Optimal Harvesting Models For Metapopulations

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May 1994

Thesis submitted for the degree of
Doctor of Philosophy
in
The University of Adelaide
(Department of Applied Mathematics)

Awarded 1995

Contents

Summary

This thesis considers harvesting strategies for populations that show a distinct spatial structure. The exploited population is assumed to be a single species that is composed of two or more spatially homogeneous subpopulations, or local populations. The local populations are connected by the dispersal of individuals, and together the local populations form a metapopulation. Many species occur as metapopulations. The landscape over which a population ranges is rarely homogeneous. Due to environmental heterogeneity, local populations often experience different conditions and hence population characteristics vary between local populations. Metapopulation models give us the ability to model these situations. This thesis is the first to formally document optimal harvesting strategies for a harvested stock with a metapopulation structure. It is important to realise the effect of metapopulation structure on harvesting strategies, for both harvester financial viability and stock conservation.

Various metapopulation models are considered in the thesis and optimal harvesting strategies are then determined. Discrete coupled difference equations form the basis of the population dynamic modelling and methods such as dynamic programming and the method of Lagrange multipliers are used to determine optimal harvesting policies. We compare the optimal harvesting strategies of the local populations to obtain a rough guide to the relative harvesting intensity required for each local population. We also consider the effect on harvests of alternative strategies that incorrectly assume that

the metapopulation is spatially homogeneous. For example, the local populations may be managed as unconnected single populations, or the managing authority may believe that the metapopulation is a well-mixed single population.

In Chapter 1 we familiarise the reader with some of the concepts, definitions and notations used throughout the thesis. The first section outlines some of the problems associated with managing harvested populations. We then review the literature concerned with harvesting spatially unstructured populations, and introduce mathematical notation by solving the basic model of single population optimal harvesting. Metapopulation theory is then discussed. We define what a metapopulation is, and briefly describe some of the previous models and applications. We then review the harvesting models that include spatial structure and conclude with some of the model assumptions that hold throughout the thesis.

The basic model that we introduce in Chapter 2 considers a metapopulation consisting of two local populations where adults are sedentary and juveniles, e.g. larvae, migrate between local populations, joining the exploited adult spawning stock in the following generation. An economic framework is established and dynamic programming is used to maximise the discounted net revenue obtained from both local populations. Two equations are produced, one for each local population, that determine the optimal equilibrium escapement. Simplifying assumptions are then used to facilitate comparisons between the harvesting strategies of each local population, and comparisons between incorrect exploitation policies and the metapopulation theory.

The basic model is extended in Chapter 3 by including a delay in juvenile recruitment to the adult stock. Models are considered where the delay is related to the receiving local population and where the delay is associated with the parent local population. As before, comparisons are made between the harvesting strategies of the individual local populations. We also consider the harvesting effects of policies that are adopted with the false belief that the metapopulation is spatially homogeneous.

Chapter 4 assumes that adults can migrate between local populations. The first model that we consider assumes that only adults migrate, whereas the second model includes both adult and juvenile migration.

In Chapter 5 we model a metapopulation that includes an unharvested local population. Harvested populations may have sections of habitat preserved in a marine park or closed as a mechanism of harvest regulation and stock protection. We find optimal harvesting strategies for the exploited local population, and argue that our results can be used to determine the best choice of reserves if a reserve system is to be established that includes a harvested species.

In Chapter 6 we consider metapopulations with multiple patches. This extends the results of the two local population model presented in Chapter 2. The basic rules-of-thumb developed in Chapter 2 are generalised, and we briefly discuss generalisations of our other models.

Finally, the Conclusion summarises the main results of each chapter and suggests future directions of research that expand upon the work that we present in this thesis.

Declaration

I declare that this work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I also give consent to this thesis being available for photocopying and loan if accepted for the award of the degree.

Geoffrey N. Tuck
May 26, 1994

Acknowledgements

There are a number of people whose assistance has been invaluable in the preparation of this thesis.

I wish to thank Hugh Possingham for his supervision, enthusiasm and valuable insight over the duration of the thesis. I also thank Hugh for encouraging in me a greater appreciation of our natural heritage.

For my family, no thanks are enough for their love, guidance and understanding throughout my life. I am also indebted to my father for many helpful discussions and constructive criticisms of the work presented in this thesis.

Special thanks are extended to Anna Ting for her type-setting assistance. I am also sincerely grateful to Jemery Day and Ian Lundy for proof reading earlier drafts and for their assistance over the last few years.

For invaluable discussions and advice, I thank Alan Butler, Colin Clark, Karen Edyvane, Ray Hilborn, Scoresby Shepherd and Philip Sluczanowski.

In addition, I thank all of my friends who have made the last few years an enjoyable and more tolerable period of my life.

And finally, I would like to thank my wife Belinda for her love, patience and humour.

Chapter 1

Review

In this chapter we review the literature on single population optimal harvesting, define terminology and notation, and conclude with an outline of the assumptions of the models presented in this thesis. In the first section we review work on optimal harvesting models when the population considered is assumed to be spatially homogeneous. This is followed by an introduction to the notation and modelling format used throughout the thesis. This is achieved by solving the optimal harvesting problem for a single population using the methodology of Clark (1976; 1990), and a new method that we call the *escapement comparison method.* We then define what a metapopulation is, and discuss previous theoretical models of metapopulations and their applications. A review of the literature associated with harvesting spatially structured populations is presented and we conclude with a brief description of the model assumptions that we use in the chapters that follow.

1.1 Renewable resource exploitation

The management of the world's exploited natural resources has become an increasingly important research area since the turn of the century, when advancements in technology, mismanagement (or no management) and an ever expanding human presence began to push the earth's natural resources to, and beyond, ecological sustainability.

Bioeconomics, as its name suggests, deals with the economics of biological resources under human utilisation. This incorporates not only fisheries (a general term which includes invertebrate, as well as vertebrate, harvested marine or freshwater stocks), but also the management of exploited vegetation and terrestrial wildlife. This review concentrates on literature concerned with fisheries management; however many of the concepts and models can be related to other problems of natural resource management. A detailed review discussing all the enumerable papers in this growing field, including their assumptions and results, is obviously not possible due to temporal and spatial considerations. However, we attempt to give an overview of what has been achieved in the harvesting literature.

Why do our natural renewable resources need to be carefully regulated? Consider the exploitation of a new, unregulated fishery, i.e. it is an open-access, common-property resource. Fishers enter the unrestricted fishery and harvest the population which then provides a profit. This not only entices new fishers into the fishery, but the existing fishers use their profits to improve their harvesting ability. Thus, the amount of effort expended on catching fish increases. However, eventually it is possible that so much effort is put into the fishery that some fishers make a net loss and are forced to leave, causing a decrease in fishing effort. As Gordon (1954) shows, eventually fishing effort reaches an equilibrium, the *bionomic equilibrium*, where there is no net revenue accruing to the fishers, i.e. total revenue equals total costs. Thus the open-access, common-property fishery can lead to fishers making very little money, and subsequently overfishing the stock; an economically and socially unacceptable situation (Clark, 1990; Cocheba, 1990).

Now, rather than assuming no fishery regulation whatsoever, assume that there is a sole owner of the exploited stock. This fishery may no longer suffer from the *Tragedy of the Commons* (Hardin, 1968) described above, but as Clark (1973) shows, if the maximum growth rate of the fished population is less than the growth rate from capital invested elsewhere (the interest rate), then it can be optimal for the sole owner to harvest the fish stock to extinction. This, once more, is an unacceptable situation.

These examples are simplistic, but nonetheless informative, ideas about resource exploitation (for further discussion, see Clark (1990), Reed (1991) and Munro (1992)). The problems associated with ownership are further complicated by migratory species that cross international fishing zones or enter unregulated oceanic waters (Levhari and Mirman, 1980; Harden Jones, 1984; Hilborn, 1987).

Assuming that managers have some control over stock regulation, what can be done to ensure the financial survival of current fishers and future generations of fishers while also maintaining the existence of the harvested stock? This is the key question that fishery bioeconomics attempts to address. It is by no means an easy question to answer, as every fishery has its own special characteristics. Assumptions holding for one fishery may not be valid for another, even if the same species is being harvested (e.g different size limits and open seasons for sub-stocks of southern Australian abalone (Shepherd and Branden, 1991)).

The fisheries manager has various tools which may assist in the regulation of the fishery. These include controls on fishing effort such as limits on the number, size or type of vessels used. Controlling mesh sizes and net types or the location and time allowed to harvest are also used. These controls are designed to limit total catch, but may not reduce catch significantly and can lead to inefficient harvesting (Cocheba, 1990; Quinn *et al.*, 1994). Controlling effort is an input control, whereas introducing quotas on fish caught is an output control. One such quota is the total allowable catch (TAC) quota, where a limit is placed on the total legal catch of fish from all vessels in the fishery. Another is the individual transferable quota (ITQ), where a certain fraction of the total allowable catch can be bought and sold between fishers. Quota systems can lead to efficient cost reducing techniques, however problems with quotas include fishers discarding by-catch, enforcement of the quotas, and the possibility that a small number of fishers may become dominant in a fishery. They also rely on accurate forecasts of catch levels (see Sissenswine and Kirkley (1982), Clark (1990) and Cocheba (1990) for reviews).

The potential problems facing managers are obviously quite daunting. How are decisions made regarding the type of policy that should be adopted and how many fish should be caught? With such a complex system of interacting forces, it would be nice to have a simplified characterisation of reality which could provide a guide and an understanding of the original problem. This is where a *mathematical model* is useful. Mathematical models are an essential part of providing management advice. They can identify critical variables and processes and suggest predictions which can then guide further research. However, mathematical models can vary widely in their degree of simplicity and eventual usefulness. As has been pointed out by Fournier and Warburton (1989), a complex model may not out-perform a simpler one, and so the design of a constructive model is not a trivial task in itself.

Hotelling (1931) was one of the first authors to address the problem of the optimal exploitation of (exhaustible) resources over time. While not being directly related to fishery bioeconomics, his model structure and solution methodology, namely the calculus of variations, provided a framework for future bioeconomic modelling. The problems associated with open-access exploitation of common-property resources were first discussed by Gordon (1954) and the idea of sole ownership was realised by Scott (1955). Schaefer (1954) produced a dynamic model of the interactions between fish populations and human harvesting but did not find optimal policies over time. A complete analytical solution to the proposed models of Gordon, Schaefer and Scott was not achieved until Clark's (1973) paper, and the field has developed rapidly since then. Reed (1991) provides a detailed review of the papers of Hotelling, Gordon and Schaefer, while Clark (1990) describes the mathematical aspects of these models.

In 1954, Schaefer introduced a dynamic, differential equation model of fish population dynamics and harvesting. Continuous, deterministic, population dynamic models, such as Schaefer's, have been used by many modellers since. In general, the dynamics of these models is of the form,

$$\frac{dx}{dt} = F(x) - h(E, x), \tag{1.1}$$

where $x(t)$ is the population size at time t, $F(x)$ is a function representing the growth rate or productivity of the unharvested population and $h(E, x)$ represents the harvesting rate, a function of effort, E and abundance. If we let,

$$F(x) = rx(1 - x/K), \tag{1.2}$$

where r is the intrinsic growth rate, K is the equilibrium population size or "carrying capacity", and $h(E, x) = qEx$, where q is a constant called the catchability coefficient, then we have the "Schaefer model". Equilibrium population levels are found by setting $dx/dt = 0$ and solving for $x(t)$ and the corresponding equilibrium catch or yield can then be found as a function of effort.

If we assume that $h(E, x) = h$, a constant, then we can find the maximum sustainable yield, MSY. The point at which we harvest the maximum sustainable yield

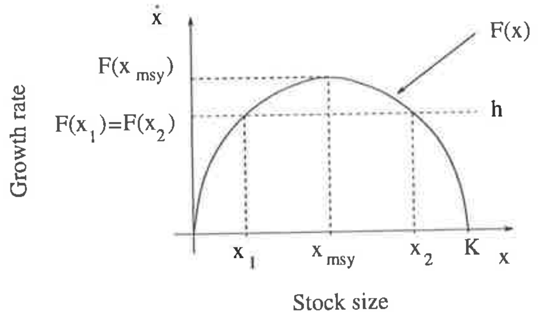

FIGURE 1.1: The maximum sustainable yield, MSY, is achieved at the point of maximum growth. The points x_1 and x_2 produce a smaller yield, and x_1 is actually unstable.

corresponds to the population's maximum sustainable growth rate. The maximum sustainable yield equals this maximum growth (Cocheba, 1990). Figure 1.1 shows the growth rate as a function of stock size. The two stock sizes, x_1 and x_2, represent the equilibria of equation (1.1) for harvests less than the optimal yield. In fact, if the initial population size is less than x_1, then the harvest is not compensated by growth, $\dot{x} = F(x) - h < 0$, and the population becomes extinct. A similar result is obtained for initial population sizes if the harvest is greater than growth for all x. If the initial population size is above x_1 and less than x_2, then $\dot{x} > 0$ and the population approaches x_2. Similarly, x_2 is approached from above if the initial population size is greater than x_2, as we now have $\dot{x} < 0$. Clark (1990) calls the population level at maximum sustainable yield "semi-stable", as growth from initial stock sizes less than x_{msy} will tend to zero, whereas those above approach x_{msy}. Maximum sustainable yield was the popular harvesting criteria of fisheries managers for many years; however it is now generally believed that this concept is too great a simplification to warrant consideration as a management objective (Clark, 1990). The main objection is that it is an unstable quantity derived from the maximisation of long-term yield, and so ignores the economics of the system. (It also ignores biological factors including inter/intraspecies dynamics, age-structure and population and environmental variability).

A more acceptable economic objective is to maximise a function of net revenue over time, thus incorporating both the benefits and the *costs* of harvesting. This was suggested by Hotelling in 1931 for exhaustible resources, where the total discounted net revenue or *total present value* was maximised. In the following section, Section 1.2, we briefly discuss the reasoning behind the present value formulation (in the discrete case). The continuous-time present value expression is given by,

$$PV = \int_0^\infty e^{-\delta t}(pqx(t) - c)E(t)\,dt, \tag{1.3}$$

where δ is the continuous rate of discount, p is the unit price of harvested stock and c is the unit cost of fishing effort, E. Equation (1.3) is subject to equation (1.1) with $h(E, x) = qEx$, $x(t) \geq 0$ and $h(t) \geq 0$. This problem can be solved using the Euler equation or by optimal control theory (for a detailed analysis see Clark and Munro (1975), and Clark (1990)), yielding an implicit equation for the optimal population level,

$$\delta = F'(x) - \frac{c'(x)F(x)}{p - c(x)}, \tag{1.4}$$

where $c(x) = c/qx$ is the unit cost of harvesting when the abundance is x. Equation (1.4) is known as "the fundamental equation of renewable resources" or a modified golden rule (MGR) equation (Conrad and Clark, 1987; Conrad, 1992; Munro, 1992).

If we assume that equation (1.4) has a unique solution, $x = x^*$, then the optimal strategy is to harvest as rapidly as possible if the stock level is above the optimal population, x^*, or to not harvest at all if below x^*. Specifically, the harvest strategy is,

$$h^*(t) = \begin{cases} h_{\max} & \text{if } x(t) > x^* \\ F(x) & \text{if } x(t) = x^* \\ 0 & \text{if } x(t) < x^*, \end{cases} \tag{1.5}$$

where $h_{\max}$ is the maximum harvest rate. The optimal population level, x^*, is frequently called the optimal *escapement*. The escapement represents the stock abundance that escapes capture, and is then able to contribute to future productivity. The "bang-bang" type behaviour of the approach path to equilibrium is called the "most-rapid-approach" path strategy.

The above model has been extended to include various economic and biological complexities. We describe some of these extensions here, including economic modifications, discrete-time models, age-structured, stochastic and multi-species models.

As Getz *et al* (1987) and Munro (1992) point out, closure of a fishery when the population is below x^* could be disastrous socially and economically. However, Clark *et al* (1979) show that the zero harvest or closure policy is a consequence of the restrictive assumption of perfect fleet malleability, i.e. that capital (e.g. vessels) can be moved to other fisheries with no financial loss. Indeed, if this assumption is relaxed, it is no longer optimal to have a zero harvest. The authors find an equilibrium stock level, x^*, defined by an equation similar to equation (1.4), except that replacing the "variable costs" term, c, is a "total costs" expression that includes both "fixed costs" (e.g. cost of vessel manufacture or purchase) and variable costs (e.g. fuel, wages). The path to the equilibrium shows "boom and bust" behaviour, with an initial capital investment (vessels are bought), depreciation, stock depletion and a recovery to x^* that coincides with a final smaller capital investment (see Clark and Lamberson (1982), Figure A1). Clark and Lamberson apply the model to the pelagic whale fishery, and Clark (1990) notes that fishery boom and bust behaviour has been observed in the real world in some circumstances. Further references on irreversible investment and non-malleability include Botsford and Wainwright (1985) and McKelvey (1985).

On a similar note, Clark (1990) considers the effects of nonlinearities in the cost function, and including a constant seasonal (or trip) set-up cost that is imposed for every harvest excursion (unlike an initial fixed cost investment, described above). Both of these extension can produce optimal harvesting strategies that suggest "pulse fishing", where it is not necessarily optimal to harvest in every season (or on every ground).

Clark and Munro (1975) derive equation (1.4) and also consider a linear model where the price and cost vary with time. This nonautonomous model uses optimal control theory to maximise the discounted present value and produces optimal harvesting equations similar to equation (1.4). They find the possibility of "blocked intervals", where, due to limits on harvest rates, we can not follow the optimal singular path, $x^*(t)$, and are forced to harvest at a minimum or maximum level for a certain time. The paper also discusses a nonlinear autonomous model, producing possible multiple equilibria which are approached asymptotically, unlike the most-rapid-approach policy seen for the linear case.

Clark and Kirkwood (1979) investigate the performance of two classes of vessels, brine and freezer trawlers, harvesting different stocks of prawns in the Gulf of Carpentaria, northern Australia. This model uses optimal control theory to maximise annual net economic revenue; thus within-year dynamics are of interest and so discounting is not included. The model predicts the optimal number of the two classes of trawlers that should be allowed entry into the fishery, as well as the prawn stocks that should be harvested, the opening date and the optimal switching time from banana prawns to alternative stocks. Features of the results include that a single fleet fishery should harvest one species of prawn or the other, and not both at the same time. In the two-fleet case, the results suggest that either one type of vessel or the other should be used, not a combination of the two.

In the preceding discussion we only considered continuous-time models. A disadvantage of continuous-time models is that the fished population is assumed to react immediately to harvesting and reproduction (growth). Analysis of age-structure, including delays and reproductive truncations, is not facilitated by the continuous-time frame of the models. As reproduction and harvesting often occur at distinct periods (e.g. breeding seasons and fishing seasons), discrete-time models can offer greater realism than continuous-time models (Horwood and Shepherd, 1981; Reed, 1983).

Continuous-time models use differential equations to describe the population dynamics. In discrete-time, difference equations are used. For example, the recurrence relation

$$x_{k+1} = F(x_k), \tag{1.6}$$

relates the population abundance in period $k+1$, given by x_{k+1}, to the abundance, x_k, of the previous period, k. The function $F(x_k)$ is called the stock-recruitment relation. An example of a stock-recruitment relation is Schnute's (1985) equation,

$$x_{k+1} = F(x_k) = \alpha x_k (1 - \beta\gamma x_k)^{1/\gamma}. \tag{1.7}$$

This form not only allows constant recruitment ($\gamma = -\infty$), but also incorporates many of the classic stock-recruitment relations, such as those of Beverton and Holt (1957) with $\gamma = -1$, Schaefer (1954) with $\gamma = 1$ and Ricker (1954) for $\gamma = 0$.

The discrete-time maximisation criterion analogous to the continuous-time present value expression, equation (1.3), is

$$PV = \sum_{k=0}^{\infty} \alpha^k \Pi(x_k, h_k), \tag{1.8}$$

where $\alpha = 1/1 + d$, is the discount factor and d is the periodic discount rate. The expression, $\Pi(x_k, h_k)$, is the net revenue in period k from a harvest of h_k, and is a function of the benefits and costs of harvesting. We do not go into the details of this model here as the full model is described in the following section.

Maximisation of equation (1.8) is achieved using a method analogous to integration by parts (Clark, 1990) or, in the finite horizon case, by dynamic programming. The equation that implicitly defines the optimal population level is,

$$\frac{1}{\alpha} = \frac{F'(x)(p - c(F(x)))}{p - c(x)}. \tag{1.9}$$

This equation is the discrete-time analogy of equation (1.4). We derive equation (1.9) in the following section. The optimal harvesting policy is the most-rapid-approach to the optimal population level x^*, as seen in the continuous case. This result depends on conditions involving $F(x_k)$ and the ability of the net revenue, $\Pi(x_k, h_k)$, to be separated into functions of state, x_k, and action, h_k. Models that have this property are called "myopic" (Sobel, 1981; Lovejoy, 1988).

The models discussed to this point have assumed that juveniles either immediately join the sexually mature or adult stock (in the continuous case), or do so in the following season (in the discrete case). However, it may take several years for juveniles to become sexually mature. For example, the abalone species *Haliotis laevigata* and *Haliotis ruber* mature after approximately 3 years (Shepherd and Laws, 1974), while the age at which 50% of the male American Pacific coast halibut become mature is estimated to be 8 years of age, while for females it is 13 years (St-Pierre, 1984). Other examples are described in Chapter 3. Clark (1976) models a maturation delay with the delay-difference equation,

$$x_{k+1} = \lambda x_k + F(x_{k-\beta}) \qquad 0 \leq \lambda \leq 1 \tag{1.10}$$

where x_k is the adult breeding population abundance, λ is the proportion of adults that survive in each period and $F(x_{k-\beta})$ represents recruitment with a delay of β years. Clark examines unharvested equilibria, stability conditions, and optimal harvesting strategies by maximising equation (1.8). A more detailed discussion of the model proposed by Clark can be found in Chapter 3, where we show that equation (1.10) approximates a more complex age-structured model (Beddington, 1978). Other papers that consider delay-difference equation population models include Goh and Agnew (1978), Bergh and Getz (1988) and Botsford (1992).

The above models have only considered the single variable x_k to represent the exploited population. This "lumped-parameter" approach ignores age-dependent factors such as length, weight, sex and reproductive capacity which all might affect optimal harvesting policies (Mendelssohn, 1978; Lovejoy, 1986). The main advantage of the lumped-parameter models is in their simplicity, as an age-structured model may have n-cohorts which require an n-dimensional state vector, not just a single variable. For models of this form, optimal harvesting behaviour typically has a two-age or bimodal form, where either a single age-class is partially or fully harvested, or an age-class is partially harvested to some optimal level and then fully harvested at a later date (Beddington and Taylor, 1973; Getz, 1980; Reed, 1980). Other models that incorporate age or size-structure include Deriso (1980), Horwood and Shepherd (1981), Reed (1983), Schnute (1985; 1987), while PDE models are considered by Botsford (1981), Botsford and Wainwright (1985), Murphy and Smith (1990) and Medhin (1992). Age-structure is discussed further in Chapter 3.

Variability is another important consideration. The models described so far have only considered deterministic dynamics, i.e. models that assume no environmental, population or system variability. However, uncertainty abounds in fisheries, whether it be in biological variables such as stock abundance, natural mortality and recruitment, or the nonbiological variables catch, price, fishing efficiency, or even in searching for fish. The environment also plays a significant role in catch and stock variability and adds to the difficulty in improving predictions (Walters and Collie, 1988).

One way of introducing stochasticity into a discrete model is to include a random variable, Z_k, in the stock recruitment relation of equation (1.6),

$$x_{k+1} = F(x_k, Z_k). \tag{1.11}$$

The stochasticity in equation (1.11) can be multiplicative, $F(x_k, Z_k) = Z_k f(x_k)$, or additive, $F(x_k, Z_k) = f(x_k) + Z_k$. The maximisation criterion used is analogous to equation (1.8), namely we maximise the *expected* discounted net revenue,

$$EPV = E\left[\sum_{k=0}^{T} \alpha^k \Pi(x_k, h_k)\right]. \tag{1.12}$$

Stochastic dynamic programming is commonly used to solve this problem. This iterative procedure is extremely useful for the numerical computation of optimal harvests; however in this case analytic results can also be found (Reed, 1979; Lovejoy, 1988; Clark, 1990). Once more, the optimal solution is to harvest as rapidly as possible until the optimal population level, x_s^*, is reached. Reed (1979) and Lovejoy (1988) investigate conditions under which the stochastic optimal population level, x_s^*, is greater than or less than the corresponding deterministic optimal population level, x_d^*. These authors find that the difference depends on the cost function and the stock-recruitment relation; however, for most realistic cases, $x_s^* > x_d^*$. This suggests that random fluctuations in the exploited population lead to more conservative harvesting strategies.

Other authors that have utilised stochastic dynamic programming include Walters (1981) and Smith and Walters (1981). They consider optimal harvesting policies when there is uncertainty regarding the form of the stock recruitment relation. The authors conclude that a probing or *actively adaptive* strategy, where escapements are deliberately altered, should form an integral part of managing a fishery. Mendelssohn (1978) considers a stochastic, multiple age-class model. Using stochastic dynamic programming he finds sufficient conditions for an optimal *age-at-first-capture* policy.

Stochasticity can also be incorporated into continuous-time models. For example, May *et al* (1978) and Ludwig (1980) model population dynamics with a stochastic differential equation where the stochasticity is applied to the stock-recruitment relationship. Maximising the expected discounted yield, neglecting costs,

$$EPV = E\left[\int_0^{\infty} e^{-\delta t} p h(t)\, dt\right], \tag{1.13}$$

Ludwig derives an optimal fixed escapement policy, as seen previously. He also examines the effect of various growth functions and different harvesting policies on alternative performance criteria, such as the coefficient of variation of the discounted yield and the expected time for the population to reach ten percent of the carrying capacity. For further discussions of stochastic, continuous-time problems in bioeconomics, the book by Mangel (1985) is recommended.

The effects of harvesting a species may not only impact the target species, but also have dramatic effects on associated species or ecosystems. For example, blue shark, *Prionace glauca*, is a significant by-catch of the Japanese longline harvest targeting bluefin tuna, *Thunnus macoyii*, in Tasmanian waters. The annual by-catch of blue shark has been estimated at more than 34 000, most of which are immature and subadult females. The effect on blue shark stock structure is not known. The impact is likely to be significant due to the typically low growth and reproductive rates of elasmobranchs (Stevens, 1992). In this fishery, the non-targeted species has little commercial value (the fins are taken). However, some fisheries target more than one species. For example, the northern Australian prawn trawlers harvest several species of prawn (Clark and Kirkwood, 1979). Harvested species may also be a major predator or prey species in the ecosystem (Mesterton-Gibbons, 1988; Strobele and Wacker, 1991). Thus, the interaction of harvested species with their community is likely to be extremely important. Multi-species models are employed in an attempt to determine optimal harvesting strategies and the effect of harvesting on species composition, distribution and abundance.

Multi-species models are more complex both in formulation and in mathematical analysis. Under simplifying assumptions, Clark (1990) shows that it is possible for one or more species to be harvested to extinction while another more productive or easily accessible species is "saved" for exploitation. Considering a deterministic, continuous model for the optimal combined exploitation of independent species, Clark is able to derive optimal harvesting equations; however the path to equilibrium is not clear. Similarly, the harvesting of dependent species with selective harvesting is also considered. Equations defining the optimal equilibrium solution are given and are a generalisation of the single-population case. The approach to equilibrium is conjectured, and although not optimal, the "most-rapid-approach" is suggested as a practical alternative to the unknown optimal approach. A more complex study can be found in Mesterton-Gibbons (1987; 1988) while Strobele and Wacker (1991) derive yield-effort curves and stability conditions when harvested species are mutualistic, competitive or form a predator-prey relationship.

We conclude the review at this point. The model descriptions have concentrated on fishery applications, however bioeconomic modelling can be applied to many other fields, including forestry (Reed, 1986), seaweed exploitation (Lee and Ang Jr, 1991) and elephant ivory harvesting (Basson *et al.*, 1991). As mentioned earlier, the field is a rapidly growing one and it has not been possible to describe all of the various applications of bioeconomic modelling here. A more detailed description of many of the models described here, and more, can be found in Colin Clark's book *Mathematical Bioeconomics*, which is highly recommended.

In the following section we explicitly derive the fundamental equation of renewable resources for a discrete-time model.

1.2 Optimal harvesting strategies for a single population

To introduce some of the ideas and notations used throughout the thesis, we briefly review Clark's (1973; 1976; 1990) model for the optimal exploitation of a single population.

1.2.1 The model

Consider an unharvested single species population that is spatially unstructured (or assumed to be spatially homogeneous). Assume that this unexploited population is governed by the following recurrence relation,

$$R_{k+1} = F(R_k), \tag{1.14}$$

where R_k is the population's abundance in period k, and $F(R_k)$ is the reproduction curve or stock-recruitment relation. This function determines the abundance in any period from the stock abundance in the previous period. If we assume that harvesting occurs before growth but directly after the population is "surveyed" then equation (1.14) becomes,

$$\begin{aligned} R_{k+1} &= F(R_k - H_k) \\ &= F(S_k), \end{aligned} \tag{1.15}$$

where H_k is the harvest taken from the population in period k and $R_k - H_k = S_k$ is called the escapement (the total stock that escapes capture).

Assume that the cost incurred from harvesting a unit of fish when the stock size is x is $c(x)$ (a decreasing function of x) and that harvested fish can be sold at a fixed price, p.

The net revenue from a harvest of H_k in period k is then,

$$\Pi(R_k, S_k) = \int_{S_k}^{R_k} (p - c(x))\, dx. \tag{1.16}$$

For a detailed derivation of equation (1.16) and alternative net revenue expressions, see Clark (1990).

Using the escapement, S_k, as the control variable, we maximise the present value of net revenue over T seasons, i.e. maximise

$$P.V. = \sum_{k=0}^{T} \alpha^k \Pi(R_k, S_k), \tag{1.17}$$

where $\alpha = 1/(1+d)$ is the discounting factor, d is the periodic discount rate or interest rate, and $\Pi(R_k, S_k)$ is the net revenue from a harvest of H_k in period k. The inclusion of a discount rate takes into account the fact that a harvest today is considered of more value than the same catch in the future. To explain the present value expression in more detail, consider the value in "today's" terms (the present value) of the net revenue, Π_k, obtained from a catch H_k in k years time, i.e.

$$P.V. = \frac{\Pi_k}{(1+d)^k}. \tag{1.18}$$

For example, a catch resulting in a net revenue of \$100 000 in 10 years time, is equivalent to a catch yielding a net revenue of \$38 554 today, if we assume a periodic discount rate of 10%. Thus, the stream of revenues, $\Pi_1, \Pi_2, \ldots, \Pi_T$, produces the present value expression of equation (1.17).

1.2.2 Derivation of the optimal harvesting strategy

Clark (1976; 1990) solves this problem using the recursive technique of dynamic programming and his results are presented here for comparison later.

Firstly, assign the value function, $J_T(R_0)$ as follows,

$$J_T(R_0) = \max_{0 \leq S_k \leq R_k} \sum_{k=0}^{T} \alpha^k \Pi(R_k, S_k). \tag{1.19}$$

The value function is the sum of all discounted net revenues up until season T maximised by an appropriate choice of the escapements S_k. The value function depends on the initial population size R_0.

From expression (1.19) we obtain Bellman's equation (Bellman, 1957),

$$J_{T+1}(R_0) = \max_{0 \leq S_0 \leq R_0} \Big(\Pi(R_0, S_0) + \alpha J_T(F(S_0)) \Big). \tag{1.20}$$

This expression states that the value function with time horizon $T+1$ is the maximum of the immediate returns in the first period plus the returns from future harvests if the population moves to $F(S_0)$ by an appropriate choice of S_0.

Consider first $T = 0$, i.e. we maximise the net revenue expression with no consideration of future generations,

$$\begin{aligned} J_0(R_0) &= \max_{0 \leq S_0 \leq R_0} \Pi(R_0, S_0) \\ &= \Pi(R_0, S_\infty), \qquad (1.21) \end{aligned}$$

where we have chosen S_∞ such that $p - c(S_\infty) = 0$. The value S_∞ is called the zero net profit stock level, and harvesting a population from R_0 down to S_∞ will produce the greatest profit. However, if $R_0 \leq S_\infty$ then the optimal policy is to not harvest at all. With negligible costs, $c(x) = 0$, we have $S_\infty = 0$, and we harvest all available stock.

If we consider next the $T = 1$ time horizon, then, using equation (1.21),

$$\begin{aligned} J_1(R_0) &= \max_{0 \leq S_0 \leq R_0} \Big(\Pi(R_0, S_0) + \alpha J_0(F(S_0)) \Big) \qquad (1.22) \\ &= \max_{0 \leq S_0 \leq R_0} \Big(\Pi(R_0, S_0) + \alpha \Pi(F(S_0), S_\infty) \Big). \qquad (1.23) \end{aligned}$$

This expression gives the profit over the first two periods in terms of the immediate profits acquired from a harvest using S_0 and the profits in the next period if the population moves to $R_1 = F(S_0)$. Maximising equation (1.23) by differentiating with respect to S_0 we obtain

$$0 = -(p - c(S_0)) + \alpha\big(p - c(F(S_0))\big)F'(S_0), \tag{1.24}$$

or,

$$\frac{1}{\alpha} = \frac{F'(S_0)\big(p - c(F(S_0))\big)}{p - c(S_0)}. \tag{1.25}$$

Equation (1.25) is called the fundamental equation of renewable resources and it implicitly defines the first period optimal escapement, S_0. The optimal harvesting strategy is an "all or nothing" type of policy. If the initial stock, R_0, is below the optimal escapement, S_0^*, then we do not harvest at all, and if it is above S_0^* then the harvest is $H_0 = R_0 - S_0^*$. Equation (1.25) holds for all time horizons $T \geq 1$ (Clark, 1976; Clark, 1990) and thus the optimal approach path is the most-rapid-approach to $S_0^* = S^*$. The analogous proof is shown in Chapter 2 for spatially structured populations. If $F(R)$ is concave and deterministic (Clark, 1971; Reed, 1979; Lovejoy, 1988) then once the stock is above S^* it will never fall below S^* again, and the equilibrium harvest is $H^* = F(S^*) - S^*$.

1.2.3 No costs analysis

If we assume that the cost of harvesting the stock is negligible, i.e. $c(x) = 0$, or that costs do not depend on the stock size, $c(x) = c$, a constant (for example, this may apply to some fisheries that harvest clupeids (Munro, 1992)) then equation (1.25) reduces to,

$$\frac{1}{\alpha} = F'(S^*), \tag{1.26}$$

where S^* is the optimal escapement. Assuming that $F''(S) < 0$ for all S then there will be at most one value of S^* such that equation (1.26) holds. For example, suppose the stock-recruitment relation is logistic,

$$F(S) = \delta S + rS(1 - S/K), \tag{1.27}$$

where δ is the proportion of the adult stock that survive per period, r is a population growth rate and K is a constant that causes density dependence in the per capita growth rate, then the optimal escapement is,

$$S^* = \frac{K}{2} - \frac{K}{2r}(1 + d - \delta), \tag{1.28}$$

with optimal harvest $H^* = F(S^*) - S^* \geq 0$. Note that if $1 + d - \delta > r$ then it is optimal to harvest the whole population, $S^* = 0$. This is a consequence of not including costs. When costs are included S^* is unlikely to be zero (depending on the cost function chosen) due to the high cost of harvesting a small population.

1.3 The escapement comparison method

In this section, we present an alternative method to derive the optimal harvesting equation, equation (1.25). The method, called the escapement comparison method, compares the present value derived from a currently administered escapement and an alternative escapement. In this way we are able to determine if, and under what circumstances, a switch in escapements is economically worthwhile.

Consider an unharvested single species population. As in the previous section, we model the population dynamics with the difference equation (1.14), i.e.

$$R_{k+1} = F(R_k). \tag{1.29}$$

Recall that R_k is the population's abundance in period k, and $F(R_k)$ is the reproduction curve or stock-recruitment relation. Including harvesting, equation (1.29) becomes,

$$\begin{aligned} R_{k+1} &= F(R_k - H_k) \\ &= F(S_k), \end{aligned} \tag{1.30}$$

where H_k is the harvest taken from the population in period k and $R_k - H_k = S_k$ is the escapement.

The net revenue from a harvest of H_k in period k is,

$$\Pi(R_k, S_k) = \int_{R_k - H_k}^{R_k} (p - c(x))\, dx, \tag{1.31}$$

as defined in the previous section.

Choose S_∞ such that $p - c(S_\infty) = 0$ and define $\Phi(R)$ as follows,

$$\Phi(R) = \int_{S_\infty}^{R} (p - c(x))\, dx. \tag{1.32}$$

The expression for $\Phi(R)$ represents the total net revenue obtained from harvesting a population from R down to the zero net profit level, S_∞. For $R \geq S_\infty$, $\Phi(R)$ is an increasing function of R, however, for $R < S_\infty$, costs from harvesting outweigh profits and so it is not optimal to harvest until the stock has recovered to a level such that $R \geq S_\infty$.

We wish to maximise the present value of net revenue, i.e. maximise

$$\begin{aligned} P.V. &= \sum_{k=1}^{\infty} \alpha^{k-1} \Pi(R_k, S_k) \\ &= \sum_{k=1}^{\infty} \alpha^{k-1} \Big(\Phi(R_k) - \Phi(R_k - H_k) \Big) \\ &= \sum_{k=1}^{\infty} \alpha^{k-1} \Big(\Phi(F(S_{k-1})) - \Phi(S_k) \Big), \end{aligned} \tag{1.33}$$

where $\alpha = 1/(1+d)$ is the discount factor. This present value expression differs from equation (1.17), as we now sum the discounted net revenues over infinite time, rather

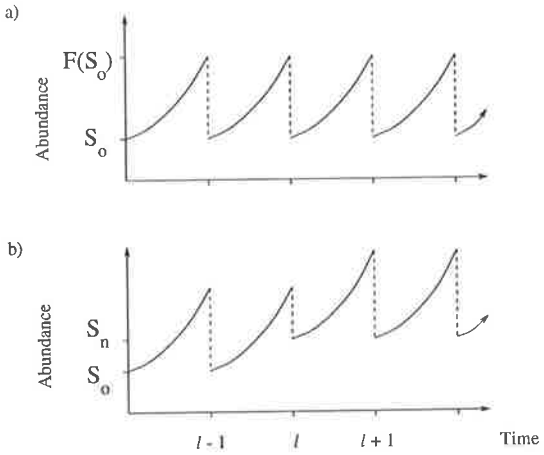

FIGURE 1.2: Figure a) shows the harvesting strategy employed if we remain harvesting at S_o. This is compared with the return provided by a switch in escapements to S_n, as shown in b). The escapement comparison method determines the circumstances under which the change is advisable.

than over a finite time. However, as we shall see, the optimal harvesting strategy does not differ.

Assume that we are currently using the escapement, S_o. We would like to determine under what conditions it is economically beneficial to move to a new escapement, say S_n (see Figure 1.2). If we remain using the old escapement, S_o, then $S_{k-1} = S_k = S_o$ for all k and we obtain the following as the present value of revenues over infinite time,

$$\begin{aligned} P.V.S_o &= \sum_{k=1}^{\infty} \alpha^{k-1}\Big(\Phi(F(S_o)) - \Phi(S_o)\Big) \\ &= \frac{1}{1-\alpha}\Big(\Phi(F(S_o)) - \Phi(S_o)\Big), \end{aligned} \tag{1.34}$$

noting that,

$$\sum_{k=1}^{\infty} \alpha^{k-1} = \frac{1}{1-\alpha}, \tag{1.35}$$

for $|\alpha| < 1$.

Consider the decision to change the escapement from S_o to the new escapement S_n

(S_n can be greater or less than S_o) at the period $k = l$. For $k < l$ the escapements are $S_k = S_o$ and for $k \geq l$ we have $S_k = S_n$. Assuming that $F(S_n) > S_n$ and $F(S_o) > S_n$ the present value obtained when the change in escapements is included is,

$$\begin{aligned} P.V.S_n &= \sum_{k=1}^{l-1} \alpha^{k-1}\Big(\Phi(F(S_o)) - \Phi(S_o)\Big) + \alpha^{l-1}\Big(\Phi(F(S_o)) - \Phi(S_n)\Big) \\ &\qquad + \sum_{k=l+1}^{\infty} \alpha^{k-1}\Big(\Phi(F(S_n)) - \Phi(S_n)\Big) \\ &= \frac{1-\alpha^{l-1}}{1-\alpha}\Big(\Phi(F(S_o)) - \Phi(S_o)\Big) + \alpha^{l-1}\Big(\Phi(F(S_o)) - \Phi(S_n)\Big) \\ &\qquad + \frac{\alpha^l}{1-\alpha}\Big(\Phi(F(S_n)) - \Phi(S_n)\Big), \end{aligned} \tag{1.36}$$

where we use,

$$\sum_{k=l}^{\infty} \alpha^k = \frac{\alpha^l}{1-\alpha}, \tag{1.37}$$

for $|\alpha| < 1$.

We would like to know when it is profitable to swap to the new escapement, i.e. when is $P.V.S_n > P.V.S_o$ or $P.V.S_n - P.V.S_o > 0$? Subtracting $P.V.S_o$ from $P.V.S_n$ we obtain the following,

$$\begin{aligned} P.V.S_n - P.V.S_o &= \alpha^{l-1}\Big(\Phi(F(S_o)) - \Phi(S_n)\Big) + \frac{\alpha^l}{1-\alpha}\Big(\Phi(F(S_n)) - \Phi(S_n)\Big) \\ &\qquad - \frac{\alpha^{l-1}}{1-\alpha}\Big(\Phi(F(S_o)) - \Phi(S_o)\Big) \\ &= \frac{\alpha^{l-1}}{1-\alpha}\Big[-\Phi(F(S_o)) + \Phi(S_o) + \alpha\Phi(F(S_n)) - \Phi(S_n) \\ &\qquad + (1-\alpha)\Big(\Phi(F(S_o)) - \Phi(S_n)\Big)\Big] \\ &= \frac{\alpha^{l-1}}{1-\alpha}\Big[\Phi(S_o) + \alpha\Phi(F(S_n)) - \alpha\Phi(F(S_o)) - \Phi(S_n)\Big] > 0. \end{aligned} \tag{1.38}$$

As $\alpha^{l-1}/(1-\alpha) > 0$ and the term in square brackets is independent of k (and independent of the time at which we swap escapements, l) we observe that,

$$\alpha\Phi(F(S_n)) - \Phi(S_n) > \alpha\Phi(F(S_o)) - \Phi(S_o), \tag{1.39}$$

for it to be profitable to swap escapements.

If we make the left hand side large enough by an appropriate choice of S_n we can ensure that this condition will always hold for the new escapement S_n and, once S_n is adopted, we will never need to change to a new escapement thereafter, i.e. we will have the optimal escapement.

Maximising $\alpha\Phi(F(S_n)) - \Phi(S_n)$ by differentiating with respect to S_n we obtain,

$$\frac{1}{\alpha} = \frac{F'(S_n)(p - c(F(S_n)))}{p - c(S_n)}. \tag{1.40}$$

This equation specifies the optimal new escapement, S_n, to choose when a swap is necessary. This equation is the same as that derived in the previous section, namely equation (1.25). A similar result holds when we require a temporary closure of the fishery, i.e. when $S_n > F(S_o)$.

The escapement comparison method is applicable where the preferred regulatory mechanism is a constant escapement policy, with the optimal approach to the escapement being the most-rapid-approach. Fixed escapement policies are not always optimal and the optimal approach path to the equilibrium optimal escapement is not always the most-rapid-approach (see Chapter 3 on maturation delays and Chapter 5 on harvest closures as examples). For this reason, the method has not been applied in the following chapters. However, the method may be fruitful in circumstances where managers wish to determine the optimal fixed escapement when the most-rapid-approach is not optimal, explicitly compare the benefits of various escapements, or determine under what circumstances temporary closures are profitable. We also suspect that the method will be able to identify policies that are locally stable, i.e. due to the costs of altering current or local harvesting strategies, it may be optimal, in some circumstances, to remain at the local solution. This is a new way of looking at the harvesting problem, akin to "evolutionary stable strategy" theory (Maynard Smith, 1982), and is an area of future research.

1.4 Metapopulations: definitions, theory and applications

In this section we introduce the concept of a metapopulation. We present definitions that we use throughout the thesis, and briefly review some of the historically significant metapopulation models to introduce notation and build a conceptual understanding of the field. We conclude this section with a description of some of the real world applications of the theory.

1.4.1 Metapopulations: what are they?

Due to factors such as habitat fragmentation and modification, and environmental variability in time and space, the population structure of a species is seldom homogeneous. Instead, it often exists in distinct patches of suitable habitat; it is patchily distributed. The patches that are occupied are called *local populations.* More specifically, a local population is an interacting collection of individuals occupying a single, geographically distinct patch. The frequency of interactions between individuals *within* a local population is considered greater than the frequency of interactions *between* local populations. Interactions include feeding, competition for resources, social behaviour and especially reproduction.

If a local population experiences occasional (infrequent compared to within patch dynamics) migration from one or more other local populations, then the set of connected local populations is called a *metapopulation.* According to Levins (1970), who is widely credited as being the first to formally define the term, a metapopulation is a "population of populations". Furthermore, Hanski and Gilpin (1991) define a metapopulation as a system of local populations connected by dispersing individuals.

