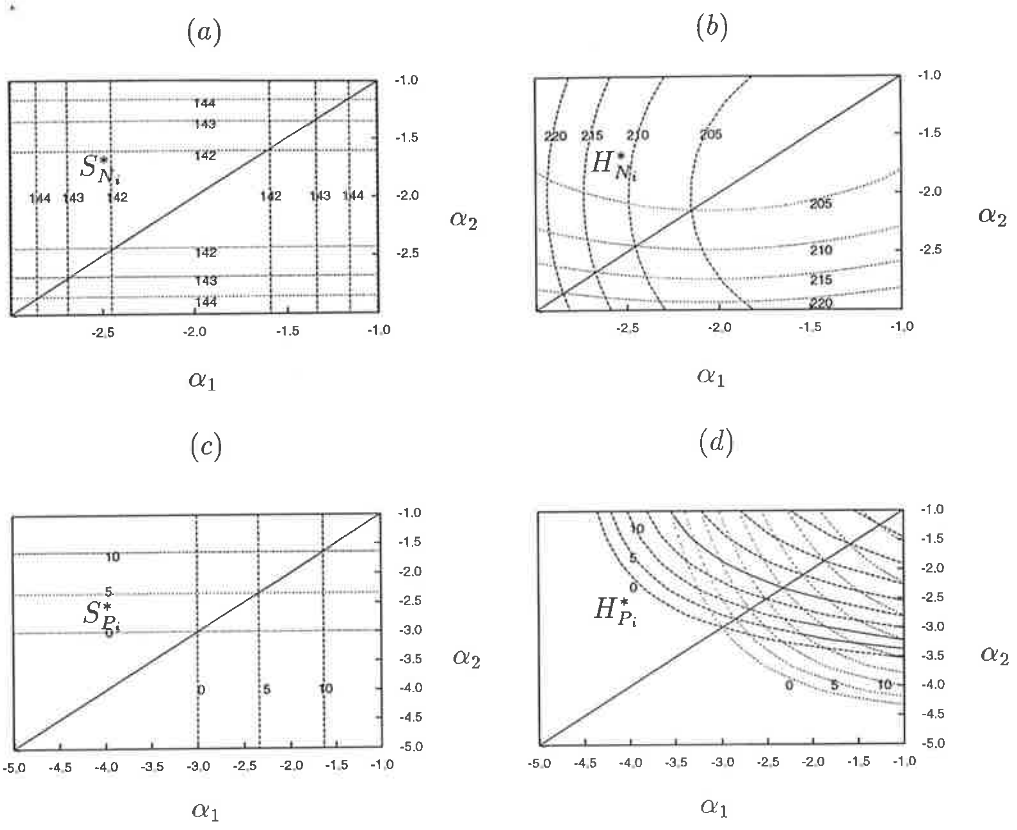


Figure 5.3: Contour plots of optimal escapements $S^*_{N_i}$ (Figure 5.3.a), prey optimal harvests $H^*_{N_i}$ (Figure 5.3.b), predator optimal escapements $S^*_{P_i}$ (Figure 5.3.c), and predator optimal harvests $H^*_{P_i}$ (Figure 5.3.d) as functions of prey vulnerability α_i [escapements and harvests are in 1000s; vulnerabilities are in 10^{-5}s]. Contour plots for the populations in patch one are given by dashes (-- ---) and contour plots for the populations in patch two are given by dots (.....). In this case β_1 and β_2 are constant with the value 0.00001, $p_{11} = p_{22} = q_{11} = q_{22} = 0.001$ and $p_{12} = p_{21} = q_{12} = q_{21} = 0.003$. See text for detail.

$$Q_{ci} = q_{ii}(p_P - c_{Pi}) + q_{ij}(p_P - c_{Pj}). \tag{5.18}$$

Similar results to the four results discussed in the negligible cost analysis can also be obtained, with some additional conditions such as:

1. *For Result 8* Prey subpopulation one is a relative source subpopulation with $p_{11}r_1 \geq p_{21}r_2$ and $p_{12}r_1 > p_{22}r_2$ (or $p_{11}r_1 > p_{21}r_2$ and $p_{12}r_1 \geq p_{22}r_2$).

2. *For Results 9 and 10* The marginal net revenue from prey subpopulation one is lower than, or equal to, the marginal revenue from prey subpopulation two, that is, $p_N - c_{N1} \leq p_N - c_{N2}$, and its ratio satisfies

$$\frac{p_N - c_{N1}}{p_N - c_{N2}} \geq \frac{r_2 p_{22}}{r_1 p_{11}}. \tag{5.19}$$

The details of the results are as follows.

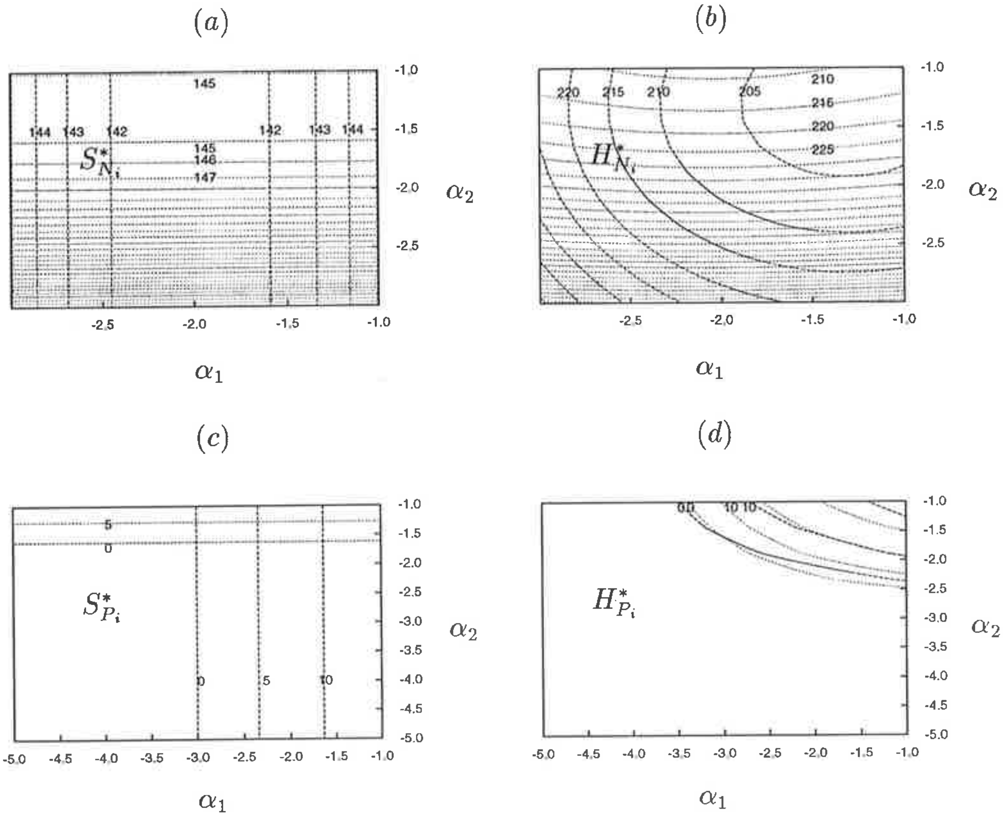


Figure 5.4: Contour plots of optimal escapements $S^*_{N_i}$ (Figure 5.4.a), prey optimal harvests $H^*_{N_i}$ (Figure 5.4.b), predator optimal escapements $S^*_{P_i}$ (Figure 5.4.c) and predator optimal harvests $H^*_{P_i}$ (Figure 5.4.d) as functions of prey vulnerability α_i [escapements and harvests are in 1000s; vulnerabilities are in 10^{-5}s]. Contour plots for the populations in patch one are given by dashes (- - - - -) and contour plots for the populations in patch two are given by dots (.....). In this case β_1 and β_2 are constant with the value 0.00001, $p_{11} = p_{22} = 0.001$, $p_{12} = p_{21} = 0.003$, $q_{11} = q_{21} = q_{22} = 0.001$ and $q_{12} = 0.003$. See text for detail.

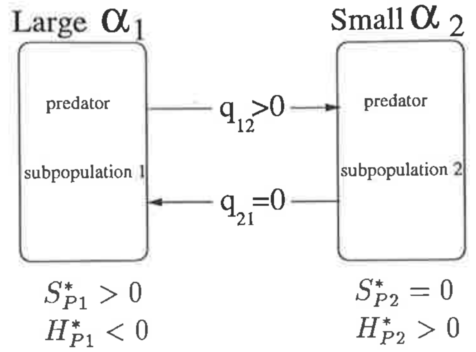


Figure 5.5: Seeding strategy for predator subpopulation one ($H^*_{P_1} < 0$) and clearing strategy for predator subpopulation two ($S^*_{P_2} = 0$) if prey vulnerability α_1 is low and prey vulnerability α_2 is high.

Result 12 *(Escapement comparison between subpopulations with costs included) Let one of the prey subpopulations be a relative source while all other parameters of the prey and the predator are identical for both subpopulations except* a_1 *and* α_1 *may differ from* a_2 *and* α_2*. Without loss of generality let us assume that prey subpopulation one is a relative source, that is,* $(p_{11} + p_{12})r_1 > (p_{22} + p_{21})r_2$*. Furthermore,* $p_{11}r_1 \geq p_{21}r_2$ *and* $p_{12}r_1 > p_{22}r_2$ *(or* $p_{11}r_1 > p_{21}r_2$ *and* $p_{12}r_1 \geq p_{22}r_2$*) and there is no harvesting cost differential between patches for the predator. If* A_{ci} *and* B_{ci} *are negative,* $a_1/a_2 = \alpha_1/\alpha_2 = (p_N - c_{N_2})/(p_N - c_{N_1})$ *and* C_{ci} *is non-positive with* $C_{ci} > max\{\frac{2B_{ci}}{K}, \frac{2A_{ci}}{L}\}$*, then:*

1. $S^*_{N_1} > S^*_{N_2}$,
2. $S^*_{P_1} \leq S^*_{P_2}$.

Proof

Rewrite escapements in equations (5.12) and (5.13) in the following form:

$$S^*_{N_{ci}} = \frac{(R_{ci} - r_{cim})\frac{2s_{cim}}{L_i} + C_{ci}(S_{ci} - s_{cim})}{\Delta_{ci}}, \tag{5.20}$$

$$S^*_{P_{ci}} = \frac{(S_{ci} - s_{cim})\frac{2r_{cim}}{K_i} + C_{ci}(R_{ci} - r_{cim})}{\Delta_{ci}}, \tag{5.21}$$

where

$$R_{ci} = (\frac{1}{\rho} - a_i)(p_N - c_{Ni}),$$

$$S_{ci} = (\frac{1}{\rho} - b_i)(p_P - c_{Pi}),$$

$$r_{cim} = [p_{ii}(p_N - c_{Ni}) + p_{ij}(p_N - c_{Nj})]r_i,$$

$$s_{cim} = [q_{ii}(p_P - c_{Pi}) + q_{ij}(p_P - c_{Pj})]s_i.$$

1. Let $\Delta_{S_N} = (S^*_{N_{c1}} - S^*_{N_{c2}})\Delta_{c1}\Delta_{c2}$. If there is no harvesting cost differential between patches for the predator, that is, $c_{P1} = c_{P2}$, then $S_{c1} = S_{c2} = S_c$, $s_{c1m} = s_{c2m} = s_{cm}$ and $B_{c1} = B_{c2} = B_c$. Since it can be shown that $C_{c1} = C_{c2} = C_c$ and $R_{c1} = R_{c2} = R_c$, then following the proof in Result 8, we only need to show

   $$\Delta_{S_N} \;=\; s_{cm}\left[\frac{2}{L}\left(C_c\left(C_c - \frac{2B_c}{K}\right) - \frac{4s_{cm}R_c}{KL}\right)\right](r_{c2m} - r_{c1m}) > 0.$$

   Since $\frac{2B_c}{K} \leq C_c \leq 0$ then $\Delta_{S_N} > 0$ if $p_{11}r_1 \geq p_{21}r_2$ and $p_{12}r_1 > p_{22}r_2$ (or $p_{11}r_1 > p_{21}r_2$ and $p_{12}r_1 \geq p_{22}r_2$). □

2. This part can be proved analogously. □

As for the case of negligible cost, I interpret the condition $C_{ci} > max\{\frac{2B_{ci}}{K}, \frac{2A_{ci}}{L}\}$ in the above result as a relatively high predator economic efficiency. However, here the predator biological efficiency $\frac{\beta_i}{|\alpha_i|}$ should be lower than or equal to the ratio of the prey marginal revenue and the predator marginal revenue $\frac{p_N - c_{Ni}}{p_P - c_{Pi}}$. Furthermore, the conditions $p_{11}r_1 \geq p_{21}r_2$ and $p_{12}r_1 > p_{22}r_2$ (or $p_{11}r_1 > p_{21}r_2$ and $p_{12}r_1 \geq p_{22}r_2$) need to be satisfied. In this case, prey subpopulation one contributes more to the larval production of both prey subpopulations, for example when prey subpopulation one is a relative source and exporter subpopulation and has intrinsic growth rate greater than, or equal to, the intrinsic growth rate of the other prey subpopulation.

The following result is a generalisation of Result 9 in the previous section. Result 10 can also be generalised in the similar way.

Result 13 *(Comparison of strategy with an unconnected two-patch predator-prey system) Let $S^*_{N_{ci}}$ and $S^*_{P_{ci}}$ denote the optimal escapement from a predator-prey metapopulation given by the equations (5.12) and (5.13), and let $S^*_{N_{ciu}}$ and $S^*_{P_{ciu}}$ denote the optimal escapement if we incorrectly consider the system as a system consisting of two unconnected predator-prey systems. Let us assume that one of prey subpopulation is a relative exporter and also a relative source while all other parameters of the prey and the predator are identical for both subpopulations. Without lost of generality let $p_{12}r_1 > p_{21}r_2$ and $p_{11}r_1 \geq p_{22}r_2$. Assume A_{ci} and B_{ci} are negative and $C_{ci} > max\{\frac{2B_{ci}}{K}, \frac{2A_{ci}}{L}\}$ and there is no harvesting cost differential between patches for the predator. If the marginal net revenue from the prey subpopulation one is lower than or equal to the marginal revenue from the prey subpopulation two, that is $p_N - c_{N1} \leq p_N - c_{N2}$, and its ratio satisfies $\frac{p_N - c_{N1}}{p_N - c_{N2}} \geq \frac{r_2 p_{22}}{r_1 p_{11}}$, then:*

1. $S^*_{N_{c1}} > S^*_{N_{c1u}}$,
2. $S^*_{N_{c2}} < S^*_{N_{c2u}}$,
3. $S^*_{P_{c1}} < S^*_{P_{c1u}}$,
4. $S^*_{P_{c2}} > S^*_{P_{c2u}}$.

Furthermore if a_1 and α_1 differ from a_2 and α_2 with $a_1/a_2 = \alpha_1/\alpha_2 = (p_N - c_{N_2})/(p_N - c_{N_1})$, and $p_{11}r_1 \geq p_{21}r_2$ and $p_{12}r_1 > p_{22}r_2$ (or $p_{11}r_1 > p_{21}r_2$ and $p_{12}r_1 \geq p_{22}r_2$), then:

5 $S^*_{N_{c1}} + S^*_{N_{c2}} \leq S^*_{N_{c1u}} + S^*_{N_{c2u}}$,

6 $S^*_{P_{c1}} + S^*_{P_{c2}} \geq S^*_{P_{c1u}} + S^*_{P_{c2u}}$.

Proof

1. Following the proof in Result 12, we obtain

$$(S^*_{N_{c1}} - S^*_{N_{c1u}})\Delta_{c1u}\Delta_{c1} = (r_{c1u} - r_{c1m})\left(C_c(C_c - \frac{2B_c}{K}) - \frac{4R_c s_{c1m}}{KL}\right)\frac{2s_{c1m}}{L},$$

where $\Delta_{c1u} = C_c^2 - \frac{4r_{c1u}s_{c1m}}{KL} < 0$ and $\Delta_{c1} = C_c^2 - \frac{4r_{c1m}s_{c1m}}{KL} < 0$. Since $0 > C_c > \frac{2B_c}{K}$, then we only need to show $r_{c1m} > r_{c1u}$, with

$$r_{c1m} = [p_{11}(p_N - c_{N1}) + p_{12}(p_N - c_{N2})]r_1,$$

$$r_{ciu} = p_{11}(p_N - c_{N1})r_1 + p_{21}(p_N - c_{N1})r_2.$$

Since $\frac{p_{12}r_1}{p_{21}r_2} > 1$, then $r_{c1m} > r_{c1u}$ is satisfied by $p_N - c_{N_1} \leq p_N - c_{N_2}$. □

2,3,4. These parts can be proved similarly. □

5. Let $X_c = \left(C_c(C_c - 2B_c/K) - \frac{4R_c s_{cim}}{KL}\right)\frac{2s_{im}}{L} < 0$ with $s_{1m} = s_{2m}$, and $\Delta S_{Nu} = (S^*_{N_{c1}} + S^*_{N_{c2}}) - (S^*_{N_{c1u}} + S^*_{N_{c2u}})$. Following the proof of Result 9, we obtain

$$\Delta S_{Nu} = \frac{(8s_{c1m}/(KL)(\frac{2(r_{c1m}+r_{c2m})s_{c1m}}{KL} - C_c^2))(r_{c1u}r_{c2u} - r_{c1m}r_{c2m})}{\Delta_{c1}\Delta_{c1u}\Delta_{c2}\Delta_{c2u}}X_c.$$

Since $\Delta_{ci} < 0$ with $i = 1, 2$, then $C_c^2 - \frac{2(r_{c1m}+r_{c2m})s_{c1m}}{KL} < 0$. To prove the result, we only need to show $(r_{c1u}r_{c2u} - r_{c1m}r_{c2m}) \geq 0$ as follow. Let $\Delta = r_{c1m}r_{c2m} - r_{c1u}r_{c2u}$ and $A_{ij} = r_i p_{ij}(p_N - c_{Nj})$.

$$\begin{aligned}\Delta &= (A_{11} + A_{12})(A_{21} + A_{22}) - (A_{11} + A_{21})(A_{22} + A_{12}) \\ &= A_{11}A_{21} + A_{12}A_{22} - A_{11}A_{12} - A_{22}A_{21} \\ &= (A_{11} - A_{22})(A_{21} - A_{12}).\end{aligned}$$

Since $\frac{p_N - c_{N1}}{p_N - c_{N2}} \geq \frac{r_2 p_{22}}{r_1 p_{11}}$ then $A_{11} - A_{22} \geq 0$, and since $p_{12}r_1 > p_{21}r_2$ and $p_N - c_{N2} \geq p_N - c_{N1}$ then $A_{21} - A_{12} < 0$, which means $\Delta \leq 0$. The last inequality can be proved similarly. □

5.1.8 Dealing with an optimal harvest that is negative

In the results presented so far, the optimal harvest for a predator-prey metapopulation may be negative. In general a negative harvest is not possible. However, a negative harvest can be interpreted as a seeding strategy. A seeding strategy may be optimal for a particular year or as an equilibrium strategy. For instance, in the previous example, if the price of the predator is seven times of the price of the prey, and the cost of harvesting is negligible, then $S^*_{N_1} = 231646$, $S^*_{N_2} = 216386$, $S^*_{P_1} = 28865$ and $S^*_{P_2} = 23779$ are obtained. Clearly using these optimal escapements produces a negative first period harvest for prey subpopulation two, since the initial population size is $\bar{N}_2 = 205331$. However, using this negative harvest strategy in the first period of harvesting produces positive optimal equilibrium harvests $H^*_{N_1} = 97203$, $H^*_{N_2} = 124194$, $H^*_{P_1} = 55707$ and $H^*_{N_2} = 61448$, with total harvests $H^*_N = 221398$ and $H^*_P = 117155$.

Another example is a negative equilibrium harvest. Tuck and Possingham (1994) showed that if one subpopulation is a relative exporter but has a smaller proportion of juveniles which do not migrate, then the optimal harvest for that subpopulation is negative. I use the same parameters as them to show that in the presence of a predator this negative harvest is also optimal. In practice, a negative harvest is impossible to be applied . There are two possible ways of dealing with a negative harvest. First, we can use a constrained harvest function

$$H^*_{X_i} = \begin{cases} X_i - S^*_{X_i} & \text{if } X_i \geq S^*_{X_i} \\ 0 & \text{if } X_i < S^*_{X_i}. \end{cases} \tag{5.22}$$

Using this harvest function, if the suggested optimal escapement is higher than the existing population size we should not harvest the population at all. Second, as suggested by Tuck and Possingham (1994), if the optimal equilibrium harvest for subpopulation i is negative, we set $H_{X_i} = 0$ and find a new optimal escapement from equation (4.11) under this zero harvest constraint.

Assume that a negative harvest occurs in prey subpopulation two. If a negative harvest is impossible, then we need to maximise $J_1(S_{N_{10}}, S_{N_{20}}, S_{P_{10}}, S_{P_{20}})$ subject to $H_{N_2} = 0$, that is, a zero harvest for prey subpopulation two. Assuming all optimal escapements are constant, an equilibrium zero harvest for this subpopulation is obtained if the equilibrium population size for this subpopulation is the optimal escapement, that is, $N_{2k} = S_{N_{2(k-1)}}$. Hence this problem reduces to maximisation of the net present value PV in equation (4.11) subject to equations (5.3) and (5.4), with non-negative escapement less than, or equal to, the population size and

$$S_{N_{20}} = N_{21}, \tag{5.23}$$

with

$$\begin{aligned} N_{11} &= a_1 S_{N_{10}} + p_{11} F_1(S_{N_{10}}) + p_{21} F_2(S_{N_{20}}) + \alpha_1 S_{N_{10}} S_{P_{10}}, & (5.24) \\ N_{21} &= a_2 S_{N_{20}} + p_{12} F_1(S_{N_{10}}) + p_{22} F_2(S_{N_{20}}) + \alpha_2 S_{N_{20}} S_{P_{20}}, & (5.25) \\ P_{11} &= b_1 S_{P_{10}} + q_{11} G_1(S_{P_{10}}) + q_{21} G_2(S_{P_{20}}) + \beta_1 S_{N_{10}} S_{P_{10}}, & (5.26) \\ P_{21} &= b_2 S_{P_{20}} + q_{12} G_1(S_{P_{10}}) + q_{22} G_2(S_{P_{20}}) + \beta_2 S_{N_{20}} S_{P_{20}}. & (5.27) \end{aligned}$$

The Lagrangian for the maximisation is

$$\begin{aligned} \mathcal{L} &= J_1(S_{N_{10}}, S_{N_{20}}, S_{P_{10}}, S_{P_{20}}) - \lambda \left[S_{N_{20}} - (a_2 S_{N_{20}} + p_{12} F_1(S_{N_{10}}) \right. \\ &\quad \left. + \, p_{22} F_2(S_{N_{20}}) + \alpha_2 S_{N_{20}} S_{P_{20}}) \right]. \end{aligned} \tag{5.28}$$

A necessary condition for the maximum is $\frac{\partial \mathcal{L}}{\partial S_{N_{10}}} = \frac{\partial \mathcal{L}}{\partial S_{N_{20}}} = \frac{\partial \mathcal{L}}{\partial S_{P_{10}}} = \frac{\partial \mathcal{L}}{\partial S_{P_{20}}} = 0$. Using these necessary conditions and considering the facts that $N_{21} = S_{N_{20}}$ and $S_{N_{20}}$ is constant with respect to $S_{N_{10}}$ we obtain

$$\begin{aligned} \frac{\partial \mathcal{L}}{\partial S_{N_{10}}} &= -\left(p_N - c_{N_1}(S_{N_{10}})\right) \\ &\quad + \rho \left[\left(p_N - c_{N_1}(N_{11})\right) \frac{\partial N_{11}}{\partial S_{N_{10}}} + \left(p_N - c_{N_2}(N_{21})\right) \frac{\partial N_{21}}{\partial S_{N_{10}}} \right. \\ &\quad \left. + \left(p_P - c_{P_1}(P_{11})\right) \frac{\partial P_{11}}{\partial S_{N_{10}}} + \left(p_P - c_{P_2}(P_{21})\right) \frac{\partial P_{21}}{\partial S_{N_{10}}} \right] \\ &\quad - \lambda[-p_{12} F_1'(S_{N_{10}})] = 0. \end{aligned} \tag{5.29}$$

Since $N_{21} = S_{N_{20}}$ and $S_{N_{20}}$ is a constant with respect to $S_{N_{10}}$, then

$$\begin{aligned} \frac{\partial \mathcal{L}}{\partial S_{N_{10}}} &= -(p_N - c_{N_1}(S_{N_{10}})) + \rho\left[(p_N - c_{N_1}(N_{11}))\,(a_1 + p_{11}F_1'(S_{N_{10}})\right. \\ &\quad \left. + \; \alpha_1 S_{P_{10}}) + (p_P - c_{P_1}(P_{11}))(\beta_1 S_{P_{10}})\right] + \lambda[p_{12}F_1'(S_{N_{10}})] = 0. \end{aligned} \tag{5.30}$$

Similarly,

$$\begin{aligned} \frac{\partial \mathcal{L}}{\partial S_{N_{20}}} &= -(p_N - c_{N_1}(S_{N_{20}})) \\ &\quad +\rho\left[(p_N - c_{N_1}(N_{11}))\,\frac{\partial N_{11}}{\partial S_{N_{20}}} + (p_N - c_{N_2}(N_{21}))\,\frac{\partial N_{21}}{\partial S_{N_{20}}}\right. \\ &\quad \left. + \; (p_P - c_{P_1}(P_{11}))\,\frac{\partial P_{11}}{\partial S_{N_{20}}} + (p_P - c_{P_2}(P_{21}))\,\frac{\partial P_{21}}{\partial S_{N_{20}}}\right] \\ &\quad -\lambda[1 - (a_2 + p_{22}F_1'(S_{N_{20}}) + \alpha_2 S_{P_{20}})] \\ &= -(p_N - c_{N_2}(S_{N_{20}})) + \rho\left[(p_N - c_{N_1}(N_{11}))\,(p_{21}F_2'(S_{N_{20}}))\right. \\ &\quad \left. + \; (p_N - c_{N_2}(N_{21})) + (p_P - c_{P_2}(P_{21}))(\beta_2 S_{P_{20}})\right] \\ &\quad -\lambda[1 - (a_2 + p_{22}F_2'(S_{N_{20}}) + \alpha_2 S_{P_{20}})] = 0. \end{aligned} \tag{5.31}$$

$$\begin{aligned} \frac{\partial \mathcal{L}}{\partial S_{P_{10}}} &= -(p_P - c_{P_1}(S_{P_{10}})) \\ &\quad +\rho\left[(p_N - c_{N_1}(N_{11}))\frac{\partial N_{11}}{\partial S_{P_{10}}} + (p_N - c_{N_2}(N_{21}))\frac{\partial N_{21}}{\partial S_{P_{10}}}\right. \\ &\quad \left. + \; (p_P - c_{P_1}(P_{11}))\frac{\partial P_{11}}{\partial S_{P_{10}}} + (p_P - c_{P_2}(P_{21}))\frac{\partial P_{21}}{\partial S_{P_{10}}}\right] \\ &= -(p_P - c_{P_1}(S_{P_{10}})) + \rho\left[(p_N - c_{N_1}(N_{11}))\alpha_1 S_{N_{10}}\right. \\ &\quad +(p_P - c_{P_1}(P_{11}))(b_1 + q_{11}G_1'(S_{P_{10}}) + \beta_1 S_{N_{10}}) \\ &\quad \left. + \; (p_P - c_{P_2}(P_{21}))q_{12}G_1'(S_{P_{10}})\right] = 0. \end{aligned} \tag{5.32}$$

$$\begin{aligned} \frac{\partial \mathcal{L}}{\partial S_{P_{20}}} &= -(p_P - c_{P_2}(S_{P_{20}})) \\ &\quad +\rho\left[(p_N - c_{N_1}(N_{11}))\frac{\partial N_{11}}{\partial S_{P_{20}}} + (p_N - c_{N_2}(N_{21}))\frac{\partial N_{21}}{\partial S_{P_{20}}}\right. \\ &\quad \left. + \; (p_P - c_{P_1}(P_{11}))\frac{\partial P_{11}}{\partial S_{P_{20}}} + (p_P - c_{P_2}(P_{21}))\frac{\partial P_{21}}{\partial S_{P_{20}}}\right] \\ &= -(p_P - c_{P_2}(S_{P_{20}})) + \rho[(p_P - c_{P_1}(P_{11}))(q_{21}G_2'(S_{P_{20}}) \\ &\quad +(p_P - c_{P_2}(P_{21}))(b_2 + q_{22}G_2'(S_{P_{20}}) + \beta_2 S_{N_{20}}) + \lambda\alpha_2 S_{N_{20}} \\ &= 0. \end{aligned} \tag{5.33}$$

Since $N_{21} = S_{N_{20}}$, then from equation (5.31)

$$\begin{aligned} \lambda &= \frac{(\rho - 1)(p_N - c_{N_2}(S_{N_{20}})) + \rho p_{21}F_2'(S_{N_{20}})(p_N - c_{N_1}(N_{11}))}{1 - (a_2 + p_{22}F_2'(S_{N_{20}}) + \alpha_2 S_{P_{20}})} \\ &\quad + \frac{\rho\beta_2 S_{P_{20}}(p_P - c_{P_2}(P_{21}))}{1 - (a_2 + p_{22}F_2'(S_{N_{20}}) + \alpha_2 S_{P_{20}})}. \end{aligned} \tag{5.34}$$

Let $X_\alpha = 1 - (a_2 + p_{22}F_2'(S_{N_{20}}) + \alpha_2 S_{P_{20}})$. Substitute λ into equations (5.30), (5.32), and (5.33) to obtain

$$\begin{aligned}
\frac{(p_N - c_{N_1}(S_{N_{10}}))}{\rho} &= (p_N - c_{N_1}(N_{11}))\,[a_1 + p_{11}F_1'(S_{N_{10}}) + \alpha_1 S_{P_{10}})] \\
&\quad + (p_P - c_{P_1}(P_{11}))\,[\beta_1 S_{P_{10}}] \\
&\quad + (p_N - c_{N_2}(S_{N_{20}}))\left[\frac{p_{12}F_1'(S_{N_{10}})(1 - 1/\rho)}{X_\alpha}\right] \\
&\quad + (p_N - c_{N_1}(N_{11}))\left[\frac{p_{12}p_{21}F_1'(S_{N_{10}})F_2'(S_{N_{20}})}{X_\alpha}\right] \\
&\quad + (p_P - c_{P_2}(P_{21}))\left[\frac{p_{12}F_1'(S_{N_{10}})\beta_2 S_{P_{20}})}{X_\alpha}\right],
\end{aligned} \tag{5.35}$$

$$\begin{aligned}
\frac{(p_P - c_{P_2}(S_{P_{20}}))}{\rho} &= (p_P - c_{P_2}(P_{21}))\,[b_2 + q_{22}G_2'(S_{P_{20}}) + \beta_2 S_{N_{20}})] \\
&\quad + (p_P - c_{P_1}(P_{11}))\,[q_{21}G_2'(S_{P_{20}})] \\
&\quad + (p_N - c_{N_2}(S_{N_{20}}))\left[\frac{\alpha_2 S_{N_{20}}(1 - 1/\rho)}{X_\alpha}\right] \\
&\quad + (p_N - c_{N_1}(N_{11}))\left[\frac{p_{21}F_2'(S_{N_{20}})\alpha_2 S_{N_{20}}}{X_\alpha}\right] \\
&\quad + (p_P - c_{P_2}(P_{21}))\left[\frac{\alpha_2 S_{N_{20}}\beta_2 S_{P_{20}})}{X_\alpha}\right],
\end{aligned} \tag{5.36}$$

$$\begin{aligned}
\frac{(p_P - c_{P_1}(S_{P_{10}}))}{\rho} &= (p_P - c_{P_1}(P_{11}))\,[b_1 + q_{11}G_1'(S_{P_{10}}) + \beta_1 S_{N_{10}})] \\
&\quad + (p_P - c_{P_2}(P_{21}))\,[q_{12}G_1'(S_{P_{10}})] \\
&\quad + (p_N - c_{N_1}(N_{11}))\,[\alpha_1 S_{N_{10}}],
\end{aligned} \tag{5.37}$$

with $X_\alpha = 1 - (a_2 + p_{22}F_2'(S_{N_{20}}) + \alpha_2 S_{P_{20}})$. Solving the last three equations together with $S_{N_{20}} = N_{21}$ produces new optimal escapements for the metapopulation. These escapements give a non-negative harvest for prey subpopulation two. The net present value generated by applying this non-negative harvest method is higher than the net present value resulting from the "suboptimal" zero-harvest method in equation (5.22). To see the comparison between these two different methods, I will present a numerical example.

I assume all parameters for the predator-prey system are identical to the parameters in the first example, except that there is a relative exporter prey subpopulation which has a smaller proportion of juveniles being retained than the other prey subpopulation, that is, $p_{11} = p_{21} = 0.002$, and $p_{12} = p_{22} = 0.0001$, and $|\alpha_i| = \beta_i = 0.000001$. The equilibrium optimal escapements are $S^*_{N_1} = S^*_{N_2} = 95333$, $S^*_{P_1} = 14505$ and $S^*_{P_2} = 9010$, with equilibrium optimal harvests $H^*_{N_1} = 193828$, $H^*_{N_2} = -81574$, $H^*_{P_1} = 3118$ and $H^*_{N_2} = 26574$. If a negative harvest is not feasible, using the first method we find equilibrium optimal harvests $H^*_{N_1} = 64685$, $H^*_{N_2} = 0$, $H^*_{P_1} = 3118$ and $H^*_{N_2} = 25789$, while using the second method we find new optimal escapements $S^*_{N_1} = 100103$, $S^*_{N_2} = 8247$, $S^*_{P_1} = 14505$ and $S^*_{P_2} = 8927$, with equilibrium optimal

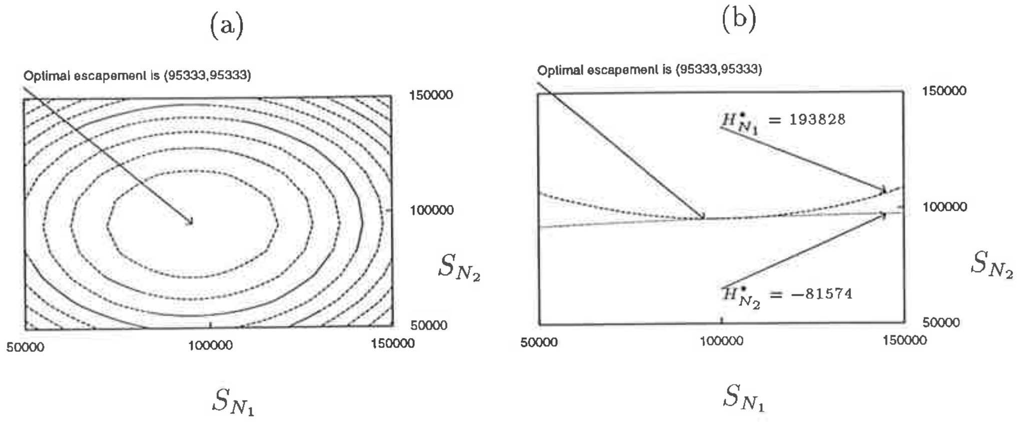


Figure 5.6: Contour plot for the profit as a function of prey escapements (Figure 5.6.a) and contour plot for the prey harvests as a function of prey escapements (Figure 5.6.b). Escapements $S^*_{N_1} = 95333$ and $S^*_{N_2} = 95333$ are found as the prey optimal escapements. These escapements produce a negative harvest $H^*_{N_2} = -81574$.

harvests $H^*_{N_1} = 64803$, $H^*_{N_2} = 0$, $H^*_{P_1} = 3142$ and $H^*_{N_2} = 25826$. If I assume the cost to put fish into the fishery is equal to the current price of the fish, in this example 8000/unit, then, neglecting all associated costs, the total revenue from the harvest is $(H_{N_1} + H_{N_2} + H_{P_1} + H_{P_2})8000 = 1136$ millions. This revenue is far above the revenue if we use the zero harvest from either the first or second method, that is, 749 millions from the first method and 750 millions from the second method. This shows that if it were possible to have a negative harvest then it could improve profit significantly (Figure 5.6). However, if it were not possible to have a negative harvest then using a harvesting strategy from the second method (equations (5.35) - (5.37)) gives a higher net present value than using a harvesting strategy from the first method (equation (5.22)).

5.1.9 Harvesting only the prey species

In this section, where only the prey species is harvested, I use the method of Lagrange multipliers (Clark, 1976a) to obtain the optimal harvesting strategy for the population. In this method the time horizon is set to infinity, hence the value function that should be maximised is

$$PV = \sum_{k=0}^{\infty} \rho^k \left[\Pi_{N_1}(N_{1k}, H_{N_{1k}}) + \Pi_{N_2}(N_{2k}, H_{N_{2k}})\right] \tag{5.38}$$

subject to equations (5.1) and (5.2), and $0 \leq H_{N_{ik}} \leq N_{ik}$, where

$$\Pi_{N_i}(N_{ik}, H_{N_{ik}}) = \int_{N_{ik}-H_{N_{ik}}}^{N_{ik}} (p - c_{N_i}(\xi))d\xi. \tag{5.39}$$

The Lagrangian for the maximisation is

$$\mathcal{L} = \sum_{k=0}^{\infty} \{\rho^k \Pi_{N_1}(N_{1k}, H_{N_{1k}}) + \Pi_{N_2}(N_{2k}, H_{N_{2k}})$$

$$\begin{aligned}
&-\lambda_{1k}[N_{1(k+1)} - a_1(N_{1k} - H_{N_{1k}}) - p_{11}F_1(N_{1k} - H_{N_{1k}}) \\
&-p_{21}F_2(N_{2k} - H_{N_{2k}}) - \alpha_1(N_{1k} - H_{N_{1k}})P_{1k}] \\
&-\lambda_{2k}[N_{2(k+1)} - a_2(N_{2k} - H_{N_{2k}}) - p_{12}F_1(N_{1k} - H_{N_{1k}}) \\
&-p_{22}F_2(N_{2k} - H_{N_{2k}}) - \alpha_2(N_{2k} - H_{N_{2k}})P_{2k}] \\
&-\lambda_{3k}[P_{1(k+1)} - b_1(P_{1k}) - q_{11}G_1(P_{1k}) - q_{21}G_2(P_{2k}) - \beta_1(N_{1k} - H_{N_{1k}})P_{1k} \\
&-\lambda_{4k}[P_{2(k+1)} - b_2(P_{2k}) - q_{12}G_1(P_{1k}) - q_{22}G_2(P_{2k}) - \beta_2(N_{2k} - H_{N_{2k}})P_{2k}.
\end{aligned} \tag{5.40}$$

To maximise the value function PV the following necessary conditions need to be satisfied:

1. $\frac{\partial \mathcal{L}}{\partial N_{ik}} = 0$, $\frac{\partial \mathcal{L}}{\partial P_{ik}} = 0$ for $k \geq 1$,
2. $\frac{\partial \mathcal{L}}{\partial H_{N_{ik}}} = 0$ for $k \geq 0$.

These conditions are equivalent to

$$\begin{aligned}
0 &= \rho^k \frac{\partial \Pi_{N_1}}{\partial N_{1k}} - \lambda_{1(k-1)} + \lambda_{1k}(a_1 + p_{11}F_1'(N_{1k} - H_{N_{1k}}) + \alpha_1 P_{1k}) \\
&\quad +\lambda_{2k}p_{12}F_1'(N_{1k} - H_{N_{1k}}) + \lambda_{3k}\beta_1 P_{1k},
\end{aligned} \tag{5.41}$$

$$\begin{aligned}
0 &= \rho^k \frac{\partial \Pi_{N_2}}{\partial N_{2k}} - \lambda_{2(k-1)} + \lambda_{2k}(a_2 + p_{22}F_2'(N_{2k} - H_{N_{2k}}) + \alpha_2 P_{2k}) \\
&\quad +\lambda_{1k}p_{21}F_2'(N_{2k} - H_{N_{2k}}) + \lambda_{4k}\beta_2 P_{2k},
\end{aligned} \tag{5.42}$$

$$\begin{aligned}
0 &= -\lambda_{3(k-1)} + \lambda_{3k}(b_1 + q_{11}G_1'(P_{1k}) + \beta_1(N_{1k} - H_{N_{1k}})) + \lambda_{4k}q_{12}G_1'(P_{1k}) \\
&\quad +\lambda_{1k}\alpha_1(N_{1k} - H_{N_{1k}})
\end{aligned} \tag{5.43}$$

$$\begin{aligned}
0 &= -\lambda_{4(k-1)} + \lambda_{4k}(b_2 + q_{22}G_2'(P_{2k}) + \beta_2(N_{2k} - H_{N_{2k}})) + \lambda_{3k}q_{21}G_2'(P_{2k}) \\
&\quad +\lambda_{2k}\alpha_2(N_{2k} - H_{N_{2k}})
\end{aligned} \tag{5.44}$$

$$\begin{aligned}
0 &= \rho^k \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} - \lambda_{1k}(a_1 + p_{11}F_1'(N_{1k} - H_{N_{1k}}) + \alpha_1 P_{1k}) \\
&\quad -\lambda_{2k}p_{12}F_1'(N_{1k} - H_{N_{1k}}) - \lambda_{3k}\beta_1 P_{1k},
\end{aligned} \tag{5.45}$$

$$\begin{aligned}
0 &= \rho^k \frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}} - \lambda_{2k}(a_2 + p_{22}F_2'(N_{2k} - H_{N_{2k}}) + \alpha_2 P_{2k}) \\
&\quad -\lambda_{1k}p_{21}F_2'(N_{2k} - H_{N_{2k}}) - \lambda_{4k}\beta_2 P_{2k}.
\end{aligned} \tag{5.46}$$

We obtain λ_1 and λ_2 by substituting equation (5.41) into (5.45) and equation (5.42) into (5.46), that is,

$$\lambda_{1(k-1)} = \rho^k \left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} \right), \tag{5.47}$$

$$\lambda_{2(k-1)} = \rho^k \left(\frac{\partial \Pi_{N_2}}{\partial N_{2k}} + \frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}} \right). \tag{5.48}$$

From equations (5.45) and (5.46) we obtain $\lambda_{3k}\beta_1 P_{1k}$ and $\lambda_{4k}\beta_2 P_{2k}$. Recall that $S_{N_{ik}} = N_{ik} - H_{N_{ik}}$, and let

$$F_{N_{ik}} = a_i + p_{ii} F_i'(S_{N_{ik}}) + \alpha_i P_{ik}, \tag{5.49}$$

$$G_{P_{ik}} = b_i + q_{ii} G_i'(P_{ik}) + \beta_i S_{N_{ik}}. \tag{5.50}$$

To reduce the complexity, let us consider the equilibrium escapement $S_{N_{i(k+1)}} = S_{N_{ik}}$, and equilibrium harvest $H_{N_{i(k+1)}} = H_{N_{ik}}$ with equilibrium population size $P_{i(k+1)} = P_{ik}$ for $k \geq 0$ and $N_{i(k+1)} = N_{ik}$ for $k > 0$. Multiply equation (5.43) with $\beta_1 P_{1k} \beta_2 P_{2k}$, and substitute λ_{1k}, λ_{2k}, $\lambda_{3k}\beta_1 P_{1k}$, and $\lambda_{4k}\beta_2 P_{2k}$ from equations (5.45) and (5.46) to obtain

$$\begin{aligned}
0 \;=\; & -\left[\rho^{k-1} \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} - \rho^k \left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} \right) F_{N_{1k}} \right] \beta_2 P_{2k} \\
& + \left[\rho^k \left(\frac{\partial \Pi_{N_2}}{\partial N_{2k}} + \frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}} \right) p_{12} F_1'(S_{N_{1k}}) \right] \beta_2 P_{2k} \\
& + \left[\rho^k \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} - \rho^{k+1} \left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} \right) F_{N_{1k}} \right] G_{P_{1k}} \beta_2 P_{2k} \\
& - \left[\rho^{k+1} \left(\frac{\partial \Pi_{N_2}}{\partial N_{2k}} + \frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}} \right) p_{12} F_1'(S_{N_{1k}}) \right] G_{P_{1k}} \beta_2 P_{2k} \\
& + \left[\rho^k \frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}} - \rho^{k+1} \left(\frac{\partial \Pi_{N_2}}{\partial N_{2k}} + \frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}} \right) F_{N_{2k}} \right] q_{12} G_1'(P_{1k}) \beta_1 P_{1k} \\
& - \left[\rho^{k+1} \left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} \right) p_{21} F_2'(S_{N_{2k}}) \right] q_{12} G_1'(P_{1k}) \beta_1 P_{1k} \\
& + \left[\rho^{k+1} \left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} \right) \alpha_1 S_{N_{1k}} \beta_1 \beta_2 P_{1k} P_{2k} \right].
\end{aligned} \tag{5.51}$$

Next divide this equation by ρ^{k+1}, and rearrange to obtain

$$\begin{aligned}
0 \;=\; & \left[\frac{1}{\rho} - G_{P_{1k}} \right] \left[\left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} \right) F_{N_{1K}} - \frac{1}{\rho} \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} \right] \beta_2 P_{2k} \\
& + \left[\left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} \right) \alpha_1 \beta_1 S_{N_{1k}} P_k \right] \beta_2 P_{2k} \\
& + \left[\frac{1}{\rho} - G_{P_{1k}} \right] \left[\left(\frac{\partial \Pi_{N_2}}{\partial N_{2k}} + \frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}} \right) p_{12} F_1'(S_{N_{1K}}) \right] \beta_2 P_{2k} \\
& + \left[\frac{1}{\rho} \frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}} - \left(\frac{\partial \Pi_{N_2}}{\partial N_{2k}} + \frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}} \right) F_{N_{2k}} \right] q_{12} G_1'(P_{1k}) \beta_1 P_{1k} \\
& - \left[\left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} \right) p_{21} F_2'(S_{N_{2k}}) \right] q_{12} G_1'(P_{1k}) \beta_1 P_{1k}.
\end{aligned} \tag{5.52}$$

Now multiply by $\rho/(\frac{1}{\rho} - G_{P_{1k}})$, and rearrange to obtain

$$\begin{aligned}
0 \;=\; & \left[-\frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} + \rho \left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} \right) F_{N_{1K}} + \rho^2 \left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} \right) \frac{\alpha_1 \beta_1 S_{N_{1k}} P_{1k}}{1 - \rho G_{P_{1k}}} \right. \\
& \left. + \rho \left(\frac{\partial \Pi_{N_2}}{\partial N_{2k}} + \frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}} \right) p_{12} F_1'(S_{N_{1K}}) \right] \beta_2 P_{2k}
\end{aligned}$$

$$\begin{aligned}&+\rho^2\left[\frac{1}{\rho}\frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}} - \left(\frac{\partial \Pi_{N_2}}{\partial N_{2k}} + \frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}}\right) F_{N_{2k}}\right.\\ &\left. - \left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}}\right) p_{21} F_2'(S_{N_{2k}})\right] \frac{q_{12} G_1'(P_{1k})\beta_1 P_{1k}}{1-\rho G_{P_{1k}}}.\end{aligned} \tag{5.53}$$

Similarly we can obtain

$$\begin{aligned} 0 \;=\; & \left[-\frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}} + \rho\left(\frac{\partial \Pi_{N_2}}{\partial N_{2k}} + \frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}}\right) F_{N_{2K}} + \rho^2\left(\frac{\partial \Pi_{N_2}}{\partial N_{2k}} + \frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}}\right)\frac{\alpha_2\beta_2 S_{N_{2k}} P_{2k}}{1-\rho G_{P_{2k}}}\right.\\ & \left. + \,\rho\left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}}\right) p_{21} F_2'(S_{N_{2K}})\right] \beta_1 P_{1k}\\ & +\rho^2\left[\frac{1}{\rho}\frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} - \left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}}\right) F_{N_{1k}}\right.\\ & \left. - \left(\frac{\partial \Pi_{N_2}}{\partial N_{2k}} + \frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}}\right) p_{12} F_1'(S_{N_{1k}})\right] \frac{q_{21} G_2'(P_{2k})\beta_2 P_{2k}}{1-\rho G_{P_{2k}}},\end{aligned} \tag{5.54}$$

with

$$\frac{\partial \Pi_{N_i}}{\partial H_{N_{ik}}} = p - c_N(S_{N_{ik}}), \tag{5.55}$$

$$\frac{\partial \Pi_{N_i}}{\partial N_{ik}} + \frac{\partial \Pi_{N_i}}{\partial H_{N_{ik}}} = p - c_N(N_{ik}). \tag{5.56}$$

These implicit escapement equations are difficult to interpret. In the following section I give a numerical example to give some insight of how these escapements differ from the escapements which occur if either we harvest both species using predator-prey harvesting theory as in the previous section or if we harvest only the prey species by ignoring the presence of the predator. Furthermore, I make the following assumptions.

