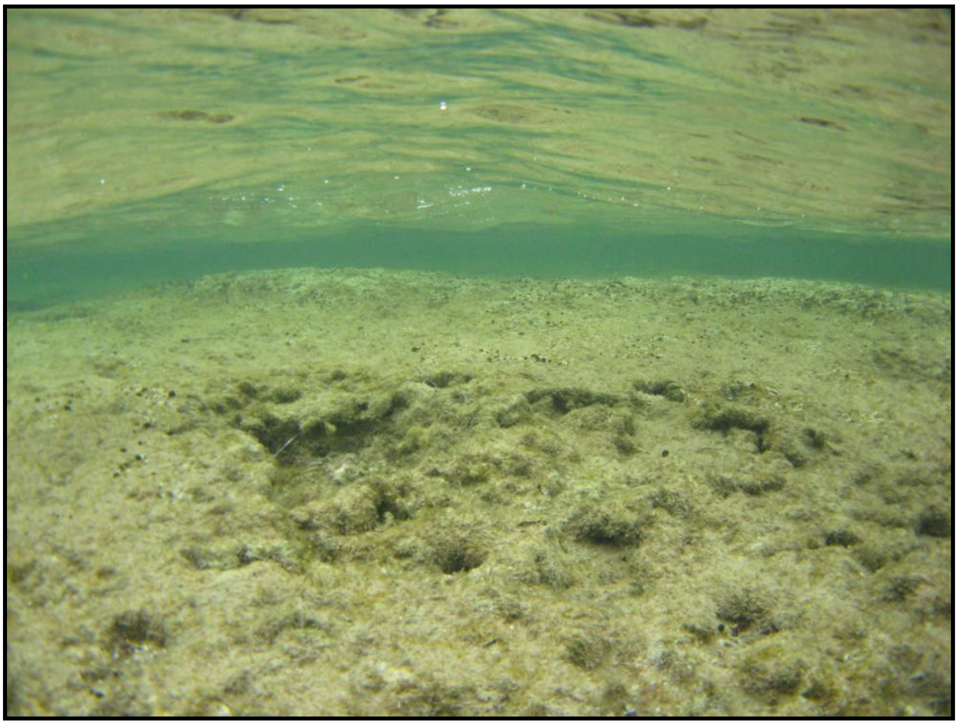
Declining Water Quality as a Driver of Changes to Subtidal Communities



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School of Earth and Environmental Sciences
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DEDICATION

I dedicate this thesis to my late father, Phillip Roy Gorman. The help and encouragement Dad gave me throughout undergraduate years and at the onset of my PhD were key influences that drove me to the finishing line. Not only did he push me to reach my goals, but he was also the first to celebrate success. Phillip died on the 19th October 2004, aged 53 years. You will be missed by all who knew you, and remembered as the “king of your castle”. As part of this dedication I include the following lyric – from a favourite poet of Dad’s and one that I read at his funeral.

A Lyric
If space and time, as sages say,
Are things that cannot be,
The fly that lives a single day
Has lived as long as we.
But let us live while yet we may,
While love and life are free
For time is time, and runs away,
Though sages disagree.
The flowers I sent thee when the dew
Was trembling on the vine,
Were withered ere the wild bee flew
To suck the eglantine.
But let us haste to pluck anew
Nor mourn to see them pine,
And though the flowers of life be few
Yet let them be divine.
T.S. ELIOT

Declaration of Authorship

This work contains no material which has been accepted for the award of any other degree or diploma in any university or tertiary institution to Daniel Gorman 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.

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Cover image: Regime-shifted landscape? An example of structurally simple turfed habitat, common along southern Australia‟s urbanised coastlines. Photograph taken along the Adelaide metropolitan coast in 2008 by the author.

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“Man has only recently come to realise the finite limitations of the coast as a place to live, work and play and as a source of valuable resources. This realisation has come along with overcrowding, overdevelopment in some areas, and destruction of valuable resources by his misuse of this unique environment”. Ketchum 1972

Abstract

This body of work examines the influence of land use on nearshore water quality, and how this can drive changes to algal and invertebrate communities along Australia‟s southern coastline. The overall aim of the thesis was to investigate links between increasing coastal water-column nitrogen concentrations (derived from terrestrial inputs) and the expansion of turf-forming habitats that can alter the structure and function of subtidal ecosystems.

I initially tested whether human activities in coastal catchments can increase subsidies of nitrogen to open rocky coasts. I identified landscape-scale variation in the supply of Dissolved Inorganic Nitrogen (DIN) to coastal waters adjacent to natural, agricultural and urban catchments. Compared to natural catchments, subsidies of DIN were 8 - 407 times greater in urban catchments, and 1 - 63 times greater in agricultural catchments. Subsidies of nitrogen from urban catchments were attributed to the release of sewage effluent, as delineated by δ^{15}N isotopic values of transplanted algae.