Hansson (1991) describes three important factors that contribute to population dispersal. They are (a) economic thresholds, i.e. dispersal triggered by resource (e.g. food, water, mates) scarcity, (b) conflicts over resources, and (c) inbreeding avoidance. The author suggests that the first two factors are likely to cause a density-dependent response, while the third influences dispersal in a density-independent fashion. Some species exhibit density-independent dispersal (e.g. species of insect where dispersal is often weather regulated, and small mammals (Fahrig and Merriam, 1985)), while others (e.g. some mammals, locusts, snails) often show density-dependent dispersal (Hansson, 1991; and authors cited therein). The age and sex of dispersers often depends on the species and particularly on the reproductive behaviour of the species. Hansson (1991) cites evidence that immature individuals and mature males are frequently the dispersers in polygynous mammal species. Waser and Jones (1983) cite evidence suggesting that where the risk associated with emigration is less for adults than offspring (due to size or experience), some species show parental abandonment of territories in favour of their young (e.g. field voles, woodrats, Algerian sandrats and field cats (Waser and Jones, 1983; and authors cited therein)). Benthic marine organisms, such as abalone, urchins, barnacles, lobsters and some species of fish, often disperse through a pelagic larval life stage (Strathmann, 1974; Hill and White, 1990; Karlson and Levitan, 1990; Carr, 1991; Booth, 1992; Levin, 1993; Shepherd and Brown, 1993). Other marine invertebrates that lack a pelagic larval phase may disperse by drifting in the water column as juveniles or adults (e.g. some bivalves and gastropods (Martel and Chia, 1991)).

An important aspect of metapopulation theory is the concept of local population extinction and recolonisation. Namely, that patches can temporarily be unoccupied due to local population extinction, and be recolonised by the immigration of dispersing individuals at a subsequent date. (However, as Hanski and Thomas (1994) state, "any assemblage of local populations which are connected by migration may be called a metapopulation, regardless of the frequency of local extinctions"). This has lead to the theory's greatest area of application; the study of threatened species. Conservation biologists are frequently interested in the probability that a population will become extinct in a given period of time, and also the persistence time of a metapopulation, i.e. the length of time for all local populations in a metapopulation to become extinct (Hanski and Gilpin, 1991). These can be used as a guide to management and conservation. The theory can predict which local populations (or species) will be most adversely affected by say, habitat loss, increased fire frequency and the introduction of non-indigenous species.

There may be some ambiguity over local population identification, unless the environment is clearly fragmented into suitable and unsuitable habitat (for example, mallee habitat that supports fragmented populations of the threatened malleefowl of southern Australia (Day and Possingham, 1994)). High levels of migration between distinct patches can lead to metapopulation delineation being unnecessary (Hanski and Thomas, 1994). Conversely, if occupied patches are isolated due to a lack of migration, then they can be considered as entities unto themselves, i.e. single homogeneous populations. However, as subjective as the definitions appear to be, the existence of metapopulations is now widely accepted on both qualitative and quantitative grounds.

Extending the concept further, patches may include more than one-species. Within patch interactions between species may be significant. As such, the metapopulation definitions are easily extended to *metacommunities*. However, in this thesis we concentrate on single species dynamics, rather than multi-species dynamics. A comprehensive model of metacommunity dynamics and harvesting would no doubt be informative, but mathematically arduous. References for metacommunity modelling include Nachman (1991), Diekmann (1993) and Nisbet *et al* (1993) on predator-prey dynamics, and Case (1991) looks at interspecies competition and metapopulation dynamics.

1.4.2 Modelling

Levins (1969) study of pest control is generally regarded as the inaugural metapopulation model. Some earlier works had a similar notional flavour. These included: Andrewartha and Birch (1954), who emphasised the importance of spatial heterogeneity in population dynamics, MacArthur and Wilson (1967), for their island biogeography study, and den Boer (1968) who recognised that spatially structured populations can "spread the risk" of extinction caused by unstable local population dynamics over all local populations. However, Levins was the first to formalise the idea in conceptual and mathematical terms and in doing so, explicitly model the local dynamics of extinction and recolonisation.

The Levins Model

In this section we briefly describe the Levins model, outlining the basic assumptions and results. Consider a single species population that inhabits several indistinguishable, but geographically isolated, patches. A proportion of these patches are occupied by members of the species, defined by $p(t)$, and a proportion are unoccupied, $1 - p(t)$. This designation immediately assumes (a) that we model the presence or absence of the species in a patch rather than the abundance, and (b) that the fraction of occupied patches, a discrete variable, can be approximated by the continuous variable $p(t)$. The first assumption is valid for a species that, on colonisation, rapidly grows to the capacity of the occupied patch, whereas the second assumption is feasible for large metapopulations (large in the sense of numerous local populations; see the review by Day (1994)).

Assume that the rate of local extinction, e, is proportional to the fraction of occupied patches, $p(t)$. This assumes that all patches experience the same probability of extinction. The rate of colonisation, m, is assumed proportional to both the fraction of patches that are occupied, and the fraction that are not occupied; the more occupied patches the more possible migrants, and the greater the number of unoccupied habitats the greater the number of sites for migrants to settle. Assume that within patch interactions do not influence $p(t)$. Levins models the metapopulation dynamics with the deterministic, differential equation,

$$\frac{dp}{dt} = mp(1-p) - ep. \tag{1.41}$$

Equation (1.41) can be rewritten in logistic form,

$$\frac{dp}{dt} = (m-e)p\Big(1 - \frac{p}{1-e/m}\Big), \tag{1.42}$$

which, for $m \neq e$, has the solution,

$$p(t) = \frac{(e-m)}{\big((p_0 m + (e-m))/p_0\big)\exp\{(e-m)t\} - m}. \tag{1.43}$$

The initial proportion of occupied patches is given by p_0. Equation (1.41) has the solution,

$$p(t) = \frac{p_0}{mtp_0 + 1}, \tag{1.44}$$

for $m = e$ (Day, 1994). Thus, if the colonisation rate exceeds the extinction rate, the equilibrium solution is,

$$\hat{p} = 1 - e/m. \tag{1.45}$$

However, if the extinction rate is greater than the colonisation rate, then the metapopulation becomes extinct, $\hat{p} = 0$. Hence, the model predicts metapopulation persistence as long as the extinction and colonisation rates are either below, or above, some threshold level (Hanski, 1991). Hanski (1991) relates this to the geography of the metapopulation; explaining that extinction rates may decrease with habitat area and increase with isolation, thus possibly pushing the rates over the threshold persistence values.

Criticisms of the Levins model include the presence-absence description of the state space, that the model does not differentiate between patches (size, quality, separation, migration or extinction rates) or the biology of the organism (age, size-structure, reproductive behaviour). A further criticism is that the model is deterministic, whereas the dynamics of migration, extinction and recolonisation are inherently stochastic (Day and Possingham, 1994). However, the Levins model was the first to explicitly consider the dynamics of local populations; namely that local populations experience occasional migration, local extinctions and recolonisation.

Space limitation - Roughgarden and Iwasa

A model with applicability to marine systems is the space-limited population model of Roughgarden and Iwasa (1986). They assume that the larvae produced from several local populations combine to form a pelagic larval "pool". Larvae then move from the larval pool into the vacant space of the local populations. The model is suggested for sessile marine invertebrates that have a pelagic larval phase, such as barnacles.

For simplicity, we consider the two local population case. Let $R_i(t)$, for $i = 1, 2$, be the adult abundance of local population i. Unlike the Levins model, Roughgarden and Iwasa explicitly model the site abundances, rather than just the presence or absence of individuals. The abundance of the local populations increases with larval settlement and decreases with adult mortality. Consider local population 1,

$$\frac{dR_1}{dt} = c_1 L F_1 - u_1 R_1, \tag{1.46}$$

where $F_1 = A_1 - a_1 R_1$ is the free space in local population 1. The total area available is A_1, and a_1 is the effective average area occupied by a single organism. The accessibility of local population 1 to larvae is given by the constant c_1, and u_1 is the average adult mortality. The abundance of larvae in the larval pool is defined by L, which increases with the average fertility of the local populations, m_i, and decrease with settlement and larval mortality, v. The rate of change of the larval pool is given by the differential equation,

$$\frac{dL}{dt} = m_1 R_1 + m_2 R_2 - c_1 L F_1 - c_2 L F_2 - vL. \qquad (1.47)$$

Roughgarden and Iwasa (1986) consider the fixed points of the model by setting the rates of change to zero, deriving a quadratic expression, the zeros of which give the fixed points. The local stability of the fixed points depends on features of the parameters, including the existence of *source* patches, where the average number of larvae produced by a settled organism is larger than one, i.e. $m_i/u_i > 1$ or $m_i > u_i$, and *sink* patches, where $m_i < u_i$. The authors find that if all patches are sources, then there is a unique equilibrium set of abundances of adults and larval organisms that is globally stable. However, if some patches are sources and some are sinks, then multiple steady states are possible. It is also shown that uninhabited but suitable patches may require an initial input of larvae above a threshold level for the metapopulation to become established. This has important implications for foreign species introductions. A more explicit age-structured model is considered, leading to the possibility of oscillatory fixed points.

Improvements over the Levins model include the recognition that patches may differ in size, fertility rates, mortality rates and thus quality. A more detailed population structure is modelled, with adults contributing larvae to a common pelagic larval pool. The larvae then settle back into the local populations according to the available free space in the patches. The model is thus specifically aimed at populations with this particular life-history; a life-history with applications to sessile marine invertebrates with pelagic larvae. The authors suggest that further models should include stochastic migration and larval mortality, adult induced larval mortality (larvaphagy) and the incomplete mixing of larvae.

Breeding site limitation - Pulliam

Pulliam (1988) considers a discrete-time model that assumes that birth, death, emigration and immigration rates can differ between local populations. The model is used to show that migration from a *source* local population can maintain an otherwise nonsustainable *sink* local population. Here, a source is defined as a net exporter of individuals and a sink is a net importer.

For simplicity, Pulliam initially considers two patches, in which local population 1 is a source patch and local population 2 is a sink patch. The adult abundance in local population i at the end of period k is defined by R_{ik}. Adult survival is given by the constant P_A, and juvenile survival is defined by P_J. Thus, survival is not patch dependent; this is a possible criticism of the model. The breeding adults of local population i produce β_i juveniles in each generation. The difference equation model is,

$$R_{ik+1} = P_A R_{ik} + P_J \beta_i R_{ik} = \lambda_i R_{ik}, \tag{1.48}$$

where λ_i represents the finite rate of increase of local population i, without migration. Thus, if $\lambda_i > 1$ then local population i is a source, and if $\lambda_i < 1$ then local population i is a sink. For the sink population to persist, it requires net immigration, while the source requires emigration for stability (Day, 1994).

Assume that the source local population is limited by the number of available breeding sites, which number $\hat{n}$ in total. Individuals that obtain a breeding site are able to breed, while others can either migrate in search of alternative breeding sites, or remain as non-breeders. Pulliam shows that the equilibrium population size of the source is greater than the number of breeding sites. This suggests the existence of a surplus of non-breeding stock that can input members to surrounding sink habitats. With a connected sink, Pulliam shows that the equilibrium abundances at the source and sink are,

$$\begin{aligned} R_1^* &= \hat{n} && (1.49) \\ R_2^* &= \hat{n}\frac{(\lambda_1 - 1)}{(1 - \lambda_2)}, && (1.50) \end{aligned}$$

where $(\lambda_1 - 1)$ is the per capita surplus of local population 1, the source, and $(1 - \lambda_2)$ is the per capita deficit of local population 2, the sink.

Pulliam's model shows that sink populations can persist due to the migration of surplus individuals from adjacent source patches. Holt and Gaines (1993) cite examples where such a relationship exists for plants (Keddy, 1981; Kadman and Shmida, 1990), and suggest that populations of small mammals, such as cotton rats, prairie voles and deer mice, may also exhibit immigration reliant sink patches. Pulliam notes that management considerations should not discount the importance of source habitats, as a small source patch may be maintaining numerous surrounding sink habitats. Disturbance of the source patch may then lead to metapopulation extinction.

The model of Pulliam is extended by Howe, Davis and Mosca (1991) by including survival parameters that depend on the habitat of the local population, and pooled emigrants that settle evenly across the metapopulation (unlike the space-limitation settlement of Roughgarden and Iwasa (1986)). Their discrete-time model is,

$$R_{ik+1} = R_{ik}P_{Ai} + B_{ik}\beta_i P_{Ji}(1 - \gamma_i) - E_{ik} + \sum_{j \neq i} \frac{A_{jk}}{M - 1}, \qquad (1.51)$$

for M local populations. The annual adult and juvenile survival are given by P_{Ai} and P_{Ji}, respectively. The number of breeding adults in patch i is B_{ik} and is bounded above by $\hat{n}_i$. The proportion of migrating juveniles is given by γ_i, and so the second term represents the surviving sedentary juveniles. The third term is the density-dependent emigration from patch i, and is defined by all the the individuals that do not obtain a breeding site (Day, 1994). The fourth term represents the immigration from all other habitats into local population i, and A_{jk} are the emigrants of patch j.

For example, if juveniles do not migrate, $\gamma_i = 0$, and we consider two patches, then the immigrants of one patch are the emigrants of the other, and so we have,

$$R_{1k+1} = P_{A1}R_{1k} + P_{J1}\beta_1 B_{1k} - E_{1k} + E_{2k} \tag{1.52}$$

$$R_{2k+1} = P_{A2}R_{2k} + P_{J2}\beta_2 B_{2k} - E_{2k} + E_{1k}. \tag{1.53}$$

The authors consider the fixed points of the system, deriving equilibrium total population sizes, and find similar sink persistence results to those of Pulliam. However, if $\gamma \neq 0$, then under some circumstances the metapopulation can become extinct.

We do not go into detail with any more of the theoretical metapopulation models, as the main objective of this section is to familiarise the reader with the concepts, notation and basic modelling framework that has been used. Numerous other papers consider extensions of the models discussed here, or include other metapopulation features. Examples include, the "rescue effect" (Brown and Kodric-Brown, 1977; Hanski, 1982), where high levels of immigration depress extinction rates, and the "propagule rain" concept of Gotelli (1991), where local populations experience recolonisation from say, a seed bank or possibly a mainland source. Stochastic models are considered by several authors including Richter-Dyn and Goel (1972), Hanski (1983), Chesson (1984), Harrison and Quinn (1989) and Verboom *et al* (1991a). Models have also been developed that incorporate local population size-structure, i.e. patches have abundances that are either high, intermediate or low, and coupled differential equations are used to model the dynamics (Hanski, 1985; Hastings, 1991).

1.4.3 Areas of application

The main area of application of metapopulation models has been in conservation biology. Due to increasing habitat fragmentation and modification (most noticeably terrestrial), the habitat over which some species may have once ranged has reduced dramatically. These species are now confined to sparse patches of suitable habitat. It is well recognised that a reduction in habitat reduces species persistence, and the management of remnant patches then becomes of great importance for species conservation. This is especially evident for species that ranged widely across a once homogeneous environment that is now a fragmented landscape. These species, now confined to scattered refugia, may not be well adapted to migration, or at least more susceptible to mortality in the migratory transition (Hanski, 1991; Verboom *et al.*, 1991a).

As mentioned, the importance of maintaining remnant patches (especially source patches (Pulliam, 1988)) then becomes a primary concern. As a guide to management, models have been developed that investigate mean times to extinction (Richter-Dyn and Goel, 1972; Harrison and Quinn, 1989; Verboom *et al.*, 1991a), and the probability of extinction over a given period (Menges, 1990; Lacy and Clark, 1990; Boyce, 1992; Burgman *et al.*, 1993; Possingham *et al.*, 1994). These models are commonly called Population Viability Analysis models. Detailed population biology (birth, death, age-structure, migration), habitat structure (patch size, quality, separation) and environmental processes (seasons, catastrophes such as fire, drought or flood) can be built into the models to determine the effects of various management policies, including variations in fire burning regimes or patch removal, on the probability of extinction.

In Table 1.1 we list some of the organisms to which the metapopulation concept has been applied. An interesting feature is the few marine applications of the theory. This may be due to the more noticeable terrestrial effects of habitat fragmentation and

Organism	Reference
Plants	Hanski (1982)
	Collins and Glenn (1991)
Furbish's Lousewort	Menges (1990)
Mites	Walde (1991)
Butterflies	Harrison *et al* (1988)
	Hanski and Thomas (1994)
Milkweed Beetle	McCauley (1989)
Bush Cricket	Kindvall and Ahlen (1992)
Red-spotted Newt	Gill (1978)
Pool Frog	Sjorgen (1991)
Natterjack Toad	Sinsch (1992)
Spruce Grouse	Fritz (1985)
Forest Birds	Van Dorp and Opdam (1987)
Java Hawk Eagle	Thiollay and Meyburg (1988)
Spotted Owl	Lamberson *et al* (1992)
	Harrison *et al* (1994)
	LaHaye *et al* (1994)
European Nuthatch	Verboom *et al* (1991b)
Sooty Shearwater	Hamilton and Muller (1993)
Malleefowl	Day and Possingham (1994)
Pika	Smith (1974; 1980)
White-footed Mouse	Fahrig and Merriam (1985)
Eastern Chipmunk	Henderson *et al* (1985)
Shrew	Peltonen and Hanski (1991)
European Badger	Verboom *et al* (1991a)
Monk Seal	Durant and Harwood (1992)
Mountain Brush-tail Possum	Lindenmayer and Lacy (1993)
Greater Glider	Possingham *et al* (1994)
Copepods	Kurdziel and Bell (1992)
Sea Urchin	Karlson and Levitan (1990)
Red Sea Urchin	Quinn *et al* (1994)
Crown-of-thorns Starfish	James and Scandol (1992)
	Scandol and James (1992)
Abalone	Shepherd and Brown (1993)
Sea Hare	Pennings (1991)

TABLE 1.1: Organisms that are believed to have a metapopulation structure or that have been modelled using metapopulation theory.

heterogeneity. The consequences of agriculture, forestry, roads and human habitation have an obvious and dramatic effect on the terrestrial landscape, with remnant patches often remaining in road-side verges, small and scattered reserves, and inaccessible or economically unproductive land. Marine systems have been spared much of this broad scale destruction; however, pollution and exploitation are having profound effects on populations and are possible causes of habitat fragmentation (McGuiness, 1990). The marine environment, just as the terrestrial, is not homogeneous in its natural state. Differences in habitat suitability (rocky shore, crevices, seagrass beds, temperature, salinity, food availability, tidal fluctuations, upwellings, gyres, sunlight, turbidity) can cause variations in population structure in both time and space.

Many marine organisms are threatened with extinction. These include species that are of some commercial value (e.g. whales (Clark and Lamberson, 1982)) and others that are threatened due to the introduction of foreign species. Marine populations can benefit from the application of metapopulation models, for both threatened species management and commercial management.

1.5 Harvesting spatially structured populations

The spatial heterogeneity of marine populations has been recognised for some time now (Beverton and Holt, 1957). However, models of harvest dynamics have concentrated on stocks that are either unit stock based, i.e. a single homogeneous stock, or several stocks that are reproductively isolated and mix at the point of harvesting (e.g. salmon of northern America, (Hilborn, 1985)), but are not connected by the transfer of individuals.

The first section of this chapter discussed homogeneous stocks. Models that recognise the discrete stock structure of harvested populations include Ricker (1958), Paulik *et al* (1967) and Hilborn (1976; 1985). Ricker and Paulik *et al* use deterministic models to consider optimal harvesting rates that maximise sustained yield. Both authors show that yields from a non-selective fishery are less than if the stocks can be managed on an individual basis. Furthermore, employing an equal harvest rate across all stocks may exterminate one or more of the less productive populations.

Hilborn (1976) considers two reproductively isolated stocks of salmon with population dynamics defined by the Ricker stock-recruitment model,

$$R_{k+1} = R_k \exp(\alpha(1 - R_k/\beta)), \tag{1.54}$$

where R_k is the population abundance in period k, α is a measure of productivity and β is the unharvested equilibrium population size. The annual average yield is maximised using stochastic dynamic programming. To facilitate numerical calculations, the abundance is classified into twenty stock levels. Eighteen harvest rates and ten stochastic deviations from the Ricker curve are considered. Optimal non-equilibrium harvest rates are determined as a function of the stock abundances for different combinations of the parameters α and β. Under non-equilibrium conditions, Hilborn (1976) concludes that fixed escapement policies are not always optimal (in fact, only when the stock parameters are equal, implying a uniform stock, is a constant escapement optimal). Surprisingly, if one of the stocks is depleted, results suggest that the mixed stock should be harvested at a rate higher than if both stock levels are equal.

It may not always be possible to differentiate between stocks, and so estimates of individual stock abundance may not be forthcoming. This scenario is considered by Hilborn (1985). Monte-Carlo simulation is used to maximise average annual yield over 30 years for a mixed-stock fishery comprising ten discrete stocks. The population dynamics of the stock is given by a stochastic Ricker equation, namely equation (1.54) multiplied by $\exp(\omega)$, where ω is a normally distributed random variable with mean zero and an input variance. The author considers three policies: constant escapement, fixed harvest rate and fixed constant yield, and their effect on annual yield, average natural logarithm of catch (an estimate of declining marginal value from increased catch) and the coefficient of variation of the annual catch. The productivity of the stock and year-to-year natural variation of the stock is varied. Features of the results include that a fixed escapement policy appears to be sub-optimal for maximisation of the natural logarithm of catch. However, a fixed escapement policy is optimal for the maximisation of average annual yield when population productivities vary, but natural variation is perfectly correlated. There is also a trade-off between average yield and yield variability; with constant escapement policies producing larger coefficients of variation than either fixed harvest rate or constant harvest policies.

These papers have recognised that stocks are not homogeneous, as harvested populations are often composed of several distinguishable stocks. However, the papers assume that there is no migration between the stocks, and as such, they are reproductively isolated. We now consider the (rather limited) literature that assumes that there is migration between stocks.

Hilborn and Walters (1987) consider stock and fleet dynamics when harvesting six spatially distinct stocks of southern Australian abalone. They use the difference-equation technique of Deriso (1980) and Schnute (1985) to simulate stock dynamics, and assume that fishers allocate effort to each stock to maximise the value of the catch. Simulations consider the development of the fishery from a virgin state. Results show that catch rates can remain high while each stock is gradually fished down, until total abundance has dropped considerably. Catch rates then fall and the stock recovers. Their analysis only considers discrete stocks; however, they suggest that if migration between stocks is evident, then density independent movement can be incorporated into the Deriso-Schnute recruitment expression, R_t, using a spatial transition matrix.

Recruitment becomes

$$R_t = P_r G^*, \tag{1.55}$$

where $P_r = [p_{ij}]$ is the transition matrix, components of which give the probability of a successful migration from area j to i, and G^* is the area-specific recruitment. This is analogous to the method employed in this thesis.

Clark and Mangel (1979) consider a fishery that harvests stocks that form surface schools. The surface schools interact with an unharvested subsurface (or geographically distinct) population. Yellowfin tuna, *Thunnus albacores*, often form surface schools that associate with marine mammals (e.g. porpoises) or floating debris. Evidence suggests that a population of subsurface tuna exists, with (unknown) interchange between the stocks. The authors consider two models of surface population dynamics. The first assumes that the equilibrium biomass of the surface school is dependent on the subsurface stocks, the other model assumes that it is independent. For brevity, we consider the first case (Clark and Mangel's model A). Let $R_1(t)$ be the total surface stock abundance (of all K schools) at time t. The surface stock increases with immigration from the subsurface population, and decreases with emigrating tuna and harvesting. The population is modelled with the deterministic differential equation,

$$\frac{dR_1}{dt} = d_{21}R_2 - d_{12}R_1 - Y(E, R_1), \tag{1.56}$$

where, $R_2(t)$, is the number of tuna in the subsurface stock at time t, d_{21} is the intrinsic schooling rate, d_{12} is the instantaneous rate of movement from the surface to subsurface schools, and the yield, Y, is a function of effort, E, and surface school population size.

The subsurface stock increases with density-dependent growth (given by the Schaeffer logistic model) and disassociation from the surface stock, and decreases with exchange to the surface stock,

$$\frac{dR_2}{dt} = rR_2(1 - R_2/\bar{R}_2) - d_{21}R_2 + d_{12}R_1, \tag{1.57}$$

where r is the intrinsic growth rate and $\bar{R}_2$ is the carrying capacity. The authors consider the equilibrium behaviour of the system by setting the rates of change to zero, and show that if the intrinsic schooling rate is less than the intrinsic growth rate, $d_{21} < r$, then the surface fishery persists for any fishing effort. However, if $d_{21} > r$ then extinction is possible if effort is excessive.

The authors' model that assumes that the surface school's unharvested equilibrium is independent of the subsurface stock (Clark and Mangel's (1979) model B) shows more complicated behaviour (including bifurcations) and is not discussed here. Thus, these models explicitly assume spatial segregation of a single species population, with differential stock dynamics that includes immigration and emigration between populations. However, "birth" is only possible in the subsurface stock and so we do not consider the population model to be characteristic of typical metapopulation models.

Hilborn (1989a) applies model A of Clark and Mangel (1979) to a population of skipjack tuna, *Euthynnus pelamis*, and suggests that there is evidence for the existence of a subsurface (or invulnerable) stock in that fishery. Mangel (1982) considers the models in more detail by investigating non-equilibrium behaviour, environmental fluctuations and times to extinction.

Hilborn (1989b) extends Clark and Mangel's (1979) model A by assuming that the subsurface stock is harvested by a longline fishery. A size or age-structured model is considered. The abundance in the surface and subsurface stocks of age a are given by $R_{1a}(t)$ and $R_{2a}(t)$ respectively. The model for a single cohort is,

$$\frac{dR_{1a}}{dt} = -(F_1V_{1a} + M + d_{12})R_{1a} + d_{21}R_{2a} \qquad (1.58)$$

$$\frac{dR_{2a}}{dt} = -(F_2V_{2a} + M + d_{21})R_{2a} + d_{12}R_{1a}, \qquad (1.59)$$

where F_i is the fishing mortality for stock i, V_{ia} is the relative vulnerability for members of population i at age a, M is the natural mortality rate and d_{ij} is the instantaneous movement rate from population i to j. Recruitment to each substock is either independent of stock size (constant), or a Beverton-Holt type stock-recruitment relation.

Yield-per-recruit analysis using simulation techniques is employed to determine the effect of the longline and surface fishery on yield and total dollar value ($600 per tonne for surface stock, which is usually canned; and $1800 per tonne for the larger subsurface fish, which are transported to the sashimi market). For the parameters chosen, analyses show that total yield is maximised by a mixed fishery, for both constant recruitment and when recruitment is related to spawner abundance. However, total dollar value is maximised by a sole longline fishery for both methods of recruitment.

Hilborn's model, as with Clark and Mangel's (1979) models, explicitly considers a spatially structured population with interacting substocks. Although not an objective of the paper, an improvement may have been to to specifically consider the effect of different migration rates, as in all analyses Hilborn assumes $d_{12} = d_{21}$. The models that we present in this thesis explictly consider non-symmetric migration.

Clark (1990) considers an inshore-offshore fishery where interactions between the two substocks are through a diffusion process. Let $R_1(t)$ and $R_2(t)$ be the abundance of the inshore and offshore populations respectively at time t. Assume that diffusion occurs from the population with the larger abundance, to the population with the smaller, weighted by the constant σ. The model is,

$$\frac{dR_1}{dt} = F_1(R_1) + \sigma(R_2 - R_1) - E_1R_1 \tag{1.60}$$

$$\frac{dR_2}{dt} = F_2(R_2) + \sigma(R_1 - R_2) - E_2R_2, \tag{1.61}$$

where $F_i(R_i)$ represents the natural growth rate of substock i, and E_i is the fishing effort exerted in substock i. The discounted net revenues (present value) of both populations is maximised,

$$P.V. = \int_0^\infty e^{-\delta t}\Big((pR_1 - c_1)E_1 + (pR_2 - c_2)E_2\Big)\,dt, \tag{1.62}$$

where p is the price (equal for both populations) and c_i is the harvest cost associated with substock i (Clark assumes that costs are less for the the inshore fishery). Maximisation by integration by parts yields the optimal equilibrium equations,

$$\begin{aligned}(F_1'(R_1) - \delta)(p - C_1(R_1)) - F_1(R_1)C_1'(R_1) &= \frac{\sigma}{R_1^2 R_2}(c_2 R_1^2 - c_1 R_2^2) && (1.63)\\ (F_2'(R_2) - \delta)(p - C_2(R_2)) - F_2(R_2)C_2'(R_2) &= \frac{\sigma}{R_2^2 R_1}(c_1 R_2^2 - c_2 R_1^2), && (1.64)\end{aligned}$$

where $C_i(R_i) = c_i/R_i$. Note that if there is no diffusion, $\sigma = 0$, then we recover equation (1.4). Clark argues that if the marginal cost of harvesting the inshore fishery with no diffusion is less than the marginal cost, $\partial C/\partial R_2$, of the offshore fishery with diffusion, then the optimal with-diffusion escapement of the inshore fishery decreases over the non-diffusion model, while the offshore escapement increases. Clark suggests that this allows stock from offshore to move inshore to be harvested at a lower cost.

Thus Clark models a spatially structured population, and uses present value maximisation to obtain optimal population levels for each substock. Similarly, maximisation of the discounted net revenues accruing from the substocks of a metapopulation is employed in this thesis. Clark, again, essentially assumes symmetric migration as rates of diffusion between substocks are the same for a particular difference in abundance.

Other models that explicitly consider the spatial structure of harvested populations include search models, transboundary models and models of harvest closures. Within a fishing area, many fishing grounds may exist, each varying in year-to-year productivity. Search models are concerned with determing how and where to allocate effort across the fishing grounds. We do not go into the detail of these models and the interested reader is directed to Mangel and Clark (1983) and Clark (1990). Transboundary fishery problems occur when a common stock is delineated due to its range crossing the boundaries of jurisdiction of two or more nations. An interesting case may occur where distinct local populations exist in each country's waters, and exchange of individuals occurs between the local populations. We do not consider this here, and recommend Munro (1979), Levhari and Mirman (1980), Kaitala (1985) and Hilborn (1987). Homogeneous (or otherwise) stocks are also delineated due to harvest regulations. For example, sections of a population's range may be preserved in an unharvested marine park, or closed as a harvest management tool to protect stocks. Polacheck (1990), DeMartini (1993) and Quinn *et al* (1994) consider this scenario and we discuss these papers in Chapter 5.

The only modelling work that explicitly considers the effects of harvesting a population exhibiting a metapopulation structure is that of Quinn, Wing and Botsford (1994) on the red sea urchin, *Strongylocentrotus franciscanus*, fishery of California. The red sea urchin is a benthic marine invertebrate that exhibits broadcast spawning and pelagic larvae. Evidence suggests that both pre and post-dispersal Allee effects are an important feature of urchin population dynamics. Fertilisation success decreases significantly with adult separation. The authors suggest that densities need to be greater than one spawner per metre for successful larval production. Furthermore, the presence of adults is believed to enhance larval settlement success. The adults' canopy of spines protects juveniles from predation (Tegner and Dayton, 1977).

Quinn *et al* model the metapopulation dynamics with deterministic differential equations. Adult densities are nondimensionalised so that the population density of local population i at equilibrium is given by $R_i = 1$. The first model considers pre-dispersal Allee effects. The function $f(R_i) = rR_i/(z_f + R_i)$ represents the per capita reproductive output, which decreases with small population densities. The parameters r and z_f are constant. The fraction of larvae that successfully disperse from local population to another is given by m, with $(1-m)$ remaining in the parent local population. The harvesting intensity, h is partitioned between local populations according to the fraction k, where $(1-k)$ is the proportion of harvesting effort allocated to local population 2, and k is allocated to local population 1. In this way, the authors are able to investigate the effect of a harvest refuge ($k = 0, 1$) on metapopulation dynamics and yields. The model is,

$$\begin{aligned} \frac{dR_1}{dt} &= (1-m)f(R_1)R_1 + mf(R_2)R_2 - dR_1 - cR_1^2 - khR_1 && (1.65) \\ \frac{dR_2}{dt} &= (1-m)f(R_2)R_2 + mf(R_1)R_1 - dR_2 - cR_2^2 - (1-k)hR_2, && (1.66) \end{aligned}$$

where c and d are constants associated with mortality.

If post-dispersal Allee effects are considered (ignoring pre-dispersal Allee effects, $f(R_i) = r$), the model is,

$$\begin{aligned} \frac{dR_1}{dt} &= g(R_1)\{(1-m)rR_1 + mrR_2\} - dR_1 - cR_1^2 - khR_1 && (1.67) \\ \frac{dR_2}{dt} &= g(R_2)\{(1-m)rR_2 + mrR_1\} - dR_2 - cR_2^2 - (1-k)hR_2, && (1.68) \end{aligned}$$

where the effect of adult presence on larval recruitment is given by the function $g(R_i) = R_i/(z_g + R_i)$.

The equilibrium behaviour of the system is then considered. Results for the first model suggest that unless a harvest refuge exists, excessive harvest pressure can lead to extinction. The maximum sustainable yield is obtained when the harvest intensity applied to the local populations is equal ($k = 0.5$). However, a small increase in effort produces a dramatic reduction in abundance, and eventual extinction. Similar results are found for the post-dispersal Allee effect model, except that harvesting pressure can be marginally greater before collapse, and an asymmetric harvest ($k \neq 0.5$) produces the maximum sustainable yield.

The two-patch models described by Quinn *et al* are followed by a more complex deterministic simulation model that includes age and spatial structure. The model is applied to a hypothetical red sea urchin metapopulation composed of twenty-four local populations that run parallel to a linear coastline. Four age-classes are considered: zygotes, juveniles, subadults and adults. The zygotes disperse to other sites (local populations), remain in the site of origin or are lost to the system. The proportion of the larvae that successfully migrate to surrounding sites is varied between 0.1 and 1%, as is the sedentary larvae. The migrating larvae are evenly distributed over an input number of the surrounding sites. Similar results to the previous analyses are found, including that harvests can cause the population to become extinct if there are no refugia in the metapopulation. If a reserve is allocated to every other local population, or every third local population, then the population persists under intensive harvesting but collapses if reserves are allocated to every sixth local population. Larger harvests are produced without reserves, but this requires strict control of harvesting effort, as a small increases in effort leads to population extinction. Results also show that reserves increase the time to extinction, and, as the authors suggest, this provides time for the adoption of alternative sustainable management policies.

The models presented in this thesis differ from those of Quinn *et al* (1994) and the other authors mentioned in this section in several important respects. We model spatially structured populations with juvenile and/or adult migration using coupled difference equations. We are then able to consider explicitly the effects of non-symmetric migration on optimal harvesting strategies. We include local population dependent harvesting costs and find analytic solutions that maximise the present value of the net revenues obtained from each local population. We compare our results with alternative management policies based on conventional single population harvesting theory. In this way we are able to identify the potential economic benefits of our theory and the costs of incorrect harvesting policies, and determine the circumstances which may lead to over or under-harvesting of the local populations. Finally, we compare the harvesting strategy of each local population to obtain a rough guide to the relative harvesting intensity required.

1.6 Assumptions

In this section we briefly outline some of the basic assumptions of the models that follow. Although restrictive, many of the economic and biological assumptions are made to simplify an otherwise complex system, and to facilitate mathematical analysis and interpretation.

Economic assumptions consistent throughout the thesis include the maximisation of discounted net revenues, perfect fleet malleability, myopic revenue expressions and the ability to selectively harvest the local populations.

Maximisation of present value is generally considered to be the objective function with most applicability in real world fisheries, and is superior to the objectives of maximum sustainable yield and the assumption of open-access harvesting (Clark, 1990). However, other factors may have a significant influence on the choice of objective function; most notably these are social objectives (e.g. to keep the abundance of a population such as whales above certain socially acceptable thresholds) and industry objectives (e.g. minimising the variance of yield, maintaining employment and financial viability).

We assume perfect fleet malleability, (e.g. transfer of vessels between fisheries), and myopic net revenue expressions, to facilitate mathematical analyses and interpretation of results. We assume that harvesting can be regulated according to the individual local populations of the metapopulation (selective harvesting); and that costs are local-population dependent. Whether regulation on a local population basis is feasible is likely to depend on the dimensions of the metapopulation. A geographically large metapopulation with local population separation in the order of kilometres, will be more easily regulated than local populations with smaller separations. For marine populations where harvesting is site-specific, such as sedentary benthic invertebrates, selective harvesting is likely to be feasible.

Many of the analytic results are derived with the assumption of negligible harvest costs, or that costs are constant for any population density. The costs associated with harvesting will rarely, if ever, be negligible, and, as mentioned, some species of clupeid are harvested with approximately fixed costs (Munro, 1992). This assumption allows analytic insights into the behaviour of the system, and many of the conclusions appear (from numerical examples) to be robust to the inclusion of density-dependent costs.

A more detailed economic model including vessel restriction, multiple jurisdiction, employment and investment could be informative; however, these factors are likely to cloud the general relationships that we seek regarding immigration and emigration. Thus, a basic economic model is considered so we can concentrate on the main extension of the thesis; namely the effects of metapopulation structure on optimal harvesting policies.

As with the economic conjectures, several biological assumptions are made to simplify the complexity of the environmental system and facilitate analysis. All models considered here use discrete-time rather than continuous-time. As explained earlier, many biological characteristics (e.g. discrete spawning events, delays) are most easily described in discrete-time, as is harvesting. Thus, we assume that harvesting occurs soon after a "census" of the population and before reproduction (inter-period dynamics can be modelled in continuous-time (Clark, 1990)).

Commercially harvested metapopulations are likely to have significant interactions with other species. Multi-species, or metacommunity, harvesting models are not considered due to their inherent complexity (Mesterton-Gibbons, 1987; Mesterton-Gibbons, 1988; Clark, 1990). Detailed age-structure is also not explicitly analysed; however Chapter 3 considers a simple age-structured population where juveniles experience a delay of arbitrary length before attaining sexual maturity (Clark, 1976; Getz and Haight, 1989).

The metapopulation models that we adopt are coupled difference-equation models where local population abundances are explicitly defined in the state space. We do not consider presence-absence metapopulation models, as these are not amenable to harvesting analysis. Our metapopulation model is an extension into two dimensions of the basic discrete-time single population harvesting model, $R_{k+1} = F(R_k - H_k)$. We assume density-independent migration between local populations. This is the simplest form of migration that allows an intoductory investigation of metapopulation dynamics. Density-dependent migration, for example, where the range of migration increases with abundance (due to space-limitation), decreases with abundance (due to a lack of territories (Hansson, 1991)) or where migration acts to even out variations in density across the metapopulation (Hilborn and Walters, 1987), add further complexity to the models, and are an area of future research. We assume that the migration parameters can be chosen to represent either distance effects (e.g. successful migration decreasing with local population separation (Hanski and Thomas, 1994)) or local environmental effects (e.g. water currents). The models that we present emphasise the effects of non-symmetric migration between local populations which is indicative of heterogeneous environments.

The chapters that follow include several numerical examples. The main purpose of these examples is to explore the behaviour of the system in greater detail than would be possible using analytic methods and to present results in an understandable fashion.

Examples are used to compare numeric results with analytic solutions, and to investigate the effect of harvesting strategies across a broad range of parameter values. Explicit use of data is not used here. As Polacheck (1990) observes, the literature contains little quantitative information on movement rates, and so the model parameters that we use here are estimates, chosen to reflect possible real world applications. For all examples we assume that the unharvested equilibrium abundances are locally stable. A more detailed analysis of local stability can be found in Agnew (1982) and Fisher (1984) for analogous multi-species models. In most discussions we assume that the models apply to marine or freshwater fisheries. However, the models are generic and applicable to terrestrial systems where the assumptions are acceptable.

No environmental or economic stochastic effects are considered; we only consider deterministic dynamics. Including random events and parameter uncertainty would certainly be informative and be an important improvement for future models. Fisheries abound with uncertainty and there is wide scope for the inclusion of stochasticity in these models. Metapopulation theory emphasises the importance of variability in local extinction and recolonisation. The effects of harvesting vulnerable populations is important for the sustainable management of metapopulations as a whole. For example, recovery from local catastrophes (e.g. overfishing, oil spillage), a stochastic event itself (Reed and Echavarria, 1992), may be reliant on immigration, and practical harvesting policies will be required. As important as stochasticity may be, this thesis presents new theories about the management of spatially structured populations; the simple rules generated from deterministic dynamics give valuable insights for management.

Chapter 2

Optimal harvesting strategies for a metapopulation

In this chapter we extend Clark's homogeneous population model by assuming the existence of two local populations which, due to the migration of juveniles between them, form a metapopulation (see Figure 2.1). The metapopulation concept allows us to introduce spatial heterogeneity into the model. Local populations can have different growth and mortality rates, reflecting geographic variability. This chapter presents the first work to find analytic optimal harvesting strategies for a spatially structured, single species population with juvenile migration between occupied patches of habitat.

It is clear that many species occur as metapopulations. In Australia, harvested species like abalone have a well-defined metapopulation structure (Shepherd and Brown, 1993). Other marine populations, such as scallops, sea hares, cod, starfish, urchins and prawns, also have spatially structured populations containing local populations that experience immigration and emigration of individuals (Fairbridge, 1953; Pennings, 1991; Frank, 1992; Scandol and James, 1992; O'Brien, 1994; Quinn *et al.*, 1994). We cannot expect the environment of a population to be homogeneous, nor to be unstructured spatially. Due to environmental heterogeneity, local populations experience different conditions and hence population parameters will vary between local populations.

In this chapter we assume that the fished population is a single species, composed of two well-mixed, spatially homogeneous sub-populations which we shall henceforth refer to as local populations. The local populations are connected by the dispersal of juveniles and together form a metapopulation. In this introductory chapter we concentrate on the case where there are just two local populations, so as to assist the interpretation of results. Chapter 6 extends the results to N local populations. We assume that the metapopulation is exploited by a single owner or authority. Managers are able to uniquely define the local populations and we assume that regulation measures can be applied to the individual sites (examples where reproductively isolated stocks are harvested and the individual stock abundances either can or can not be identified are considered by Hilborn (1976; 1985); see Chapter 1).

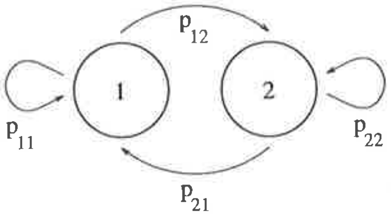

FIGURE 2.1: A metapopulation with two local populations. The circles represent the local populations, and the proportion of juveniles migrating from local population i to j in each generation is given by p_{ij}.

We begin by describing the metapopulation using coupled deterministic difference equations. The state space is composed of the abundances of these local populations. Following Clark (1976), we establish an economic framework and use dynamic programming to find optimal policies for the maximisation of the discounted net revenue obtained from both local populations. Results are discussed with simplifying assumptions which facilitate analytic comparisons between the local populations and with alternative policies that are made without the managing body recognising the metapopulation structure of the stock. These results are interpreted in relation to some simple local population classifications, and are illustrated with specific examples.

In this model we assume that adults are sedentary and that after a period of spawning, larvae produced by the adults of the local populations either remain in the parental population, move to the other local population or are lost from the system. A model of this form may be most applicable to benthic marine invertebrates with pelagic larvae, commercial examples of which include urchins (Quinn *et al.*, 1994), scallops (Fairbridge, 1953; Brand, 1991), abalone (Brown and Murray, 1992; Shepherd and Brown, 1993), oysters (Matthiessen, 1991) and lobster (Hill and White, 1990).

Features of the results include the conservative harvesting of *relative exporter* and *relative source* local populations in comparison to alternative incorrect harvesting policies. A relative exporter is defined as the local population that exports more larvae per capita than it imports. A relative source is the local population that produces the greater per capita number of larvae. Relative source local populations should also have the larger equilibrium population level (escapement) of the two habitats.

Under some circumstances we find harvesting policies that require a negative harvest from *one* (the relative exporter) of the local populations. This situation does not arise in conventional single population optimal harvesting theory. If we interpret a negative harvest as an optimal seeding policy, then our results suggest that stock should be placed in a local population to enhance abundance for future harvests. Seeding populations is a common (where financially feasible) stock management procedure in many fisheries, for example, abalone and scallop populations in Japan. Schiel (1992) quotes figures from the Iwate Prefecture Mariculture Centre that from 1984 to 1986, over 30% of the total weight of caught abalone was seeded stock, with rearing programs releasing hundreds of thousands of seed abalone per year (see Tegner and Butler (1992)). Scallops have had artificially replenished stocks in Japan's Mutsu Bay for many years now (Aoyama, 1988). Salmon ranching is used on the west coast of North America to enhance Pacific salmon production (Pitcher and Hart, 1987; Brannon, 1984). Enhancements are also used to replenish depleted stocks (Tegner, 1992; Mackie and Ansell, 1993). If a negative harvest is infeasible, we discuss a method for eliminating the possibility of a negative harvest and negative harvests are discussed further in the Closing Remarks of this chapter.

2.1 Theory

Assume that adults do not migrate between local populations. The adults produce juveniles, e.g. larvae, of which a proportion remain within the natal local population, a proportion migrate to the connected local population and the remaining juveniles are lost from the system. The migrating juveniles become members of their new local population and, together with the sedentary juveniles and adults, form the adults of the following generation.

2.1.1 The basic model

Assume that the two interacting local populations can be modelled with the following population equations,

$$R_{1k+1} = \delta_1 R_{1k} + p_{11} G_1(R_{1k}) + p_{21} G_2(R_{2k}) \tag{2.1}$$

$$R_{2k+1} = \delta_2 R_{2k} + p_{12} G_1(R_{1k}) + p_{22} G_2(R_{2k}), \tag{2.2}$$

where R_{ik+1} is the number of fish in the i^{th} population at the beginning of the $k+1^{th}$ period. The proportion of adults surviving per generation in the i^{th} local population is represented by δ_i and p_{ij} is the proportion of the juveniles produced by population i that recruit to population j. Assume that the remaining proportion of the juveniles of population i, ϵ_i, are lost from the system, so $p_{i1} + p_{i2} + \epsilon_i = 1$. The function $G_i(R_{ik})$ is the recruit production function for population i. For example, we might assume a logistic form for the recruit production (as in Chapter 1), namely

$$G_i(R_{ik}) = r_i R_{ik}(1 - R_{ik}/K_i), \tag{2.3}$$

where r_i is a growth rate and K_i is a form of carrying capacity that causes density dependence in the per capita growth rate of local population i. Abundance in a particular local population thus increases with adult survival, juvenile retention and immigration.