1. Costs are negligible and prices are not different between the patches.
2. There is no migration between predator subpopulations, that is, $q_{12} = q_{21} = 0$.

Numerical example

In this section I present a numerical example to illustrate optimal escapements for a two-patch predator-prey metapopulation when we harvest only the prey species. For the purpose of comparison, parameters for the prey population are those used by Tuck and Possingham (1994).

Assume that the prey, N_i, in both patches have carrying capacities $K_1 = K_2 = 400000$, with intrinsics growth rates $r_1 = r_2 = 1000$ and adult survival rates per period $a_1 = a_2 = 0.001$. The prey has symmetrical migration, that is, $p_{11} = p_{22} = 0.001$ and $p_{12} = p_{21} = 0.003$, hence there is no relative source/sink or exporter/importer prey subpopulation. The discounting rate δ is 10%. Before the exploitation begins, it is assumed that the population is in the equilibrium state. In the absence of the predator, the unharvested population sizes for prey subpopulations one and two are $\bar{N}_1 = \bar{N}_2 = 300100$. The optimal escapements for prey subpopulations one and two are $S^*_{N_{1s}} = S^*_{N_{2s}} = 145050$, hence both prey subpopulation are harvested equally with

Migration parameters		PPM (prey)	PPM (both)	SSM
	$q_{11} = 0.004$	$S^*_{N_1} = 118348$	$S^*_{N_1} = 145050$	$S^*_{N_1} = 145050$
$p_{11} = 0.001$	$q_{22} = 0.002$	$S^*_{N_2} = 112955$	$S^*_{N_2} = 145050$	$S^*_{N_2} = 145050$
$p_{22} = 0.001$	$q_{11} = 0.002$	$S^*_{N_1} = 112955$	$S^*_{N_1} = 145050$	$S^*_{N_1} = 145050$
$p_{12} = 0.003$	$q_{22} = 0.004$	$S^*_{N_2} = 118348$	$S^*_{N_2} = 145050$	$S^*_{N_2} = 145050$
$p_{21} = 0.003$	$q_{11} = 0.003$	$S^*_{N_1} = 116424$	$S^*_{N_1} = 145050$	$S^*_{N_1} = 145050$
	$q_{22} = 0.003$	$S^*_{N_2} = 116424$	$S^*_{N_2} = 145050$	$S^*_{N_2} = 145050$
	$p_{11} = p_{22} = 0.001$	$S^*_{N_1} = 116424$	$S^*_{N_1} = 145050$	$S^*_{N_1} = 145050$
$q_{11} = 0.003$	$p_{12} = p_{21} = 0.003$	$S^*_{N_2} = 116424$	$S^*_{N_2} = 145050$	$S^*_{N_2} = 145050$
$q_{22} = 0.003$	$p_{11} = p_{12} = 0.001$	$S^*_{N_1} = 50272$	$S^*_{N_1} = 90100$	$S^*_{N_1} = 90100$
$q_{12} = 0.000$	$p_{21} = p_{22} = 0.003$	$S^*_{N_2} = 142028$	$S^*_{N_2} = 163367$	$S^*_{N_2} = 163367$
$q_{21} = 0.000$	$p_{11} = p_{12} = 0.003$	$S^*_{N_1} = 142028$	$S^*_{N_1} = 163367$	$S^*_{N_1} = 163367$
	$p_{21} = p_{22} = 0.001$	$S^*_{N_2} = 50272$	$S^*_{N_2} = 90100$	$S^*_{N_2} = 90100$

Table 5.7: Escapement comparisons from three different methods: From predator-prey metapopulation harvesting theory when harvesting only targets the prey species (PPM (prey)); From predator-prey metapopulation harvesting theory when harvesting targets both species (PPM (both)); From single-species harvesting theory, that is, when the presence of predator is ignored (SSM). In this example predator efficiency is 100%.

first period optimal harvests $H^*_{N_{1s}} = H^*_{N_{2s}} = 155050$ and equilibrium optimal harvests $H^*_{N_{1s}} = H^*_{N_{2s}} = 224900$.

Now suppose the predator, P_i, is present. For simplicity I choose intrinsic growth rates of the predator as $s_1 = s_2 = 1000$ with the carrying capacities $L_1 = L_2 = 40000$. I assume the predator's adult survival per period do not different from the prey's adult survival and do not differ between patches, hence $b_1 = b_2 = 0.001$. The predator in patch one is assumed to be a relative source and exporter subpopulation, with migration parameters $q_{12} = q_{21} = 0$, $q_{11} = 0.004$, and $q_{22} = 0.002$. Let us assume $|\alpha_i| = \beta_i = 0.00001$, that is, the predator has a high biomass conversion efficiency. Using NAG routine c05nbf, one of the positive equilibrium population sizes for this two-patch predator-prey system, that is, $(\bar{N}_1, \bar{N}_2, \bar{P}_1, \bar{P}_2) = (250123, 228804, 55022, 65781)$, is obtained. From equations (5.53) and (5.54) together with $P_{i(k+1)} = P_{i(k)}$, equilibrium escapements when we harvest only the prey population are found. These escapements are $S^*_{N_1} = 118348$ and $S^*_{N_2} = 112955$. These escapements are lower than the escapements we get if we use single-species metapopulation theory which produces $S^*_{N_{1s}} = S^*_{N_{2s}} = 145050$ (see Table 5.7).

Both escapements from single-species metapopulation harvesting theory are equal. This is because both prey subpopulations are identical, for example, there is no source or sink subpopulation. However, using escapements from equations (5.53) and (5.54), the optimal escapement for the prey subpopulation living in the same patch with the relative source predator subpopulation is higher than the escapement for the other prey subpopulation that lives in the same patch with the relative sink subpopulation. It suggests that the rule of thumb to harvest a predator-prey metapopulation described in Result 8 may no longer true if we only harvest one of the species. However, we still harvest a relative source prey subpopulation more conservatively than a relative sink subpopulation (see Tables 5.7 and 5.8 for the value of $q_{11} = q_{22} = 0.003$ with predator efficiency 100% and 75%, respectively). Tables 5.7 and 5.8 show that if both

Migration parameters		PPM (prey)	PPM (both)	SSM
	$q_{11} = 0.004$	$S^*_{N_1} = 121077$	$S^*_{N_1} = 143461$	$S^*_{N_1} = 145050$
$p_{11} = 0.001$	$q_{22} = 0.002$	$S^*_{N_2} = 117813$	$S^*_{N_2} = 144375$	$S^*_{N_2} = 145050$
$p_{22} = 0.001$	$q_{11} = 0.002$	$S^*_{N_1} = 117813$	$S^*_{N_1} = 144375$	$S^*_{N_1} = 145050$
$p_{12} = 0.003$	$q_{22} = 0.004$	$S^*_{N_2} = 121077$	$S^*_{N_2} = 143461$	$S^*_{N_2} = 145050$
$p_{21} = 0.003$	$q_{11} = 0.003$	$S^*_{N_1} = 119918$	$S^*_{N_1} = 143765$	$S^*_{N_1} = 145050$
	$q_{22} = 0.003$	$S^*_{N_2} = 119918$	$S^*_{N_2} = 143765$	$S^*_{N_2} = 145050$
	$p_{11} = p_{22} = 0.001$	$S^*_{N_1} = 119918$	$S^*_{N_1} = 143765$	$S^*_{N_1} = 145050$
$q_{11} = 0.003$	$p_{12} = p_{21} = 0.003$	$S^*_{N_2} = 119918$	$S^*_{N_2} = 143765$	$S^*_{N_2} = 145050$
$q_{22} = 0.003$	$p_{11} = p_{12} = 0.001$	$S^*_{N_1} = 53027$	$S^*_{N_1} = 87295$	$S^*_{N_1} = 90100$
$q_{12} = 0.000$	$p_{21} = p_{22} = 0.003$	$S^*_{N_2} = 144961$	$S^*_{N_2} = 162536$	$S^*_{N_2} = 163367$
$q_{21} = 0.000$	$p_{11} = p_{12} = 0.003$	$S^*_{N_1} = 144961$	$S^*_{N_1} = 162536$	$S^*_{N_1} = 163367$
	$p_{21} = p_{22} = 0.001$	$S^*_{N_2} = 53027$	$S^*_{N_2} = 87295$	$S^*_{N_2} = 90100$

Table 5.8: Escapement comparisons from three different methods: From predator-prey metapopulation harvesting theory when harvesting only targets the prey species (PPM (prey)); From predator-prey metapopulation harvesting theory when harvesting targets both species (PPM (both)); From single-species harvesting theory, that is, when the presence of predator is ignored (SSM). In this example predator efficiency is 75%.

predator subpopulations are identical, and so are the prey subpopulations, then both prey optimal escapements are equal, that is, $S^*_{N_1} = S^*_{N_2} = 116424$ if predator efficiency is 100% and $S^*_{N_1} = S^*_{N_2} = 119918$ if predator efficiency is 75%.

To summarise, in this section I have discussed optimal escapements for a predator-prey metapopulation when only the prey population is harvested. Similar to optimal escapements for one period to go discussed in Chapter 4, numerical examples in this section suggest that the rule described in Result 8 is only partially true, when only the prey species is harvested. That is, we still harvest a relative source prey subpopulation conservatively if the predator populations are identical in both patches. On the other hand, if one of the predator subpopulations is a relative source subpopulation, we may not harvest the prey living in the same patch with the relative sink predator subpopulation conservatively.

5.2 The second model: Predator recruitment model

In the previous section I showed that Tuck and Possingham's (1994) rules of thumb are preserved in the presence of a predator under some circumstances. It was also shown that if the cost of harvesting is negligible and there is no market price differential between the prey and predator, then to establish the third rule of thumb the predator efficiency needs to be extremely high – the predator has to be able to convert all food from eating one prey into one offspring. This is unlikely to occur in nature. However, if the predator is very valuable compared to the prey, then we can establish a rule similar to Tuck and Possingham's (1994) third rule of thumb, that is, we would harvest a relative source prey/predator subpopulation more conservatively than if we use the strategy from well-mixed predator-prey harvesting theory, without requiring extremely high predator efficiency.

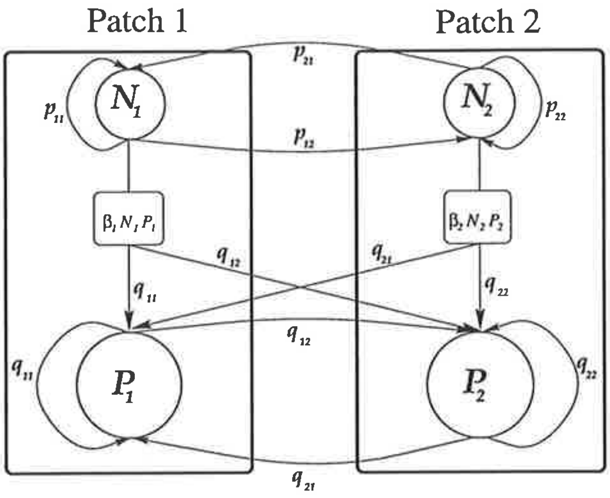


Figure 5.7: The relationships between the dynamics of the populations in a two-patch predator-prey metapopulation. The number of prey and predator are N_i and P_i, respectively. The prey and predator juvenile migration rates are p_{ij} and q_{ij}, respectively. The number of predator's offsprings in patch i from the conversion of eaten prey is $\beta_i N_i P_i$, which is distributed into patch i and j with proportion q_{ii} and q_{ij} respectively, while some of them $(1-q_{ii}-q_{ij})$ either die or are lost from the system.

The model in the previous section assumes that prey conversion in a patch translates into an increased reproduction in that patch only. The model can also be interpreted as meaning that increased predation increases predator survival. Usually predation will affect predator reproductive more than its survival. In this section, I modify the model to allow some of the enhanced reproduction to migrate between patches and to assume that predation affects predator recruitment (see Figure 5.7). This section helps us to determine that the rules described in the previous model are robust to a change in model structure. I also provide an example of dealing with a negative harvest.

Consider a predator-prey metapopulation that coexists in two different patches, patch one and patch two. Using the same notation as the model in the previous section, let the dynamics of the exploited metapopulation of these two species be given by the equations

$$N_{i(k+1)} = a_i S_{N_{ik}} + \alpha_i S_{N_{ik}} S_{P_{ik}} + p_{ii} F_i(S_{N_{ik}}) + p_{ji} F_j(S_{N_{jk}}), \tag{5.57}$$

$$\begin{aligned} P_{i(k+1)} &= b_i S_{P_{ik}} + q_{ii}(G_i(S_{P_{ik}}) + \beta_i S_{N_{ik}} S_{P_{ik}}) \\ &\quad + q_{ji}(G_j(S_{P_{jk}}) + \beta_j S_{N_{jk}} S_{P_{jk}}), \end{aligned} \tag{5.58}$$

where the functions $F_i(N_{ik})$ and $G_i(P_{ik}) + \beta_i S_{N_{ik}} S_{P_{ik}}$, $i = 1, 2$, are the recruit production functions of the prey and predator in patch i at time period k, respectively. I will assume that $F_i(N_{ik}) = r_i N_{ik}(1 - N_{ik}/K_i)$ and $G_i(P_{ik}) = s_i P_{ik}(1 - P_{ik}/L_i)$, where r_i

(s_i) denotes the intrinsic growth rate of the prey (predator) and K_i (L_i) denotes the local carrying capacity of the prey (predator), respectively, with $\alpha_i < 0$ and $\beta_i > 0$.

Moreover, if Π_{Xi} represents the present value of net revenue from harvesting population X in patch i, and ρ is a discounting factor, then to obtain the optimal harvest from the fishery we should maximise the net present value

$$PV = \sum_{k=0}^{T} \rho^k \sum_{i=1}^{2} \sum_{X \in \{N,P\}} \Pi_{Xi}(X_{ik}, S_{X_{ik}}) \tag{5.59}$$

subject to equations (5.57) and (5.58), with non-negative escapement less than, or equal to, the population size. I will assume $\rho = 1/(1+\delta)$ for the remainder of this chapter, where δ denotes a periodic discounting rate, with $\Pi_{Xi}(X_{ik}, S_{X_{ik}}) = \int_{S_{X_{ik}}}^{X_{ik}} (p_X - c_{Xi}(\xi))d\xi$, which reflects the net revenue from the harvest $H_{X_{ik}}$ of the local population X_i in period k. Following the previous section for the first model, implicit expression of optimal escapements $S^*_{N_{i0}}$ and $S^*_{P_{i0}}$ are found in the form

$$\begin{aligned}\frac{p_N - c_{Ni}(S^*_{N_{i0}})}{\rho} &= \big(a_i + \alpha_i S^*_{P_{i0}} + p_{ii}F'_i(S^*_{N_{i0}})\big)\big(p_N - c_{Ni}(N_{i1})\big) \\ &\quad + p_{ij}F'_i(S^*_{N_{i0}})(p_N - c_{Nj}(N_{j1})) \\ &\quad + q_{ii}\beta_i S^*_{P_{i0}}\,(p_P - c_{Pi}(P_{i1})) \\ &\quad + q_{ij}\beta_i S^*_{P_{i0}}\,(p_P - c_{Pj}(P_{j1}))\,,\end{aligned} \tag{5.60}$$

$$\begin{aligned}\frac{p_P - c_{Pi}(S^*_{P_{i0}})}{\rho} &= \big(b_i + q_{ii}\beta_i S^*_{N_{i0}} + q_{ii}G'_i(S^*_{P_{i0}})\big)\big(p_P - c_{Pi}(P_{i1})\big) \\ &\quad + q_{ij}\beta_i S^*_{N_{i0}}(p_P - c_{Pj}(P_{j1})) \\ &\quad + q_{ij}G'_i(S^*_{P_{i0}})(p_P - c_{Pj}(P_{j1})) \\ &\quad + \alpha_i S^*_{N_{i0}}\,(p_N - c_{Ni}(N_{i1}))\,.\end{aligned} \tag{5.61}$$

These equations are the general form of the optimal harvesting equation for a two-patch predator-prey metapopulation. If $\alpha_i = \beta_i = 0$ then the optimal harvesting equation for a single-species metapopulation (Tuck and Possingham, 1994) is obtained. Furthermore if there is no migration between patches, $p_{ij} = q_{ij} = 0$ for $i \neq j$ and $F'(S) = a_i + p_{ii}F'_i(S_{N_{i0}})$ together with $\alpha_i = \beta_i = 0$ then the equation reduces to the optimal harvesting equation for a single-species population (Clark, 1976a). Using a similar proof to the one in Chapter 4, it can be shown that the escapements $S^*_{X_{i0}}$ found by solving these implicit equations are independent of the time horizon considered. I discuss some properties of these escapements in the following section.

5.2.1 Results and discussion

In this section, I discuss some properties of the optimal escapements in equations (5.60) and (5.61). I compare the optimal escapements between the two subpopulations. I also compare the optimal escapement to the escapements if the migration is ignored to see how important it is to use the theory presented here for choosing optimal escapements. Specifically, how important it is for the fishery manager to recognise and measure connections between subpopulations. For the remainder of the chapter I assume that the market price for the predator is higher than or equal to the price for the prey, that is $p_P = mp_N$ with $m \geq 1$, and prey vulnerability is the same in both patches, that is, $\alpha_1 = \alpha_2 = \alpha$.

Negligible costs analysis

To simplify the analysis and discussion, the costs of harvesting are assumed to be negligible. Using these assumptions, and substituting all derivatives of the logistic recruitment functions, F_i and G_i, into equations (5.60) and (5.61) we can find the optimal escapements $S^*_{N_i}$ and $S^*_{P_i}$, which are given by

$$S^*_{N_i} = \frac{A_i m(q_{i1} + q_{i2})\frac{2s_i}{L_i} + C_i B_i}{\Delta_i}, \tag{5.62}$$

$$S^*_{P_i} = \frac{B_i(p_{i1} + p_{i2})\frac{2r_i}{K_i} + C_i A_i}{\Delta_i}, \tag{5.63}$$

provided $\Delta_i = C_i^2 - m(p_{i1} + p_{i2})\frac{2r_i}{K_i}(q_{i1} + q_{i2})\frac{2s_i}{L_i} \neq 0$, with $A_i = \frac{1}{\rho} - (p_{i1} + p_{i2})r_i - a_i$, $B_i = \frac{m}{\rho} - m(q_{i1} + q_{i2})s_i - mb_i$, and $C_i = \alpha_i + m(q_{i1} + q_{i2})\beta_i$. It can be shown that if A_i and B_i are negative and C_i is non-positive with $C_i > max\{\frac{2B_i}{K_i}, \frac{2mA_i}{L_i}\}$ then $\Delta_i < 0$ and all resulting escapements, $S^*_{N_i}$ and $S^*_{P_i}$, are positive. If this is the case, I can also establish the following result.

Result 14 *(Escapement and harvest comparisons between subpopulations) Assume prey subpopulation one is a relative source, that is,* $(p_{11} + p_{12})r_1 > (p_{22} + p_{21})r_2$, *while all other parameters of the prey and the predator are identical for both subpopulations. If* A_i *and* B_i *are negative, and* C_i *is non-positive with* $C_i > max\{\frac{2B}{K}, \frac{2mA}{L}\}$, *then:*

$$S^*_{N_1} > S^*_{N_2} \text{ and } S^*_{P_1} \leq S^*_{P_2}.$$

Furthermore, if, in addition, $p_{i1} \leq p_{i2}$, $q_{i1} = q_{i2}$, $S^*_{N_i} \leq K_i$, $S^*_{P_i} \leq L_i$ *with* $S^*_{N_1}S^*_{P_1} > S^*_{N_2}S^*_{P_2}$, *then*

$$H^*_{N_1} < H^*_{N_2} \text{ and } H^*_{P_1} \geq H^*_{P_2}.$$

Proof

The first two parts can be proved analogously to the proof of Result 8 while the last two parts can be proved by substituting optimal escapements, $S^*_{N_i}$ and $S^*_{P_i}$, into the harvest equations $H^*_{N_i} = N_i - S^*_{N_i}$ and $H^*_{P_i} = P_i - S^*_{P_i}$, where N_i and P_i are given by prey and predator dynamic equations (5.57) and (5.58). ☐

Result 14 suggests that if the growth rate of the populations are higher than the reciprocal of the discounting factor $1/\rho$ (indicated by $A_i < 0$ and $B_i < 0$) and $C_i > max\{\frac{2B}{K}, \frac{2mA}{L}\}$ then we should protect the relative source prey subpopulation in two different ways: directly, with a higher escapement of the relative source prey subpopulation, and indirectly, with a lower escapement of the predator living in the same patch with the relative source prey subpopulation. Since $C_i > max\{\frac{2B}{K}, \frac{2mA}{L}\}$ can be written as $m(q_{ii} + q_{ij})\frac{\beta}{|\alpha|} > 1 + max\{\frac{2B}{K}, \frac{2mA}{L}\}/|\alpha|$, then we can interpret $C_i > max\{\frac{2B}{K}, \frac{2mA}{L}\}$ as a relatively high predator economic efficiency. Furthermore, if every escapement is less than each subpopulation's carrying capacity, lower escapement means higher harvest. This result is similar to the result in the previous model, only in the present model the predator economic efficiency is discounted by the predator migration survival $q_{ii} + q_{ij}$.

The following result enables us to compare escapements from the present methods to escapements if spatial heterogeneity is ignored. There are two different ways we could misinterpret the spatial structure of a metapopulation, first we could assume that there is no connection between the two patches, and second we could lump the two patches into one patch whose populations are well-mixed. In the following result, r_{iu} is the growth of prey subpopulation i if it is assumed there is no connection between the two prey subpopulations. This growth would be measured $r_{iu} = p_{ii}r_i + p_{ji}r_j$. Similarly, r_w is the growth of prey if it is assumed to be a well-mixed prey population. This growth would be measured $r_w = [(p_{11} + p_{12})r_1 + (p_{21} + p_{22})r_2]/2$. The growth of the predator populations, s_{iu} and s_w are measured analogously.

Result 15 *(Comparison of strategy with incorrect harvesting strategies) Let* $S^*_{N_i}$ *and* $S^*_{P_i}$ *denote the optimal escapement from the predator-prey metapopulation given by equations (5.62) and (5.63). Let* $S^*_{N_{iu}}$ *and* $S^*_{P_{iu}}$ *denote the optimal escapement if we incorrectly consider the system as a system consisting of two unconnected predator-prey systems and let* $S^*_{N_w}$ *and* $S^*_{P_w}$ *denote the optimal escapement if we incorrectly consider the system as a well-mixed predator-prey system. Let us assume prey subpopulation one is a relative exporter and source subpopulation with* $p_{12}r_1 > p_{21}r_2$ *and* $p_{11}r_1 \geq p_{22}r_2$*, all other parameters of the prey and the predator are identical for both subpopulations. Let* A_i *and* $B_1 = B_2 = B$ *are negative,* $C_1 = C_2 = C \leq 0$ *with* $C > max\{\frac{2B}{K}, \frac{2mA_i}{L}\}$*. If there is no predator mortality associated with migration,* $q_{ii} + q_{ij} = 1$*, then*

$$S^*_{N_1} > S^*_{N_{1u}},\ S^*_{N_2} < S^*_{N_{2u}},\ S^*_{P_1} \leq S^*_{P_{1u}} \text{ and } S^*_{P_2} \geq S^*_{P_{2u}}.$$

Furthermore, if the biological predator efficiency is equal to the ratio of the prey market price and predator market price, that is, $\frac{\beta}{|\alpha|} = \frac{1}{m}$*, then*

$$S^*_{N_1} > \tfrac{1}{2}S^*_{N_w},\ S^*_{N_2} < \tfrac{1}{2}S^*_{N_w},\ S^*_{P_1} \leq \tfrac{1}{2}S^*_{P_w} \text{ and } S^*_{P_2} \geq \tfrac{1}{2}S^*_{P_w}.$$

I do not provide the proof of the result above, since it is analogous to the proof of a similar result in the predator survival model (Section 5.1).

In reality, the condition that the biological predator efficiency, $\frac{\beta}{|\alpha|}$, is exactly the same as the inverse of the relative predator market price, m, is improbable. The biological predator efficiency could be any value equal to, or less than, as well as more than the inverse of the relative predator market price, as long as it is less than 100%. In this general case, Appendix 5A shows that, in some circumstances, if the two prey subpopulations have a non-overlapping generation and their total natural growth, $r_1(p_{11} + p_{12}) + r_2(p_{21} + p_{22})$, is less than three times of the reciprocal of the annual discounting factor, $1/\rho$, then assuming a predator-prey metapopulation as a well-mixed predator-prey population would over-harvest the relative source and exporter prey subpopulation. Note that individual natural growth $r_i(p_{ii} + p_{ij})$ should be more than the reciprocal of the annual discounting factor to ensure that optimal escapements from the predator-prey metapopulation are non-negative. A similar conclusion for the predator can be drawn, that is, we would over-harvest the predator living in the same patch with the relative sink and importer prey subpopulation if we incorrectly manage the population as a well-mixed predator prey system, whenever the total growth of the two predator subpopulations is less than three times of the reciprocal of the annual discounting factor and the growths of both predator subpopulations do not overlap.

5.2.2 Numerical examples

Let us assume that there is a two-patch predator-prey metapopulation where the prey in both patches have carrying capacities $K_1 = K_2 = 50000000$, intrinsic growth rates

$r_1 = r_2 = 10$, and adult survival rates per period $a_1 = a_2 = 0.001$. Prey juveniles migrate with $p_{11} = p_{12} = 0.3$ and $p_{21} = p_{22} = 0.1$, hence prey subpopulation one is a relative source and exporter subpopulation. Let the discounting rate δ be 10%. Now suppose predators are present in both patches with intrinsic growth rates $s_1 = s_2 = 4$, carrying capacities $L_1 = L_2 = 50000$, and adult survival rates per period $b_1 = b_2 = 0.001$. Predator juveniles migration is symmetrical with $q_{11} = q_{12} = q_{21} = q_{22} = 0.5$. Let $|\alpha_i| = 0.000001$ and $\beta_i = 0.0000001$, that is, the biological predator efficiency is 10%. Using equations (5.57) and (5.58), it can be shown that one of the positive equilibrium population sizes for this two-patch predator-prey metapopulation is $(\bar{N}_1, \bar{N}_2, \bar{P}_1, \bar{P}_2) = (36473692, 36473692, 83105, 83105)$. I assume harvesting begins with this equilibrium as the initial population size.

Using equations (5.62) and (5.63), the optimal escapements for the system, $S^*_{N_1} = 20420833$, $S^*_{N_2} = 11262500$ and $S^*_{P_1} = S^*_{P_2} = 18131$, are found with the first period optimal harvests $H^*_{N_1} = 16052859$, $H^*_{N_2} = 25211192$ and $H^*_{P_1} = H^*_{P_2} = 64973$, and the equilibrium optimal harvests $H^*_{N_1} = 24196828$, $H^*_{N_2} = 33512055$ and $H^*_{P_1} = H^*_{P_2} = 56835$. As suggested by Result 14, we should harvest the relative exporter and source prey subpopulation more conservatively than the relative importer and sink prey subpopulation (in terms of escapement $S^*_{N_1} > S^*_{N_2}$ and in terms of harvest $H^*_{N_1} < H^*_{N_2}$). There is no difference in escapement and harvest between both predator subpopulations. This is because the predator biological efficiency is exactly the same as the inverse of m, (m is the relative market value of the predator, where in this case $m = 10$ and $\beta/|\alpha| = 0.1$). Figure 5.8 shows that if $0 < m < 10$ then all rules in Result 14 are satisfied. However, if m is sufficiently large, in our example if $m > 10$, these rules may be violated. This is because large m causes predator economic efficiency to be more than 100% or $C > 0$ (see Result 14).

Figure 5.8 shows escapements and harvests which are plotted as functions of the ratio of the predator market price to the prey market price, m. The figures suggest that, in this example where the growth of the predator is relatively low ($s_i = 4$ while $r_i = 10$), if there is no difference between the market price of predator and prey ($m = 1$) then it is optimal to harvest the predator to extinction (Figure 5.8.b). While if m is very large (m is approximately more than 550) then it is optimal to leave the relative sink, which is also the relative importer, prey subpopulation unharvested, and eventually it is optimal to leave both prey subpopulations unharvested if m is even larger (lines in Figure 5.8.c). This rule is also observed for a single patch predator-prey system (Ragozin and Brown, 1985) and also observed in the first model in the previous section. This situation is different if there is no relative source/sink prey subpopulation. For example, if $p_{11} = p_{21} = 0.12$ and $p_{12} = p_{22} = 0.28$ then we should not harvest the relative exporter prey subpopulation (dots in Figure 5.8.c). [Note that in the example of the first model in Section 5.1.3, optimal equilibrium harvests are $H^*_{N_1} = 97203$, $H^*_{N_2} = 124194$, $H^*_{P_1} = 55707$ and $H^*_{N_2} = 61448$, with total harvests $H^*_N = 221398$ and $H^*_P = 117155$ if $p_N = \frac{1}{7}p_P$, while if $p_N = p_P$ then $H^*_N = 415692$ and $H^*_P = 61559$, and if $p_N = \frac{1}{5}p_P$ then $H^*_N = 326144$ and $H^*_P = 101375$. Therefore, the total harvest for the prey when $p_N = \frac{1}{7}p_P$ is lower and the total harvest for the predator is higher than the total harvest for the prey and predator, respectively, when $p_N = \frac{1}{5}p_P$ and $p_N = p_P$. This suggests that if the prey is less valuable in the market than the predator, then it is better to leave it as food for the predator which is more valuable.]

Furthermore, even when m is very small, that is, a high prey value compared to predator value, if the growth of the predator is sufficiently high, then predator extinction is not optimal. For example, if $s_i = 20$ with $m = 1$ then predator optimal escapements are $S^*_{N_1} = 656$ and $S^*_{N_2} = 11096$. Predator escapement in patch one is less than in patch two, this is because prey subpopulation one is a relative exporter and source subpopulation which should be more protected by leaving a lower predator escapement in that patch (see Result 14).

Dealing with an optimal harvest that is negative

As seen in the example above, the analysis presented here may produce negative harvests. A negative harvest could be interpreted as a seeding or restocking strategy. However, in many situations such a strategy is not practical. In this case, as in single population exploitation, we can use the harvest function

$$H^*_{X_i} = \begin{cases} X_i - S^*_{X_i} & \text{if } X_i \geq S^*_{X_i} \\ 0 & \text{if } X_i < S^*_{X_i}. \end{cases} \tag{5.64}$$

Another alternative is suggested by Tuck and Possingham (1994). To avoid a negative harvest, they use the following procedure. Assume that using the metapopulation harvesting theory, optimal equilibrium harvest for subpopulation i is negative. They set $H_{X_i} = 0$ and find a new optimal escapement from the maximisation of the value function under this zero harvest constraint. I apply the same procedure if the method presented in the previous section produces a negative harvest.

A negative harvest may be optimal for the subpopulation that exports a high proportion of larvae but only contributes a low proportion of the larvae to its own subpopulation. For example, if the juvenile migration parameters for the prey in the previous example are $p_{11} = p_{21} = 0.2$ and $p_{12} = p_{22} = 0.065$ with $m = 10$, then the optimal equilibrium harvest for prey subpopulation two is $H^*_{N_2} = -1427582$, while all other subpopulations have a positive harvest. This strategy suggests that we should seed prey into subpopulation two and harvest the results from prey subpopulation one and both predator subpopulations. Using the procedure suggested by Tuck and Possingham (1994), I set $H_{N_2} = 0$ and maximise the present value in equation (5.59) with this additional constraint. The new equilibrium optimal escapements $S^*_{N_1}$, $S^*_{N_2}$, $S^*_{P_1}$, and $S^*_{P_2}$ are found and satisfy equations

$$\begin{aligned} \frac{(p_N - c_{N_1}(S_{N_{10}}))}{\rho} &= (p_N - c_{N_1}(N_{11}))\left[a_1 + p_{11}F_1'(S_{N_{10}}) + \alpha_1 S_{P_{10}}\right] \\ &\quad + (p_P - c_{P_1}(P_{11}))\left[q_{11}\beta_1 S_{P_{10}}\right] \\ &\quad + (p_P - c_{P_2}(P_{21}))\left[q_{12}\beta_1 S_{P_{10}}\right] \\ &\quad + (p_N - c_{N_2}(S_{N_{20}}))\left[\frac{p_{12}F_1'(S_{N_{10}})(1 - 1/\rho)}{X_\alpha}\right] \\ &\quad + (p_N - c_{N_1}(N_{11}))\left[\frac{p_{12}p_{21}F_1'(S_{N_{10}})F_2'(S_{N_{20}})}{X_\alpha}\right] \\ &\quad + (p_P - c_{P_2}(P_{21}))\left[\frac{p_{12}F_1'(S_{N_{10}})q_{22}\beta_2 S_{P_{20}}}{X_\alpha}\right] \\ &\quad + (p_P - c_{P_1}(P_{11}))\left[\frac{p_{12}F_1'(S_{N_{10}})q_{21}\beta_2 S_{P_{20}}}{X_\alpha}\right], \end{aligned} \tag{5.65}$$

$$\frac{(p_P - c_{P_2}(S_{P_{20}}))}{\rho} = (p_P - c_{P_2}(P_{21}))\left[b_2 + q_{22}G_2'(S_{P_{20}}) + q_{22}\beta_2 S_{N_{20}}\right]$$

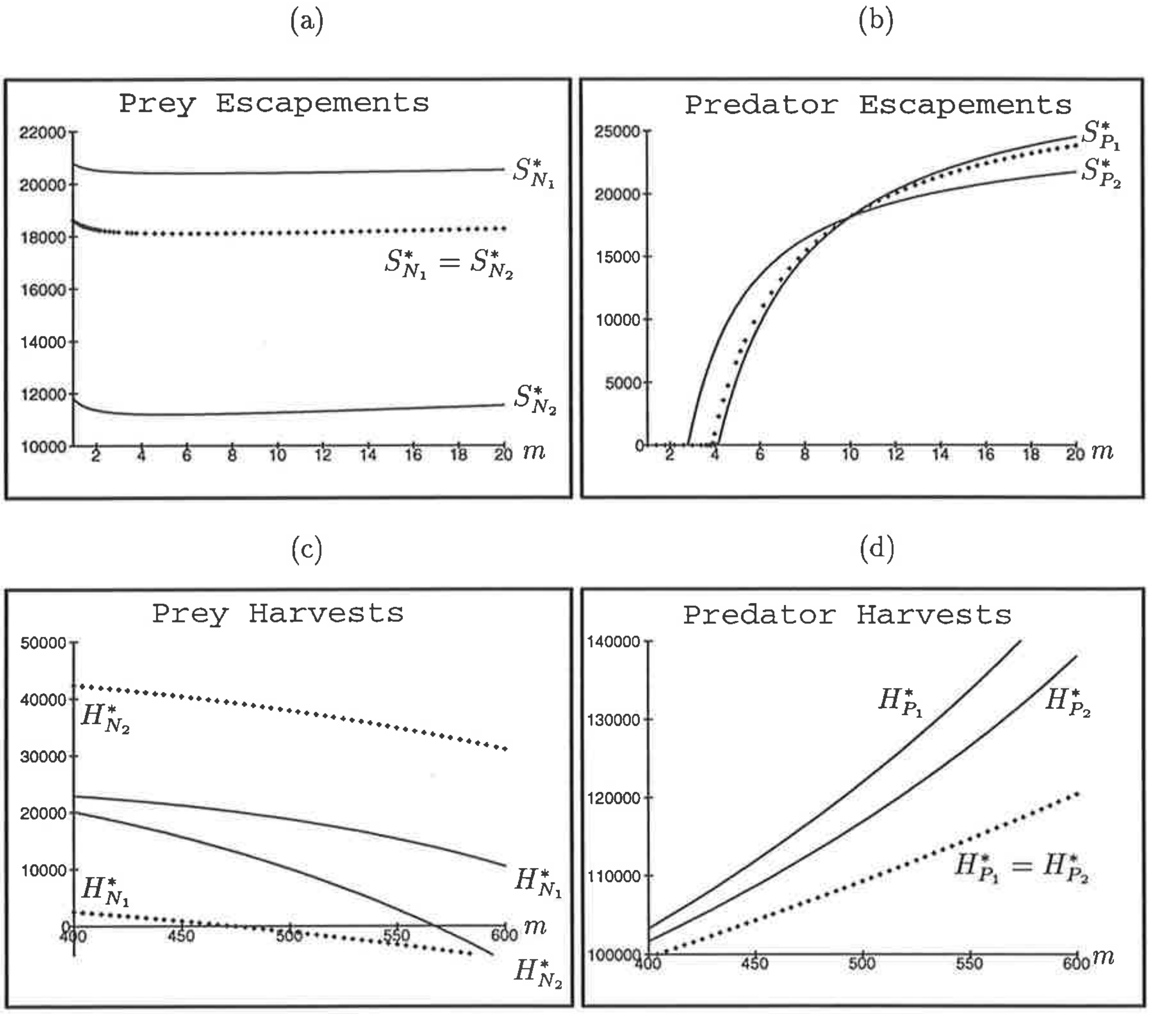

(a) (b) (c) (d)

Figure 5.8: Escapements and harvests are plotted as functions of ratio predator market price to prey market price, m. The prey numbers are in thousands. Lines indicate results if prey subpopulation one is a relative source subpopulation and dots indicate results if prey subpopulation one is a relative exporter subpopulation with no source/sink subpopulation (see text for details). The figures suggest that, in this example where the growth of the predator is relatively low, if there is no difference between both market price ($m = 1$) then it is optimal to harvest the predator to extinction (Figure 5.8.b). While if m is sufficiently large (m between 550 and 600) then it is optimal to leave the relative sink prey subpopulation (line in Figure 5.8.c) and the relative exporter prey subpopulation (dots in Figure 5.8.c) unharvested.

$$
\begin{aligned}
&+(p_P - c_{P_1}(P_{11}))\left[q_{21}G_2'(S_{P_{20}}) + q_{21}\beta_2 S_{N_{20}}\right] \\
&+(p_N - c_{N_2}(S_{N_{20}}))\left[\frac{\alpha_2 S_{N_{20}}(1-1/\rho)}{X_\alpha}\right] \\
&+(p_N - c_{N_1}(N_{11}))\left[\frac{p_{21}F_2'(S_{N_{20}})\alpha_2 S_{N_{20}}}{X_\alpha}\right] \\
&+(p_P - c_{P_2}(P_{21}))\left[\frac{\alpha_2 S_{N_{20}} q_{22}\beta_2 S_{P_{20}})}{X_\alpha}\right] \\
&+(p_P - c_{P_1}(P_{11}))\left[\frac{\alpha_2 S_{N_{20}} q_{21}\beta_2 S_{P_{20}})}{X_\alpha}\right], \qquad (5.66)
\end{aligned}
$$

$$
\begin{aligned}
\frac{(p_P - c_{P_1}(S_{P_{10}}))}{\rho} &= (p_P - c_{P_1}(P_{11}))\left[b_1 + q_{11}G_1'(S_{P_{10}}) + q_{11}\beta_1 S_{N_{10}}\right] \\
&\quad +(p_P - c_{P_2}(P_{21}))\left[q_{12}G_1'(S_{P_{10}}) + q_{12}\beta_1 S_{N_{10}}\right] \\
&\quad +(p_N - c_{N_1}(N_{11}))\left[\alpha_1 S_{N_{10}}\right], \qquad (5.67)
\end{aligned}
$$

with $X_\alpha = 1 - (a_2 + p_{22}F_2'(S_{N_{20}}) + \alpha_2 S_{P_{20}})$. Solving the last three equations together with $S_{N_{20}} = N_{21}$, and assuming $X_\alpha \neq 0$, produces a non-negative harvest for prey subpopulation two. Figure 5.9 shows total profit differences among the three methods, that is, a negative harvest from (5.62) and (5.63), a zero harvest from (5.64), and a zero harvest from (5.65) - (5.67).

If it is possible to implement a negative harvest, equilibrium optimal harvests $H^*_{N_1} = 26517750$, $H^*_{N_2} = -1427582$, and $H^*_{P_1} = H^*_{P_2} = 54642$ are found. However, if we can not use a negative harvest in managing the exploitation, then using the first method (equation (5.64)) we find that equilibrium optimal harvests are $H^*_{N_1} = 24720979$, $H^*_{N_2} = 0$ and $H^*_{P_1} = H^*_{P_2} = 52849$, while using the second method (equation (5.65) - (5.67)) we find new optimal escapements $S^*_{N_1} = 15249769$, $S^*_{N_2} = 12923857$, $S^*_{P_1} = 18131$, and $S^*_{P_2} = 16045$ with equilibrium optimal harvests $H^*_{N_1} = 24852974$, $H^*_{N_2} = 0$, $H^*_{P_1} = 50985$ and $H^*_{N_2} = 53069$ (see Figure 5.9). If we assume that the cost to put fish into the fishery is equal to the profit per fish harvested, then, neglecting all associated costs, the total revenue from the harvest, if a negative harvest is allowable, is $H_{N_1} + H_{N_2} + 10(H_{P_1} + H_{P_2}) = 26183008$ currency units. This revenue is above the revenue if we use zero harvest from either the first or second method, that is, 25777959 from the first method and 25893514 from the second method. This suggests the optimality of a negative harvest for the system or in other words shows that if it were possible to have a negative harvest then it would improve profit significantly. However, if the cost of seeding prey is higher than the profit from catching prey then zero harvest will be the best. In the example above if the cost to put fish into the fishery is twice the profit per fish from harvesting then the total revenue by allowing seeding strategy is 24755426 currency units, which is smaller than if we use zero harvest from the first or the second method.

5.3 Concluding remarks

In this chapter harvesting strategies for a spatially-structured predator-prey system were established. It was assumed that the interaction between the prey and the predator occurs in the adult stage. I investigated optimal harvesting strategies for two

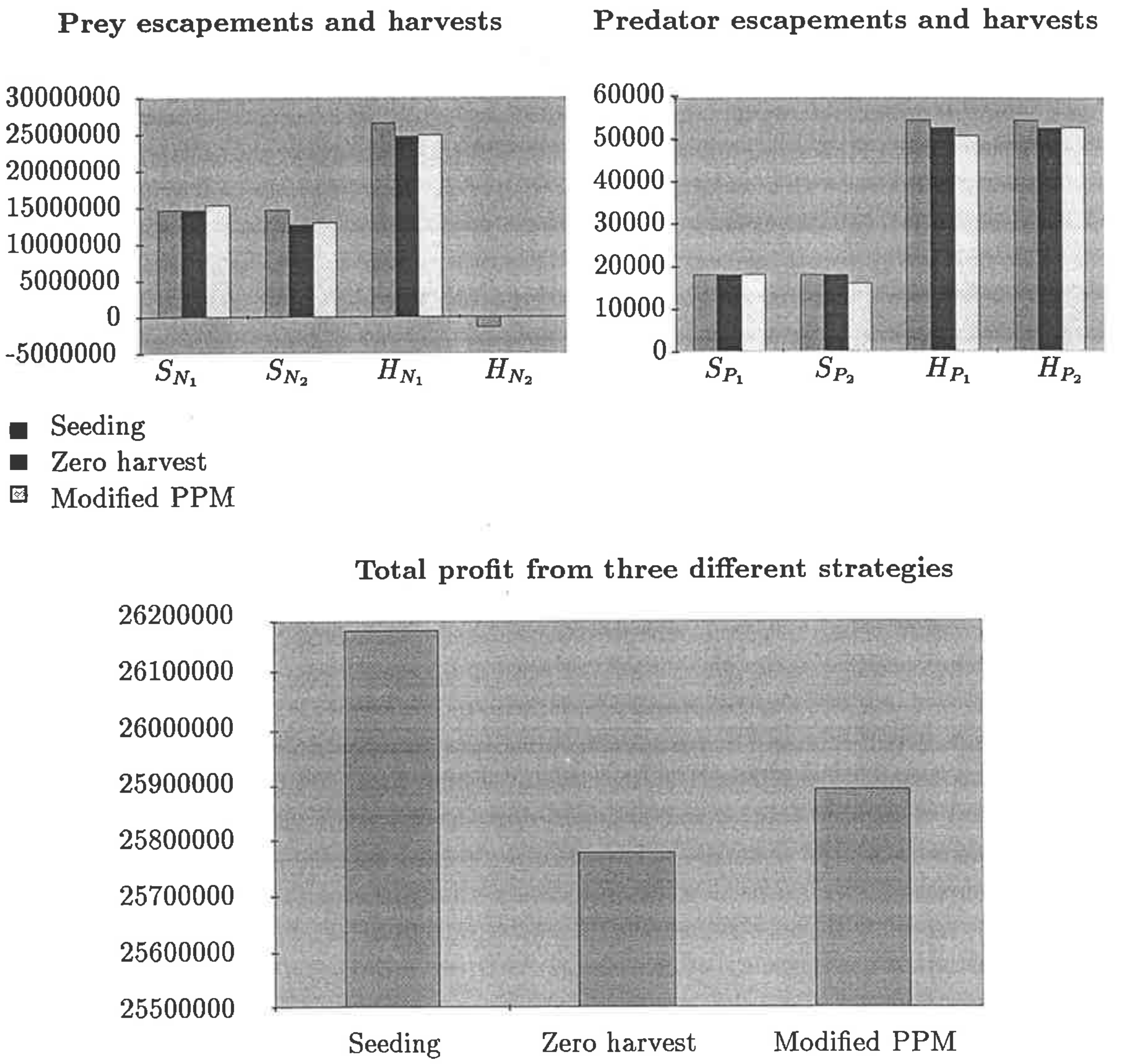


Figure 5.9: Escapement, harvest, and profit comparisons among three different methods in dealing with a negative harvest. In this example a negative harvest occurs in prey subpopulation two. Escapements in the negative harvest column are derived from (5.62) and (5.63), escapements in zero harvest column are derived from (5.64), and escapements in modified PPM (predator-prey metapopulation with zero harvest constraint) are derived from (5.65) - (5.67). Equilibrium harvests are computed using $H^*_{N_i} = N_i - S^*_{N_i}$ and $H^*_{P_i} = P_i - S^*_{P_i}$ where N_i and P_i are determined by (5.57) and (5.58).

structurally different models. The first model assumes that predation affects the predator's adult survival and the second model assumes that predation affects the predator's recruitment. Results show that the most significant rule in single-species metapopulation harvesting theory, that is, we should harvest a relative source subpopulation more conservatively than a relative sink subpopulation, remains true in the presence of a predator, if we harvest both species and if the predator efficiency is above a certain threshold, regardless of the structure of the population.