Having made this link, I then assessed whether catchment-scale variation in nitrogen subsidies may predict patterns of subtidal habitat structure, particularly as related to theories of regime shifts from forested landscapes to structurally depauperate turf-forming habitats. I validated this hypothesis, demonstrating that both relative covers and patch-sizes of turfed habitat were greater where the ratio of terrestrial nitrogen inputs to ambient coastal resources was large. An important realisation was that loss of forests may be more strongly related to the size of subsidy (i.e. the relative increases in water column nitrogen concentrations along urban coasts) rather than the size of coastal populations. Together, these data link coastal development with modified land-to-sea subsidies, and indirectly support the model that ecological effects may be proportional to the disparity between donor and recipient resources.

Having demonstrated a link between nitrogen subsidies and subtidal habitat change, I then investigated factors likely to initiate and maintain such shifts. My results demonstrate that nutrient elevation can alter the natural phenology of turfs, sustaining dense covers throughout periods of natural senescence (winter). Perennial turf covers are able to accumulate large volumes of sediment; a synergy can impede the winter recruitment of canopy-forming species (kelps and fucoid algae). My observations of reduced forest recovery along urban coasts serve to highlight the complex interaction between elevated nutrients, persistent turf covers and increased sediment accumulation, which can reduce the resilience of coastal ecosystems to disturbance.

In recognition that regime shifts are likely to have consequences for higher trophic levels, I compared the diet of invertebrate herbivores from healthy and degraded coastlines using stable isotope analysis (δ^{13}C and δ^{15}N). Dietary modelling showed that turfs contributed more to the diet of consumers along degraded coastlines where turfed landscapes have replaced extensive covers of macroalgal forest. Additionally, there were strong correlations between covers of turfed habitat, herbivore diet and relative densities. Changes to ambient food quality associated with regime shift may be an important aspect of nutrient-driven change along human-dominated coastlines.

The final component of my thesis redressed some of the uncertainty about restoration initiatives for urban coasts by demonstrating that regime shifts are not necessarily permanent. I showed that turf removal can facilitate the recovery of degraded forests. Future restoration, therefore, is a possible outcome of polices that aim to decouple the link between nutrient inputs and recalcitrant turfed habitats that prevent forest recovery. Initiatives that reduce nutrient discharge to coastal waters (e.g., wastewater recycling) are likely to restore the resilience of nearshore marine ecosystems and promote their rehabilitation.

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I am indebted to my supervisors Sean Connell and Bronwyn Gillanders, whose energy and enthusiasm for subtidal and estuarine ecology is truly inspiring. To colleagues and members of the Southern Seas Ecology Laboratories (past and present) who helped with fieldwork, labwork, and to make time spent in the office both stimulating as well as entertaining. Special thanks, in addition to photo credits (below) to, The Livore family, A. Irving, T. Saunders, S. Hart, B. Roberts, C. Izzo and J. Brooks. Thanks also, to the many who offered passionate discussions about science held on the green couch or in various Rundle Street hotels. I am also thankful for the love and support of my family and friends, especially Mum and Rainer; Amy Vomiero, Delphine Fleury, Claire Doughty and the group-of-8 brotherhood (while not exactly beneficial to a life of study, were always there when needed).

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Chapter Acknowledgements

(As per individual manuscripts)

Chapter two

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Chapter three

This research was motivated by the requirement of policy makers (South Australian Department of Premier and Cabinet) for improved understanding of the factors contributing to habitat loss along Adelaide‟s metropolitan coastline. Field assistance was provided by A. D. Irving, J. Brooks and F. Colosio. Paul Burch (SARDI Aquatic Sciences) provided helpful advice on statistical analysis. This research was funded by a Wildlife Conservation Fund South Australia Grant to Gorman (0254) and an ARC Discovery grant to Sean Connell.

Chapter four

This research was driven by the need to understand the affects and the potential for reversing subtidal regime shifts along the southern coastline of Australia. We are thankful for the helpful comments of Bronwyn M. Gillanders and Bayden D. Russell. Financial support was provided through an Australian Research Council Grant to Sean Connell and a Lirabenda Endowment Fund Research Grant to Daniel Gorman. We thank R. Diocares for mass spectrometry, I.J. Carlson for assistance with nutrient analysis, T. Saunders and A.F. Dobrovolskis for field assistance. The experiments performed in this study comply with the current laws of Australia.