The local populations are harvested, H_{ik}, and the escapements $S_{ik} = R_{ik} - H_{ik}$ then grow according to equations (2.1) and (2.2) to R_{ik+1}. Thus, including harvesting, equations (2.1) and (2.2) become,

$$\begin{aligned} R_{1k+1} &= \delta_1 S_{1k} + p_{11} G_1(S_{1k}) + p_{21} G_2(S_{2k}) & (2.4) \\ R_{2k+1} &= \delta_2 S_{2k} + p_{12} G_1(S_{1k}) + p_{22} G_2(S_{2k}). & (2.5) \end{aligned}$$

Now, using the escapements, S_{ik}, as the control variables, our objective is to maximise the present value of net revenue over T seasons, namely maximise

$$P.V. = \sum_{k=0}^{T} \alpha^k \sum_{i=1}^{2} \Pi_i(R_{ik}, S_{ik}), \tag{2.6}$$

subject to equations (2.4) and (2.5) and $0 \leq S_{ik} \leq R_{ik}$. The function $\Pi_i(R_{ik}, S_{ik})$ represents the net revenue from harvesting local population i.

Equation (2.6) is similar to equation (1.16) except that the discounted net revenues from both local populations are added to form our present value expression. As before, α is a discounting factor. The net revenue produced in period k from a harvest of H_{ik}

from local population i is,

$$\Pi_i(R_{ik}, S_{ik}) = \int_{S_{ik}}^{R_{ik}} (p - c_i(x))\, dx, \tag{2.7}$$

where p is the price of the stock and $c_i(x)$ is the cost of harvesting a unit of stock from local population i when its abundance is x. See Clark (1990) for a detailed derivation of the single population analogy of equation (2.7). The cost of harvesting can vary from local population to local population. Local populations may have different harvesting costs associated with them due to factors such as the cost of travelling to the population, differences in weather or depth to the population, or even risks to health (Hilborn and Kennedy, 1992). However, we shall assume that the price of the harvested stock is independent of its source.

2.1.2 Derivation of the optimal harvesting strategy

Dynamic programming is used to determine the optimal harvesting strategy. We assign the value function, $J_T(R_{10}, R_{20})$, as follows,

$$J_T(R_{10}, R_{20}) = \max_{0 \le S_{ik} \le R_{ik}} \sum_{k=0}^{T} \alpha^k \sum_{i=1}^{2} \Pi_i(R_{ik}, S_{ik}). \tag{2.8}$$

The value function is the sum of the discounted net revenues from both local populations up until season T, maximised by an appropriate choice of the escapements S_{ik}. The value function depends on the initial local population sizes, R_{10} and R_{20}.

A recursive equation in terms of the value functions is then obtained from equation (2.8),

$$J_{T+1}(R_{10}, R_{20}) = \max_{0 \le S_{i0} \le R_{i0}} \left(\sum_{i=1}^{2} \Pi_i(R_{i0}, S_{i0}) + \alpha J_T(R_{11}, R_{21}) \right). \tag{2.9}$$

Equation (2.9) is Bellman's equation (Bellman, 1957). This expression states that the value function with time horizon $T+1$ is the maximum of the immediate returns in the first period plus the returns from future harvests if the local populations' abundances move to R_{11} and R_{21}. This maximum is achieved by an appropriate choice of the escapements S_{i0}.

Consider first the value function with $T = 0$, i.e. our objective is to maximise our immediate net revenue without any consideration of future generations. In this case,

$$\begin{aligned} J_0(R_{10}, R_{20}) &= \max_{0 \leq S_{i0} \leq R_{i0}} \sum_{i=1}^{2} \Pi_i(R_{i0}, S_{i0}) \\ &= \sum_{i=1}^{2} \Pi_i(R_{i0}, S_{i\infty}), \end{aligned} \tag{2.10}$$

where $S_{i\infty}$ is called the zero net profit level for local population i and is chosen so that $p - c_i(S_{i\infty}) = 0$ and harvesting a local population from R_{i0} down to $S_{i\infty}$ will produce the maximum possible profit from that local population.

For the next time horizon $T = 1$ we obtain the following recursive equation,

$$\begin{aligned} J_1(R_{10}, R_{20}) &= \max_{0 \leq S_{i0} \leq R_{i0}} \left(\sum_{i=1}^{2} \Pi_i(R_{i0}, S_{i0}) + \alpha J_0(R_{11}, R_{21}) \right) \\ &= \max_{0 \leq S_{i0} \leq R_{i0}} \left(\sum_{i=1}^{2} \Pi_i(R_{i0}, S_{i0}) + \alpha \left\{ \sum_{i=1}^{2} \Pi_i(R_{i1}, S_{i\infty}) \right\} \right). \end{aligned} \tag{2.11}$$

Equation (2.11) is maximised by partial differentiation with respect to S_{10} and S_{20}. Define $V(R_{1k}, R_{2k})$ as follows,

$$\begin{aligned} V(R_{1k}, R_{2k}) &= \sum_{i=1}^{2} \Pi_i(R_{ik}, S_{i\infty}) \\ &= \sum_{i=1}^{2} \int_{S_{i\infty}}^{R_{ik}} (p - c_i(x))\, dx, \end{aligned} \tag{2.12}$$

where

$$\begin{aligned} R_{1k} &= \delta_1 S_{1k-1} + p_{11} G_1(S_{1k-1}) + p_{21} G_2(S_{2k-1}) \\ R_{2k} &= \delta_2 S_{2k-1} + p_{22} G_2(S_{2k-1}) + p_{12} G_1(S_{1k-1}). \end{aligned}$$

Thus, partially differentiating the first summed term in equation (2.11) with respect to S_{i0}, we find

$$\frac{\partial \Pi_i(R_{i0}, S_{i0})}{\partial S_{i0}} = -(p - c_i(S_{i0})). \tag{2.13}$$

Noting that,

$$\frac{\partial V(R_{11}, R_{21})}{\partial S_{10}} = (p - c_1(R_{11}))(\delta_1 + p_{11}G_1'(S_{10})) + (p - c_2(R_{21}))p_{12}G_1'(S_{10}), \tag{2.14}$$

and similarly for $\frac{\partial V(R_{11}, R_{21})}{\partial S_{20}}$, we obtain

$$\begin{aligned}
\frac{\partial J(R_{10}, R_{20})}{\partial S_{10}} &= -(p - c_1(S_{10})) + \alpha\Big[(p - c_1(R_{11}))(\delta_1 + p_{11}G_1'(S_{10})) \\
&\qquad + (p - c_2(R_{21}))p_{12}G_1'(S_{10})\Big] = 0, \\
\frac{\partial J(R_{10}, R_{20})}{\partial S_{20}} &= -(p - c_2(S_{20})) + \alpha\Big[(p - c_2(R_{21}))(\delta_2 + p_{22}G_2'(S_{20})) \\
&\qquad + (p - c_1(R_{11}))p_{21}G_2'(S_{20})\Big] = 0.
\end{aligned}$$

After minor rearrangements, we produce equations (2.15) and (2.16),

$$\frac{1}{\alpha} = \frac{(\delta_1 + p_{11}G_1'(S_{10}))(p - c_1(R_{11})) + p_{12}G_1'(S_{10})(p - c_2(R_{21}))}{p - c_1(S_{10})}, \tag{2.15}$$

$$\frac{1}{\alpha} = \frac{(\delta_2 + p_{22}G_2'(S_{20}))(p - c_2(R_{21})) + p_{21}G_2'(S_{20})(p - c_1(R_{11}))}{p - c_2(S_{20})}. \tag{2.16}$$

These equations are generalisations of the optimal harvesting equation for a single population. If we remove migration by setting $p_{ij} = 0$ for $i \neq j$ and assign $F'(S) = \delta_i + p_{ii}G_i'(S_i)$ then equation (1.25) is recovered. From equations (2.15) and (2.16) it is possible to find the optimal escapements, S_{10}^* and S_{20}^*, for each local population. There are also second derivative conditions which must hold to ensure a maximum, rather than a minimum or turning point. These conditions are given in Appendix 1.

Equations (2.15) and (2.16) hold for all time horizons $T \geq 1$. To prove this we adjust Clark's (1976; 1990) proof for the analogous single population case. Rewrite

$J_1(R_{10}, R_{20})$ as,

$$J_1(R_{10}, R_{20}) = \max_{0 \leq S_{i0} \leq R_{i0}} V(R_{10}, R_{20}) - V(S_{10}, S_{20}) + \alpha V(R_{11}, R_{21}), \tag{2.17}$$

where $V(R_{1k}, R_{2k})$ is defined by equation (2.12). Assume that we have found optimal escapements, S^*_{10} and S^*_{20}, from equations (2.15) and (2.16). Equation (2.17) becomes,

$$J_1(R_{10}, R_{20}) = V(R_{10}, R_{20}) - V(S^*_{10}, S^*_{20}) + \alpha V(R^*_{11}, R^*_{21}), \tag{2.18}$$

where the star in the terms R^*_{i1} indicates that they are functions of the escapements, S^*_{i0}. Consider the next time horizon, $T = 2$,

$$\begin{aligned}
J_2(R_{10}, R_{20}) &= \max_{0 \leq S_{i0} \leq R_{i0}} V(R_{10}, R_{20}) - V(S_{10}, S_{20}) + \alpha J_1(R_{11}, R_{21}) \\
&= \max_{0 \leq S_{i0} \leq R_{i0}} V(R_{10}, R_{20}) - V(S_{10}, S_{20}) \\
&\qquad + \alpha\Big(V(R_{11}, R_{21}) - V(S^*_{10}, S^*_{20}) + \alpha V(R^*_{12}, R^*_{22})\Big) \\
&= \max_{0 \leq S_{i0} \leq R_{i0}} V(R_{10}, R_{20}) - V(S_{10}, S_{20}) \\
&\qquad + \alpha\Big(V(R_{11}, R_{21}) + A(S^*_{10}, S^*_{20})\Big) \\
&= J_1(R_{10}, R_{20}) + \alpha A(S^*_{10}, S^*_{20}). \qquad (2.19)
\end{aligned}$$

When maximising $J_2(R_{10}, R_{20})$ with respect to S_{10} and S_{20}, the term $A(S^*_{10}, S^*_{20})$ is constant, and we simply maximise $J_1(R_{10}, R_{20})$. Thus, the maximisation of $J_2(R_{10}, R_{20})$ is mathematically equivalent to maximising $J_1(R_{10}, R_{20})$, and so we produce the same optimal escapements, S^*_{10} and S^*_{20}. This is also true for time horizons $T > 2$, and so the optimal first-year escapements are independent of the time horizon considered.

2.1.3 Optimal negative harvests

The optimal escapements will depend on the initial population levels, R_{10} and R_{20}. If $R_{i0} > S^*_{i0}$ then the optimal harvest is $H^*_{i0} = R_{i0} - S^*_{i0}$. However, if $R_{i0} < S^*_{i0}$ then population i will have escapement R_{i0}, and there is no harvest from local population i. This assumes that the optimal escapements produce harvests that are non-negative, or equivalently, that if $R_{i0} < S^*_{i0}$ then local population i will experience an increase in abundance when optimally harvesting.

Unlike the analysis of single population exploitation, it is possible that one of the optimal escapements will produce negative harvests, even if $R_{i0} > S^*_{i0}$. Thus our globally optimal solution may be infeasible unless we can produce a negative harvest, by placing stock into the population rather than removing stock. This harvesting strategy is called *seeding* and is used to restock depleted populations or to enhance stocks for future harvesting.

Assuming that a negative harvest is impossible, we should harvest no stock from that local population. Thus we can still maximise J_1 as defined by equation (2.11) (assuming that the concavity conditions in Appendix 1 hold) by setting $H^{*'}_{i0} = 0$ and searching along the curve determined by this constraint for the maximum of the surface defined by equation (2.11). In general it will not be optimal to remain harvesting at S^*_{j0} if local population i has a globally optimal negative harvest. Thus we produce new optimal escapements $S^{*'}_{i0}$ and $S^{*'}_{j0}$. A numerical example of a globally optimal negative harvest is given later in this chapter. We discuss the feasibility of negative harvests in the Closing Remarks of this chapter, and an analytic solution to the non-negative harvest problem is produced in Appendix 4.

Equations (2.15) and (2.16) are sufficient to find optimal harvests; however they give little indication of their meaning. In the following sections we make simplifying assumptions to help further our understanding of the optimal harvesting policies suggested by the equations.

2.2 Discussion of the two local population results

To facilitate interpretations of the above results, we define two types of local population according to their per capita larval production. The assumption of negligible costs is then used to produce analytic results that can be readily interpreted. Finally, examples comparing optimal and sub-optimal strategies for the costs and no costs case are examined.

2.2.1 Local population classifications

Before proceeding with the no costs theory, we make two biological classifications of local populations according to their per capita larval production, i.e. the number of larvae produced per individual in a local population.

Relative exporters/importers

Firstly, consider a local population, say local population i, that exports a greater per capita number of larvae to the other local population, local population j, than local population j exports to it. We call such a local population a *relative exporter* local population. Mathematically it is a local population i with

$$r_i p_{ij} > r_j p_{ji} \qquad \forall j \neq i. \tag{2.20}$$

Similarly, a local population that imports a greater per capita number of larvae than it exports we call a *relative importer* local population and it is defined by reversing the above inequality. For the two local population case, if local population i is a relative exporter then local population j is a relative importer.

Relative sources/sinks

Consider a local population whose per capita larval production is greater than the other local population's per capita larval production. We call this local population a *relative source* local population and mathematically a relative source local population i has

$$r_i(1-\epsilon_i) > r_j(1-\epsilon_j) \qquad \forall j \neq i. \tag{2.21}$$

A *relative sink* is the local population that has the smaller per capita larval production and it has $r_i(1-\epsilon_i) < r_j(1-\epsilon_j)$. For the two local population case, if local population i is a relative source then local population j is automatically a relative sink.

2.2.2 No costs analysis

Assume that the cost of harvesting the resource is either negligible or independent of the density and local population. Equations (2.15) and (2.16) respectively simplify to,

$$\frac{1}{\alpha} = \delta_1 + G_1'(S_1^*)(p_{11}+p_{12}) \tag{2.22}$$

$$\frac{1}{\alpha} = \delta_2 + G_2'(S_2^*)(p_{21}+p_{22}), \tag{2.23}$$

where S_i^* is the optimal equilibrium escapement for local population i.

Assume that $G_i''(S_i) < 0$ so that these equations determine no more than one solution for S_i^*. For example, assume logistic growth for $G_i(S_{ik})$ of the form seen in equation (2.3). In this case the optimal escapements are,

$$S_1^* = \frac{K_1}{2} - \frac{K_1}{2r_1}\frac{(1+d-\delta_1)}{(p_{11}+p_{12})} \tag{2.24}$$

$$S_2^* = \frac{K_2}{2} - \frac{K_2}{2r_2}\frac{(1+d-\delta_2)}{(p_{21}+p_{22})}, \tag{2.25}$$

and the conditions for a maximum are satisfied.

A comparison of the above equations with the escapement derived for the optimal economic harvesting of a single population shows that if we set $r = r_i(p_{ii} + p_{ij})$ then the equations are of the same general form.

Comparisons with incorrect harvesting policies

The theory generates optimal harvesting policies, but we may be interested in how the policies differ from those predicted by existing single population theory. There are two possible incorrect harvesting policies that could be employed if the metapopulation structure has not been recognised. Firstly, the local populations themselves have been recognised but they are believed to be reproductively isolated, i.e. recruitment is assumed to be local and there is no migration between the stocks (see (a) of Figure 2.2). Secondly, the metapopulation is incorrectly assumed to be a well-mixed single population, i.e. a population with reproductive interactions equally likely across the whole population (see (b) of Figure 2.2).

We would then like to know under what circumstances the metapopulation escapements are larger (or smaller) than the escapements used if the metapopulation is mismanaged, and if the local populations are over or under-harvested. For the following analyses we assume that the optimal escapements defined by equations (2.24) and (2.25) produce positive harvests.

Assume that the two local populations have $K_1 = K_2$ and that the local populations are harvested as two unconnected single populations. Further, assume that observations of a local population suggest that its growth rate, r_{is}, would be measured as

$$r_{is} = r_i p_{ii} + r_j p_{ji}, \tag{2.26}$$

if we did not know that the population was connected by migration to another local

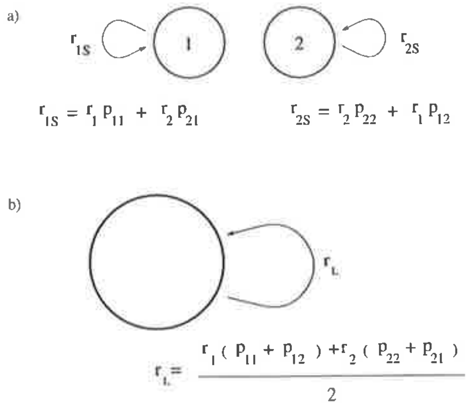

FIGURE 2.2: a) Two unconnected single populations with their estimated growth rates. b) A well-mixed single population with its estimated growth rate.

population. This is essentially the "flow in" to local population i. The estimate assumes that the growth rate is measured from the sedentary juveniles of local population i and, unwittingly, the immigrants from local population j. It also assumes that the population sizes are roughly equal, and that measurements are made after dispersal. A suggested alternative pre-dispersal measure of the growth rate, $r_{is} = r_i(p_{ii} + p_{ij})$, is not employed here, as measurements made before dispersal are not likely to be able to predict with confidence the proportion of juveniles that successfully migrate or remain within the parental population, i.e. the migration parameters p_{ij}.

The optimal escapement of local population i derived from metapopulation harvesting theory will be larger than that from unconnected single population harvesting theory, $S_i^* > S_{is}^*$, if $r_i p_{ij} > r_j p_{ji}$. If this inequality holds for local population i then the reverse is automatically true for the other local population, i.e. if $S_i^* > S_{is}^*$ then $S_j^* < S_{js}^*$ for $i \neq j$. We conclude that relative exporter populations will be over-harvested if unconnected single population harvesting theory is the preferred guide to managing the stock, while relative importer populations will be under-harvested. The sum of the optimal escapements from both local populations will be greater than the sum of the escapements when the populations are believed to be unconnected single populations, $S_1^* + S_2^* > S_{1s}^* + S_{2s}^*$, if $r_i p_{ij} > r_j p_{ji}$ and $r_i p_{ii} < r_j p_{jj}$ (see Appendix 2). Thus if the metapopulation is a relative exporter/importer system with the relative exporter local population retaining fewer of its larvae per capita than the importer local population, we should leave more of the total stock than if the metapopulation were managed as two unconnected populations.

The metapopulation could also be managed as a well-mixed single population. In making a comparison of the optimal escapements for the local populations we estimate the escapements for the local populations from the single population theory by dividing the single optimal escapement by two (we are assuming $K_1 = K_2$). For simplicity, assume that $\delta_1 = \delta_2$ and that the growth rate measured for the single merged population is the average per capita juvenile production,

$$r_L = \frac{r_1(p_{11} + p_{12}) + r_2(p_{22} + p_{21})}{2}. \tag{2.27}$$

The escapement from local population i will be larger than the estimated optimal escapement from single population exploitation, $S_i^* > S_L^*/2$, if $r_i(p_{ii} + p_{ij}) > r_L$, i.e. $r_i(1 - \epsilon_i) > r_j(1 - \epsilon_j)$. We conclude that, to harvest the metapopulation as a well-mixed single population will over-harvest relative source populations and under-harvest relative sink populations. The sum of the optimal escapements from both local populations will never be greater than the escapement derived from the well-mixed single population exploitation, i.e. $S_1^* + S_2^* \leq S_L^*$ (see Appendix 3). Thus a metapopulation that is managed as a well-mixed single population may be harvested too conservatively.

Comparisons between local populations

Finally, assume that we have recognised the metapopulation structure of the stock. We would like to know how a particular local population's escapement differs from the other local population's escapement. In this way we can develop rough guides that determine how heavily different stocks should be harvested.

For example, assuming $K_1 = K_2$ and $\delta_1 = \delta_2$ and that $r_i(p_{ii} + p_{ij}) > r_j(p_{jj} + p_{ji})$, (or $r_i(1 - \epsilon_i) > r_j(1 - \epsilon_j)$), then $S_i^* > S_j^*$. This means that relative source populations should be harvested more conservatively than relative sink populations. If a local population has no juvenile production at all or there is total juvenile wastage from that local population, i.e. $\epsilon_i = 1$, then that local population should be completely harvested, $S_i^* = 0$. For example, if migration were uni-directional such that $p_{ij} > 0$ and $p_{j\cdot} = 0$ then we should fully harvest local population j. Uni-directional migration may be observed in a river hatchery/put and take fishery where the source is the hatchery and the sink local population is the fishing ground. Oceanic currents may also produce juvenile migration that is uni-directional (Pennings, 1991).

The escapement for local population i will also be larger than that of local population j, $S_i^* > S_j^*$, if $K_i > K_j$ or $\delta_i > \delta_j$, if all other population parameters remain equal. (These conditions are analogous to increasing a single population's size or adult survival, as can be seen from equation (1.28)). Thus, local populations that produce a large per capita number of larvae, have a large density-dependence parameter K_i, or have low adult mortality, should be harvested more conservatively than those local populations that do not. However, if one local population has, say, a larger K_i but is a relative sink then there is a trade-off in escapement sizes.

Examples

In the following sections we use numerical examples to investigate the harvesting behaviour of the models in more detail. The initial examples consider the numerical iteration of the dynamic programming equations. The results are compared with the analytic conclusions to confirm (a) that the optimal harvesting strategies are given by equations (2.15) and (2.16), and (b) that the optimal approach to equilibrium is indeed the most-rapid-approach. Specific examples are then considered to facilitate the interpretation of the optimal harvesting results and the incorrect harvesting policies. The initial examples assume negligible costs, and then costs are included in the latter examples. The main effect of including costs appears to be an increase in optimal escapements (a zero escapement is not possible for the cost function that we consider). The general behaviour of the models remains the same, as does the harvesting results.

2.3 Examples with no costs

2.3.1 Iteration of the dynamic programming equations

In this example we compare the analytic results with optimal escapements obtained by iterating Bellman's equation. Suppose that we wish to harvest the two local populations of a previously unharvested metapopulation. We can express the migratory parameters using a migration matrix where the $(i, j)^{th}$ entry is the proportion of juveniles migrating from local population i to local population j. In this example, the local populations' dispersal is represented by the migration matrix,

$$P = \begin{pmatrix} 0.1 & 0.1 \\ 0.15 & 0.1 \end{pmatrix}.$$

T	R_1	R_2	S_1	S_2	H_1	H_2
5	133	105	50	60	83	45
4	106	86	50	60	56	26
3	106	86	50	60	56	26
2	106	86	50	60	56	26
1	106	86	50	60	56	26
0	106	86	0	0	106	86

TABLE 2.1: Escapements and harvests from iterating the dynamic programming equations. The left hand column is time to go, and so $T = 5$ is the present or initial period.

The juvenile production function is logistic, with growth rates $r_1 = r_2 = 10$, adjusted carrying capacities $K_1 = K_2 = 200$ and adult survival per period $\delta_1 = \delta_2 = 0.1$. Thus, local population 2 is a relative source/exporter, while local population 1 is a relative sink/importer. The unharvested equilibrium population sizes are $\bar{R}_1 = 133$ for local population 1 and $\bar{R}_2 = 105$ for local population 2. The discount rate is 10%.

The optimal escapements from the analytic solutions, equations (2.24) and (2.25), are $S_1^* = 50$ and $S_2^* = 60$, with equilibrium harvests, $H_1^* = 56$ and $H_2^* = 26$. Thus we protect the relative source/exporter local population and more heavily exploit the relative sink/importer local population.

We can compare the above analytic solutions with the solutions obtained from iterating Bellman's equation, equation (2.9). The escapements and harvests produced are shown in Table 2.1.

As we do not consider generations after the final period, the terminal period's escapements for both local populations are zero. The initial conditions are the unharvested equilibrium population sizes, $\bar{R}_1 = 133$ and $\bar{R}_2 = 105$. The equilibrium escapements found are $S_1^* = 50$ and $S_2^* = 60$, with harvests $H_1^* = 56$ and $H_2^* = 26$. Thus, the analytic and numerical solutions produce the same optimal harvesting strategy. Note that the optimal escapements, S_1^* and S_2^*, hold for all time horizons $T > 0$, as expected.

2.3.2 Variation of the migration parameters

In this example we consider the behaviour of our analytic results, equations (2.24) and (2.25), as the juvenile migration parameters, p_{12} and p_{21}, vary. This allows greater insight into the effect of migration on escapements and harvests. Only the migration parameters are varied; all other parameters remain constant. We only consider the analytic solution, as numerical solutions are not facilitated by the large state space.

Assume that the metapopulation shows logistic juvenile production, with parameters $r_1 = r_2 = 1\,000$, $K_1 = K_2 = 400\,000$ and adult survival $\delta_1 = \delta_2 = 0.001$. The discount rate is 10%, and we assume that costs are negligible. The migration matrix is,

$$P = \begin{pmatrix} 0.001 & p_{12} \\ p_{21} & 0.001 \end{pmatrix}.$$

A contour plot of the optimal equilibrium escapements of local population 1 is shown in Figure 2.3. The escapements of local population 2 are not shown as they can be found by reflecting Figure 2.3 about the line $p_{12} = p_{21}$. Local population 1 is a relative source/exporter if the point (p_{12}, p_{21}) is below the line $p_{12} = p_{21}$, and it is a relative sink/importer if above.

We can see from Figure 2.3, and from equation (2.24), that the escapement of local population 1 is independent of p_{21}. We can explicitly define the change in the escapement for a particular change in the migration variables by using partial differentiation.

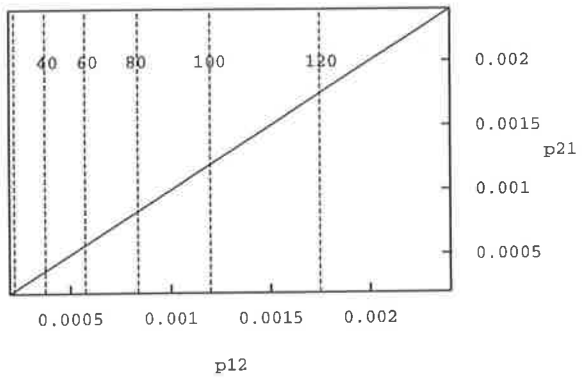

FIGURE 2.3: A contour plot of the escapements of local population 1 as a function of the migration parameters. Numbers on the contours are escapements $\times 10^3$. The escapements of local population 2 can be found by reflecting the contours about the line $p_{12} = p_{21}$.

For example, the rate of change of S_i^* with respect to p_{ij}, is given by

$$\frac{\partial S_i^*}{\partial p_{ij}} = \frac{K_i(1 + d - \delta_i)}{2r_i(p_{ii} + p_{ij})^2}. \tag{2.28}$$

For the parameters of our example, this equation simplifies to,

$$\frac{\partial S_i^*}{\partial p_{ij}} = \frac{219.8}{(0.001 + p_{ij})^2}. \tag{2.29}$$

Thus, with an increment in p_{12} of 0.0005, we expect a change in the escapement of approximately 49 000 near $p_{12} = 0.0005$, and near $p_{12} = 0.002$ we expect a change of approximately 12 000. Indeed, this is observed in Figure 2.3. Thus, for a particular increment, small p_{ij} values have a greater effect on the optimal escapement than larger values of p_{ij}. As far as management implications are concerned, if p_{ij} is large, then uncertainty about its exact value should not influence the choice of escapement as much as it would if p_{ij} were small.

In Figure 2.4 we plot the contours of the equilibrium harvests of local population 1. In the lower-right of Figure 2.4, local population 1 is a strong relative source/exporter, and this produces an optimal negative harvest. If we consider a negative harvest as

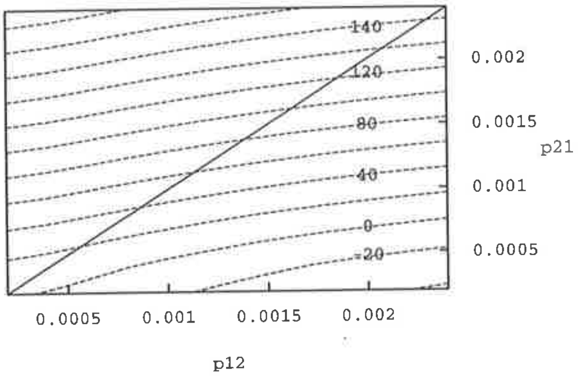

FIGURE 2.4: Contours of local population 1 harvests as a function of the migration parameters. Numbers on the contours are harvests $\times 10^3$.

being equivalent to seeding the population, i.e. placing stock into a local population rather than taking stock out, then the optimality of a negative harvest suggests that strong source/exporter local populations should be used to "boost" or enhance stock abundance in harvested sink/importer local populations. Note that the seeded stock are adults, and so they become part of the spawning stock abundance of local population 1.

As shown for the optimal escapements, we can explicitly define the change in the harvest as the migration variables change. Recall that the equilibrium harvest of local population 1 is,

$$H_1^* = \delta_1 S_1^* + p_{11} G_1(S_1^*) + p_{21} G_2(S_2^*) - S_1^*, \tag{2.30}$$

where S_1^* and S_2^* are the optimal equilibrium escapements given by equations (2.24) and (2.25). Partially differentiating the harvest with respect to p_{12}, we obtain,

$$\frac{\partial H_1^*}{\partial p_{12}} = \frac{K_1(1+d-\delta_1)}{2r_1(p_{11}+p_{12})^2}\left[\delta_1 - 1 + \frac{p_{11}}{p_{11}+p_{12}}(1+d-\delta_1)\right], \tag{2.31}$$

and similarly, partial differentiation with respect to p_{21} yields,

$$\frac{\partial H_1^*}{\partial p_{21}} = \frac{K_2(1+d-\delta_2)}{2r_2(p_{22}+p_{21})^2}\left[\frac{(r_2(p_{22}+p_{21}))^2}{2(1+d-\delta_2)} + \left(\frac{p_{21}}{p_{22}+p_{21}} - \frac{1}{2}\right)(1+d-\delta_2)\right]. \tag{2.32}$$

For the parameters of our example, equation (2.31) simplifies to,

$$\frac{\partial H_1^*}{\partial p_{12}} = \frac{219.8}{(0.001 + p_{12})^2}\left[-0.999 + \frac{0.001(1.099)}{0.001 + p_{12}}\right]. \tag{2.33}$$

Thus, we expect a decrease in harvest of approximately 13 000 for a change in p_{12} of 0.0005 near $p_{12} = 0.0005$, and near $p_{12} = 0.002$ the decrease is approximately 7 700. Figure 2.4 confirms these results.

Similarly, equation (2.32) reduces to,

$$\frac{\partial H_1^*}{\partial p_{21}} = \frac{219.8}{(0.001 + p_{21})^2}\left[\frac{(1\,000(0.001 + p_{21}))^2}{2.198} + \left(\frac{p_{21}}{p_{21} + 0.001} - \frac{1}{2}\right)(1.099)\right]. \tag{2.34}$$

Thus, an increment of 0.0005 near $p_{21} = 0.0005$ produces a change in harvest of approximately 41 000, while near $p_{21} = 0.002$ we expect an increase of around 52 000. Again, this is observed in Figure 2.4.

Similar results can be found by partially differentiating the escapement and harvest of local population 2; however, we do not include these equations here. In other models presented in this thesis we can also use partial differentiation to investigate the rates of change of our negligible costs escapements and harvests. However it appears that the graphical representation is more easily interpreted, and so we do not include the explicit mathematical forms for the rates of change in the models of the following chapters.

2.3.3 Harvesting relative sources and sinks

In the following examples we restrict attention to more specific situations and consider optimal harvesting behaviour from our theory, and harvesting strategies where managers have not recognised the metapopulation structure of the stock. We assume that the initial population size is the stable equilibrium of the unharvested metapopulation, $R_{i0} = \bar{R}_i$, and equilibrium harvesting behaviour is then considered.

The local populations' parameters are $r_1 = r_2 = 1\,000$, $K_1 = K_2 = 400\,000$ and $\delta_1 = \delta_2 = 0.001$. The migratory parameters, p_{ij}, are given in the examples and the discount rate is 10%. Consider a metapopulation whose local populations are indistinguishable except that $p_{12} > p_{21}$, i.e. local population 1 is a relative source and exporter population. In this example, the migration matrix is,

$$P_1 = \begin{pmatrix} 0.001 & 0.003 \\ 0.001 & 0.001 \end{pmatrix}. \tag{2.35}$$

The unharvested metapopulation has a stable equilibrium of $\bar{R}_1 = 148\,028$ and $\bar{R}_2 = 334\,710$.

In Figure 2.5 we plot the contours of the objective function given by equation (2.11), along with the contours of the harvests from each local population that are produced from using particular escapements. The zero harvest contours indicate where the escapements produce a zero harvest in one or the other local population. Negative harvests are possible but in this case, they are not optimal. The optimal escapements derived from equations (2.24) and (2.25) are $S_1^* = 145\,050$ and $S_2^* = 90\,100$ (see Table 2.2) which is the maximum observed from Figure 2.5.

The equilibrium harvests produced using the optimal escapements are $H_1^* = 17\,351$ and $H_2^* = 257\,149$. Thus we protect the relative source population and heavily harvest the relative sink population.

Comparisons with incorrect harvesting policies

If the metapopulation is managed assuming it to be two unconnected single populations then the escapements and harvests derived for each local population are $S_{1s}^* = 90\,100$ and $S_{2s}^* = 145\,050$ with harvests $H_{1s}^* = 72\,246$ and $H_{2s}^* = 156\,961$. The total harvest, $H_{1s}^* + H_{2s}^* = 229\,207$ is less than the total harvest from optimal metapopulation harvesting, $H_1^* + H_2^* = 274\,500$. Note that the escapements are the direct opposite of those

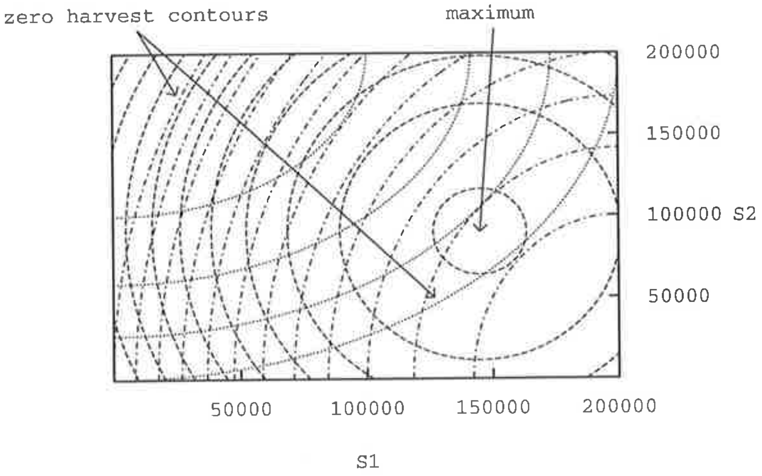

FIGURE 2.5: The objective function and harvest contours as functions of escapements S_1 and S_2 for P_1 with negligible costs. The objective function is represented by the dash contours, harvests H_1 by dot contours, and H_2 by the dash-dot contours. The global maximum is found at $S_1^* = 145\,050$ and $S_2^* = 90\,100$ with harvests $H_1^* = 17\,351$ and $H_2^* = 257\,149$. The contour increment is 25 000, starting from zero.

derived for metapopulation harvesting. This is due to the difference in the growth rate terms. In the metapopulation theory, local population i has $r = r_i(p_{ii} + p_{ij})$ whereas $r_{is} = r_i p_{ii} + r_j p_{ji}$ in the unconnected single population case. Thus if this metapopulation is exploited assuming that the local populations are unconnected single populations then we will be under-harvesting the relative sink/importer local population while over-harvesting the relative source/exporter local population.

The single escapement derived if the metapopulation is believed to be a well-mixed single population is $S_L^* = 253\,467$, which, as shown above, is greater than the sum of the two escapements from metapopulation harvesting, $S_1^* + S_2^* = 235\,150$. The estimated harvest is $H_L^* = 266\,267$ which is less than the total harvest from metapopulation exploitation, $H_1^* + H_2^* = 274\,500$. Thus if we manage the population believing it to be a single well mixed population, we will be under-exploiting the resource.

	Metapopulation	Unconnected Single Populations	Well-mixed Single Population
S_1^*	145	90	-
S_2^*	90	145	-
S_{Total}^*	235	235	S_L^*=253
H_1^*	17	72	-
H_2^*	257	157	-
H_{Total}^*	274	229	H_L^*=266

TABLE 2.2: Management policy comparisons with migration matrix P_1 and negligible costs. Table escapements and harvests are rounded to the nearest thousand $\times 10^3$.

2.3.4 An example with an optimal harvest that is negative

As an example that produces negative harvests on applying the escapements from equations (2.24) and (2.25), consider a local population that has $p_{22} = p_{12}$ and p_{11} and p_{21} equal and extremely small, i.e. few recruits remain within local population 1 and few migrate there.

Assume that the migration matrix is,

$$P_2 = \begin{pmatrix} 0.0001 & 0.002 \\ 0.0001 & 0.002 \end{pmatrix}. \tag{2.36}$$

Thus, local population 1 is a relative exporter, but it is not a relative source. The local populations have unharvested stable equilibria $\bar{R}_1 = 10\,982$ and $\bar{R}_2 = 219\,651$.

Equations (2.24) and (2.25) produce equal optimal escapements for both local populations, $S_1^* = S_2^* = 95\,333$. However, the equilibrium harvests are $H_1^* = -80\,715$ and $H_2^* = 195\,210$. If we assume that no harvest is taken from local population 1 while $R_{10} < S_1^*$ (this is the procedure for a single population), and attempt to use the

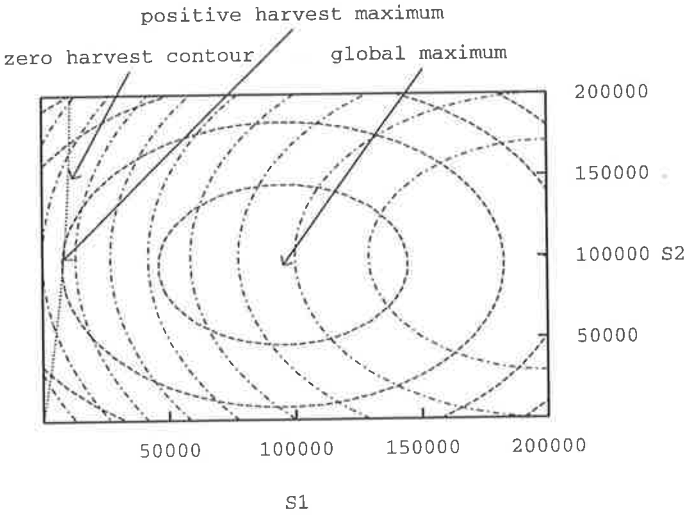

FIGURE 2.6: The objective function and harvest contours as functions of escapements S_1 and S_2 for P_2 with negligible costs. The objective function is represented by the dash contours, harvests H_1 by dot contours, and H_2 by dash-dot contours. The global maximum produces a negative harvest from local population 1. The positive harvest maximum is found along the $H_1 = 0$ contour. The contour increment is 25 000, starting from zero.

above escapements, local population 1 does not approach S_1^* but actually decreases (see Table 2.3). From Figure 2.6 we see that negative harvests are indeed produced from local population 1. To find the feasible non-negative optimal escapements we set $H_1^{*'} = 0$ and find the new maximum of equation (2.11). In this example the new optimal escapements are $S_1^{*'} = 8\,333$ and $S_2^{*'} = 100\,174$, with harvests $H_1^{*'} = 0$ and $H_2^{*'} = 66\,419$ (see Table 2.4). Thus we protect the relative exporter local population and harvest the relative importer local population.

Comparison with an incorrect harvesting policy

Due to the negative harvests produced, in this case it is difficult to make a comparison with the escapements and harvests produced from well-mixed single population management. We find that the estimated escapements from the incorrect policy produce a

	S_1^*	S_2^*	H_1^*	H_2^*
1	10 983	95 333	0	124 318
2	8 340	95 333	0	71 349
3	8 086	95 333	0	66 319
4	8 061	95 333	0	65 832
5	8 059	95 333	0	65 785
6	8 059	95 333	0	65 780
7	8 059	95 333	0	65 780

TABLE 2.3: Escapements and harvests for the migration matrix P_2. The global optimal escapements are $S_1^* = S_2^* = 95\,333$. However, starting from the unharvested equilibria, local population 1 does not increase to S_1^*, suggesting the optimality of a "negative" harvest .

negative harvest as well. However, we can make a comparison if the metapopulation is assumed to be two unconnected single populations. The escapement for local population 1 is negative and thus is set to zero, while $S_{2s}^* = 145\,050$. The harvests produced are $H_{1s}^* = 9\,245$ and $H_{2s}^* = 39\,998$ with a total harvest considerably less than that achieved using metapopulation harvesting. Thus, local population 1 is over-harvested while local population 2 is under-harvested. The harvest for local population 1 is not zero even though its escapement is zero due to the seasonal migration of juveniles from local population 2.

Note that if $p_{11} = p_{21} = 0$ in the above example then local population 1 is doomed to extinction ($S_1^* = 0$) and we harvest local population 2 as a single population.

	Metapopulation	Unconnected Single Populations
S_1^*	8	0
S_2^*	100	145
S_{Total}^*	108	145
H_1^*	0	9
H_2^*	66	40
H_{Total}^*	66	49

TABLE 2.4: Management policy comparisons with migration matrix P_2 and negligible costs. Table escapements and harvests are rounded to the nearest thousand $\times 10^3$.

2.4 Examples that include harvest costs

So far we have ignored the costs associated with harvesting the local populations. The inclusion of costs makes interpretations more difficult, so in the next section we use specific examples to illustrate our results.

2.4.1 Iteration of the dynamic programming equations

In this example, we simply iterate the dynamic programming equations so as to compare the results from our analytic solution with the numeric solution, and to observe the effect of including costs on optimal exploitation strategies.

Suppose that we have an unharvested metapopulation that is composed of two connected local populations. Both local populations are to be exploited. The local populations' dispersal is represented by the migration matrix,

$$P = \begin{pmatrix} 0.1 & 0.1 \\ 0.15 & 0.1 \end{pmatrix}.$$

T	R_1	R_2	S_1	S_2	H_1	H_2
5	133	105	65	68	68	37
4	118	96	65	68	53	28
3	118	96	65	68	53	28
2	118	96	65	68	53	28
1	118	96	65	68	53	28
0	118	96	33	33	85	63

TABLE 2.5: Escapements and harvests from iterating the dynamic programming equations.

Thus, local population 2 is a relative source/exporter, while local population 1 is a relative sink/importer. The juvenile production function is logistic, as seen earlier, with growth rates $r_1 = r_2 = 10$, adjusted carrying capacities $K_1 = K_2 = 200$ and adult survival per period $\delta_1 = \delta_2 = 0.1$. The unharvested equilibrium population sizes are $\bar{R}_1 = 133$ for local population 1 and $\bar{R}_2 = 105$ for local population 2.

The cost function is defined by,

$$c_i(x_i) = \frac{a_i}{q_i x_i}, \tag{2.37}$$

where $a_i = 30$ and $q_i = 1.3 \times 10^{-2}$. The price of a unit of stock is $p = 70$. Thus the zero net profit escapement level is,

$$S_{i\infty} = a_i/q_i p = 33.$$

for $i = 1, 2$. The discount rate is 10%. If the dynamic programming equations (2.9) are iterated, we produce the escapements and harvests shown in Table 2.5.

The initial conditions are the unharvested equilibrium population sizes, $\bar{R}_1 = 133$ and $\bar{R}_2 = 105$. The final period's escapements is the zero net profit level, $S_{i\infty}$, as expected. The equilibrium escapements found are $S_1^* = 65$ and $S_2^* = 68$, with harvests $H_1^* = 53$ and $H_2^* = 28$. Thus we protect the relative source/exporter local population and take a greater harvest from the relative sink/importer local population.

Comparing the numerical results from the above analysis to the analytic results derived from equations (2.15) and (2.16), we see that similar equilibrium escapements and harvests are found; $S_1^* = 66$ and $S_2^* = 70$ with harvests $H_1^* = 53$ and $H_2^* = 27$. The small differences may be due to rounding errors in the computer programs. Comparisons with the negligible costs harvests from the example in Section 2.3.1 suggest that the rule of thumb source/sink results appear to be robust when costs are included.

2.4.2 Variation of the migration parameters

To further investigate the effect of the migration parameters on optimal harvesting policies, in this example we vary the proportion of juveniles that migrate between local populations, p_{12} and p_{21}, while the other parameters remain constant. The section extends the no costs example of Section 2.3.2.

Consider a metapopulation with parameters, $r_1 = r_2 = 1\,000$, $K_1 = K_2 = 400\,000$ and $\delta_1 = \delta_2 = 0.001$, and migration matrix,

$$P = \begin{pmatrix} 0.001 & p_{12} \\ p_{21} & 0.001 \end{pmatrix}.$$

The cost function is defined by equation (2.37), with $a_i = 5\,000$ and $q_i = 1.3 \times 10^{-5}$ for $i = 1, 2$. The price of a unit of fished stock is $p = 7\,000$. The discount rate is 10%.

In Figure 2.7 we plot the escapements and harvests of local population 1 as contour lines. Local population 1 is a relative source/exporter if the point (p_{12}, p_{21}) is below the line $p_{12} = p_{21}$, and it is a relative sink/importer if above. To determine the optimal escapement and harvest of local population 2 we can transpose the migration matrix P. This reflects Figure 2.7 about the line $p_{12} = p_{21}$.