Silvert and Smith (1977), May *et al.* (1979), and Ragozin and Brown (1985) suggested that in a multi-species fisheries a species may be more protected than the other species if it enhances the profit from the fisheries through its bioeconomic role. For example, if the prey in a predator-prey system grows slowly then it would be better to use a zero harvest strategy for the prey, that is, not to harvest the prey population. The unharvested prey can increase the profit significantly if it is left as food for the predator. This is also observed in the result presented in this chapter for harvesting a two-patch predator-prey metapopulation. The result in this chapter generalises the result of Silvert and Smith (1977), May *et al.* (1979), and Ragozin and Brown (1985) to include the importance of exporter/importer subpopulations in determining the optimal harvesting strategy for the population. In the present result, where spatial structure is taken into account, the decision to protect a prey population applies especially to the exporter prey subpopulation, hence a zero harvest strategy will generally apply to only one prey subpopulation. On the other hand, if spatial structure is neglected, such as in Silvert and Smith (1977), May *et al.* (1979), and Ragozin and Brown (1985), prey protection applies to the whole prey population, which may not be economically, politically, or socially acceptable (Gary *et al.*, 1998).

In addition, a negative harvest may be optimal in harvesting a two-patch predator-prey metapopulation. This negative harvest is interpreted as a seeding strategy. Numerical examples show that if the predator market price is much higher than the prey market price, then it is optimal to seed the prey and harvest the predator which has a higher market price. If in addition one prey subpopulation is a relative exporter subpopulation, then the seeding strategy should be applied to this relative exporter subpopulation. However, the seeding strategy only works if the cost of seeding equals the price of stock unless the relative value of the predator, m, is even bigger. For this reason, as in the previous chapter, I also provided an alternative procedure to determine optimal escapements if negative harvesting is not possible.

In addition to results presented in the previous chapter, in this chapter I presented optimal equilibrium escapements when harvesting only targets one species for the first model. Numerical examples suggest that the rule to heavily harvest the prey subpopulation living in the same patch with a relative source predator subpopulation may no longer hold if harvesting only targets the prey species. However, we still harvest a relative source prey subpopulation more conservatively than a relative sink subpopulation.

I also established rules when the cost of harvesting differs, either between prey subpopulations, or between predator subpopulations. For example, if prey subpopulation one is a relative source/exporter subpopulation and has intrinsic growth greater than or equal to the intrinsic growth of the other prey subpopulation, that is, $p_{11}r_1 \geq p_{21}r_2$ and $p_{12}r_1 > p_{22}r_2$ (or $p_{11}r_1 > p_{21}r_2$ and $p_{12}r_1 \geq p_{22}r_2$) then we should protect the relative source prey subpopulation whenever the ratio of adult survival in patch one to adult survival in patch two equals the ratio of the marginal net revenue in patch two to the marginal net revenue in patch one. If adult survivals of all populations are the same and there is differences in the marginal net revenue status between the populations, optimal escapements are determined by the trade-off between the source/sink status and the marginal net revenue status, because there is a tendency for the exploiter to conserve the subpopulation with a higher marginal net revenue. This tendency is also observed in harvesting a single-species population with spatial structure (see Clark (1976a) for his inshore and offshore model and Gatto *et al.* (1982) for their effort-allocation model).

As in the previous chapter, populations can be protected in two different ways – directly, with a higher escapement of the relative source prey subpopulation, and indirectly, with a lower escapement of the predator living in the same patch. Furthermore, if the marginal net revenue from the relative source and exporter prey subpopulation is lower than the marginal net revenue from the relative sink and importer prey subpopulation, the present theory would harvest the relative source and exporter prey subpopulation more conservatively than if we use unconnected predator-prey harvesting theory. The predator living in the same patch with the relative source and exporter prey subpopulation would be harvested more heavily than if we use unconnected predator-prey harvesting theory.

It is important to realise the limitations of the results in this chapter. To establish Results 10 and 15, that using predator-prey metapopulation harvesting strategy would harvest a relative source subpopulation more conservatively than using strategy from well-mixed predator-prey population, we may need an extreme predator efficiency, that is $\frac{\beta}{|\alpha|} = 1$. However, if there is a price differential between the prey and predator then the rule requires that the predator "bioeconomic conversion", $m\beta$, equals the absolute value of prey vulnerability, $|\alpha|$. If we assume that predation affects predator recruitment, we need an additional requirement that there is no predator mortality during migration. If these conditions are not satisfied then the rule may not true. The models in this chapter ignore age-structure and only consider Lotka-Volterra predator-prey functional form. Future models should include age-structure and take into account various types of predator-prey functional forms to generalise results presented in this chapter. In the next chapter I investigate optimal harvesting strategies for a simple predator-prey metapopulation where age-structure is included using a recruitment delay.

5.4 Appendices

Appendix 5A: Non-overlapping prey generations

If both prey subpopulations in predator-prey metapopulation with predator reruitment model (Section 5.2) have a non-overlapping generation and their total natural growth, $r_1(p_{11} + p_{12}) + r_2(p_{21} + p_{22})$, is less than three times of the reciprocal of the annual discounting factor, $1/\rho$, and if C in Result 15 satisfies $0 > C > max\{B/K, mA/L\}$ and $r_1(p_{11} + p_{12}) + r_2(p_{21} + p_{22}) < \frac{3}{\rho}$, then assuming a predator-prey metapopulation as a well-mixed predator-prey population would over-harvest the relative source and exporter prey subpopulation, that is, then $\frac{1}{2}S^*_{N_w} < S^*_{N_1}$. This can be proved as follows.

Following the proof of Result 10, we can obtain $S^*_{N_1} > S^0$ for $r_{1m} > r_w$, and

$$\Delta_1\Delta_0\left(S^0 - \frac{1}{2}S^*_{N_w}\right) = \frac{3A_w s_m C}{L}\left(C - \frac{2B}{K}\frac{r_w}{(-3A_w)}\right) + BC^3. \qquad (5.68)$$

It can be proved that if $r_1 + r_2 \leq \frac{3}{\rho}$, then $\frac{r_w}{-3A_w} \geq 1$, hence

$$\Delta_1 \Delta_0 \left(S^0 - \frac{1}{2} S^*_{N_w} \right) \geq \frac{3A_w s_m C}{L} \left(C - \frac{2B}{K} \right) + BC^3 > 0. \tag{5.69}$$

Since $C > B/K$ and $C > mA/L$, following the proof in Result 9, it can be shown that $\Delta_0 < 0$. Since $\Delta_1 < 0$ then $S^0 - \frac{1}{2}S^*_{N_w} > 0$. Finally, $S^*_1 > S^0 > \frac{1}{2}S^*_{N_w}$. Similarly, it can be proved that if $s_1(q_{11} + q_{12}) + s_2(q_{21} + q_{22}) < \frac{3}{\rho}$ then $\frac{1}{2}S^*_{P_w} \leq S^*_{P_2}$.

Chapter 6

Predator-prey metapopulations with delayed juvenile recruitment

In the previous chapters I derived and discussed optimal harvesting strategies for several predator-prey metapopulation models. The underlying biological models assume that the population in each patch is a single homogeneous and well-mixed population. The model for each patch is described by a single variable representing the number of individuals and assumes that the offsprings of the current population are immediately recruited to the adult population in the next period. This model has a very simple age structure. In reality, many exploited populations consist of several different age classes. Population models that include yearly age classes are known as "age-structured models" (Clark, 1985a).

Some examples of the early models for age-structured populations can be found in Leslie (1945, 1948), Von Foerster (1959), Sinko and Streifer (1967) and Cushing (1976) for unexploited populations, and Beddington and Taylor (1973), Rorres and Fair (1975), Beddington (1978) and Reed (1980) for exploited populations. In general, Clark (1985a) divided age-structured population models into three groups, that is, Leslie's matrix models, delay-recruitment models and dynamic pool models.

Leslie (1945, 1948) pioneered the use of matrices to study age-structure in population modelling. The Leslie matrix model is extended by Williamson (1959) and widely used in ecology (Lefkovitch 1965; Usher, 1971; Emlen, 1984; Caswell, 1989), demography (Keyfitz, 1985), forestry (Usher, 1966, 1976) and fishery (Reed, 1980; Botsford, 1981; Horwood and Whittle, 1986). Dunkel (1970) and Mendelssohn (1976) argued that Leslie's matrix model is ecologically uninteresting because it only models density-independent growth of a population, and hence produces unbounded sustainable yield (Reed, 1980). Reed (1980) and Botsford (1981) were among the first authors who introduced density-dependence into Leslie's matrix model. They found an optimal harvesting strategy for their system. This has solved the limitation of Leslie's model.

Leslie's age-structured model deals only with the females of a population, and can be written in a matrix form

$$[N_{i(k+1)}] = [F_{ij}][N_{i(k)}], \tag{6.1}$$

where $N_{i(k)}$ denotes the number of females of age i in year k and $[F_{ij}]$ is a transition matrix relating the abundance of the females in generation $k+1$ to the abundance of the females in generation k. If it is assumed that $N_{i(k)}$ with $i = 0, 1, \dots, \gamma - 1$ is the number non-reproductive females of age less than γ in year k, $N_{\gamma(k)}$ is the number of reproductive females of age γ or more in year k, a_i is the survivorship of the females

Organism:	Age at maturity:	Reference:
Red lip abalone	≥ 3 years	Shepherd and law, 1974
Sauces scallop	1 year	Dredge, 1981
Iceland scallop	6 years	Vahl, 1981
Baleen whale	≥ 5 years	Clark and Lamberson, 1982
Sei whale	≥ 9 years	Allen, 1963; Fisher and Goh, 1984
Fin whale	±8 years	Allen, 1963; Fisher and Goh, 1984
Orange roughy	≥ 23 years	Francis, 1992
Chinook salmon	3 to 7 years	Hankin *et al.*, 1993
Sturgeons	10 to 20 years	Auer, 1996
Pacific ocean perch	8 to 10 years	Gunderson, 1997
Atka mackerel	≥ 3.6 years	McDermott and Lowe, 1997
Squid	≥ 270 days	Arkhipkin and Silvanovich, 1997

Table 6.1: Some known delay time for commercial marine populations.

of age i, and $F(N_{\gamma(k)})$ is the fecundity of females in year k then the transition matrix $[F_{ij}]$ can be written as

$$[F_{ij}] = \begin{bmatrix} 0 & 0 & 0 & \dots & 0 & F(N_{\gamma(k)}) \\ a_0 & 0 & 0 & \dots & 0 & 0 \\ 0 & a_1 & 0 & \dots & 0 & 0 \\ 0 & 0 & a_2 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & a_{\gamma-1} & a_\gamma \end{bmatrix}. \tag{6.2}$$

Many studies on the exploitation of age-structured populations use a Leslie model. For example, Reed (1980) used Leslie's matrix in a slightly different form, where he assumed that the first year survival rate of the population is density-dependent. Beddington (1978) showed that if the right hand side of the Leslie matrix model is solved for $N_{\gamma(k+1)}$, it ends up with

$$N_{\gamma(k+1)} = a_{\gamma-1}a_{\gamma-2}\dots a_0 F(N_{\gamma(k-\gamma)})N_{\gamma(k-\gamma)}) + a_\gamma N_{\gamma(k)}, \tag{6.3}$$

that is, the number of mature individuals in the next period can be obtained as a function of the number of mature individuals in the present period and γ periods ago. Assuming $F(N_{k-\gamma}) = a_{\gamma-1}a_{\gamma-2}\dots a_0 F(N_{\gamma(k-\gamma)})N_{\gamma(k-\gamma)})$, $N_k = N_{\gamma(k)}$, and $a = a_\gamma$, equation (6.3) can be rewritten as

$$N_{k+1} = aN_k + F(N_{k-\gamma}), \tag{6.4}$$

which is known as the "delay-recruitment model". Equation (6.4) is a model where recruitment to the reproductive population occurs γ years after birth. Clark (1976b) used equation (6.4) to model the growth of the Antarctic fin whale, *Balaenoptera physalus*, where each individual has five years delay before it enters the mature class. Other commercial marine populations with known delayed-recruitment are shown in Table 6.1. Some of the species listed in the table are either prey or predator or both in complex food-webs (Jones, 1982).

Clark (1976b) analysed the stability of an equilibrium solution of the delay-recruitment model, equation (6.4), and investigated optimal harvesting strategies for the population. In Clark's (1976b) model, if the number of harvested individuals in year k is H_k and assuming that recruitment is determined by escapement $S_k = N_k - H_k$, then the delay-recruitment equation becomes

$$N_{k+1} = aS_k + F(S_{k-\gamma}). \tag{6.5}$$

As in the case of the non-delay-recruitment model, Clark (1976b) assumed that the net economic return from exploitation in year k is

$$\Pi(N_k, H_k) = \int_{S_k}^{N_k} (p - c(\xi))d\xi, \tag{6.6}$$

with value function

$$J = \sum_{k=0}^{\infty} \rho^k \Pi(N_k, H_k). \tag{6.7}$$

The parameters p, $c(\cdot)$ and ρ have the usual meaning, that is, market price, cost of harvesting and discounting rate, respectively. Clark (1976b) found an implicit expression for the optimal equilibrium escapement, S^*,

$$\frac{p - c(S^*)}{\rho} = (p - c(N(S^*))(a + \rho^{\gamma} F'(S^*)), \tag{6.8}$$

where $N(S^*)$ is given by equation (6.5). Assuming the cost of harvesting is negligible or independent of the abundance of the population, and assuming the recruitment function, F, is logistic, then the optimal equilibrium escapement can be written explicitly in exactly the same form as the case of the non-delay model with ρ^{γ} term added, that is,

$$S^* = \frac{K}{2} - \frac{K}{2}\left(\frac{1 + \delta - a}{\rho^{\gamma} r}\right). \tag{6.9}$$

It is clear from the last equation that the optimal escapement for the delay model, with a delay of more than two years, $\gamma \geq 2$, is lower than the optimal escapement for the non-delay model. The larger the time-delay, the lower the optimal escapement. It suggests that if the delay is large enough, then it is not optimal to wait for juveniles to be recruited into the reproductive adult class and we should exploit the stock to extinction (Tuck, 1994).

Tuck (1994) developed two delay-recruitment metapopulation models as generalisations of Clark's (1976b) model for a single-species. One of his models has a similar structure to Agnew's (1982) model. The difference is Agnew (1982) considered delay-recruitment for two species having an interspecific biological interaction while Tuck (1994) considered delay-recruitment for a species with the interchange of individuals between subpopulations. The first model of Tuck (1994) assumes that the delay experienced by the newborn is related to the subpopulation in which the newborn is recruited, known as the "receptor delay model" (RDM). The second model assumes that the delay experienced by the newborn is related to the origin subpopulation of the newborn, known as the "parental delay model" (PDM). Using the same symbols as the previous non-delay single-species metapopulation model, the receptor local population delay-recruitment model with exploitation is written as

$$N_{1(k+1)} = a_1 S_{1k} + p_{11} F_1(S_{1k} - \gamma_1) + p_{21} F_2(S_{2k} - \gamma_1), \tag{6.10}$$

$$N_{2(k+1)} = a_2 S_{2k} + p_{12} F_1(S_{1k} - \gamma_2) + p_{22} F_2(S_{2k} - \gamma_2), \tag{6.11}$$

and the parental delay model is written as

$$N_{1(k+1)} = a_1 S_{1k} + p_{11} F_1(S_{1k} - \gamma_1) + p_{21} F_2(S_{2k} - \gamma_2), \tag{6.12}$$

$$N_{2(k+1)} = a_2 S_{2k} + p_{12} F_1(S_{1k} - \gamma_1) + p_{22} F_2(S_{2k} - \gamma_2), \tag{6.13}$$

where γ_i denotes the delay for subpopulation i. Optimal harvesting strategies for each model are found by maximising the present value of net revenue

$$J = \sum_{k=0}^{\infty} \rho^k \sum_{i=1}^{2} \Pi_i(N_{ik}, H_{ik}), \tag{6.14}$$

subject to equations (6.10) and (6.11) for the receptor local population delay model and subject to equations (6.12) and (6.13) for the parental delay model, where Π_i is defined as in the non-delay model. Using the Lagrange multipliers method, Tuck (1994) found an implicit expression for the equilibrium optimal escapements, S_i^*, for each model as generalisations of Clark's (1976b) optimal escapement for the single-species delay model, equation (6.8). Explicit forms are found by assuming the costs of harvesting are independent of the population size. The escapements are

$$S_1^* = \frac{K_1}{2} - \frac{K_1}{2}\left(\frac{1+\delta-a_1}{r_1(p_{11}\rho^{\gamma_1} + p_{12}\rho^{\gamma_2})}\right), \tag{6.15}$$

$$S_2^* = \frac{K_2}{2} - \frac{K_2}{2}\left(\frac{1+\delta-a_2}{r_2(p_{21}\rho^{\gamma_1} + p_{22}\rho^{\gamma_2})}\right), \tag{6.16}$$

for the receptor local population delay model, and

$$S_1^* = \frac{K_1}{2} - \frac{K_1}{2}\left(\frac{1+\delta-a_1}{r_1\rho^{\gamma_1}(p_{11} + p_{12})}\right), \tag{6.17}$$

$$S_2^* = \frac{K_2}{2} - \frac{K_2}{2}\left(\frac{1+\delta-a_2}{r_2\rho^{\gamma_2}(p_{21} + p_{22})}\right), \tag{6.18}$$

for the parental delay model.

Tuck (1994) showed that if both populations have the same carrying capacities, adult survival rates and delays, then the escapements from both models are equal. In this case, the presence of a delay does not alter decisions on how we should harvest the population optimally. As in the case of a non-delay model, the relative source subpopulation should be more conservatively harvested than the relative sink subpopulation. On the other hand, if the per capita larval production for both subpopulations are equal, the parental delay model suggests that the subpopulation with the larger delay should be harvested less conservatively than the other subpopulation. This is not always the case in the receptor local population delay model. Furthermore, Tuck (1994) showed that the rules of thumb for harvesting a non-delay single-species metapopulation, that is, that we would over-harvest the relative exporter subpopulation if we incorrectly manage the population as an unconnected single population and that we would over-harvest the relative source subpopulation if we incorrectly manage the population as a well-mixed single population, are confirmed from the parental delay model regardless of the differences in recruitment delays. However, the same rules are confirmed in the receptor local subpopulation delay model only if both recruitment delays are equal.

Tuck (1994) added that, in some circumstances, if the difference between recruitment delays are very high, both models may suggest that a seeding strategy may be an optimal policy. For example, if subpopulation one has a large delay but subpopulation two has a small delay, the optimal harvesting policy is to seed subpopulation one and harvest the adults in subpopulation two as long as the receptor local population delay model is concerned. However, the parental delay model suggests the opposite, that is, that we should seed subpopulation two and harvest the adults in the subpopulation one. This is logical in terms of minimising the time between seeding and getting a harvest.

In the following section, I investigate the optimal harvesting strategy for a predator-prey metapopulation in the presence of recruitment delays, by generalising the receptor local population delay and the parental delay models discussed in Tuck (1994).

6.1 Predator-prey receptor delay model

This section describes a deterministic, discrete-time model for a spatially-structured predator-prey population with a time-delay. I generalise the receptor local population delay model (Tuck, 1994) to include predator-prey interactions. In nature the delay-recruitment of marine species may result from the need of the juveniles of a species to travel from their original/spawning habitat to the destination habitat and also may reflect the time needed to get big enough to breed (Potter and Hyndes, 1994). I model this by assigning recruitment delays which are specific to the subpopulation where these juveniles are recruited. I use the method of Lagrange multipliers to derive optimal harvesting strategies for the population and compare the strategies to other existing strategies in which either spatial structure or predator-prey interaction is ignored

6.1.1 The model

As in the previous chapter, let us assume that there is a predator-prey population in each of two different patches, namely patch one and patch two. Let the movement of individuals between the local populations be through the dispersal of juveniles. Adults are assumed to be sedentary, they do not migrate from one patch to another patch. Let the population size of the prey and predator in patch i at the beginning of period k be denoted by N_{ik} and P_{ik}, respectively. The number of mature adults of the prey and predator subpopulation i in the time period $k+1$ is the sum of adult survival from period k and recruitment from juveniles that were born γ_i periods ago for the prey and τ_i periods ago for the predator. In the absence of a predator-prey interaction, the growth of the prey and predator assuming receptor local population delay are

$$N_{i(k+1)} = a_i N_{ik} + p_{ii} F_i(N_{ik-\gamma_i}) + p_{ji} F_j(N_{jk-\gamma_i}), \tag{6.19}$$

$$P_{i(k+1)} = b_i P_{ik} + q_{ii} G_i(P_{ik-\tau_i}) + q_{ji} G_j(P_{jk-\tau_i}), \tag{6.20}$$

respectively. All parameters have the same meaning to those in the non-delay model (Chapter 4). In addition, I model adult prey mortality and predator recruitment as a result of predator-prey interaction explicitly. I use assumptions analogous to those in the paper of Wangersky and Cunningham (1957) to describe prey mortality and adult recruitment resulting from predator-prey interaction, that is, adult prey mortality caused by predation in period k is proportional to the number of prey and predator in that period, and predator recruitment as a result of biomass conversion from the

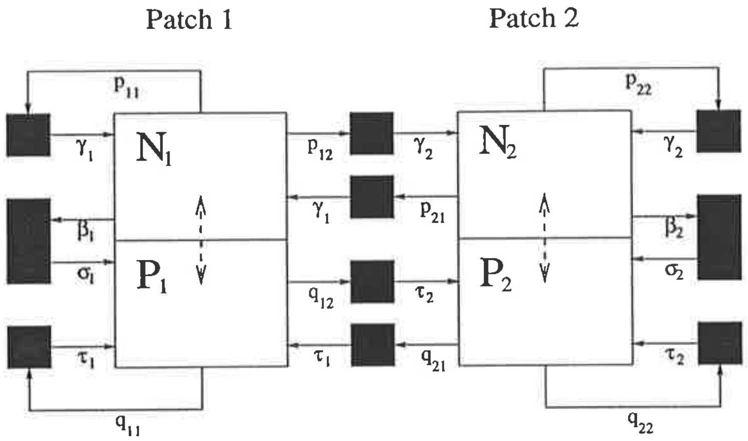


Figure 6.1: Juvenile migrations and delayed recruitment diagram for a spatially-structured predator prey metapopulation. As in Chapter 4, p_{ij} and q_{ij} is the proportion of juveniles which successfully migrate from prey subpopulation i to prey subpopulation j and from predator subpopulation i to predator subpopulation j, respectively. The symbol $\leftarrow - - - - \rightarrow$ represents predator-prey interaction in each patch, and the black boxes represent the prey (predator) juveniles density which will be recruited to prey (predator) adult class after a delay γ_i (τ_i). In addition, I assume that the number of the predator subpopulation i depends on the number of prey σ_i time ago, where $\sigma_i \geq \tau_i$.

interaction is proportional to the number of contacts between prey and predator, in which the predator successfully kills the prey, some σ_i periods ago. Mathematically the prey mortality is given by $\alpha_i N_{ik} P_{ik}$ and predator recruitment is $\beta_i N_{ik-\sigma_i} P_{ik-\sigma_i}$, where $|\alpha_i| \geq \beta_i > 0$. With these additional assumptions, a complete model of a predator-prey metapopulation assuming receptor local population delay can be written as

$$N_{i(k+1)} = a_i N_{ik} + p_{ii} F_i(N_{ik-\gamma_i}) + p_{ji} F_j(N_{jk-\gamma_i}) + \alpha_i N_{ik} P_{ik}, \tag{6.21}$$

$$P_{i(k+1)} = b_i P_{ik} + q_{ii} G_i(P_{ik-\tau_i}) + q_{ji} G_j(P_{jk-\tau_i}) + \beta_i N_{ik-\sigma_i} P_{ik-\sigma_i}, \tag{6.22}$$

and illustrated by Figure 6.1. Equation (6.22) assumes that the delay impacts local predator recruitment. In this case, there is a delay of σ_i time units between predation and recruitment to the local predator population. If predation only aids predator's adult survival then $\sigma_i = 0$.

As in the previous chapter, I assume that we harvest prey and predator subpopulation i at the beginning of period k with the rate of harvesting $H_{N_{ik}}$ and $H_{P_{ik}}$, respectively. Let $S_{N_{ik}} = N_{ik} - H_{N_{ik}}$ and $S_{P_{ik}} = P_{ik} - H_{P_{ik}}$ be prey and predator escapements on patch i at the end of that period. Substituting these escapements into equations (6.21) and (6.22) produces equations for a harvested predator-prey metapopulation

$$N_{1(k+1)} = a_1 S_{N_{1k}} + p_{11} F_1(S_{N_{1k-\gamma_1}}) + p_{21} F_2(S_{N_{2k-\gamma_1}}) + \alpha_1 S_{N_{1k}} S_{P_{1k}}, \tag{6.23}$$

$$N_{2(k+1)} = a_2 S_{N_{2k}} + p_{22} F_2(S_{N_{2k-\gamma_2}}) + p_{12} F_1(S_{N_{1k-\gamma_2}}) + \alpha_2 S_{N_{2k}} S_{P_{2k}}, \tag{6.24}$$

$$P_{1(k+1)} = b_1 S_{P_{1k}} + q_{11} G_1(S_{P_{1k-\tau_1}}) + q_{21} G_2(S_{P_{2k-\tau_1}}) + \beta_1 S_{N_{1k-\sigma_1}} S_{P_{1k-\sigma_1}}, \tag{6.25}$$

$$P_{2(k+1)} = b_2 S_{P_{2k}} + q_{22} G_2(S_{P_{2k-\tau_2}}) + q_{12} G_1(S_{P_{1k-\tau_2}}) + \beta_2 S_{N_{2k-\sigma_2}} S_{P_{2k-\sigma_2}}. \tag{6.26}$$

In the following sections I derive optimal escapements for the population and compare them to escapements from non-delay predator-prey metapopulation.

6.1.2 Optimal escapements

To obtain the optimal harvesting strategy for the metapopulation I use the method of Lagrange multipliers. The non-linearity of the net revenue function due to the inclusion of the delays has made it difficult to use dynamic programming (Tuck, 1994). Using the Lagrange multipliers method, the net revenue

$$PV = \sum_{k=0}^{\infty} \rho^k \sum_{i=1}^{2} \sum_{X \in \{N,P\}} \Pi_{Xi}(X_{ik}, S_{X_{ik}}) \tag{6.27}$$

is maximised over infinite time subject to equations (6.23) - (6.26), with a non-negative escapement less than, or equal to, the population size. As in the previous chapter I also assume $\rho = 1/(1+\delta)$ where δ denotes a periodic discounting rate and

$$\Pi_{X_i}(X_{ik}, H_{X_{ik}}) = \int_{X_{ik}-H_{X_{ik}}}^{X_{ik}} (p_X - c_{X_i}(\xi)) d\xi. \tag{6.28}$$

The Lagrangian for the maximisation is

$$\begin{aligned}
\mathcal{L} \; = \; & \sum_{k=0}^{\infty} \{\rho^k [\Pi_{N_1}(N_{1k}, H_{N_{1k}}) + \Pi_{N_2}(N_{2k}, H_{N_{2k}}) \\
& + \Pi_{P_1}(P_{1k}, H_{P_{1k}}) + \Pi_{P_2}(P_{2k}, H_{P_{2k}})] \\
& - \lambda_{1k}[N_{1(k+1)} - a_1(N_{1k} - H_{N_{1k}}) - p_{11} F_1(N_{1k-\gamma_1} - H_{N_{1k-\gamma_1}}) \\
& - p_{21} F_2(N_{2k-\gamma_1} - H_{N_{2k-\gamma_1}}) - \alpha_1(N_{1k} - H_{N_{1k}})(P_{1k} - H_{P_{1k}})] \\
& - \lambda_{2k}[N_{2(k+1)} - a_2(N_{2k} - H_{N_{2k}}) - p_{12} F_1(N_{1k-\gamma_2} - H_{N_{1k-\gamma_2}}) \\
& - p_{22} F_2(N_{2k-\gamma_2} - H_{N_{2k-\gamma_2}}) - \alpha_2(N_{2k} - H_{N_{2k}})(P_{2k} - H_{P_{2k}})] \\
& - \lambda_{3k}[P_{1(k+1)} - b_1(P_{1k} - H_{P_{1k}}) - q_{11} G_1(P_{1k-\tau_1} - H_{P_{1k-\tau_1}}) \\
& - q_{21} G_2(P_{2k-\tau_1} - H_{P_{2k-\tau_1}}) \\
& - \beta_1(N_{1k-\sigma_1} - H_{N_{1k-\sigma_1}})(P_{1k-\sigma_1} - H_{P_{1k-\sigma_1}})] \\
& - \lambda_{4k}[P_{2(k+1)} - b_2(P_{2k} - H_{P_{2k}}) - q_{12} G_1(P_{1k-\tau_2} - H_{P_{1k-\tau_2}}) \\
& - q_{22} G_2(P_{2k-\tau_2} - H_{P_{2k-\tau_2}}) \\
& - \beta_2(N_{2k-\sigma_2} - H_{N_{2k-\sigma_2}})(P_{2k-\sigma_2} - H_{P_{2k-\sigma_2}})]\}.
\end{aligned} \tag{6.29}$$

To maximise the value function PV in (6.27), the conditions $\frac{\partial \mathcal{L}}{\partial N_{ik}} = \frac{\partial \mathcal{L}}{\partial P_{ik}} = 0$ for $k \geq 1$ and $\frac{\partial \mathcal{L}}{\partial H_{N_{ik}}} = \frac{\partial \mathcal{L}}{\partial H_{P_{ik}}} = 0$ need to be satisfied. In Appendix 6A these equations are solved to obtain an implicit expression for the optimal escapements in the form

$$\begin{aligned}
\frac{p_N - c_{N1}(S^*_{N_{10}})}{\rho} \; = \; & (p_N - c_{N1}(N_{11}))(a_1 + p_{11} F_1'(S^*_{N_{10}}) \rho^{\gamma_1} + \alpha_1 S^*_{P_{10}}) \\
& + (p_N - c_{N2}(N_{21})) p_{12} F_1'(S^*_{N_{10}}) \rho^{\gamma_2} \\
& + (p_P - c_{P1}(P_{11})) \beta_1 S^*_{P_{10}} \rho^{\sigma_1},
\end{aligned} \tag{6.30}$$

$$\begin{aligned}\frac{p_N - c_{N2}(S^*_{N_{20}})}{\rho} &= (p_N - c_{N2}(N_{21}))(a_2 + p_{22}F'_2(S^*_{N_{20}})\rho^{\gamma_2} + \alpha_2 S^*_{P_{20}}) \\ &\quad + (p_N - c_{N1}(N_{11}))p_{21}F'_2(S^*_{N_{20}})\rho^{\gamma_1} \\ &\quad + (p_P - c_{P2}(P_{21}))\beta_2 S^*_{P_{20}}\rho^{\sigma_2}, \qquad (6.31)\end{aligned}$$

$$\begin{aligned}\frac{p_P - c_{P1}(S^*_{P_{10}})}{\rho} &= (p_P - c_{P1}(P_{11}))(b_1 + q_{11}G'_1(S^*_{P_{10}})\rho^{\tau_1} + \beta_1 S^*_{N_{10}}\rho^{\sigma_1}) \\ &\quad + (p_P - c_{P2}(P_{21}))q_{12}G'_1(S^*_{P_{10}})\rho^{\tau_2} \\ &\quad + (p_N - c_{N1}(N_{11}))\alpha_1 S^*_{N_{10}}, \qquad (6.32)\end{aligned}$$

$$\begin{aligned}\frac{p_P - c_{P2}(S^*_{P_{20}})}{\rho} &= (p_P - c_{P2}(P_{21}))(b_2 + q_{22}G'_2(S^*_{P_{20}})\rho^{\tau_2} + \beta_2 S^*_{N_{20}}\rho^{\sigma_2}) \\ &\quad + (p_P - c_{P1}(P_{11}))q_{21}G'_2(S^*_{P_{20}})\rho^{\tau_1} \\ &\quad + (p_N - c_{N2}(N_{21}))\alpha_2 S^*_{N_{20}}. \qquad (6.33)\end{aligned}$$

These equations are the general form of the optimal escapement equations for a two-patch predator-prey metapopulation with a time-delay.

Note that in the absence the delay ($\gamma_i = \sigma_i = \tau_i = 0$), the equations reduce to equations (5.5) and (5.6) from Chapter 5. If $\alpha_i = \beta_i = 0$, then Tuck's (1994) optimal escapement equation for a single-species metapopulation with time delay is obtained. On the other hand, if there is no migration between patches, $p_{ij} = q_{ij} = 0$ for $i \neq j$, and if $N_i = N_j = N$ and $P_i = P_j = P$, then the implicit optimal escapements equation for patch one is

$$\begin{aligned}\frac{p_N - c_N(S^*_{N_0})}{\rho} &= (p_N - c_N(N_1))(F_{1N} + \rho^{\gamma_i} D_{1N}) \\ &\quad + (p_P - c_P(P_1))(G_{1N} + \rho^{\tau_1} E_{1N}), \qquad (6.34)\end{aligned}$$

$$\begin{aligned}\frac{p_P - c_P(S^*_{P_0})}{\rho} &= (p_N - c_N(N_1))(F_{1P} + \rho^{\gamma_i} D_{1P}) \\ &\quad + (p_P - c_P(P_1))(G_{1P} + \rho^{\tau_1} E_{1P}), \qquad (6.35)\end{aligned}$$

where $F_{1N} = a_1 + \alpha_1 S^*_{P_0}$, $G_{1N} = \beta_1 S^*_{P_0}\rho^{\sigma_1}$, $D_{1N} = p_{11}F'_1(S^*_{N_0})$, $E_{1N} = 0$, $F_{1P} = \alpha_1 S^*_{N_0}$, $G_{1P} = b_1 + \beta_1 S^*_{N_0}\rho^{\sigma_1}$, $D_{1P} = 0$ and $E_{1P} = q_{11}G'_1(S^*_{P_0})$. Optimal escapements for patch two can be obtained similarly in this form. These equations are implicit optimal harvesting equations for two species derived by Agnew (1982) in the presence of a time-delay in the predator numerical response such as in Wangersky and Cunningham (1957). Finally, if both juvenile migration and predator-prey interaction are ignored, equations (6.30) - (6.33) collapse to Clark's (1976b) optimal escapement equation for a single-species with time-delay

$$\frac{p_N - c_{N1}(S^*_{N_{10}})}{\rho} = (p_N - c_{N1}(N_{11}))(a_1 + p_{11}F'_1(S^*_{N_{10}})\rho^{\gamma_1}). \qquad (6.36)$$

The following section discusses further the optimal escapements and gives some interpretations of the results by comparing them with other escapements.

6.1.3 Results with negligible costs

To facilitate the interpretations of equations (6.30) - (6.33) I assume that there is no difference between the prey and predator price and to simplify the analysis I also assume the costs of harvesting are negligible or density and subpopulation independent. Using these assumptions, substitute all derivatives of the logistic recruitment functions $F_i(N_{ik}) = r_i N_{ik}(1 - N_{ik}/K_i)$ and $G_i(P_{ik}) = s_i P_{ik}(1 - P_{ik}/L_i)$ into equations (6.30) - (6.33), to obtain

$$\frac{1}{\rho} = a_i + (p_{i1}\rho^{\gamma_1} + p_{i2}\rho^{\gamma_2})\left(r_i - \frac{2r_i}{K_i}S^*_{Ni}\right) + (\alpha_i + \beta_i\rho^{\sigma_i})S^*_{Pi}, \tag{6.37}$$

$$\frac{1}{\rho} = b_i + (q_{i1}\rho^{\tau_1} + q_{i2}\rho^{\tau_2})\left(s_i - \frac{2s_i}{L_i}S^*_{Pi}\right) + (\alpha_i + \beta_i\rho^{\sigma_i})S^*_{Ni}. \tag{6.38}$$

Let

$$A_i = \frac{1}{\rho} - (p_{i1}\rho^{\gamma_1} + p_{i2}\rho^{\gamma_2})r_i - a_i, \tag{6.39}$$

$$B_i = \frac{1}{\rho} - (q_{i1}\rho^{\tau_1} + q_{i2}\rho^{\tau 2})s_i - b_i, \tag{6.40}$$

and

$$C_i = \alpha_i + \beta_i\rho^{\sigma_i}. \tag{6.41}$$

As in the previous chapters I interpret C_i as a predator efficiency, but here it is discounted by the delay σ_i. Solving equations (6.37) and (6.38) produces optimal escapements S^*_{Ni} and S^*_{Pi}

$$S^*_{Ni} = \frac{A_i(q_{i1}\rho^{\tau_1} + q_{i2}\rho^{\tau_2})\frac{2s_i}{L_i} + C_iB_i}{\Delta_i}, \tag{6.42}$$

$$S^*_{Pi} = \frac{B_i(p_{i1}\rho^{\gamma_1} + p_{i2}\rho^{\gamma_2})\frac{2r_i}{K_i} + C_iA_i}{\Delta_i}, \tag{6.43}$$

provided

$$\Delta_i = C_i^2 - (p_{i1}\rho^{\gamma_1} + p_{i2}\rho^{\gamma_2})\frac{2r_i}{K_i}(q_{i1}\rho^{\tau_1} + q_{i2}\rho^{\tau_2})\frac{2s_i}{L_i} \neq 0. \tag{6.44}$$

In the following discussions I will only deal with positive escapements. I establish the following result to guarantee that the escapements are all positive. The escapements are then compared to the escapements which occur if we ignored predator-prey interaction, that is, escapements from single-species metapopulation harvesting theory.

Result 16 *(Sufficient conditions for positive escapements) Let $S^*_{N_i}$ and $S^*_{P_i}$ denote the optimal escapement from a predator-prey metapopulation given by equations (6.42) and (6.43). If A_i and B_i are negative, and C_i is non-positive with $C_i > max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}$, then:*

1. *Δ_i is negative,*
2. *S^*_{Ni} and S^*_{Pi} are positive.*

Proof

1. Since $-\frac{(p_{i1}\rho^{\gamma_1}+p_{i2}\rho^{\gamma_2})r}{A} = \frac{(p_{i1}\rho^{\gamma_1}+p_{i2}\rho^{\gamma_2})r}{(p_{i1}\rho^{\gamma_1}+p_{i2}\rho^{\gamma_2})r+(a-(1+\delta))} \geq 1$, the condition $C > \frac{2B}{K}$ implies $C > -\frac{(p_{i1}\rho^{\gamma_1}+p_{i2}\rho^{\gamma_2})r}{A}\frac{2B}{K}$. Hence $C_i > max\{-\frac{2B_i(p_{i1}\rho^{\gamma_1}+p_{i2}\rho^{\gamma_2})r_i}{A_iK_i}, -\frac{2A_i(q_{i1}\rho^{\tau_1}+q_{i2}\rho^{\tau_2})s_i}{B_iL_i}\}$. It follows $B_i(p_{i1}\rho^{\gamma_1}+p_{i2}\rho^{\gamma_2})\frac{2r_i}{K_i} < -C_iA_i$ or alternatively $B_i < \frac{-C_iA_i}{(p_{i1}\rho^{\gamma_1}+p_{i2}\rho^{\gamma_2})\frac{2r_i}{K_i}}$.
   If $C = 0$ then clearly $\Delta_i < 0$. If $-C > 0$ then $-C_iB_i < -C_i\left(\frac{-C_iA_i}{(p_{i1}\rho^{\gamma_1}+p_{i2}\rho^{\gamma_2})\frac{2r_i}{K_i}}\right)$. On the other hand, since $A_i(q_{i1}\rho^{\tau_1}+q_{i2}\rho^{\tau_2})\frac{2s_i}{L_i} < -C_iB_i$ then $A_i(q_{i1}\rho^{\gamma_1}+q_{i2}\rho^{\gamma_2})\frac{2s_i}{L_i} < -C_i\left(\frac{-C_iA_i}{(p_{i1}\rho^{\gamma_1}+p_{i2}\rho^{\gamma_2})\frac{2r_i}{K_i}}\right)$. Finally, since A_i negative, then $(q_{i1}\rho^{\tau_1}+q_{i2}\rho^{\tau_2})\frac{2s_i}{L_i}(p_{i1}\rho^{\gamma_1}+p_{i2}\rho^{\gamma_2})\frac{2r_i}{K_i} > C_i^2$ which means $\Delta_i < 0$. □

2. It is clear from equations (6.42) and (6.43). □

As in the non-delay case, an analogous result can be obtained if A_i and B_i are positive and C_i is non-negative. However, $C_i > 0$ is biologically unacceptable since it means the discounted predator efficiency is more than 100%. An interpretation of the condition $A_i < 0$ is that the sum of the proportion of surviving adults, a_i, and the discounted per capita larval production, $(p_{ii}\rho^{\gamma_1}+p_{ij}\rho^{\gamma_2})r_i$, is higher than the reciprocal of the discounting factor, $1/\rho$. As in the case of no time delay, this is the normal situation, otherwise it is best to harvest the populations down to zero escapements (Clark, 1976a). The condition $B_i < 0$ is interpreted similarly, while C_i is non-positive with $C_i > max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}$ interpreted as a high predator efficiency. Hence, if one of the subpopulations has a very high adult mortality, or a very small intrinsic growth, a very high proportion of losing juveniles from the system, or a very small predator efficiency, then negative escapements may occur. For the remainder of this chapter, to ensure that the optimal escapements are positive, I assume A_i and B_i are negative, and C_i is non-positive with $C_i > max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}$.

Using Result 16 I explore the relationship between escapements from the predator-prey metapopulation presented in this chapter and escapements from a single-species metapopulation with the receptor population delay model discussed in Tuck (1994). The relationship is summarised in the following result.

Result 17 *(Escapement comparison with a single-species metapopulation) Let $S^*_{N_i}$ and $S^*_{P_i}$ denote the optimal escapement from a predator-prey metapopulation given by equations (6.42) and (6.43), and let $S^*_{N_{is}}$ and $S^*_{P_{is}}$ denote the optimal escapement from a single-species metapopulation with receptor population delay model given by the same equations by assigning $\alpha_i = \beta_i = 0$. If A_i and B_i are negative, and C_i is non-positive with $C_i > max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}$, then:*

1. $S^*_{N_i} - S^*_{N_{is}} = \frac{C_i}{(p_{i1}\rho^{\gamma_1}+p_{i2}\rho^{\gamma_2})2r_i/K_i}S^*_{N_i} < 0,$

2. $S^*_{P_i} - S^*_{P_{is}} = \frac{C_i}{(q_{i1}\rho^{\tau_1}+q_{i2}\rho^{\tau_2})2s_i/L_i}S^*_{P_i} < 0.$

Proof

1. We need to determine the sign of $S^*_{N_i} - S^*_{N_{is}}$.

$$S^*_{N_i} - S^*_{N_{is}} = \frac{A_i(q_{i1}\rho^{\tau_1}+q_{i2}\rho^{\tau_2})\frac{2s_i}{L_i} + C_iB_i}{\Delta_i} - \frac{A_i}{-(p_{i1}\rho^{\gamma_1}+p_{i2}\rho^{\gamma_2})\frac{2r_i}{K_i}}$$

$$
\begin{aligned}
&= \frac{C_iB_i(p_{i1}\rho^{\gamma_1}+p_{i2}\rho^{\gamma_2})\frac{2r_i}{K_i}+C_i^2A_i}{\Delta_i(p_{i1}\rho^{\gamma_1}+p_{i2}\rho^{\gamma_2})\frac{2r_i}{K_i}}\\
&= \frac{B_i(p_{i1}\rho^{\gamma_1}+p_{i2}\rho^{\gamma_2})\frac{2r_i}{K_i}+C_iA_i}{\left(\Delta_i(p_{i1}\rho^{\gamma_1}+p_{i2}\rho^{\gamma_2})\frac{2r_i}{K_i}\right)/C_i}\\
&= \frac{C_i}{(p_{i1}\rho^{\gamma_1}+p_{i2}\rho^{\gamma_2})2r_i/K_i}S^*_{P_i}.
\end{aligned}
$$

Because the denominator is positive and $B_i(p_{i1}\rho^{\gamma_1}+p_{i2}\rho^{\gamma_2})\frac{2r_i}{K_i} < -C_iA_i$, then we have $S^*_{N_i} - S^*_{N_{is}} < 0$. □

2. The proof is analogous to the proof above. □

Hence, in general, optimal escapements from predator-prey metapopulations with the receptor subpopulation delay model are smaller than the escapement from a single-species metapopulation with receptor subpopulation delay model and has the same value if $C_i = 0$. The condition $C_i = 0$ is biologically unacceptable since it means that the discounted predator efficiency is zero ($\alpha_i + \beta_i\rho^{\sigma_i} = 0$) which means that if there is no delay in converting energy (food) from predation into predator organism, the immediate predator efficiency is higher than 100% ($\alpha_i + \beta_i > 0$). However, if there are differences between the price of the prey and the price of the predator, say the predator is m times more valuable than the prey, then $C_i = \alpha_i + m\beta_i\rho^{\sigma_i} = 0$. This condition can occur without requiring extremely high predator efficiency. It can be interpreted as a condition where the discounted predator efficiency weighted by the relative predator value is high.