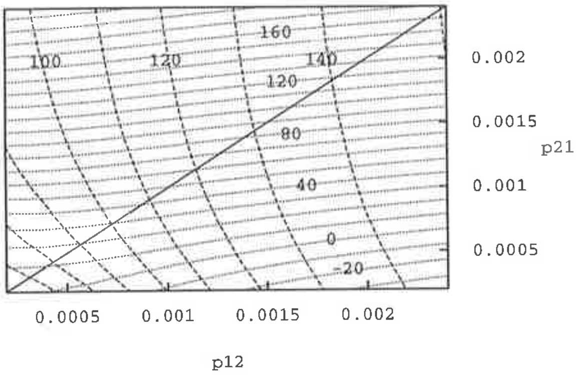

FIGURE 2.7: Escapements (dashes) and harvests (dots) of local population 1 as a function of the migration parameters. Numbers on the contours are escapements and harvests $\times 10^3$.

As observed in the example of Section 2.3.2, a negative harvest is obtained from local population 1 if it is a strong relative exporter/source. As an example, take $p_{12} = 0.0014$ and $p_{21} = 0.0002$. This produces optimal escapements, $S_1^* = 117\,621$ and $S_2^* = 90\,701$, with harvests $H_1^* = -20\,442$ and $H_2^* = 95\,772$. Assuming that seeding a unit of stock costs the same as harvesting the same unit of stock, then the net harvest from the metapopulation is $H_1^* + H_2^* = 75\,330$. If a negative harvest is not possible from local population 1 then, setting $H_1^{*\prime} = 0$ and maximising equation (2.11), we find $S_1^{*\prime} = 77\,047$ and $S_2^{*\prime} = 97\,658$ with a harvest from local population 2 of $H_2^{*\prime} = 63\,344$. Thus, the net harvest is greater if we seed local population 1 (however, see the Closing Remarks of this chapter for a discussion on the optimality of a negative harvest).

2.4.3 Harvesting relative sources and sinks

We now consider the two examples with migration matrices P_1 and P_2 when costs are no longer considered negligible. The cost function used is defined by equation (2.37), with $a_i = 5\,000$ and $q_i = 1.3 \times 10^{-5}$ for $i = 1, 2$. The price of a unit of fished stock is $p = 7\,000$.

	Metapopulation	Unconnected Single Populations	Well-mixed Single Population
S_1^*	156	114	-
S_2^*	122	158	-
S_{Total}^*	278	272	S_L^*=270
H_1^*	24	63	-
H_2^*	249	182	-
H_{Total}^*	273	245	H_L^*=267

TABLE 2.6: Management policy comparisons with migration matrix P_1 and costs included. Table escapements and harvests are rounded to the nearest thousand$\times 10^3$.

For the first example, where the migration matrix is P_1, equations (2.15) and (2.16) yield optimal escapements, $S_1^* = 156\,169$ and $S_2^* = 121\,953$ (see Table 2.6). The optimal harvests are $H_1^* = 23\,956$ and $H_2^* = 248\,532$. Thus we still harvest the relative source population conservatively.

Comparisons with incorrect harvesting policies

If the local populations are believed to be reproductively isolated then the optimal escapements for each local population are $S_{1_s}^* = 114\,121$ and $S_{2_s}^* = 158\,141$ with harvests $H_{1_s}^* = 63\,175$ and $H_{2_s}^* = 182\,323$. Once again, the sum of the metapopulation escapements is greater than the sum of the escapements if the local populations were managed believing them to be unconnected, $S_{1_s}^* + S_{2_s}^* = 272\,262$. The total harvest, $H_{1_s}^* + H_{2_s}^* = 245\,498$, is also less than the harvest from metapopulation management.

The escapement derived from well-mixed single population harvesting is $S_L^* = 269\,996$, which is no longer greater than the sum of the escapements from metapopulation harvesting, $S_1^* + S_2^* = 278\,122$. The harvest produced using S_L^* is $H_L^* = 266\,895$, which is less than the total harvest from metapopulation harvesting, $H_1^* + H_2^* = 272\,488$. Thus we not only leave more stock but we also harvest more than if the population was managed as a well-mixed single population.

Thus, in comparison to alternative management schemes, metapopulation harvesting not only leaves more of the stock behind but it also increases the combined harvest from the local populations.

2.4.4 An example with an optimal harvest that is negative

Using the migration matrix P_2 the optimal escapements from equations (2.15) and (2.16) are $S_1^* = 118\,129$ and $S_2^* = 118\,397$ (see Table 2.7). As before this produces a negative harvest in local population 1. Setting $H_1^{*'} = 0$ and searching for the maximum of equation (2.11), we produce new optimal escapements $S_1^{*'} = 9\,509$ and $S_2^{*'} = 124\,400$ with harvest $H_2^{*'} = 65\,713$.

Comparison with an incorrect harvesting policy

If the local populations were managed believing them to be unconnected single populations then the escapements produced would be $S_{1s}^* = 7\,164$ and $S_{2s}^* = 158\,141$ with harvests $H_{1s}^* = 3\,109$ and $H_{2s}^* = 47\,328$. The total harvest, $H_{1s}^* + H_{2s}^* = 50\,437$ is less than the harvest achieved using metapopulation harvesting theory.

2.5 Closing Remarks

In this chapter we have extended the single population optimal harvesting model of Clark (1972; 1973) by assuming that the exploited stock is spatially structured. We

	Metapopulation	Unconnected Single Populations
S_1^*	10	7
S_2^*	124	158
S_{Total}^*	134	165
H_1^*	0	3
H_2^*	66	47
H_{Total}^*	66	50

TABLE 2.7: Management policy comparisons with migration matrix P_2 and costs included. Table escapements and harvests are rounded to the nearest thousand $\times 10^3$.

no longer assume that the exploited stock is a single homogeneous population, but assume it is composed of two interacting sub-populations or local populations. The local populations have their own specific growth and death characteristics. Together the local populations form a dynamic heterogeneous unit that is connected by migrating juveniles and referred to as a metapopulation.

Modelling the metapopulation dynamics with discrete, coupled difference equations, we optimised the present value of net revenues derived from each local population. This maximisation used the dynamic programming techniques of Clark (1976). We showed that the equations for optimal harvesting are generalisations of the fundamental equation of renewable resources derived for the exploitation of a single population.

To facilitate our understanding of the system, results were derived under some simplifying assumptions (negligible costs, equivalence of some local population parameters, logistic growth). In this way we were able to compare escapements between local populations and compare harvesting strategies from incorrect management policies. These comparisons were then discussed in relation to two biological classifications of local populations, namely *relative source/sink* local populations and *relative exporter/importer* local populations. These populations are defined according to their per capita larval production.

Under the simplifying assumptions, our results suggest that relative source local populations should have the larger optimal escapement of the two local populations. Relative sinks should have the smaller escapement. We also compared the escapements derived from the metapopulation theory with the estimated escapements from harvesting policies that are employed without the managing body recognising the metapopulation structure of the stock. If the local populations are managed as two unconnected single populations, results suggest that relative exporter local populations will have a smaller escapement than that proposed by the metapopulation theory. Over-exploitation of relative exporters is therefore a possible consequence of this mismanagement. Conversely, relative importer local populations will be harvested too conservatively. The metapopulation could also be managed as a well-mixed single population. In this case, we find that the relative source local population will be over-exploited, while the relative sink local population is under-exploited. Numerical examples for the special case of negligible or density and local population independent costs confirm these results and the above rules-of-thumb also appear to be robust when costs are included.

An interesting result which is a direct consequence of the extension into two dimensions is the optimality of a negative harvest. Long (1992), in a note on the model of Feichtinger *et al* (1992), discovers that by a change of variable, Feichtinger *et al*'s model on resource-employment dynamics can be transformed into a predator-prey model. Long applies the model to squid-krill interactions and finds an optimal negative harvest of squid when krill abundance is high and squid stocks are low. The negative harvest is interpreted as an optimal seeding policy, i.e. replenish the squid stock and encourage growth in the population. The negative harvest is optimal until the squid abundance begins to decrease due to a decline in krill stocks (see Feichtinger *et al* (1992), Figure 5).

In our formulation, we also find an optimal negative harvest which is interpreted as an optimal seeding strategy, i.e. placing stock into a particular local population so as to maximise economic gains from the harvest of the other local population. However, we now consider what a negative harvest actually means in terms of the net revenue expression for local population i,

$$NR_i = \int_{R_i - H_i}^{R_i} \left(p - \frac{a_i}{q_i x}\right) dx. \tag{2.38}$$

Evaluating the integral, this can be rewritten as,

$$NR_i = pH_i - \frac{a_i}{q_i} \ln\left(\frac{R_i}{R_i - H_i}\right). \tag{2.39}$$

For a positive or zero harvest this expression states that the net revenue is equal to the benefits received from the sale of a harvest H_i, minus the costs of harvesting the population down to $R_i - H_i$. How do we interpret the above equations when harvests are less than zero?

The first term, pH_i can be interpreted as the cost (remember $H_i < 0$) of buying (or raising) H_i juveniles for seeding. However, the price per unit of juveniles is not likely to be equal to the sale price of adults. In a more realistic model we could have a different price, say p', for the sale price (or raising cost) per individual. The second term is the benefit (positive) of restocking the population up to $R_i - H_i$. This is unrealistically positive in the current form and should actually be the cost, possibly independent of stock size, of restocking a local population. In a more realistic model we could have C_i representing this cost.

Thus, a model where seeding is considered a possible harvest strategy, the net revenue for local population i could be of the form,

$$NR_i = \begin{cases} \int_{R_i - H_i}^{R_i} (p - \frac{a_i}{q_i x})\, dx. & \text{if } H_i > 0 \\ p' H_i - C_i & \text{if } H_i < 0. \end{cases} \tag{2.40}$$

This model is not analysed in this thesis and is a possible area for future research. In the basic model described in this chapter, and in the models that follow, the limitation described above should be kept in mind when optimal negative harvests are found. As unrealistic as the negative harvests are, they are a good indication of where seeding strategies could be considered. If negative harvests are not possible then the best strategy is to set the harvest of that local population to zero and search for the escapements which maximise the particular objective function with which we are concerned. We suspect that a revised model of the form shown above will show regions in parameter space where fully harvested metapopulations are optimal, then move into a region where a local population should be unharvested, then as parameters change further, a region where it has become economically feasible for the seeding of the local population.

Chapter 3

Delayed juvenile recruitment

In this chapter we consider populations where there is a delay in recruitment to the adult breeding stock. Previous chapters have assumed that the juveniles produced from the breeding adults of one generation become members of the spawning stock themselves in the following generation. In a sense, there is already a one year delay inherent in the discrete models. However, it may take several years for juveniles to reach sexual maturity.

A well-documented example of species that have an extended period of growth before sexual maturity are the baleen whales. Baleen whales have a maturation period of at least five years (Clark and Lamberson, 1982). Sei whales are believed to reach sexual maturity after approximately nine years, while for southern hemisphere Fin whales the maturation period is around eight years (Allen, 1963; Fisher and Goh, 1984).

Australia's orange roughy fishery is a recently established and valuable fishery, exploiting stock off the north-east and southern coast of Tasmania. Radiometric aging of otoliths (the ear bone) have estimated that orange roughy live past 100 years and do not become sexually mature until 20-25 years old (Francis (1992) uses an estimate of

23 years in a risk assessment model). This can have a dramatic affect on management strategies due to lower rates of growth, natural mortality and thus productivity than other harvested stocks. Determining the stock structure of the population has yet to be fully addressed (Elliott and Ward, 1992) and the degree of mixing between the two populations will be important for the sustainable management of the fishery (Sustainable Development Fisheries Working Group, 1991).

The age at maturity of scallops varies widely depending on the species and locality (Orensanz *et al.*, 1991). The saucer scallop *Amusium japonicum balloti* of the central Queensland coast begins spawning after approximately one year (no delay as far as our models are concerned) (Dredge, 1981), while arctic species may take up to 6 years, (e.g. the Iceland scallop *Chlamys islandica* (Vahl, 1981)). Scallops also show marked differences in reproductive schedules within species. These differences have been attributed to genetic or environmental factors (for a review see Orensanz *et al* (1991)).

The size and age at sexual maturity of five species of southern Australian abalone is investigated by Shepherd and Laws (1974). They find that the commercially valuable abalone species *Haliotis laevigata* and *Haliotis ruber* both become sexually mature after around 3 years and between 75-120mm, depending on locality. Interestingly, *H. ruber* of Tipara Reef appear to mature later than at the other localities, maturing at 4 years of age. The local environment of the abalone species also plays an important role in determining the size at maturity, through its affect on growth rates, and on spawning times, which is related to factors like sea temperature and food availability. This emphasises the importance of local habitats on population dynamics and ultimately on management policies.

In this chapter we first consider optimal harvesting policies for a spatially homogeneous population with a maturation delay. Clark (1976) uses Lagrange multipliers to determine the optimal harvesting equation that implicitly defines the optimal escapement for arbitrary recruitment delays. Clark then employs dynamic programming to show that the most-rapid-approach is not optimal when costs are density-dependent. We show that Clark's dynamic programming procedure can be extended to derive his optimal harvesting equation.

We then consider two models that include spatial structure. The first model assumes that larvae that settle at a particular local population experience a delay in sexual maturation that is related to the local population they settle in. This delay effect may be due to environmental conditions (food availability, local temperature). The second model assumes that the delay experienced by the larvae is related to the source of the larvae, i.e. the parent local population. We assume that either genetic (however, there is not likely to be great genetic differences in such a well-mixed population) or environmental conditions cause the delay. For example, larvae may remain in the parent local population while immature and before migration occurs.

These two models are then mathematically described using coupled delay-difference equations, and the method of Lagrange multipliers is used to determine optimal harvesting policies. Using the simplifying assumption of negligible costs we produce analytic results that allow comparisons between each local population's escapement and comparisons between incorrect harvesting policies and the metapopulation theory. We conclude each model with hypothetical examples which allow us to investigate optimal harvesting strategies in more detail.

3.1 Single population recruitment delay model

In 1976, Colin Clark determined the optimal harvesting equation for a single population that has delayed juvenile recruitment to the breeding stock. The delay-difference equation used to model the population dynamics is,

$$R_{k+1} = \delta R_k + G(R_{k-\beta}), \tag{3.1}$$

where R_k is the stock abundance in generation k, δ is the per generation adult survival, the function $G(\cdot)$ is called the recruit production function and defines the number of surviving juveniles produced β years ago that join the mature stock. The recruit production function is a function of the adult abundance β years ago (β is the juvenile recruitment delay).

This model presents a simple way in which to include age-structure in a lumped-parameter population model. Beddington (1978) showed that the delay-difference equation model is a simplification of a more detailed age-structured Leslie matrix model (Leslie, 1945). Let $N_i(k)$ be the number of immature females of age i in generation or year k, with associated survivorship δ_i. Let $N_\beta(k)$ be the number of mature and reproductive females of age β or more in year k, with δ_β their annual survivorship. Let $F(N_\beta(k))$ be a density dependent function representing the fecundity of reproducing females in year k. We can then relate the abundance in generation $k+1$ to that of generation k using the matrix formulation below,

$$\begin{bmatrix} N_0(k+1) \\ N_1(k+1) \\ N_2(k+1) \\ \vdots \\ N_\beta(k+1) \end{bmatrix} = \begin{bmatrix} 0 & 0 & \cdots & 0 & F(N_\beta(k)) \\ \delta_0 & 0 & \cdots & 0 & 0 \\ 0 & \delta_1 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & \delta_{\beta-1} & \delta_\beta \end{bmatrix} \begin{bmatrix} N_0(k) \\ N_1(k) \\ N_2(k) \\ \vdots \\ N_\beta(k) \end{bmatrix}. \tag{3.2}$$

Multiplying this matrix equation out and back substituting iteratively, beginning with the equation for $N_\beta(k+1)$, we find

$$N_\beta(k+1) = \delta_{\beta-1}\delta_{\beta-2}\ldots\delta_0 F(N_\beta(k-\beta))N_\beta(k-\beta) + \delta_\beta N_\beta(k), \tag{3.3}$$

which can then be simplified to the difference equation (3.1) if we assume that $R_k = N_\beta(k)$, $\delta = \delta_\beta$ and $G(R_{k-\beta}) = \delta_{\beta-1}\delta_{\beta-2}\dots\delta_0 F(R_{k-\beta})R_{k-\beta}$.

The Leslie matrix model described lumps female abundances into the single variable $N_\beta(k)$ and then assumes that all females that reach sexual maturity have an equal effect on recruitment. In many cases this assumption should be relaxed and several different adult female age-classes should be followed. The effect of truncations in reproduction, where after a fixed period of time individuals are no longer reproductive, can then be investigated (see Levin and Goodyear (1980), Reed (1983), Silva and Hallam (1993)). In this analysis we only consider the delay-difference equation (3.1) and its extension to include spatially heterogeneous populations.

3.1.1 Derivation of the optimal harvesting strategy

We now derive the equation that defines the optimal harvesting strategy for the delay-difference equation model (3.1).

An interesting feature of this model is that the most-rapid-approach policy is not optimal when harvest costs are included due to the nonlinearity of the net revenue expression. To show this, we extend the dynamic programming framework proposed by Clark (1976) and attempt to find an optimal equilibrium solution. For simplicity, consider a juvenile recruitment delay of one year, $\beta = 1$. Assume that we are able to selectively harvest the breeding adults from the local populations. Following Clark, we define the value function,

$$J_T(R_0; R_{-1}) = \max_{0 \le S_k \le R_k} \sum_{k=0}^{T} \alpha^k \Pi(R_k, S_k), \tag{3.4}$$

which is subject to equation (3.1), and where R_{-1} is the stock abundance (or escapement) of the generation before the initial period.

From the value function, equation (3.4), we derive Bellman's equation,

$$J_{T+1}(R_0; R_{-1}) = \max_{0 \leq S_0 \leq R_0} \Big(\Pi(R_0, S_0) + \alpha J_T(\delta S_0 + G(R_{-1}); S_0) \Big). \tag{3.5}$$

If the time horizon is zero, $T = 0$, then

$$\begin{aligned} J_0(R_0; R_{-1}) &= \max_{0 \leq S_0 \leq R_0} \Pi(R_0, S_0) \\ &= \Pi(R_0, S_\infty), \end{aligned} \tag{3.6}$$

where S_∞ is chosen such that $p - c(S_\infty) = 0$. Consider next the time horizon $T = 1$,

$$\begin{aligned} J_1(R_0; R_{-1}) &= \max_{0 \leq S_0 \leq R_0} \Big(\Pi(R_0, S_0) + \alpha J_0(\delta S_0 + G(R_{-1}); S_0) \Big) \\ &= \max_{0 \leq S_0 \leq R_0} \Big(\Pi(R_0, S_0) + \alpha \Pi(\delta S_0 + G(R_{-1}), S_\infty) \Big). \end{aligned} \tag{3.7}$$

Differentiating equation (3.7) with respect to S_0 we find,

$$0 = -(p - c(S_0)) + \alpha(p - c(\delta S_0 + G(R_{-1})))\delta \tag{3.8}$$

or,

$$\frac{1}{\alpha} = \frac{(p - c(\delta S_0 + G(R_{-1})))\delta}{(p - c(S_0))}. \tag{3.9}$$

This equation defines the first year optimal escapement with one period to go. We call this escapement S_1^*. Note that if costs are negligible then there is no solution and it is optimal to harvest the whole population, $S_1^* = 0$. This no-costs result is found by Clark (1976). For the final two-periods we harvest all available stock. This is intuitive; the juveniles produced in the last two periods will not benefit future harvests, as they join the adult stock after the terminal period. However, when there are three or more periods to go, juvenile production is important.

Placing S_1^* back into J_1, we produce

$$J_1(R_0; R_{-1}) = \Pi(R_0, S_1^*) + \alpha \Pi(\delta S_1^* + G(R_{-1}), S_\infty). \tag{3.10}$$

Consider the time horizon $T = 2$,

$$\begin{aligned} J_2(R_0; R_{-1}) = \max_{0 \le S_0 \le R_0} \Big(\Pi(R_0, S_0) &+ \alpha J_1(\delta S_0 + G(R_{-1}); S_0) \Big) \\ = \max_{0 \le S_0 \le R_0} \Big(\Pi(R_0, S_0) &+ \alpha \Pi(\delta S_0 + G(R_{-1}), S_\infty) \\ &+ \alpha^2 \Pi(\delta S_1^* + G(S_0), S_\infty) \Big). \end{aligned} \tag{3.11}$$

Differentiating with respect to S_0 we find,

$$\begin{aligned} 0 = -(p - c(S_0)) &+ \alpha(p - c(\delta S_0 + G(R_{-1})))\delta \\ &+ \alpha^2 (p - c(\delta S_1^* + G(S_0))) F'(S_0). \end{aligned} \tag{3.12}$$

Equation (3.12) implicitly defines the optimal escapement when there are two periods to go, S_2^*. In the non-delay model (see Chapter 2 for the two local population non-delay analogy), the second discounted term is not a function of S_0, and so we produce the same optimal equation for $T \ge 2$ as $T = 1$ and this equation is optimal for all periods. The approach path to the equilibrium escapement is thus the most-rapid-approach. Here, the second discounted term is a function of S_0, and so the optimal equation that defines S_2^*, equation (3.12), is different from equation (3.9).

Placing S_2^* back into equation (3.11),

$$\begin{aligned} J_2(R_0; R_{-1}) = \Pi(R_0, S_2^*) &+ \alpha \Pi(\delta S_2^* + G(R_{-1}), S_1^*) \\ &+ \alpha^2 \Pi(\delta S_1^* + G(S_2^*), S_\infty). \end{aligned} \tag{3.13}$$

Now consider the following time horizon, $T = 3$,

$$\begin{aligned} J_3(R_0; R_{-1}) = \max_{0 \le S_0 \le R_0} \Big(\Pi(R_0, S_0) &+ \alpha J_2(\delta S_0 + G(R_{-1}); S_0) \Big) \\ = \max_{0 \le S_0 \le R_0} \Big(\Pi(R_0, S_0) &+ \alpha \Pi(\delta S_0 + G(R_{-1}), S_2^*) \\ &+ \alpha^2 \Pi(\delta S_2^* + G(S_0), S_1^*) \\ &+ \alpha^3 \Pi(\delta S_1^* + G(S_2^*), S_\infty) \Big). \end{aligned} \tag{3.14}$$

Differentiating with respect to S_0, we produce,

$$\begin{aligned} 0 = -(p - c(S_0)) \quad &+ \quad \alpha(p - c(\delta S_0 + G(R_{-1})))\delta \\ &+ \quad \alpha^2(p - c(\delta S_2^* + G(S_0)))F'(S_0). \end{aligned} \tag{3.15}$$

Equation (3.15) can be implicitly solved for the optimal escapement when there are three periods to go, S_3^*.

We generalise this procedure to the N periods to go case,

$$J_N(R_0; R_{-1}) = \max_{0 \leq S_0 \leq R_0} \Big(\Pi(R_0, S_0) \quad + \quad \alpha J_{N-1}(\delta S_0 + G(R_{-1}); S_0) \Big) \tag{3.16}$$

$$\begin{aligned} = \max_{0 \leq S_0 \leq R_0} \Big(\Pi(R_0, S_0) \quad &+ \quad \alpha \Pi(\delta S_0 + G(R_{-1}), S_{N-1}^*) \\ &+ \quad \alpha^2 \Pi(\delta S_{N-1}^* + G(S_0), S_{N-2}^*) \\ &+ \quad \alpha^3 \Pi(\delta S_{N-2}^* + G(S_{N-1}^*), S_{N-3}^*) \\ &+ \quad \cdots \\ \cdots \quad &+ \quad \alpha^{N-1} \Pi(\delta S_2^* + G(S_3^*), S_1^*) \\ &+ \quad \alpha^N \Pi(\delta S_1^* + G(S_2^*), S_\infty) \Big), \end{aligned} \tag{3.17}$$

and so we have,

$$\begin{aligned} J_N(R_0; R_{-1}) = \max_{0 \leq S_0 \leq R_0} \Big(\Pi(R_0, S_0) \quad &+ \quad \alpha \Pi(\delta S_0 + G(R_{-1}), S_{N-1}^*) \\ &+ \quad \alpha^2 \Pi(\delta S_{N-1}^* + G(S_0), S_{N-2}^*) + A(S_c^*) \Big), \end{aligned} \tag{3.18}$$

where $A(S_c^*)$ is constant in terms of S_0. Differentiating with respect to S_0 we find,

$$\begin{aligned} 0 = -(p - c(S_0)) \quad &+ \quad \alpha(p - c(\delta S_0 + G(R_{-1})))\delta \\ &+ \quad \alpha^2(p - c(\delta S_{N-1}^* + G(S_0)))F'(S_0). \end{aligned} \tag{3.19}$$

If we assume that the system is in equilibrium, then $S_0 = R_{-1} = S_{N-1}^*$ and $R_{k+1} = R_k = \delta S^* + G(S^*)$ where S^* is the equilibrium optimal escapement. We can rewrite equation (3.19) as,

$$0 = -(p - c(S^*)) + \alpha(p - c(\delta S^* + G(S^*)))(\delta + \alpha F'(S_0)), \tag{3.20}$$

or,

$$\frac{1}{\alpha} = \frac{(p - c(\delta S^* + G(S^*)))}{(p - c(S^*))}(\delta + \alpha F'(S^*)). \tag{3.21}$$

This equation implicitly defines the optimal equilibrium escapement S^*, when there is a one year delay in juvenile recruitment to the adult breeding stock. Clark (1976) derives the optimal equation for a general delay β using the method of Lagrange multipliers. The details of this method are not given for the single population case, as we use the method in the two local population theory that follows.

The equation that defines the optimal equilibrium escapement for a general delay β is,

$$\frac{1}{\alpha} = \frac{p - c(F(S^*))}{p - c(S^*)}\left(\delta + \alpha^\beta G'(S^*)\right), \tag{3.22}$$

where,

$$F(S^*) = \delta S^* + G(S^*). \tag{3.23}$$

Clark notes that even though the most-rapid-approach policy is sub-optimal to an asymptotic approach, it is only marginally sub-optimal.

When harvest costs are negligible or density-independent, the most-rapid-approach is the optimal approach policy. Equation (3.22) becomes,

$$\frac{1}{\alpha} = \delta + \alpha^\beta G'(S^*), \tag{3.24}$$

and this equation holds for all time horizons, unlike when harvesting costs are included. If we assume that the population has logistic juvenile production, then the optimal equilibrium escapement is,

$$S^* = \frac{K}{2} - \frac{K}{2}\left(\frac{1 + d - \delta}{\alpha^\beta r}\right), \tag{3.25}$$

and clearly, if S^* is negative then we reassign the escapement to zero. The inclusion of a delay in recruitment results in a decrease in the optimal escapement over the non-delay model ($\beta = 0$). This result is intuitive if we consider the complete harvesting of a population due to a large (infinite say) delay. It can not be optimal to wait (infinitely long) for the juveniles to mature.

Clark (1976) also considers local stability conditions for the unexploited delay-difference equation (3.1). Using linearised stability analysis, Clark analytically determines a sufficient condition for stability and numerically determines, for combinations of δ and β, the necessary and sufficient condition for stability. Goh and Agnew (1978), Fisher and Goh (1984), Bergh and Getz (1988) and Botsford (1992), among other authors, have looked at the stability of various extensions of the model.

We now consider strategies for the optimal harvesting of a spatially structured population with juvenile recruitment delays. The first model assumes that the delay experienced by the larvae is related to the receiving local population; we call this model the receptor local population delay model. The second model assumes that the delay is related to the source of the larvae; we call this the parental delay model. A general two-species model formulated by Agnew (1982) has a similar structure to the receptor delay model analysed here. Agnew considers two species (or two sexes) that reach sexual maturity after a specified delay (or no delay) and investigates stability and optimal exploitation regimes. The single-species model employed here can be seen as a special case of Agnew's model, but with additional features such as spatial structure and local population interaction.

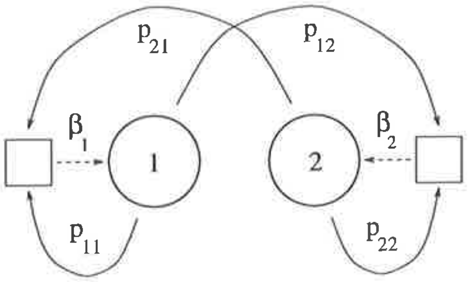

FIGURE 3.1: A metapopulation that shows delayed juvenile recruitment. The delay for local population i is given by β_i. The boxes represent the immature stock before it joins the sexually mature adults represented by the circles.

3.2 Receptor local population delay model

Assume that we have an unharvested metapopulation composed of two local populations. The proportion of juveniles that migrate from local population i and successfully recruit to local population j after the maturation delay is given by p_{ij}. We assume that the sedentary larvae of local population i and those larvae that migrate to local population i from local population j, will experience a delay of β_i periods before recruiting to the adult stock (see Figure 3.1). This assumes that the delay is related to the environment of the receptor local population, and not the parent local population.

Thus, suppose that the two interacting unharvested local populations are modelled by the following stock-recruitment relation,

$$\begin{aligned} R_{1k+1} &= \delta_1 R_{1k} + p_{11}G_1(R_{1k-\beta_1}) + p_{21}G_2(R_{2k-\beta_1}) && (3.26) \\ R_{2k+1} &= \delta_2 R_{2k} + p_{12}G_1(R_{1k-\beta_2}) + p_{22}G_2(R_{2k-\beta_2}), && (3.27) \end{aligned}$$

where parameters and variables retain their usual meaning.

The local populations are harvested, H_{ik}, and the escapements $S_{ik} = R_{ik} - H_{ik}$ then grow according to equations (3.26) and (3.27) to R_{ik+1}. Thus, including harvesting, equations (3.26) and (3.27) become,

$$R_{1k+1} = \delta_1 S_{1k} + p_{11}G_1(S_{1k-\beta_1}) + p_{21}G_2(S_{2k-\beta_1}) \tag{3.28}$$

$$R_{2k+1} = \delta_2 S_{2k} + p_{12}G_1(S_{1k-\beta_2}) + p_{22}G_2(S_{2k-\beta_2}), \tag{3.29}$$

As in the single population case, analyses that use dynamic programming are not facilitated by the non-linearity of the net revenue function, and so in this section (and for the parental delay model) we use the method of Lagrange multipliers to determine the equilibrium optimal harvesting strategy. The objective is to maximise the present value of net revenue, as before, only the maximisation is over infinite time, rather than having a final period, T. Thus, we maximise,

$$P.V. = \sum_{k=0}^{\infty} \alpha^k \sum_{i=1}^{2} \Pi_i(R_{ik}, H_{ik}), \tag{3.30}$$

subject to equations (3.28) and (3.29) and $0 \leq S_{ik} \leq R_{ik}$.

The net revenue produced in period k from a harvest of H_{ik} from local population i is

$$\Pi_i(R_{ik}, H_{ik}) = \int_{R_{ik}-H_{ik}}^{R_{ik}} (p - c_i(x))\, dx. \tag{3.31}$$

3.2.1 Derivation of the optimal harvesting strategy

The method of Lagrange multipliers is used to determine the optimal harvesting strategy. See Clark (1976; 1990) for a description of the application of the method of Lagrange multipliers to problems of this form. We define the Lagrangian,

$$\begin{aligned} L = \sum_{k=0}^{\infty} \Big[& \alpha^k(\Pi_1(R_{1k}, H_{1k}) + \Pi_2(R_{2k}, H_{2k})) \\ & - \lambda_{1k}\Big(R_{1k+1} - \delta_1(R_{1k} - H_{1k}) \\ & - p_{11}G_1(R_{1k-\beta_1} - H_{1k-\beta_1}) - p_{21}G_2(R_{2k-\beta_1} - H_{2k-\beta_1})\Big) \end{aligned}$$

$$
\begin{aligned}
&- \lambda_{2k}\Big(R_{2k+1} - \delta_2(R_{2k} - H_{2k}) \\
&- p_{12}G_1(R_{1k-\beta_2} - H_{1k-\beta_2}) - p_{22}G_2(R_{2k-\beta_2} - H_{2k-\beta_2})\Big)\Big], \qquad (3.32)
\end{aligned}
$$

with necessary conditions,

$$
\begin{aligned}
\frac{\partial L}{\partial R_{ik}} &= 0 \qquad k = 1, 2, 3, \ldots && (3.33) \\
\frac{\partial L}{\partial H_{ik}} &= 0 \qquad k = 0, 1, 2, \ldots, && (3.34)
\end{aligned}
$$

for $i = 1, 2$. Necessary condition (3.33) does not include $k = 0$ as R_{i0} is predefined.

Assume that there exist equilibrium solutions S_1 and S_2. Consider local population 1, i.e. $i = 1$. Equations (3.33) and (3.34) become,

$$
\begin{aligned}
\frac{\partial L}{\partial R_{1k}} &= \alpha^k \Pi_{1R_{1k}} - \lambda_{1k-1} + \delta_1 \lambda_{1k} \\
&\quad + p_{11}\lambda_{1k+\beta_1} G_1'(S_1) + p_{12}\lambda_{2k+\beta_2} G_1'(S_1) = 0 && (3.35) \\
\frac{\partial L}{\partial H_{1k}} &= \alpha^k \Pi_{1H_{1k}} - \delta_1 \lambda_{1k} \\
&\quad - p_{11}\lambda_{1k+\beta_1} G_1'(S_1) - p_{12}\lambda_{2k+\beta_2} G_1'(S_1) = 0. && (3.36)
\end{aligned}
$$

Adding equations (3.35) and (3.36) we find,

$$
\lambda_{1k-1} = \alpha^k(\Pi_{1H_{1k}} + \Pi_{1R_{1k}}), \qquad (3.37)
$$

and similarly for local population 2,

$$
\lambda_{2k-1} = \alpha^k(\Pi_{2H_{2k}} + \Pi_{2R_{2k}}). \qquad (3.38)
$$

Placing equations (3.37) and (3.38) into equation (3.36), we obtain,

$$
\begin{aligned}
\alpha^k \Pi_{1H_{1k}} &- \delta_1 \alpha^{k+1}(\Pi_{1H_{1k}} + \Pi_{1R_{1k}}) \\
&- p_{11} G_1'(S_1) \alpha^{k+\beta_1+1}(\Pi_{1H_{1k}} + \Pi_{1R_{1k}}) \\
&- p_{12} G_1'(S_1) \alpha^{k+\beta_2+1}(\Pi_{2H_{2k}} + \Pi_{2R_{2k}}) = 0,
\end{aligned}
$$

and so,

$$\begin{aligned}\alpha^k &= \frac{\Pi_{1H_{1k}}+\Pi_{1R_{1k}}}{\Pi_{1H_{1k}}}\Big[\delta_1\alpha^{k+1}+p_{11}G_1'(S_1)\alpha^{k+\beta_1+1}\Big] \\ &\qquad + \frac{\Pi_{2H_{2k}}+\Pi_{2R_{2k}}}{\Pi_{1H_{1k}}}\Big[p_{12}G_1'(S_1)\alpha^{k+\beta_2+1}\Big].\end{aligned}$$

Dividing through by α^{k+1} and rearranging we obtain,

$$\frac{1}{\alpha} = \frac{\Pi_{1H_{1k}}+\Pi_{1R_{1k}}}{\Pi_{1H_{1k}}}\Big[\delta_1+p_{11}G_1'(S_1)\alpha^{\beta_1}\Big]+\frac{\Pi_{2H_{2k}}+\Pi_{2R_{2k}}}{\Pi_{1H_{1k}}}\Big[p_{12}G_1'(S_1)\alpha^{\beta_2}\Big] \tag{3.39}$$

$$\frac{1}{\alpha} = \frac{\Pi_{2H_{2k}}+\Pi_{2R_{1k}}}{\Pi_{2H_{2k}}}\Big[\delta_2+p_{22}G_2'(S_2)\alpha^{\beta_2}\Big]+\frac{\Pi_{1H_{1k}}+\Pi_{1R_{1k}}}{\Pi_{2H_{2k}}}\Big[p_{21}G_2'(S_2)\alpha^{\beta_1}\Big]. \tag{3.40}$$

If $\Pi_i(R_{ik}, H_{ik})$ is given by equation (2.7) then equations (3.39) and (3.40) become,

$$\frac{1}{\alpha} = \frac{(p-c_1(R_1))\Big[\delta_1+p_{11}G_1'(S_1)\alpha^{\beta_1}\Big]+(p-c_2(R_2))\Big[p_{12}G_1'(S_1)\alpha^{\beta_2}\Big]}{p-c_1(S_1)} \tag{3.41}$$

$$\frac{1}{\alpha} = \frac{(p-c_2(R_2))\Big[\delta_2+p_{22}G_2'(S_2)\alpha^{\beta_2}\Big]+(p-c_1(R_1))\Big[p_{21}G_2'(S_2)\alpha^{\beta_1}\Big]}{p-c_2(S_2)}, \tag{3.42}$$

where,

$$\begin{aligned}R_1 &= \delta_1S_1+p_{11}G_1(S_1)+p_{21}G_2(S_2)\\ R_2 &= \delta_2S_2+p_{12}G_1(S_1)+p_{22}G_2(S_2).\end{aligned}$$

Equations (3.41) and (3.42) implicitly define the optimal equilibrium escapements S_1^* and S_2^*. These equations can be seen as a special case of equations (18a) and (18b) of the general two-species model of Agnew (1982). Unlike Agnew, we consider the model from the perspective of a single species that interacts via the migration of juveniles. Thus, in the following subsection we investigate the effect of migration and delays on optimal harvesting strategies. As in previous sections, results are facilitated with the assumption of negligible costs.

3.2.2 No costs analysis

If we assume that the costs associated with harvesting are negligible, or that they are density and local population independent, equations (3.41) and (3.42) simplify to,

$$\begin{aligned} \frac{1}{\alpha} &= \delta_1 + G_1'(S_1^*)(p_{11}\alpha^{\beta_1} + p_{12}\alpha^{\beta_2}) & (3.43) \\ \frac{1}{\alpha} &= \delta_2 + G_2'(S_2^*)(p_{21}\alpha^{\beta_1} + p_{22}\alpha^{\beta_2}), & (3.44) \end{aligned}$$

where S_i^* is the optimal equilibrium escapement for local population i.

If the recruit production function is logistic (see equation (2.3) of Chapter 2), then the optimal escapements derived from equations (3.43) and (3.44) are,

$$\begin{aligned} S_1^* &= \frac{K_1}{2} - \frac{K_1}{2}\Big(\frac{1+d-\delta_1}{r_1(p_{11}\alpha^{\beta_1} + p_{12}\alpha^{\beta_2})}\Big) & (3.45) \\ S_2^* &= \frac{K_2}{2} - \frac{K_2}{2}\Big(\frac{1+d-\delta_2}{r_2(p_{21}\alpha^{\beta_1} + p_{22}\alpha^{\beta_2})}\Big). & (3.46) \end{aligned}$$

As β_i, the delay in recruitment to local population i, increases, the optimal escapement decreases, as with single population model. If both delays are infinite, implying that the juveniles never recruit, then the optimal escapements are zero, as we would expect. However, if one of the delays is infinite and the other is not, then neither local population has a zero escapement.

Comparisons with incorrect harvesting policies

Assume that the metapopulation is being managed as two unconnected single populations. For local population i, the estimated per capita growth rate measured might be,

$$r_{is} = r_i p_{ii} + r_j p_{ji}. \qquad (3.47)$$

As described in Chapter 2, this assumes that abundances are roughly equal and that the measurements are made after dispersal (see Section 2.2.2).

If we assume that $K_1 = K_2$ and $\delta_1 = \delta_2$, then the optimal escapement of local population i derived from harvesting the population as a spatially structured metapopulation is greater than that from the incorrect harvesting policy, $S_i^* > S_{is}^*$, if,

$$r_i p_{ij} \alpha^{\beta_j} > r_j p_{ji} \alpha^{\beta_i}. \tag{3.48}$$

Due to the introduction of the delay, we can no longer conclude that relative exporters should be more conservatively harvested. We interpret local population i as relative exporter of discounted larvae, while local population j is a relative importer of discounted larvae. The discounted per capita value of juveniles exported from local population i, taking into account the time it takes to mature, is $r_i p_{ij} \alpha^{\beta_j}$. Note that if the delays are equal, $\beta_i = \beta_j$, then condition (3.48) simplifies to, $r_i p_{ij} > r_j p_{ji}$ for $S_i^* > S_{is}^*$. Thus, with equal recruitment delays, the analogous result of Chapter 2 holds, i.e. relative exporters should have a greater escapement if metapopulation harvesting, than if the population were managed as a single unconnected population. If the per capita larval migration is equal for both local populations, $r_i p_{ij} = r_j p_{ji}$, then $S_i^* > S_{is}^*$ if $\beta_i > \beta_j$. In this case, the local population with larger recruitment delay is being over-harvested, while the local population with the smaller delay is under-harvested.

If the metapopulation is managed as a well-mixed single population, then an estimate of the growth rate may be the averaged juvenile production,

$$r_L = \frac{r_1(p_{11} + p_{12}) + r_2(p_{21} + p_{22})}{2}, \tag{3.49}$$

with averaged delay,

$$\beta_L = \frac{\beta_1 + \beta_2}{2}. \tag{3.50}$$

Assume that $K_1 = K_2$ and $\delta_1 = \delta_2$. The optimal escapement from harvesting local population i using the metapopulation harvesting theory is greater than the estimated escapement from exploiting the population as a well-mixed population, $S_i^* > S_L^*/2$, if,

$$\alpha^{\frac{\beta_1+\beta_2}{2}} \frac{r_1(p_{11}+p_{12})+r_2(p_{21}+p_{22})}{2} < r_i(p_{ii}\alpha^{\beta_i}+p_{ij}\alpha^{\beta_j}). \tag{3.51}$$

Again, the relative source results from previous analyses without delays, do not hold in this instance. However, as before, if the recruitment delays are equal, $\beta_i = \beta_j$, then $S_i^* > S_L^*/2$ if $r_i(p_{ii}+p_{ij}) > r_j(p_{ji}+p_{jj})$. Thus, with equal recruitment delays, relative source local populations should be more conservatively harvested than if the metapopulation were managed as a well-mixed single population. Thus, only where the recruitment delays are different, $\beta_1 \neq \beta_2$, do the results of Chapter 2 fail.

Comparisons between local populations

Assuming that we have recognised the metapopulation structure of the population, we now consider how the escapements differ between local populations. Assume that $K_1 = K_2$ and $\delta_1 = \delta_2$. The escapement of local population 1 is greater than that of local population 2, $S_1^* > S_2^*$, if

$$r_1(p_{11}\alpha^{\beta_1}+p_{12}\alpha^{\beta_2}) > r_2(p_{21}\alpha^{\beta_1}+p_{22}\alpha^{\beta_2}). \tag{3.52}$$

Thus, if the delays are equal, $\beta_1 = \beta_2$, then local population 1 has the higher escapement if it is a relative source local population, and local population 2 the smaller escapement if it is a relative sink local population. Note that if $r_1p_{11} = r_2p_{21}$ and $r_1p_{12} = r_2p_{22}$ then the escapements will be equal, regardless of the difference in the delay.

3.2.3 Variation of the delay parameters

In this example we consider a metapopulation that is essentially homogeneous, except for differences in the juvenile recruitment delays, β_i. Consider a metapopulation with

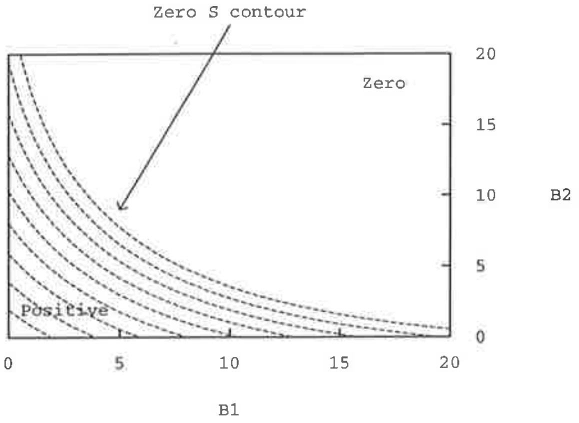

FIGURE 3.2: The escapement of local population 1 (and 2) for the receptor delay model as a function of the delay in recruitment to the adult breeding stock. In this example, the metapopulation is homogeneous except for differences in the delays. The contour increment is 10,000 and escapements decrease from the origin.

the following parameters; $\delta_1 = \delta_2 = 0.001$, a logistic juvenile production function with $r_1 = r_2 = 1\,000$, $K_1 = K_2 = 400\,000$ and symmetric migration matrix,

$$P = \begin{pmatrix} 0.001 & 0.001 \\ 0.001 & 0.001 \end{pmatrix}.$$

Assuming that costs are negligible, $c_i(x) = 0$, we vary the delay in recruitment to the adult breeding stock for each local population between zero (no delay) and twenty, $\beta_i = 0, \ldots, 20$ for $i = 1, 2$. All other parameters remain constant and we consider the equilibrium solutions produced by equations (3.45) and (3.46). In this example and the examples that follow, we plot contours of the escapements and harvests. The actual grid points are the integer values of the delays β_i, as fractional delays are not possible in the current model formulation. However, we interpolate the data to include partial delays to facilitate graphical interpretation.

For the symmetric example, the optimal escapements and harvests of the local populations are exactly the same for a particular delay (β_1, β_2). To see this, notice that equations (3.43) and (3.44) are equivalent for the populations' parameters given above (in fact, equations (3.41) and (3.42) are also equivalent).

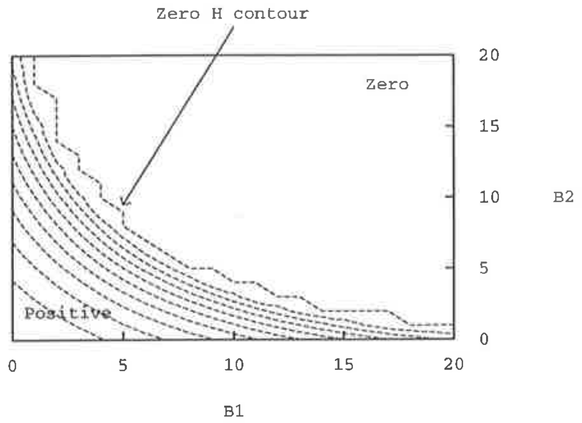

FIGURE 3.3: The harvests from local population 1 (and 2) for the receptor delay model and a homogeneous metapopulation except for the delays. The contour increment is 5,000 and harvests decrease away from the origin.

In Figure 3.2 we plot the escapement of the local populations as a function of the delays β_i. As expected, the delays cause a decrease in the optimal escapement as the delay in either local population increases. Eventually, an optimal negative escapement is produced and thus it is optimal to harvest the whole population. As previously stated, when the delays become large we reach a point where it is no longer profitable to wait for the juveniles to join the breeding adult stock. The zero escapement contour is given by the equation,

$$\beta_i = \frac{\ln\left(\frac{1+d-\delta_i}{r_i p_{ii}} - \frac{p_{ij}}{p_{ii}}\alpha^{\beta_j}\right)}{\ln(\alpha)}. \tag{3.53}$$

This equation is derived by setting the equations (3.43) and (3.44) to zero and rearranging. For example, if $\beta_1 = \beta_2 = \beta$ we find $\beta = 6.28$ and if $\beta_2 = 2$ then $\beta_1 = 13.63$.

The harvest contours plotted in Figure 3.3 are the same for both local populations for a particular delay (β_1, β_2). The harvests decrease away from the origin (no delay) until the optimal escapements become zero and therefore the equilibrium harvest is also zero. The zero harvest contour is not smooth due to problems in its estimation with the package (GNUPLOT) used.

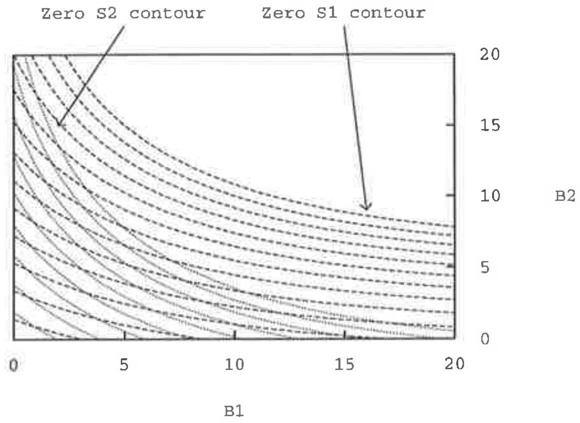

FIGURE 3.4: The escapements of local populations 1 and 2 for the receptor delay model as a function of the delays. For the non-symmetric migration matrix, with $p_{12} > p_{21}$, the escapement of local population 1 increases over that of the symmetric example. The contour increment is 10,000 and escapements decrease from the origin.

If we replace the migration matrix from the above symmetric example with,

$$P = \begin{pmatrix} 0.001 & 0.002 \\ 0.001 & 0.001 \end{pmatrix},$$

then we can investigate the effect of sources, sinks and delays on optimal harvesting policies.

Figure 3.4 shows a contour plot of the escapements of both local populations. In this example, the escapement of local population 1 is always larger than that of local population 2, conforming to the source/sink rules of the non-delay model; to see this, consider the inequality (3.52). From this inequality we see that it is conceivable that a relative exporter local population could have a smaller optimal escapement than the relative importer local population if the juvenile recruitment delay of the relative exporter local population is large enough. As in the previous example, eventually the equilibrium escapements become negative for large delays. Local population 2 has a non-negative escapement for a greater range of β_1 and β_2 due to an increase in the parameter p_{12} (see inequality (3.52) and equation (3.53)).

We note that a delay of β in local population j produces a greater decrease in the

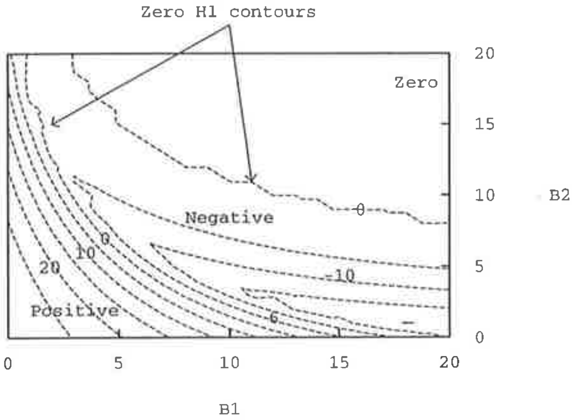

FIGURE 3.5: The harvests from local population 1 as a function of the delay parameters for the non-symmetric migration matrix and the receptor delay model. The contour increment is 5,000. Numbers on the contours are harvests $\times 10^3$.

optimal escapement of the relative exporter local population i than the same delay in local population i. For example, with no delay $(\beta_1, \beta_2) = (0, 0)$, local population 1 has escapement $S_1^* = 126\,733$. When $(\beta_1, \beta_2) = (0, 4)$ we find $S_1^* = 107\,101$. Conversely, when $(\beta_1, \beta_2) = (4, 0)$ the escapement is $S_1^* = 118\,077$. This appears to be counterintuitive as we would expect the delay in local population i to decrease that local population's escapement to a greater extent than if the delay were in local population j. With the above delays, the escapement of local population 2 is exactly the same, $S_2^* = 69\,401$, for both $(\beta_1, \beta_2) = (0, 4)$ and $(\beta_1, \beta_2) = (4, 0)$. (see the inequality (3.54)). With the delay $(\beta_1, \beta_2) = (4, 0)$, the escapement of local population 1 is higher as more stock can then migrate to local population 2 where it is heavily harvested. In this way, we "avoid" the delay in local population 1. If $(\beta_1, \beta_2) = (0, 4)$, then the delay in local population 2 counter-acts the flow of juveniles into that population.

In general, if we assume negligible costs, local population i in a metapopulation with delays (β_1', β_2') will have a greater escapement than local population i with delays (β_1'', β_2'') if,

$$(p_{ii}\alpha^{\beta_i'} + p_{ij}\alpha^{\beta_j'}) > (p_{ii}\alpha^{\beta_i''} + p_{ij}\alpha^{\beta_j''}). \tag{3.54}$$

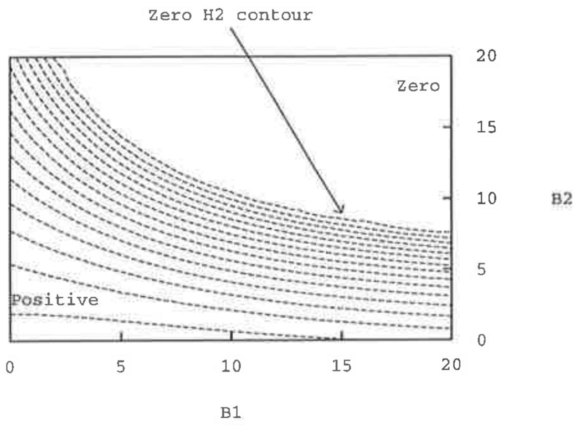

FIGURE 3.6: The harvests from local population 2 as a function of the delay parameters for the receptor delay model and the non-symmetric migration matrix. The contour increment is 10,000 and increases monotonically from zero.

Thus, with $(\beta_1', \beta_2') = (4, 0)$, $(\beta_1'', \beta_2'') = (0, 4)$, and the parameters from the non-symmetric migration matrix, we find $S_1^{*\prime} > S_1^{*\prime\prime}$ and $S_2^{*\prime} = S_2^{*\prime\prime}$.

Unlike the symmetric migration example, we find that under some circumstances optimal negative harvests are produced by local population 1. In Figure 3.5 we plot the contours of the equilibrium harvests of local population 1 as a function of the delays. As the delays increase, eventually a negative harvest is produced in local population 1. As the delays increase further, the harvest becomes zero due to the escapements in both local populations becoming zero (see Figure 3.4).

Figure 3.6 plots the equilibrium harvests of local population 2 as a function of the delays. In the mid-right region we observe that a positive harvest is produced even though the equilibrium escapement from local population 2 is zero (see Figure 3.4). This is due to the seasonal migration of juveniles from the relative exporter, local population 1. As the delays increase, eventually a zero harvest is optimal due to the escapements both becoming zero.

We now attempt to explain some of the results from this model. Firstly, from Figure 3.5 we observe that negative harvests are produced for high values of β_1 and

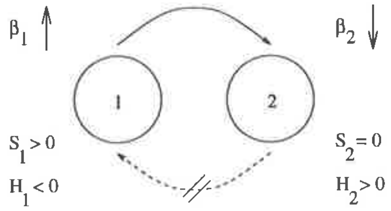

FIGURE 3.7: For large values of the delay in local population 1, β_1, (and for some small β_1 delays) the optimal policy is to seed that local population, and then harvest the adults in local population 2. The seeded juveniles take less time to mature and join the harvestable stock in local population 2, than if maturing in local population 1.

low β_2 delays. In the same range, the escapement of local population 1 is positive, the escapement of local population 2 is zero, and the harvest from local population 2 is always positive. If a negative harvest is interpreted as placing stock into a local population, then we seed local population 1 and harvest local population 2. This strategy takes the yield from the local population with the smallest delay in juvenile recruitment, thus minimising the time taken for juveniles to join the harvestable stock (see Figure 3.7).

The seeding strategy is also optimal for β_1 low and β_2 high, only over a smaller range. This is due to local population 1 being a relative source/exporter local population. It is still optimal to seed local population 1 due to the large migration of juveniles from the relative source/exporter, local population 1, to the relative sink/importer, local population 2, which can then be harvested. As the delay in local population 2 increases further eventually this policy is no longer optimal and both escapements approach zero. Thus there is a trade-off between the benefits of the migration from local population 1 to 2 and the costs of the delay in local population 2.

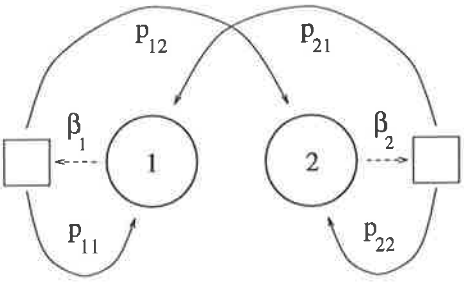

FIGURE 3.8: A metapopulation where juveniles experience a delay before recruiting to the adult breeding stock. The delay, β_i, for local population i depends on the source of the larvae, i.e. it is determined by the larvae's parents and/or birth place.

3.3 Parental delay model

In the previous section, we assume that the recruitment delay occurs in the local population that receives the juveniles. However, the delay may occur due to effects originating in the parent local population (see Figure 3.8). For example, genetic influences on age at sexual maturity may cause juvenile stock from local population i to take β_i years to reach maturity, regardless of where it migrates. Another possibility is that the juveniles produced by the parent stock of local population i take β_i years to reach sexual maturity, at which time they disperse to find mates and acquire new territories.

Thus, including harvesting, we replace equations (3.28) and (3.29) by,

$$\begin{aligned} R_{1k+1} &= \delta_1 S_{1k} + p_{11} G_1(S_{1k-\beta_1}) + p_{21} G_2(S_{2k-\beta_2}) && (3.55) \\ R_{2k+1} &= \delta_2 S_{2k} + p_{12} G_1(S_{1k-\beta_1}) + p_{22} G_2(S_{2k-\beta_2}). && (3.56) \end{aligned}$$

As before, we use the method of Lagrange multipliers to determine the equilibrium optimal harvesting equations. The details of the derivation are not given here. The equations found are,

$$\frac{1}{\alpha} = \frac{(p-c_1(R_1))\Big[\delta_1 + p_{11}G_1'(S_1)\alpha^{\beta_1}\Big] + (p-c_2(R_2))\Big[p_{12}G_1'(S_1)\alpha^{\beta_1}\Big]}{p-c_1(S_1)} \tag{3.57}$$

$$\frac{1}{\alpha} = \frac{(p-c_2(R_2))\Big[\delta_2 + p_{22}G_2'(S_2)\alpha^{\beta_2}\Big] + (p-c_1(R_1))\Big[p_{21}G_2'(S_2)\alpha^{\beta_2}\Big]}{p-c_2(S_2)}, \tag{3.58}$$

where,

$$\begin{aligned} R_1 &= \delta_1 S_1 + p_{11}G_1(S_1) + p_{21}G_2(S_2) \\ R_2 &= \delta_2 S_2 + p_{12}G_1(S_1) + p_{22}G_2(S_2). \end{aligned}$$

3.3.1 No costs analysis

Assuming that harvest costs are negligible, the equilibrium escapements, S_i^*, are defined by,

$$\frac{1}{\alpha} = \delta_1 + \alpha^{\beta_1}G_1'(S_1^*)(p_{11}+p_{12}) \tag{3.59}$$

$$\frac{1}{\alpha} = \delta_2 + \alpha^{\beta_2}G_2'(S_2^*)(p_{21}+p_{22}). \tag{3.60}$$

If we assume that the recruit production function is logistic, then the optimal escapements from equations (3.59) and (3.60) are,

$$S_1^* = \frac{K_1}{2} - \frac{K_1}{2}\frac{1+d-\delta_1}{\alpha^{\beta_1}r_1(p_{11}+p_{12})} \tag{3.61}$$

$$S_2^* = \frac{K_2}{2} - \frac{K_2}{2}\frac{1+d-\delta_2}{\alpha^{\beta_2}r_2(p_{21}+p_{22})}. \tag{3.62}$$

As before, an increase in the delay decreases the optimal escapement. If the delay in local population i is infinite, implying that the juveniles never recruit, then the optimal escapement for local population i is zero.

Comparisons with incorrect harvesting policies

If the metapopulation is incorrectly managed as two unconnected single populations, the estimated growth rate for local population i is given by equation (3.47). Assuming that $K_1 = K_2$ and $\delta_1 = \delta_2$, then $S_i^* > S_{is}^*$ if,

$$r_i p_{ij} > r_j p_{ji}. \tag{3.63}$$

Thus, relative exporters will be over-exploited if the metapopulation is mismanaged, and relative importers under-exploited. This is the same result that we derived when there are no delays (see Chapter 2).

The estimated growth rate if the metapopulation is managed as a well-mixed single population is defined by equation (3.49), with the averaged delay of equation (3.50).

If we assume that $K_1 = K_2$ and $\delta_1 = \delta_2$, then the optimal escapement from harvesting local population i as a metapopulation is greater than the escapement from incorrectly exploiting the population as a well-mixed population, $S_i^* > S_L^*/2$, if,

$$r_i(p_{ii} + p_{ij}) > r_j(p_{jj} + p_{ji}). \tag{3.64}$$

Relative source local populations should be more conservatively harvested than is suggested by the incorrect harvesting policy. Similarly, relative sink local populations are under-exploited if the metapopulation is managed as a well-mixed single population

Thus, the rules-of-thumb for incorrect harvesting policies that we derive in Chapter 2 are insensitive to parent site induced delays in recruitment.

Comparisons between local populations

If we have recognised the spatial structure of the population, then we may like to know how the escapements differ between local populations. We have already mentioned that

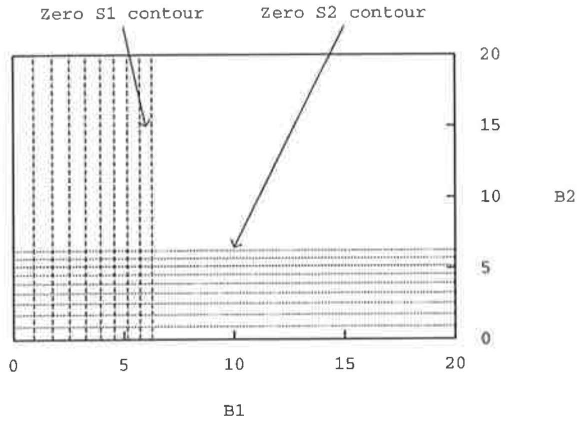

FIGURE 3.9: The escapements plotted as a function of the delay parameters for the parental delay model and the symmetric migration matrix. The contour increment is 10,000 and escapements increase monotonically from the zero contour toward the origin.

an increase in the delay will decrease the optimal escapements. Assume that $K_1 = K_2$ and $\delta_1 = \delta_2$, then $S_1^* > S_2^*$ if,

$$\alpha^{\beta_1} r_1(p_{11} + p_{12}) > \alpha^{\beta_2} r_2(p_{21} + p_{22}). \tag{3.65}$$

The per capita discounted juvenile production for local population i is given by $\alpha^{\beta_i} r_i(p_{ii} + p_{ij})$. This takes into account the time taken for juveniles to reach sexual maturity. To facilitate interpretations of the inequality (3.65), we consider two special cases. If the per capita juvenile production is the same in both local populations, i.e. $r_1(p_{11} + p_{12}) = r_2(p_{21} + p_{22})$, then $S_1^* > S_2^*$ if the delay in local population 1 is smaller than that of local population 2. If the delays are equal, then the relative source local population has the larger optimal escapement, while the relative sink local population has the smaller.

3.3.2 Variation of the delay parameters

In this section we repeat the receptor delay examples of the previous section only now we assume that the delay is related to the parental stock. Therefore, we begin by

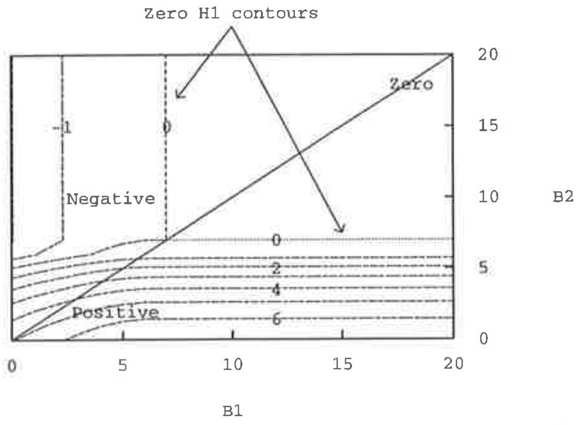

FIGURE 3.10: The harvests from local population 1 as a function of the delay parameters for the parental delay model and the symmetric migration matrix. The contour increment is 10,000. Numbers on the contours are harvests $\times 10^4$.

considering a homogeneous metapopulation and vary the delay parameters, β_i between zero and twenty. The parameters of the metapopulation are; $\delta_1 = \delta_2 = 0.001$, a logistic juvenile production function with $r_1 = r_2 = 1\,000$, $K_1 = K_2 = 400\,000$ and the symmetric migration matrix,

$$P = \begin{pmatrix} 0.001 & 0.001 \\ 0.001 & 0.001 \end{pmatrix}.$$

As before, we assume negligible costs and that the discount rate is 10%.

In Figure 3.9 we plot the escapements of both local populations as functions of the delays. Unlike the receptor delay model, the escapements are no longer equivalent for all (β_1, β_2). We also note that the escapement of local population i is independent of the delay in local population j (see equations (3.61) and (3.62)) and decreases as β_i increases. Eventually the escapements become zero when it is no longer optimal to conserve the stock due to the excessive time for the juveniles to join the breeding adults. The zero escapement contour is given by,

$$\beta_i = \frac{\ln\left(\dfrac{1 + d - \delta_i}{r_i(p_{ii} + p_{ij})}\right)}{\ln(\alpha)}, \tag{3.66}$$

where we have rearranged equations (3.61) and (3.62). For the symmetric migration matrix, the zero escapement contour is found at $\beta_i = 6.83$ and so a delay of seven years or more in local population i produces a zero optimal escapement for that local population.

The harvest from local population 1 is plotted in Figure 3.10. Harvests from local population 2 are not shown as they can be found by reflecting Figure 3.10 about the line $\beta_1 = \beta_2$. The greatest harvest, $H_1 = 69\,805$, is produced with $\beta_1 > 6$ and $\beta_2 = 0$. In some circumstances a negative harvest is produced and, as the delays increase, eventually both escapements become zero and so the equilibrium harvest also becomes zero. For $\beta_1 > 6$ and $\beta_2 < 7$ a positive yield is taken from local population 1 even though the optimal escapement is zero. As seen in the receptor delay model, this is due to the seasonal migration of juveniles from local population 2.

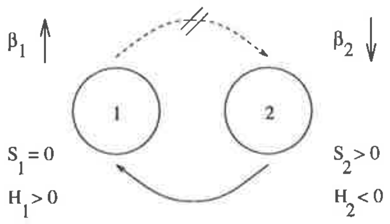

FIGURE 3.11: For large values of the delay in local population 1, β_1, the optimal policy is to seed local population 2 and harvest all of local population 1. This takes advantage of the small maturation delay associated with juveniles that mature in local population 1.

If we assume that a negative harvest can be interpreted as seeding a local population then for large values of β_1 and low β_2 delays it is optimal to seed local population 2. In the same range, the optimal escapement for local population 2 is positive, the optimal escapement for local population 1 is zero and the equilibrium harvest is positive (see Figure 3.10). It is optimal to place stock into local population 2 so that the time taken

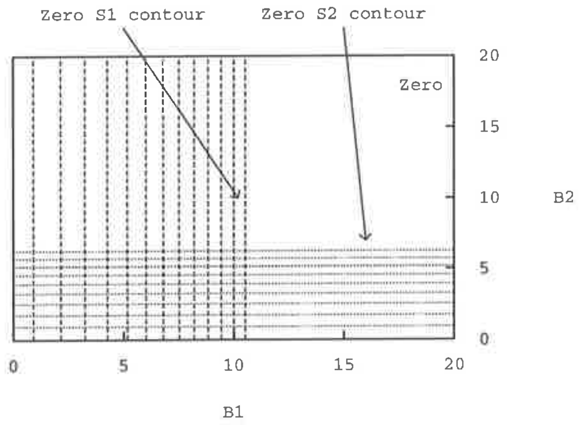

FIGURE 3.12: The escapements as a function of the delay parameters for the parental delay model and the non-symmetric migration matrix. The contour increment is 10,000 and escapements increase monotonically from the zero escapement contour towards the origin.

for juveniles to join the harvestable stock (in local population 1) is minimised (see Figure 3.11). This policy is reversed for a large β_1 delay and a small β_2 delay. In this case, we seed stock in local population 1 so we can take advantage of the shorter delay in local population 2.

Consider next the non-symmetric migration matrix,

$$P = \begin{pmatrix} 0.001 & 0.002 \\ 0.001 & 0.001 \end{pmatrix},$$

where local population 1 is a relative source/exporter local population.

The optimal escapements of the local populations are shown in Figure 3.12. Increasing the proportion of juveniles migrating from local population 1 to local population 2 increases the optimal escapements of local population 1 but has no effect on the escapement of local population 2. This can be seen by observing the equations that define the optimal escapements, equations (3.61) and (3.62). The increase in p_{12} also increases the range over which the escapement of local population 1 is non-negative (see equation (3.66)). For local population 1 the zero escapement contour is found at $\beta_1 = 6.83$, and for local population 2, $\beta_2 = 10.54$. Thus if the delay is seven years or

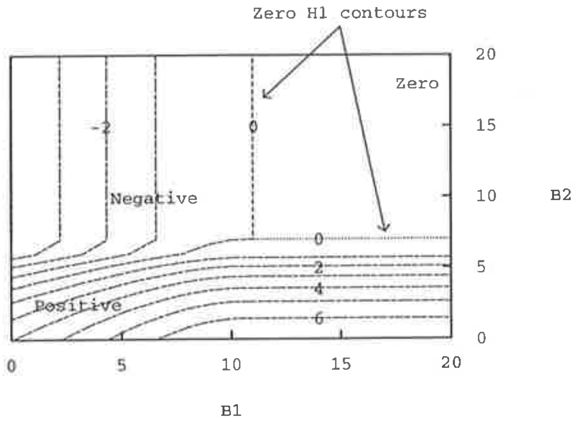

FIGURE 3.13: The harvests from local population 1 as a function of the delay parameters for the parental delay model and the non-symmetric migration matrix. The contour increment is 10,000. Numbers on the contours are harvests $\times 10^4$.

more in local population 1, or fourteen years or more in local population 2, then the optimal escapements should be zero.

The harvest of local population 1 is shown as a contour plot in Figure 3.13. The greatest harvest from local population 1, $H_1 = 69\,805$, is found for parameters $\beta_1 > 10$ and $\beta_2 = 0$ (however, local population 2 has a negative optimal harvest in this range). In the range $\beta_1 > 11$ and $\beta_2 < 7$ positive harvests are produced from local population 1 when the escapement of that local population is zero. This is due to the seasonal migration of juveniles from local population 2. In this delay range, local population 2 experiences an optimal negative harvest. As in previous examples, as the escapements both become zero, the equilibrium harvest also becomes zero. As β_2 increases, we find optimal negative harvests for local population 1.

Note that under some circumstances it is optimal to seed local population 1 when the delay in that local population is greater than the delay in local population 2. This is due to the increase in the migration parameter, p_{12}. There is a trade-off between the harvest benefits (to local population 2) due to the migrating juveniles and the cost of an increase in the delay of local population 1.

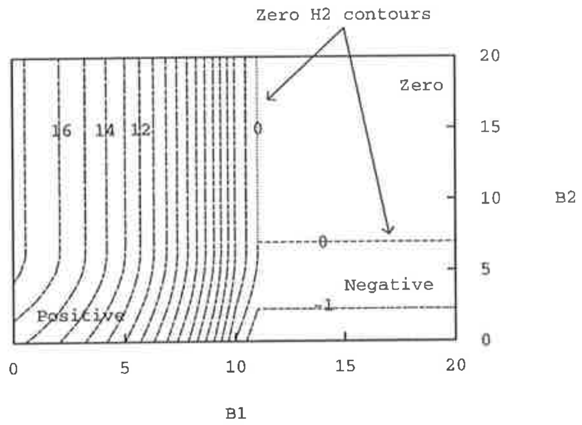

FIGURE 3.14: The harvests from local population 2 as a function of the delay parameters. The contour increment is 10,000. Numbers on the contours are harvests $\times 10^4$.

Figure 3.14 shows a contour plot of the harvests of local population 2 as function of the delays β_i. The greatest harvest for local population 2 is 173 160, when $\beta_1 = 0$ and $\beta_2 > 6$. The harvests are zero where the escapements are zero, and there is a region of optimal negative harvests as β_1 becomes large and β_2 is less than 6.83. Similar to the harvests of local population 1, there exists a region of positive local population 2 harvests when the escapement of that local population is zero, due to the migration of juveniles from local population 1. This occurs in the range $\beta_1 < 11$ and $\beta_2 > 7$.

3.4 Closing Remarks

In this chapter we have extended the basic metapopulation model by including simple age structure in the form of two age-classes where the juvenile age-class exists for an arbitrary number of years. In the rest of this thesis organisms are assumed to breed the year after they are born. Many populations experience a period of growth over several years before attaining sexual maturity, and even then may take further years to fully contribute to the population's recruits. For example, some species of abalone take 3 years to reach sexual maturity at which time their larval production is much less than those of older age classes (Shepherd and Laws, 1974; Shepherd, 1976).

We considered two models where the delay is related either to the receiving local population or where it is due to the parent local population. Results depended not only on the per capita larval production but also on the delays.

For the receptor model, comparisons between incorrect harvesting policies and the metapopulation theory, and comparisons between the local population's escapements themselves, showed that the relative source/sink rules of the non-delay model no longer necessarily hold (see Chapter 2). However, if the delays are equal then the relative source/sink rules remain, i.e. relative exporters (importers) should be more (less) conservatively harvested than if the local populations are managed as single unconnected populations and relative sources (sinks) should be more (less) conservatively harvested than if the metapopulation were managed as a well-mixed single population. Relative sources (sinks) should also have the larger escapement of the metapopulation if the delays are equal.

The parental delay model adheres to the above relative source/sink results for the harvest policy comparisons regardless of the population delays. However, the difference between the local population's escapements does depend upon the delays, except for the special case of equal maturation delays. In this case the relative source (sink) local population has the larger (smaller) escapement, as before.

The examples that varied the delay parameters suggest that local populations with juveniles that cause large delays should be harvested conservatively, if at all. For example, if an optimal negative harvest is interpreted as an optimal seeding policy, then in some circumstances it is optimal to place stock into populations that cause large delays and harvest the population with the smaller delay. This, in effect, minimises the time for juveniles to reach sexual maturity, at which point they can be harvested.

These examples assume that costs are negligible. If harvesting costs are included then the strategy of placing little harvesting effort into large delay local populations remains optimal; however it is less pronounced than the no costs case.

We can enhance our understanding of the effects of introducing a delay in maturation if we consider the annual juvenile survival. The delay models that we have discussed assume that there is either no juvenile mortality or that juvenile mortality is subsumed within the migration parameter p_{ij}. Assume that the proportion of juveniles surviving each period in local population i is D_i. Let p'_{ij} be the initial proportion of the juveniles of local population i that migrate to local population j. Therefore, if annual juvenile survival and the delay are related to the local population of settling (the receptor model), the proportion of juveniles that migrated from local population i to j and are still alive after β_j years is,

$$p_{ij} = p'_{ij} D_j^{\beta_j} \qquad i, j = 1, 2. \tag{3.67}$$

Substituting this expression into our no costs optimal escapement for local population 1 say, equation (3.45), we find,

$$S_1^* = \frac{K_1}{2} - \frac{K_1}{2}\left[\frac{1 + d - \delta_1}{r_1(p'_{11}(D_1\alpha)^{\beta_1} + p'_{12}(D_2\alpha)^{\beta_2})}\right]. \tag{3.68}$$

Similarly, if the annual juvenile survival and delay are associated with the parental local population (the parental model) then,

$$p_{ij} = p'_{ij} D_i^{\beta_i} \qquad i, j = 1, 2 \tag{3.69}$$

and the optimal escapement for local population 1 is,

$$S_1^* = \frac{K_1}{2} - \frac{K_1}{2}\left[\frac{1 + d - \delta_1}{(D_1\alpha)^{\beta_1} r_1(p'_{11} + p'_{12})}\right]. \tag{3.70}$$

We can now appreciate the effects of the delay, discounting and juvenile survival. The inclusion of a delay in maturation essentially acts as a dampener on the growth of the population (most easily seen if $\alpha = 1$, i.e. no discounting; also see equations (3.67) and (3.69)). Discounting then acts multiplicatively with juvenile survival, and as far as economic decisions and management are concerned, an increase in interest rates is equivalent to a decrease in annual juvenile survival.

In the introduction to the parental delay model, one of the justifications for the delay's association with the parent population was that local genetics influenced the time at maturation, regardless of where the juveniles migrated. On recollection, this seems unlikely. Assume that juveniles of local population j with a gene for a β_j delay migrate to local population i. These juveniles reach maturity after β_j years and then produce juveniles themselves. Now, ignoring the complications of breeding with β_i delay individuals, assume that the β_j gene is passed on to these juveniles. Some of these juveniles then migrate back to their parent's birth local population with delay β_j. However, individuals born in local population i should have that local population's delay, β_i, not a β_j delay. We therefore have a contradiction, suggesting that the formulated model as stands is not appropriate for the genetic application described. The current parental delay model is better suited to delays caused by environmental effects of the local population (temperature, food availability affecting growth and maturation) before eventual migration.

In the examples of the previous chapter, and in the chapters that follow, we iterate the dynamic programming equations to compare numerical solutions with the derived analytic solutions. In this chapter we have not been able to do this due to computational difficulties with the large state space. The state space has increased over the non-delay models because we have to iterate over all possible previous abundances, as well as over all initial abundances. For a one-period delay in both local populations, the dimension of the state space becomes $K^4 \times T$. Attempts to overcome this problem by contracting the state space to a region surrounding the optimal solution derived from the analytic equations also proved fruitless due to the most-rapid-approach policy no longer being optimal. Results were produced when one of the local populations has no delay and the other has a one period delay, i.e. say $\beta_1 = 0$ and $\beta_2 = 1$. However due to the reduction in K, ($K = 50$ was used), it was difficult to differentiate between effects caused by the delays, migration or any possible rounding errors. For this reason, the results are not shown here.

In a number of examples, we varied the delay parameters between zero and twenty and investigated optimal harvesting regimes. Thus, it is possible for one local population's juveniles to recruit immediately to the spawning stock (no delay) while the other local population has a very large delay before sexual maturation. This does not seem likely for a single species population. When interpreting the results, it may be more realistic to consider differences between the local population delays of ϵ_β, where ϵ_β is small (results near the line $\beta_1 = \beta_2$ of the diagrams) or an increasing function of the delays.

As mentioned, if there is no difference in delay between the local populations then the two models, the receptor model and the parental delay model, are mathematically equivalent. The relative source/sink results from the non-delay analyses hold for this special case. Thus, if there is little to no difference in the delays, the general rules-of-thumb from the non-delay model should suffice.

Botsford (1992), in a summary of the future directions of delay difference and age structured models, suggests a need for further research into the behaviour of these models when there are several subpopulations connected by dispersing larvae. In this chapter, we have considered the problem of spatial structure and dispersal when there are arbitrary maturation delays. Our major conclusions are (a) results differ if the delay is determined by the destination site or birth site of the larvae (b) results only differ from those of Chapter 2 if the delays differ between local populations (or if annual juvenile mortality differs between local populations) and (c) harvests should be conservative if juveniles recruited to a local population take time to reach maturity; we are then able to take advantage of possible smaller delays in the connected local population. Although we have not considered a size-structured model, we suspect that a similar strategy should be adopted for connected local populations that vary in size-at-maturity, i.e. conservatively harvest local populations with a propensity for small sized individuals, and take advantage of migration to the connected local population where larger stock can then be harvested.

Chapter 4

Adult migration

The models of the previous chapters assume that juveniles migrate between local populations, but that adults are sedentary. In this chapter we investigate the effect of adult migration on optimal harvesting strategies. In the first section we assume that only adults migrate and that juveniles remain in their parental local population until the following period, when they become sexually mature and are then able to migrate. This model is followed by a model that assumes that both adults and juveniles migrate between local populations.

We model the population dynamics in discrete-time using coupled difference equations. The optimal harvesting strategies are described without detailed analysis as the solution method is analogous to the dynamic programming procedure of Chapter 2. We produce optimality equations that implicitly define the equilibrium optimal escapements for both local populations. As in the previous chapters, we use simplifying assumptions to further analyse the results. Comparisons are made between the local population's escapements and between escapements produced when incorrect management policies are employed. In various respects, the results are qualitatively similar to the relative source/sink and relative exporter/importer results of Chapter 2.

Broad scale migrations of adult stocks are well documented, examples including Pacific salmon (Brannon, 1984; Harden Jones, 1984), tuna (Harden Jones, 1984), halibut (St-Pierre, 1984), whales (Clark and Lamberson, 1982) and shark (Walker, 1992). However, these migrations are often seasonal and relate to factors such as movements to feeding habitat, spawning grounds or refugia (Wootton, 1990) and seldom is there a clearly defined metapopulation-like structure to the life-history strategy. Most metapopulation models assume that juveniles are the source of spatial interaction. However, there is evidence of adult dispersal, including "artificial" adult migrations, and we describe these examples below.

The anadromous salmonids of the northern Pacific and Atlantic often have large scale migrations from their freshwater natal rivers to various oceanic feeding habitats, and return again after a number years (depending on the species) to a freshwater environment where they spawn. The semelparous salmon of the genus *Oncorhynchus* die during or immediately after spawning, while the the closely related iteroparous genus *Salmo* survive to breed in following seasons (Wootton, 1990). These salmon are well known for their ability to return to the river at which they were spawned, i.e. their home river. For example, less than one percent of the sockeye salmon, *Oncorhynchus nerka*, are believed to have strayed from their natal stream during a study by Quinn *et al* (1987). However, some spawners become lost or *stray* to alternate, usually adjacent, non-natal streams. Many studies have ignored the effect of strays on population dynamics and management (Legget, 1984; Quinn, 1984). Quinn and Nemeth (1991), however, believe that strays are vital for the colonisation of new habitats or recolonisation of restored habitat, and that they are an essential response to the degradation of spawning habitat. Their study on fall chinook salmon suggests that up to 27.5% of the stock from certain streams of the Columbia River strayed.

If we consider the spawning habitats to be local populations (Schaffer and Elson,

1975) that are connected by the migration of strays, then we have defined a metapopulation. Salmon populations show many of the characteristics of metapopulations, including local extinction and recolonisation, occasional migration between breeding local populations and a distinct geographical structure. The population dynamics are also appropriate for the models proposed in this thesis. The model described in Chapter 2 may be appropriate for the semelparous salmon if we set $\delta_i = 0$. While, iteroparous species, where adults survive for more than a single spawning event, may be modelled with the adult migration models that we introduce in this chapter.

Further examples of adult migrations occur due to human interference. As discussed in Chapter 2, some populations are enhanced by the introduction of adults (or juveniles) from foreign or human raised stocks. If adult stock are transplanted from one local population to another, then an "artificial" metapopulation may have been created. For example, due to the excessive costs and low survival rates of larval seedings (Schiel, 1992; Tegner, 1992), mature stocks of abalone and scallop are used to enhance their respective stocks (Aoyama, 1988; Tegner, 1992), while legal-sized trout are placed in rivers for recreational fishers (Cooper, 1952). Artificial colonisation is an accepted practice for the conservation of threatened species, and metapopulation models are recognised as important guides to management in these cases (Hanski and Gilpin, 1991).

Evidence exists for amphibians (Sinsch, 1992) and barnacles and gastropods (Martel and Chia, 1991) that both adults and juveniles disperse. Waser and Jones (1983) and Hansson (1991) describe situations in which the adults of some species of mammals (e.g. woodrats, Algerian sandrats, field voles) disperse due to the abandonment of their home range in favor of their offspring. The authors suggest that this strategy may be related to a lower risk of migration mortality in adults due to size and experience. Anecdotal evidence of adult migration and colonisation is provided by John (1979), as cited by John (1984), for ichthyoneuston and by Elliot and Ward (1992) for orange roughy.

Metapopulation models that explicitly include adult migration include Freedman and Wu (1994), and Wu and Freedman (1991), with a model suggested for the western tent caterpillar, *Malacosoma californicum pluviale.* Both papers assume a multiple patch environment occupied by a single species population that has an immature and a mature stage structure. Migration can occur in both stages. In Freedman and Wu, dispersal is linear, while in Wu and Freedman, migration of immature individuals is rare, while adult migration is more frequent and non-linear. The age at maturity is assumed constant across the metapopulation. A partial differential equation model is used do describe the population dynamics, and they find conditions for the global stability of the positive equilibrium. Exploitation is not considered.

In the first section of this chapter we consider a metapopulation model where only adults migrate between the local populations. Optimal harvesting equations are found and we then illustrate the results with numerical examples. This model is extended in the following section where both adult and juvenile migration between local populations occurs.

4.1 Adult migration and no juvenile migration

4.1.1 The model

In this section we consider a model where adults migrate between local populations, but juveniles are sedentary. Assume that a proportion of the surviving adult stock from local population i migrates to local population j. This proportion is defined by m_{ij}. The proportion of the adults that are lost from the system is given by ω_i. Thus,

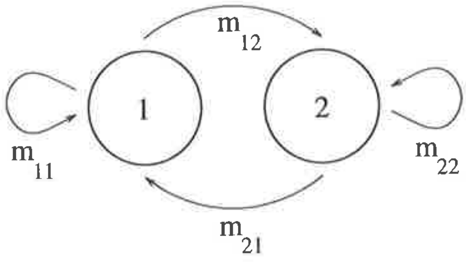

FIGURE 4.1: A metapopulation with two local populations. The proportion of surviving adults migrating from local population i to j in each generation is given by m_{ij}.

we have $m_{i1} + m_{i2} + \omega_i = 1$. The stock-recruitment relation is then,

$$R_{1k+1} = \delta_1 m_{11} R_{1k} + \delta_2 m_{21} R_{2k} + G_1(R_{1k}) \tag{4.1}$$

$$R_{2k+1} = \delta_2 m_{22} R_{2k} + \delta_1 m_{12} R_{1k} + G_2(R_{2k}), \tag{4.2}$$

where δ_i is the pre-migration survival of local population i adults (may be subsumed within the m_{ij} terms). Other parameters and variables have their usual meaning.

We do not go into the details of the derivation of the optimal harvesting equations here as small changes to the dynamic programming procedure used in Chapter 2, Section 2.1.2, are all that is required.

The equations that define the optimal escapements are,

$$\frac{1}{\alpha} = \frac{(\delta_1 m_{11} + G_1'(S_{10}))(p - c_1(R_{11})) + \delta_1 m_{12}(p - c_2(R_{21}))}{p - c_1(S_{10})} \tag{4.3}$$

$$\frac{1}{\alpha} = \frac{(\delta_2 m_{22} + G_2'(S_{20}))(p - c_2(R_{21})) + \delta_2 m_{21}(p - c_1(R_{11}))}{p - c_2(S_{20})}. \tag{4.4}$$

These equations implicitly define the optimal equilibrium escapements, S_1^* and S_2^*, for each local population. We can prove that these equations hold for all time horizons $T > 1$ by modifying the analogous proof in Chapter 2, Section 2.1.2.

4.1.2 No costs analysis

In this section we assume that harvesting costs are negligible or independent of the local populations and density. This will facilitate comparisons between various management policies and the interpretation of the results. With no harvesting costs, equations (4.3) and (4.4) simplify to,

$$\frac{1}{\alpha} = \delta_1(m_{11}+m_{12}) + G_1'(S_1^*) \tag{4.5}$$

$$\frac{1}{\alpha} = \delta_2(m_{21}+m_{22}) + G_2'(S_2^*), \tag{4.6}$$

where S_i^* is the optimal equilibrium escapement for local population i.

If we assume that $G_i''(S_i) < 0$ then these equations determine no more than one solution for S_i^*. Assuming logistic growth for the juvenile production function, $G_i(S_{ik})$ (see equation (2.3)), the optimal escapements from equations (4.5) and (4.6) are,

$$S_1^* = \frac{K_1}{2} - \frac{K_1}{2r_1}\Big(1 + d - \delta_1(m_{11}+m_{12})\Big) \tag{4.7}$$

$$S_2^* = \frac{K_2}{2} - \frac{K_2}{2r_2}\Big(1 + d - \delta_2(m_{21}+m_{22})\Big). \tag{4.8}$$

Thus, as the adult migration survival, $\delta_{im} = \delta_i(m_{ii}+m_{ij})$, for local population i increases, the optimal escapement for local population i also increases.

Comparisons with incorrect harvesting policies

In a similar fashion to the previous chapters, we compare the escapements derived from metapopulation harvesting theory to escapements that assume that the local populations are either unconnected by migration or that the metapopulation is a well-mixed single population. In this way, we are able to determine the advantage of using the metapopulation theory and the effect of incorrect harvesting policies on the population.

Assume that the local populations are managed as two unconnected single populations. For simplicity, assume that the density-dependent parameters K_i and the growth rates r_i for each population are equal. Measurements of the adult survival in local population i are taken as,

$$\delta_{is} = \delta_i m_{ii} + \delta_j m_{ji}. \tag{4.9}$$

This measures the "flow in" of adults to a local population, and is analogous to equation (2.26) of Chapter 2, Section 2.2.2. As in Chapter 3, this assumes that the local population's abundances are approximately the same, and that measurements are made after dispersal. The optimal escapement of local population i from harvesting the population as a metapopulation is greater than the optimal escapement if the local populations are incorrectly assumed to be unconnected, $S_i^* > S_{is}^*$, if

$$\delta_i m_{ij} > \delta_j m_{ji}. \tag{4.10}$$

This suggests that local populations with high adult export survival should be harvested more conservatively than would be recommended from managing the population as an unconnected single population.

If the local populations are managed as a well-mixed single population, adult survival may be measured as

$$\delta_L = \frac{\delta_1(m_{11} + m_{12}) + \delta_2(m_{22} + m_{21})}{2}. \tag{4.11}$$

This quantity measures the average adult migration survival. Assume that $K_1 = K_2$ and $r_1 = r_2$. The optimal escapement from our metapopulation harvesting theory is larger than the estimated escapement from the well-mixed single population, $S_i^* > S_L^*/2$, if

$$\delta_i(m_{ii} + m_{ij}) > \delta_j(m_{jj} + m_{ji}). \tag{4.12}$$

Thus harvesting the metapopulation as a well-mixed single population will over-harvest local populations with high adult migration survival, and under-harvest those with low adult migration survival.

Comparisons between local populations

If we have recognised the metapopulation structure of the population, then we may like to know how the local populations' escapements compare. Thus, if we assume that $K_1 = K_2$ and $r_1 = r_2$ then the escapement from local population i, S_i^*, should be greater than S_j^* if $\delta_i(m_{ii} + m_{ij}) > \delta_j(m_{jj} + m_{ji})$. We conclude that local populations with high adult migration survival should be harvested more conservatively than those with lower adult migration survival.

4.1.3 Iteration of the dynamic programming equations

In this section we iterate the dynamic programming equations so as to compare numerical solutions with our analytic solutions, equations (4.3) and (4.4). Further assume that a metapopulation with two local populations is currently unharvested. Assume that juvenile production function is logistic (see equation (2.3)), with parameters $r_1 = r_2 = 1$ and $K_1 = K_2 = 200$. Pre-migration adult survival is given by $\delta_1 = \delta_2 = 1$ (thus we concentrate our attention on the migration parameters, m_{ij}), and the adult migration matrix is,

$$M = \begin{pmatrix} 0.2 & 0.2 \\ 0.4 & 0.2 \end{pmatrix}.$$

The unharvested equilibrium local population sizes are $\bar{R}_1 = 106$ and $\bar{R}_2 = 88$. If the cost function is defined by equation (2.37) with parameters $a_i = 30$ and $q_i = 1.3 \times 10^{-2}$, the price of a unit of stock is $p = 70$ and the discount rate is 10%, then iterating the dynamic programming equations produces the escapements and harvests

T	R_1	R_2	S_1	S_2	H_1	H_2
5	106	88	59	63	47	25
4	79	68	59	63	20	5
3	79	68	59	63	20	5
2	79	68	59	63	20	5
1	79	68	59	63	20	5
0	79	68	33	33	46	35

TABLE 4.1: Escapements and harvests from iterating the dynamic programming equations.

shown in Table 4.1.

The optimal escapement for local population 1 is $S_1^* = 59$ with equilibrium harvest $H_1^* = 20$. Local population 2 has optimal escapement $S_2^* = 63$ with equilibrium harvest $H_2^* = 5$. The terminal period escapements are the zero profit escapement levels $S_\infty = 33$. Thus we conservatively harvest local population 2 and take a greater harvest from local population 1. This reiterates the analytic results which suggest that a local population with high adult migration survival should have a larger optimal escapement than a local population with lower adult migration survival.