In the next section, I compare escapements between patches if there is parameter variability. These escapements are also compared to the escapements we get if we ignore the spatial structure of the population. As expected, the result is a generalisation of harvesting theory for a single-species metapopulation with recruitment delay (Tuck 1994) and the harvesting theory for predator-prey metapopulation discussed in the previous chapter.

Escapement comparisons between subpopulations

To make an escapement comparison between patches, I use the following lemma, which I do not prove here since it can be proved analogously to a similar lemma in the non-delay model (Chapter 5). The lemma is also used to establish results in comparing the escapements from a predator-prey metapopulation to escapements where the spatial structure is ignored.

Lemma 5 *(Migration trade-off equations) Let $S^*_{N_i}$ and $S^*_{P_i}$ denote the optimal escapement from predator-prey metapopulation with receptor local population delay model given by equations (6.42) and (6.43). If $a_i = a$, $b_i = b$, $K_i = K$, $L_i = L$, $C_i = C$, $R = \frac{1}{\rho} - a$, $S = \frac{1}{\rho} - b$, $r_{im} = (p_{i1}\rho^{\gamma_1} + p_{i2}\rho^{\gamma_2})r_i$ and $s_{im} = (q_{i1}\rho^{\tau_1} + q_{i2}\rho^{\tau_2})s_i$, for $i = 1, 2$, then*

$$
\begin{aligned}
(S^*_{N_1} - S^*_{N_2})\Delta_1\Delta_2 &= \left(C^2(s_{1m} - s_{2m}) - \frac{4s_{1m}s_{2m}}{KL}(r_{2m} - r_{1m})\right)\left(\frac{2R}{L} - C\right)\\
&\quad -\frac{2C}{L}\left(C - \frac{2S}{K}\right)(r_{1m}s_{1m} - r_{2m}s_{2m}),
\end{aligned}
$$

and

$$\begin{aligned}(S^*_{P_1} - S^*_{P_2})\Delta_1\Delta_2 &= \left(C^2(r_{1m} - r_{2m}) - \frac{4r_{1m}r_{2m}}{KL}(s_{2m} - s_{1m})\right)\left(\frac{2S}{K} - C\right) \\ &\quad -\frac{2C}{K}\left(C - \frac{2R}{L}\right)(r_{1m}s_{1m} - r_{2m}s_{2m}),\end{aligned}$$

where $\Delta_i = C^2 - r_{im}s_{im}\frac{4}{KL}$, $i = 1, 2$.

Result 18 *(Escapement comparison between subpopulations) Let one of prey subpopulation be a relative source while all other parameters of the prey and the predator are identical for both subpopulations except for the delay parameters for the prey. Without loss of generality let us assume that prey subpopulation one is a relative source, that is* $(p_{11} + p_{12})r_1 > (p_{22} + p_{21})r_2$, *and also* $r_{1m} > r_{2m}$. *If* A_i *and* B_i *are negative, and* C_i *is non-positive with* $C > max\{\frac{2B}{K}, \frac{2A}{L}\}$, *then:*

1. $S^*_{N_1} > S^*_{N_2}$,
2. $S^*_{P_1} \leq S^*_{P_2}$.

Proof

1. Let $\Delta_{S_N} = (S^*_{N_1} - S^*_{N_2})\Delta_1\Delta_2$. Using lemma 5 Δ_{S_N} can be written as

$$\begin{aligned}\Delta_{S_N} &= \left(-\frac{4s^2_{1m}}{KL}(r_{2m} - r_{1m})\right)\left(\frac{2R}{L} - C\right) - \frac{2C}{L}\left(C - \frac{2S}{K}\right)s_{1m}(r_{1m} - r_{2m}) \\ &= s_{1m}\left[-\left(\frac{4s_{1m}}{KL}\right)\left(\frac{2R}{L} - C\right) + \frac{2C}{L}\left(C - \frac{2S}{K}\right)\right](r_{2m} - r_{1m}) \\ &= s_{1m}\left[\frac{2}{L}\left(C^2 - \frac{4s_{1m}R}{KL} - C\left(\frac{2S}{K} - \frac{2s_{1m}}{K}\right)\right)\right](r_{2m} - r_{1m}) \\ &= s_{1m}\left[\frac{2}{L}\left(C^2 - \frac{4s_{1m}R}{KL} - \frac{2C}{K}(S - s_{1m})\right)\right](r_{2m} - r_{1m}) \\ &= s_{1m}\left[\frac{2}{L}C\left(C - \frac{2B}{K}\right) - \frac{4s_{1m}R}{KL}\right](r_{2m} - r_{1m})\end{aligned}$$

   Since $C > \frac{2B}{K}$, then $\Delta_{S_N} > 0$ only if $r_{2m} < r_{1m}$. □

2. The proof is similar to above. □

Hence, we can conclude that as for the non-delay case, there is a region of parameters where we protect a relative source prey subpopulation more than a relative sink prey subpopulation in the sense that we allow more escapement in the source than the sink subpopulation. However, this source subpopulation has to have an additional property, it has to be a source prey subpopulation with the time delays included, that is

$$(p_{11}\rho^{\gamma_1} + p_{12}\rho^{\gamma_2})r_1 > (p_{21}\rho^{\gamma_1} + p_{22}\rho^{\gamma_2})r_2. \qquad (6.45)$$

This inequality redefines what a source subpopulation is for the receptor delay model. It means that the per capita larval production of subpopulation one which is discounted by its cumulative death rate, needs to be larger than the discounted per capita larval production of subpopulation two. If both prey subpopulations have the same delay, $\gamma_1 = \gamma_2$, then Result 18 simply says that the relative source prey subpopulation should be harvested more conservatively than the relative sink prey subpopulation and that the predator living in the same patch with the relative source prey subpopulation should be harvested more heavily than the predator living in the other patch. This is a generalisation of the rule of thumb for single-species metapopulation harvesting theory (Tuck, 1994). Furthermore, if the retention rate of prey subpopulation i, $(i = 1, 2)$, is equal to the immigration rate in that subpopulation, that is, $p_{ii} = p_{ji}$, then both subpopulations should be harvested equally, regardless of the value of the recruitment delays γ_1 and γ_2.

In the single-species metapopulation harvesting theory, if there is no source/sink subpopulations and there is no differences between the time delays for prey and predator juveniles to recruit into the adult populations, or if $r_1 p_{1i} = r_2 p_{2i}$ with any value of the delay, both subpopulations should be harvested equally. In contrast, optimal escapements in the present theory also depend on other quantities, prey vulnerability to predation α_i and discounted predator efficiency C_i. I use the following Lemma to investigate optimal escapement differences if discounted predator efficiency are different between subpopulations.

Lemma 6 *(Discounted efficiency trade-off equations) Let* $S^*_{N_i}$ *and* $S^*_{P_i}$ *denote the optimal escapement from a predator-prey metapopulation given by equations (6.42) and (6.43). If* $a_1 = a_2 = a$, $b_1 = b_2 = b$, $K_i = K$, $L_i = L$, $p_{11} = p_{22}, p_{12} = p_{21}, q_{11} = q_{22}, q_{12} = q_{21}, r_1 = r_2, s_1 = s_2$, $r_{im} = (p_{i1}\rho^{\gamma_1} + p_{i2}\rho^{\gamma_2})r_i = r_m$ *and* $s_{im} = (q_{i1}\rho^{\tau_1} + q_{i2}\rho^{\tau_2})s_i = r_m$ *then*

$$(S^*_{N_1} - S^*_{N_2})\Delta_1\Delta_2 = (C_2 - C_1)\left[\frac{2As_m}{L}(C_2 + C_1) + \frac{4r_m s_m B}{KL} + B(C_1 C_2)\right]$$

and

$$(S^*_{P_1} - S^*_{P_2})\Delta_1\Delta_2 = (C_2 - C_1)\left[\frac{2Br_m}{K}(C_2 + C_1) + \frac{4r_m s_m A}{KL} + A(C_1 C_2)\right].$$

Using this lemma I establish the following result.

Result 19 *(Escapement comparison between subpopulations) Let us assume one of the predator subpopulations is relatively more efficient with respect to time delay, while all other parameters of the prey and the predator are identical for both subpopulations, without loss of generality let us also assume that predator subpopulation one is relatively more efficient, that is* $C_1 > C_2$. *If* $A_1 = A_2 = A$ *and* $B_1 = B_2 = B$ *are negative, and* C_i *is non-positive with* $C_i > max\{\frac{B}{K}, \frac{A}{L}\}$, *then:*

1. $S^*_{N_1} > S^*_{N_2}$,
2. $S^*_{P_1} > S^*_{P_2}$.

Proof

1. From Lemma 6, we only need to show that $\left[\frac{2As_m}{L}(C_2 + C_1) + \frac{4r_m s_m B}{KL} + B(C_1 C_2)\right] < 0$ which is satisfied by $C_i > -\frac{r_m B}{AK}$; this is true since $C_i > \frac{B}{K}$ and $-\frac{r_m}{A} \geq 1$. □
2. The proof is analogous to the proof above. □

To facilitate interpretations of the result, without loss of generality, I consider two special cases for $C_1 > C_2$. First, if the predator conversion delay is the same in both patches, that is, $\sigma_1 = \sigma_2$, and prey vulnerability α_i is the same for both prey subpopulations, then $C_1 > C_2$ reduces to $\frac{\beta_1}{|\alpha|} > \frac{\beta_2}{|\alpha|}$. In this case I interpret that we should harvest the prey and predator subpopulations living in the patch that has the greater predator biological efficiency more conservatively than those living in the patch that has a lower efficiency. Second, if $\alpha_1 = \alpha_2$ and $\beta_1 = \beta_2$ then $C_1 > C_2$ is satisfied by $\sigma_1 < \sigma_2$. In this case, we should harvest prey and predator subpopulations in a lower predator conversion delay patch more conservatively than those in a greater conversion delay patch. The following section describes comparisons of the optimal escapements if the metapopulation is incorrectly managed as an unconnected two-patch predator-prey or a well-mixed predator-prey population.

Escapement comparisons to incorrect escapements policies

Result 20 *(Comparison of strategy with escapements from an unconnected two-patch predator-prey system) Let* $S^*_{N_i}$ *and* $S^*_{P_i}$ *denote optimal escapements from a predator-prey metapopulation given by equations (6.42) and (6.43). Let* $S^*_{N_{iu}}$ *and* $S^*_{P_{iu}}$ *denote optimal escapements if we incorrectly consider the population as a system consisting of two unconnected predator-prey populations. If all hypothesis in Lemma 5 are satisfied and also* $s_{1m} = s_{2m} = s_m$, $\Delta S_{N_u} = (S^*_{N_1} + S^*_{N_2}) - (S^*_{N_{1u}} + S^*_{N_{2u}})$ *and* $\Delta S_{P_u} = (S^*_{P_1} + S^*_{P_2}) - (S^*_{P_{1u}} + S^*_{P_{2u}})$ *then:*

1. $S^*_{N_1} - S^*_{N_{1u}} = \frac{(r_{1u} - r_{1m})X}{\Delta_{1u}\Delta_1}$,
2. $S^*_{N_2} - S^*_{N_{2u}} = \frac{(r_{2u} - r_{2m})X}{\Delta_{2u}\Delta_2}$,
3. $S^*_{P_1} - S^*_{P_{1u}} = \frac{(r_{1u} - r_{1m})Y}{\Delta_{1u}\Delta_1}$,
4. $S^*_{P_2} - S^*_{P_{2u}} = \frac{(r_{2u} - r_{2m})Y}{\Delta_{2u}\Delta_2}$,
5. $\Delta S_{N_u} = \frac{(8s_m/(KL)(\frac{2(r_{1m}+r_{2m})s_m}{KL} - C^2))(r_{1u}r_{2u} - r_{1m}r_{2m})}{\Delta_1\Delta_{1u}\Delta_2\Delta_{2u}} X$,
6. $\Delta S_{P_u} = \frac{(8s_m/(KL)(\frac{2(r_{1m}+r_{2m})s_m}{KL} - C^2))(r_{1u}r_{2u} - r_{1m}r_{2m})}{\Delta_1\Delta_{1u}\Delta_2\Delta_{2u}} Y$,

where $X = \left(C(C - 2B/K) - \frac{4Rs_m}{KL}\right)\frac{2s_m}{L}$ *and* $Y = \left(C(C - \frac{2B}{K}) - \frac{4Rs_m}{KL}\right)C$. *Furthermore, if* A_i *and* B_i *are negative, and* C_i *is non-positive with* $C > max\{\frac{2B}{K}, \frac{2A}{L}\}$, *then* $X < 0$ *and* $Y > 0$.

I do not provide a proof of the result above since it is only a minor modification of the proof for the similar result in the previous chapter. Assuming $r_1 = r_2$, I interpret the result above as follows. Recall that $r_{im} = (p_{ii}\rho^{\gamma_i} + p_{ij}\rho^{\gamma_j})r_i$ and $r_{iu} = p_{ii}r_i\rho^{\gamma_i} + p_{ji}r_j\rho^{\gamma_i}$.

1. If $p_{11} = p_{22}$, $p_{12} = p_{21}$ and $\gamma_1 = \gamma_2$ then $r_{im} = r_{iu}$. Hence, if there is no source/sink and no exporter/importer prey subpopulation and there is also no recruitment delay difference between the two prey subpopulations, then optimal escapements from a predator-prey metapopulation are exactly the same as escapements from the two-patch unconnected predator-prey harvesting theory.

2. If $p_{11}\rho^{\gamma_1} \geq p_{22}\rho^{\gamma_2}$, $p_{12} = p_{21}$ and $\gamma_1 > \gamma_2$ then $r_{1m} > r_{1u}$ and $r_{2m} < r_{2u}$, assuming that the discounting rate is not zero. If there is no discounting rate, then there is no difference between optimal escapements from a predator-prey metapopulation and from the unconnected two-patch predator-prey harvesting theory. The following discussion assumes that the discounting rate is not zero. Since $\Delta_{iu} < 0$, $C^2 - \frac{2(r_{1m}+r_{2m})s_m}{KL} < 0$ and $r_{1m}r_{2m} - r_{1u}r_{2u} \leq 0$ (see Appendix 6B), then:

   (a) $S^*_{N_1} > S^*_{N_{1u}}$,
   (b) $S^*_{N_2} < S^*_{N_{2u}}$,
   (c) $S^*_{P_1} \leq S^*_{P_{1u}}$,
   (d) $S^*_{P_2} \geq S^*_{P_{2u}}$,
   (e) $(S^*_{N_1} + S^*_{N_2}) - (S^*_{N_{1u}} + S^*_{N_{2u}}) \leq 0$,
   (f) $(S^*_{P_1} + S^*_{P_2}) - (S^*_{P_{1u}} + S^*_{P_{2u}}) \geq 0$.

   Here, as in the single-species metapopulation delay model (Tuck, 1994), the prey subpopulation with the larger recruitment delay is over-exploited if it is managed as an unconnected two-patch predator-prey population. This incorrect policy also under-harvests the prey subpopulation with the smaller recruitment delay and the over-all prey population would be under-exploited. In contrast to single-species metapopulation theory, incorrectly assuming that the population is an unconnected two-patch predator-prey population would under-harvest the predator living in the same patch with the larger recruitment delay prey subpopulation and over-exploit the predator living in the same patch with the smaller recruitment delay prey subpopulation.

3. If $p_{11} \geq p_{22}$, $p_{12} > p_{21}$ and $\gamma_1 = \gamma_2$ then $r_{1m} > r_{1u}$ and $r_{2m} < r_{2u}$, assuming that the discounting rate is not zero. The result is the same to the case of $p_{11}\rho^{\gamma_1} \geq p_{22}\rho^{\gamma_2}$, $p_{12} = p_{21}$ and $\gamma_1 > \gamma_2$. Therefore, incorrectly managing a predator-prey metapopulation as an unconnected two-patch predator-prey population would over-harvest the relative exporter prey subpopulation and the predator living in the same patch with the relative importer prey subpopulation. On the other hand, the relative importer prey subpopulation and the predator living in the same patch with the relative exporter prey subpopulation would be under-harvested.

Result 21 *(Comparison of strategy with escapements from a well-mixed predator-prey system) Let $S^*_{N_i}$ and $S^*_{P_i}$ denote optimal escapements from a predator-prey metapopulation given by equations (6.42) and (6.43). Let $S^*_{N_w}$ and $S^*_{P_w}$ denote optimal escapements if we incorrectly consider the population as a well-mixed system. If all hypothesis in Lemma 5 are satisfied and also $s_{1m} = s_{2m} = s_m$, $\Delta S_{N_w} = (S^*_{N_1} + S^*_{N_2}) - S^*_{N_w}$ and $\Delta S_{P_w} = (S^*_{P_1} + S^*_{P_2}) - S^*_{P_w}$, and in addition C satisfies $C\left(BC^2 + \frac{3(R-r_w)s_m}{L}C - \frac{2Br_ws_m}{KL}\right) = 0$ then:*

1. $S^*_{N_1} - \frac{1}{2}S^*_{N_w} = \frac{(r_w - r_{1m})X}{\Delta_0\Delta_1}$,

2. $S^*_{N_2} - \frac{1}{2}S^*_{N_w} = \frac{(r_w - r_{2m})X}{\Delta_0\Delta_2}$,

3. $S^*_{P_1} - \frac{1}{2}S^*_{P_w} = \frac{(r_w - r_{1m})Y}{\Delta_0\Delta_1}$,

4. $S^*_{P_2} - \frac{1}{2}S^*_{P_w} = \frac{(r_w - r_{2m})Y}{\Delta_0\Delta_2}$,
5. $\Delta S_{N_w} = \frac{(8s_m/(KL)(\frac{2(r_{1m}+r_{2m})s_m}{KL} - C^2))(r_w r_w - r_{1m}r_{2m})}{\Delta_1\Delta_0\Delta_2\Delta_0} X$,
6. $\Delta S_{P_w} = \frac{(8s_m/(KL)(\frac{2(r_{1m}+r_{2m})s_m}{KL} - C^2))(r_w r_w - r_{1m}r_{2m})}{\Delta_1\Delta_0\Delta_2\Delta_0} Y$,

where $X = \left(C(C - 2B/K) - \frac{4Rs_m}{KL}\right)\frac{2s_m}{L}$, $Y = \left(C(C - \frac{2B}{K}) - \frac{4Rs_m}{KL}\right)C$ *and* $\Delta_0 = C^2 - \frac{4s_m r_w}{KL}$. *Furthermore, if* A_i *and* B_i *are negative, and* C_i *is non-positive with* $C > max\{\frac{2B}{K}, \frac{2A}{L}\}$, *then* $X < 0$ *and* $Y > 0$.

I interpret the result above for the case of $r_1 = r_2$ as follows. Recall that $r_{im} = (p_{ii}\rho^{\gamma_i} + p_{ij}\rho^{\gamma_j})r_i$ and $r_w = \left(\frac{r_1(p_{11}+p_{12})+r_2(p_{21}+p_{22})}{2}\right)\rho^{(\gamma_1+\gamma_2)/2}$.

1. If $p_{11} = p_{22}$, $p_{12} = p_{21}$ and $\gamma_1 = \gamma_2$ then $r_{im} = r_w$. Hence, if there is no source/sink and no exporter/importer prey subpopulation and there is also no recruitment delay differences between the two prey subpopulations, then optimal escapements from a predator-prey metapopulation are exactly the same as escapements from the well-mixed predator-prey harvesting theory.

2. If $p_{11} = p_{22}$, $p_{12} = p_{21}$ and if there is no discounting rate, then there is no difference between optimal escapements from a predator-prey metapopulation and from the well-mixed predator-prey harvesting theory regardless of the value of recruitment delays γ_1 and γ_2.

3. If $p_{11} \geq p_{22}$, $p_{12} > p_{21}$ and $\gamma_1 = \gamma_2$ then $r_{1m} > r_w$ and $r_{2m} < r_w$, assuming that the discounting rate is not zero. Furthermore it can be proved that $r_{1m}r_{2m} - r_w^2 \leq 0$ (see Appendix 6C), and hence:

    (a) $S^*_{N_1} > \frac{1}{2}S^*_{N_w}$,
    (b) $S^*_{N_2} < \frac{1}{2}S^*_{N_w}$,
    (c) $S^*_{P_1} \leq \frac{1}{2}S^*_{P_w}$,
    (d) $S^*_{P_2} \geq \frac{1}{2}S^*_{P_w}$,
    (e) $(S^*_{N_1} + S^*_{N_2}) \leq S^*_{N_w}$,
    (f) $(S^*_{P_1} + S^*_{P_2}) \geq S^*_{P_w}$.

    Therefore, incorrectly managing a predator-prey metapopulation as a well-mixed predator-prey population would over-harvest the relative exporter prey subpopulation and the predator living in the same patch with the relative importer prey subpopulation. On the other hand, the relative importer prey subpopulation and the predator living in the same patch with the relative exporter prey subpopulation would be under-harvested. Incorrectly managing the population as a well-mixed predator-prey would under-harvest the prey and over-harvest the predator at the metapopulation level.

To illustrate the results discussed above, I present numerical examples in the following section. I also investigate optimal harvesting strategies for the other model, that is, the parental delay predator-prey metapopulation model, in the subsequent section. The optimal escapements in this section will be compared to the optimal escapements from the parental delay predator-prey metapopulation.

6.1.4 Numerical examples

Consider a metapopulation with two subpopulations, N_1 and N_2. The two subpopulations have the same carrying capacities $K_1 = K_2 = 500000$, the same intrinsic growth rates $r_1 = r_2 = 1000$ and the same adult survival rates per period $a_1 = a_2 = 0.001$. The metapopulation has a symmetrical migration $p_{11} = p_{22} = p_{12} = p_{21} = 0.001$, hence there is no relative source/sink and exporter/importer subpopulation. The discounting rate δ is 10%. Before the exploitation begins, it is assumed that the metapopulation is in its equilibrium population size $\bar{N}_1 = \bar{N}_2 = 250250$. Optimal escapements for this metapopulation are $S^*_{N_{1s}} = S^*_{N_{2s}} = 112625$, hence both prey subpopulations are harvested equally with first period optimal harvests $H^*_{N_{1s}} = H^*_{N_{2s}} = 137625$ and equilibrium optimal harvests $H^*_{N_{1s}} = H^*_{N_{2s}} = 62000$.

Now assume that the predator, P_i, is present. Let us assume that the intrinsic growth rate of the predator is $s_i = 1000$ with the carrying capacity $L_i = 10000$. The predator's adult survival per period is not different from the prey's adult survival and is not different between patches, hence $b_1 = b_2 = 0.001$. To see the effect of predator's recruitment delays on the optimal escapements of prey populations, I assume that the predator has migration parameters $q_{11} = q_{12} = q_{21} = q_{22} = 0.01$. Let $|\alpha_i| = \beta_i = 0.00001$, that is, the predator has a high conversion efficiency. Let $\tau_1 = \tau_2 = 2$, $\sigma_1 = 3$, $\sigma_2 = 4$, and the prey do not experience recruitment delay, that is, $\gamma_1 = \gamma_2 = 0$. With these parameters, a positive equilibrium population size, $(\bar{N}_1, \bar{N}_2, \bar{P}_1, \bar{P}_2) = (223702, 223702, 10619, 10619)$, is obtained. Using equations (6.42) and (6.43) the optimal escapements for the system are found, that is, $S^*_{N_1} = 111200$, $S^*_{N_2} = 110818$, $S^*_{P_1} = 4584$ and $S^*_{P_2} = 4561$. These escapements are smaller than the escapements we get if we do not take into account the recruitment delays (recruitment delays are zero), that is, $S^*_{N_1} = S^*_{N_2} = 112625$ and $S^*_{P_1} = S^*_{P_2} = 4668$.

Note that even though both prey subpopulation are identical, in terms of their biological parameters, their optimal escapements are different. We should harvest the prey living in the same patch with the predator subpopulation which has a lower conversion delay (in patch one) more conservatively than the other prey subpopulation ($S^*_{N_1} > S^*_{N_2}$). We should also harvest the predator subpopulation with a lower conversion delay more conservatively than the other predator subpopulation ($S^*_{P_1} > S^*_{P_2}$). This is because predator subpopulation one has a higher discounted efficiency, that is, $C_1 > C_2$ due to the lower delay in energy conversion ($\sigma_1 < \sigma_2$) (see Result 19 and Figure 6.2). If we ignore conversion delays, or if predation only aids predator survival, optimal escapements for both patches are equal. This is because in the absence of the delays, predator efficiency in both patches are equal, that is, $C_1 = C_2$.

Figure 6.2.a shows a contour plot of the difference between two prey subpopulation optimal escapements ($S^*_{N_1} - S^*_{N_2}$) with the variation of $\alpha_1 = \alpha_2 = \alpha$ and $\beta_1 = \beta_2 = \beta$. The contour line 0 is the contour line where $S^*_{N_1} = S^*_{N_2}$. The region below this line is the region for $S^*_{N_1} < S^*_{N_2}$, where the conditions in Result 19 may be violated. For example if $\alpha = -0.0001$ and $\beta = 0.00001$ then $S^*_{N_1} < S^*_{N_2}$ (see Figure 6.2.a) and $C \leq max\{\frac{B}{K}, \frac{A}{L}\}$ (see Result 19). If we ignore the predator-prey interaction, that is, if we consider the system as a single-species metapopulation with delay, then optimal escapements for both prey subpopulation would be the same due to the symmetric delay, since $\gamma_1 = \gamma_2$ and $\tau_1 = \tau_2$. If we only consider the presence of predator-prey interaction but not the delays, then optimal escapements for both prey subpopulations would be equal along the line $\beta = |\alpha|$. Figure 6.2.b is interpreted similarly.

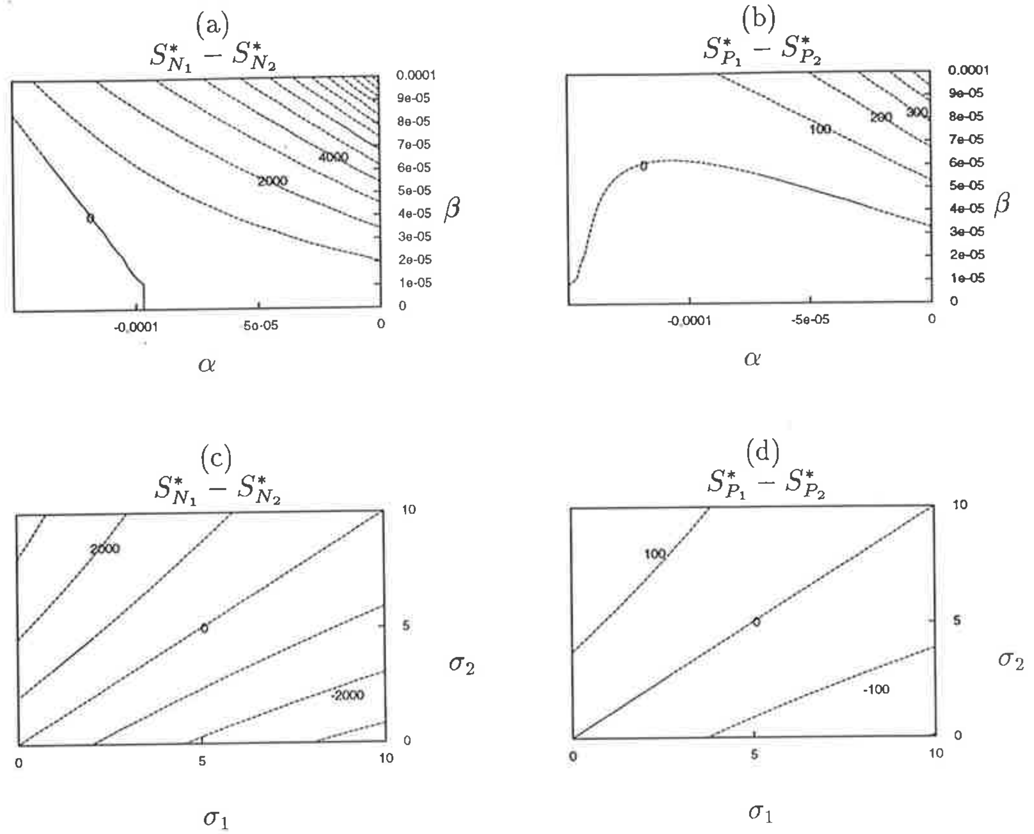


Figure 6.2: Contour plot of $S^*_{N_1} - S^*_{N_2}$ (Figure 6.2.a) and $S^*_{P_1} - S^*_{P_2}$ (Figure 6.2.b) with the variation of $\alpha_1 = \alpha_2 = \alpha$ and $\beta_1 = \beta_2 = \beta$ and contour plot of $S^*_{N_1} - S^*_{N_2}$ (Figure 6.2.c) and $S^*_{P_1} - S^*_{P_2}$ (Figure 6.2.d) with the variation of σ_1 and σ_2.

Figure 6.2.c shows a contour plot of the difference between two prey subpopulation optimal escapements ($S^*_{N_1} - S^*_{N_2}$) with the variation of σ_1 and σ_2. The contour line 0 (or the line $\sigma_2 = \sigma_1$) is the contour line where $S^*_{N_1} = S^*_{N_2}$. The region below this line is the region for $S^*_{N_1} < S^*_{N_2}$. In this region predator subpopulation two has a lower conversion delay than predator subpopulation one and hence has a higher discounted efficiency than predator subpopulation one. In this case, we should protect both prey and predator subpopulation in patch two more conservatively than prey and predator in patch one (see Result 19).

As mentioned earlier in this section, the optimal escapements in this example are smaller than the escapements if we do not take into account the recruitment delays. This is typical for harvesting a population with delayed recruitment in general. It is not optimal to wait until juvenile reach maturity if the recruitment delays of the populations are too large. Hence optimal escapement is zero (Clark, 1976b; Tuck, 1994). This is also true in general for the optimal harvesting of a predator-prey metapopulation. Other examples as in Figures 6.3.a and 6.3.c, where $q_{11} = q_{21} = q_{22} = 0.002$ and $q_{12} = 0.003$, show that a prey subpopulation with a larger delay has a smaller optimal escapement, until finally it is zero, that is, all the population should be harvested. In this example, optimal escapements for both predator subpopulations are increasing with the increase of the prey recruitment delay (Figures 6.3.b and 6.3.d). However, their equilibrium harvests are decreasing, due to the decrease of their food (the prey), until they reach

t	N_1	N_2	$S^*_{N_1}$	$S^*_{N_2}$	$H^*_{N_1}$	$H^*_{N_2}$
0	220533	216539	111588	111718	108945	104821
1	169831	170293	111588	111718	58243	58575
2	169831	170293	111588	111718	58243	58575
3	169831	170293	111588	111718	58243	58575
4	169831	170293	111588	111718	58243	58575
5	169831	170293	0	0	169831	170293

t	P_1	P_2	$S^*_{P_1}$	$S^*_{P_2}$	$H^*_{P_1}$	$H^*_{P_2}$
0	11659	13717	3334	2918	8325	10799
1	3	3	3334	2918	-3331	-2915
2	3	3	3334	2918	-3331	-2915
3	8581	10803	3334	2918	5247	7885
4	12302	14063	3334	2918	8968	11145
5	12302	14063	0	0	12302	14063

Table 6.2: Optimal escapements and harvests from a predator-prey metapopulation. The t^{th} row indicates the value for $5 - t$ periods to go.

a constant harvest for any large values of prey recruitment delays, γ_i. In this example predator subpopulation one produces $H^*_{P_1} = 5500$ and predator subpopulation two produces $H^*_{P_2} = 6500$, regardless of the values of γ_i (Figures 6.3.c and 6.3.d). These harvests are exactly the same as harvests from a single-species metapopulation.

On the other hand, with the increase of predator recruitment delays, optimal escapements for both predator subpopulations decrease (Figures 6.4.b) while optimal escapements for both prey subpopulations increase (Figures 6.4.a). Unlike the case where the variation takes the form of prey recruitment delays (Figure 6.3), in which the increase of predator escapement does not mean the increase of predator equilibrium harvest, here the increase of prey escapement due to the decrease of predator recruitment delay means the increase of prey equilibrium harvest (Figure 6.4.c) and the decrease of predator escapement means the decrease of predator equilibrium harvest (Figure 6.4.d). We harvest the relative exporter/importer predator subpopulations more/less conservatively, but we no longer harvest prey subpopulations living within the same patch as the relative importer/exporter predator subpopulations more/less conservatively (see Figure 6.4.a). This is because the predator discounted efficiency between the two subpopulations are different. It does not satisfy the condition described in Result 18. If there is no difference between the two discounted efficiencies, for example if $\sigma_1 = \sigma_2 = 3$, then the rule described in the Result 18 above holds (see Table 6.2).

To illustrate the comparison between predator-prey metapopulation policy and the incorrect harvesting policy I give a different example where one predator subpopulation is a relative exporter and source subpopulation. For the following example I assume that all parameters are equal to the previous example, except that $q_{12} = 0.003$, $q_{11} = q_{21} = q_{22} = 0.002$, and $\sigma_1 = \sigma_2 = 3$, that is, predator subpopulation one is a relative exporter and source subpopulation. If we correctly manage the population as a predator-prey metapopulation we find optimal escapements and harvests as in

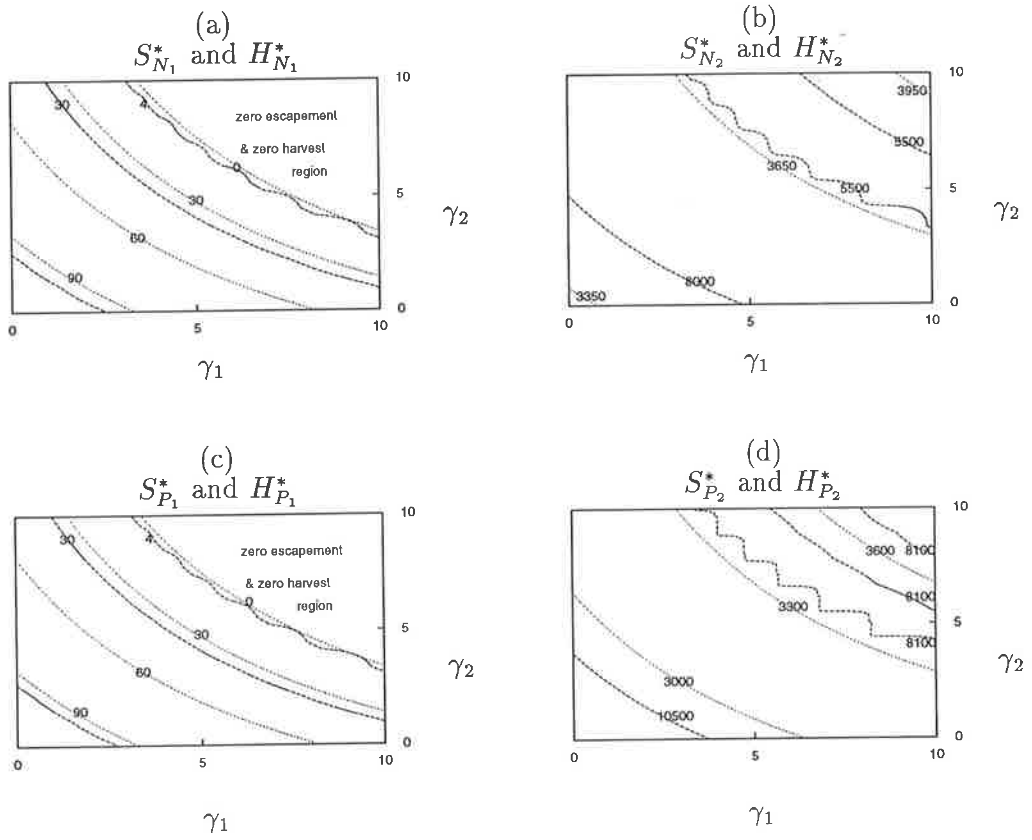


Figure 6.3: Contour plots of the optimal escapements (dots) and equilibrium harvests (dashes) for prey subpopulation one (Figure 6.3.a), prey subpopulation two (Figure 6.3.b), predator subpopulation one (Figure 6.3.c) and predator subpopulation two (Figure 6.3.d). Prey numbers are in thousands. Prey escapements are always smaller than escapements if there is no recruitment delay and decreasing with the increase of the delays. If the delays are extremely high (upper-right corner in the figure) then it is optimal to harvest all prey in both subpopulations. This is consistent with the result for single-species metapopulation harvesting theory. Figures 6.3.b and 6.3.d show that we should harvest the exporter predator subpopulation which has a lower conversion delay (subpopulation one) more conservatively than predator subpopulation two.

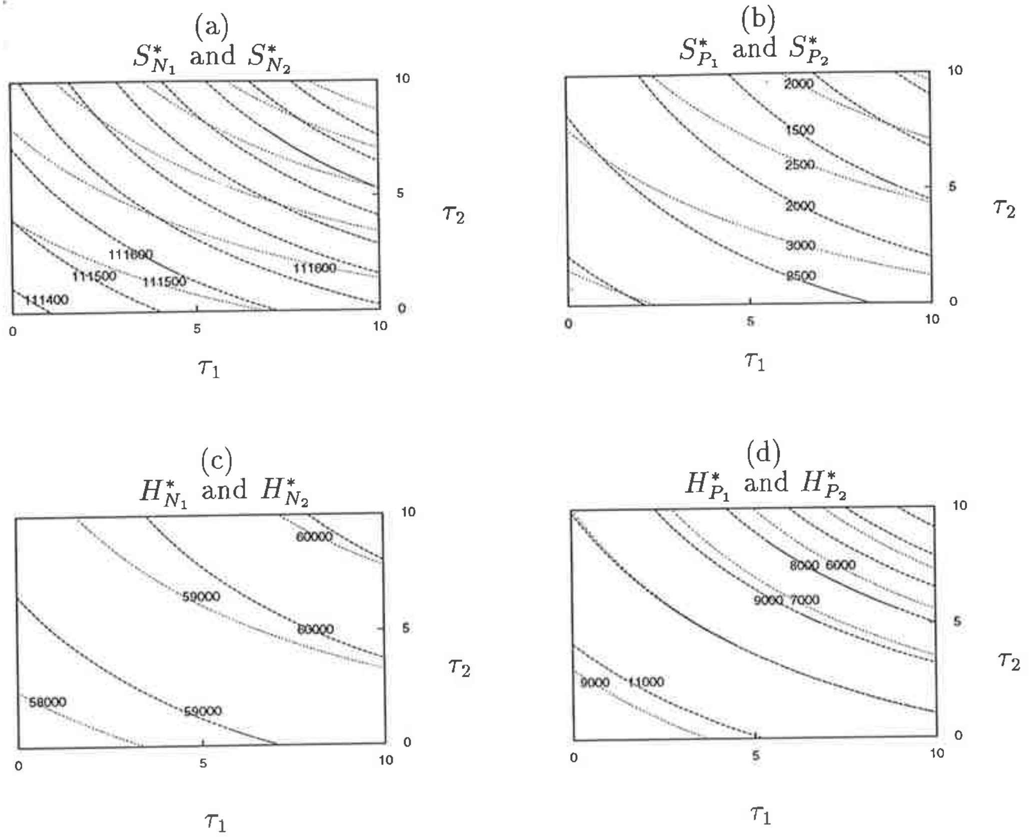


Figure 6.4: Figure 6.4.a shows contour plots of prey optimal escapements $S^*_{N_1}$ (dots) and $S^*_{N_2}$ (dashes), Figure 6.4.b shows contour plots of predator optimal escapements $S^*_{P_1}$ (dots) and $S^*_{P_2}$ (dashes), Figure 6.4.c shows contour plots of prey equilibrium harvests $H^*_{N_1}$ (dots) and $H^*_{N_2}$ (dashes), and Figure 6.4.d shows contour plots of predator equilibrium harvests $H^*_{P_1}$ (dots) and $H^*_{P_2}$ (dashes) with the variation of the predator recruitment delays τ_1 and τ_2.

Table 6.2.

Because there is no recruitment and energy conversion delay differences between subpopulations, the relative exporter predator subpopulation is harvested more conservatively than the relative importer predator subpopulation. As in the case of the non-delay predator-prey metapopulation, the prey living in the same patch with the relative exporter predator subpopulation is harvested less conservatively. Furthermore, assuming that in the beginning of the exploitation the metapopulation consists of adult individuals only, since both predator subpopulations experience two periods recruitment delay, we should leave both predator subpopulations unharvested for the first two periods (indicated by the negative harvests $H^*_{P_1} = -3331$ and $H^*_{P_2} = -2915$). As in the case of the non-delay model, there are two different ways to handle these negative escapements, if they impossible to implement. However, seeding strategy using these negative escapements gives a higher profit than the other two methods.

If we incorrectly consider the population to be an unconnected two-patch predator-prey population, we find that $S^*_{N_{1u}} = S^*_{N_2}$, $S^*_{N_{2u}} = S^*_{N_1}$, $S^*_{P_{1u}} = S^*_{P_2}$ and $S^*_{P_{2u}} = S^*_{P_1}$ with equilibrium harvests $H^*_{N_{1u}} = H^*_{N_2}$, $H^*_{N_{2u}} = H^*_{N_1}$, $H^*_{P_{1u}} = 8923 < H^*_{P_1}$ and $H^*_{P_{2u}} = 11034 < H^*_{P_2}$. As in the non-delay case, the incorrect harvesting policy fails to recognise the importance of the relative exporter and source subpopulation, hence this important subpopulation is over-harvested while the less important subpopulation is under-harvested. As a result, the total harvest from this incorrect harvesting policy is less than the total harvest if the population is managed properly.

If we incorrectly consider the population as a well-mixed predator-prey population, we find that $S^*_{N_{1w}} = S^*_{N_{2w}} = \frac{1}{2}S^*_{N_w} = 110896$ and $S^*_{P_{1w}} = S^*_{P_{2w}} = \frac{1}{2}S^*_{P_w} = 2781$. Here we see the rule holds that if we incorrectly manage a predator-prey metapopulation as a well-mixed predator-prey population we would over-harvest the relative exporter predator subpopulation and the prey living in the same patch with the relative importer predator subpopulation. But, the rule that a relative importer predator subpopulation and the prey living in the same patch with the relative exporter predator subpopulation would be under-harvested, as suggested by the explanation of Result 21, does not hold. This is because the discounted predator efficiency C_i does not satisfy the assumptions in Result 21.

If now, for example, we chose $\beta_1 = \beta_2 = 0.00001331$ and incorrectly manage the population as a well-mixed predator-prey population we would produce escapements $S^*_{N_{1w}} = S^*_{N_{2w}} = \frac{1}{2}S^*_{N_w} = 112625$ and $S^*_{P_{1w}} = S^*_{P_{2w}} = \frac{1}{2}S^*_{P_w} = 3522$. While if we manage the population correctly as a two-patch predator-prey metapopulation, we would find optimal escapements $S^*_{N_1} = S^*_{N_2} = 112625$, $S^*_{P_1} = 3670$ and $S^*_{P_2} = 3338$. Here the rule described in Result 21 is satisfied.

The last example shows that to satisfy the rule in Result 21, we need the discounted predator efficiency, C_i, to be equal to zero (which is satisfied by $\beta_i = 0.00001331 > |\alpha_i| = 0.00001$). In nature, this is impossible, since it means that the predator biological efficiency is greater than 100%. This is because it is assumed that there is no price difference between prey and predator. If we take price differences into account, say the price of predator is ten times the price of the prey, then we only need $\beta_i = 0.000001331$ or the predator biological efficiency is about thirteen per cent, which is plausible for many species (Rand and Stewart, 1998). As in the case of the non-delay model, the analysis with the inclusion of harvesting cost is similar to the analysis where harvesting cost is neglected.

6.2 Predator-prey parental delay model

A predator-prey receptor delay model assumes that the recruitment delays occur in the subpopulations that receive the juveniles. Tuck (1994) argued that delay may occur due to some genetic effects, hence all juveniles from subpopulation i experience the same delay, regardless of where they go. He called this type of delay "parental recruitment delay". This model can also describe delays related by environmental effects on a subpopulation before the juvenile migrate to other subpopulations.

In nature, there is much evidence to show that parental recruitment delays can occur, for example in Chinook salmon, *Oncorhynchus tshawytscha* (Hankin *et al.*, 1993). Quinn and Hendry (1997) studied adult life history of Sockeye salmon, *Oncorhynchus nerka*, in Lake Washington which has five subpopulations. Two of the subpopulations are native to the lake while the other three are native to a different lake, Lake Baker. They found that spawning salmon in one of the non-native subpopulations are older than the native species. The age of these non-native spawning salmon in Lake Washington is relatively the same as the age of spawning salmon in their original habitat (Lake Baker). Furthermore, they pointed out that the existence of local adaptation is difficult to prove, they argued that habitat variations are not sufficient to make differences in age at maturity. The model in the following section is more appropriate to describe this type of delay than the previous predator-prey receptor delay model. I refer to the model in this section as a predator-prey parental delay model.