The numerical solutions above compare favourably with solutions produced from the analytic equations derived in the previous section, equations (4.3) and (4.4). The optimal escapements from these equations are $S_1^* = 57$ and $S_2^* = 63$ with optimal equilibrium harvests $H_1^* = 20$ and $H_2^* = 4$. Differences between analytic and numerical solutions are likely to be due to rounding errors in the computer programs.

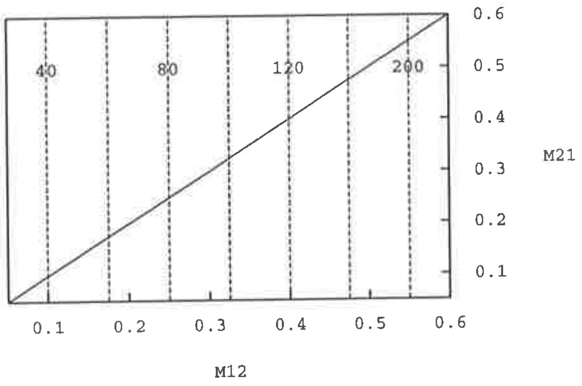

FIGURE 4.2: Contours of the escapement of local population 1 from equation (4.7) as a function of the adult migration parameters. Numbers on the contours are escapements $\times 10^3$. The contours of the escapements of local population 2 can by found be reflecting the figure about the line $m_{12} = m_{21}$.

4.1.4 Variation of the adult migration parameters

In this example we investigate the effect of varying the adult migration parameters m_{12} and m_{21} on escapements and harvests. All other parameters remain constant. Assume that the metapopulation shows logistic juvenile production with parameters: $K_1 = K_2 = 400\,000$, $r_1 = r_2 = 0.75$, adult survival $\delta_1 = \delta_2 = 1$ and migration matrix,

$$M = \begin{pmatrix} 0.4 & m_{12} \\ m_{21} & 0.4 \end{pmatrix}.$$

The cost of harvesting the stock is assumed negligible, and the discount rate is 10%.

The escapements of local population 1 are plotted as contour lines in Figure 4.2. Local population 1 has high adult migration survival if the point (m_{12}, m_{21}) is below the line $m_{12} = m_{21}$ and low adult migration survival if above. The escapements of local population 2 are not shown as they can be found by reflecting Figure 4.2 about the line $m_{12} = m_{21}$. The escapement of local population 1 is always greater than, or equal to, that of local population 2 if $m_{12} \geq m_{21}$. This conforms to the negligible costs analytic results derived in Section 4.1.2.

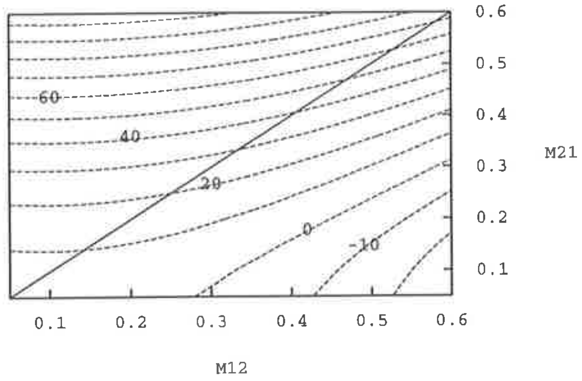

FIGURE 4.3: Contours of the harvests of local population 1 as a function of the adult migration parameters. Numbers on the contours are harvests $\times 10^3$. The contours of the harvests of local population 2 can be found by reflecting the figure about the line $m_{12} = m_{21}$.

In Figure 4.3 we plot the contours of the equilibrium harvests of local population 1. We note that if local population 1 has greater adult migration survival than local population 2, $m_{12} > m_{21}$, then local population 1 is the more conservatively harvested population, $H_1^* < H_2^*$. The general form of Figure 4.3 is similar to that of Figure 2.4 in Chapter 2. A negative equilibrium harvest is produced if local population 1 shows strong adult migration survival, just as strong relative exporters/sources did in Chapter 2. Thus, in both cases, it is optimal to conservatively harvest local populations that are sources of dispersing individuals.

In the following section we assume that both adults and juveniles can migrate between local populations.

4.2 Adult and juvenile migration

Some populations show both adult and juvenile dispersive stages, for example, the models by Wu and Freedman (1991) and Freedman and Wu (1994) for butterfly metapopulations. Sinsch (1992) describes a natterjack toad metapopulation where adult

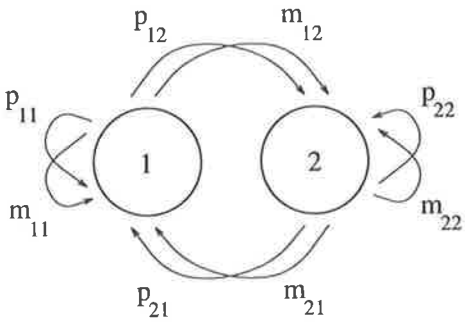

FIGURE 4.4: A metapopulation with two local populations. The proportion of juveniles migrating from local population i to j in each generation is given by p_{ij}, and the proportion of surviving adults that migrate from local population i to j in each generation is given by m_{ij}.

females and young males are the main source of spatial interaction. Martel and Chia (1991) give evidence for adult and juvenile dispersal in bivalves and gastropods that do not have a planktonic larval stage.

4.2.1 The model

In this section we extend the previous model by including juvenile migration, in addition to adult migration. Recall that the juvenile migration parameter, p_{ij}, represents the proportion of juveniles that migrate from local population i to local population j in each period. Similarly, adult migration is given by m_{ij} and represents the proportion of adults that migrate from local population i to j. The stock-recruitment relation is,

$$\begin{aligned} R_{1k+1} &= \delta_1 m_{11} R_{1k} + \delta_2 m_{21} R_{2k} + p_{11} G_1(R_{1k}) + p_{21} G_2(R_{2k}) \qquad (4.13) \\ R_{2k+1} &= \delta_2 m_{22} R_{2k} + \delta_1 m_{12} R_{1k} + p_{12} G_1(R_{1k}) + p_{22} G_2(R_{2k}), \qquad (4.14) \end{aligned}$$

where parameters and variables have their usual meaning.

Minor amendments to the dynamic programming procedure used in Chapter 2 will determine the optimal harvesting strategy, and so the details are not given here.

The equations that define the optimal escapements are,

$$\frac{1}{\alpha} = \frac{(\delta_1 m_{11} + p_{11}G_1'(S_{10}))(p - c_1(R_{11})) + (\delta_1 m_{12} + p_{12}G_1'(S_{10}))(p - c_2(R_{21}))}{p - c_1(S_{10})} \tag{4.15}$$

$$\frac{1}{\alpha} = \frac{(\delta_2 m_{22} + p_{22}G_2'(S_{20}))(p - c_2(R_{21})) + (\delta_2 m_{21} + p_{21}G_2'(S_{20}))(p - c_1(R_{11}))}{p - c_2(S_{20})}. \tag{4.16}$$

These equations implicitly define the optimal equilibrium escapements, S_1^* and S_2^*, for each local population. These equations hold for all time horizons $T > 1$ (see the analogous proof in the Chapter 2).

4.2.2 No costs analysis

If we assume that harvesting costs are negligible, equations (4.15) and (4.16) become,

$$\frac{1}{\alpha} = \delta_1(m_{11} + m_{12}) + G_1'(S_1^*)(p_{11} + p_{12}) \tag{4.17}$$

$$\frac{1}{\alpha} = \delta_2(m_{21} + m_{22}) + G_2'(S_2^*)(p_{21} + p_{22}), \tag{4.18}$$

where S_i^* is the optimal equilibrium escapement for local population i.

Assuming logistic growth for the juvenile production function, $G_i(S_{ik})$, the optimal escapements from equations (4.17) and (4.18) are,

$$S_1^* = \frac{K_1}{2} - \frac{K_1}{2r_1}\frac{(1 + d - \delta_1(m_{11} + m_{12}))}{(p_{11} + p_{12})} \tag{4.19}$$

$$S_2^* = \frac{K_2}{2} - \frac{K_2}{2r_2}\frac{(1 + d - \delta_2(m_{21} + m_{22}))}{(p_{21} + p_{22})}. \tag{4.20}$$

Comparisons with incorrect harvesting policies

If the local populations are managed as two unconnected single populations, then the estimated growth rate, r_{is}, and adult survival, δ_{is}, may be given by equations

(2.26) and (4.9) respectively. Assume that $K_1 = K_2$. The optimal escapement of local population 1 determined from our metapopulation harvesting theory will be larger than the escapement if the local population is managed as an unconnected single population, $S_1^* > S_{1s}^*$, if,

$$\frac{(1+d-\delta_1(m_{11}+m_{12}))}{r_1(p_{11}+p_{12})} < \frac{(1+d-(\delta_1 m_{11}+\delta_2 m_{21}))}{r_1 p_{11}+r_2 p_{21}}. \tag{4.21}$$

Assume that local population 1 is a relative exporter, $r_1 p_{12} > r_2 p_{21}$, and has higher adult export survival than local population 2, $\delta_1 m_{12} > \delta_2 m_{21}$. In this case, if the metapopulation structure is recognised, then the optimal escapement of local population 1 is larger than if the local populations are harvested as single unconnected populations, $S_1^* > S_{1s}^*$. Thus, a local population that is an exporter of adults and juveniles is over-harvested if the metapopulation is managed as two unconnected single populations. Similarly, if a local population is an importer of adults and juveniles, then it is under-harvested.

If local population i is a relative exporter but has a lower adult export survival than local population j, then the difference in escapements from the alternative management policies will depend on the inequality (4.21).

The metapopulation could also be managed as a well-mixed single population. The growth rates and adult survival are given by the average per capita juvenile production, equation (2.27), and the average adult migration survival, equation (4.11). Assume that $K_1 = K_2$. The optimal escapement of local population 1 from our metapopulation theory, namely equation (4.19), is larger than the estimated escapement if the metapopulation is managed as a well-mixed single population if,

$$\frac{(1+d-\delta_1(m_{11}+m_{12}))}{r_1(p_{11}+p_{12})} < \frac{(1+d-(\delta_1(m_{11}+m_{12})+\delta_2(m_{22}+m_{21}))/2)}{(r_1(p_{11}+p_{12})+r_2(p_{22}+p_{21}))/2}. \tag{4.22}$$

Thus, if local population 1 is a relative source, $r_1(p_{11}+p_{12}) > r_2(p_{22}+p_{21})$, and has greater adult survival, $\delta_1(m_{11}+m_{12}) > \delta_2(m_{22}+m_{21})$, then harvesting the metapopulation as a well-mixed single population will over-exploit local population 1 and under-exploit local population 2. We conclude that if local population i is a juvenile and adult source, then local population i should be more conservatively harvested than would be suggested from harvesting the metapopulation as a well-mixed single population. Similarly, juvenile and adult sinks should be exploited to a greater degree. Thus, the conclusions of Chapter 2 and the adult migration only model of Section 4.1 are enhanced. As mentioned in the discussion above, if a local population is a relative source, but has lower adult survival than the other local population, then differences in optimal escapements will depend on the inequality (4.22).

Comparisons between local populations

Having recognised the metapopulation structure of the population, we may like to know how the escapements compare between local populations. If we assume that $K_1 = K_2$ and $r_1 = r_2$, then the optimal escapement of local population 1 should be greater than that of local population 2, $S_1^* > S_2^*$, if

$$\frac{(1+d-\delta_1(m_{11}+m_{12}))}{r_1(p_{11}+p_{12})} < \frac{(1+d-\delta_2(m_{21}+m_{22}))}{r_2(p_{21}+p_{22})}. \tag{4.23}$$

This result reinforces the relative source/sink results of Chapter 2 and the adult migration results of Section 4.1. For example, if local population 1 is a relative source and has greater adult survival than local population 2, then local population 1 has the larger optimal escapement. However, if a local population is a relative source, but has lower adult migration survival than the other local population, then differences in the escapements will depend upon the inequality (4.23).

4.2.3 Iteration of the dynamic programming equations

Case 1

As in Section 4.1.3, assume that we are to harvest a previously unexploited metapopulation composed of two local populations. Assume that the juvenile production function is logistic, with parameters $r_1 = r_2 = 10$ and $K_1 = K_2 = 200$. Adult survival is given by $\delta_1 = \delta_2 = 1$. The adult migration matrix is,

$$M = \begin{pmatrix} 0.2 & 0.2 \\ 0.4 & 0.2 \end{pmatrix},$$

and the juvenile migration migration matrix is,

$$P = \begin{pmatrix} 0.1 & 0.1 \\ 0.15 & 0.1 \end{pmatrix}.$$

In this example local population 2 is a relative source/importer local population *and* has greater adult migration survival than local population 2. The unharvested equilibrium local population sizes are $\bar{R}_1 = 176$ for local population 1 and $\bar{R}_2 = 128$ for local population 2. The cost function is defined by equation (2.37) with parameters $a_i = 30$ and $q_i = 1.3 \times 10^{-2}$, the price of a unit of stock is $p = 70$, and the discount rate is 10%. The dynamic programming equations produce the escapements and harvests shown in Table 4.2.

The optimal escapement for local population 1 is $S_1^* = 80$ and for local population 2, $S_2^* = 87$. The optimal equilibrium harvests are $H_1^* = 93$ and $H_2^* = 44$. The terminal period escapements are the zero profit escapement levels $S_\infty = 33$. As expected, the relative source/exporter local population, local population 2, has the larger optimal escapement and smaller equilibrium harvest.

The analytic solutions from equations (4.15) and (4.16) are $S_1^* = 79$ and $S_2^* = 89$ with equilibrium harvests $H_1^* = 94$ and $H_2^* = 42$. Thus, results suggest that local populations with high per capita juvenile production and high adult migration survival should be conservatively harvested. This is shown even more markedly in the negligible costs case where the optimal escapements are $S_1^* = 65$ and $S_2^* = 80$.

T	R_1	R_2	S_1	S_2	H_1	H_2
5	176	128	80	87	96	41
4	173	131	80	87	93	44
3	173	131	80	87	93	44
2	173	131	80	87	93	44
1	173	131	80	87	93	44
0	173	131	33	33	140	98

TABLE 4.2: Escapements and harvests from iterating the dynamic programming equations.

Case 2

In this example we transpose the adult migration matrix to determine the impact on harvesting strategies of a relative source/exporter local population that has low adult migration survival. The parameters are the same as those of the previous example, except that the adult migration matrix is,

$$M = \begin{pmatrix} 0.2 & 0.4 \\ 0.2 & 0.2 \end{pmatrix}.$$

Iterating the dynamic programming equations (not shown here), we find optimal equilibrium escapements $S_1^* = 86$ and $S_2^* = 83$. The harvests are $H_1^* = 70$ and $H_2^* = 66$. Transposing the adult migration matrix has increased the escapement of local population 1 while decreasing that of local population 2, the effect being to "equalise" the escapements. If we assume negligible harvesting costs, this equalising is even more pronounced. The no-costs optimal escapements are $S_1^* = 75$ and $S_2^* = 72$. This trend reversal was expected from our analytic work of Section 4.2.2.

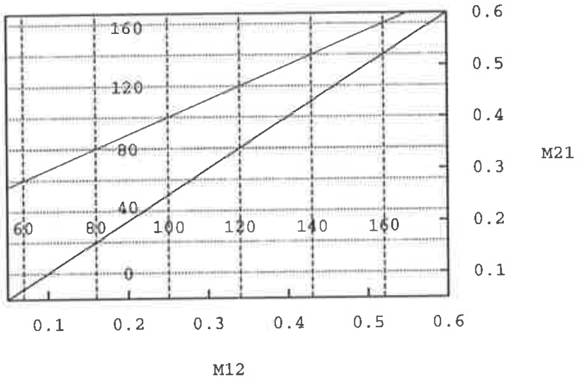

FIGURE 4.5: The escapements of the local populations from equations (4.19) and (4.20) as a function of the adult migration parameters. The vertical contour lines are local population 1 escapements, and the horizontal contours represent local population 2 escapements. Numbers on the contours are escapements $\times 10^3$. The uppermost diagonal line separates the parameters for which $S_1^* > S_2^*$ (below) and $S_1^* < S_2^*$ (above).

4.2.4 Variation of the migration parameters

To investigate the behaviour of the system in more detail, we vary the adult and juvenile migration parameters while all other parameters remain constant. In this way we are able to determine the effect of migration on the local populations' optimal escapements and harvests.

In this example we use the parameter values from the example presented in Section 4.1.4. However, as we now have juvenile migration effects as well, it is more difficult to fully investigate the parameter space. Thus, in the first example we hold the juvenile migration constant, and vary the adult migration parameters. This is followed by an example where adult migration is constant and juvenile migration is varied.

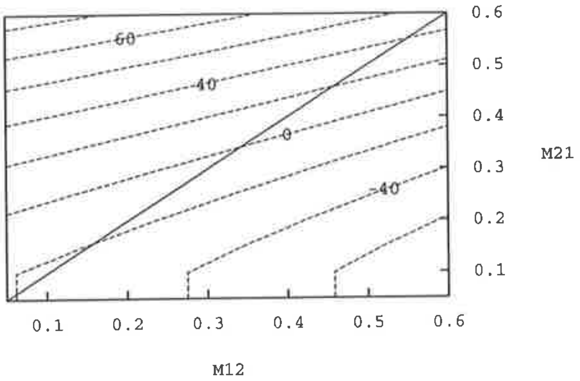

FIGURE 4.6: The harvest of local population 1 as a function of the adult migration parameters. Numbers on the contours are harvests $\times 10^3$.

Example 1

Consider a metapopulation with a logistic recruit production function, parameters, $r_1 = r_2 = 300$, $K_1 = K_2 = 400\,000$, and juvenile migration matrix,

$$P = \begin{pmatrix} 0.001 & 0.002 \\ 0.001 & 0.001 \end{pmatrix}.$$

Adult survival is $\delta_1 = \delta_2 = 1.0$ and the adult migration matrix is,

$$M = \begin{pmatrix} 0.4 & m_{12} \\ m_{21} & 0.4 \end{pmatrix}.$$

Costs associated with harvesting are assumed negligible and the discount rate is 10%.

The escapements of local population 1 and local population 2 are shown in Figure 4.5. If $m_{21} > m_{12}$ the optimal escapement of local population 2 is not always greater than that of local population 1 (unlike the example of Section 4.1.4), as local population 1 is a relative source. Local population 2 has a greater escapement than local population 1 if $2m_{12} < 3m_{21} - 0.7$ (see equation (4.23) and Figure 4.5). Note that the escapement of local population 2 is zero for m_{21} less than 0.1, and thus harvests in local population 2 rely on immigration from local population 1.

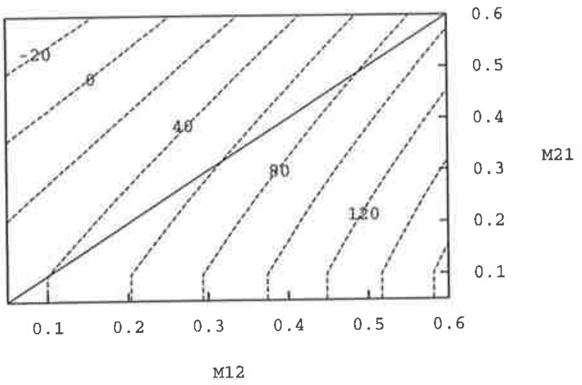

FIGURE 4.7: The harvest of local population 2 as a function of the adult migration parameters. Numbers on the contours are harvests $\times 10^3$.

Figures 4.6 and 4.7 show the equilibrium harvests from local population 1 and local population 2 respectively. These figures have a similar form to those of Chapter 2, Figure 2.4, and the adult-migration-only model, Figure 4.3. The harvests from local population 1 are less than those of local population 2 over a greater range of the parameter space. This is a consequence of the non-symmetric juvenile migration, $p_{12} > p_{21}$, causing more conservative harvesting in the relative exporter/source local population. The discontinuity in harvest contours observed for populations with $m_{21} < 0.1$ is due to local population 2 having a zero optimal escapement over this range. The equilibrium harvest of local population 2 is not zero in this range due to the seasonal migration of juveniles and adults from local population 1.

Example 2

In this example, we hold the adult migration parameters constant and vary the juvenile migration parameters. The parameters are the same as those defined in the previous example except the migration matrices are now,

$$P = \begin{pmatrix} 0.001 & p_{12} \\ p_{21} & 0.001 \end{pmatrix},$$

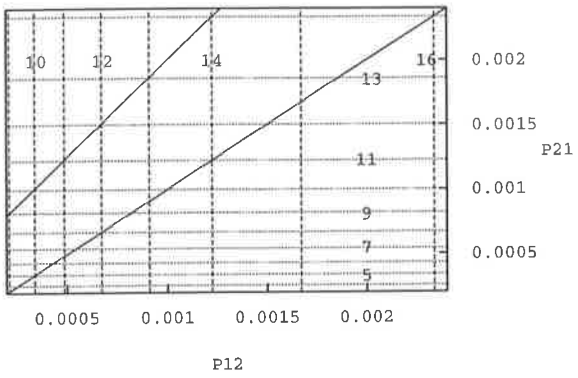

FIGURE 4.8: Contours of the escapements of both local populations derived from equations (4.19) and (4.20) as a function of the juvenile migration parameters. Numbers on the contours are escapements $\times 10^4$. Contours labelled with even numbers are local population 1 escapements, and those odd are local population 2 escapements. Local population 1 has a greater escapement than local population 2 for parameters below the upper diagonal line, and local population 2 has the larger escapement above the line.

and,

$$M = \begin{pmatrix} 0.4 & 0.5 \\ 0.4 & 0.4 \end{pmatrix}.$$

The optimal escapements of local population 1 and 2 are shown in Figure 4.8. The escapement contours are of the same form as those shown in Chapter 2, Figure 2.3. The effect of adult migration is most noticeable when $p_{12} = p_{21}$. Without adult migration, or with $m_{12} = m_{21}$, we would expect the optimal escapements to be equal. However, as $m_{12} > m_{21}$, we find that the optimal escapement of local population 1 is greater than that of local population 2. Similarly, if $p_{ij} > p_{ji}$ we can not say that local population i has the larger escapement (as we did in Chapter 2, Section 2.2.2), as adult migration now effects the equilibrium escapement. In fact, from equation (4.23), the optimal escapement of local population 1 is greater than the optimal escapement of local population 2 if $0.2p_{21} < 0.0001 + 0.3p_{12}$ (see Figure 4.8).

The equilibrium harvests from local population 1 and 2 are plotted in Figures 4.9

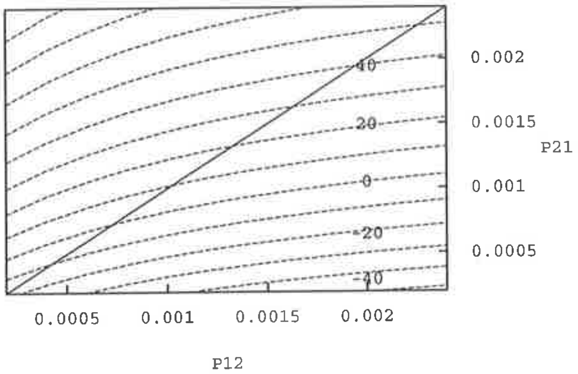

FIGURE 4.9: The harvest of local population 1 as a function of the juvenile migration parameters. Numbers on the contours are harvests $\times 10^3$.

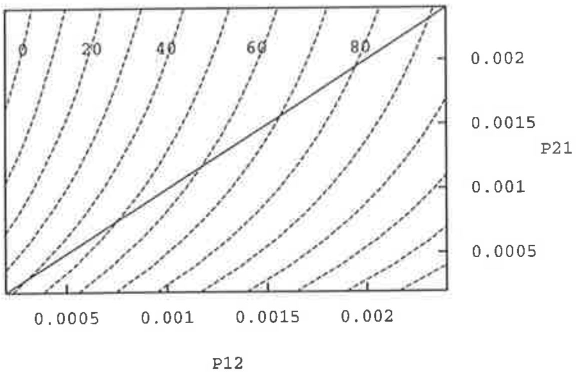

FIGURE 4.10: The harvest of local population 2 as a function of the juvenile migration parameters. Numbers on the contours are harvests $\times 10^3$.

and 4.10 respectively. Once again, the harvest contours are of the same general form as those shown in Figure 2.4. The local populations show an optimal negative harvest when the proportion of immigrating larvae is low compared to the proportion of emigrating larvae. Local population 1 is more conservatively harvested than local population 2 over a greater range of the parameters. This is due to the greater adult export survival of local population 1, $m_{12} > m_{21}$. As mentioned earlier, this suggests that local populations that are sources of migration should be protected from harvesting.

4.3 Closing Remarks

In this chapter we have considered adult migration between local populations. Some species show spatial interactions that involve dispersing adults (Waser and Jones, 1983; Hansson, 1991; Martel and Chia, 1991; Wu and Freedman, 1991; Sinsch, 1992). We considered two models; the first assumed that only adults are able to migrate, and the second assumed that both adults and juveniles migrate. The metapopulations are modelled with coupled difference equations, and equations are derived that implicitly define the optimal equilibrium escapements for each local population.

To obtain a greater understanding of our results, some simplifying assumptions are made (e.g. no costs). Comparisons between local populations are used to obtain rough guides to the relative harvest intensity that is required for each local population. For the adult-migration-only model, we find that the local population with the higher adult migration survival should be harvested more conservatively than the local population with lower migration survival. This is analogous to our rule-of-thumb from the juvenile migration only model of Chapter 2, i.e. that the local population with the greater per capita larval production should be more conservatively harvested.

Comparisons are then made between the optimal escapements from our metapopulation theory and incorrect harvesting strategies. Firstly, if the local populations have been recognised but the managing authority does not believe that they are connected by migration, then we find that the local population with the greater adult export survival is over-harvested, while the other local population remains under-harvested. Secondly, if the metapopulation is managed as a well-mixed single population, then the local population with the greater adult migration survival is over-exploited, while the other is under-exploited. Again, these results are analogous to those found in Chapter 2, Section 2.2.2 for the juvenile migration only models. If we include both adult and juvenile migration, the results described here for the adult migration only model and the results from Chapter 2 are reinforced, e.g. conservative harvesting of relative exporters/sources with high adult migration survival. However, there is a trade-off in harvest if a local population is, say, a relative exporter/source local population but has low adult migration survival.

Note that the adult survival terms that we have used in this chapter's examples are significantly greater than that of Chapter 2, where adult survival is $\delta = 0.001$. The increase in parameter values is necessary to obtain the richness of behaviour observed in the examples; very low levels of adult survival, while still plausible, have little effect on optimal harvesting strategies. In fact, in the examples of Chapter 2, we could have increased adult survival by a factor of 100 with no qualitative difference and little quantitative difference to the results.

Chapter 5

Optimal harvesting of a partially closed or reserved metapopulation

In Chapter 2 we considered optimal harvesting policies for a fully harvested metapopulation, where all local populations are available for exploitation. In this chapter we consider the possibility that particular local populations cannot be harvested. An example where local populations may be closed, or otherwise unharvested, is the prohibition of harvesting from breeding habitats, where protection of juveniles and breeding adults is vital for stock persistence. Fishing may also be financially undesirable in certain local populations due to these regions being prone to under-sized or unmarketable individuals. Sub-populations of harvested stock may be unreachable due to depth or distance from port, as was the case for many populations before new technologies made these remote populations accessible (Davis, 1989). Another example is the temporary closure of fishing grounds to allow stock recovery from overfishing or damage from pollutants (Cook and McGaw, 1991; Tegner, 1992). This is all too common a problem, as seen in South Australia's Gulf St. Vincent prawn fishery, and the oil spill in Spencer's Gulf in 1992 (Noye *et al.*, 1994). Fishing activities may be restricted in marine sanctuaries or protected areas, for example West Island's Marine Reserve in South Australia (Shepherd, 1991). Marine habitats are worthy of protection for ecological reasons and these preserved areas may have commercially viable populations that are connected to exploited populations by the dispersal of juveniles or adults.

Harvesting a partially closed metapopulation.

Fishery managers are often faced with the problem of deciding how best to serve their fishery with the knowledge that a significant part of the stock cannot be harvested, and is interacting with the exploitable population. For example, a harvested metapopulation may require the closure of a local population because of overfishing (Cook and McGaw, 1991; Orensanz *et al.*, 1991). How then should the exploited local population be harvested to maximise the fishery's financial viability and improve stock recovery in the closed patch? How will the closed local population react to closure? How should we manage sources and sinks?

Harvest closures can also be applied as a fishery stock and harvest regulatory mechanism. Prohibiting the exploitation of known areas of high stock production or breeding grounds can be used to boost abundance and possibly future catch. Refugia can also be applied as an alternative to other regulatory measures such as restricting season lengths, as a means to reduce fishing effort and maintain stocks (Davis, 1989; Shepherd and Brown, 1993; Quinn *et al.*, 1994).

Shepherd (1991) suggests that marine reserves should be used to help manage the recovery of declining abalone stocks. He lists three main reasons why reserves are a potentially valuable management tool. Firstly, for research, as fishing can bias measurements of growth and make estimates of natural mortality difficult to obtain. Secondly, harvest reserves can protect genetic diversity. Due to harvesters selecting faster growing individuals, over time selective harvesting may result in a reduction of growth rates, increases in fecundity at age, reductions in age at maturity and decreases in size at maturity (Brown and Parman, 1993; Policansky, 1993). It has been suggested that at least one local population of abalone be preserved every few hundred kilometres, which is the scale of genetic change across the population. The final purpose is that reserves could provide a restocking source for populations that experience dramatic declines in abundance (Tegner, 1992).

Given that the metapopulation is over-exploited, rather than close the whole fishery down (a rather drastic decision economically), managers may wish to close only a portion of the fishing zone. Or, perhaps a manager wishes to introduce a harvest refuge as a regulatory measure. How should the refuge choice be made to maximise economic benefits and/or stock recovery? What is the influence of sources and sinks on the optimal choice of habitat for closure?

Managers may also have to determine optimal harvesting policies when their stock is intimately connected to a reserve system or marine sanctuary.

Harvesting within a reserve system.

Scientific and social desires for species and ecosystem conservation have led to the preservation of a variety of ecologically valuable habitats. While terrestrial habitats have received greater attention as far as preservation and management are concerned, the benefits of preserving marine and estuarine habitats are only now beginning to be realised (Fairweather and McNeill, 1993). The Green Island Marine Park was Australia's first marine reserve, being declared in 1938, while in 1879 the first Australian terrestrial park was proclaimed at Royal National Park in New South Wales. In 1991, less than one percent of Australia's maritime area was protected outside of the Great Barrier

Reef Marine Park, which comprised 88% of the total preserved area of approximately 4.1%, whereas 5.3% of Australia's land was under park protection (Bridgewater and Ivanovici, 1993; Fairweather and McNeill, 1993). Taking a world view, coastal and marine reserves comprise approximately 850 of the 4500 protected areas of the world (Elder, 1993). This is contrast to the fact that the marine environment is the most phyla rich environment on the planet, and far outweighs Earth's land in terms of surface area (Bridgewater and Ivanovici, 1993; Elder, 1993).

Marine sanctuaries, or Marine and Estuarine Protected Areas (MEPAs), are discrete areas of coastal waters and underlying terrain where commercial and recreational activities are limited or prohibited entirely (see Ballantine (1987) and Elder (1993)). The merits of MEPAs for conservation are obvious. Protection from pollution, over-exploitation, and habitat destruction benefits both recreational users and the environment. There are also likely to be beneficial effects on recreational and commercial fisheries, especially if fished habitat is connected to the reserved region. This is due to the protection of stock, breeding habitats and sources of food (Davis, 1989; McNeill, 1991).

When establishing a reserve system our decision may be determined by issues of nature conservation, profitability or a combination of these alternatives. Firstly, there may be a predetermined site for the reserve, a region of significant biodiversity, or an important refuge of a threatened species. In this case, conservation goals are the main objective. The other extreme is that the impact of the reservation on a fishery is the primary concern. If a commercially valuable species inhabits the area proposed for preservation, and is relevant to the reserve choice (for example the abalone population off West Island (Shepherd, 1991)), then we may like to know which area will preserve the greatest number of the species. The exploited habitat that is likely to maximise economic gain to commercial industry may also be an important factor in reserve choice. Thus, the choice of habitat for preservation will depend upon the objectives of the MEPA in question, namely, if conservation is the primary objective, if commercial interests are to have an influence on the decision (Peterson, 1993), or some combination of these two objectives. Regardless of the circumstances surrounding the reserve choice, once the reserve system is established, we still need to determine optimal harvesting policies for the exploited local populations.

Once established, the influence of the reserve system should be monitored (for examples, see Alcala (1981; 1988); Cole *et al.* (1990)). We might like to know what effect harvesting has on the reserved habitat. If it is detrimental to the conservation goals of the MEPA, then alternative management policies need to be investigated. Conversely, the effect of the reserve population on harvesting may be of interest. Fish catch and quality may improve with the increase in environmental quality. If the reserve system had previously been harvested, either correctly as a metapopulation or incorrectly as unconnected single populations, then a comparison of harvests and escapements would be informative. The influence of sources and sinks may also be important, especially in reserve choice. Should sources or sinks be reserved to achieve economic or conservation goals? How does the preservation of a source patch affect harvests in sink populations (and vice versa) and the metapopulation as a whole?

Thus, similar questions need to be answered regardless of the reasons behind the closure of a local population. For example, how do we optimally harvest the exploitable local populations? What is the effect of sources and sinks on the metapopulation? How is the closed habitat affected?

5.1 Previous modelling of harvest closures

The effects of harvest refugia on fisheries has received little attention in the fisheries modelling literature. However, with increasing desires for marine protection, two recent papers (Polacheck, 1990; DeMartini, 1993) use deterministic simulation techniques, while Quinn *et al.* (1994) use a two patch differential equation model, to determine if year-round closures or marine reserves can be an effective management tool.

Polacheck (1990) uses an extension of the Beverton-Holt equation (Beverton and Holt, 1957) to model the effects of a marine fishery reserve on surrounding harvested temperate zone fish, Georges Bank cod *Gadus morhua* and haddock *Melanogrammus aeglefinus*. Measurements of spawning stock biomass (SSB) and yield are made under changes in refuge size, ranging from 1-50% of the possible fished area, transfer rates between the refuge and the exploited habitat, and the fishing mortality rate. For species with rapid growth rates and moderate transfer rates, Polacheck found that marine sanctuaries could increase the spawning stock and biomass.

The model of Polacheck is used by DeMartini (1993) to model the effects of closure size, fishing mortality, emigration-immigration rates, fishing effort and age at first capture on spawning stock biomass per recruit (SSB/R) and yield per recruit (Y/R) for three types of tropical Pacific reef fish. Unlike Polacheck, DeMartini uses a three-sided reserve, noting that most tropical harvest refugia have a shoreline edge, with migration only occurring between the downcoast, upcoast and offshore boundaries. DeMartini also considered the SLOSS (single large or several small) problem with respect to marine reserves, namely if several small reserves (ten 1% closures) or a single large reserve (one 10% closure) can increase SSB/R.

Similar results to those of Polacheck were found. Spawning stock biomass per recruit increased with increasing closure size, but yield per recruit generally decreased. Unlike natural and fishing mortality rates, transfer rates had little effect on SSB/R. Due to the difference in perimeter-to-area ratios, DeMartini concluded that the contribution to SSB/R of several small reserves will be less than that of a single large reserve.

Both authors believe that harvesting refugia have the potential to increase spawning stock biomass per recruit, but will have little effect on increasing yield per recruit. However, fishing effort and age at first capture, among other factors listed, will have to be controlled for this potential to be realised.

Quinn *et al.* (1994) investigate the effectiveness of harvest refugia for conservation and for harvest regulation. They apply their model to the red sea urchin, *Strongylocentrotus franciscanus*, which exhibits both pre-larval and post-larval Allee effects. The proportion of harvesting effort is varied in each patch, allowing the possibilities of reserves (zero effort) or poaching (small effort). They find that harvest refugia are necessary for the population and the fishery to remain viable with certainty. It is further suggested that harvest refugia may be especially useful where harvesting effort is difficult to control, and sanctuaries can provide a useful management alternative to limiting harvest efficiency.

As mentioned in Chapter 1, Clark and Mangel (1979) model two subpopulations of tuna where the underlying subpopulation is unharvested, but connected by migration to the harvested subpopulation above. Yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) are harvested by tuna purse seine fleets that take advantage of the aggregating behaviour of these fish. Floating objects, marine mammals or man-made rafts (fish-aggregating devices, FADs) appear to attract significant surface schools of exploitable fish (Hilborn and Medley, 1989). Interacting with these surface schools is a subsurface population that remains unharvested and is essentially a reserved population. Clark and Mangel (1979) model this situation using two coupled differential equations where individuals diffuse from one population to the other. They find that under some circumstances the underlying population may become extinct, in spite of not being harvested. Mangel (1982), Samples and Sproul (1985), Hilborn and Medley (1989) and Hilborn (1989a) consider various extensions of this model, including removing the steady state assumptions, stochastic fluctuations, different assumptions regarding recruitment to fish-aggregating devices, effects of fish-aggregating devices and vessel number on profitability and parameter estimation from tagging data.

We consider the problem of optimally exploiting a local population that is connected to an unharvested local population by explicitly defining the spatial population dynamics using coupled difference equations, and then searching for analytic solutions using dynamic programming and the method of Lagrange multipliers. We then consider how the optimal harvesting strategies affect yield and spawning stock abundances, and relate this to problems associated with reserve establishment and management.

5.2 Theory

Assume that we have recognised the spatial structure of the population. For simplicity, assume that the metapopulation has two local populations and one is to be reserved or closed. Without loss of generality assume that local population 1 is closed and local population 2 is harvested.

We set up the problem as in the previous chapters, only the escapement for local population 1 is the unharvested abundance, $S_{ik} = R_{ik}$, and the present value expression is the sum of discounted net revenues from the harvested local population, local population 2. Local population 2 is harvested, H_{2k}, and its escapement $S_{2k} = R_{2k} - H_{2k}$ then grows according to equations (2.1) and (2.2) to R_{2k+1}. Thus, including harvesting, equations (2.1) and (2.2) become,

$$R_{1k+1} = \delta_1 R_{1k} + p_{11} G_1(R_{1k}) + p_{21} G_2(S_{2k}) \tag{5.1}$$

$$R_{2k+1} = \delta_2 S_{2k} + p_{12} G_1(R_{1k}) + p_{22} G_2(S_{2k}) \tag{5.2}$$

Now, using the escapement, S_{2k}, as the control variable, our objective is to maximise the present value of net revenue over T seasons, namely maximise

$$P.V. = \sum_{k=0}^{T} \alpha^k \Pi_2(R_{2k}, S_{2k}), \tag{5.3}$$

subject to equations (5.1) and (5.2) and $0 \leq S_{2k} \leq R_{2k}$.

The net revenue produced in period k from a harvest of H_{2k} from local population two is

$$\Pi_2(R_{2k}, S_{2k}) = \int_{S_{2k}}^{R_{2k}} (p - c_2(x))\, dx, \tag{5.4}$$

where p is the price of the stock and $c_2(x)$ is the cost of harvesting a unit of stock from local population 2 when its abundance is x.

5.2.1 Derivation by dynamic programming

As in the previous chapter, dynamic programming is used to determine the optimal harvesting strategy. Let the value function be,

$$J_T(R_{10}, R_{20}) = \max_{0 \leq S_{2k} \leq R_{2k}} \sum_{k=0}^{T} \alpha^k \Pi_2(R_{2k}, S_{2k}). \tag{5.5}$$

The value function is the sum of the discounted net revenue from local population 2 up until season T, maximised by an appropriate choice of the escapement S_{2k}. The value function depends on the initial local population sizes, R_{10} and R_{20}.

A recursive equation for the value functions is obtained from equation (5.5),

$$J_{T+1}(R_{10}, R_{20}) = \max_{0 \leq S_{20} \leq R_{20}} \Big(\Pi_2(R_{20}, S_{20}) + \alpha J_T(R_{11}, R_{21}) \Big). \tag{5.6}$$

This expression states that the value function with time horizon $T+1$ is the maximum of the immediate returns in the first period plus the returns from future harvests if the local population's abundances move to R_{11} and R_{21}. This maximum is achieved by an appropriate choice of the escapement S_{20}.

Consider first the value function with time horizon $T = 0$, i.e. we wish to maximise our immediate net revenue without any consideration of future generations. Then,

$$\begin{aligned} J_0(R_{10}, R_{20}) &= \max_{0 \le S_{20} \le R_{20}} \Pi_2(R_{20}, S_{20}) \\ &= \Pi_2(R_{20}, S_{2\infty}), \end{aligned} \tag{5.7}$$

where $S_{2\infty}$ is the zero-profit escapement size for local population 2.

If we consider next the time horizon $T = 1$ we obtain the following recursive equation,

$$\begin{aligned} J_1(R_{10}, R_{20}) &= \max_{0 \le S_{20} \le R_{20}} \Big(\Pi_2(R_{20}, S_{20}) + \alpha J_0(R_{11}, R_{21}) \Big) \\ &= \max_{0 \le S_{20} \le R_{20}} \Big(\Pi_2(R_{20}, S_{20}) + \alpha \big[\Pi_2(R_{21}, S_{2\infty}) \big] \Big). \end{aligned} \tag{5.8}$$

Equation (5.8) is maximised by partial differentiation with respect to S_{20},

$$0 = -(p - c_2(S_{20})) + \alpha \big[(p - c_2(R_{21}))(\delta_2 + p_{22} G_2'(S_{20})) \big]$$

or,

$$\frac{1}{\alpha} = \frac{(\delta_2 + p_{22} G_2'(S_{20}))(p - c_2(R_{21}))}{p - c_2(S_{20})}. \tag{5.9}$$

From equation (5.9) we implicitly find the optimal escapement when there is one period to go, $S_2^{1*}(R_{10})$. The optimal escapement's dependence on the abundance of local population 1, R_{10} (through $R_{21} = \delta_2 S_{20} + p_{22} G_2(S_{20}) + p_{12} G_1(R_{10})$), is due to the connection of the local populations through migration. The optimal escapement of local population 2 derived when harvesting both local populations also depended on the abundance of local population 1, only in that case the population sizes were "controlled" by harvesting. Obviously, a single, unconnected population has no such reliance.

To find the optimal escapement if there are two periods to go, first recall

$$\begin{aligned} J_1(R_{10}, R_{20}) &= \max_{0 \le S_{20} \le R_{20}} \Big(\Pi_2(R_{20}, S_{20}) + \alpha \big[\Pi_2(R_{21}, S_{2\infty}) \big] \Big) \\ &= \Big(\Pi_2(R_{20}, S_2^{1*}) + \alpha \big[\Pi_2(R_{21}, S_{2\infty}) \big] \Big), \end{aligned} \tag{5.10}$$

where,

$$R_{21}(R_{10}, S_2^{1*}) = \delta_2 S_2^{1*} + p_{22} G_2(S_2^{1*}) + p_{12} G_1(R_{10}).$$

Now if we let,

$$V(R_{2k}) = \int_{S_{2\infty}}^{R_{2k}} (p - c_2(x))\, dx, \tag{5.11}$$

then

$$\Pi_2(R_{20}, S_{20}) = V(R_{20}) - V(S_{20}). \tag{5.12}$$

Thus,

$$J_1(R_{10}, R_{20}) = V(R_{20}) - V(S_2^{1*}) + \alpha V(R_{21}). \tag{5.13}$$

If there are two periods to go, i.e. $T = 2$, we have,

$$\begin{aligned} J_2(R_{10}, R_{20}) &= \max_{0 \le S_{20} \le R_{20}} \Big(\Pi_2(R_{20}, S_{20}) + \alpha J_1(R_{11}, R_{21}) \Big), \\ &= \max_{0 \le S_{20} \le R_{20}} \Big(V(R_{20}) - V(S_{20}) + \alpha \big[V(R_{21}) - V(S_2^{1*}) + \alpha V(R_{22}) \big] \Big), \end{aligned} \tag{5.14}$$

where,

$$\begin{aligned} R_{21}(R_{10}, S_{20}) &= \delta_2 S_{20} + p_{22} G_2(S_{20}) + p_{12} G_1(R_{10}), \\ R_{22}(R_{11}, S_2^{1*}) &= \delta_2 S_2^{1*} + p_{22} G_2(S_2^{1*}) + p_{12} G_1(R_{11}), \end{aligned}$$

and

$$R_{11}(R_{10}, S_{20}) \quad = \quad \delta_1 R_{10} + p_{11} G_1(R_{10}) + p_{21} G_2(S_{20}).$$

Differentiating equation (5.14) with respect to S_{20} we produce the following equation,

$$\begin{aligned} 0 \;=\; & -(p - c_2(S_{20})) \\ & +\alpha\Big[(p - c_2(R_{21}))(\delta_2 + p_{22}G_2'(S_{20})) - (p - c_2(S_2^{1*}))\frac{\partial S_2^{1*}}{\partial R_{11}} p_{21} G_2'(S_{20})\Big] \\ & +\alpha^2\Big[(p - c_2(R_{22}))\Big(\frac{\partial S_2^{1*}}{\partial R_{11}} p_{21} G_2'(S_{20})(\delta_2 + p_{22}G_2'(S_2^{1*})) + p_{12}G_1'(R_{11}) p_{21} G_2'(S_{20})\Big)\Big]. \end{aligned} \tag{5.15}$$

In Chapter 2, where both local populations are harvested (with no delay in recruitment), the terms $V(S_2^{1*})$ and $V(R_{22})$ of equation (5.14) were not functions of the escapement, S_{20}, and so dropped out under differentiation. This was vital for the proof that the equations for optimal harvesting (and thus the escapements) held for all $T > 1$. However, in this case we have an extra dependence on S_{20}, producing an optimal equation for the 2-periods to go escapement which is different from the 1-period to go escapement. For the remaining sections of the derivation, we assume that $S_2^{k*}(R_{10}) = S_2^{k*}$ for $k > 0$. This assumption simplifies the mathematics and does not affect the resulting equilibrium optimal solution.

Assume that we can implicitly solve equation (5.15) to find the optimal escapement when there are two periods to go, S_2^{2*}. Placing this escapement back into $J_2(R_{10}, R_{20})$ we find,

$$J_2(R_{10}, R_{20}) = V(R_{20}) - V(S_2^{2*}) + \alpha\big[V(R_{21}) - V(S_2^{1*}) + \alpha V(R_{22})\big].$$

Now, if there are three periods to go, i.e. $T = 3$, then,

$$J_3(R_{10}, R_{20}) \quad = \quad \max_{0 \leq S_{20} \leq R_{20}} \Big(\Pi_2(R_{20}, S_{20}) + \alpha J_2(R_{11}, R_{21})\Big)$$

$$= \max_{0 \le S_{20} \le R_{20}} \Big(V(R_{20}) - V(S_{20}) + \alpha \Big[V(R_{21}) - V(S_2^{2*}) + \alpha \Big[V(R_{22}) - V(S_2^{1*}) + \alpha V(R_{23}) \Big] \Big] \Big) \tag{5.16}$$

where,

$$\begin{aligned} R_{21}(R_{10}, S_{20}) &= \delta_2 S_{20} + p_{22} G_2(S_{20}) + p_{12} G_1(R_{10}), \\ R_{22}(R_{11}, S_2^{2*}) &= \delta_2 S_2^{2*} + p_{22} G_2(S_2^{2*}) + p_{12} G_1(R_{11}), \\ R_{23}(R_{12}, S_2^{1*}) &= \delta_2 S_2^{1*} + p_{22} G_2(S_2^{1*}) + p_{12} G_1(R_{12}), \\ R_{11}(R_{10}, S_{20}) &= \delta_1 R_{10} + p_{11} G_1(R_{10}) + p_{21} G_2(S_{20}), \end{aligned}$$

and

$$R_{12}(R_{11}, S_2^{2*}) = \delta_1 R_{11} + p_{11} G_1(R_{11}) + p_{21} G_2(S_2^{2*}).$$

Differentiating equation (5.16) with respect to S_{20}, we produce the following equation,

$$\begin{aligned} 0 = & -(p - c_2(S_{20})) + \alpha \Big[(p - c_2(R_{21}))(\delta_2 + p_{22} G_2'(S_{20})) \Big] \\ & + \alpha^2 \Big[(p - c_2(R_{22})) p_{12} G_1'(R_{11}) p_{21} G_2'(S_{20}) \Big] \\ & + \alpha^3 \Big[(p - c_2(R_{23})) p_{12} G_1'(R_{12}) p_{21} G_2'(S_{20})(\delta_1 + p_{11} G_1'(R_{11})) \Big]. \end{aligned} \tag{5.17}$$

This equation can be implicitly solved for the optimal escapement when there are three periods to go, S_2^{3*}. The terms R_{21}, R_{22} and R_{23} are functions of S_{20}, through R_{11}, and this produces a different optimal equation again from equation (5.15).

Generalising this procedure to the case when there are N periods to go, we find,

$$\begin{aligned} J_N(R_{10}, R_{20}) &= \max_{0 \le S_{20} \le R_{20}} \Big(\Pi_2(R_{20}, S_{20}) + \alpha J_{N-1}(R_{11}, R_{21}) \Big), \\ &= \max_{0 \le S_{20} \le R_{20}} \Big(V(R_{20}) - V(S_{20}) + \alpha \Big[V(R_{21}) - V(S_2^{N-1*}) \\ &\qquad + \alpha \Big[V(R_{22}) - V(S_2^{N-2*}) \end{aligned}$$

$$
\begin{aligned}
&+\alpha\Big[V(R_{23}) - V(S_2^{N-3*})\\
&+\cdots\\
\cdots&+\alpha V(R_{2N})\Big]\cdots\Big]\Big]\Big).
\end{aligned}
\tag{5.18}
$$

Differentiating with respect to S_{20} we determine the equation that defines the N^{th} period to go escapement,

$$
\begin{aligned}
0 = & - \quad (p - c_2(S_{20}))\\
& + \quad \alpha\Big[(p - c_2(R_{21}))(\delta_2 + p_{22}G_2'(S_{20}))\Big]\\
& + \quad \alpha^2\Big[(p - c_2(R_{22}))p_{12}G_1'(R_{11})p_{21}G_2'(S_{20})\Big]\\
& + \quad \alpha^3\Big[(p - c_2(R_{23}))p_{12}G_1'(R_{12})p_{21}G_2'(S_{20})(\delta_1 + p_{11}G_1'(R_{11}))\Big]\\
& + \quad \alpha^4\Big[(p - c_2(R_{24}))p_{12}G_1'(R_{13})p_{21}G_2'(S_{20})(\delta_1 + p_{11}G_1'(R_{11}))(\delta_1 + p_{11}G_1'(R_{12}))\Big]\\
& + \quad \cdots\\
\cdots & + \quad \alpha^N\Big[(p - c_2(R_{2N}))p_{12}G_1'(R_{1N-1})p_{21}G_2'(S_{20})(\delta_1 + p_{11}G_1'(R_{11}))\\
& \qquad \ldots(\delta_1 + p_{11}G_1'(R_{1N-2}))\Big],
\end{aligned}
\tag{5.19}
$$

where we have used mathematical induction to prove that, for $k > 2$,

$$
\frac{\partial V(R_{2k})}{S_{20}} = (p - c_2(R_{2k}))p_{12}p_{21}G_1'(R_{1k-1})G_2'(S_{20})\prod_{j=1}^{k-2}(\delta_1 + p_{11}G_1'(R_{1j})).
\tag{5.20}
$$

Simplifying equation (5.19) we find,

$$
\begin{aligned}
0 \ = & \ - \ (p - c_2(S_{20})) + \alpha\Big[(p - c_2(R_{21}))(\delta_2 + p_{22}G_2'(S_{20}))\Big]\\
& + \sum_{k=2}^{N}\alpha^k\Big[(p - c_2(R_{2k}))p_{12}p_{21}G_1'(R_{1k-1})G_2'(S_{20})\prod_{j=1,k>2}^{k-2}(\delta_1 + p_{11}G_1'(R_{1j}))\Big].
\end{aligned}
\tag{5.21}
$$

This equation gives little insight into the optimal strategy. However, we can search for equilibrium solutions to this equation. Setting $R_{ik} = R_{ik+1}$ for $i = 1, 2$ and $k > 0$

and letting N tend to infinity, equation (5.21) becomes,

$$\begin{aligned} 0 &= -(p - c_2(S_{20})) + \alpha\Big[(p - c_2(R_{21}))(\delta_2 + p_{22}G_2'(S_{20}))\Big] \\ &+ \alpha^2(p - c_2(R_{21}))p_{12}p_{21}G_1'(R_{11})G_2'(S_{20})\sum_{j=0}^{\infty}\Big(\alpha(\delta_1 + p_{11}G_1'(R_{11}))\Big)^j. \end{aligned} \quad (5.22)$$

We use the result,

$$\sum_{j=0}^{\infty}\gamma^j = \frac{1}{1-\gamma}, \quad (5.23)$$

for $|\gamma| < 1$, to show that if $|\alpha(\delta_1 + p_{11}G_1'(R_{11}))| < 1$ then,

$$\begin{aligned} 0 = -(p - c_2(S_{20})) &+ \alpha\Big[(p - c_2(R_{21}))(\delta_2 + p_{22}G_2'(S_{20}))\Big] \\ &+ \alpha^2\frac{(p - c_2(R_{21}))p_{12}p_{21}G_1'(R_{11})G_2'(S_{20})}{1 - \alpha(\delta_1 + p_{11}G_1'(R_{11}))}, \end{aligned} \quad (5.24)$$

or,

$$\frac{1}{\alpha} = \left(\frac{p - c_2(R_{21})}{p - c_2(S_{20})}\right)\left[\delta_2 + p_{22}G_2'(S_{20}) + \frac{\alpha p_{12}p_{21}G_1'(R_{11})G_2'(S_{20})}{1 - \alpha(\delta_1 + p_{11}G_1'(R_{11}))}\right]. \quad (5.25)$$

Equation (5.25) defines the optimal escapement for the harvested patch, local population 2, for any initial population sizes R_{10} and R_{20}. This equilibrium solution is the solution to the infinite time horizon problem (shown later) and so is only an approximation for small time horizons, T.

To solve this equation, the initial abundances are input and the escapement, S_2^*, is then found implicitly. The local populations grow after harvesting and the following period's escapement is found by placing these abundances back into the equation, and so on. Eventually an equilibrium is found that is independent of the initial population sizes. Alternatively, we can replace R_{11} by S_{10}, due to the zero equilibrium harvest, and numerically search over S_{i0} for the solution.

In the derivation of equation (5.24) we required the condition,

$$|\alpha(\delta_1 + p_{11}G_1'(S_{10}))| < 1,$$

(we have replaced R_{11} by S_{10}). This condition is equivalent to,

$$\frac{-1-d-\delta_1}{p_{11}} < G_1'(S_{10}) < \frac{1+d-\delta_1}{p_{11}},$$

and if the juvenile production function is logistic, then $G_1'(S_{10}) = r_1(1-2S_{10}/K_1)$, and so we have,

$$\frac{K_1}{2}\Big(1-\frac{1+d-\delta_1}{rp_{11}}\Big) < S_{10} < \frac{K_1}{2}\Big(1+\frac{1+d+\delta_1}{rp_{11}}\Big).$$

This inequality will hold for most realistic parameter values. In the next section we no longer require this condition to derive equation (5.25).

5.2.2 Derivation by the method of Lagrange multipliers

Before proceeding further, we first show that equation (5.25) can be derived in a much simpler fashion using the method of Lagrange multipliers. In this case, we produce equation (5.25) directly and do not require the back-stepping procedures of dynamic programming. Unlike the dynamic programming method, the present value expression is summed over infinite time instead of having a final time, T. Thus, we maximise,

$$P.V. = \sum_{k=0}^{\infty} \alpha^k \Pi(R_{2k}, H_{2k}), \tag{5.26}$$

subject to equations (5.1) and (5.2) and $0 \le H_{2k} \le R_{2k}$.

To facilitate calculations, the net revenue expression is written as a function of population size and harvest, rather than escapement. Hence, the net revenue produced in period k from a harvest of H_{2k} from local population 2 is,

$$\Pi(R_{2k}, H_{2k}) = \int_{R_{2k}-H_{2k}}^{R_{2k}} (p - c_2(x))\, dx, \tag{5.27}$$

where parameters and variables have their usual meaning.

The method of Lagrange multipliers is used to determine the optimal harvesting strategy. We assign the Lagrangian,

$$\begin{aligned} L &= \sum_{k=0}^{\infty}\Big\{\alpha^k\Pi(R_{2k},H_{2k}) - \lambda_{1k}\Big[R_{1k+1} - \delta_1 R_{1k} - p_{11}G_1(R_{1k}) - p_{21}G_2(R_{2k}-H_{2k})\Big] \\ &\qquad - \lambda_{2k}\Big[R_{2k+1} - \delta_2(R_{2k}-H_{2k}) - p_{12}G_1(R_{1k}) - p_{22}G_2(R_{2k}-H_{2k})\Big]\Big\}, \end{aligned} \tag{5.28}$$

with necessary conditions,

$$\frac{\partial L}{\partial R_{ik}} = 0 \qquad k \geq 1, \qquad i = 1,2 \tag{5.29}$$

$$\frac{\partial L}{\partial H_{2k}} = 0 \qquad k \geq 0. \tag{5.30}$$

If we expand equations (5.29) we find,

$$\frac{\partial L}{\partial R_{1k}} = -\lambda_{1k-1} + \lambda_{1k}(\delta_1 + p_{11}G_1'(R_{1k})) + \lambda_{2k}p_{12}G_1'(R_{1k}) = 0 \tag{5.31}$$

$$\frac{\partial L}{\partial R_{2k}} = \alpha^k\Pi_{R_2} + \lambda_{1k}p_{21}G_2'(S^*) - \lambda_{2k-1} + \lambda_{2k}(\delta_2 + p_{22}G_2'(S^*)) = 0, \tag{5.32}$$

and equation (5.30) becomes,

$$\frac{\partial L}{\partial H_{2k}} = \alpha^k\Pi_{H_2} - \lambda_{1k}p_{21}G_2'(S^*) - \lambda_{2k}(\delta_2 + p_{22}G_2'(S^*)) = 0, \tag{5.33}$$

where S^* is the optimal equilibrium escapement. Adding equation (5.32) and (5.33) we produce,

$$\lambda_{2k} = \alpha^{k+1}(\Pi_{R_2} + \Pi_{H_2}). \tag{5.34}$$

Now, rewrite equation (5.33) as,

$$\lambda_{1k} = \frac{\alpha^k\Pi_{H_2} - \alpha^{k+1}(\Pi_{R_2} + \Pi_{H_2})(\delta_2 + p_{22}G_2'(S^*))}{p_{21}G_2'(S^*)}. \tag{5.35}$$

Substituting equations (5.35) and (5.34) into equation (5.31), we have,

$$\begin{aligned} 0 &= -\left[\frac{\alpha^{k-1}\Pi_{H_2} - \alpha^k(\Pi_{R_2} + \Pi_{H_2})(\delta_2 + p_{22}G_2'(S^*))}{p_{21}G_2'(S^*)}\right] \\ &\quad + \left[\frac{\alpha^k\Pi_{H_2} - \alpha^{k+1}(\Pi_{R_2} + \Pi_{H_2})(\delta_2 + p_{22}G_2'(S^*))}{p_{21}G_2'(S^*)}\right](\delta_1 + p_{11}G_1'(R_1)) \\ &\quad + \alpha^{k+1}(\Pi_{R_2} + \Pi_{H_2})p_{12}G_1'(R_1). \end{aligned}$$

Multiplying through by $p_{21}G_2'(S^*)$ and dividing by α^{k+1} we produce,

$$\begin{aligned} &\frac{\Pi_{H_2}}{\alpha^2} - \frac{1}{\alpha}(\Pi_{R_2} + \Pi_{H_2})(\delta_2 + p_{22}G_2'(S*)) \\ &\qquad = \left[\frac{\Pi_{H_2}}{\alpha} - (\Pi_{R_2} + \Pi_{H_2})(\delta_2 + p_{22}G_2'(S^*))\right](\delta_1 + p_{11}G_1'(R_1)) \\ &\qquad\quad + (\Pi_{R_2} + \Pi_{H_2})p_{12}p_{21}G_1'(R_1)G_2'(S^*), \end{aligned} \tag{5.36}$$

and so,

$$\begin{aligned} 0 &= \left[\frac{1}{\alpha} - (\delta_1 + p_{11}G_1'(R_1))\right]\left[(\Pi_{R_2} + \Pi_{H_2})(\delta_2 + p_{22}G_2'(S^*)) - \frac{\Pi_{H_2}}{\alpha}\right] \\ &\quad +(\Pi_{R_2} + \Pi_{H_2})p_{12}p_{21}G_1'(R_1)G_2'(S^*). \end{aligned}$$

After algebraic rearrangement we find,

$$\frac{1}{\alpha} = \frac{(\Pi_{R_2} + \Pi_{H_2})}{\Pi_{H_2}}\left[\delta_2 + p_{22}G_2'(S^*) + \frac{\alpha p_{12}p_{21}G_1'(R_1)G_2'(S^*)}{1 - \alpha(\delta_1 + p_{11}G_1'(R_1))}\right], \tag{5.37}$$

which is equivalent to equation (5.25). Note that $\Pi_{R_2} = (p - c_2(R_2)) - (p - c_2(S^*))$ and $\Pi_{H_2} = (p - c_2(S^*))$.

A further method to derive equation (5.25) uses difference equation techniques to solve equation (5.31), a linear first-order recurrence relation in λ_{1k}. The solution can then be substituted into equation (5.35) and rearranged, producing equation (5.25).

5.2.3 Interpretation of the result

It is difficult to interpret our main result, equation (5.25), directly, and so we discuss some special cases.

Uni-directional migration

If there is no migration between the local populations in one direction or in both directions, i.e. $p_{12} = 0$ and/or $p_{21} = 0$, then equation (5.25) reduces to,

$$\frac{1}{\alpha} = \left(\frac{p - c_2(R_{21})}{p - c_2(S_{20})}\right)\left[\delta_2 + p_{22}G_2'(S_{20})\right]. \tag{5.38}$$

To explain this, first consider $p_{12} = 0$. If $p_{12} = 0$ then the harvested local population's abundance is independent of the closed local population and it is harvested as a single population with population dynamics,

$$R_{2k+1} = \delta_2 S_{2k} + p_{22}G_2(S_{2k}).$$

As expected, equation (5.38) defines the optimal escapement for a population with the above growth characteristics. The harvested local population sends juveniles to the closed local population; however this does not affect the optimal harvesting decision for local population 2.

If $p_{21} = 0$, the explanation is not intuitively obvious. Recall the optimal equation for harvesting local population 2 when both patches are harvested,

$$\frac{1}{\alpha} = \frac{(\delta_2 + p_{22}G_2'(S_{20}))(p - c_2(R_{21})) + p_{21}G_2'(S_{20})(p - c_1(R_{11}))}{p - c_2(S_{20})}.$$

This reduces to equation (5.38) if $p_{21} = 0$. If costs are assumed negligible, then the optimal escapement for the exploited local population is,

$$S_2^* = \frac{K}{2} - \frac{K}{2}\left[\frac{1 + d - \delta_2}{r_2 p_{22}}\right]. \tag{5.39}$$

This suggests that the escapement of local population 2 is not influenced by the input of juveniles from local population 1. This is because the abundance of local population 1 is independent of the harvested stock of local population 2, and so any juveniles that migrate to the exploited local population are "bonuses" to the harvest, and do not influence the equilibrium harvesting decision.

Mathematically, we can show that equation (5.38) holds by observing that the term $V(R_{22})$ in equation (5.14) is not a function of S_{20} if $p_{12} = 0$ and/or $p_{21} = 0$. This term is held constant under partial differentiation with respect to S_{20} and we produce equation (5.35). This is true for all $T > 0$ and thus equation (5.38) determines the optimal equilibrium escapement.

Using the method of Lagrange multipliers with $p_{21} = 0$ we place $\lambda_{2k} = \alpha^{k+1}(\Pi_R + \Pi_H)$ back into equation (5.32) to produce equation (5.38). Equation (5.32) is not a function of λ_{1k} and so equation (5.31) is redundant. Similarly, for $p_{12} = 0$ we substitute equation (5.35) into (5.32) to produce the optimal harvesting equation.

Comparisons with incorrect harvesting policies

In this section we compare harvest strategies from our metapopulation theory and policies where the managing authority has not recognised the metapopulation structure of the stock. As described in the previous section, analytic results are not facilitated by the nonlinear form of equation (5.25), and so we only consider the special case of uni-directional migration and negligible or density-independent costs.

Assume that $p_{21} = 0$ and/or $p_{12} = 0$. With no costs, equation (5.25) simplifies to,

$$\frac{1}{\alpha} = \delta_2 + p_{22}G_2'(S_2), \tag{5.40}$$

and with logistic juvenile production, equation (2.3), the optimal escapement for local population 2 is,

$$S_2^* = \frac{K}{2} - \frac{K}{2}\left[\frac{1 + d - \delta_2}{r_2 p_{22}}\right]. \tag{5.41}$$

Assume that the authority managing the metapopulation has recognised the two local populations but does not believe there to be any larval exchange between them. One of the local populations is reserved, say local population 1, and the other local population is harvested. The estimated growth rate for local population 2 is the "flow in" to the local population,

$$r_{2s} = r_2 p_{22} + r_1 p_{12}, \tag{5.42}$$

as described in Chapter 2, Section 2.2.2.

There are two possibilities for the uni-directional flow. Firstly, assume that there is no larval migration from the exploited population to the reserve, i.e. $p_{21} = 0$. In this case, the escapement of local population 2 from our metapopulation theory is greater than that if the local populations are assumed unconnected, $S_2^* > S_{2s}^*$, if $r_1 p_{12} < 0$. This inequality is not feasible, suggesting that the exploited local population will always be harvested too conservatively. The incorrect harvesting strategy does not take advantage of the migrants to the exploited local population, p_{12}.

The second case of uni-directional flow occurs when larval migration only occurs from the exploited population to the reserve, and so we have $p_{12} = 0$. We find that the escapements from both the correct metapopulation harvesting strategy and the incorrect policy are exactly the same, i.e equation (5.41). As described in the previous section, in these special circumstances, the optimal escapement is not influenced by migration in and out of local population 2, and now that $p_{21} = 0$, the incorrect harvesting policy will estimate the correct growth rate for local population 2, and ultimately produce the same optimal escapement.

The metapopulation could also be managed as though it is one large well-mixed single population. Establishing a reserve system then requires half of the population to be set aside for preservation, the other half for exploitation. The estimated growth rate of the exploited half of the population is assumed to be the average per capita juvenile production, as seen in Chapter 2, Section 2.2.2,

$$r_L = \frac{r_1(p_{11} + p_{12}) + r_2(p_{22} + p_{21})}{2}. \tag{5.43}$$

Assume that there is no larval flow from the exploited local population to the reserved local population, i.e. $p_{21} = 0$. The escapement from our metapopulation theory is greater than the estimated escapement if the local population is assumed to be part of a well-mixed single population, $S_2^* > S_L^*/2$, if $r_2 p_{22} > r_1(p_{11}+p_{12})$. This result is similar to our rule-of-thumb from Chapter 2; namely, that if the per capita juvenile production in local population 2 is greater than the per capita juvenile production in local population 1, then we should harvest local population 2 more conservatively than local population 1. Thus, if the exploited population is a relative source (to itself) then management that assumes that the metapopulation is a single population may over-harvest the population.

Now assume that the uni-directional flow is from the exploited local population to the reserve, and there is no larval flow in the opposite direction, i.e. $p_{12} = 0$. In this case the optimal escapement if the metapopulation structure is recognised is greater than that if it is not, $S_2^* > S_L^*/2$, if $r_2 p_{22} > r_1 p_{11} + r_2 p_{21}$. Thus, the exploited local population will be over-harvested if more larvae per capita remain within the harvested local population than flow in to the reserve.

As far as management implications are concerned, it appears that it is better to err on the side of unconnected single population management, where either the harvest policy is correct or under-harvests the stock, than a management policy that assumes that the metapopulation is a well-mixed single population.

5.3 Examples

In this section we consider some examples that help explore our main result in more detail. The first example simply iterates the dynamic programming equations and compares numerical results with the escapement and harvest of our analytic solution,

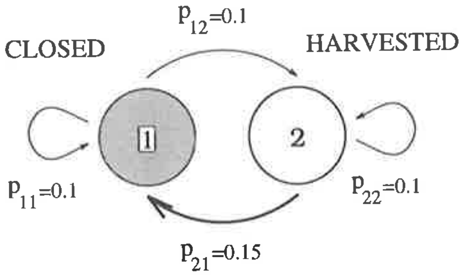

FIGURE 5.1: The reserve system of the example of Section 5.3.1. The shaded region represents the unharvested relative sink/importer local population.

equation (5.25). We then vary the migration parameters, p_{12} and p_{21}, to determine how sources and sinks may effect harvesting strategies and reserve choice. Comparisons are then made between policies from the harvest closure theory presented in the previous sections of this chapter and the theory of Chapter 2, where the metapopulation is fully harvested.

5.3.1 Iteration of the dynamic programming equations

Suppose that we have an unharvested metapopulation that is composed of two connected local populations. Local population 1 is an unharvested reserve and we wish to harvest local population 2. Movement of juveniles within and between the populations is represented by the migration matrix,

$$P = \begin{pmatrix} 0.1 & 0.1 \\ 0.15 & 0.1 \end{pmatrix}.$$

Thus, local population 2 is a relative source/exporter local population, while local population 1 is a relative sink/importer local population. In this example we harvest the relative source/exporter local population and preserve the relative sink/importer local population (see Figure 5.1).

The juvenile production function is logistic, as seen earlier, with growth rates $r_1 = r_2 = 10$, density-dependent factors $K_1 = K_2 = 200$ and adult survival per period $\delta_1 = \delta_2 = 0.1$. The unharvested equilibrium population sizes are $\bar{R}_1 = 133$ for local population 1 and $\bar{R}_2 = 105$ for local population 2.

The cost function is defined by,

$$c_2(x) = \frac{a}{qx},$$

where $a = 30$ and $q = 1.3 \times 10^{-2}$. The price of a unit of stock is $p = 70$. Thus the zero net profit escapement level is,

$$S_{2\infty} = a/qp = 33.$$

If the dynamic programming equations (5.6) are iterated, we produce the escapements and harvests shown in Table 5.1.

The final period's escapement (the first period determined in the dynamic programming procedure) is the zero net profit level, $S_{2\infty}$, as expected. The penultimate period, $T = 1$, has its escapement defined by equation (5.9). An equilibrium escapement is reached, $S^* = 47$, for the preceding periods until the first (last according to the iteration) two periods. The initial conditions are the unharvested equilibrium population sizes, $\bar{R}_1 = 133$ and $\bar{R}_2 = 105$ and the iteration quickly finds the harvested equilibrium thereafter.

Comparing the numerical results from the above analysis to our analytic result, equation (5.25), we find that the same equilibrium escapement and harvest are produced, namely $S_2^* = 47$ and $H_2^* = 43$.

Consider the reverse situation where local population 2, the relative source/exporter local population, is reserved and local population 1, the sink/importer local population, is harvested. Rather than solving the corresponding equations for the harvesting of

T	R_1	R_2	S_2	H_2
7	133	105	46	59
6	111	85	48	37
5	115	91	47	44
4	114	90	47	43
3	114	90	47	43
2	114	90	47	43
1	114	90	50	40
0	117	92	33	59

TABLE 5.1: Escapements and harvests from iterating the dynamic programming equations. Here we harvest the relative source/exporter local population. T is time-to-go, and $T = 0$ is the final period. The abundances immediately prior to harvesting are given by R_1 and R_2. The escapement of the exploited local population is S_2 and the harvest is H_2.

local population 1, for the analyses we transpose the migration matrix, so we have,

$$P = \begin{pmatrix} 0.1 & 0.15 \\ 0.1 & 0.1 \end{pmatrix},$$

and remain harvesting local population 2. To minimise confusion the results are displayed as if we are indeed harvesting local population 1. Thus we now preserve the source/exporter local population and harvest the sink/importer local population. Iterating the dynamic programming equations, we produce the results shown in Table 5.2. The equilibrium optimal escapement derived from the numerical iteration of the dynamic programming equations is $S_1^* = 52$ with equilibrium harvest $H_1^* = 67$.

It may be important, especially in reserve choice, to determine which closed local population maximises economic and/or conservation benefits. We can compare the results from harvesting the relative sink/importer local population with those from har-

T	R_2	R_1	S_1	H_1
7	105	133	54	79
6	100	120	50	70
5	98	118	52	66
4	98	119	52	67
3	98	119	52	67
2	98	119	52	67
1	98	119	52	67
0	98	119	33	86

TABLE 5.2: Escapements and harvests from exploiting the relative sink/importer local population.

vesting the relative source/exporter local population. We observe that the escapement and harvest is larger if we exploit the relative sink/importer local population. This is an ideal situation for the harvested local population, i.e. we are able to conserve more of the exploited stock while also harvesting more. Total equilibrium population sizes are also larger if the relative source/exporter local population is reserved, with $R_T = R_1 + R_2 = 227$ for the harvesting of the sink/importer, and $R_T = 204$ otherwise. However, the preserved local population will have less stock in it, with $R_2 = 98$ compared with $R_1 = 114$.

Thus, if we have to select one of the two patches for preservation, the ultimate choice depends on the objectives of the policy makers. If we wish to conserve as much of the harvested stock as possible in the reserved local population then, according to the analyses, we reserve local population 1, the relative sink/importer local population. However, if we wish to maximise total population size over the metapopulation, or maximise harvest, then local population 2 should be reserved, the relative source/exporter local population.

Comparison with the analytic solution shows that the equilibrium escapements differ by one, with the analytic solution being, $S^* = 53$ and harvest $H^* = 66$. Numerical errors in the computer programs (possibly rounding error) account for the small difference in escapement size.

5.3.2 Variation of the migration parameters

In this section we vary the migration parameters, p_{12} and p_{21}, so we can further explore the effect of migration on optimal harvesting policies. Consider a metapopulation with the following parameters; $\delta_1 = \delta_2 = 0.001$, a logistic juvenile production function with $r_1 = r_2 = 1\,000$, $K_1 = K_2 = 400\,000$ and migration matrix,

$$P = \begin{pmatrix} 0.001 & p_{12} \\ p_{21} & 0.001 \end{pmatrix}.$$

The migration parameters p_{12} and p_{21} are free while other parameters remain constant. In this way we produce a contour plot of the escapements and harvests as functions of the migration parameters. For this example we only consider the equilibrium solution derived from equation (5.25), as numerical solutions are not facilitated by the large state space.

In Figure 5.2 we plot the escapement of the exploited local population as contour lines, where the migration parameters range from 0.0001 to 0.0025. Similarly, in Figure 5.3 the corresponding harvests are plotted. Local population 2 is a relative sink/importer if the point (p_{12}, p_{21}) is below the line $p_{12} = p_{21}$, and it is a relative source/exporter if above. Thus, in the upper-left region, relative source/exporter local populations are harvested while in the lower-right relative sink/importer local populations are harvested.

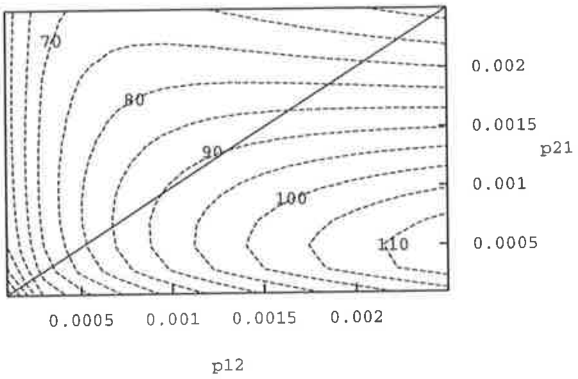

FIGURE 5.2: Escapements of local population 2 as a function of the migration parameters. Numbers on the contours are escapements $\times 10^3$.

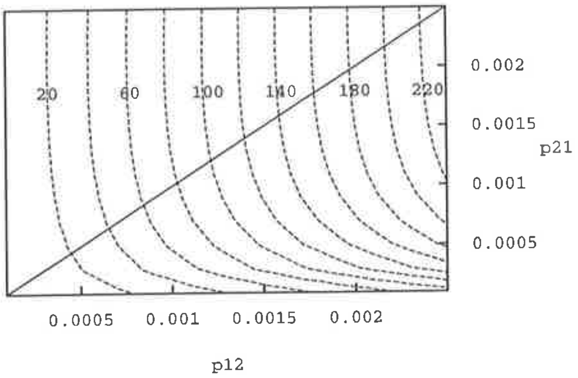

FIGURE 5.3: Harvests from local population 2 as a function of the migration parameters. Numbers on the contours are harvests $\times 10^3$.

We can see from Figures 5.2 and 5.3 that if the relative sink/importer local population is exploited, then both the escapement and harvest in the exploited local population is larger than if the relative source/exporter local population is exploited. This was seen in the previous example with the specified migration matrix. This suggests that to maximise the escapement of the exploited local population, relative sink/importer local populations should be harvested. Commercial industry also benefits the most if this strategy is employed, through an increase in harvests.

Figure 5.4 shows the equilibrium abundance of the unharvested local population

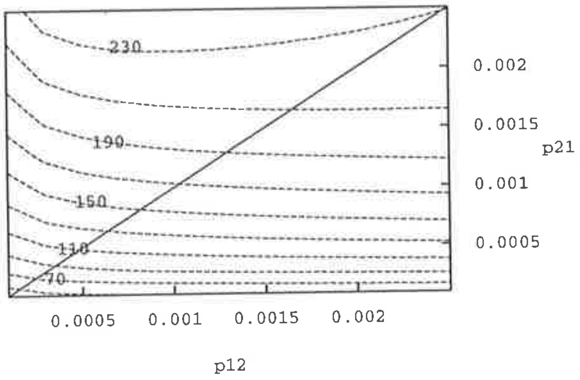

FIGURE 5.4: The equilibrium abundance in the closed local population. Numbers on the contours are the abundance $\times 10^3$.

size as a function of the migration parameters. If the objective is to maintain as large a population size as possible, relative sink/importer local populations should be preserved. However, the over-exploitation of a relative source/exporter local population could have a devastating effect on the preserved relative sink/importer local population, especially if the sink is reliant on the influx of immigrants from the source for its existence. The possibility of stock collapse, which may be even more evident in a stochastically varying population, may sway the reserve decision in favour of the preservation of relative source/exporter local populations. This is an area of future research.

It should be noted that if relative source/exporter local populations are preserved then, even though abundance in the reserve is lower, the overall metapopulation size, $R_T = R_1 + R_2$, is in general greater than if we had reserved the relative sink/importer local population. However, this measure of total population size includes the "soon-to-be-harvested" stock of the exploited local population. An alternative measure is the total spawning stock abundance (SSA). The spawning stock abundance is the number of adults that are left after harvesting and that contribute to the reproductive growth of the population. If we have a fully harvested metapopulation, then the SSA is $S_1^* + S_2^*$,

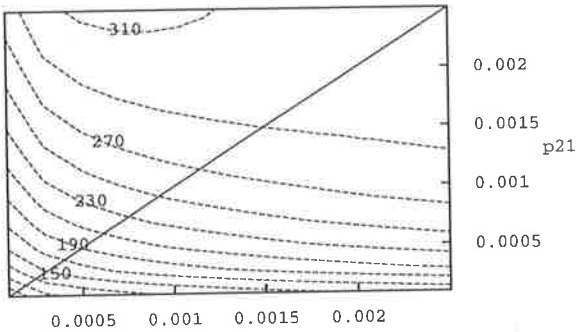

FIGURE 5.5: The spawning stock abundance (SSA) of the metapopulation. Numbers on the contours are SSA $\times 10^3$.

whereas with a closed local population the SSA is $R + S^*$. Figure 5.5 plots contours of the spawning stock abundance as a function of the migration parameters. From this figure we can see that spawning stock abundance is greatest when source local populations are harvested.

In this section we have explored the general behaviour of the system when sources and sinks are harvested in a reserve system. In the following section, we consider a more specific example where we compare harvesting strategies for a metapopulation that is partially closed with that of harvesting both local populations.

5.3.3 Comparison with a fully harvested metapopulation

Assume that the metapopulation has the parameters of the previous example, only with migration matrix,

$$P = \begin{pmatrix} 0.001 & 0.003 \\ 0.001 & 0.001 \end{pmatrix}.$$

This example is analysed in Chapter 2, where both local populations are exploited. The unharvested equilibrium population sizes are $\bar{R}_1 = 148\,028$ and $\bar{R}_2 = 334\,710$. The optimal escapements produced are, $S_1^* = 156\,169$ and $S_2^* = 121\,953$, with equilibrium harvests $H_1^* = 23\,956$ and $H_2^* = 248\,532$. We might now like to know how these escapements and harvests differ if one of the local populations is reserved.

If local population 1 is reserved then the escapement for local population 2, the harvested local population, is $S_2^* = 106\,990$ with harvest $H_2^* = 267\,611$. The stock abundance in local population 1 is $R_1 = 177\,257$. If local population 2 is reserved then the escapement for local population 1, is $S_1^* = 64\,825$ with harvest $H_1^* = 81\,856$. The stock abundance in local population 2, is $R_2 = 255\,510$. As expected, this shows that reserving local population 1, the relative source/exporter, produces the greatest harvest for the exploited patch. The results are summarised in Table 5.3. The starred numbers represent local population sizes before harvesting.

The total harvest from exploiting both local populations is $H_T = H_1 + H_2 = 272\,488$ compared to $H_2 = 267\,611$ if the relative sink/importer local population is harvested. This suggests that similar catches can be made in a reserve system to catches utilising both patches in the metapopulation, if the stock is optimally harvested. The spawning stock abundance is only marginally more in the sink harvested reserve system than in the fully harvested metapopulation. The spawning stock abundance in the fully harvested metapopulation is $S_1^* + S_2^* = 278\,122$, while in the sink harvested reserve system it is $S_2^* + R_1 = 284\,247$. As fas as management is concerned, the benefits of reservation (e.g. minimal environmental degradation, improved quality of catch, tourism) may outweigh the small economic cost of reserving the relative source local population.

If the relative sink is reserved, and the relative source exploited, there is a dramatic drop in the equilibrium harvest; the economic consequences of which may be disastrous for fishers reliant on the resource. However, there is a substantial increase in spawning stock abundance. If economic benefits are associated with increased abundance (e.g. tourism), then reserving the relative sink may be worthwhile. This situation may occur where coral reefs are important for both tourism and, to a lesser extent, harvesting (Ballantine, 1987; Alcala, 1988; Craik, 1993).

The escapements and harvests can also be compared to those derived from incorrectly harvesting the metapopulation. In Chapter 2 we investigated the harvesting strategies if the metapopulation is believed to be composed of two unconnected single populations, or of one well-mixed single population. If the local populations are assumed to be unconnected by larval exchange, then harvests are lower than if we managed the metapopulation as a sink harvested reserve system. The spawning stock abundance is significantly greater if the sink is reserved, however this is at the expense of harvests from the relative source. If the metapopulation is managed as a well-mixed single population, harvests are not greater than if the relative sink is harvested when the metapopulation structure has been recognised. Note that the numbers for the well-mixed single population harvesting policy when both local populations are harvested are for the whole metapopulation, not just local population 1, as shown in Table 5.3. Again, incorrect management produces large spawning stock abundances, but harvests are poor; possibly disastrously so if the source local population is harvested and the sink reserved.

Variation of the migration parameters

In this section we vary the parameters p_{ij} where $i \neq j$ to see how the spawning stock abundance and harvests differ if the metapopulation has a closed local population and if it is fully harvested. As in previous analyses, we consider the migration matrix,

$$P = \begin{pmatrix} 0.001 & p_{12} \\ p_{21} & 0.001 \end{pmatrix},$$

with the following parameters; $\delta_1 = \delta_2 = 0.001$, a logistic juvenile production function with $r_1 = r_2 = 1\,000$, $K_1 = K_2 = 400\,000$.

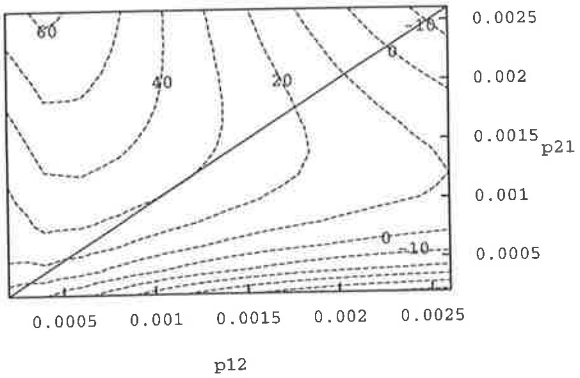

FIGURE 5.6: The difference in spawning stock abundance between a fully harvested metapopulation and a metapopulation with local population 1 closed. Numbers on the contours are the difference $\times 10^3$. A positive number indicates that spawning stock abundance is greater when local population 1 is closed.

The difference between the spawning stock abundances of the two harvesting policies are plotted in Figure 5.6. In this plot we assume that a negative harvest is possible and we use the escapements that produce the negative harvests for the comparisons. The SSA is exactly the same where local population 1 moves from having a positive harvest to a negative harvest in the fully harvested metapopulation case (see Chapter 2, Figure 2.7). Another region where the SSA is the same is in the upper right region of Figure 5.6.

The difference in harvest produced by fully harvesting the metapopulation and reserving local population 2 is shown in Figure 5.7. This shows that using closures as a management tool does not increase harvests. The harvests are the same only when the fully harvested metapopulation moves from positive harvests in local population 1, to negative harvests. For all other parameter values, fully exploiting the metapopulation provides the greater harvests. This result is intuitive as removing a local population from harvesting decreases harvest potential, and if it were optimal to close a local population, the theory of Chapter 2 should indicate this (as it does for the transition

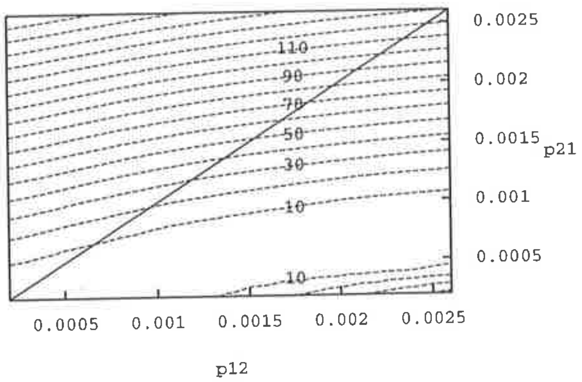

FIGURE 5.7: The difference in harvests between a fully harvested metapopulation and a metapopulation with local population 2 closed. Numbers on the contours are the harvests difference $\times 10^3$. This difference is always non-negative, indicating that total harvests are always greater from a fully harvested metapopulation.

from positive to negative harvests).

5.4 Closing Remarks

In this chapter we have considered the effects of closing a local population on optimal harvesting strategies. Harvest closures are currently receiving great attention because of their role in conservation and fishery regulation.

Fishing closures provide a place of refuge for threatened species or communities and as such are of great importance for marine biodiversity conservation. Protected communities are likely to be connected to surrounding habitat that is experiencing some kind of human impact (Ballantine, 1987). This connection may be through adult or larval migration or through nutrient or chemical (e.g. pollutant) exchange. Human impact may involve harvesting, waste disposal or perhaps mineral or oil extraction. All of these factors (and more) influence the effectiveness of a reserve system. In this chapter we have concentrated on the possible effects of exploitation on harvest closures, and vice versa.

Another important application of harvest closures is as a harvest regulatory mechanism. Due to overfishing or some other unforeseen catastrophe (e.g. oil spillage), harvest closures may be forced upon a fishery for stock recovery purposes. Harvest refugia are also used as a method to regulate stock and harvest effort. For example, prohibition of harvesting in spawning grounds is used to increase future abundance and ultimately catch (for example, prawn nursery grounds (O'Brien, 1994), and haddock spawning habitat (Sissenwine and Kirkley, 1982)). Closures are also used as an alternative to some of the more common regulatory mechanisms that are administratively costly (e.g. to police) and costly to fishers. Thus, in an area of conflict, harvest refugia can provide a medium of compromise between conservation and economic goals.

Using coupled difference equations to model the harvested and closed local populations of a two patch metapopulation, we derived an equation that implicitly defines the optimal equilibrium escapement for the harvested stock. This was achieved using both dynamic programming and the method of Lagrange multipliers.

In a brief discussion of this result for the special case of uni-directional migration (and negligible costs for $p_{21} = 0$) we showed that the optimal equation, equation (5.25), reduces to an equation that does not involve p_{12} or p_{21}. Recall that we harvest local population 2. With no migration into the exploited habitat, $p_{12} = 0$, local population 2 is independent (through a lack of incoming juveniles) of the reserve and so is harvested as a single population. Thus, optimal policies for exploiting local population 2 do not depend upon migrating larvae leaving that local population. Now, when $p_{21} = 0$ the abundance of the unharvested reserve is independent of the exploited habitat, and additional juveniles are then a "bonus" to the controlled, harvested stock. This somewhat surprising result has important implications for the management of harvested reserve systems. If we can ascertain that there is uni-directional migration (or none at all) then the harvested population should be managed using the parameters of that patch, regardless of the juvenile migration.

Comparisons with incorrect harvesting policies were then made with the assumption of uni-directional migration. As described above, this assumption facilitates analytic results. If the local populations are believed to be unconnected by larval exchange, we find that the exploited local population is either under-harvested or correctly harvested, depending on the direction of larval flow. However, if the metapopulation is managed as a well-mixed single population, harvesting may over or under-utilise the resource. This suggests that it is better to err on the side of unconnected single population management if uni-directional flow is suspected. In a numerical study with larval exchange between both local populations, we have shown that incorrect harvesting strategies (with either both local populations harvested or one reserved) do not harvest more than the fully harvested metapopulation or the sink harvested reserve system. In fact, if the metapopulation structure is not recognised, and the relative source local population is exploited, then harvests reduce dramatically, the consequences of which may be catastrophic for the fishery.

Further results in the chapter were obtained from more specific examples. Analytic results that could be easily interpreted were not forthcoming due to nonlinearities in the optimal equilibrium equation, and the assumption of negligible costs also was ineffective except in the special case of uni-directional migration. The numerical examples suggest that maximum yield is obtained from exploiting the relative sink local population, rather than the relative source. This is a sensible strategy to adopt, as harvesting source local populations is fraught with the danger of collapse (Shepherd and Brown, 1993). However, to maximise the metapopulation's spawning stock abundance our results suggest that relative source local population's should be harvested (with a significant decrease in harvest over sink harvesting). As previously mentioned, this strategy will require strict regulation for the conservation goals to be realised.

Fairbridge (1953, as cited by Orensanz *et al.* (1991)) states that the preservation of "upstream" stocks whose larvae are transported to populations in the direction of water flow can be used to protect populations such as scallops. This is analogous to results presented in this chapter regarding the preservation of relative source local populations. Orensanz *et al.* (1991) cite Caddy (1988) as suggesting that scallop populations that experience consistent larval retention are appropriate choices for refugia. These populations may be sink populations, in which case reservation may be optimal to preserve maximum spawning stock. However, as mentioned in our discussion above, and by Fairbridge, it may be more worthwhile preserving the larval source.

The examples show that, while yield is never greater than a fully harvested metapopulation (assuming optimal policies are adopted), it is comparable for populations with low per capita migration into the reserve local population. Once again, this suggests that relative sink local populations should be harvested to keep yield at a level that approximates that taken for a fully harvested metapopulation. The small economic loss due to a decrease in harvests may be countered by the potential environmental and economic benefits of the reserve. However, a reserve system in which a relative source is harvested, while increasing spawning stock abundance, produces a dramatic decrease in yield. This strategy may be financially unwise, unless significant gains can be made from the increase in abundance.