6.2.1 The model and its optimal escapements

If all the symbols in the predator-prey parental delay model have the same meaning as the previous predator-prey metapopulation with receptor delay recruitment, then the growth of the exploited populations in the predator-preý parental model are given by

$$N_{1(k+1)} = a_1 S_{N_{1k}} + p_{11} F_1(S_{N_{1k-\gamma_1}}) + p_{21} F_2(S_{N_{2k-\gamma_2}}) + \alpha_1 S_{N_{1k}} S_{P_{1k}}, \tag{6.46}$$

$$N_{2(k+1)} = a_2 S_{N_{2k}} + p_{22} F_2(S_{N_{2k-\gamma_2}}) + p_{12} F_1(S_{N_{1k-\gamma_1}}) + \alpha_2 S_{N_{2k}} S_{P_{2k}}, \tag{6.47}$$

$$P_{1(k+1)} = b_1 S_{P_{1k}} + q_{11} G_1(S_{P_{1k-\tau_1}}) + q_{21} G_2(S_{P_{2k-\tau_2}}) + \beta_1 S_{N_{1k-\sigma_1}} S_{P_{1k-\sigma_1}}, \tag{6.48}$$

$$P_{2(k+1)} = b_2 S_{P_{2k}} + q_{22} G_2(S_{P_{2k-\tau_2}}) + q_{12} G_1(S_{P_{1k-\tau_1}}) + \beta_2 S_{N_{2k-\sigma_2}} S_{P_{2k-\sigma_2}}. \tag{6.49}$$

Optimal escapements for the present model satisfy implicit equations

$$\begin{aligned}\frac{p_N - c_{N1}(S^*_{N_{10}})}{\rho} &= (p_N - c_{N1}(N_{11}))(a_1 + p_{11} F_1'(S^*_{N_{10}})\rho^{\gamma_1} + \alpha_1 S^*_{P_{10}}) \\ &\quad + (p_N - c_{N2}(N_{21})) p_{12} F_1'(S^*_{N_{10}})\rho^{\gamma_1} \\ &\quad + (p_P - c_{P1}(P_{11}))\beta_1 S^*_{P_{10}} \rho^{\sigma_1},\end{aligned} \tag{6.50}$$

$$\begin{aligned}\frac{p_N - c_{N2}(S^*_{N_{20}})}{\rho} &= (p_N - c_{N2}(N_{21}))(a_2 + p_{22} F_2'(S^*_{N_{20}})\rho^{\gamma_2} + \alpha_2 S^*_{P_{20}}) \\ &\quad + (p_N - c_{N1}(N_{11})) p_{21} F_2'(S^*_{N_{20}})\rho^{\gamma_2} \\ &\quad + (p_P - c_{P2}(P_{21}))\beta_2 S^*_{P_{20}} \rho^{\sigma_2},\end{aligned} \tag{6.51}$$

$$\begin{aligned}\frac{p_P - c_{P1}(S^*_{P_{10}})}{\rho} &= (p_P - c_{P1}(P_{11}))(b_1 + q_{11} G_1'(S^*_{P_{10}})\rho^{\tau_1} + \beta_1 S^*_{N_{10}} \rho^{\sigma_1}) \\ &\quad + (p_P - c_{P2}(P_{21})) q_{12} G_1'(S^*_{P_{10}})\rho^{\tau_1} \\ &\quad + (p_N - c_{N1}(N_{11}))\alpha_1 S^*_{N_{10}},\end{aligned} \tag{6.52}$$

$$\begin{aligned}\frac{p_P - c_{P2}(S^*_{P_{20}})}{\rho} &= (p_P - c_{P2}(P_{21}))(b_2 + q_{22} G_2'(S^*_{P_{20}})\rho^{\tau_2} + \beta_2 S^*_{N_{20}} \rho^{\sigma_2}) \\ &\quad + (p_P - c_{P1}(P_{11})) q_{21} G_2'(S^*_{P_{20}})\rho^{\tau_2} \\ &\quad + (p_N - c_{N2}(N_{21}))\alpha_2 S^*_{N_{20}}.\end{aligned} \tag{6.53}$$

6.2.2 Results with negligible costs

As in the predator-prey receptor delay model, results are interpreted by neglecting all costs associated with harvesting. I also assume that there is no difference between the price of the prey and predator. Using these assumptions, substitute all derivatives of the logistic recruitment functions $F_i(N_{ik}) = r_i N_{ik}(1 - N_{ik}/K_i)$ and $G_i(P_{ik}) = s_i P_{ik}(1 - P_{ik}/L_i)$, into equations (6.50) - (6.53) to obtain

$$\frac{1}{\rho} = a_i + (p_{i1} + p_{i2})\rho^{\gamma_i}\left(r_i - \frac{2r_i}{K_i} S^*_{N_i}\right) + (\alpha_i + \beta_i \rho^{\sigma_i}) S^*_{P_i}, \tag{6.54}$$

$$\frac{1}{\rho} = b_i + (q_{i1} + q_{i2})\rho^{\tau_i}\left(s_i - \frac{2s_i}{L_i}S^*_{P_i}\right) + (\alpha_i + \beta_i\rho^{\sigma_i})S^*_{N_i}. \tag{6.55}$$

Solving equations (6.54) and (6.55) produces explicit expressions of optimal escapements,

$$S^*_{Ni} = \frac{A_i(q_{i1} + q_{i2})\rho^{\tau_i}\frac{2s_i}{L_i} + C_iB_i}{\Delta_i}, \tag{6.56}$$

$$S^*_{Pi} = \frac{B_i(p_{i1} + p_{i2})\rho^{\gamma_i}\frac{2r_i}{K_i} + C_iA_i}{\Delta_i}, \tag{6.57}$$

provided

$$\Delta_i = C_i^2 - (p_{i1} + p_{i2})\rho^{\gamma_i}\frac{2r_i}{K_i}(q_{i1} + q_{i2})\rho^{\tau_i}\frac{2s_i}{L_i} \neq 0, \tag{6.58}$$

with

$$A_i = \frac{1}{\rho} - (p_{i1} + p_{i2})\rho^{\gamma_i}r_i - a_i, \tag{6.59}$$

$$B_i = \frac{1}{\rho} - (q_{i1} + q_{i2})\rho^{\tau_i})s_i - b_i, \tag{6.60}$$

and

$$C_i = \alpha_i + \beta_i\rho^{\sigma_i}. \tag{6.61}$$

As in the case of the predator-prey receptor delay model, I deal only with positive escapements. The following result guarantees that the escapements are all positive, and the result is used to obtain escapement comparison between the current method and the method where we ignore the predator-prey interaction. I do not go into the details of the proof of the following result, since it can be proved analogously to the result in the previous section.

Result 22 *(Sufficient conditions for positive escapements) Let $S^*_{N_i}$ and $S^*_{P_i}$ denote the optimal escapement from a predator-prey metapopulation given by equations (6.56) and (6.57). If A_i and B_i are negative, and C_i is non-positive with $C_i > max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}$, then*

$$\Delta_i \textit{ is negative, and } S^*_{N_i} \textit{ and } S^*_{P_i} \textit{ are positive.}$$

Result 23 *(Escapement comparison to a single-species metapopulation) Let $S^*_{N_i}$ and $S^*_{P_i}$ denote the optimal escapement from a predator-prey metapopulation given by equations (6.56) and (6.57), and let $S^*_{N_{is}}$ and $S^*_{P_{is}}$ denote the optimal escapement from the single-species metapopulation with receptor population delay model given by the same equations by assigning $\alpha_i = \beta_i = 0$. If A_i and B_i are negative, and C_i is non-positive with $C_i > max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}$, then*

$$S^*_{N_i} - S^*_{N_{is}} = \frac{C_i}{(p_{i1}+p_{i2})\rho^{\gamma_i}2r_i/K_i}S^*_{N_i} < 0 \textit{ and } S^*_{P_i} - S^*_{P_{is}} = \frac{C_i}{(q_{i1}+q_{i2})\rho^{\tau_i}2s_i/L_i}S^*_{P_i} < 0.$$

Hence, in general escapements from a predator-prey metapopulation with a parental delay model are smaller than escapements from a single-species metapopulation with a parental delay model and has the same value if $C_i = 0$. This properties is also found for the receptor delay model discussed in the previous section. The condition $C_i = 0$ is only acceptable, biologically, if the predator is more valuable than the prey, otherwise it requires extreme predator efficiency.

Escapement comparisons between subpopulations

This section discusses some comparisons of escapements from the predator-prey parental delay model if there is parameter variability between patches.

Lemma 7 *(Migration trade-off equations) Let* $S^*_{N_i}$ *and* $S^*_{P_i}$ *denote the optimal escapement from a predator-prey metapopulation with receptor local population delay model given by equations (6.56) and (6.57). If* $i = 1, 2$, *let* $a_i = a$, $b_i = b$, $K_i = K$, $L_i = L$, $C_i = C$, $R = \frac{1}{\rho} - a$, $S = \frac{1}{\rho} - b$, $r_{im} = (p_{i1} + p_{i2})\rho^{\gamma_i} r_i$ *and* $s_{im} = (q_{i1} + q_{i2})\rho^{\tau_i} s_i$, *for* $i = 1, 2$, *then*

$$\begin{aligned}(S^*_{N_1} - S^*_{N_2})\Delta_1\Delta_2 \;=\;& \left(C^2(s_{1m} - s_{2m}) - \frac{4s_{1m}s_{2m}}{KL}(r_{2m} - r_{1m})\right)\left(\frac{2R}{L} - C\right)\\ & -\frac{2C}{L}\left(C - \frac{2S}{K}\right)(r_{1m}s_{1m} - r_{2m}s_{2m}),\end{aligned}$$

and

$$\begin{aligned}(S^*_{P_1} - S^*_{P_2})\Delta_1\Delta_2 \;=\;& \left(C^2(r_{1m} - r_{2m}) - \frac{4r_{1m}r_{2m}}{KL}(s_{2m} - s_{1m})\right)\left(\frac{2S}{K} - C\right)\\ & -\frac{2C}{K}\left(C - \frac{2R}{L}\right)(r_{1m}s_{1m} - r_{2m}s_{2m}).\end{aligned}$$

Result 24 *(Escapement comparison between subpopulations) Let one of the prey subpopulations be a relative source while all other parameters of the prey and the predator are identical for both subpopulations except delay parameters for the prey. Without loss of generality let us assume that prey subpopulation one is the relative source, that is,* $(p_{11} + p_{12})r_1 > (p_{22} + p_{21})r_2$, *and also* $r_{1m} > r_{2m}$. *If* A_i *and* B_i *are negative,* C_i *is non-positive with* $C > max\{\frac{2B}{K}, \frac{2A}{L}\}$, *then*

$$S^*_{N_1} > S^*_{N_2} \text{ and } S^*_{P_1} \leq S^*_{P_2}.$$

Result 24 shows that, as for the non-delay case, there is a region of parameters where we protect a relative source prey subpopulation better than a relative sink prey subpopulation in the sense that we harvest the relative source prey subpopulation with more escapement than the sink subpopulation. However, this source subpopulation has to have an additional property, it has to be a source prey subpopulation with respect to time delay, that is,

$$(p_{11} + p_{12})\rho^{\gamma_1} r_1 > (p_{21} + p_{22})\rho^{\gamma_2} r_2. \tag{6.62}$$

In this case, the per capita larval production of subpopulation one, discounted by its cumulative death rate, needs to be larger than the per capita larval production of subpopulation two, discounted by its cumulative death rate. Similar to the case of the receptor delay model (inequality (6.45)), inequality (6.62) redefines what a source subpopulation is for the parental delay model. The difference is, here migration rate p_{ij} is discounted by the delay of subpopulation j, while in the previous model migration rate p_{ij} is discounted by the delay of subpopulation i.

If both prey subpopulations have the same delay, $\gamma_1 = \gamma_2$, or $\gamma_1 \leq \gamma_2$, then Result 24 tells us that the relative source prey subpopulation should be harvested more conservatively than the relative sink prey subpopulation and that the predator living in the same patch with the relative source prey subpopulation should be harvested more heavily than the predator living in the other patch. This is a generalisation of the rule of thumb for single-species metapopulation exploitation (Tuck, 1994). In contrast to the predator-prey receptor delay model, here we can still establish the same result for $\gamma_1 < \gamma_2$. Furthermore, if there is no source/sink and no exporter/importer subpopulation, but $\gamma_1 < \gamma_2$, then we should harvest the prey subpopulation with a lower recruitment delay (subpopulation one) more conservatively than the prey subpopulation with a higher recruitment delay (subpopulation two). This is not the case in the predator-prey receptor delay model, where it suggests that we should harvest both prey subpopulations equally.

In harvesting theory for a single-species metapopulation, if there is no source/sink subpopulations and there is no differences between time delay for prey and predator juveniles to recruit into the adult populations, or if $r_1 p_{1i} = r_2 p_{2i}$ with any value of the delay, both subpopulations should be harvested equally. In contrast, in the present theory, optimal escapements also depend on other quantities, prey vulnerability to predation, α_i, and discounted predator efficiency, C_i. I use the following lemma to investigate optimal escapement differences if discounted predator efficiency are different between patches.

Lemma 8 *(Discounted efficiency trade-off equations) Let* $S^*_{N_i}$ *and* $S^*_{P_i}$ *denote the optimal escapement from a predator-prey metapopulation given by equations (6.56) and (6.57). If* $a_1 = a_2 = a$, $b_1 = b_2 = b$, $K_1 = K_2 = K$, $L_1 = L_2 = L$, $p_{11} = p_{22}, p_{12} = p_{21}, q_{11} = q_{22}, q_{12} = q_{21}, r_1 = r_2, s_1 = s_2$, $r_{im} = (p_{i1} + p_{i2})\rho^{\gamma_i} r_i = r_m$ *and* $s_{im} = (q_{i1} + q_{i2})\rho^{\tau_i} s_i = r_m$ *then*

$$(S^*_{N_1} - S^*_{N_2})\Delta_1\Delta_2 = (C_2 - C_1)\left[\frac{2As_m}{L}(C_2 + C_1) + \frac{4r_m s_m B}{KL} + B(C_1C_2)\right]$$

and

$$(S^*_{P_1} - S^*_{P_2})\Delta_1\Delta_2 = (C_2 - C_1)\left[\frac{2Br_m}{K}(C_2 + C_1) + \frac{4r_m s_m A}{KL} + A(C_1C_2)\right]$$

Using this lemma I establish the following result

Result 25 *(Escapement comparison between subpopulations) Let one of the predator subpopulations be relatively more efficient with respect to time delay, while all other parameters of the prey and the predator are identical for both subpopulations, without loss of generality we assume that predator subpopulation one is relatively more efficient, that is,* $C_1 > C_2$. *If* $A_1 = A_2 = A$ *and* $B_1 = B_2 = B$ *are negative, and* C_i *is non-positive with* $C_i > max\{\frac{B}{K}, \frac{A}{L}\}$, *then*

$$S^*_{N_1} > S^*_{N_2} \text{ and } S^*_{P_1} > S^*_{P_2}.$$

Interpretation of the result above is similar to the same result in the predator-prey receptor delay model.

Comparison of optimal escapement to incorrect escapements policies

Result 26 *(Comparison of strategy with escapements from an unconnected two-patch predator-prey system) Let* $S^*_{N_i}$ *and* $S^*_{P_i}$ *denote optimal escapements from a predator-prey metapopulation given by equations (6.56) and (6.57). Let* $S^*_{N_{iu}}$ *and* $S^*_{P_{iu}}$ *denote optimal escapements if we incorrectly consider the population as a system consisting of* *two unconnected predator-prey populations. Let* $\Delta S_{N_u} = (S^*_{N_1} + S^*_{N_2}) - (S^*_{N_{1u}} + S^*_{N_{2u}})$ *and* $\Delta S_{P_u} = (S^*_{P_1} + S^*_{P_2}) - (S^*_{P_{1u}} + S^*_{P_{2u}})$. *If all assumptions in Lemma 7 are satisfied,* A_i *and* B_i *are negative,* C_i *is non-positive with* $c_i > max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}$ *and also* $s_{1m} = s_{2m} = s_m$ *then:*

1. $S^*_{N_1} - S^*_{N_{1u}} = \frac{(r_{1u} - r_{1m})X}{\Delta_{1u}\Delta_1}$,
2. $S^*_{N_2} - S^*_{N_{2u}} = \frac{(r_{2u} - r_{2m})X}{\Delta_{2u}\Delta_2}$,
3. $S^*_{P_1} - S^*_{P_{1u}} = \frac{(r_{1u} - r_{1m})Y}{\Delta_{1u}\Delta_1}$,
4. $S^*_{P_2} - S^*_{P2u} = \frac{(r_{2u} - r_{2m})Y}{\Delta_{2u}\Delta_2}$,
5. $\Delta S_{N_u} = \frac{(8s_m/(KL)(\frac{2(r_{1m}+r_{2m})s_m}{KL} - C^2))(r_{1u}r_{2u} - r_{1m}r_{2m})}{\Delta_1\Delta_{1u}\Delta_2\Delta_{2u}}X$,
6. $\Delta S_{P_u} = \frac{(8s_m/(KL)(\frac{2(r_{1m}+r_{2m})s_m}{KL} - C^2))(r_{1u}r_{2u} - r_{1m}r_{2m})}{\Delta_1\Delta_{1u}\Delta_2\Delta_{2u}}Y$,

where $X = \left(C(C - 2B/K) - \frac{4Rs_m}{KL}\right)\frac{2s_m}{L} < 0$, $Y = \left(C(C - \frac{2B}{K}) - \frac{4Rs_m}{KL}\right)C > 0$.

Assuming $r_1 = r_2$, I interpret the result above as follows. Recall that $r_{im} = (p_{ii} + p_{ij})\rho^{\gamma_i} r_i$ and $r_{iu} = (p_{ii}r_i + p_{ji}r_j)\rho^{\gamma_i}$.

1. If $p_{12} = p_{21}$ then $r_{im} = r_{iu}$ regardless of the value of recruitment delays γ_i. In contrast to the predator-prey metapopulation with receptor delay model, the present model suggests that if there is no exporter/importer prey subpopulation then results from the correct and incorrect policy are the same, that is, $S^*_{N_i} = S^*_{N_{iu}}$ and $S^*_{P_i} = S^*_{P_{iu}}$, regardless of the values of the discounting rate (δ), prey discounted retention rate ($r_i p_{ii} \rho^{\gamma_i}$) and prey recruitment delays (γ_i).

2. If $p_{11} \geq p_{22}$, $p_{12} > p_{21}$ and $\gamma_1 = \gamma_2$ then $r_{1m} > r_{1u}$ and $r_{2m} < r_{2u}$. The result is the same to the case of predator-prey receptor delay recruitment in the previous section. Therefore, incorrectly managing a predator-prey metapopulation as an unconnected two-patch predator-prey population would over-harvest the relative exporter prey subpopulation and the predator living in the same patch with the relative importer prey subpopulation. On the other hand, the relative importer prey subpopulation and the predator living in the same patch with the relative exporter prey subpopulation would be under-harvested. In contrast to the parental recruitment delay model for a single-species metapopulation (Tuck, 1994), to obtain the result here we need both of the delays to be equal, that is, $\gamma_1 = \gamma_2$. In the single-species metapopulation model, the same result can be obtained regardless of the values of the delays γ_i (Tuck, 1994).

Result 27 *(Comparison of strategy with escapements from a well-mixed predator-prey system) Let* $S^*_{N_i}$ *and* $S^*_{P_i}$ *denote optimal escapements from a predator-prey metapopulation given by equations (6.56) and (6.57). Let* $S^*_{N_w}$ *and* $S^*_{P_w}$ *denote the optimal escapements if we incorrectly consider the population as a well-mixed system. Let* $\Delta S_{N_w} = (S^*_{N_1} + S^*_{N_2}) - S^*_{N_w}$ *and* $\Delta S_{P_w} = (S^*_{P_1} + S^*_{P_2}) - S^*_{P_w}$. *If all assumptions in Lemma 7 are satisfied,* A_i *and* B_i *are negative,* C_i *is non-positive with* $c_i > max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}$, $s_{1m} = s_{2m} = s_m$, *and in addition* C *satisfies* $C\left(BC^2 + \frac{3(R - r_w)s_m}{L}C - \frac{2Br_w s_m}{KL}\right) = 0$ *then:*

1. $S^*_{N_1} - \frac{1}{2}S^*_{N_w} = \frac{(r_w - r_{1m})X}{\Delta_0\Delta_1}$,

2. $S^*_{N_2} - \frac{1}{2}S^*_{N_w} = \frac{(r_w - r_{2m})X}{\Delta_0\Delta_2}$,

3. $S^*_{P_1} - \frac{1}{2}S^*_{P_w} = \frac{(r_w - r_{1m})Y}{\Delta_0\Delta_1}$,

4. $S^*_{P_2} - \frac{1}{2}S^*_{P_w} = \frac{(r_w - r_{2m})Y}{\Delta_0\Delta_2}$,

5. $\Delta S_{N_w} = \frac{(8s_m/(KL)(\frac{2(r_{1m}+r_{2m})s_m}{KL} - C^2))(r_w r_w - r_{1m} r_{2m})}{\Delta_1\Delta_0\Delta_2\Delta_0} X$,

6. $\Delta S_{P_w} = \frac{(8s_m/(KL)(\frac{2(r_{1m}+r_{2m})s_m}{KL} - C^2))(r_w r_w - r_{1m} r_{2m})}{\Delta_1\Delta_0\Delta_2\Delta_0} Y$,

where $X = \left(C(C - 2B/K) - \frac{4Rs_m}{KL}\right)\frac{2s_m}{L} < 0$, $Y = \left(C(C - \frac{2B}{K}) - \frac{4Rs_m}{KL}\right) C > 0$ *and* $\Delta_0 = C^2 - \frac{4s_m r_w}{KL}$.

Assuming $r_1 = r_2$, I interpret the result above as follows. Recall that $r_{im} = (p_{ii} + p_{ij})\rho^{\gamma_i})r_i$ and $r_w = \left(\frac{r_1(p_{11}+p_{12})+r_2(p_{21}+p_{22})}{2}\right)\rho^{(\gamma_1+\gamma_2)/2}$.

1. If $p_{11} = p_{22}$, $p_{12} = p_{21}$ and $\gamma_1 = \gamma_2$ then $r_{im} = r_w$. Hence, if there is no exporter/importer prey subpopulation and there are also no recruitment delay differences between the two prey subpopulations, then optimal escapements from the predator-prey metapopulation are exactly the same as escapements from the well-mixed predator-prey harvesting theory.

2. If $p_{11} = p_{22}$, $p_{12} = p_{21}$ and if there is no discounting rate, then there is no difference between optimal escapements from a predator-prey metapopulation and from the well-mixed predator-prey harvesting theory regardless of the value of recruitment delays γ_1 and γ_2.

3. If $p_{11} \geq p_{22}$, $p_{12} > p_{21}$ and $\gamma_1 = \gamma_2$ then $r_{1m} > r_w$ and $r_{2m} < r_w$, assuming that the discounting rate is not zero. The result is the same as the case of the receptor delay recruitment model. Hence, incorrectly managing a predator-prey metapopulation as a well-mixed predator-prey population would over-harvest the relative exporter prey subpopulation and the predator living in the same patch with the relative importer prey subpopulation. On the other hand, the relative importer prey subpopulation and the predator living in the same patch with the relative exporter prey subpopulation would be under-harvested. Incorrectly managing the population as a well-mixed predator-prey would under-harvest the prey and over-harvest the predator at the metapopulation level.

In the single-species metapopulation harvesting theory (Tuck, 1994), the parental delay model adheres to the relative source/sink results for the harvest policy comparisons regardless of the values of the delays. However, in the presence of predators, the two models in this chapter (the receptor delay and the parental delay predator-prey metapopulation models) adhere to the relative source/sink results for the harvest policy comparisons in Chapter 5 only for a special case, that is, if the population delays are equal. The following result investigates the differences between escapements from a predator-prey metapopulation assuming parental delay recruitment and escapements from a predator-prey metapopulation assuming local population receptor delay recruitment discussed in the previous section. The result can be proved analogously to Results 26 and 27.

Result 28 *(Escapement comparison between the predator-prey parental delay model and the predator-prey receptor delay model) Let* $S^*_{N_{ip}}$ *and* $S^*_{P_{ip}}$ *denote optimal escapements from a predator-prey metapopulation assuming parental recruitment delay, given by equations (6.56) and (6.57), and let* $S^*_{N_{ir}}$ *and* $S^*_{P_{ir}}$ *denote optimal escapements from a predator-prey metapopulation assuming local population receptor recruitment delay, given by equations (6.42) and (6.43). If all hypotheses in Lemma 7 are satisfied,* $s_{1m} = s_{2m} = s_m$, A_i *and* B_i *are negative, and* C_i *is non-positive with* $c_i > max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}$, *then:*

1. $S^*_{N_{1p}} - S^*_{N_{1r}} = \frac{(r_{1r}-r_{1p})X}{\Delta_{1r}\Delta_{1p}}$,
2. $S^*_{N_{2p}} - S^*_{N_{2r}} = \frac{(r_{2r}-r_{2p})X}{\Delta_{2r}\Delta_{2p}}$,
3. $S^*_{P_{1p}} - S^*_{P_{1r}} = \frac{(r_{1r}-r_{1p})Y}{\Delta_{1r}\Delta_{1p}}$,
4. $S^*_{P_{2p}} - S^*_{P_{2r}} = \frac{(r_{2r}-r_{2p})Y}{\Delta_{2r}\Delta_{2p}}$,

where $X = \left(C(C-2B/K) - \frac{4Rs_m}{KL}\right)\frac{2s_m}{L} < 0$, $Y = \left(C(C-\frac{2B}{K}) - \frac{4Rs_m}{KL}\right)C > 0$, Δ_{ip} *is* Δ_i *in (6.58) and* Δ_{ir} *is* Δ_i *in (7.52).*

To interpret the result above, let us assume that we have a predator-prey metapopulation satisfying all the assumptions in the result above, with parental recruitment delay mode. Let prey subpopulation one have a larger recruitment delay than prey subpopulation two, that is, $\gamma_1 > \gamma_2$. Recall that $r_{ir} = (p_{ii}\rho^{\gamma_i} + p_{ij}\rho^{\gamma_j})r_i$, $r_{ip} = (p_{ii}\rho^{\gamma_i} + p_{ij}\rho^{\gamma_i})r_i$. If $\gamma_1 > \gamma_2$ then $r_{1r} > r_{1p}$ and $r_{2r} < r_{2p}$, therefore

$$S_{N_{1p}} < S_{N_{1r}},\ S_{N_{2p}} > S_{N_{2r}},\ S_{P_{1p}} \geq S_{P_{1r}} \text{ and } S_{P_{2p}} \leq S_{P_{2r}}.$$

Hence, assuming that the metapopulation has local population receptor delay mode, would under-harvest the prey subpopulation with the larger recruitment delay, and over-harvest the prey subpopulation with the lower recruitment delay. On the other hand, we would also over-harvest the predator subpopulation living in the same patch with the prey subpopulation which has a larger recruitment delay, while the other predator subpopulation would be under-harvested (see Figure 6.5).

6.2.3 Numerical examples

I use a similar example to that for the receptor delay predator-prey metapopulation model discussed in the previous section, that is, a predator-prey metapopulation with the following parameters: $K_1 = K_2 = 500000$, $L_1 = L_2 = 10000$, $r_1 = r_2 = 1000$, $s_1 = s_2 = 1000$, $a_1 = a_2 = 0.001$, $b_1 = b_2 = 0.001$, $p_{11} = p_{22} = p_{12} = p_{21} = 0.001$, $q_{11} = q_{22} = q_{12} = q_{21} = 0.01$, $\beta_1 = \beta_2 = |\alpha_1| = |\alpha_2| = 0.00001$ and $\delta = 10\%$. Furthermore, to allow comparison between the predator-prey receptor delay model and the predator-prey parental delay model I assume that $\gamma_1 = \gamma_2 = 0$, $\tau_1 = 2$, $\tau_2 = 3$ and $\sigma_1 = \sigma_2 = 3$. For comparison reasons, I add subscript r and p to indicate results from the predator-prey receptor delay model and the predator-prey parental delay model, respectively. With these parameters, a positive equilibrium population size, $(\bar{N}_1, \bar{N}_2, \bar{P}_1, \bar{P}_2) = (223702, 223702, 10619, 10619)$, is obtained. Using equations (6.42) and (6.43), optimal escapements, $S^*_{N_{1r}} = S^*_{N_{2r}} = 11206$ and $S^*_{P_{1r}} = S^*_{P_{2r}} = 4564$, are

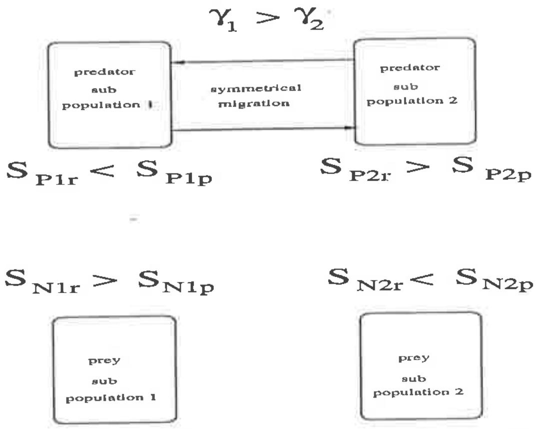


Figure 6.5: Prey subpopulation one has a larger recruitment delay than prey subpopulation two, that is, $\gamma_1 > \gamma_2$. The figure shows that assuming the metapopulation has local population receptor delay model we would under-harvest the prey subpopulation with the larger recruitment delay and over-harvest the prey subpopulation with the lower recruitment delay. On the other hand, we would also over-harvest the predator subpopulation living in the same patch with the prey subpopulation which has a larger recruitment delay, while the other predator subpopulation would be under-harvested.

obtained. Similarly, using equations (6.56) and (6.57) optimal escapements $S^*_{N_{1p}} = 111200$, $S^*_{N_{2p}} = 111213$, $S^*_{P_{1p}} = 4584$ and $S^*_{P_{2p}} = 4542$ are obtained.

Note that the predator-prey receptor delay model gives equal escapements for both patches while the predator-prey parental delay model harvests the predator subpopulation with the lower recruitment delay more conservatively than predator subpopulation with the higher recruitment delay. This is because the proportion of predator juveniles that remain in the parent patch equals the proportion of predator juveniles that migrate to the other patch, $q_{ii} = q_{ij}$ for $i = 1, 2$, and both subpopulations migrate symmetrically, $q_{ij} = q_{ji}$. As a result, recruitment delay differences does not cause escapement differences. Recall the migration trade-off equation in Lemma 5. In this case, the equation reduces to

$$\Delta_{S_P} = r_{1m}\left[\frac{2}{K}C\left(C - \frac{2A}{L}\right) - \frac{4r_{1m}S}{KL}\right](s_{2m} - s_{1m}), \tag{6.63}$$

$$\Delta_{S_N} = C(s_{1m} - s_{2m})\left(C(\frac{2A}{L} - C) + \frac{4r_{1m}S}{KL}\right), \tag{6.64}$$

with $\Delta_{S_P} = (S^*_{P_1} - S^*_{P_2})\Delta_1\Delta_2$, $\Delta_{S_N} = (S^*_{N_1} - S^*_{N_2})\Delta_1\Delta_2$, $s_{im} = (q_{i1}\rho^{\tau_1} + q_{i2}\rho^{\tau_2})s_i$, $r_{im} = (p_{i1}\rho^{\gamma_1} + p_{i2}\rho^{\gamma_2})r_i$ and $r_{im} = (p_{i1}\rho^{\gamma_1} + p_{i2}\rho^{\gamma_2})r_i$. Clearly $s_{1m} = s_{2m}$ and hence $S^*_{N_1} = S^*_{N_2}$ and $S^*_{P_1} = S^*_{P_2}$.

On the other hand, for the same parameters as above, the predator-prey parental delay model harvests the predator subpopulation with the lower delay more conservatively than the predator subpopulation with the higher delay. This is because escapement of subpopulation one is independent of the delay in subpopulation two and vice-versa (see equations (6.56) and (6.57)). The increase of the delay in predator subpopulation two only decreases escapement of predator subpopulation two and, in addition, it also increases escapement of the prey living in the same patch with this predator subpopulation. It can also be seen from the migration trade-off equations in Lemma 7 which reduce to equations (6.63) and (6.64), but with $s_{im} = (q_{ii} + q_{ij})\rho^{\tau_i} s_i$ and $r_{im} = (p_{ii} + p_{ij})\rho^{\gamma_i} r_i$. Since $\tau_1 < \tau_2$ we have $s_{1m} > s_{2m}$. Moreover, since the assumptions in Result 22 are satisfied then we have $S^*_{N_1} < S^*_{N_2}$ and $S^*_{P_1} > S^*_{P_2}$.

I compare results from the predator-prey receptor delay model and the predator-prey parental delay model for various cases, such as different delays and migration parameters for the predator as shown in Table 6.3. The table shows that when the predator migrates symmetrically with identical proportion of q_{ij}, such as in the example above, escapements from the predator-prey receptor delay model are always equal for every patch regardless of the value of recruitment delays. Escapements from the predator-prey parental delay model follow the general rule described above. However, when the predator migrate non-symmetrically, in this case predator subpopulation one is a relative source and exporter subpopulation, then we should harvest the relative exporter and source subpopulation more conservatively than the relative importer and sink predator subpopulation regardless of the value of the delays. We should also harvest the prey living in the same patch with the relative exporter and source predator subpopulation less conservatively than the other prey subpopulation (see Table 6.3 for non-symmetric migration case). This suggests that the rule in the previous chapter on how to harvest a relative source/sink and exporter/importer subpopulations is robust if the difference between delays is not large (see Figure 6.6).

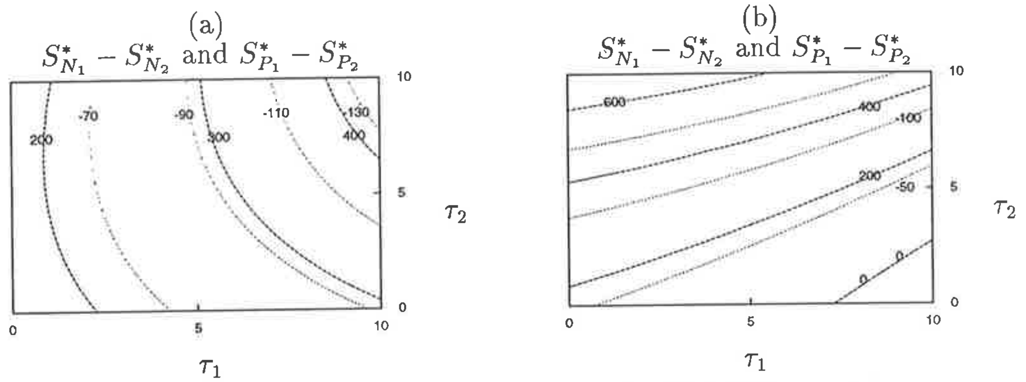
Figures 6.6.a and 6.6.b show that the rules of thumb of how to harvest a relative source and exporter subpopulation (in this example predator subpopulation one is a relative source and exporter) are valid for the predator-prey parental delay model as long as $\tau_1 < \tau_2$. However, in this special case, it is valid for the predator-prey receptor delay model regardless of the value of τ_i. Figures 6.6.c and 6.6.d show that as prey recruitment delay γ_i varies, the effects of predator parameter differential are neutralised by large values of γ_i. For small values of γ_i, the rule to harvest a relative source/sink and exporter/importer subpopulation holds for both the predator-prey receptor delay model and the predator-prey parental delay model.

6.3 Concluding Remarks

In nature, time-delays in recruitment occur for many species of fish. For example, Pacific ocean perch has a recruitment delay of at least 8 years (Gunderson, 1997). For this reason, the predator-prey metapopulation model in Chapter 5 was extended in this chapter by including a time-delay in juvenile recruitment for both species. The model takes the form of a simple age-structured model which has only two age-classes, juvenile and adult.

Recruitment delay can be modelled in two different ways. First, a recruitment delay experienced by juveniles can be related to the subpopulation in which they are recruited, this is referred to as the "local population recruitment delay model". Second, the delay may be related to their original subpopulation, and this model is known as the "parental recruitment delay model" (Tuck, 1994). I extended the basic predator-prey metapopulation model in Chapter 5 by including these two types of recruitment delay.

The results in this chapter show that if both subpopulations are identical then both models produce the same optimal escapements. However, if one of the subpop-



Receptor delay model

Parental delay model

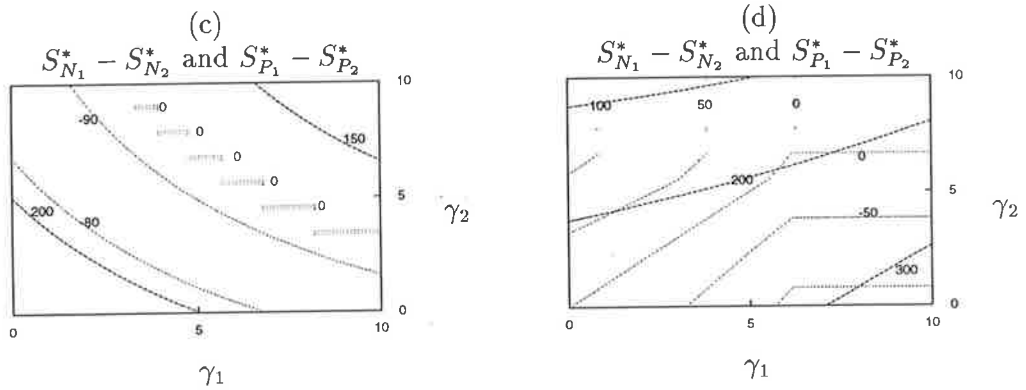


Figure 6.6: Figures 6.6.a and 6.6.c show contour plots of $S^*_{N_1} - S^*_{N_2}$ (dots) and $S^*_{P_1} - S^*_{P_2}$ (dashes) from the receptor delay model and Figures 6.6.b and 6.6.d show contour plots of $S^*_{N_1} - S^*_{N_2}$ (dots) and $S^*_{P_1} - S^*_{P_2}$ (dashes) from the parental delay model. In this case, predator subpopulation one is a relative exporter and source subpopulation. Figure 6.6.a shows that regardless of the value of predator delays, the rule to harvest a relative source and exporter subpopulation conservatively holds in the receptor delay model and Figure 6.6.b shows that the same rule holds in the parental delay model as long as $\tau_1 < \tau_2$. The sign of $S^*_{N_1} - S^*_{N_2}$ and $S^*_{P_1} - S^*_{P_2}$ are changed in the lower right part of Figure 6.6.b. Figure 6.6.d shows that if γ_i is sufficiently large then optimal escapements for both prey subpopulations are the same. In all figures $q_{12} = 0.03$, $q_{11} = q_{22} = q_{21} = 0.01$ with $\gamma_1 = \gamma_2$ (Figures 6.6.a and 6.6.b) and $\tau_1 < \tau_2$ (Figures 6.6.c and 6.6.d).

(a) Symmetrical migration case with $q_{12} = q_{21} = q_{11} = q_{22} = 0.01$.

Escapement	$\tau_1 = 2 < \tau_2 = 3$		$\tau_1 = \tau_2 = 3$		$\tau_1 = 3 > \tau_2 = 2$	
	RDM	PDM	RDM	PDM	RDM	PDM
$S^*_{N_1}$	111206	111200	111213	111213	111206	111213
$S^*_{N_2}$	111206	111213	111213	111213	111206	111200
$S^*_{P_1}$	4564	4584	4542	4542	4564	4542
$S^*_{P_2}$	4564	4542	4542	4542	4564	4584

(b) Non-symmetrical migration case with $q_{12} = 0.03$, $q_{21} = q_{11} = q_{22} = 0.01$.

Escapement	$\tau_1 = 2 < \tau_2 = 3$		$\tau_1 = \tau_2 = 3$		$\tau_1 = 3 > \tau_2 = 2$	
	RDM	PDM	RDM	PDM	RDM	PDM
$S^*_{N_1}$	111140	111135	111142	111142	111137	111142
$S^*_{N_2}$	111206	111213	111213	111213	111206	111200
$S^*_{P_1}$	4777	4792	4772	4772	4787	4772
$S^*_{P_2}$	4564	4542	4542	4542	4564	4584

Table 6.3: Escapement comparisons between the predator-prey receptor delay model (RDM) and the predator-prey parental delay model (PDM). The table shows that when the predators migrate symmetrically with identical proportion of q_{ij}, escapements from the predator-prey receptor delay model are always equal for every patch regardless of the value of recruitment delays. However, when the predator migrates non-symmetrically we should harvest the relative exporter and source subpopulation more conservatively than the relative importer and sink predator subpopulation regardless of the value of the delays. This suggests that the rule in the previous chapter on how to harvest a relative source/sink and exporter/importer subpopulations is robust if the difference between delays is not large.

ulations has a larger recruitment delay (or in general there is a biological parameter difference between patches) then the optimal escapements will differ. For example, if prey subpopulation one has a larger recruitment delay than prey subpopulation two, that is, $\gamma_1 > \gamma_2$, then escapement for prey subpopulation one from the parental delay model is lower than escapement from the receptor delay model and escapement for prey subpopulation two from the parental delay model is greater than escapement from the receptor delay model. Hence, incorrectly managing a predator-prey metapopulation having parental recruitment delay as a metapopulation with local population receptor delay model, would under-harvest the prey subpopulation with the larger recruitment delay, and over-harvest the prey subpopulation with the lower recruitment delay. On the other hand, it also would over-harvest the predator subpopulation living in the same patch with the prey subpopulation which has a larger recruitment delay, while the other predator subpopulation would be under-harvested.

In a special case, if migration parameters are uniform, that is, $p_{ij} = p_{ji}, \forall i, j = 1, 2$ and $q_{ij} = q_{ji}, \forall i, j = 1, 2$, then escapements from the receptor delay model are equal for every patch while the parental delay model produces different escapements for different patches, that is, $S_{N_{1p}} < S_{N_{1r}} = S_{N_{2r}} < S_{N_{2p}}$ or $S_{N_{1p}} > S_{N_{1r}} = S_{N_{2r}} > S_{N_{2p}}$, depending on the value of recruitment delay, γ_i. This result is not surprising if we look at equations (6.42) and (6.56) for the receptor delay model and the parental delay model, respectively. Escapement $S_{N_{1p}}$ from the parental delay model is only affected by γ_1, while escapement from the receptor delay model is also affected by γ_2, which is smaller than γ_1. This is consistent with single-species harvesting theory which concludes that we should harvest a subpopulation with a greater recruitment delay more heavily than a subpopulation with a lower recruitment delay (Tuck, 1994; see also Table 6.3).

The parental delay model would conserve a relative source prey subpopulation more conservatively than a relative sink prey subpopulation and harvest the predator living in the same patch with a relative source prey subpopulation less conservatively than the other predator subpopulation if prey subpopulation one has a lower recruitment delay, so that $(p_{11}+p_{12})\rho^{\gamma_1}r_1 > (p_{21}+p_{22})\rho^{\gamma_2}r_2$. The receptor delay model needs an additional condition, that is, $p_{11} > p_{21}$, $p_{12} \geq p_{22}$ or $p_{11} \geq p_{21}$, $p_{12} > p_{22}$ – for example, if the proportion of migrating juvenile from patch one to patch i is greater than the proportion of migrating juvenile from patch two to patch i, for $i = 1, 2$. However, numerical examples show that if the difference between delays is not large, then to establish the rule, the additional condition above is not required.

Furthermore, if there is no discounting rate or if recruitment delays in the two patches are equal, then the rules of thumb of predator-prey metapopulation harvesting theory, such as escapement comparison between patches and escapement comparison to incorrect harvesting policies, hold. If the discounting rate δ is not zero and there is a difference in the recruitment delay between patches (for example $\gamma_1 \neq \gamma_2$), then the rule of how to harvest a relative source/sink and exporter/importer subpopulation is no longer necessarily true.

In the single-species metapopulation harvesting theory (Tuck, 1994), the parental delay model is the same as the relative source/sink results for the harvest policy comparisons regardless of the values of the delays. However, in the presence of predators, the two models in this chapter adhere to the relative source/sink results for the harvest policy comparisons in Chapter 5 only for a special case, that is, if the population delays are equal. If there is no exporter/importer prey subpopulation, escapements from the predator-prey metapopulation with parental delay recruitment are equal to escapements from the incorrect unconnected two-patch predator-prey population harvesting policy, regardless of the delays, γ_i. In contrast, escapement differences between the predator-prey metapopulation with receptor delay recruitment and the incorrect unconnected two-patch predator-prey population, do depend on the delays.

The exploited population delay model discussed in this chapter was originally developed by Clark (1976b), especially the analysis of its optimal escapement. Botsford (1992) suggested that this model can be extended by considering the spatial structure of the population and larval dispersal between subpopulations. Tuck (1994) extended Clark's (19976b) model to incorporate spatial structure, dispersal and maturation delays. His major conclusion was that results from the delay model may differ depending on whether we assume that the delay related to the destination site or the birth site of the dispersing larvae. In this chapter I have extended Tuck's (1994) model by adding predator-prey interactions to the system. The results in this chapter show that Tuck's (1994) major conclusion is confirmed in the presence of predator-prey interaction, if the predator "discounted" efficiency is greater than a certain threshold. It can also be concluded that maturation delays differences of one species (e.g. the prey species) affect the optimal escapement of other species (e.g. the predator species) even when the latter species has a uniform delay, that is, delays are equal in any patches.

This result is not surprising, since delayed recruitment is considered to be one of five possible reasons for a declining population. The other four reasons are low adult survivorship, low fecundity, low juvenile survivorship and insufficient immigration (Russ and Alcala, 1996; Hitchcock and Grattotrevor, 1997). Meanwhile, the changes of a species' abundance may affect the dynamics of other species which interact with the former species (Crawford and Dyer, 1995; Agnew, 1997), and eventually affect the level of escapements of both species. Tuck (1994) showed that an increase (decrease) in recruitment delay of a single-species decreases (increases) the optimal escapement of that species. I have shown in this chapter that it can also increase (decrease) the optimal escapement of the other species which interacts with the former, especially in the predator-prey metapopulation parental delay model.

The results in this chapter are the same as those in the non-delay models when the delays between subpopulations are the same. Thus, by knowing that there is no variability in the delays between subpopulations, all strategies in the non-delay models remain the same in the presence of the delays. The results are different only when the delays differ between subpopulations, for example we might not harvest a relative source prey subpopulation more conservatively than a relative sink prey subpopulation if the delay of the relative source prey subpopulation in the parental delay model is much larger than the relative sink prey subpopulation. In this case there are two counteracting forces. First, the source/sink force, that is, in the absence of the delays, we should harvest the relative source prey subpopulation more conservatively than the other prey subpopulation. This is intuitive, since protecting the source subpopulation means protecting the replenishment of the other subpopulation (Mangel *et al.*, 1997; Gary, 1998). Second, the recruitment delay force, that is, in the absence of source/sink structure, we should harvest the prey subpopulation with a larger recruitment delay less conservatively than the other prey subpopulation. This is also intuitive, since a higher delay in maturation can be interpreted as a higher dampener on the growth of the population (Tuck, 1994). Thus if there are differences in delay and source/sink status between populations, optimal escapements are determined by the trade-off between the two forces. However, in general both results are identical if we modify the definition of source subpopulation to include the delays. That is, a subpopulation is a relative source if its per capita larval production, discounted by its cumulative death rate, is larger than the per capita larval production of the other subpopulation, discounted by its cumulative death rate [see inequality (6.62)].