	S_1	S_2	R_1	R_2	SSA	H_1	H_2	H_{Total}
True Optima								
Harvest Both	156	122	180*	371*	278	24	249	273
Harvest LP2 (si.)	-	107	177	375*	284	-	268	268
Harvest LP1 (so.)	65	-	147*	256	321	82	-	82
False Optima								
Unconnected (both)	114	158	177*	340*	272	63	182	245
Harvest LP2	-	158	196	396*	354	-	238	238
Harvest LP1	114	-	150*	313	427	36	-	36
Well-mixed (both)	270	-	537*	-	270	267	-	267
Harvest LP2	-	135	189	389*	324	-	254	254
Harvest LP1	135	-	149*	328	463	14	-	14

TABLE 5.3: A comparison of escapements and harvests from different management policies. Numbers in the table are rounded to the nearest thousand $\times 10^3$. Results under the heading of True Optima assume that the metapopulation structure has been recognised, whereas False Optima results have not. The starred numbers are abundances immediately before harvesting. Spawning stock abundance (SSA) is the total number of adults from both local populations that contribute to the abundance of the following generation. The figures for the well-mixed incorrect harvesting policy when both local populations are harvested are population-wide, not just for local population 1. The abbreviation (si.) indicates that the relative sink is harvested, and (so.) indicates that the relative source is harvested.

Chapter 6

More than two local populations

In this chapter we generalise the juvenile migration model introduced in Chapter 2. We determine optimal harvesting strategies for a spatially structured population that is composed of N interacting local populations. We assume that the local populations interact via the periodic migration of juveniles. We further assume that there is no adult migration or delay in juvenile recruitment to the adult stock.

As in Chapter 2, we model the metapopulation dynamics using coupled difference equations. In this case, we have N equations that represent the abundance of each local population. Dynamic programming is used to determine N modified golden rule equations that specify the optimal escapement for each local population. Using simplifying assumptions, including negligible costs, we find explicit equations for the equilibrium optimal escapements and investigate the effect of alternative management policies on harvests. We also compare the escapements of the local populations if the metapopulation structure has been recognised.

The comparisons are facilitated by local population classifications which are generalisations of those defined in Chapter 2. We redefine relative exporters/importers and relative sources/sinks both verbally and mathematically for the N local population case. We define an *average relative source* local population as a local population that has a per capita larval production greater than the arithmetic average per capita larval production of all other local populations. *Average relative sinks* have a per capita larval production that is smaller than the average per capita larval production of all other local populations.

Models that determine optimal exploitation regimes for commercially viable populations have mainly concentrated on single stock populations (Hilborn, 1985), and where the spatial structure of a population has been recognised, the usual assumption is that the stocks are discrete or reproductively isolated (stock here refers to a "local population" of, say, salmon that has come from a distinct spawning ground). The stocks are assumed to be unconnected by migration and the harvest taken is often a mixture of individuals from all stocks of the population. Paulik *et al* (1967) determines equilibrium harvest rates for up to twenty discrete stocks by maximising sustainable yield. Monte Carlo simulation is employed by Hilborn (1985) who assumes that the stock abundances (of a ten stock population) are unknown and the manager must rely on total abundance information only. Hilborn's paper does not assume that the fishery is in equilibrium (unlike Paulik *et al*, 1967) and results suggest that a fixed escapement policy is only optimal in special circumstances (see also Kope (1992) and Collie *et al* (1990)). Hilborn and Walters (1987) use the Deriso-Schnute model (Deriso, 1980; Schnute, 1985) to simulate the dynamics of six discrete stocks of southern Australian abalone. They suggest that the Deriso-Schnute iterative technique can also accommodate spatially connected stocks. If migration is density-independent, movement can be included into the recruitment (or biomass) expression using spatial transition matrices, analogous to the migration matrices defined here.

As discussed in previous chapters, Quinn *et al* (1994) use coupled differential equation metapopulation models to analyse the effects of harvest refugia on harvests and stock abundance. The initial two-patch models are followed by an age-structured simulation model applied to a red sea urchin (*Strongylocentrotus franciscanus*) metapopulation. The metapopulation is composed of twenty-four local populations that run along a coastline. Results show the importance of harvest refugia for metapopulation persistence when harvest intensities are excessive. Further results are described in Chapter 2. Quinn *et al* (1994) do not explicitly consider the costs of harvesting and, their model being a simulation, analytic solutions are not found.

The work presented here differs from that of previous authors because we consider a spatially structured population that is connected by the migration of juveniles. We explicitly include local population dependent costs, and present a more detailed economic framework from which analytic solutions are found.

It is clear that commercially harvested local populations are not always reproductively isolated (Fairbridge, 1953; John, 1979; Quinn, 1984; Macleod *et al.*, 1985; Orensanz *et al.*, 1991; Frank, 1992; Shepherd and Brown, 1993; O'Brien, 1994; Quinn *et al.*, 1994). In this chapter we present a simple metapopulation model that assumes that N local populations are connected by dispersing larvae. Each local population is assumed to be easily discernible from other local populations and we assume that managers can regulate harvests according to each local population. Following the mathematical description of the model, we analytically determine the optimal harvesting policies for each local population, simplify our results to facilitate our understanding of the system and conclude with some simple examples to illustrate possible applications.

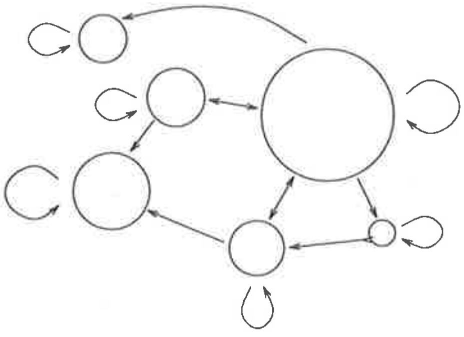

FIGURE 6.1: A metapopulation with multiple local populations. The circles represent the local populations, the area of which roughly represents the size of the patch. Arrows indicate paths of juvenile migration which may occur in one or both directions.

6.1 Theory

Consider N local populations that interact through the dispersal of their juveniles (see Figure 6.1 and the examples at the end of this chapter). To reflect geographic variability in environmental conditions, the local populations have different growth and mortality characteristics. As in Chapter 2, we assume that adults do not migrate between local populations. The adults produce juveniles of which a proportion remain within the natal local population, p_{ii}, and a proportion migrate to other local populations, p_{ij}. The remaining juveniles are lost from the system and this loss is defined by the fraction ϵ_i. The migrating juveniles recruit to their new local population and, together with the sedentary juveniles and adults, form the adults of the following generation.

6.1.1 The model

The metapopulation dynamics is modelled by N coupled difference equations,

$$R_{ik+1} = \delta_i R_{ik} + \sum_{j=1}^{N} p_{ji} G_j(R_{jk}) \qquad i = 1, \ldots, N \tag{6.1}$$

where

$$\sum_{j=1}^{N} p_{ij} + \epsilon_i = 1 \qquad i = 1, \ldots, N. \tag{6.2}$$

Equations (6.1) are generalisations of equations 2.1 and 2.2 of Chapter 2. Recall that the term R_{ik+1} defines the adult abundance of local population i in generation $k+1$. The number of juveniles produced per generation by local population j is given by the recruit production function $G_j(R_{jk})$. The proportion of adults surviving each period in local population i is δ_i.

Including harvesting, the population dynamics defined by equations (6.1) become,

$$R_{ik+1} = \delta_i S_{ik} + \sum_{j=1}^{N} p_{ji} G_j(S_{jk}) \qquad i = 1, \ldots, N \tag{6.3}$$

where

$$\sum_{j=1}^{N} p_{ij} + \epsilon_i = 1 \qquad i = 1, \ldots, N, \tag{6.4}$$

and $S_{jk} = R_{jk} - H_{jk}$ is the escapement of local population j.

We wish to maximise the present value of the total net revenue derived from all N local populations, i.e. maximise

$$P.V. = \sum_{k=0}^{T} \alpha^k \sum_{i=1}^{N} \Pi_i(R_{ik}, S_{ik}) \tag{6.5}$$

subject to equations (6.3) and (6.4), and $0 \leq S_{ik} \leq R_{ik}$ for all i and k. The parameter $\alpha = 1/(1+d)$ is the discounting factor and $\Pi_i(R_{ik}, S_{ik})$ is the net revenue of local population i from a harvest of H_{ik}.

This maximisation can be achieved using dynamic programming. The procedure is not given here as it is a simple extension of the procedure outlined in Chapter 2. The optimal equations that implicitly define the first period optimal escapement for each local population are,

$$\frac{1}{\alpha} = \frac{\delta_i(p - c_i(R_{i1})) + G_i'(S_{i0})\left[\sum_{j=1}^{N} p_{ij}(p - c_j(R_{j1}))\right]}{p - c_i(S_{i0})} \qquad i = 1, \ldots, N. \tag{6.6}$$

Here, S_{i0} is the first period escapement for local population i. The term R_{i1} is the abundance of local population i in the following generation and is a function of S_{i0}. We can prove that these equations hold for all $T \geq 1$ by adjusting the analogous proof of Chapter 2. Note that these equations are a generalisation of the optimal harvesting result derived in Chapter 2. If we assign $N = 2$, we recover equations (2.15) and (2.16). As in the two local population case, if the initial population levels are less than the optimal escapement then we do not harvest until the stock reaches an abundance greater than S_{i0}^*. If the optimal escapement of one or more populations produces a negative harvest (even if $R_{i0} > S_{i0}^*$) then we set $H_{i0}^{*'} = 0$ for all those populations and search for the new escapements for all local populations that maximise equation (6.5).

6.2 Discussion

To facilitate interpretations of the above results, we define three types of local population according to their per capita larval production. The assumption of negligible costs is then used to produce analytic results that can be readily interpreted. Finally, examples comparing optimal and sub-optimal strategies for the no costs case are examined.

6.2.1 Local population classifications

Before proceeding with the no costs theory, we make three classifications of local populations according to their per capita larval production, i.e. the number of larvae or juveniles produced per individual in a local population.

Consider a local population that exports a greater per capita number of larvae to other local populations than it imports. We call such a local population a *relative* *exporter* local population. Mathematically they are local populations i with

$$r_i \sum_{j=1}^{N} p_{ij} = r_i(1-\epsilon_i) > \sum_{j=1}^{N} r_j p_{ji}. \tag{6.7}$$

Conversely, a population that imports more larvae per capita than it exports we call a *relative importer* local population and they are mathematically defined by reversing the above inequality.

A local population whose per capita larval production is greater than that of any other local population is called a *relative source* local population. Local population i is a relative source local population if,

$$r_i(1-\epsilon_i) > r_j(1-\epsilon_j) \qquad \forall j, \quad j \neq i. \tag{6.8}$$

A *relative sink* is a local population that has the smallest per capita larval production and it has $r_i(1-\epsilon_i) < r_j(1-\epsilon_j)$ for all other local populations j.

Finally, consider a local population that has a per capita larval production greater than the average per capita larval production of all other local populations. Such populations we call *average relative source* local populations and are mathematically defined by

$$r_i(1-\epsilon_i) > \sum_{j=1, j\neq i}^{N} \frac{r_j(1-\epsilon_j)}{N-1}. \tag{6.9}$$

A local population that is not an average relative source is an *average relative sink* local population.

6.2.2 No costs analysis

Assuming negligible costs or density-independent costs, equation (6.6) becomes,

$$\frac{1}{\alpha} = \delta_i + G_i'(S_i^*)(1-\epsilon_i) \qquad i = 1, \ldots, N. \tag{6.10}$$

Assume that $G_i''(S_i) < 0$ so that equations (6.10) determine no more than one solution for each S_i^*. For example, assume that $G_i(S_i^*)$ is logistic,

$$G_i(S_i) = r_i S_i (1 - S_i/K_i), \tag{6.11}$$

where r_i is a growth rate and K_i is a form of carrying capacity that causes density dependence in the growth rate of local population i. The optimal escapement for each local population is then,

$$S_i^* = \frac{K_i}{2} - \frac{K_i}{2r_i} \frac{(1 + d - \delta_i)}{(1 - \epsilon_i)} \qquad i = 1, ..., N. \tag{6.12}$$

Comparisons with incorrect harvesting policies

We now determine in what way the metapopulation optimal escapements, defined by equations (6.12), differ from escapements that assume the population is composed either of single unconnected populations or of one well-mixed population. For the following analysis we assume that equations (6.12) produce non-negative harvests for all local populations.

Assume that $K_i = K_j$ for all i, j and that the local populations are harvested as single unconnected populations. The optimal escapement for each unconnected single population is

$$S_{is}^* = \frac{K_i}{2} - \frac{K_i}{2r_{is}}(1 + d - \delta_i). \tag{6.13}$$

Assume that observations of a particular local population i produce estimated growth rates, r_{is}, given by the total "flow in" to local population i, namely,

$$r_{is} = \sum_{j=1}^{N} r_j p_{ji}. \tag{6.14}$$

As described in previous chapters, this assumes that abundances in the local populations are roughly equal and that measurements are made after dispersal.

Thus the optimal escapement for local population i will be greater (smaller) than the escapement from the wrong harvesting policy, $S_i^* \lessgtr S_{is}^*$, if

$$r_i(1-\epsilon_i) \lessgtr \sum_{j=1}^{N} r_j p_{ji}, \tag{6.15}$$

or

$$\sum_{j=1}^{N}(r_i p_{ij} - r_j p_{ji}) \lessgtr 0. \tag{6.16}$$

Condition (6.15) defines relative exporter/importer local populations. Thus, relative exporter (importer) local populations should be harvested more (less) conservatively than if they were managed as single unconnected populations.

Now assume that the N local populations are managed as a well-mixed single population. For simplicity, assume that $K_i = K_j = K$, $\delta_i = \delta_j = \delta$ for all i, j and that the population's growth rate is measured as,

$$r_L = \sum_{j=1}^{N} \frac{r_j(1-\epsilon_j)}{N}, \tag{6.17}$$

that is, the average per capita juvenile production across all local populations.

To compare the escapement of a local population with that from the exploitation of a well-mixed single population, we estimate the local population's escapement by dividing S_L^* by N (remembering that $K_i = K$ for all i). Note that,

$$S_L^* = \frac{NK}{2} - \frac{NK(1-\delta+d)}{2r_L}. \tag{6.18}$$

Thus we find that $S_i^* \lessgtr S_L^*/N$ if,

$$r_i(1-\epsilon_i) \lessgtr \sum_{j=1, j\neq i}^{N} \frac{r_j(1-\epsilon_j)}{N-1}. \tag{6.19}$$

Recall from our definitions of local populations that condition (6.19) defines average relative source/sink local populations. Thus average relative source (sink) local populations should have a larger (smaller) escapement than if we had considered the population to be a well-mixed single population.

Comparisons between local populations

Assume that we have recognised the metapopulation structure of the stock. We would now like to know how the escapements differ from one local population to the next. As in the two local population case, if the local populations have parameters $K_i = K_j$ and $\delta_i = \delta_j$, then $S_i^* \lesseqgtr S_j^*$ if,

$$r_i(1 - \epsilon_i) \lesseqgtr r_j(1 - \epsilon_j). \tag{6.20}$$

A local population i with $r_i(1 - \epsilon_i) > r_j(1 - \epsilon_j)$ for all j is a relative source local population while a local population i with $r_i(1 - \epsilon_i) < r_j(1 - \epsilon_j)$ for all j is a relative sink local population. Thus the relative source (sink) local population has the largest (smallest) optimal escapement of all local populations. There is only one relative source local population and one relative sink local population unless one or more of the local populations have an equal per capita larval production. Note that a relative source (sink) local population is an average relative source (sink) local population, but not necessarily vice versa.

If the local populations are indistinguishable except for $K_i > K_j$ or $\delta_i > \delta_j$, then $S_i^* > S_j^*$. Thus populations that have greater per capita larval production, high adult survival or a large density dependence parameter, K_i, will have larger optimal escapements than populations that do not have those characteristics.

6.3 Examples

In this section, unlike previous chapters, we do not go into detail as far as numerical examples are concerned. The aim of these examples is simply to present some possible geographic forms of spatially structured populations with multiple local populations and add some comments regarding harvesting. We use the simplifying assumptions of negligible costs (or that costs are density and local population independent) and that the adult survival, δ_i, and density-dependent parameters, K_i, are equal for all i.

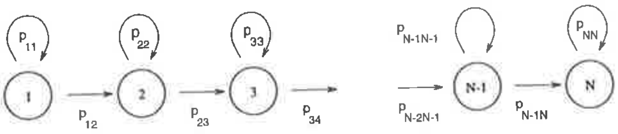

FIGURE 6.2: A metapopulation with uni-directional migration.

6.3.1 Uni-directional migration

Consider a metapopulation that has uni-directional migration, possibly due to water currents, as shown in Figure 6.2. For example, Pennings (1991) describes a mollusc metapopulation in which recruits to a local population off the coast of Santa Catalina Island, California, derive from local spawners and also migrants from spawners in Baja California, Mexico. Larvae from the Mexican local populations are carried north by summer currents; however, no evidence is described for southerly transport of Californian larvae.

Assume that the N local populations are indistinguishable except for differences in $r_i(1-\epsilon_i)$. The size of the optimal escapements increases with increasing per capita larval production, $r_i(1-\epsilon_i)$. The local population with the largest escapement is the population with the largest $r_i(1-\epsilon_i)$ and is the relative source population. Note that if no juveniles are retained in the terminal local population, $p_{NN} = 0$, then regardless of K_N and δ_N, the escapement is $S_N^* = 0$, i.e. we harvest all of the individuals in local population N in each season. The harvest from N in this special case is the juvenile emigrants from local population $N - 1$.

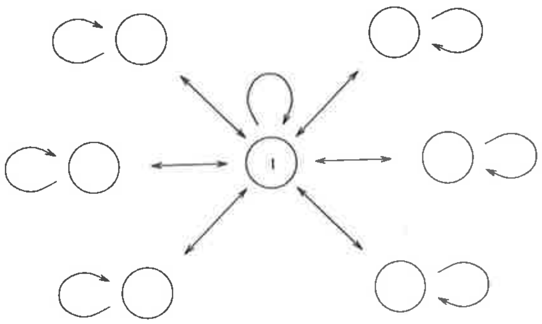

FIGURE 6.3: A metapopulation with a mainland-island spatial structure.

6.3.2 Mainland-island spatial structure

Now consider a metapopulation with a mainland-island, or wagon-wheel like spatial structure with outward migration, a schematic representation of which is shown in Figure 6.3. The position, size and number of the local populations in the figure are purely hypothetical, but may be appropriate in one form or another to some populations. In this case, a central ("mainland") local population produces abundant larvae which replenish skirting ("island") local populations that are possibly in less desirable habitat. Orensanz *et al* (1991) suggests that semi-enclosed bays are often areas which, due to water movements, are areas of enhanced settlement for scallops and may provide larvae for scarcely populated surrounding grounds.

If all migration occurred from the central local population, say local population 1, and $p_{ii} = 0$, for all $i \neq 1$, then the optimal escapement for local population i under the negligible costs assumption is $S_i^* = 0$, for all $i \neq 1$. Thus, local population 1 is a relative source local population and we harvest all of the juveniles that emigrate from local population 1. If $p_{ii} \neq 0$, for all $i \neq 1$, then the sizes of the optimal escapements depends on the quantities $r_i(1 - \epsilon_i)$ with $S_i^* > S_j^*$ if $r_i(1 - \epsilon_i) > r_j(1 - \epsilon_j)$.

We could also have a mainland-island metapopulation structure with inward migration. If local population 1 has no outward migration, $p_{1j} = 0$, for all $j \neq 1$ and no juvenile retention, $p_{11} = 0$, then its equilibrium optimal escapement is $S_1^* = 0$ and we harvest all of the immigrating larvae. The mainland-island metapopulation structures described here may arise in situations where gyres or eddies cause the aggregation of larvae (Fisk and Harriott, 1990; Orensanz *et al.*, 1991; Pennings, 1991). However, in most circumstances there would be both inward and outward migration between at least some of the local populations.

One of the main points from the mainland-island and uni-directional migration examples is that "dead-end" local populations should be fully harvested under the example's assumptions. By dead-end we mean local populations that have immigrating larvae, but no larvae emigrate and none remain in the population. Thus, even without harvesting, these local populations would be doomed to extinction if it were not for the periodic immigration of larvae.

6.4 Adult migration and delays

The previous models assume that there is no adult migration, nor any juvenile delays in recruitment to the adult breeding stock. For completeness we give the optimal harvesting equations for these model here. We do not describe the behaviour of the results here, but we suspect that many of the results from the models outlined in previous chapters will be robust to the extensions.

Assume that adults are capable of migration between local populations as well as juveniles. Initially, assume that there is no juvenile delay in recruitment. As in Chapter 4, we define the proportion of adults migrating from local population i to local population j by the parameter m_{ij}. Maximising the present value derived from all local populations, equation (6.5), we find

$$\frac{1}{\alpha} = \frac{\sum_{j=1}^{N}\Big((\delta_i m_{ij} + p_{ij}G_i'(S_{i0}))(p - c_j(R_{j1}))\Big)}{p - c_i(S_{i0})} \qquad i = 1, \ldots, N \tag{6.21}$$

where S_{i0} is the optimal equilibrium escapement. Equation (6.21) implicitly defines the optimal escapement for a local population with both adult and juvenile migration in an N local population metapopulation.

Assume that juveniles take a number of periods before they become sexually mature. If the delay is related to the local population that receives the juveniles, and the delay associated with local population i is β_i, then the optimal equilibrium escapements from maximising the present value expression are implicitly defined by the equation,

$$\frac{1}{\alpha} = \frac{\sum_{j=1}^{N}\Big((\delta_i m_{ij} + p_{ij}\alpha^{\beta_j}G_i'(S_{i0}))(p - c_j(R_{j1}))\Big)}{p - c_i(S_{i0})} \qquad i = 1, \ldots, N \tag{6.22}$$

where S_{i0} is the optimal equilibrium escapement. As explained in Chapter 3, a delay of this kind may occur due to environmental conditions (temperature, food availability) affecting the sexual maturity of juveniles in the foster local population.

If the delay is associated with the source of the larvae, i.e. the parental local population, then maximising the discounted net revenue derived from all local populations, equation (6.5), we find

$$\frac{1}{\alpha} = \frac{\sum_{j=1}^{N}\Big((\delta_i m_{ij} + p_{ij}\alpha^{\beta_i}G_i'(S_{i0}))(p - c_j(R_{j1}))\Big)}{p - c_i(S_{i0})} \qquad i = 1, \ldots, N \tag{6.23}$$

where S_{i0} is the optimal equilibrium escapement. Environmental conditions could possibly cause juveniles that migrate to alternative local populations having a time to sexual maturity that is related to the parental population (see Chapter 3 for more details).

6.5 Closing Remarks

In this chapter we generalise the juvenile migration model introduced in Chapter 2. We assume that the metapopulation is composed of N local populations connected by dispersing juveniles, e.g. larvae. The metapopulation is modelled using N difference equations; each equation representing the abundance of a local population in one generation as a function of the abundance of all local populations in the previous generation. Equations are derived that implicitly define the optimal escapement for each local population. The details of the derivation are not included here as the method is a simple generalisation of that used in Chapter 2.

To facilitate our understanding of the system, we assume that there are negligible costs and that local populations are indistinguishable except for differences in the migration parameters, p_{ij}. This enables us to find an explicit equation for the optimal escapement for the local populations. Comparisons are made between the local populations' escapements, and between the metapopulation results and harvesting strategies where managers assume that the population is not spatially structured. Results are then related to simple stock classifications, that are generalisations of those defined in Chapter 2. Features of the results included that the optimal escapements depend on the relative size of the per capita larval production; the larger the per capita larval production, the larger the escapement. The local population with the largest per capita larval production we call the relative source local population, and the relative sink has the smallest per capita larval production. We find that the relative source local population should have the largest optimal escapement of the metapopulation and the relative sink the smallest. If the local populations are believed to be unconnected by migration, we find that relative exporter local populations are over-exploited while relative importer local populations are under-exploited. A relative exporter (importer) local population is defined as a local population that exports more (less) larvae per capita than it imports. Similarly, if the metapopulation is managed as a well-mixed single population, then average relative source local populations are over-exploited and average relative sink local populations are under-exploited. Average relative source (sink) local populations are defined as local populations that have greater (lesser) per capita larval production than the average per capita larval production of all other local populations in the metapopulation. Note that if $N = 2$, then an average relative source (sink) is a relative source (sink). This explains why we only required the two classifications, relative exporter/importer and relative source/sink, in the definitions of Chapter 2.

Two examples of typical geographic structures for a multiple local population metapopulation are considered. We describe a metapopulation with uni-directional migration and a metapopulation with a mainland-island structure; however, any number of spatial formations could be applied. A feature of these examples was that "dead-end" local populations are likely to be harvested more heavily than local populations with strong connectivity.

The chapter is concluded with further multiple local population generalisations. Optimal harvesting equations are defined for both juvenile and adult migration, and when juvenile delays are associated with either the source of the juveniles or with the receiving local population. Detailed investigation of these equations is left to the reader, however we suspect that many of the basic rules from previous chapters will generalise well when more than two local populations exist in the metapopulation.

Chapter 7

Conclusion

In this thesis we have formally documented harvesting strategies for the optimal exploitation of a metapopulation. We assume that the exploited population is not homogeneous in space; distinct local populations show characteristic growth, mortality and recruitment traits. Local populations are not reproductively isolated due to the periodic exchange of individuals through dispersive activity. Together the local populations form a dynamic, heterogeneous unit known as a metapopulation.

Many natural populations can be described as metapopulations (Pennings, 1991; Frank, 1992; Shepherd and Brown, 1993; Quinn *et al.*, 1994). Habitat destruction and modification continues to reduce and fragment the range of species, creating a mosaic of habitable and uninhabitable patches. Distinct population aggregations are also a natural consequence of environmental variability in habitat suitability. Frequently, local populations are reliant on immigration for local persistence, and this can have important implications for regulation and conservation. This is one reason why metapopulation modelling is attracting a great deal of interest and the literature is rapidly expanding in complexity and applicability. Metapopulation modelling has become an important part of applied conservation biology (Hanski, 1991; Boyce, 1992; Possingham *et al.*, 1994). We believe that recognising the metapopulation structure of an exploited stock can also have a significant impact on both economic and social objectives.

In Chapter 2 we introduce a basic metapopulation model where two local populations interact through the migration of juveniles, e.g. larvae. Sedentary adults produce young, a proportion of which remain in the parental population, a proportion successfully immigrate to the connected local population and the rest are assumed to either suffer migratory mortality or are redundant non-breeders.

To facilitate interpretation of our results, we define two local population classifications according to the per capita larval production. First, we define a relative source (sink) local population as the local population with the greater (lesser) per capita larval production. Second, the local population that exports a greater (lesser) per capita number of larvae to the connected local population is called a relative exporter (importer) local population.

Maximising the discounted net revenues from both local populations, we derive two equations, one for each local population, that define the local populations' optimal population levels, or escapements. The equations are generalisations of the fundamental equation of renewable resources (Conrad and Clark, 1987) first derived by Clark (1973). Under simplifying assumptions we are able to determine some simple rules-of-thumb for the exploitation of a metapopulation. First, relative source local populations should have the larger of the two escapements, while relative sinks should have the smaller. This result gives a rough guide to the relative degree of harvesting necessary for each local population. However, we may be interested in how different our results are from conventional single population harvesting theory. The metapopulation could be managed in the false belief that the local populations are not connected by periodic migration of juveniles, or that the metapopulation is one well-mixed population. This leads to our second rule-of-thumb; if the local populations have been recognised, but the inter-population migration has not, we find that the relative exporter local population could be harvested too heavily, while the relative importer local population remains under-exploited. Finally, if the metapopulation is incorrectly managed as a well-mixed single population, the relative source local population could be over-exploited, whereas the relative importer may be under-exploited.

An interesting feature of the results is that, under some circumstances, an optimal negative harvest is obtained from one of the local populations. While problematic as far as economic interpretations are concerned in the present model format, we believe that the optimality of a negative harvest is a good indication of where seeding strategies, i.e. enhancing stock for future harvests, should be considered.

In Chapter 3 a simple form of age-structure is considered. We no longer assume that juveniles join the adult breeding population in the year following birth. Thus, an arbitrary delay in juvenile maturation is introduced. The delay in maturation can be determined by either the source of the larvae or its destination. The first model that we consider assumes that the delay is determined by the local population of settlement; we call this the receptor delay model. Second, we assume that the source of the larvae affects the time to sexual maturation; we call this the parental delay model. We assume that the delays are related to local environmental conditions (e.g. food availability, temperature).

As in Chapter 2, we maximise the discounted total net revenues and produce equations that implicitly define the optimal equilibrium escapements for each local population. Features of the results include that the optimal harvesting strategies differ according to the source of the delay, and that the rules-of-thumb from Chapter 2 hold if there is no difference in the delays between populations and if the juvenile survival is the same in both local populations. If the delays differ between local populations, we find that the local population containing juveniles that show the larger maturation delay should be conservatively harvested; in this way we are able to take advantage of the larval migration to the other local population where juveniles take less time to mature and join the harvested adult stock.

In Chapter 4 two models of adult migration are presented. The first model assumes that only adults can migrate between local populations. This model is then extended to include both adult and juvenile migration. Results for the adult migration only model are similar to the juvenile migration model of Chapter 2. For example, the local population with the higher adult migration survival should be the more conservatively harvested population, and could be over-exploited if the metapopulation is incorrectly managed as a single well mixed population. Similarly, local populations with high adult export survival could be over-exploited if the managing body believes the local populations are reproductively isolated. The inclusion of juvenile and adult migration reinforces many of the results of Chapter 2 and the adult migration only model.

Many harvested species have a portion of their population protected in a marine reserve, or as a result of a harvest regulation. This situation is considered in Chapter 5. We assume that one of the local populations is an unharvested reserve, and we find optimal harvesting policies for the exploited local population. If a reserve system is to be established, we show that the relative source local population should be preserved for maximum economic benefit. The total stock that remains unharvested and contributes to future generations, i.e. the spawning stock abundance, is maximised with the preservation of the relative sink local population. However this is countered by the possibility of local population collapse if the source population is excessively harvested. We show that harvests in a reserve system are never greater than the combined harvests from a fully harvested metapopulation, but are only marginally less in many circumstances.

In Chapter 6 we generalise the juvenile migration model of Chapter 2 to metapopulations with more than two local populations. We derive optimal harvesting equations and find that the rules-of-thumb in Chapter 2 extend to the N local population case. A modified rule is that relative average sources (sinks), defined as those local populations with greater (less) per capita larval production than the average of all other local populations, should be more conservatively harvested than predicted if the metapopulation is incorrectly managed as a well-mixed single population. Two possible geographic forms of metapopulation are considered; uni-directional migration and mainland-island (or wagon-wheel) metapopulation structures. The main result from these examples is that local populations with little emigration or larval retention (dead-end local populations) should be heavily (or fully) harvested. The models of Chapters 3 and 4 are briefly reconsidered in this context. We derive the optimal harvesting equations, and it is left to the reader to analyse the equations further. We suspect that many of the results derived in the previous chapters will extend to the general case.

The models that we have presented in this thesis are a first step in the problem of optimally harvesting metapopulations, and it is hoped that many of the concepts introduced here will stimulate further research. The models allow us to consider some simple aspects of harvesting and spatial structure and enhance our understanding of an inherently complex biological and economic system. There are many assumptions that we have made to facilitate derivations of results (outlined in Chapter 1). More complex models, while not accessible to mathematical analysis, may yield interesting results. However, for this thesis we have kept models relatively simple, and as such, we have concentrated on the main extension to the optimal harvesting literature; namely the effects of inter-population migration and spatial structure. More complex biological models (e.g. that include age-structure, seasonal effects, space-limitation, multicommunities) and economic models (e.g. employment, fleet dynamics, investment) would improve the realism of future models, but possibly to the detriment of our understanding of the implications of metapopulation structure on harvesting strategies.

However, we believe that some extensions may be particularly important and profitable. Future models should consider stochastic migration, catastrophes, local extinction and recovery, harvesting within a reserve system in the face of uncertain dynamics, the Single Large Or Several Small (SLOSS) reserve design problem, parameter estimation, and seeding strategies.

Many, if not most, populations experience recruitment that varies both in time and space. The optimal harvesting of a population with variable recruitment and migration (e.g. good and bad years of recruitment), has important implications for management. Variable recruitment may lead to population collapse or local recovery, important concepts in metapopulation theory. Harvesting these populations will intensify problems associated with management, and policies will require careful consideration to prevent local or metapopulation extinction (see Quinn *et al* (1994)). Closely linked to this is the effect of random catastrophes, e.g. oil spills, that cause local extinctions. In this case, connections between populations become vital and how harvesting will fit into this scheme is yet to be determined.

One way of mediating the effect of a possible collapse or catastrophe is with a reserve system. It has been shown that reserves can prevent extinction under excessive harvest intensities (Quinn *et al.*, 1994); however, uncertain recruitment may necessitate more conservative harvesting strategies to maintain the population even with the luxury of a reserve. It may be possible to determine, under optimal harvesting situations, the best sequence of reserves in a multiple-patch metapopulation to maximise economic and/or social objectives (the SLOSS problem; see DeMartini (1993) and Quinn *et al* (1994)).

The models and subsequent examples developed in this thesis rely upon hypothetical estimates of the migration parameters for both analytical and numerical results. Estimating the parameters of fisheries models is difficult even in models that do not include spatial structure (Hilborn and Walters, 1992). However, as we have shown here, if we can measure the mixing parameters then significant economic and social gains may be made, and so parameter estimation is an important future research area for spatially structured models.

A feature of the models that we have introduced here is the optimality (under some circumstances) of a negative harvest, which we interpret as a seeding strategy. This has relevant real world applications, and although the current model format is not strictly appropriate for seeding strategy analysis due to possible different cost structures for positive and negative harvests, we have proposed an alternative model in the Closing Remarks of Chapter 2 that is worth further consideration.

Throughout the thesis we have assumed that the local populations can be regulated on a local population basis, i.e. we can assign independent escapements to the various local populations. However, in some circumstances it may not be possible to assign different harvest limits to each separate population. This may occur where local populations are relatively close to one another, or where management feels that regulation on a local population basis is costly or otherwise infeasible. Thus, we have recognised the metapopulation structure (unlike the well-mixed single population incorrect management policies considered here) and must set a single escapement (or other harvest regulating mechanism) across the whole metapopulation, or part thereof. As in the reproductively isolated population case considered by Paulik *et al* (1967), where less productive populations could be exterminated, local populations with minimal per capita larval production (e.g. average relative sinks) could face the prospect of over-exploitation unless conservative harvesting regimes are considered.

We wish to reiterate that this thesis is by no means the final word on harvesting spatially structured populations. However, we hope that, as an introductory guide, the present study initiates further work in an interesting and rewarding research area. We can not over-emphasise the importance of diligent and enduring resource management. In a society that is placing ever increasing pressure on its natural resources, it is vital that they be managed with the interests of current *and* future generations held firmly in mind; otherwise, in the long run, we shall all be poorer for the loss.

Chapter 8

Appendices

8.1 Appendix 1

In this appendix we determine the conditions that ensure that our equations (2.15) and (2.16) define a maximum, rather than a minimum or a saddle point, for the adult and/or juvenile migration models of Chapters 2 and 4. The more general model that includes both adult and juvenile migration is considered, as the pure adult migration or pure juvenile migration models can be obtained by setting $p_{12} = p_{21} = 0$ and $p_{11} = p_{22} = 1$, or $m_{12} = m_{21} = 0$ and $m_{11} = m_{22} = 1$ respectively.

Recall that the model is,

$$\begin{aligned} R_{1k+1} &= \delta_1 m_{11} S_{1k} + \delta_2 m_{21} S_{2k} + p_{11} G_1(S_{1k}) + p_{21} G_2(S_{2k}) && (8.1) \\ R_{2k+1} &= \delta_2 m_{22} S_{2k} + \delta_1 m_{12} S_{1k} + p_{12} G_1(S_{1k}) + p_{22} G_2(S_{2k}). && (8.2) \end{aligned}$$

To ensure that our solution is a maximum, we must have,

$$\begin{aligned} J_{S_{10}S_{10}} &= c_1'(S_{10}) + \alpha\Big[G_1''(S_{10})(p_{11}(p - c_1(R_{11})) + p_{12}(p - c_2(R_{21}))) \\ &\quad - c_1'(R_{11})(\delta_1 m_{11} + p_{11}G_1'(S_{10}))^2 - c_2'(R_{21})(\delta_1 m_{12} + p_{12}G_1'(S_{10}))^2\Big] < 0 \end{aligned} \tag{8.3}$$

and

$$J_{S_{20}S_{20}} = c_2'(S_{20}) + \alpha\Big[G_2''(S_{20})(p_{21}(p - c_2(R_{21})) + p_{21}(p - c_1(R_{11})))$$
$$- c_2'(R_{21})(\delta_2 m_{22} + p_{22}G_2'(S_{20}))^2 - c_1'(R_{11})(\delta_2 m_{21} + p_{21}G_2'(S_{20}))^2\Big] < 0 \tag{8.4}$$

while also, $J_{S_{10}S_{10}}J_{S_{20}S_{20}} - (J_{S_{10}S_{20}})^2 > 0$, where,

$$J_{S_{10}S_{20}} = -\alpha\Big[c_1'(R_{11})(\delta_2 m_{21} + p_{21}G_2'(S_{20}))(\delta_1 m_{11} + p_{11}G_1'(S_{10}))$$
$$+ c_2'(R_{21})(\delta_2 m_{22} + p_{22}G_2'(S_{20}))(\delta_1 m_{12} + p_{12}G_1'(S_{10}))\Big]. \tag{8.5}$$

8.2 Appendix 2

In finding conditions under which $S_1^* + S_2^* > S_{1s}^* + S_{2s}^*$, we assume that $K_1 = K_2 = K$ and $\delta_1 = \delta_2 = \delta$ and assign $M_{ij} = r_i p_{ij}$. Consider

$$(S_1^* + S_2^*) - (S_{1s}^* + S_{2s}^*)$$
$$= \frac{K}{2}(1 + d - \delta)\Big[\frac{1}{M_{11} + M_{21}} + \frac{1}{M_{22} + M_{12}} - \frac{1}{M_{11} + M_{12}} - \frac{1}{M_{22} + M_{21}}\Big]. \tag{8.6}$$

If we multiply through to produce a positive common denominator for the square bracket terms, we need only consider the numerator. Let $\bar{M} = (M_{11} + M_{12} + M_{22} + M_{21}) > 0$. The numerator becomes,

$$(M_{22} + M_{12})(M_{11} + M_{12})(M_{22} + M_{21}) + (M_{11} + M_{21})(M_{11} + M_{12})(M_{22} + M_{21})$$
$$-(M_{11} + M_{21})(M_{22} + M_{12})(M_{22} + M_{21}) - (M_{11} + M_{21})(M_{22} + M_{12})(M_{11} + M_{12})$$
$$= \Big[(M_{11} + M_{12})(M_{22} + M_{21})\bar{M}\Big] - \Big[(M_{11} + M_{21})(M_{22} + M_{12})\bar{M}\Big]$$
$$= \bar{M}\Big[M_{11}M_{21} + M_{22}M_{12} - M_{11}M_{12} - M_{22}M_{21}\Big]$$

$$
\begin{aligned}
&= \bar{M}\Big[r_1p_{11}r_2p_{21} + r_2p_{22}r_1p_{12} - r_1^2p_{11}p_{12} - r_2^2p_{22}p_{21}\Big] \\
&= \bar{M}\Big[(r_2p_{21} - r_1p_{12})(r_1p_{11} - r_2p_{22})\Big]. \qquad (8.7)
\end{aligned}
$$

Thus, for $(S_1^* + S_2^*) - (S_{1s}^* + S_{2s}^*) > 0$ we require $r_ip_{ij} > r_jp_{ji}$ and $r_ip_{ii} < r_jp_{jj}$ for $i = 1, 2$ and $j = 1, 2$ with $j \neq i$.

8.3 Appendix 3

To prove that $S_1^* + S_2^* \leq S_L^*$ where S_L^* is determined assuming that the population is a well-mixed single population and that there are no costs associated with harvesting, we first recall the expressions $S_1^* + S_2^*$ and S_L^*,

$$
\begin{aligned}
S_1^* + S_2^* &= K - \frac{K(1+d-\delta)}{2}\Big[\frac{1}{r_1(1-\epsilon_1)} + \frac{1}{r_2(1-\epsilon_2)}\Big] \\
S_L^* &= K - \frac{2K(1+d-\delta)}{r_1(1-\epsilon_1) + r_2(1-\epsilon_2)}. \qquad (8.8)
\end{aligned}
$$

Let $A_j = r_j(1-\epsilon_j)$. Thus,

$$
\begin{aligned}
S_1^* + S_2^* - S_L^* &= K(1+d-\delta)\Big[\frac{2}{A_1+A_2} - \Big(\frac{1}{2A_1} + \frac{1}{2A_2}\Big)\Big] \\
&= K(1+d-\delta)\Big[\frac{8A_1A_2 - (A_1+A_2)2A_2 - (A_1+A_2)2A_1}{4(A_1+A_2)A_1A_2}\Big] \\
&= -K(1+d-\delta)\Big[\frac{(A_1-A_2)^2}{2(A_1+A_2)A_1A_2}\Big] \leq 0. \qquad (8.9)
\end{aligned}
$$

8.4 Appendix 4

Non-negative harvesting

In Chapter 2 we discussed the possibility of an optimal negative harvest or optimal seeding of a local population. However, if a negative harvest was infeasible, we set that local populations harvest to zero and searched for new optimal escapements that maximise the objective function, equation (2.11). In this appendix we find an analytic solution to this problem using Lagrange multipliers.

Assume that the optimal escapements from equations (2.15) and (2.16) produce a negative equilibrium harvest in local population 1. A negative harvest is not feasible. We must now maximise equation (2.11) subject to a zero harvest constraint for local population 1. Thus, we maximise

$$J_1(S_{10}, S_{20}) = \Pi_1(R_{10}, S_{10}) + \Pi_2(R_{20}, S_{20}) + \alpha(\Pi_1(R_{11}, S_{1\infty}) + \Pi_2(R_{21}, S_{2\infty})), \qquad (8.10)$$

subject to

$$S_{10} = R_{11} = \delta_1 S_{10} + p_{11} G_1(S_{10}) + p_{21} G_2(S_{20}), \qquad (8.11)$$

where

$$R_{21} = \delta_2 R_{20} + p_{12} G_1(S_{10}) + p_{22} G_2(S_{20}). \qquad (8.12)$$

Equation (8.11) ensures that local population 1 has a zero equilibrium harvest.

Note that the one-step maximisation of the objective function, J_1, disregards the initial conditions, R_{i0}, as they are held constant when maximising with respect to the escapements, S_{i0}. The Lagrangian is,

$$\begin{aligned} L &= \Pi_1(R_{10}, S_{10}) + \Pi_2(R_{20}, S_{20}) + \alpha(\Pi_1(R_{11}, S_{1\infty}) + \Pi_2(R_{21}, S_{2\infty})) \\ &\quad -\lambda(S_{10} - \delta_1 S_{10} - p_{11} G_1(S_{10}) - p_{21} G_2(S_{20})), \end{aligned} \qquad (8.13)$$

with necessary conditions,

$$\begin{aligned} \frac{\partial L}{\partial S_{10}} &= -(p - c_1(S_{10})) - \alpha(p - c_1(S_{10})) - \alpha(p - c_2(R_{21})) p_{12} G_1'(S_{10}) \\ &\quad -\lambda(1 - \delta_1 - p_{11} G_1'(S_{10})) = 0, \end{aligned} \qquad (8.14)$$

and

$$\frac{\partial L}{\partial S_{20}} = -(p - c_2(S_{20})) - \alpha(p - c_2(R_{21}))(\delta_2 + p_{22}G_2'(S_{20})) \\ -\lambda(-p_{21}G_2'(S_{20})) = 0. \tag{8.15}$$

Note that we have used,

$$\frac{\partial \Pi_i(R_{i0}, S_{i0})}{\partial S_{i0}} = -(p - c_i(S_{i0})). \tag{8.16}$$

Rearranging equation (8.14) we find,

$$\lambda = \frac{(p - c_1(S_{10}))(\alpha - 1) + \alpha p_{12}G_1'(S_{10})(p - c_2(R_{21}))}{1 - (\delta_1 + p_{11}G_1'(S_{10}))}. \tag{8.17}$$

Substituting λ into equation (8.15) and rearranging we find,

$$\frac{1}{\alpha} = \left(\frac{p - c_2(R_{21})}{p - c_2(S_{20})}\right)\left[\delta_2 + p_{22}G_2'(S_{20}) + \frac{p_{12}p_{21}G_1'(R_{11})G_2'(S_{20})}{1 - (\delta_1 + p_{11}G_1'(S_{10}))}\right] \\ +\left(\frac{p - c_1(S_{10})}{p - c_2(S_{20})}\right)\left[\frac{p_{21}G_2'(S_{20})(1 - 1/\alpha)}{1 - (\delta_1 + p_{11}G_1'(S_{10}))}\right]. \tag{8.18}$$

Equation (8.18), along with the zero equilibrium harvest condition (8.11), determines the optimal escapement to the non-negative harvest problem, defined by equations (8.10) and (8.11). Equation (8.18) is similar to equation (5.25) of Chapter 5. This is not surprising, as forcing a zero harvest from local population 1 is essentially reserving or closing that local population to harvesting. The difference in the two results occurs due to the present theory assuming a fixed escapement policy, and initial and terminal harvests. The closure theory presented in Chapter 5 assumes that there is no harvest whatsoever from local population 1, i.e. $S_{10} = R_{10}$, and escapements are not necessarily constant for all periods.

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