The model in this chapter is the simplest form of a cohort model, that is, it only has two age-classes: juvenile and adult. The model could be extended to a more general model, for example a population that has at least three age-classes: juvenile, subadult, and adult, with predator-prey interactions in at least one age-class. Exploitation may not only target the adult-class, but also the subadult-class. In this chapter I assumed that the time delays, γ_i, are constant. This could also be extended to non-constant recruitment delays, since an increasing fishing mortality may causes some fish species to mature at a younger age, such as the North Sea cod population (Rowell, 1993). In this case, recruitment delays γ_i could be extended to be functions of fishing mortality or constant times H_{X_i}. Another possibility for future work is to consider sex-structured delay-recruitment. The literature confirms that differences in male and female delays to recruitment affect population stability (Cruywagen, 1996). In effect, optimal escapements for each sex-class may be different. Sex selective harvesting is common in game or hunting practices. An example of sex selective harvesting in fisheries is the exploitation of Dungeness crabs, *Cancer magister*, along the west coast of North

America, where only the males are harvested (Higgins *et al.*, 1997).

So far I only considered optimal harvesting strategies for predator-prey metapopulations with juvenile migration. The next chapter considers optimal harvesting strategies for predator-prey metapopulations with adult migration. Optimal harvesting strategies for predator-prey metapopulations with more than two patches are also explored by assuming that both the adults and juveniles migrates, which often occurs in nature.

6.4 Appendices

Appendix 6A: Optimal escapements derivation

This appendix solves the necessary conditions for maximum $\frac{\partial \mathcal{L}}{\partial N_{ik}} = \frac{\partial \mathcal{L}}{\partial P_{ik}} = 0$ for $k \geq 1$ and $\frac{\partial \mathcal{L}}{\partial H_{N_{ik}}} = \frac{\partial \mathcal{L}}{\partial H_{P_{ik}}} = 0$ with $\mathcal{L}$ in equation (6.29). The above conditions are equivalent to

$$\begin{aligned} 0 &= \rho^k \frac{\partial \Pi_{N_1}}{\partial N_{1k}} - \lambda_{1(k-1)} + \lambda_{1k} a_1 + \lambda_{1k+\gamma_1} p_{11} F_1'(S_{N_{1k}}) + \lambda_{1k} \alpha_1 S_{P_{1k}} \\ &\quad + \lambda_{2k+\gamma_2} p_{12} F_1'(S_{N_{1k}}) + \lambda_{3k+\sigma_1} \beta_1 S_{P_{1k}}, \end{aligned} \tag{6.65}$$

$$\begin{aligned} 0 &= \rho^k \frac{\partial \Pi_{N_2}}{\partial N_{2k}} - \lambda_{2(k-1)} + \lambda_{2k} a_2 + \lambda_{2k+\gamma_2} p_{22} F_2'(S_{N_{2k}}) + \lambda_{2k} \alpha_2 S_{P_{2k}} \\ &\quad + \lambda_{1k+\gamma_1} p_{21} F_2'(S_{N_{2k}}) + \lambda_{4k+\sigma_2} \beta_2 S_{P_{2k}}, \end{aligned} \tag{6.66}$$

$$\begin{aligned} 0 &= \rho^k \frac{\partial \Pi_{P_1}}{\partial P_{1k}} - \lambda_{3(k-1)} + \lambda_{3k} b_1 + \lambda_{3k+\tau_1} q_{11} G_1'(S_{P_{1k}}) + \lambda_{3k+\sigma_1} \beta_1 S_{N_{1k}} \\ &\quad + \lambda_{4k+\tau_2} q_{12} G_1'(S_{P_{1k}}) + \lambda_{1k} \alpha_1 S_{N_{1k}}, \end{aligned} \tag{6.67}$$

$$\begin{aligned} 0 &= \rho^k \frac{\partial \Pi_{P_2}}{\partial P_{2k}} - \lambda_{4(k-1)} + \lambda_{4k} b_2 + \lambda_{4k+\tau_2} q_{22} G_2'(S_{P_{2k}}) + \lambda_{4k+\sigma_2} \beta_2 S_{N_{2k}} \\ &\quad + \lambda_{3k+\tau_1} q_{21} G_2'(S_{P_{2k}}) + \lambda_{2k} \alpha_2 S_{N_{2k}}, \end{aligned} \tag{6.68}$$

$$\begin{aligned} 0 &= \rho^k \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} - \lambda_{1k} a_1 - \lambda_{1k+\gamma_1} p_{11} F_1'(S_{N_{1k}}) - \lambda_{1k} \alpha_1 S_{P_{1k}} \\ &\quad - \lambda_{2k+\gamma_2} p_{12} F_1'(S_{N_{1k}}) - \lambda_{3k+\sigma_1} \beta_1 S_{P_{1k}}, \end{aligned} \tag{6.69}$$

$$\begin{aligned} 0 &= \rho^k \frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}} - \lambda_{2k} a_2 - \lambda_{2k+\gamma_2} p_{22} F_2'(S_{N_{2k}}) - \lambda_{2k} \alpha_2 S_{P_{2k}} \\ &\quad - \lambda_{1k+\gamma_1} p_{21} F_2'(S_{N_{2k}}) - \lambda_{4k+\sigma_2} \beta_2 S_{P_{2k}}, \end{aligned} \tag{6.70}$$

$$\begin{aligned} 0 \;=\;& \rho^k \frac{\partial \Pi_{P_1}}{\partial H_{P_{1k}}} - \lambda_{3k} b_1 - \lambda_{3k+\tau_1} q_{11} G_1'(S_{P_{1k}}) - \lambda_{3k+\sigma_1} \beta_1 S_{N_{1k}} \\ & -\lambda_{4k+\tau_2} q_{12} G_1'(S_{P_{1k}}) - \lambda_{1k} \alpha_1 S_{N_{1k}}, \end{aligned} \tag{6.71}$$

$$\begin{aligned} 0 \;=\;& \rho^k \frac{\partial \Pi_{P_2}}{\partial H_{P_{2k}}} - \lambda_{4k} b_2 - \lambda_{4k+\tau_2} q_{22} G_2'(S_{P_{2k}}) - \lambda_{4k+\sigma_2} \beta_2 S_{N_{2k}} \\ & -\lambda_{3k+\tau_1} q_{21} G_2'(S_{P_{2k}}) - \lambda_{2k} \alpha_2 S_{N_{2k}}, \end{aligned} \tag{6.72}$$

Solving equations (6.65) to (6.71) produces

$$\lambda_{1(k-1)} = \rho^k \left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} \right), \tag{6.73}$$

$$\lambda_{2(k-1)} = \rho^k \left(\frac{\partial \Pi_{N_2}}{\partial N_{2k}} + \frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}} \right), \tag{6.74}$$

$$\lambda_{3(k-1)} = \rho^k \left(\frac{\partial \Pi_{P_1}}{\partial P_{1k}} + \frac{\partial \Pi_{P_1}}{\partial H_{P_{1k}}} \right), \tag{6.75}$$

$$\lambda_{4(k-1)} = \rho^k \left(\frac{\partial \Pi_{P_2}}{\partial P_{2k}} + \frac{\partial \Pi_{P_2}}{\partial H_{P_{2k}}} \right). \tag{6.76}$$

Substituting λ_{1k}, λ_{2k}, λ_{3k}, and λ_{4k} into equation (6.69) produces

$$\begin{aligned} 0 \;=\;& \rho^k \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} - a_1 \rho^{(k+1)} \left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} \right) \\ & -p_{11} F_1'(S_{N_{1k}}) \rho^{(k+1+\gamma_1)} \left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} \right) \\ & -\alpha_1 S_{P_{1k}} \rho^{(k+1)} \left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} \right) \\ & -p_{12} F_1'(S_{N_{1k}}) \rho^{(k+1+\gamma_2)} \left(\frac{\partial \Pi_{N_2}}{\partial N_{2k}} + \frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}} \right) \\ & -\beta_1 S_{P_{1k}} \rho^{(k+1+\sigma_1)} \left(\frac{\partial \Pi_{P_1}}{\partial P_{1k}} + \frac{\partial \Pi_{P_1}}{\partial H_{P_{1k}}} \right). \end{aligned} \tag{6.77}$$

Divide this equation by ρ^{k+1}, and recall that $\frac{\partial \Pi_{N_i}}{\partial H_{N_{ik}}} = p - c_N(S_{N_{i0}})$ and $\frac{\partial \Pi_{N_i}}{\partial N_{ik}} + \frac{\partial \Pi_{N_i}}{\partial H_{N_{ik}}} = p - c_N(N_{i1})$ then

$$\begin{aligned} \frac{p_N - c_{N1}(S_{N_{10}})}{\rho} \;=\;& (p_N - c_{N1}(N_{11}))(a_1 + p_{11} F_1'(S_{N_{10}}) \rho^{\gamma_1} + \alpha_1 S_{P_{10}}) \\ & +(p_N - c_{N2}(N_{21})) p_{12} F_1'(S_{N_{10}}) \rho^{\gamma_2} \\ & +(p_P - c_{P1}(P_{11})) \beta_1 S_{P_{10}} \rho^{\sigma_1}. \end{aligned} \tag{6.78}$$

Similarly, substituting λ_{1k}, λ_{2k}, λ_{3k}, and λ_{4k} into equations (6.70) to (6.72) produces

$$
\begin{aligned}
\frac{p_N - c_{N2}(S_{N_{20}})}{\rho} &= (p_N - c_{N2}(N_{21}))(a_2 + p_{22}F_2'(S_{N_{20}})\rho^{\gamma_2} + \alpha_2 S_{P_{20}}) \\
&\quad + (p_N - c_{N1}(N_{11}))p_{21}F_2'(S_{N_{20}})\rho^{\gamma_1} \\
&\quad + (p_P - c_{P2}(P_{21}))\beta_2 S_{P_{20}}\rho^{\sigma_2}, \qquad (6.79)
\end{aligned}
$$

$$
\begin{aligned}
\frac{p_P - c_{P1}(S_{P_{10}})}{\rho} &= (p_P - c_{P1}(P_{11}))(b_1 + q_{11}G_1'(S_{P_{10}})\rho^{\tau_1} + \beta_1 S_{N_{10}}\rho^{\sigma_1}) \\
&\quad + (p_P - c_{P2}(P_{21}))q_{12}G_1'(S_{P_{10}})\rho^{\tau_2} \\
&\quad + (p_N - c_{N1}(N_{11}))\alpha_1 S_{N_{10}}, \qquad (6.80)
\end{aligned}
$$

$$
\begin{aligned}
\frac{p_P - c_{P2}(S_{P_{20}})}{\rho} &= (p_P - c_{P2}(P_{21}))(b_2 + q_{22}G_2'(S_{P_{20}})\rho^{\tau_2} + \beta_2 S_{N_{20}}\rho^{\sigma_2}) \\
&\quad + (p_P - c_{P1}(P_{11}))q_{21}G_2'(S_{P_{20}})\rho^{\tau_1} \\
&\quad + (p_N - c_{N2}(N_{21}))\alpha_2 S_{N_{20}}. \qquad (6.81)
\end{aligned}
$$

Appendix 6B: Escapement comparisons with the escapements from the unconnected metapopulation

Recall that $r_{im} = (p_{ii}\rho^{\gamma_i} + p_{ij}\rho^{\gamma_j})r_i$, $r_{iu} = p_{ii}r_i\rho^{\gamma_i} + p_{ji}r_j\rho^{\gamma_i}$, $\Delta_i = C_i^2 - r_{im}\frac{2r_i}{K_i}s_{im}\frac{2s_i}{L_i} < 0$, $\Delta_{iu} = C_i^2 - r_{iu}\frac{2r_i}{K_i}s_{im}\frac{2s_i}{L_i}$, and $r_1 = r_2$. Let us assume that $p_{11}\rho^{\gamma_1} \geq p_{22}\rho^{\gamma_2}$, $p_{12} = p_{21}$, $\gamma_1 > \gamma_2$ and $r_1 = r_2$, then:

1. $r_{1u} < r_{1m}$ and $r_{2u} > r_{2m}$
   Proof:

$$
\begin{aligned}
r_{1u} &= p_{11}r_1\rho^{\gamma_1} + p_{21}r_2\rho^{\gamma_1} \\
&< p_{11}r_1\rho^{\gamma_1} + p_{12}r_1\rho^{\gamma_2} \\
&= r_{1m}.
\end{aligned}
$$

   Hence, $r_{1u} < r_{1m}$. Similarly, it can be proven that $r_{2u} > r_{2m}$.

2. $\Delta_{iu} < 0$
   Proof:

$$
\begin{aligned}
r_{1u} &= p_{11}r_1\rho^{\gamma_1} + p_{21}r_2\rho^{\gamma_1} \\
&\geq p_{22}r_2\rho^{\gamma_2} + p_{21}r_2\rho^{\gamma_1} \\
&= r_{2m}.
\end{aligned}
$$

   Hence, $\Delta_{1u} \leq \Delta_2 < 0$. Furthermore, since $r_{2u} > r_{2m}$ then $\Delta_{2u} \leq \Delta_2 < 0$.

3. $C^2 - \frac{2(r_{1m}+r_{2m})s_m}{KL} < 0$
   Proof:
   It is clear since $r_{2m} < \frac{r_{1m}+r_{2m}}{2} < r_{1m}$ and $\Delta_i < 0$.

4. $r_{1m}r_{2m} - r_{1u}r_{2u} \leq 0$
   Proof:
   Let $A_{ij} = r_i p_{ij} \rho^{\gamma_j}$, then

$$\begin{aligned} r_{1m}r_{2m} - r_{1u}r_{2u} &= (A_{11} + A_{12})(A_{21} + A_{22}) - (A_{11} + A_{21})(A_{12} + A_{22}) \\ &= A_{11}A_{21} + A_{12}A_{22} - A_{11}A_{12} - A_{21}A_{22} \\ &= A_{11}(A_{21} - A_{12}) + A_{22}(A_{12} - A_{21}) \\ &= (A_{11} - A_{22})(A_{21} - A_{12}) \\ &= r^2(p_{11}\rho^{\gamma_1} - p_{22}\rho^{\gamma_2})(p_{21}\rho^{\gamma_1} - p_{12}\rho^{\gamma_2}). \end{aligned}$$

Since $p_{11}\rho^{\gamma_1} \geq p_{22}\rho^{\gamma_2}$, $p_{12} = p_{21}$ and $\gamma_1 > \gamma_2$ then

$$r_{1m}r_{2m} - r_{1u}r_{2u} \leq 0. \tag{6.82}$$

Appendix 6C: Escapement comparisons with the escapements from the well-mixed metapopulation

If $p_{11} \geq p_{22}$, $p_{12} > p_{21}$ and $\gamma_1 = \gamma_2$ then $r_{1m}r_{2m} - r_w^2 \leq 0$.

Proof:

Recall that $r_{im} = (p_{ii}\rho^{\gamma_i} + p_{ij}\rho^{\gamma_j})r_i$ and $r_w = \left(\frac{r_1(p_{11}+p_{12})+r_2(p_{21}+p_{22})}{2}\right)\rho^{(\gamma_1+\gamma_2)/2}$. Let $A_{ij} = r_i p_{ij}\rho^{\gamma_j}$, $B_{ij} = r_i p_{ij}$ and $V_i = B_{ii} + B_{ij}$, then

$$r_{1m}r_{2m} - r_w^2 = (A_{11} + A_{12})(A_{21} + A_{22}) - \left(\frac{B_{11} + B_{12} + B_{21} + B_{22}}{2}\right)^2 \left(\rho^{(\gamma_1+\gamma_2)}\right).$$

Since $\gamma_1 = \gamma_2 = \gamma$ then

$$\begin{aligned} r_{1m}r_{2m} - r_w^2 &= \rho^{2\gamma}\left[(B_{11} + B_{12})(B_{21} + B_{22}) - \left(\frac{(B_{11} + B_{12}) + (B_{21} + B_{22})}{2}\right)^2\right] \\ &= -\frac{1}{4}\rho^{2\gamma}\left[V_1^2 + V_2^2 - 2V_1V_2\right] = -\frac{1}{4}\rho^{2\gamma}\left[(V_1^2 - V_1V_2) + (V_2^2 - V_1V_2)\right] \\ &= -\frac{1}{4}\rho^{2\gamma}\left[V_1(V_1 - V_2) + V_2(V_2 - V_1)\right] = -\frac{1}{4}\rho^{2\gamma}(V_1 - V_2)^2 \leq 0. \end{aligned}$$

Chapter 7

Predator-prey metapopulations with adult migration

In the previous chapters I discussed optimal harvesting strategies for some predator-prey metapopulations. I have assumed throughout these chapters that local populations are connected by the dispersal of juveniles and adults are sedentery. Adult migration is not uncommon in many commercial fish stocks, although these migrations are often seasonal. Examples including Pacific salmon, Sockeye salmon, Atlantic salmon, Bull trout, shrimp and turtles, and many of these migrations are related to homing from feeding habitat to spawning habitat or nursery ground (Brannon, 1984; Harden Jones, 1984; Wooton, 1990; Creasey *et al.*, 1996; Crowley, 1996; Crozier *et al.*, 1997; Quinn *et al.*, 1997; Sakamoto *et al.*, 1997; Swanberg, 1997).

Sturgeon are a good example of a fish that is highly mobile and utilises several distinct habitats throughout its life. Different types of habitat are needed: to develop eggs and larvae in the early stage of their life, to feed during their body size development and to spawn in the mature stage (Auer, 1996). Auer (1996) showed a positive relationship between maximum migration distance and body size of sturgeon. This suggests that the adults of sturgeon are highly dispersive.

The salmonids of the Northtern Pacific and Atlantic are anadromous, that is, they hatch in freshwater but grow and mature in the ocean. After they reach maturity they home, that is, they return again to the freshwater habitat where they hatched, in order to spawn (Policansky and Magnuson, 1998). The freshwater and oceanic habitat used by the salmonids throughout their life can be described as a dendritic or tree-like structure, consisting of one trunk, in this case the oceanic feeding habitat, and many freshwater streams where they spawn as the branches (Tallman and Healey, 1994). Although the tendency of the salmonids fishes to find the site where they hatched is well known (Hartman and Raleigh, 1964), many studies show that some of them stray or fail to home (Quinn *et al.*, 1991; Pascual and Quinn, 1994). Straying levels vary from species to species. Certain species, like the Chum salmon, have a significant stray level, nearly 50% of the population (Tallman and Healey, 1994). The salmonids that stray spawn elsewhere, usually in nearby habitat. Some authors have considered the places where the salmonids hatched as local populations (Schaffer and Elson, 1975). If in addition we also consider that these habitats are connected by the migration of the strays, then we have a metapopulation with adult migration (Tuck, 1994).

In this chapter I develop predator-prey metapopulation models connected by adult migration (e.g. stray migration in the case of salmonids). Optimal harvesting strategies are investigated for three different models. The first model assumes that only the adults of the populations migrate, the second model assumes that both age-classes, the adults and juveniles, migrate. In the third model, I extend the second model by assuming that the metapopulation is made of more than two subpopulations and determine the optimal harvesting strategies for this general model.

7.1 Adult migration without juvenile migration

Many of the examples of marine metapopulations in the previous chapters are made up of several subpopulations connected by the dispersal of their larvae or juveniles. The adults are sedentary. There are also some examples of marine metapopulation where the connection is caused by the dispersal of adults, not by the dispersal of juveniles – for example, the Squat lobster (*Pleuroncodes monodon*). Roa and Bahamonde (1993) observed that the older class of this species migrate while the younger class occupied the site vacated by the older class. The first model in this chapter considers this type of metapopulation, that is, a metapopulation with adult migration where the juveniles are assumed to be immobile or sedentary. This model is extended in the subsequent chapter to include the juvenile migration.

7.1.1 The model and its optimal escapements

Let us assume that there is a predator-prey population in each of two different patches, namely patch one and patch two. Let us also assume that a proportion of the surviving prey and predator adult stock from subpopulation i migrates to subpopulation j. The proportion of the surviving prey and predator adult which migrates from patch i to patch j is defined by m_{ij} and n_{ij}, respectively. If it is assumed that a proportion of adults are lost from the system then $m_{i1} + m_{i2} < 1$ and $n_{i1} + n_{i2} < 1$. If a_i and b_i are the pre-migration adult survivals of the prey and predator subpopulations i, respectively, using the same notation as in the previous chapters, then the dynamic of the population is given by

$$N_{1(k+1)} = a_1 m_{11} N_{1k} + a_2 m_{21} N_{2k} + F_1(N_{1k}) + \alpha_1 N_{1k} P_{1k}, \tag{7.1}$$

$$N_{2(k+1)} = a_1 m_{12} N_{1k} + a_2 m_{22} N_{2k} + F_2(N_{2k}) + \alpha_2 N_{2k} P_{2k}, \tag{7.2}$$

$$P_{1(k+1)} = b_1 n_{11} P_{1k} + b_2 n_{21} P_{2k} + G_1(P_{1k}) + \beta_1 N_{1k} P_{1k}, \tag{7.3}$$

$$P_{2(k+1)} = b_1 n_{12} P_{1k} + b_2 n_{22} N_{2k} + G_2(P_{2k}) + \beta_2 N_{2k} P_{2k}, \tag{7.4}$$

where $\alpha_i < 0$ and $\beta_i > 0$.

If S^*_{Ni} and S^*_{Pi} are optimal escapements for prey and predator subpopulation i, respectively, then following the same method in the previous chapters, implicit optimal escapement equations are found and given by

$$\begin{aligned}\frac{p_N - c_{Ni}(S^*_{N_{i0}})}{\rho} &= \Big(a_i m_{ii} + F_i'(S^*_{N_{i0}}) + \alpha_i S^*_{P_{i0}})(p_N - c_{Ni}(N_{i1})\Big) \\ &\quad + a_i m_{ij}\,(p_N - c_{Nj}(N_{j1})) \\ &\quad + \beta_i S^*_{P_{i0}}\,(p_P - c_{Pi}(P_{i1}))\,,\end{aligned} \tag{7.5}$$

$$\frac{p_P - c_{Pi}(S^*_{P_{i0}})}{\rho} = \Big(b_i n_{ii} + G_i'(S^*_{P_{i0}}) + \beta_i S^*_{N_{i0}})(p_P - c_{Pi}(P_{i1})\Big) \\ + b_i n_{ij}\left(p_P - c_{Pj}(P_{j1})\right) \\ + \alpha_i S^*_{N_{i0}}\left(p_N - c_{Ni}(N_{i1})\right). \quad (7.6)$$

These equations are the general form of the optimal escapement equation for a two-patch predator-prey metapopulation with adult migration. Solving these equations produces optimal equilibrium escapements, $S^*_{N_i}$ and $S^*_{P_i}$. Like optimal escapements in the previous chapters, these escapements are independent of the time horizon considered. It can be seen that if there is no migration between patches, that is, $m_{12} = m_{21} = 0$, $m_{11} = m_{22} = 1$, $n_{12} = n_{21} = 0$ and $n_{11} = n_{22} = 1$ then the optimal escapement equations reduce to equations (3.19) and (3.20) in Chapter 3. If we set $\alpha_i = \beta_i = 0$, then Tuck's (1994) optimal escapement equation for a single-species metapopulation is obtained.

As in the case of juvenile migration, interpretations of the optimal escapements can be derived by neglecting the costs of harvesting and price differences between the prey and predator, which now satisfy equations

$$\frac{1}{\rho} = a_i(m_{ii} + m_{ij}) + F_i'(S^*_{N_{i0}}) + (\alpha_i + \beta_i)S^*_{P_{i0}}, \quad (7.7)$$

$$\frac{1}{\rho} = b_i(n_{ii} + n_{ij}) + G_i'(S^*_{P_{i0}}) + (\alpha_i + \beta_i)S^*_{N_{i0}}. \quad (7.8)$$

Furthermore, explicit expressions of the optimal equilibrium escapements are obtained by assuming that recruitment production functions, F_i and G_i, are logistic as in equations (3.3) and (3.4). The optimal escapements are now given by

$$S^*_{N_i} = \frac{A_i \frac{2s_i}{L_i} + C_i B_i}{\Delta_i}, \quad (7.9)$$

$$S^*_{P_i} = \frac{B_i \frac{2r_i}{K_i} + C_i A_i}{\Delta_i}, \quad (7.10)$$

provided $\Delta_i = C_i^2 - \frac{2r_i}{K_i}\frac{2s_i}{L_i} \neq 0$, where

$$A_i = \frac{1}{\rho} - r_i - a_i(m_{i1} + m_{i2}), \quad (7.11)$$

$$B_i = \frac{1}{\rho} - s_i - b_i(n_{i1} + n_{i2}), \quad (7.12)$$

and $C_i = \alpha_i + \beta_i \leq 0$.

Using the same method as in the previous chapters, sufficient conditions for the metapopulation to have non-negative optimal escapements can be obtained. The conditions are written in the following result.

Result 29 *(Sufficient conditions for positive escapements) Let $S^*_{N_i}$ and $S^*_{P_i}$ denote the optimal escapement from a predator-prey metapopulation given by equations (7.9) and (7.10). If A_i and B_i are negative, and C_i is non-positive with $C_i > max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}$, then*

Δ_i is negative, and S^*_{Ni} and S^*_{Pi} are positive.

The condition $A_i < 0$ has a similar interpretation to the same condition in the previous chapters, that is, the sum of the proportion of surviving adult prey and the per capita prey larval production is higher than the reciprocal of the discounting factor, $1/\rho$. In other words, the natural growth rate of the prey population is higher than the reciprocal of the discounting factor. Only here the natural growth rate of the prey population depends on adult prey migration survival, $a_i(m_{ii} + m_{ij})$, while in the previous chapters the natural growth rate of the prey population depended on the juvenile prey migration survival, $r_i(p_{ii} + p_{ij})$. In the present model, in which it is assumed that there is adult prey migration between patches, one can concludes that the lower the adult prey survival rate the higher the possibility that the prey population has a non-negative optimal escapement. This is similar to the rule in the previous chapters, where it can be concluded that the lower the juvenile prey survival rate the higher the possibility that the prey population has a non-negative optimal escapement. Both assertions reiterate the well known result in single-species harvesting theory which points out that it is best to harvest the population down to zero escapement if the growth rate of the population is lower than the discounting rate (Clark, 1976a). The condition $B_i < 0$ for the predator population is interpreted similarly.

The relationship between escapements from a predator-prey metapopulation presented in this chapter and escapements from a single-species metapopulation discussed in the paper of Tuck and Possingham (1994) can be explored using Result 29 as follow.

Result 30 *(Escapement comparison with a single-species metapopulation) Let $S^*_{N_i}$ and $S^*_{P_i}$ denote the optimal escapement from a predator-prey metapopulation given by equations (7.9) and (7.10), and let $S^*_{N_{is}}$ and $S^*_{P_{is}}$ denote the optimal escapement from a single-species metapopulation given by the same equations by assigning $\alpha_i = \beta_i = 0$. If A_i and B_i are negative and $max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\} < C_i \leq 0$, then*

$$S^*_{N_i} - S^*_{N_{is}} = \frac{C_i}{2r_i/K_i} S^*_{P_i} \leq 0 \text{ and } S^*_{P_i} - S^*_{P_{is}} = \frac{C_i}{2s_i/L_i} S^*_{N_i} \leq 0.$$

Result 30 can be proved in the same way as in the case of juvenile migration. The result suggests that optimal escapement from a predator-prey metapopulation is always less than, or equal to, optimal escapement from a single-species metapopulation depending on the predator efficiency or the sign of C_i. In the case where the predator efficiency is extremely high, $C_i = 0$ or $\frac{\beta_i}{|\alpha_i|} = 1$, both escapements are equal. This is unlikely to occur, however, if there is price differential between prey and the predator then $C_i = \alpha_i + m\beta_i$, where m is the relative predator price to the prey price. Hence, in many normal situations, where $\beta_i < |\alpha_i|$ and $m > 1$, we can manage a predator-prey metapopulation as a single-species metapopulation if $C_i = 0$.

To draw some conclusions about escapement comparisons between patches and between methods (for example an unconnected two-patch predator-prey population and a well-mixed predator-prey population), the same procedures as in juvenile migration are used in the following section. These escapement comparisons are intended to show the importance of considering spatial structure in obtaining optimal escapements for the population.

7.1.2 Escapement comparisons between subpopulations

To compare optimal escapements between patches, I use the following lemma.

Lemma 9 *(Migration trade-off equations) Let* $S^*_{N_i}$ *and* $S^*_{P_i}$ *denote the optimal escapement from a predator-prey metapopulation given by equations (7.9) and (7.10). If* $K_i = K$, $L_i = L$, $C_i = C$, $a_{im} = a_i(m_{i1} + m_{i2})$, $b_{im} = b_i(n_{i1} + n_{i2})$, $r_i = r$, *and* $s_i = s$ *for* $i = 1, 2$, *then:*

$$1.\quad (S^*_{N_1} - S^*_{N_2})\Delta_1 = [a_{2m} - a_{1m}]\frac{2s}{L} + C[b_{2m} - b_{1m}],$$

$$2.\quad (S^*_{P_1} - S^*_{P_2})\Delta_1 = [b_{2m} - b_{1m}]\frac{2r}{K} + C[a_{2m} - a_{1m}].$$

Proof

1. Note that $\Delta_1 = \Delta_2$. If $R_i = \frac{1}{\rho} - a_i(m_{i1} + m_{i2})$ and $S_i = \frac{1}{\rho} - b_i(n_{i1} + n_{i2})$, then

$$\begin{aligned} S^*_{N_1} - S^*_{N_2} &= \frac{(R_1 - r)\frac{2s}{L} + C(S_1 - s)}{\Delta_1} - \frac{(R_2 - r)\frac{2}{L} + C(S_2 - s)}{\Delta_1} \\ (S^*_{N_1} - S^*_{N_2})\Delta_1 &= (R_1 - R_2)\frac{2s}{L} + C(S_1 - S_2) \\ &= [a_{2m} - a_{1m}]\frac{2s}{L} + C[b_{2m} - b_{1m}]. \end{aligned}$$

The second part of the lemma can be proved analogously. □

It can be concluded from Lemma 9 that if A_i and B_i are negative and $C > max\{\frac{2B_i}{K}, \frac{2A_i}{L}\}$ and both predator subpopulations have the same adult migration survival, that is $b_1(n_{11}+n_{12}) = b_2(n_{21}+n_{22})$, then we should harvest a prey subpopulation with high adult migration survival more conservatively than one with lower adult migration survival. On the other hand, we should harvest the predator subpopulation living with in the same patch with the prey subpopulation which has a high adult migration survival less conservatively than the other predator subpopulation. This is an analogous result to that in the previous chapters, where we should harvest the relative source prey subpopulation more conservatively than the relative sink subpopulation and we should harvest the predator living in the same patch with the relative source prey subpopulation less conservatively than the other predator subpopulation. I rewrite this conclusion in the following result. I do not provide the proof, since it is similar to the proof for the analogous theorem in the previous chapters.

Result 31 *(Escapement comparison between subpopulations) Let one of the prey subpopulations have a higher adult migration survival while all other parameters of the prey and the predator are identical for both subpopulations. Without loss of generality, let us assume that prey subpopulation one has a higher adult migration survival, that is,* $a_{1m} = a_1(m_{11} + m_{12}) > a_{2m} = a_2(m_{22} + m_{21})$. *If* $|\alpha| = \beta$, *or if* A_i *and* B_i *are negative and* $C > max\{\frac{2B_i}{K}, \frac{2A_i}{L}\}$, *then*

$$S^*_{N_1} > S^*_{N_2} \text{ and } S^*_{P_1} \le S^*_{P_2}.$$

Result 31 assumes that both predator subpopulations have identical adult migration survival. In addition, by investigating the sign of the right hand side of equations (1) and (2) in Lemma 9, we can obtain Table 7.1 illustrating how we should harvest each subpopulation if adult migration survival is different between patches for various

Migration survival		Optimal escapement		Additional condition
Prey	Predator	Prey	Predator	
$a_{1m} > a_{2m}$	$b_{1m} = b_{2m}$	$S^*_{N_1} > S^*_{N_2}$	$S^*_{P_1} \leq S^*_{P2}$	—
$a_{1m} > a_{2m}$	$b_{1m} < b_{2m}$	$S^*_{N_1} > S^*_{N_2}$	$S^*_{P_1} < S^*_{P_2}$	—
$a_{1m} > a_{2m}$	$b_{1m} > b_{2m}$	$S^*_{N_1} > S^*_{N_2}$	$S^*_{P_1} < S^*_{P_2}$	$\frac{a_{2m}-a_{1m}}{b_{2m}-b_{1m}} > max\{\frac{\lvert C\rvert L}{2s}, \frac{2r}{\lvert C\rvert K}\}$
$a_{1m} = a_{2m}$	$b_{1m} > b_{2m}$	$S^*_{N_1} \leq S^*_{N_2}$	$S^*_{P_1} > S^*_{P_2}$	—
$a_{1m} < a_{2m}$	$b_{1m} > b_{2m}$	$S^*_{N_1} < S^*_{N_2}$	$S^*_{P_1} > S^*_{P_2}$	—
$a_{1m} > a_{2m}$	$b_{1m} > b_{2m}$	$S^*_{N_1} < S^*_{N_2}$	$S^*_{P_1} > S^*_{P_2}$	$\frac{a_{2m}-a_{1m}}{b_{2m}-b_{1m}} < min\{\frac{\lvert C\rvert L}{2s}, \frac{2r}{\lvert C\rvert K}\}$

Table 7.1: Prey and predator optimal escapements for various combinations of adult prey and predator migration survival. The additional condition column contains conditions other than the conditions or hypotheses mentioned in Result 31.

combination of adult prey and predator migration survival a_{im} and b_{im}. The first two rows in the table show that we should harvest the prey subpopulation with high adult migration survival more conservatively than that with lower adult migration survival. On the other hand, we should harvest the predator subpopulation living in the same patch with the prey subpopulation which has a high adult migration survival less conservatively than the other predator subpopulation. This is an analogous result to the result in the previous chapters, where we should harvest the relative source prey subpopulation more conservatively than the relative sink subpopulation and we should harvest the predator living in the same patch with the relative source prey subpopulation less conservatively than the other predator subpopulation. However, here adult predator migration survival is allowed to be different between patches, as long as the adult migration survival of the predator subpopulation living in the same patch with the relatively high migration survival prey subpopulation is not more than the other predator subpopulation migration survival, otherwise we need an additional condition such as the shown in the last column of the table.

7.1.3 Escapement comparisons to incorrect policies

As in the case of juvenile migration, I also perform escapement comparisons between optimal escapements from a predator-prey metapopulation and escapement if we incorrectly manage the population by ignoring its spatial structure. I use Lemma 9 from the previous section to compare the optimal escapement in this section either with escapement resulting by assuming the population as an unconnected two-patch predator-prey population or with escapement which results from assuming the population to be a well-mixed predator-prey population.

First, let us assume that each prey and predator subpopulation are managed as two unconnected predator-prey populations. I use all the assumptions described in Result 31, that is the only biological differences between patches is the adult prey migration survival, a_{im}. I also assume that adult prey survival in subpopulation i are measured as

$$a_{iu} = a_i m_{ii} + a_j m_{ji}. \tag{7.13}$$

When spatial structure is not recognised, the optimal escapement for unconnected patches are $S^*_{N_{iu}}$ and $S^*_{P_{iu}}$ given in Appendix 7A. As before, the differences between the optimal escapements from predator-prey metapopulation harvesting theory and the

Migration survival		**Optimal escapement**		**Additional condition**
Prey	Predator	Prey	Predator	
$a_1m_{12} > a_2m_{21}$	$b_1m_{12} = b_2m_{21}$	$S^*_{N_1} > S^*_{N_{1u}}$	$S^*_{P_1} \leq S^*_{P_{1u}}$	—
		$S^*_{N_2} < S^*_{N_{2u}}$	$S^*_{P_2} \geq S^*_{P_{2u}}$	—
$a_1m_{12} > a_2m_{21}$	$b_1m_{12} < b_2m_{21}$	$S^*_{N_1} > S^*_{N_{1u}}$	$S^*_{P_1} < S^*_{P_{1u}}$	—
		$S^*_{N_2} < S^*_{N_{2u}}$	$S^*_{P_2} > S^*_{P_{2u}}$	—
$a_1m_{12} > a_2m_{21}$	$b_1m_{12} > b_2m_{21}$	$S^*_{N_1} > S^*_{N_{1u}}$	$S^*_{P_1} < S^*_{P_{1u}}$	$\frac{a_{1u}-a_{1m}}{b_{1u}-b_{1m}} > max\{\frac{\lvert C\rvert L}{2s}, \frac{2r}{\lvert C\rvert K}\}$
		$S^*_{N_2} < S^*_{N_{2u}}$	$S^*_{P_2} > S^*_{P_{2u}}$	$\frac{a_{2u}-a_{2m}}{b_{2u}-b_{2m}} > max\{\frac{\lvert C\rvert L}{2s}, \frac{2r}{\lvert C\rvert K}\}$
$a_1m_{12} = a_2m_{21}$	$b_1m_{12} > b_2m_{21}$	$S^*_{N_1} \leq S^*_{N_{1u}}$	$S^*_{P_1} > S^*_{P_{1u}}$	—
		$S^*_{N_2} \geq S^*_{N_{2u}}$	$S^*_{P_2} < S^*_{P_{2u}}$	—
$a_1m_{12} < a_2m_{21}$	$b_1m_{12} > b_2m_{21}$	$S^*_{N_1} < S^*_{N_{1u}}$	$S^*_{P_1} > S^*_{P_{1u}}$	—
		$S^*_{N_2} > S^*_{N_{2u}}$	$S^*_{P_2} < S^*_{P_{2u}}$	—
$a_1m_{12} > a_2m_{21}$	$b_1m_{12} > b_2m_{21}$	$S^*_{N_1} < S^*_{N_{1u}}$	$S^*_{P_1} > S^*_{P_{1u}}$	$\frac{a_{1u}-a_{1m}}{b_{1u}-b_{1m}} < min\{\frac{\lvert C\rvert L}{2s}, \frac{2r}{\lvert C\rvert K}\}$
		$S^*_{N_2} > S^*_{N_{2u}}$	$S^*_{P_2} < S^*_{P_{2u}}$	$\frac{a_{2u}-a_{2m}}{b_{2u}-b_{2m}} < min\{\frac{\lvert C\rvert L}{2s}, \frac{2r}{\lvert C\rvert K}\}$

Table 7.2: Comparison between escapements obtained by considering spatial structure and escapements obtained by ignoring spatial structure using unconnected two-patch predator-prey population harvesting theory (with index u), for various combinations of adult prey and predator migration survival. The additional condition column contains conditions other than conditions A_i and B_i are negative and $C > max\{\frac{2B_i}{K}, \frac{2A_i}{L}\}$.

escapements from two-patch unconnected predator-prey population harvesting theory are

$$(S^*_{N_i} - S^*_{N_{iu}})\Delta \quad = \quad [a_{iu} - a_{im}]\frac{2s}{L} + C[b_{iu} - b_{im}], \tag{7.14}$$

$$(S^*_{P_i} - S^*_{P_{iu}})\Delta \quad = \quad [b_{iu} - b_{im}]\frac{2r}{K} + C[a_{iu} - a_{im}], \tag{7.15}$$

where $\Delta = \Delta_i$ and $C = C_i$. In the following discussion I assume A_i and B_i are negative and $C > max\{\frac{2B_i}{K}, \frac{2A_i}{L}\}$ to ensure that the resulting optimal escapements are positive. By exploring equations (7.14) and (7.15) I obtain Table 7.2 showing optimal escapement comparisons for several combinations of prey and predator adult export survival a_im_{ij} and b_in_{ij} for $i = 1, 2$.

Table 7.2 shows that when prey (predator) subpopulation one has a higher adult export survival, that is, $a_1m_{12} > a_2m_{21}$ ($b_1n_{12} > b_2n_{21}$), the optimal escapement of prey (predator) subpopulation one from harvesting the population as a predator-prey metapopulation is greater than the optimal escapement if the prey (predator) subpopulation is incorrectly managed as two unconnected predator-prey populations. In other words, a subpopulation with high export survival should be harvested more conservatively than if we use harvesting policy which assumes the population as an unconnected two-patch predator-prey population. This rule is analogous to the rule in harvesting predator-prey metapopulation with juveniles migration, in which assuming the population to be an unconnected predator-prey population would over-harvest a relative exporter prey (predator) subpopulation. However, here I establish a more general rule where both species may have different export survival rates between patches. Table 7.2 also suggests that incorrectly managing the population as an unconnected two-patch predator-prey population would under-harvest the predator living in the same patch with the prey which has a higher export survival. Again, compared to a similar rule when subpopulations are connected by the dispersal of juvenile, here the rule is developed for a more general case, where both species may have different export survival rates between patches.

Total escapements of each species, either from predator-prey metapopulation harvesting theory or from unconnected two-patch predator-prey population harvesting theory are equal, that is, $S^*_{N_1} + S^*_{N_2} = S^*_{N_{1u}} + S^*_{N_{2u}}$ and $S^*_{P_1} + S^*_{P_2} = S^*_{P_{1u}} + S^*_{P_{2u}}$ (see equations (7.14) and (7.15)). However, numerical examples show that their equilibrium harvests may be different (see Table 7.3). This is because escapements from predator-prey metapopulation harvesting theory recognise the importance of the subpopulation which has a greater adult export survival as a contributor to the abundance of other subpopulations, while the two-patch predator-prey population harvesting theory overlooks it.

In a special case, where both subpopulations are identical except prey subpopulation one has a greater adult export survival with $a_1 m_{12} > a_2 m_{21}$ and $a_1 m_{11} = a_2 m_{22}$, it can be shown that the total harvest of each species from the predator-prey metapopulation harvesting theory is at least as great as the harvest if we incorrectly manage the population as a two-patch predator-prey population. To prove the claim above, we need to show that $\Delta_{HN} = (H^*_{N_1} + H^*_{N_2}) - (H^*_{N_{1u}} + H^*_{N_{2u}}) \geq 0$. Recall that $S^*_{N_i}$ and $S^*_{P_i}$ are given by equations (7.9) and (7.10), while $S^*_{N_{iu}}$ and $S^*_{P_{iu}}$ are given in Appendix 7A. From equations (7.11), (7.12) and (7.13) we obtain $A_1 = A_{2u}$, $A_2 = A_{1u}$, $B_1 = B_{2u}$, and $B_2 = B_{1u}$. It follows that $S^*_{N_1} = S^*_{N_{2u}}$, $S^*_{N_2} = S^*_{N_{1u}}$, $S^*_{P_1} = S^*_{P_{2u}}$, and $S^*_{P_2} = S^*_{P_{1u}}$. Since $H^*_{N_i} = N_i(S^*_{N_i}, S^*_{N_j}, S^*_{P_i}) - S^*_{N_i}$, where N_i as in equations (7.18) and (7.19), and similarly $H^*_{N_{iu}} = N_i(S^*_{N_{iu}}, S^*_{N_{ju}}, S^*_{P_{iu}}) - S^*_{N_{iu}}$, then considering both subpopulations are identical, we conclude

$$\Delta_{HN} = (a_1 m_{12} - a_2 m_{21})(S^*_{N_1} + S^*_{N_{iu}}) > 0. \qquad (7.16)$$

Escapement comparisons to well-mixed predator-prey harvesting theory can be obtained in a similar way.

7.1.4 Numerical examples

In this section I present numerical examples to illustrate and to compare our two-patch predator-prey optimal escapements with other escapements. The results in these examples conform to the rules described in the analysis discussed above. Some interpretations that are not clearly seen in the previous analytical results can also be obtained.

Assume that there is a couple of predator-prey populations occupying two different patches. The populations are connected by adult migration. The carrying capacity of the prey in each patch is $K_i = 500000$, with intrinsic growth rate $r_i = 4$ and adult survival rate per period measured before migration is $a_i = 1$. The adults migrate non-symmetrically with $m_{11} = m_{21} = m_{22} = 0.025$ and $m_{12} = 0.050$, that is, prey subpopulation one has a greater export survival than prey subpopulation two. The predator population is assumed to be identical in both patches with the following biological parameters: carrying capacity is $L_i = 1000$, predator intrinsic growth is $s_i = 4$, pre-migration adult survival $b_i = 1$ and adult migration survival rate is $n_i = 0.25$. The parameters for the predator-prey interactions are $\alpha_i = 0.00001$ and $\beta_i = 0.000001$.

Before the commencement of exploitation, I assume that the population is in the equilibrium population size. Using equations (7.18) and (7.21), the equilibrium popula-

PPM	$S^*_{N_1} = 185816$ $S^*_{N_2} = 184253$	$H^*_{N_1} = 290078$ $H^*_{N_2} = 294662$	$S^*_{P_1} = 216$ $S^*_{P_2} = 218$	$H^*_{P_1} = 610$ $H^*_{P_2} = 612$
	$S^*_N = 370069$	$H^*_N = 584740$	$S^*_P = 434$	$H^*_P = 1222$
UPP	$S^*_{N_{1u}}=184253$ $S^*_{N_{2u}}=185816$	$H^*_{N_{1u}}=290016$ $H^*_{N_{2u}}=294684$	$S^*_{P_{1u}}=218$ $S^*_{P_{2u}}=216$	$H^*_{P_{1u}}=612$ $H^*_{P_{2u}}=610$
	$S^*_{N_u}=370069$	$H^*_{N_u}=584700$	$S^*_{P_u}=434$	$H^*_{P_u}=1222$
WPP	$S^*_{N_w}=370294$	$H^*_{N_w}=585523$	$S^*_{P_w}=17$	$H^*_{P_w}=61$

Table 7.3: Escapement and harvest comparisons between correct and incorrect assumptions, where $p_N = p_P$ and costs are negligible. PPM, UPP and WPP denote predator-prey metapopulation, unconnected predator-prey population and well-mixed predator-prey population, respectively.

tion size for each species are $\bar{N}_1 = 380063$, $\bar{N}_2 = 383112$, $\bar{P}_1 = 970$ and $\bar{P}_2 = 971$. Note that the equilibrium population size of the prey subpopulation with a greater export survival is smaller than the other prey subpopulation. This is because it exports more adults than it imports. Next I will explore the optimal escapement for the population by considering that the costs of harvesting are negligible with the discounting rate $\delta = 10\%$. The results will be compared to the previous analytical results. The effects of the inclusions of the costs of harvesting will also be explored.

Optimal escapements for the population are $S^*_{N_1} = 185816$, $S^*_{N_2} = 184253$, $S^*_{P_1} = 216$ and $S^*_{P_2} = 218$ found by substituting all biological parameters into equations (7.9) and (7.10). All escapements are positive because it is assumed that both species have relatively high intrinsic growths. Result 29 implies that if natural growth rates or adult survival rates are relatively low compared to the discounting rate, then the optimal escapements may be non-positive. For example if $s_i = 4$ is replaced by $s_i = 2$ then we obtain new optimal escapements $S^*_{N_1} = 185976$, $S^*_{N_2} = 184412$, and $S^*_{P_1}$ and $S^*_{P_2}$ are negative. [Note that here it is optimal to harvest all predators. This is not the case if we incorrectly believe that the population does not have any predator-prey interactions, where we would harvest both predator subpopulations equally, that is, $S^*_{P_{1s}} = S^*_{P_{2s}} = 280$, although we still harvest the prey subpopulation with a larger adult migration more conservatively than the other prey subpopulation ($S^*_{N_{1s}} = 185938$ and $S^*_{N_{2s}} = 184375$)].

Now let us take the cost of harvesting into consideration. Let the cost of harvesting be given by

$$c_X(X_i) = (m_{X_i} + c_i n_{X_i} X_i)/(n_{X_i} X_i). \tag{7.17}$$

If the cost of harvesting is independent of species and location with $m_{X_i} = 30$, $n_{X_i} = 1.3 \times 10^{-2}$, $c_i = 0$, and price $p_X = 70$, then optimal escapements $S^*_{N_1} = 185819$, $S^*_{N_2} = 184256$, $S^*_{P_1} = 222$ and $S^*_{N2} = 224$ are obtained (see Table 7.4). We can see that the rules of how to harvest prey and predator subpopulations with different adult migration survival remain true in the inclusion of the costs of harvesting. In this example, the rule is also robust if there are price differences between species, for example if $p_N = 70$ but $p_P = 10 \times p_N$, where in this case new optimal escapements $S^*_{N_1} = 185944$, $S^*_{N_2} = 184382$ and $S^*_{P_1} = S^*_{N_2} = 426$ are found (see Table 7.5).

PPM	$S^*_{N_1} = 185819$	$H^*_{N_1} = 290066$	$S^*_{P_1} = 222$	$H^*_{P_1} = 622$
	$S^*_{N_2} = 184256$	$H^*_{N_2} = 294651$	$S^*_{P_2} = 224$	$H^*_{P_2} = 624$
	$S^*_N = 370075$	$H^*_N = 584717$	$S^*_P = 446$	$H^*_P = 1246$
UPP	$S^*_{N_{1u}} = 184256$	$H^*_{N_{1u}} = 290005$	$S^*_{P_{1u}} = 224$	$H^*_{P_{1u}} = 624$
	$S^*_{N_{2u}} = 185819$	$H^*_{N_{2u}} = 294673$	$S^*_{P_{2u}} = 222$	$H^*_{P_{2u}} = 622$
	$S^*_{N_u} = 370075$	$H^*_{N_u} = 584678$	$S^*_{P_u} = 446$	$H^*_{P_u} = 1246$
WPP	$S^*_{N_w} = 370273$	$H^*_{N_w} = 585477$	$S^*_{P_w} = 41$	$H^*_{P_w} = 146$

Table 7.4: Escapement and harvest comparisons between correct and incorrect assumptions, where $p_N = p_P$ and costs are given by equation (7.17) with $m_{X_i} = 30$, $n_{X_i} = 1.3 \times 10^{-2}$, $c_i = 0$ and price $p_X = 70$. The rules of how to harvest prey and predator subpopulations with different adult migration survival are robust with the inclusion of the costs of harvesting.

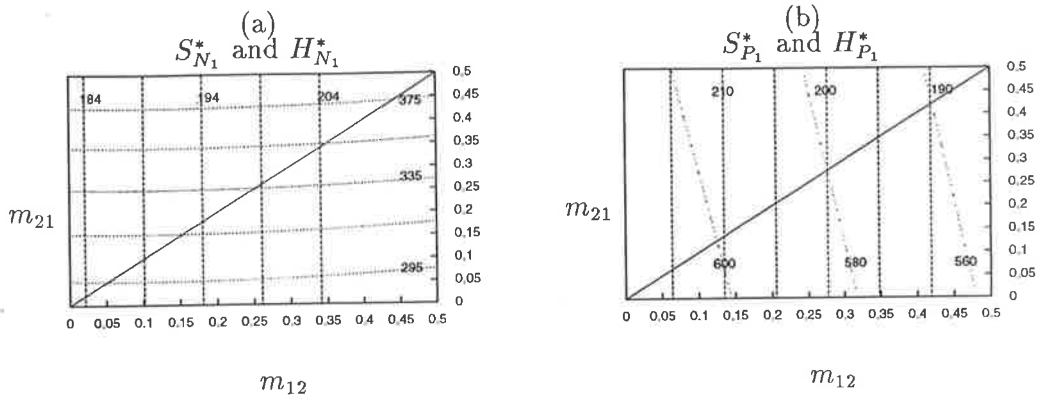
PPM	$S^*_{N_1} = 185944$	$H^*_{N_1} = 289697$	$S^*_{P_1} = 426$	$H^*_{P_1} = 844$
	$S^*_{N_2} = 184382$	$H^*_{N_2} = 294294$	$S^*_{P_2} = 426$	$H^*_{P_2} = 844$
	$S^*_N = 370326$	$H^*_N = 583991$	$S^*_P = 852$	$H^*_P = 1688$
UPP	$S^*_{N_{1u}} = 184382$	$H^*_{N_{1u}} = 289646$	$S^*_{P_{1u}} = 426$	$H^*_{P_{1u}} = 844$
	$S^*_{N_{2u}} = 185944$	$H^*_{N_{2u}} = 294307$	$S^*_{P_{2u}} = 426$	$H^*_{P_{2u}} = 844$
	$S^*_{N_u} = 370326$	$H^*_{N_u} = 583953$	$S^*_{P_u} = 852$	$H^*_{P_u} = 1688$
WPP	$S^*_{N_w} = 370318$	$H^*_{N_w} = 583982$	$S^*_{P_w} = 850$	$H^*_{P_w} = 1688$

Table 7.5: Escapement and harvest comparisons between correct and incorrect assumptions, where $p_N = p_P$ and costs are given by equation (7.17) with $m_{X_i} = 30$, $n_{X_i} = 1.3 \times 10^{-2}$, $c_i = 0$, $p_N = 70$ and $p_P = 10 \times p_N$. The table shows that the rules of how to harvest prey and predator subpopulations with different adult migration survival are robust with the inclusion of the costs of harvesting.

Impact of variation of parameters m_{ij}, α_i and β_i on optimal strategies

In this section I investigate the change to optimal escapements as a result of adult migration parameter variations. From equations (7.9) and (7.10) we can see that if all assumptions in Result 29 are true, that is, A_i and B_i are negative and C_i is non-positive, then the partial derivative $\frac{\partial S^*_{N_i}}{\partial m_{ij}}$ is positive and the partial derivative $\frac{\partial S^*_{P_i}}{\partial m_{ij}}$ is non-positive. This implies that prey optimal escapement $S^*_{N_i}$ increases with the increase of the adult migration parameter m_{ij} and predator optimal escapement $S^*_{P_i}$ does not increase with the increase of the adult migration parameter m_{ij}. As an example, I plot contour lines of escapements $S^*_{N_1}$ and $S^*_{P_1}$ of the predator-prey metapopulation in the previous example as adult migration parameters m_{12} and m_{21} vary in Figure 7.1. This figure shows that as adult migration parameter m_{12} increases, the optimal escapement for prey subpopulation one, $S^*_{N_1}$, increases (Figure 7.1.a, dashes). Optimal escapement for prey subpopulation two, $S^*_{N_2}$, can be found by reflecting the contour about the line $m_{12} = m_{21}$, which is always lower than $S^*_{N_1}$ whenever $m_{12} > m_{21}$.

Adult migration survival in patch i does not affect the optimal escapement in the other patch. However all equilibrium harvests $H^*_{N_i}$ and $H^*_{P_i}$ in both patches are influenced. For example, I plot the equilibrium harvest $H^*_{N_1}$ for prey subpopulation


(a) $S^*_{N_1}$ and $H^*_{N_1}$

(b) $S^*_{P_1}$ and $H^*_{P_1}$

Figure 7.1: Figure 7.1.a shows the contours of the escapement $S^*_{N_1}$ (dashes) and the equilibrium harvest $H^*_{N_1}$ (dots) for prey subpopulation one (in thousands). Figure 7.1.b shows the contours of the escapement $S^*_{P_1}$ (dashes) and the equilibrium harvest $H^*_{P_1}$ (dots) for predator subpopulation one. The contours for prey and predator subpopulation two can be obtained by reflecting the figure about the line $m_{12} = m_{21}$.

one. This equilibrium harvest increases as the adult migration parameters for the other species increases (Figure 7.1.a, dots). Figure 7.1.b (dashes) shows that, if the adult migration survival of prey subpopulation one increases then the optimal escapement of the predator living in the same patch with this prey subpopulation decreases. This is consistent with the result from the case of juvenile migration predator-prey metapopulation. All regions in Figure 7.1 satisfy the condition $C_i > max\{\frac{2A_i}{L_i}, \frac{2B_i}{K_i}\}$. A similar rule can also be observed if $C_i < min\{\frac{2A_i}{L_i}, \frac{2B_i}{K_i}\}$, such as shown in Figure 7.2 where the contour of escapements and equilibrium harvests are plotted as the prey adult survival migration and vulnerability vary.

As in Figure 7.1, Figure 7.2.a shows that, for a fixed prey vulnerability, prey escapement $S^*_{N_1}$ increases as the adult survival migration increases (dashes). This means that we should harvest the prey more conservatively as the prey has a larger adult survival migration. It can also be observed in Figure 7.2.b, where the harvest of the prey decreases as the adult survival migration increases (dashes). Predator escapement $S^*_{P_1}$ is relatively unaffected and remains the same for all values of adult survival migration (dots). Both prey and predator escapements in patch two are also unaffected (Figure 7.2.c). However, although prey escapement in patch two remains the same, for a fixed α_1, as adult survival migration increases, its equilibrium harvest increases (Figure 7.2.d, dashes).

Most of the values of α_1 produce zero escapements of the predator in both patches. This is because I choose a low value of $\beta_i = 0.000001$, which means that predator efficiency for most values of β_i is very small. Since it is also assumed that the price of prey and the predator are equal (the relative predator price is $m = 1$), then it is not optimal to leave the prey to be consumed by the predator. By generating a similar figure for $m = 10$, that is, the price of the predator ten times the price of the prey, it can be shown that predator escapements are positive for various value of m_{12} and α_1 in Figure 7.2.

We observe that, for a fixed adult survival migration m_{12}, prey optimal escapement increases as the prey vulnerability increases (Figure 7.2.a). This is contrary to

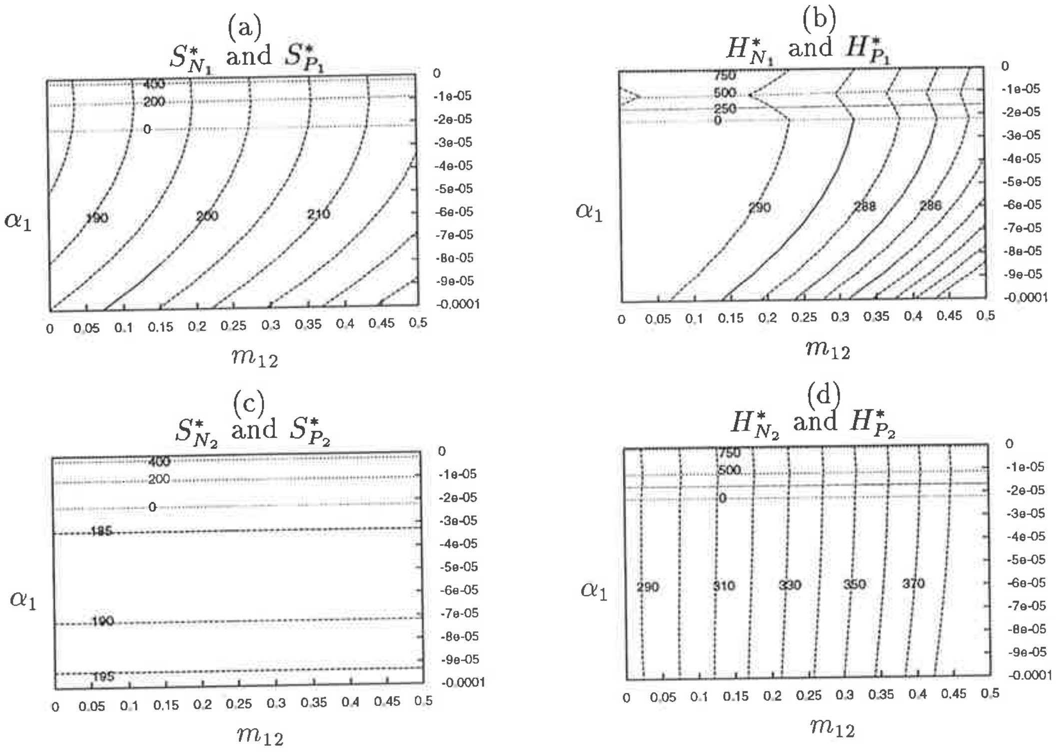
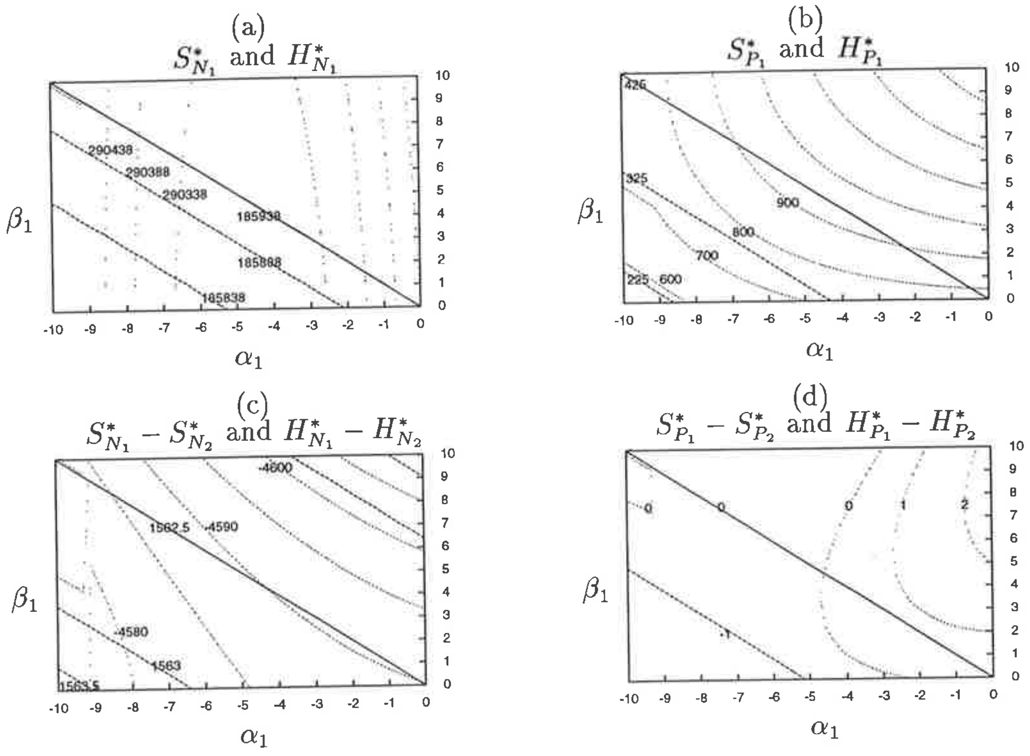


Figure 7.2: Figure 7.2.a shows the contours of the escapement $S^*_{N_1}$ for prey subpopulation one (dashes) and $S^*_{P_1}$ (dots) for predator subpopulation one. Figure 7.2.b shows the contours of the harvest $H^*_{N_1}$ for prey subpopulation one (dashes) and $H^*_{P_1}$ (dots) for predator subpopulation one. In this figure we assume $\alpha_1 = \alpha_2$, $m_{21} = 0.025$, and $\beta_i = 0.000001$. Figure 7.2.c shows $S^*_{N_2}$ and $S^*_{P_2}$, and Figure 7.2.d shows $H^*_{N_2}$ and $H^*_{P_2}$. The contours for the prey are in thousands.

the result in the previous chapter where we should harvest a prey subpopulation which has a lower vulnerability more conservatively than a prey subpopulation with a higher vulnerability. The reason is because in this case $C_i < min\{\frac{2A_i}{L_i}, \frac{2B_i}{K_i}\}$ for most regions in the Figure 7.2.a. If the condition $C_i > max\{\frac{2A_i}{L_i}, \frac{2B_i}{K_i}\}$ is satisfied, Figure 7.3 shows that, all the rules of harvesting a more (less) vulnerable prey and a more (less) efficient predator subpopulation are observed as in the case of juvenile migration.

Figure 7.3.a shows that, for a fixed β_1, prey optimal escapement $S^*_{N_1}$ diminishes as the prey vulnerability increases (lower α_1). The increase of $S^*_{N_1}$ is also observed, if we fixed the value of α_1 at a certain level, as the value β_1 increases. It can be observed in Figure 7.3.b that for a fixed β_1, predator escapement $S^*_{P_1}$ diminishes as the predator efficiency decreases (lower α_1), and for a fixed α_1, predator escapement $S^*_{P_1}$ increases as the predator efficiency increases (higher β_1). All of these observations are well established in the previous chapter. A similar result to Result 11 can be obtained analytically.

The rule that we should harvest prey subpopulations with larger adult survival migration is observed in Figure 7.3.c. In this figure the difference between escapement


(a) $S^*_{N_1}$ and $H^*_{N_1}$

(b) $S^*_{P_1}$ and $H^*_{P_1}$

(c) $S^*_{N_1} - S^*_{N_2}$ and $H^*_{N_1} - H^*_{N_2}$

(d) $S^*_{P_1} - S^*_{P_2}$ and $H^*_{P_1} - H^*_{P_2}$

Figure 7.3: Figure 7.3.a shows the contours of the escapements $S^*_{N_1}$ (dashes) and harvests $H^*_{N_1}$ (dots) for prey subpopulation one. Figure 7.3.b shows the contours of the escapements $S^*_{P_1}$ (dashes) and harvests $H^*_{P_1}$ (dots) for predator subpopulation one. Figure 7.3.c shows the contours of the difference $S^*_{N_1} - S^*_{N_2}$ (dashes) and the difference $H^*_{N_1} - H^*_{N_2}$ (dots). Figure 7.3.d shows the contours of the difference $S^*_{P_1} - S^*_{P_2}$ (dashes) and the difference $H^*_{P_1} - H^*_{P_2}$ (dots). The region below the line $\beta_1 = |\alpha_1|$ is the region which is biologically meaningful, that is, the region where predator efficiency does not exceed 100% (α_i and β_i are in 10^{-6}).

of prey subpopulation one, which has a larger adult survival migration, and escapement of prey subpopulation two, $S^*_{N_1} - S^*_{N_2}$, is always positive for every value of α and β (dashes). While in Figure 7.3.d the difference between escapement of the predator living in the same patch with the prey which has a larger adult survival migration and escapement of the other predator subpopulation is always negative, as expected, regardless of the value of α and β (dashes).

7.2 Adult and juvenile migration

In this section I extend the model of the previous section to include juvenile migration in the system. Much of the literature shows that the adults and juveniles of many marine species migrate between habitat. For example, the intertidal gastropod, *Bambicium auratum*, has high adult and juvenile migration rate (Crowley, 1996). Other examples are crustaceans, *Callinectes sapidus*, in Chesapeake Bay, USA and *Maja squinado* in

Ria de Arouse, Spain. Both adults and juveniles of these crabs species migrate between different types of habitat (Hines *et al.*, 1995).

7.2.1 The model and its optimal escapements

As in Chapter 5, I assume p_{ij} and q_{ij} denote the proportion of the juveniles of prey and predator migrating from patch i to patch j, respectively. Using the same notation as that in the previous section, the dynamic of the population is given by

$$N_{1(k+1)} = a_1 m_{11} N_{1k} + a_2 m_{21} N_{2k} + p_{11} F_1(N_{1k}) + p_{21} F_2(N_{2k}) + \alpha_1 N_{1k} P_{1k}, \tag{7.18}$$

$$N_{2(k+1)} = a_1 m_{12} N_{1k} + a_2 m_{22} N_{2k} + p_{12} F_1(N_{1k}) + p_{22} F_2(N_{2k}) + \alpha_2 N_{2k} P_{2k}, \tag{7.19}$$

$$P_{1(k+1)} = b_1 n_{11} P_{1k} + b_2 n_{21} P_{2k} + q_{11} G_1(P_{1k}) + q_{21} G_2(P_{2k}) + \beta_1 N_{1k} P_{1k}, \tag{7.20}$$

$$P_{2(k+1)} = b_1 n_{12} P_{1k} + b_2 n_{22} N_{2k} + q_{12} G_1(P_{1k}) + q_{22} G_2(P_{2k}) + \beta_2 N_{2k} P_{2k}, \tag{7.21}$$

where $\alpha_i < 0$ and $\beta_i > 0$.

Following the same method in the previous section, optimal escapements for the prey and predator populations, $S^*_{N_i}$ and $S^*_{P_i}$, can be obtained in the implicit expressions

$$\begin{aligned} \frac{p_N - c_{Ni}(S^*_{N_{i0}})}{\rho} &= \Big(a_i m_{ii} + p_{ii} F_i'(S^*_{N_{i0}}) + \alpha_i S^*_{P_{i0}}\Big)\big(p_N - c_{Ni}(N_{i1})\big) \\ &\quad + \Big(a_i m_{ij} + p_{ij} F_i'(S^*_{N_{i0}})\Big)\left(p_N - c_{Nj}(N_{j1})\right) \\ &\quad + \beta_i S^*_{P_{i0}}\left(p_P - c_{Pi}(P_{i1})\right), \end{aligned} \tag{7.22}$$

$$\begin{aligned} \frac{p_P - c_{Pi}(S^*_{P_{i0}})}{\rho} &= \Big(b_i n_{ii} + q_{ii} G_i'(S^*_{P_{i0}}) + \beta_i S^*_{N_{i0}}\Big)\big(p_P - c_{Pi}(P_{i1})\big) \\ &\quad + \Big(b_i n_{ij} + q_{ij} G_i'(S^*_{N_{i0}})\Big)\left(p_P - c_{Pj}(P_{j1})\right) \\ &\quad + \alpha_i S^*_{N_{i0}}\left(p_N - c_{Ni}(N_{i1})\right). \end{aligned} \tag{7.23}$$

These equations are the general form of the optimal escapement equation for a two-patch predator-prey metapopulation with adult and juvenile migration. As expected, if $m_{12} = m_{21} = 0$, $m_{11} = m_{22} = 1$, $n_{12} = n_{21} = 0$ and $n_{11} = n_{22} = 1$ then the optimal escapement equations reduce to equations (5.5) and (5.6) in Chapter 5 and if $p_{12} = p_{21} = 0$, $p_{11} = p_{22} = 1$, $q_{12} = q_{21} = 0$ and $q_{11} = q_{22} = 1$ then the optimal escapement equations reduce to equations (7.5) and (7.6) in the previous section.

As in the case of juvenile migration only or adult migration only, explicit expressions of the optimal escapements $S^*_{N_i}$ and $S^*_{P_i}$ can be obtained by neglecting the costs of harvesting and price differences between the prey and predator and assuming that recruitment production functions, F_i and G_i, are logistic as in equations (3.3) and (3.4). These escapements are

$$S^*_{N_i} = \frac{A_i(q_{i1} + q_{i2})\frac{2s_i}{L_i} + C_i B_i}{\Delta_i}, \tag{7.24}$$

$$S^*_{P_i} = \frac{B_i(p_{i1} + p_{i2})\frac{2r_i}{K_i} + C_i A_i}{\Delta_i}, \tag{7.25}$$

provided $\Delta_i = C_i^2 - (p_{i1} + p_{i2})\frac{2r_i}{K_i}(q_{i1} + q_{i2})\frac{2s_i}{L_i} \neq 0$, where

$$A_i = \frac{1}{\rho} - (p_{i1} + p_{i2})r_i - a_i(m_{i1} + m_{i2}), \tag{7.26}$$

$$B_i = \frac{1}{\rho} - (q_{i1} + q_{i2})s_i - b_i(n_{i1} + n_{i2}), \tag{7.27}$$

and

$$C_i = \alpha_i + \beta_i. \tag{7.28}$$

Using the same method as in the previous chapters, sufficient conditions for the metapopulation to have non-negative optimal escapements are obtained. The conditions are written in the following result.

Result 32 *(Sufficient conditions for positive escapements) Let $S^*_{N_i}$ and $S^*_{P_i}$ denote the optimal escapement from a predator-prey metapopulation given by equations (7.24) and (7.25). If A_i and B_i are negative, and C_i is non-positive with $C_i > max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}$, then*

Δ_i is negative, and S^*_{Ni} and S^*_{Pi} are positive.

The condition $A_i < 0$ has a similar interpretation to the same condition in the previous section. The relationship between escapements from a predator-prey metapopulation presented in this chapter and escapements from a single-species metapopulation with adult and juvenile migration discussed in Tuck (1994) can be explored using Result 2 in Chapter 5 where A_i and B_i are given by equations (7.26) and (7.27). To draw some conclusions about escapement comparisons between patches I construct the following lemma.

Lemma 10 *(Migrations trade-off equations) Let $S^*_{N_i}$ and $S^*_{P_i}$ denote the optimal escapement from a predator-prey metapopulation given by equations (7.24) and (7.25). If $K_i = K$, $L_i = L$, $C_i = C$, $x_{im} = (p_{ii} + p_{ij})r_i + (m_{ii} + m_{ij})a_i$ and $y_{im} = (q_{ii} + q_{ij})s_i + (n_{ii} + n_{ij})b_i$ then:*

1. $$\begin{aligned}(S^*_{N_1} - S^*_{N_2})\Delta_1\Delta_2 &= \left(C^2(y_{1m} - y_{2m}) - \frac{4y_{1m}y_{2m}}{KL}(x_{2m} - x_{1m})\right)\left(\frac{2}{\rho L} - C\right)\\ &\quad -\frac{2C}{L}\left(C - \frac{2}{\rho K}\right)(x_{1m}y_{1m} - x_{2m}y_{2m}),\end{aligned}$$

2. $$\begin{aligned}(S^*_{P_1} - S^*_{P_2})\Delta_1\Delta_2 &= \left(C^2(x_{1m} - x_{2m}) - \frac{4x_{1m}x_{2m}}{KL}(y_{2m} - y_{1m})\right)\left(\frac{2}{\rho K} - C\right)\\ &\quad -\frac{2C}{K}\left(C - \frac{2}{\rho L}\right)(x_{1m}y_{1m} - x_{2m}y_{2m}).\end{aligned}$$

In a special case, where both predator subpopulations are identical, we can compare optimal escapements if one of the prey subpopulations has a higher adult export survival or is a relative exporter subpopulation, so that the total surviving individuals of that population, that is, $(p_{i1} + p_{i2})r_i + (m_{i1} + m_{i2})a_i$, is greater than the total surviving individuals of the other patch. This comparison is summarised in the following result.

Result 33 *(Escapement comparisons between subpopulations) Let prey subpopulation one be a relative exporter subpopulation or have a higher adult migration survival, so that the total surviving individuals of that prey subpopulation is higher than the total surviving individuals of the other prey subpopulation. All other parameters of the prey and the predator are identical for both subpopulations. If* $|\alpha| = \beta$, *or if* A_i *and* B_i *are negative and* $C > max\{\frac{2B_i}{K}, \frac{2A_i}{L}\}$, *then*

$$S^*_{N_1} > S^*_{N_2} \text{ and } S^*_{P_1} \leq S^*_{P_2}.$$

Lemma 10 can also be used to compare escapements given by equations (7.24) and (7.25) to the escapements we get if we incorrectly manage the metapopulation as an unconnected two-patch predator-prey population. In this case we would measure the adult survival of subpopulation i as a_{iu} given by equation (7.13) and the growth rate as r_{iu} given by equation (4.44). The adult survival and growth rate of the predator would be measured similarly. The comparison between these escapements are summarised in the following result.

Result 34 *(Escapement Comparison to an unconnected two-patch predator-prey population). Let* $S^*_{N_i}$ *and* $S^*_{P_i}$ *denote the optimal escapement from a predator-prey metapopulation given by equations (7.24) and (7.25), and let* $S^*_{N_{iu}}$ *and* $S^*_{P_{iu}}$ *denote the optimal escapement if we incorrectly consider the metapopulation as a system consisting of two unconnected predator-prey populations. Let prey subpopulation one be a relative exporter and also be a relative source subpopulation or have a higher adult migration survival, so that the total surviving individuals of that prey subpopulation is higher than the total surviving individuals of the other prey subpopulation, that is* $x_{1m} > x_{2m}$, *with* $p_{12}r_1 > p_{21}r_2$ *and* $p_{11}r_1 \geq p_{22}r_2$. *All other parameters of the prey and the predator are identical for both subpopulations. If* A_i *and* $B_1 = B_2 = B$ *are negative and* $C_1 = C_2 = C$ *is non-positive with* $C > max\{\frac{2B}{K}, \frac{2A}{L}\}$ *then:*

1. $S^*_{N_1} > S^*_{N_{1u}}$,
2. $S^*_{N_2} < S^*_{N_{2u}}$,
3. $S^*_{P_1} \leq S^*_{P_{1u}}$,
4. $S^*_{P_2} \geq S^*_{P_{2u}}$,
5. $S^*_{N_1} + S^*_{N_2} \leq S^*_{N_{1u}} + S^*_{N_{2u}}$,
6. $S^*_{P_1} + S^*_{P_2} \geq S^*_{P_{1u}} + S^*_{P_{2u}}$.

The proof of this result is analogous to the proof of Result 9.

It can be concluded from Result 33, that we should harvest a relative source prey subpopulation that has a higher adult migration survival more conservatively than a relative sink prey subpopulation that has a lower adult migration survival. It can also be concluded that we should harvest the predator living in the same patch with the relative source prey subpopulation that has a higher adult migration survival, less conservatively than the other predator subpopulation. In general, if adult migration survival and the per capita larval production for both species are different between subpopulations, then the difference in escapements are determined by the migration trade-off equations in Lemma 10.

Furthermore, Result 34 concludes that if we ignore spatial structure and manage the metapopulation as two unconnected predator-prey populations then we would over-harvest the relative source prey subpopulation that has a higher adult migration survival and under-harvest the relative sink prey subpopulation that has a lower adult migration survival. On the other hand, we would also under-harvest the predator living in the same patch with the relative source prey subpopulation that has a higher adult migration survival and over-harvest the predator living in the same patch with the relative sink prey subpopulation that has a lower adult migration survival. A similar result can also be obtained if we incorrectly manage the metapopulation as a well-mixed predator-prey population.

7.2.2 Numerical examples

In this section I present numerical examples to illustrate the analytical results in the previous section. The examples are similar to examples in the previous section in order to compare how the escapements would change if the migration of juveniles is included into the system.

As in the previous section I assume that there are a couple of predator-prey populations occupying two different patches. The populations are connected both by the migration of adults and the migration of juveniles. All parameters are the same as the parameters in Section 7.1.4 with the addition that the parameters of the juveniles migration are given by $p_{11} = p_{21} = p_{22} = 0.050$ and $p_{12} = q_{ij} = 0.065$. As before, harvesting begins when the populations are at their equilibrium population size. Next, I determine optimal escapement for the metapopulation by considering that the costs of harvesting are negligible with the discounting rate $\delta = 10\%$. The results will be compared to the analytical results of the previous section. The effects of the inclusion of the costs of harvesting will also be explored.

Substituting all the parameters above into equations (7.24) and (7.25) produces negative escapements for both prey subpopulations, that is, $S^*_{N_1} = -320244$ and $S^*_{N_2} = -426582$, with $C_i < min\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}$. To obtain positive optimal escapements, the condition $C_i > max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}$ needs to be satisfied. This can be attained by setting a higher intrinsic growth of the population. Let us assume that the population has a higher intrinsic growth rate, for example, ten times the original intrinsic growth, that is, $r_i = s_i = 40$, then new optimal escapements $S^*_{N_1} = 194159$, $S^*_{N_2} = 184216$, $S^*_{P_1} = 274$ and $S^*_{P_2} = 283$ are found. As suggested by Result 33, we should harvest the relative source prey subpopulation that has a higher adult migration survival more conservatively than the relative sink prey subpopulation that has a lower adult migration survival. We can also observe that the optimal escapement for the predator living in the same patch with the relative source prey subpopulation that has a higher adult migration survival is less than the optimal escapement for the other predator subpopulation. Profit generated from these escapements is greater than profit generated by escapements if we ignored the spatial structure (see Table 7.6).

Next, let us take the costs of harvesting into consideration, where the costs of harvesting are given by equation (7.17). The parameters in the costs function are $m_{X_i} = 30$, $n_{X_i} = 1.3 \times 10^{-2}$, $c_i = 0$, and price $p_X = 70$. Using this cost function optimal escapements $S^*_{N_1} = 194163$, $S^*_{N_2} = 184221$, $S^*_{P_1} = 279$ and $S^*_{N_2} = 288$ are found (see Table 7.7). We can see that the inclusion of the costs of harvesting does not change the rules described in Result 33. Tables 7.7 and 7.8 compare escapements from equations (7.22) and (7.23) to escapements if we ignored the spatial structure of

PPM	$S^*_{N_1} = 194159$ $S^*_{N_2} = 184216$	$H^*_{N_1} = 284985$ $H^*_{N_2} = 371052$	$S^*_{P_1} = 274$ $S^*_{P_2} = 283$	$H^*_{P_1} = 963$ $H^*_{P_2} = 953$
	$S^*_N = 378375$	$H^*_N = 656037$	$S^*_P = 557$	$H^*_P = 1916$
UPP	$S^*_{N_{1u}}$=184216 $S^*_{N_{2u}}$=194159	$H^*_{N_{1u}}$=294939 $H^*_{N_{2u}}$=359397	$S^*_{P_{1u}}$=283 $S^*_{P_{2u}}$=274	$H^*_{P_{1u}}$=953 $H^*_{P_{2u}}$=963
	$S^*_{N_u}$ =378375	$H^*_{N_u}$ =654336	$S^*_{P_u}$=557	$H^*_{P_u}$=1916
WPP	$S^*_{N_w}$ =379122	$H^*_{N_w}$ =656311	$S^*_{P_w}$ =1210	$H^*_{P_w}$=981

Table 7.6: Escapement and harvest comparisons between correct and incorrect assumptions, where $p_N = p_P$ and costs of harvesting are negligible. PPM, UPP and WPP denote predator-prey metapopulation, unconnected predator-prey population and well-mixed predator-prey population, respectively.

PPM	$S^*_{N_1} = 194163$ $S^*_{N_2} = 184221$	$H^*_{N_1} = 284976$ $H^*_{N_2} = 371043$	$S^*_{P_1} = 279$ $S^*_{P_2} = 288$	$H^*_{P_1} = 973$ $H^*_{P_2} = 963$
	$S^*_N = 378384$	$H^*_N = 656019$	$S^*_P = 567$	$H^*_P = 1936$
UPP	$S^*_{N_{1u}} = 184220$ $S^*_{N_{2u}} = 194163$	$H^*_{N_{1u}} = 294930$ $H^*_{N_{2u}} = 359389$	$S^*_{P_{1u}} = 288$ $S^*_{P_{2u}} = 279$	$H^*_{P_{1u}} = 963$ $H^*_{P_{2u}} = 973$
	$S^*_{N_u} = 378383$	$H^*_{N_u} = 654319$	$S^*_{P_u} = 567$	$H^*_{P_u} = 1936$
WPP	$S^*_{N_w} = 379122$	$H^*_{N_w} = 656300$	$S^*_{P_w} = 234$	$H^*_{P_w} = 1002$

Table 7.7: Escapement and harvest comparisons between correct and incorrect assumptions, where $p_N = p_P$ and costs are given by equation (7.17) with $m_{X_i} = 30$, $n_{X_i} = 1.3 \times 10^{-2}$, $c_i = 0$ and price $p_X = 70$. Compared to escapements with negligible costs of harvesting, the escapements in this table are slightly higher, but the rule to conserve the relative exporter prey subpopulation that has a higher adult migration survival remains unchanged.

the population for various parameters of the costs of harvesting.

I plot the contour of the optimal escapements and the equilibrium harvests as the adult and juvenile migration survivals, m_{12} and p_{12}, vary in Figure 7.4. Figure 7.4.a shows that the optimal escapement for prey subpopulation one increases as the adult and juvenile migration increase (dashes), while the equilibrium harvest decreases as the adult and juvenile migration increase (dots) as suggested by Result 33. The variations of the adult and juvenile survival of prey subpopulation one do not affect the optimal escapements of prey and predator subpopulation two. However, their equilibrium harvests are affected (Figures 7.4.b and 7.4.d). The equilibrium harvest of prey subpopulation two increases as the adult and juvenile migration survival of the prey subpopulation one increase (Figure 7.4.b). As expected optimal escapement of the predator subpopulation one decreases (Figure 7.4.c).

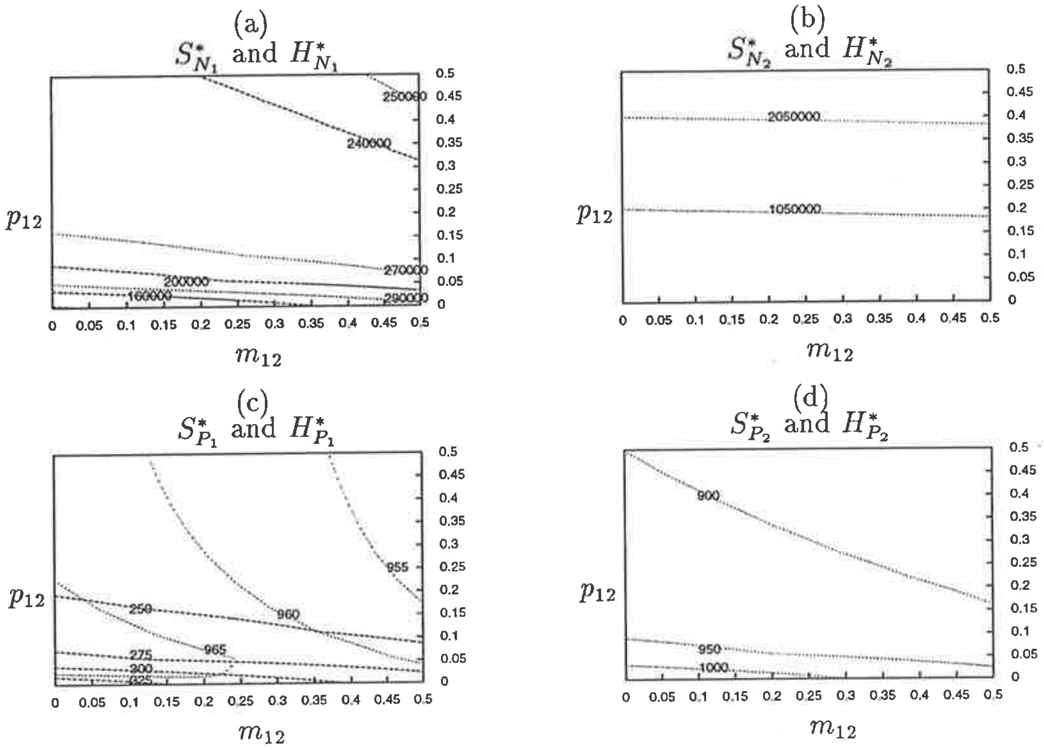


Figure 7.4: Contour plot of the optimal escapements and the equilibrium harvests as the adult and juvenile migration survivals, m_{12} and p_{12}, vary. Figure 7.4.a shows that the optimal escapement for prey subpopulation one increases as the adult and juvenile migration increase (dashes), while the equilibrium harvest decreases (dots). The variations of the adult and juvenile survival of prey subpopulation one do not affect the optimal escapements of prey and predator subpopulation two. However, their equilibrium harvests are affected (Figures 7.4.b and 7.4.d). The equilibrium harvest of prey subpopulation two increases as the adult and juvenile migration survival of the prey subpopulation one increase (Figure 7.4.b). As expected by the Result 33 optimal escapement of the predator subpopulation one decreases (Figure 7.4.c).

PPM	$S^*_{N_1} = 194299$ $S^*_{N_2} = 184382$	$H^*_{N_1} = 284674$ $H^*_{N_2} = 370770$	$S^*_{P_1} = 443$ $S^*_{P_2} = 443$	$H^*_{P_1} = 1148$ $H^*_{P_2} = 1143$
	$S^*_N = 378681$	$H^*_N = 655444$	$S^*_P = 886$	$H^*_P = 2291$
UPP	$S^*_{N_{1u}} = 184382$ $S^*_{N_{2u}} = 194300$	$H^*_{N_{1u}} = 294636$ $H^*_{N_{2u}} = 359117$	$S^*_{P_{1u}} = 443$ $S^*_{P_{2u}} = 443$	$H^*_{P_{1u}} = 1143$ $H^*_{P_{2u}} = 1147$
	$S^*_{N_u} = 378682$	$H^*_{N_u} = 653753$	$S^*_{P_u} = 886$	$H^*_{P_u} = 2291$
WPP	$S^*_{N_w} = 379366$	$H^*_{N_w} = 655089$	$S^*_{P_w} = 886$	$H^*_{P_w} = 2291$

Table 7.8: Escapement and harvest comparisons between correct and incorrect assumptions, where $p_N = p_P$ and costs are given by equation (7.17) with $m_{X_i} = 30$, $n_{X_i} = 1.3 \times 10^{-2}$, $c_i = 0$, $p_N = 70$ and $p_P = 10 \times p_N$. In this case the equilibrium harvest level for both prey subpopulations decline suggesting that some proportions of these prey should be conserved for the consumption of the predator, which is more valuable than the prey.

7.3 Adult and juvenile migrations with more than two subpopulations

In the previous section I discussed optimal harvesting strategies for a two-patch predator-prey metapopulation connected by adult and juvenile migration. In this section I extend the model to a predator-prey metapopulation consisting of more than two subpopulations. Many commercial aquatic population consist of more than two subpopulations. For example, Sockeye salmon, *Oncorchynchus nerka* in Lake Washington has five subpopulations (Quinn and Hendry, 1997). Other examples are red sea urchin, *Strongylocentrotus franciscanus*, and southern Australian abalone (genus *Haliotis*) which are reproductively connected among subpopulations (Shepherd, 1973; Shepherd and Brown, 1993; Quinn *et al.*, 1993). Authors who investigated harvesting strategies for stocks with multiple subpopulations include Hilborn (1985), Hilborn and Walters (1987), Quinn *et al.* (1993) and Tuck (1994). Most of these authors studied harvesting strategies using simulation techniques and they did not find analytic solutions. In contrast, Tuck (1994) found analytic solutions of optimal harvesting strategies for a general M patches single-species metapopulation and also considered the costs of harvesting, which depend on locations, explicitly. In this section, I extend Tuck's (1994) model to include predator-prey interactions in the metapopulation.

7.3.1 The model and its optimal escapements

Let us assume that prey and predator populations both occupy M different patches connected by the dispersal of their juveniles and the migration of the adults. The dynamics of the metapopulation is modelled by $2M$ coupled difference equations,

$$N_{i(k+1)} = \sum_{l=1}^{M} a_l m_{li} N_{lk} + \sum_{l=1}^{M} p_{li} F_l(N_{lk}) + \alpha_i N_{ik} P_{ik}, \tag{7.29}$$

$$P_{i(k+1)} = \sum_{l=1}^{M} b_l n_{li} P_{lk} + \sum_{l=1}^{M} q_{li} G_l(G_{lk}) + \beta_i N_{ik} P_{ik}, \tag{7.30}$$

where $\alpha_i < 0$, $\beta_i > 0$, $\sum_{l=1}^{M} a_{il} < 1$ and $\sum_{l=1}^{M} p_{il} < 1$, for $i = 1, 2, ..., M$. As in the two-patch case, $N_{i(k+1)}$ and $P_{i(k+1)}$ are the adult abundances of prey and predator subpopulation i in generation $k+1$ while $F_i(N_{ik})$ and $G_i(P_{ik})$ are the numbers of juveniles produced by prey and predator subpopulation i in generation k. Including harvesting and recalling that the escapement of prey and predator subpopulations i are given by $S_{N_{ik}} = N_{ik} - H_{N_{ik}}$ and $S_{P_{ik}} = P_{ik} - H_{P_{ik}}$, the dynamics of the metapopulation become

$$N_{i(k+1)} = \sum_{l=1}^{M} a_l m_{li} S_{N_{lk}} + \sum_{l=1}^{M} p_{li} F_l(S_{N_{lk}}) + \alpha_i S_{N_{ik}} S_{P_{ik}}, \tag{7.31}$$

$$P_{i(k+1)} = \sum_{l=1}^{M} b_l n_{li} S_{P_{lk}} + \sum_{l=1}^{M} q_{li} G_l(S_{G_{lk}}) + \beta_i S_{N_{ik}} S_{P_{ik}}. \tag{7.32}$$

Optimal harvesting strategies are found by maximising the net present value from harvesting all species from all patches, that is, by maximising

$$PV = \sum_{k=0}^{T} \rho^k \sum_{i=1}^{M} \sum_{X \in \{N,P\}} \Pi_{Xi}(X_{ik}, S_{Xik}) \tag{7.33}$$

subject to the state variable equations (7.31) and (7.32), with non-negative escapement less than or equal to the population size, where $\Pi_{Xi}(X_{ik}, S_{Xik})$ is given by equation (4.14). As in the two-patch models, the discounting factor is given by $\rho = \frac{1}{(1+\delta)}$.

Following the same method as in the previous section, optimal escapements for the prey and predator populations, $S^*_{N_i}$ and $S^*_{P_i}$, are found in their implicit expressions

$$\begin{aligned} \frac{p_N - c_{Ni}(S^*_{N_{i0}})}{\rho} &= \sum_{l=1}^{M} \left[\left(a_i m_{il} + p_{il} F'_i(S^*_{N_{i0}}) \right) \left(p_N - c_{Nl}(N_{l1}) \right) \right] \\ &\quad + \alpha_i S^*_{P_{i0}} \left(p_N - c_{Ni}(N_{i1}) \right) \\ &\quad + \beta_i S^*_{P_{i0}} \left(p_P - c_{Pi}(P_{i1}) \right), \end{aligned} \tag{7.34}$$

$$\begin{aligned} \frac{p_P - c_{Pi}(S^*_{P_{i0}})}{\rho} &= \sum_{l=1}^{M} \left[\left(b_i n_{il} + q_{il} G'_i(S^*_{P_{i0}}) \right) \left(p_P - c_{Pl}(P_{l1}) \right) \right] \\ &\quad + \beta_i S^*_{N_{i0}} \left(p_P - c_{Pi}(P_{i1}) \right) \\ &\quad + \alpha_i S^*_{N_{i0}} \left(p_N - c_{Ni}(N_{i1}) \right), \end{aligned} \tag{7.35}$$

for $i = 1, 2, ..., M$. These equations are the general form of the optimal escapement equation for a M-patch predator-prey metapopulation with adult and juvenile migrations. To obtain explicit expressions of the optimal escapements, $S^*_{N_i}$ and $S^*_{P_i}$, I assume that the costs of harvesting are negligible or independent of the population abundance and that there is no price difference between prey and predator. Furthermore I also assume that the recruitment production functions, F_i and G_i, are logistic as in (3.3) and (3.4). Using these assumptions, optimal escapements are found as

$$S^*_{N_i} = \frac{A_i \frac{2s_i}{L_i} \sum_{l=1}^{M} q_{il} + C_i B_i}{\Delta_i}, \tag{7.36}$$

$$S^*_{P_i} = \frac{B_i \frac{2r_i}{K_i} \sum_{l=1}^{M} p_{il} + C_i A_i}{\Delta_i}, \tag{7.37}$$

for $i = 1, 2, ..., M$, where

$$\Delta_i = C_i^2 - \left(\frac{2r_i}{K_i} \sum_{l=1}^{M} p_{il} \right) \left(\frac{2s_i}{L_i} \sum_{l=1}^{M} q_{il} \right), \tag{7.38}$$

$$A_i = \frac{1}{\rho} - r_i \sum_{l=1}^{M} p_{il} - a_i \sum_{l=1}^{M} m_{il}, \tag{7.39}$$

$$B_i = \frac{1}{\rho} - s_i \sum_{l=1}^{M} q_{il} - b_i \sum_{l=1}^{M} n_{il}, \tag{7.40}$$

and

$$C_i = \alpha_i + \beta_i, \tag{7.41}$$

provided $\Delta_i \neq 0$. Using the same method as in the previous chapters, we can obtain sufficient conditions for the metapopulation to have non-negative optimal escapements. The conditions are written in the following result.

Result 35 *(Sufficient conditions for positive escapements) Let $S^*_{N_i}$ and $S^*_{P_i}$ denote the optimal escapement from a predator-prey metapopulation given by equations (7.36) and (7.37). If A_i and B_i are negative, and C_i is non-positive with $C_i > max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}$, then*

Δ_i is negative, and S^*_{Ni} and S^*_{Pi} are positive.

To draw some conclusions about escapement comparisons between patches I use Lemma 10 in the previous section with additional definitions

$$x_{im} = r_i \sum_{l=1}^{M} p_{il} + a_i \sum_{l=1}^{M} m_{il} \tag{7.42}$$

and

$$y_{im} = s_i \sum_{l=1}^{M} q_{il} + b_i \sum_{l=1}^{M} n_{il}, \tag{7.43}$$

and, following Tuck (1994), I redefine and generalise the concept *relative exporter/ importer* and *relative source/sink* subpopulations in the following way.

A prey subpopulation i is called *a relative exporter (importer)* prey subpopulation if it exports (imports) a greater per capita number of larvae to the other prey subpopulations than it imports (exports), that is,

$$r_i \sum_{l=1}^{M} p_{il} > (<) \sum_{l=1}^{M} r_l p_{li}. \tag{7.44}$$

A prey subpopulation i has *a higher (lower) adult export survival* if

$$a_i \sum_{l=1}^{M} m_{il} > (<) \sum_{l=1}^{M} a_l m_{li}. \tag{7.45}$$

A relative exporter (importer) and *a higher (lower) adult export survival* are defined analogously for the predator population.

A prey subpopulation i is called *a relative source (sink)* prey subpopulation if it has a greater (lower) per capita larval production than that of the other subpopulations, that is,

$$r_i \sum_{l=1}^{M} p_{il} > (<) r_j \sum_{l=1}^{M} p_{jl}, \; \forall j \; j \neq i. \tag{7.46}$$

A prey subpopulation i has *a higher (lower) adult migration survival* if

$$a_i \sum_{l=1}^{M} m_{il} > (<) a_j \sum_{l=1}^{M} m_{jl}, \ \forall j\, j \neq i. \tag{7.47}$$

A relative source (sink) and *a higher (lower) adult migration survival* are defined analogously for the predator population.

In a special case, where all predator subpopulations are identical, we can compare optimal escapements if one of the prey subpopulations, say prey subpopulation i, has a higher adult export survival or is a relative exporter subpopulation, so that the total surviving individuals of that population, that is, x_i, is greater than the total surviving individuals of the other prey subpopulation. The comparison is summarised in the following result.

Result 36 *(Escapement comparison among subpopulations) Let prey subpopulation i be a relative source subpopulation or have a higher adult migration survival, so that the total surviving individuals of that prey subpopulation is higher than the total surviving individuals of the other prey subpopulation, that is, $x_i > x_j$, $\forall j\, j \neq i$. All other parameters of the prey and the predator are identical for both subpopulations. If $|\alpha| = \beta$, or if A_l and B_l are negative and $C > max\{\frac{2B_l}{K}, \frac{2A_l}{L}\}$ with $l = 1,.., M$, then*

1. $S^*_{N_i} > S^*_{N_j}$,
2. $S^*_{P_i} \leq S^*_{P_j}$.

Proof

1. Let $\Delta_{S_{N_{ij}}} = (S^*_{N_i} - S^*_{N_j})\Delta_i\Delta_j$. Following the proof of Result 8, we only need to show

$$\Delta_{S_{N_{ij}}} = y_m \left[\frac{2}{L} \left(C \left(C - \frac{2B}{K} \right) - \frac{4y_m(\frac{1}{\rho})}{KL} \right) \right] (x_{jm} - x_{im}) > 0, \tag{7.48}$$

which is satisfied by $x_{im} > x_{jm}$, since $\frac{2B}{K} \leq C \leq 0$. The second part can be proved analogously. □

Using the same method as above, we can compare the escapements in this section to escapements if we ignore the spatial structure of the population and incorrectly consider the predator-prey population to be an unconnected M-patch predator-prey population. In this case, the optimal escapements for the prey and predator subpopulation i are given by $S^*_{N_{iu}}$ and $S^*_{P_{iu}}$ in Appendix 7A with the growth rates r_{iu} and s_{iu}, and adult survival after migration, a_{iu} and b_{iu}, are given by

$$r_{iu} = \sum_{l=1}^{M} r_l p_{li}, \quad s_{iu} = \sum_{l=1}^{M} s_l q_{li}, \quad a_{iu} = \sum_{l=1}^{M} a_l m_{li}, \quad b_{iu} = \sum_{l=1}^{M} b_l n_{li}. \tag{7.49}$$

Result 37 *(Escapement Comparison to an unconnected M-patch predator-prey population). Let $S^*_{N_i}$ and $S^*_{P_i}$ denote the optimal escapement from a predator-prey metapopulation given by equations (7.36) and (7.37), and let $S^*_{N_{iu}}$ and $S^*_{P_{iu}}$ denote the optimal escapement if we incorrectly consider the metapopulation as a system consisting of M unconnected predator-prey populations. Let prey subpopulation i be a relative exporter* *(importer) prey subpopulation or have a higher (lower) adult export survival, so that* $r_{im} + a_{im} > (<) r_{iu} + a_{iu}$ *with the total surviving individuals of that prey subpopulation higher (lower) than the total surviving individuals of the other prey subpopulation, that is* $x_{im} > (<) r_{iu} + a_{iu}$*, with* $C^2 - \frac{2r_{iu}}{K_i}\frac{2s_{iu}}{L_i}$. *All other parameters of the prey and the predator are identical for both subpopulations. If* A_l *and* $B_l = B$ *are negative and* $C_l = C$ *is non-positive with* $C > max\{\frac{2B}{K}, \frac{2A}{L}\}$ *then*

$$S^*_{N_i} > (<) S^*_{N_{iu}} \text{ and } S^*_{P_i} \leq (\geq) S^*_{P_{iu}}.$$

The proof of this result is analogous to the proof of Result 9.

7.3.2 Numerical examples

In this section I present a numerical example to illustrate the analytical results in the previous section. In this example I use $M = 3$, that is, the predator-prey metapopulation consists of three different patches. Let us assume that the three subpopulations are connected by the migration of adults and the migration of juveniles, where the migration parameters for the prey and predator given by $p_{11} = p_{13} = p_{21} = p_{22} = p_{31} = p_{32} = p_{33} = 0.050$, $p_{12} = p_{23} = q_{ij} = 0.065$, $m_{11} = m_{13} = m_{21} = m_{22} = m_{31} = m_{32} = m_{33} = n_{ij} = 0.025$, $m_{12} = 0.050$ and $m_{23} = 0.035$. All other parameters for the three subpopulations are indistinguisable as in Section 7.2.2. As before, harvesting begins when the populations are at their equilibrium population size. Next, I determine the optimal escapement for the metapopulation by considering the costs of harvesting as negligible with the discounting rate $\delta = 10\%$. The results will be compared to the analytical results in the previous section. The effects of the inclusions of the costs of harvesting will also be explored.

Subtituting all the parameters above into equations (7.36) and (7.37) produces optimal escapements $S^*_{N_1} = 212000$, $S^*_{N_2} = 211432$, $S^*_{N_3} = 207157$, $S^*_{P_1} = 355$, $S^*_{P_2} = 356$ and $S^*_{P_3} = 358$. In this example $x_{1m} > x_{2m} > x_{3m}$ and as suggested by Result 36, the relations $S^*_{N_1} > S^*_{N_2} > S^*_{N_3}$ and $S^*_{P_1} < S^*_{P_2} < S^*_{P_3}$ are obtained. Hence, we should harvest the relative source prey subpopulation which has a higher adult migration more conservatively than the other prey subpopulations and we should harvest the predator living in the same patch with this relative source prey subpopulation less conservatively than the other predator subpopulations. If we incorrectly manage the population as a three-patch unconnected predator-prey population then we would over-harvest the relative source prey subpopulation while under-harvesting the other prey subpopulations and also we would under-harvest the predator living in the same patch with the relative source prey subpopulation while under-harvesting the other predator subpopulations (see Table 7.9). This rule is also observed when the costs of harvesting are included in the analysis (see Table 7.10).

7.4 Concluding Remarks

In this chapter I generalised the predator-prey metapopulation model introduced in Chapter 5 by including the migration of adults. The first section in this chapter considered only the migration of the adults and the second section considered both the migration of the adults and juveniles.

Optimal escapement properties for predator-prey metapopulation with adult-only migration are analogous to optimal escapements when only juvenile are able to migrate.

PPM	$S^*_{N_1} = 212000$	$H^*_{N_1} = 533944$	$S^*_{P_1} = 355$	$H^*_{P_1} = 1776$
	$S^*_{N_2} = 211432$	$H^*_{N_2} = 613080$	$S^*_{P_2} = 356$	$H^*_{P_2} = 1776$
	$S^*_{N_3} = 207157$	$H^*_{N_3} = 614127$	$S^*_{P_3} = 358$	$H^*_{P_3} = 1772$
	$S^*_{N} = 630589$	$H^*_{N} = 1761151$	$S^*_{P} =1069$	$H^*_{P} = 5324$
UPP	$S^*_{N_{1u}}=207157$	$H^*_{N_{1u}}=538798$	$S^*_{P_{1u}}=358$	$H^*_{P_{1u}}=1772$
	$S^*_{N_{2u}}=212000$	$H^*_{N_{2u}}=611920$	$S^*_{P_{2u}}=355$	$H^*_{P_{2u}}=1776$
	$S^*_{N_{3u}}=211432$	$H^*_{N_{3u}}=609900$	$S^*_{P_{3u}}=356$	$H^*_{P_{3u}}=1776$
	$S^*_{N_u} =630589$	$H^*_{N_u} =1760618$	$S^*_{P_u}=1069$	$H^*_{P_u}=5324$
WPP	$S^*_{N_w} =731601$	$H^*_{N_w} =1727302$	$S^*_{P_w} = 1254$	$H^*_{P_w}=5685$

Table 7.9: Escapement and harvest comparisons between correct and incorrect assumptions, where $p_N = p_P$ and costs of harvesting are negligible. PPM, UPP and WPP denote predator-prey metapopulation, unconnected predator-prey population and well-mixed predator-prey population, respectively.

PPM	$S^*_{N_1} = 212004$	$H^*_{N_1} = 533937$	$S^*_{P_1} = 359$	$H^*_{P_1} = 1784$
	$S^*_{N_2} = 211435$	$H^*_{N_2} = 613074$	$S^*_{P_2} = 359$	$H^*_{P_2} = 1783$
	$S^*_{N_3} = 207161$	$H^*_{N_3} = 614120$	$S^*_{P_3} = 361$	$H^*_{P_3} = 1780$
	$S^*_{N} = 630600$	$H^*_{N} = 1761131$	$S^*_{P} = 1079$	$H^*_{P} = 5347$
UPP	$S^*_{N_{1u}}= 207161$	$H^*_{N_{1u}}= 538791$	$S^*_{P_{1u}}= 361$	$H^*_{P_{1u}}= 1780$
	$S^*_{N_{2u}}= 212004$	$H^*_{N_{2u}}= 611913$	$S^*_{P_{2u}}= 359$	$H^*_{P_{2u}}= 1784$
	$S^*_{N_{3u}}= 211435$	$H^*_{N_{3u}}= 609894$	$S^*_{P_{3u}}= 359$	$H^*_{P_{3u}}= 1783$
	$S^*_{N_u} = 630600$	$H^*_{N_u} = 1760598$	$S^*_{P_u} = 1079$	$H^*_{P_u}= 5347$
WPP	$S^*_{N_w} = 731601$	$H^*_{N_w} = 1727300$	$S^*_{P_w} = 1254$	$H^*_{P_w}= 5686$

Table 7.10: Escapement and harvest comparisons between correct and incorrect assumptions, where $p_N = p_P$ and costs are given by equation (7.17) with $m_{X_i} = 30$, $n_{X_i} = 1.3 \times 10^{-2}$, $c_i = 0$ and price $p_X = 70$. Compared to escapements with negligible costs of harvesting, the escapements in this table are slightly higher, but the rule to conserve the relative esporter prey subpopulation that has a higher adult migration survival remains true.

For example, we should harvest a prey subpopulation with a high adult migration survival more conservatively than that with a lower adult migration survival. On the other hand, we should harvest the predator subpopulation living in the same patch with the prey subpopulation which has a high adult migration survival less conservatively than the other predator subpopulation. If both age-classes are able to migrate then there is a trade-off between high/low adult migration survival and sink/source properties of the populations.

Many commercially exploited aquatic populations are believed to be made of several separate subpopulations, for example the Sockeye salmon in Lake Washington which has five subpopulations (Quinn and Hendry, 1997). These populations are often reproductively connected (Shepherd and Brown, 1993; Quinn *et al.*, 1993). The two most common or typical structures of non-symmetric reproductive connection among subpopulations are the "uni-directional migration" structure, where migration occurs in one direction, and the "mainland-island" structure, where migration occurs only from one subpopulation (Tuck, 1994). Examples of populations with the first structure are a mollusc, *Aplysia californica*, along the coast off California and the Eastern king prawn, *Penaeus plebejus*, in New South Wales. These populations are well-known to migrate northward. The northern subpopulations recruit individuals from their spawners and also from the southern subpopulations (Penning, 1991; Gordon *et al.*, 1995). Examples of populations with the second structure are scallops (Orensanz *et al.*, 1991).

The third section in this chapter generalises the model for a predator-prey metapopulation with adult and juvenile migrations where the metapopulation consists of M subpopulations, incuding the uni-directional migration and mainland-island spatial structures as special cases. For these special cases, harvesting theory for an M-patch single-species metapopulation with uni-directional migration (Tuck, 1994), assuming that the migration of the juveniles occurs from subpopulation one to subpopulation two, from subpopulation two to subpopulation three, and so forth, suggests that if no juveniles are retained in the last subpopulation (subpopulation M) then we should harvest all individuals in the last subpopulation. However, in the presence of a predator, the optimal escapement for the last prey subpopulation need not be zero, unless $C_M = 0$ (see equation 7.36). In the presence of the predator, the theory in this chapter suggests that the optimal escapement for the last or the terminal prey subpopulation should not be greater than the optimal escapement for any other prey subpopulations, as long as the assumptions in Results 36 are satisfied.

Similarly, if the population has a mainland-island structure, for example all migration of juveniles occur from subpopulation one and no juveniles are retained in any subpopulation other than subpopulation one, the harvesting theory for an M-patch single-species metapopulation, assuming the costs of harvesting are negligible, suggests that we should harvest all individuals from all the subpopulations other than subpopulation one. Again, in the presence of the predator, the theory in this chapter suggests that the optimal escapement for prey subpopulation one should be bigger than the optimal escapements for any of the other subpopulations, as long as the hypotheses in Result 36 are satisfied. In the previous section I argued that adult-migration metapopulations are common. Among the examples are salmonid populations connected by straying individuals. Although the straying behaviour of these salmonids is well documented, it is still not certain whether the strays can successfully reproduce. Policansky and Magnuson (1998) believed that the connection among local populations by straying is responsible for the current dynamics and distributions of the salmonid populations. However, Tallman and Healey (1994) showed that a high level of straying does not necessarily reflect a high level of genetic migration among local populations. This can be interpreted to mean that the salmonids that stray do not necessarily successfully reproduce. The difficulty the strays have in reproducing may be due to the difficulty of the stray in finding a mate, because "stray only mated with stray through some unknown mechanism of mate choice" (Tallman and Healey, 1994). Another possibility is that interbreeding between stray and the local population does occur, but their offsprings are too weak to survive. For example, hybrids between Kokanee and Sockeye salmons have poor swimming capabilities (Taylor and Foote, 1991) which may lead to a problem in predator avoidance. For this reason, Tallman and Healey (1994) argued that strays do not reproduce successfully in nature.

The models in this chapter assume that the strays successfully reproduce. Future models of adult-migration predator-prey metapopulations may include the assumption that strays do not successfully reproduce and other relevant factors, such as different functional forms of the predator-prey interaction, environmental stochasticity, etc., to improve the understanding of optimal harvesting strategies for the metapopulations.

7.5 Appendices

Appendix 7A: General escapements formula for an unconnected M-patch predator-prey population

Consider an M-patch predator-prey metapopulation. If the only differences between patches are adult and juvenile migration parameters, and if we incorrectly manage the metapopulation as M patches unconnected predator-prey populations, assuming the costs of harvesting are negligible, then optimal escapements for subpopulation i ($i = 1, 2, ..., M$) are given by

$$S^*_{N_{iu}} = \frac{A_{iu}\frac{2s_{iu}}{L_i} + B_{iu}C_{iu}}{\Delta_{iu}} \tag{7.50}$$

and

$$S^*_{P_{iu}} = \frac{B_{iu}\frac{2r_{iu}}{K_i} + A_{iu}C_{iu}}{\Delta_{iu}}, \tag{7.51}$$

where

$$\Delta_{iu} = C^2_{iu} - \frac{2r_{iu}}{K_i}\frac{2s_{iu}}{L_i} \neq 0, \tag{7.52}$$

$$A_{iu} = \frac{1}{\rho} - r_{iu} - a_{iu}, \tag{7.53}$$

$$B_{iu} = \frac{1}{\rho} - s_{iu} - b_{iu}, \tag{7.54}$$

$$C_{iu} = \alpha_i + \beta_i. \tag{7.55}$$

In this case, r_{iu} and s_{iu} are the growth rate of the prey and predator subpopulation i measured after migration and given by $r_{iu} = \sum_{l=1}^{M} r_l p_{li}$ and $s_{iu} = \sum_{l=1}^{M} s_l q_{li}$. Similarly, a_{iu} and b_{iu} are adult survival after migration of the population i and given by $a_{iu} = \sum_{l=1}^{M} a_l m_{li}$ and $b_{iu} = \sum_{l=1}^{M} b_l n_{li}$.

Appendix 7B: General escapements formula for a well-mixed predator-prey population

Consider an M-patch predator-prey metapopulation. If the only differences between patches are adult and juvenile migration parameters, and if we incorrectly manage the metapopulation as a well-mixed predator-prey population, assuming the costs of harvesting are negligible, then optimal escapements for the metapopulation are:

$$S^*_{N_w} = \frac{A_w\frac{2s_w}{L_w} + B_wC_w}{\Delta_w} \tag{7.56}$$

and

$$S^*_{P_w} = \frac{B_w\frac{2r_w}{K_w} + A_wC_w}{\Delta_w}, \tag{7.57}$$

where

$$\Delta_w = C^2_w - \frac{2r_w}{K_w}\frac{2s_w}{L_w} \neq 0, \tag{7.58}$$

$$A_w = \frac{1}{\rho} - r_w - a_w, \tag{7.59}$$

$$B_w = \frac{1}{\rho} - s_w - b_w, \tag{7.60}$$

$$C_w = \alpha_w + \beta_w. \tag{7.61}$$

In this case, r_w and s_w are the average growth rate of the prey and predator population given by

$$r_w = \frac{\sum_{i=1}^{M} r_i \sum_{j=1}^{M} p_{ij}}{M}, \tag{7.62}$$

$$s_w = \frac{\sum_{i=1}^{M} s_i \sum_{j=1}^{M} q_{ij}}{M}. \tag{7.63}$$

The average adult migration survivals, a_w and b_w, are defined similarly. Predator-prey coefficients are taken as the average value $\alpha_w = \frac{\sum_{i=1}^{M} \alpha_i}{M}$ and $\beta_w = \frac{\sum_{i=1}^{M} \beta_i}{M}$. The carrying capacities for the prey and predator population are the total carrying capacities $K_w = \sum_{i=1}^{M} K_i$ and $L_w = \sum_{i=1}^{M} L_i$.

Chapter 8

Conclusion

In this thesis I have developed mathematical models of commercially exploited populations. I have addressed the question of how to harvest a predator-prey metapopulation. Rules about harvesting source/sink subpopulations, more/less vulnerable prey subpopulations and more/less efficient predator subpopulations were found. The costs of not harvesting the population properly, that is, if we did not realise that the population was a metapopulation, were also discussed.

Although in general it is impossible to include all relevant details in simple population models (Spencer and Collie, 1996), major factors need to be included in population modelling if the models are intended to give a better understanding of the behaviour and management of the populations. Among the major factors we need to include are biological interactions, such as predator-prey interactions, and the spatial structure of the population (Sih *et al.*, 1998; Czárán, 1998; Parma *et al.*, 1998; Hall, 1998).

Explicit study on optimal harvesting strategies for spatially-structured predator-prey populations has received little attention (Semmler and Sieveking, 1995; Shea *et al.*, 1998). In this thesis I simultaneously incorporated predator-prey interactions and spatial structure into population models and investigated optimal harvesting strategies of the populations. At first glance, examining spatial structure and biological interactions in exploited living marine resources will only complicate the management task (OECD, 1997). However, some authors have shown that this kind of study produces results which can be summarised in simple rules and used to improve the existing management of the resources (Tuck and Possingham, 1994; Pelletier and Magal, 1996; Brown and Roughgarden, 1997).

In nature, many populations have a discrete spatial structure (Quinn *et al.*, 1993; Quinn and Hendry, 1997; Brown and Roughgarden, 1997). The populations occupy several distinct habitat patches separated by a large distance (Frank, 1992). Metapopulation modelling has became a popular and important tool in understanding these kinds of populations and has contributed better alternatives in managing the populations (Tuck and Possingham, 1994; Lindenmayer and Possingham, 1996; Hanski and Gilpin, 1997). In Chapter 4 I developed predator-prey metapopulation models assuming the populations live in two different patches, and there are predator-prey interactions in both patches. Both the prey and predator populations are connected by the dispersal of the juveniles. I modelled the dynamics of the metapopulation using coupled difference equations.

Several assumptions have been made, including the assumptions that exploitation can be carried out selectively, for each species in each patch, and optimal harvesting strategies were sought by maximising the discounted net revenues generated from both species in two different patches. The predator-prey interaction was modelled in a very simple form, that is the classic Lotka-Volterra predator-prey interaction, so that an explicit form of the optimal escapements could be obtained. Following Tuck and Possingham (1994), interpretations of the resulting optimal escapements are facilitated by classifying subpopulations according to the per capita larval production, prey vulnerability and predator efficiency.

I call a prey subpopulation which has a greater (lesser) per capita larval production a relative source (sink) prey subpopulation. A prey subpopulation which exports more (less) per capita number of larvae than it imports is called a relative exporter (importer) prey subpopulation. A relative source (sink) and a relative exporter (importer) predator subpopulation are defined similarly. A prey subpopulation that is more (less) vulnerable to predation than the other prey subpopulation is called a more (less) vulnerable prey subpopulation. Furthermore, I call a predator subpopulation that is more (less) efficient in converting biomass, from the prey they eat into new predator individuals, than the other predator subpopulation as a more (less) biologically efficient predator subpopulation.

In the absence of predator-prey interactions, Tuck and Possingham (1994) investigated optimal harvesting strategies for a metapopulation and found the following rules of thumb:

TP 1 A relative source subpopulation should be harvested more conservatively than a relative sink subpopulation.

TP 2 If we use single-species metapopulation harvesting theory, a relative exporter subpopulation would be harvested more conservatively than if we use unconnected single-species population theory, while a relative importer subpopulation would be harvested more heavily.

TP 3 If we use single-species metapopulation harvesting theory, a relative source subpopulation would be harvested more conservatively than if we use well-mixed single-species population theory, while a relative sink subpopulation would be harvested more heavily.

Although, in general, rules derived from single-species harvesting theory are not necessarily true in harvesting ecologically interrelated stocks (Semmler and Sieveking, 1994), in this thesis, in the presence of predator-prey interactions, I established harvesting strategy rules for a predator-prey metapopulation as a generalisation of the harvesting strategy rules for a single-species metapopulation. Some properties of the escapements for a single-species metapopulation are preserved in the presence of predators, such as the strategies of how to harvest a relative source/sink and exporter/importer local population, similar to the rules of thumb TP 1 to TP 3 above. With two species an important issue throughout the thesis is which species is being harvested, or both, and if both what is the relative profit per unit biomass for each species. This adds another dimension to the problem not present in the single-species work.

Interpretations of the resulting optimal escapements are derived for two different cases. In the first case I assume that both species are harvested. In this case optimal escapements for the two species in both patches are obtained and they are independent of the time horizon considered. In the second case I assume that harvesting targets only one species, either the prey or the predator. In this case optimal escapements for the exploited species are functions of the abundance of the unexploited species. However, if there is no discounting then these escapements are equal for any period of exploitation. This is because when there is no discounting, profit in any period generated from escapements has exactly the same value to profit from the same escapements in any other period.

When harvesting targets both species, I generalised the concept of predator biological efficiency to include a delay in predator biomass conversion, a predator survival rate and a predator relative value to the prey in the following way. Assume that the the predator is m times more valuable than the prey. I defined predator economic efficiency as the predator biological efficiency weighted by the relative value of the predator, m. Furthermore, if the predator has a delay of σ in converting biomasses from eating the prey into predator's offsprings, assuming that the discounting factor is ρ, I defined discounted predator efficiency as the predator economic efficiency discounted by ρ^{σ}. Post-dispersal predator efficiency can take three forms: either as the predator biological efficiency discounted by the proportion of the surviving predators, the predator economic efficiency or the discounted predator efficiency.

If the post-dispersal predator efficiency is above a threshold, the two prey (predator) subpopulations are indistinguishable except for the prey migration rate and the cost of harvesting is negligible or independent of the stock abundance, then the first rule of thumb for harvesting a single-species metapopulation (TP 1) can be used to manage a predator-prey metapopulation. In other words, in this case, we should harvest the relative source prey subpopulation more conservatively than the relative sink prey subpopulation. Furthermore, we protect the relative source prey subpopulation directly with a higher escapement for the prey, and indirectly, with a lower escapement of the predator living in the same patch with this prey subpopulation. If, in addition, the relative source prey subpopulation is also a relative exporter subpopulation then incorrectly managing the metapopulation as an unconnected two-patch predator-prey population would over-harvest the relative exporter and source prey subpopulation while under-harvesting the relative importer and sink prey subpopulation, as long as the predator efficiency measured before and after dispersal is the same for both patches. This rule generalises the second rule of single-species metapopulation harvesting theory (TP 2). On the other hand, if the migrations between subpopulations are symmetric (no exporter/importer and source/sink hierarchy), and there is no biological variability except the vulnerability of the prey, then we should harvest the less vulnerable prey subpopulation more conservatively than the other prey subpopulation which is more vulnerable to predation. A special case occurs when there is no predation in one of the patches. This rule makes sense because it shows we should harvest the prey living in a refugial habitat (as reflected by low vulnerability) more conservatively than the prey living in the habitat where predation occurs. This is intuitive and agree with the belief of many fishery biologists that we should be more protective in dealing with critical subpopulations, such as those act as source subpopulations and those living in spawning and refugial areas (Hall, 1998).

Furthermore, if the prey vulnerabilities of the two prey subpopulations are exactly the same, but the predator efficiencies differ between the two predator subpopulations, then we should harvest the prey living in the same patch with the relatively more efficient predator more conservatively than the other prey subpopulation. This result suggests that if the predator has a high biological efficiency, then we should leave enough prey to sustain the predator population. This result is well known in harvesting theory for homogeneous predator-prey populations (Silvert and Smith, 1977; May *et al.*, 1979; Ragozin and Brown, 1985). However, with two patches here there can be a conflict between a high predator efficiency (also a high predator natural growth) and the source/sink or exporter/importer properties of the prey populations. A prey living in the same patch with a relatively more efficient predator might not need to be more protected than the other prey subpopulation if it is a relative sink or importer subpopulation.

Another complication arises when we consider the relative market prices of prey and predator. If the market value of the predator is large enough compared to the market value of the prey, then the equilibrium harvest for the prey can be negative. A negative harvest might be considered a "seeding strategy", where prey are put into the system from another patch. In many situations a seeding strategy is impracticable, so in this case an alternative strategy of imposing zero harvest, for the population which has a negative harvest, is the best that can be done. However, if it is possible to implement a negative harvest, numerical examples show that this strategy increases the total net revenue compared to a zero prey harvest strategy. Again, this is consistent with the belief of many fisheries managers that proper harvesting strategies which include biological interactions, such as predator-prey interactions, may have a positive effect on overall yield (Christensen, 1996). This is not surprising considering the "bioeconomic role" of the prey population which can be converted into a more economically valuable species through the predator-prey interaction.

The seeding or feeding strategy discussed here has another limitation, that is it assumes that the cost of seeding (negative harvest profit) equals the price of prey. This might not be true. In this case the optimal harvesting strategy is to apply a zero harvest until the prey abundance is higher than the prey optimal escapement. I also provide an alternative method for dealing with a negative harvest by considering a zero harvest as a constraint in the maximisation.

If harvesting only targets the prey (predator) species and if the only difference between the populations is prey (predator) migration parameters, assuming that there is no discounting, then the rules described above hold (that is, we should harvest the relative source prey (predator) subpopulation conservatively) regardless of the value of the predator efficiency. Hence, in this case, a high predator efficiency is not a necessary condition for this rule. Protecting a relative source subpopulation, by harvesting it conservatively, is intuitively sensible; protecting the source subpopulation means protecting the replenishment of the other subpopulation, so that the exploitation can be carried out sustainably (Mangel *et al.*, 1997; Gary *et al.*, 1998).

In Chapter 5 I looked at optimal harvesting strategies for predator-prey metapopulations which have different biological structures. The rationale is that I want to know the robustness of the results in Chapter 4 to the biological relationships between predator and prey. In Chapter 4 I assumed that predator-prey interactions occur in the juvenile life-stage of the population while in Chapter 5 I assumed that the interactions take place in the adult life-stage of the population. Predation was modelled in two different ways depending on the effect on the dynamics of the predator. The first model assumes that predation affects the predator survival while the second model assumes that predation affects the predator recruitment, which is probably more likely than the first one (this is because both models also assume that the predator has another main food and hence predation is likely to affect birth more than death).

The results in Chapter 5 show that the most significant rule, that we should harvest a relative source prey subpopulation more conservatively than a relative sink prey subpopulation, while we should also harvest the predator living in the same patch with the relative source prey subpopulation more heavily than the other predator subpopulation, is robust regardless of the biological structure of the population. If predation occurs in the adult life-stage and it affects the survival of the predator, then incorrectly managing the metapopulation as an unconnected two-patch predator-prey population would over-harvest the relative exporter and source prey subpopulation while under-harvesting the relative exporter and sink prey subpopulation. On the other hand, we might under-harvest the predator living in the same patch with the relative exporter and source prey subpopulation while over-harvesting the other predator subpopulation. Unlike the case where predation occurs in the juvenile life-stage of the populations, this result was derived without requiring equal predator efficiencies measured before and after migration.

In Chapter 4, when harvesting only targets one species, we only investigated optimal escapements for one period to go. These escapements may give useful information if there is no discounting, since in this case profit generated from any escapements in one period is the same as the profit generated from the same escapements in any periods (Agnew, 1982). However, they might be less informative if there is a non zero discounting rate. In Chapter 5 some properties of the optimal escapements with a non-zero discounting rate were explored. Numerical examples suggest that, when harvesting only targets the prey population, the rule to harvest the prey subpopulation living in the same patch with a relative source predator subpopulation may no longer hold. However, in some circumstances, we still harvest a relative source prey subpopulation more conservatively than a relative sink subpopulation.

The results mentioned above are derived by assuming the costs of harvesting are negligible. In the absence of the predators, Tuck (1994) argued that the analogous results for the single-species metapopulation harvesting theory would not change if the costs of harvesting are taken into account. However, in this thesis, that is in the presence of the predators, when the costs of harvesting are included in the analysis, several requirements need to be satisfied to obtain the same results. For example, let the prey subpopulation one be a relative source subpopulation and the costs of harvesting of the prey population be constant but different between patches. In this case we should still protect this relative source prey subpopulation in the two different ways explained above if: (1) the retention rate of the relative source prey subpopulation larval production, $p_{11}r_1$, is greater than the larval immigration rate from the other prey subpopulation, $p_{21}r_2$; (2) the larval emigration rate of the relative source prey subpopulation, $p_{12}r_1$, is greater than the retention rate of the other prey subpopulation larval production, $p_{22}r_2$; (3) the product of the predation rate, α_i, and the marginal net revenue, $p_N - c_{N_i}$, is the same for the two patches.

Furthermore, if the costs of harvesting for the predator are the same regardless of the location of the populations and the marginal net revenue from the relative source prey subpopulation is lower than, or equal to, the marginal net revenue from the relative sink prey subpopulation, then incorrectly managing the population as a well-mixed predator-prey population or an unconnected two-patch predator-prey population would over-harvest the relative source prey subpopulation while it would also under-harvest the relative sink prey subpopulation. The predator living in the same patch with the relative source prey subpopulation would be under-harvested and the predator living in the same patch with the relative sink prey subpopulation would be over-harvested. At the metapopulation level, the prey subpopulation would be over-harvested and the predator subpopulation would be under-harvested. As a result, the total profit from predator-prey metapopulation harvesting theory is greater than the total profit from strategies that ignore the true spatial structure of the populations.

The biological structure of the models in Chapters 4 and 5 was very simple, ignoring the age structure of the population. The model for each patch is described by a single variable representing the number of individuals and assumes that the offspring of the current population are immediately recruited to the adult population in the next period. In other words the population in each patch is a single homogeneous and well-mixed population. In reality, many exploited populations consist of several different age classes. In Chapter 6 I derived and discussed optimal harvesting strategies for the simplest form of age-structured predator-prey metapopulation, by considering that either the prey or predator juveniles may experience a delay in recruitment. I modelled the recruitment delay in two different ways. First, a recruitment delay experienced by juveniles can be related to the subpopulation in which they eventually recruit, this is referred to as "local population receptor delay model". Second, the delay may be related to their origin subpopulation, and the model is known as "parental recruitment delay model" (Tuck, 1994). I extended the basic predator-prey metapopulation model in Chapters 4 and 5 by including these two types of recruitment delay.

The results in Chapter 6 show that if there is no discounting rate then the rules of thumb of predator-prey metapopulation harvesting theory, such as escapement comparison between patches and escapement comparison to incorrect harvesting policies, hold regardless of the delays. However, if the discounting rate δ is not zero then the rule on how to harvest a relative source/sink and exporter/importer subpopulation is no longer necessarily true unless the delays of the two subpopulations are equal. If there is no exporter/importer prey subpopulation, escapements from the predator-prey metapopulation with parental delay recruitment are equal to escapements from the incorrect unconnected two-patch predator-prey population harvesting policy, regardless of the population delays, γ_i. In contrast, escapement differences between the predator-prey metapopulation with receptor delay recruitment and the incorrect unconnected two-patch predator-prey population do depend on the delays.

The results in Chapter 6 also show that if both subpopulations are identical then both models produce the same optimal escapements. However, if one of the subpopulations has a larger recruitment delay then results from both models are different. For example, if prey subpopulation one has a larger recruitment delay than prey subpopulation two, that is, $\gamma_1 > \gamma_2$, then the escapement for prey subpopulation one from the parental delay model is lower than the escapement from the receptor delay model and the escapement for prey subpopulation two from the parental delay model is greater than the escapement from the receptor delay model. Hence, incorrectly managing a predator-prey metapopulation having parental recruitment delay as a metapopulation with local population receptor delay mode, would under-harvest the prey subpopulation with larger recruitment delay, and over-harvest the prey subpopulation with the lower recruitment delay. On the other hand, it also would over-harvest the predator subpopulation living in the same patch with the prey subpopulation which has a larger recruitment delay, while the other predator subpopulation would be under-harvested.

The exploited population delay model discussed in Chapter 6 was originally developed by Clark (1976b). Botsford (1992) suggested that this model can be extended by considering the spatial structure of the population and larval dispersal between subpopulations. Tuck (1994) extended Clark's (1976b) model to incorporate spatial structure, dispersal and maturation delays. His major conclusion is that results from the delay model may differ depending on whether we assume the delay related to destination site or birth site of the dispersing larvae. In Chapter 6 we have extended Tuck's (1994) model by adding predator-prey interactions into the system. Our results show that Tuck's (1994) major conclusion is confirmed in the present of predator-prey interactions, if the predator "discounted" efficiency is greater than a certain threshold.

Tuck (1994) showed that an increase (decrease) in recruitment delay of a single species decreases (increases) the optimal escapement of that species. We have shown in Chapter 6 that it can also increase (decrease) the optimal escapement of the other species which interacts with the former, especially in the predator-prey metapopulation parental delay model. In other words, maturation delay differences in one species (e.g. prey species) influences the optimal escapement of the other species (e.g. predator species) even though the later species has a uniform delay, that is, the delays are equal in any patches. The result is not surprising, since delayed recruitment is considered one of the important factors in declining fish populations (Russ and Alcala, 1996; Hitchcock and Grattotrevor, 1997). The collapse of these fish populations may affect the abundance of other species which interact with them, as observed by Crawford and Dyer (1995) and Agnew (1997).

Chapter 7 considered predator-prey metapopulation models connected by adult migration, such as strays migration in the case of salmonids. Optimal harvesting strategies were investigated for two different models. The first model assumed that only the adults of the populations migrate and the second model assumed that both age-classes, the adults and juveniles, migrate. The results in Chapter 7 indicate that optimal escapements properties for predator-prey metapopulation with adult-only migration are analogous to optimal escapements with juvenile-only migration. For example we should harvest prey subpopulations with high adult migration survival more conservatively than those with lower adult migration survival. On the other hand, we should harvest the predator subpopulation living in the same patch with the prey subpopulation which has a high adult migration survival less conservatively than the other predator subpopulation. If both stages are able to migrate then there is a trade-off between high/low adult migration survival and source/sink properties of the populations.

Many commercially exploited aquatic populations are made up of more than two subpopulations, for example the sockeye salmon in Lake Washington has five subpopulations (Quinn and Hendry, 1997). These populations are often reproductively connected to each other (Shepherd and Brown, 1993; Quinn *et al.*, 1993). The two most common or typical types of reproductive connection among subpopulations are "uni-directional migration", where migration occurs in one direction, and a "mainland-island" structure, where migration occurs only from one subpopulation (Penning, 1991; Orensanz *et al.*, 1991; Gordon *et al.*, 1995). In Chapter 7 I have also generalised the model for a predator-prey metapopulation with adult and juvenile migrations assuming the metapopulation consists of M subpopulations, including the uni-directional migration and mainland-island spatial structures as special cases.

For the case of uni-directional migration, (Tuck, 1994) suggests that if no juveniles are retained in the last subpopulation (subpopulation M) then we should harvest all individuals in the last subpopulation. However, in the presence of a predator, the optimal escapement for the last prey subpopulation need not be zero, unless the biological predator efficiency in that patch is extremely efficient. In the presence of the predator, the result in this chapter suggests that the optimal escapement for the last or the terminal prey subpopulation should not be greater than optimal escapement for any other prey subpopulations.

Throughout the discussion in the thesis I assumed that prey and predator species operate at the same scales. In reality, they often operate at different scales. For example, the prey population may be patchily distributed but the predator may be completely well-mixed. Detailed investigation of optimal harvesting strategies for this system is not included in this thesis, however, many rules discussed in this thesis will also hold for this system, with some minor modifications. We still should harvest a relative source prey subpopulation (and also a relatively less vulnerable prey subpopulation) more conservatively than the other prey subpopulations. Conversely, in the case where the predator is patchily distributed with a well-mixed prey, then the rule to harvest a relative source predator subpopulation (and also a relatively more efficient predator subpopulation) more conservatively than the other predator subpopulation will also hold.

In this thesis, not all important economic and biological aspects of the resources are included. Future research should include other important economic and biological aspects of the resources and see how these aspects may influence the results derived here. For example, the last section in the last chapter assumed that the strays successfully reproduce. Future models of adult-migration predator-prey metapopulation may include an assumption that strays do not successfully reproduce as often observed in many real situations (Taylor and Foote, 1991; Tallman and Healey, 1994). Other relevant factors, such as different functional forms of the predator-prey interaction, environmental stochasticity, etc., need to be included into the models to improve the understanding of optimal harvesting strategies for the metapopulations. Other constraints could also be added in the optimisation process to ensure population size can be maintained above a certain level, which may be relevant in the case where harvesting only targets the prey population if the prey is also the main food for a protected predator species, as in krill and whales interaction (Krishna *et al.*, 1998).

Other limitations that I realise in this thesis include the following biological and economical aspects. Throughout the thesis I have assumed that dispersal rates are constant. In reality the dispersal rates may not constant. Many studies revealed that prey dispersal rate responses to predation. The prey may increase or decrease their movement rate depending to predation intensity (Wooster *et al.*, 1997). Dispersal can also be affected by the size of individuals, hence dispersal rate may differ between different age-classes (Roa and Bahamonde, 1993). Weather and tides may cause a huge variation in dispersal rate and recruitment success. In this case modelling optimal solutions would be best found using stochastic dynamic programming.

All results in this thesis are derived by assuming that predator-prey interactions are those of the Lotka-Volterra type. Although the Lotka-Volterra model has proved to be useful in deriving insights in studying predator-prey interactions, there are some objections from some scientists. One drawback of the Lotka-Volterra predator-prey model is what is known as the "paradox of enrichment", where an increase of nutrients may destabilise the predator-prey system (Hairston *et al.*, 1960; Rosenzweig, 1971; Brauer, 1976). Whenever this type of predator-prey interaction is applied to multi-species fishery management, a controversial conclusion may occur, that is, in some circumstances predator extermination is an "optimal" strategy (Flaaten, 1988; Yodzis, 1994). This situation is undesirable for conservation. Berryman (1992) and Ginzburg and Akçakaya (1992) pointed out that this paradox can be avoided by using different types of functional responses or trophic functions. The original Lotka-Volterra model uses what they call "prey-dependent" trophic function, that is, the rate of predator consumption on prey depends only on the density of the prey. They suggested that the paradox can be eliminated if we use the "ratio-dependent" trophic function, that is, the functional responses should be a function of the ratio of the prey and predator. Using this functional response, predator density will respond proportionately to changes in prey density (Arditi and Ginzburg, 1989; Arditi and Berryman, 1991; Ginzburg and Akçakaya, 1992). The work in this thesis could also be extended to consider this type of predator-prey systems, and assess the robustness of the results.

Economic assumptions in this thesis are simple. For example, all interpretations were derived with the assumption of a fixed market price of the harvested resource. A more realistic model may include the possibility that the market price depends on the amount of harvested biomass. In this case I suspect that demand elasticity may affect the optimal escapement. Another possibility to extend and improve the model in this thesis is to allow the resource to be owned by at least two bodies (countries), which is relevant for a highly migratory or transboundary stock (Brander and Taylor, 1998), and might be best tackled within a game theoretic framework rather than the dynamic programming approach used in this thesis. Other fishing controls, such as taxes, quotas and licences, could also be considered in future development of the models.

In this thesis I kept the models simple and general insights into how we should harvest a spatially-structured predator-prey population were obtained. In general, spatially-structured models can produce a better understanding of natural resource management (Dunning *et al.*, 1995). However, even the simplest spatially implicit models, such as the models in this thesis, may be difficult to parameterise and test – especially when we need dispersal parameters and recruit production functions, things which are difficult to measure (Conroy *et al.*, 1995; Spencer and Collie, 1996; Blondel and Lebreton, 1996). However, by recognising the metapopulation structure of the population, the basic rules of thumb I describe are still worthwhile guidance for managing the populations if one can identify which subpopulation is a relative exporter/importer, source/sink, more/less vulnerable or more/less efficient.

To conclude, the results presented in this thesis represents a start on a theory of harvesting complex stocks. Further understanding of optimal harvesting strategies for spatially-structured and biologically-interconnected populations is still needed. I hope that this work motivate others to extend and improve the models so that better management of our natural resources can be attained.

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