Chapter five

We thank the farsighted recognition of P. von Baumgarten (Principle Marine Policy Adviser) and her department (The Department of Environment and Heritage) for commissioning this research to guide development of new policy on coastal management. The Australian Research Council (ARC Linkage) provided leverage funds to assist DEH achieve our work in an applied context. These research outcomes have been used by the South Australian Department of Premier and Cabinet as part of its coastal planning and water recycling initiatives. Helpful comments were provided by T. Wernberg. Field assistance was provided by J. Brooks, J.P. Livore and J.R. Naumann. Daniel Gorman was supported by a Wildlife Conservation Foundation Research Grant (0254), and Sean Connell by a QEII Fellowship.

Conducting broad-scale subtidal research along Australia‟s southern coastline requires a great deal of logistical planning, and a „big‟ boat. Research vessel „Odax‟ in front of Australia‟s parliament house. Photograph taken by the author during the Southern Ocean trip 2005.

CHAPTER ONE

CHAPTER ONE:

General Introduction

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General Introduction

The physical structure and biological function of natural ecosystems is strongly influenced by disturbance (Petraitis et al. 1989). Natural disturbance whether physical (e.g., climate and catastrophe) or biological (e.g., predation and competition), can disrupt community equilibrium to bring about shifts in the dominant assemblages of an ecosystem (Dayton et al. 1984). Indeed, there is ample evidence that many opportunistic (and competitively inferior) species would cease to exist in the absence of disturbance events (Sousa 1984). Whilst disturbed states may occur over different spatial extents and durations and in doing so contribute to physical and biological heterogeneity (Pickett & White 1985), the high capacity for renewal displayed by most ecosystems acts as a buffer to permanent change. The ability of an ecosystem to recover (i.e., the rate or degree to which community characteristics are restored following disturbance) is defined as „resilience‟ (sensu, Holling 1973) and differs from its sister concept of „resistance‟, which is defined as the extent to which a system can resist change by disturbance. Typically, resilience remains static over time (Gunderson 2000) because of its dependence on interactions among biota (e.g., herbivores-algae) and their environment (e.g., water quality).

Whilst most ecosystems are readily able to recover from disturbance under natural conditions, there is concern that those under pressure from human activities display reduced resilience (Gunderson 2000, Hughes et al. 2005). Human impacts such as resource extraction (Jackson et al. 2001), nutrient loading (Carpenter et al. 1998) and sedimentation (Airoldi 2003) can alter environmental conditions making recovery from disturbance slow or impossible (Fig. 1.1; Gunderson 2000). Failure to recover from disturbance can lead to a permanent change in community structure termed a „regime shift‟ (sensu, Scheffer & Carpenter 2003) that is generally characterised by the replacement of complex and productive assemblages by comparatively depauperate ones (e.g., „weedy species‟; Tilman & Lehman 2001). Altered communities can have dramatic effects on the overall ecological function of a system by reducing its ability to generate resources, absorb wastes and provide services to animal and human populations (Vitousek et al. 1997b, Loreau et al. 2001, Folke et al. 2004).

Figure 1.1 Ball and cup heuristic of „ecosystem state‟ (as shown by stability landscapes) referring to the ability of the ecosystem to remain in a stability domain, as the shape of the domain changes in response to altered environmental „conditions‟. The stability landscapes (front to back) represent reductions in resilience from an undisturbed system with high resilience, through to a point where a perturbation of a significant size can induce a regime shift. (Figure from, Scheffer et al. 2001, reproduced with permission from Nature).

1.1 Regime shifts in temperate rocky marine communities

The alteration of coastal landscapes by humans (e.g., urbanisation and agriculture) can result in considerable changes to macrophyte communities, and ultimately, the degradation of subtidal ecosystems (e.g., Duarte 1995, Deegan et al. 2002). Coastal marine habitats are particularly susceptible to land-based human activities as they act as reservoirs for terrestrially evolved materials (e.g., McCulloch et al. 2003, Seitzinger et al. 2005). Coastal eutrophication (in particular dissolved nitrogen; see reviews, Cloern 2001, Rabalais 2002) can dramatically alter nearshore water quality, creating novel conditions that favour the persistence of opportunistic species (Worm & Lotze 2006). These conditions can lead to undesirable changes to assemblages of submerged aquatic vegetation that can affect many ecosystem attributes (Duarte 1995, Bowen & Valiela 2001). Replacement of perennial macrophyte communities by simple or un-vegetated habitats can represent a significant loss of structural complexity (i.e., refuge for animals; Connolly 1994, Warfe et al. 2008) and primary productivity (e.g., energy and organic matter; Mann 1973). These losses are increasingly recognised as a substantial threat to the biodiversity and functioning of temperate rocky coasts globally (Vitousek et al. 1997a, Steneck et al. 2002, Worm & Lotze 2006, Connell 2007b).

Along temperate coastlines, concerns over degraded or regime-shifted landscapes have generally centred on the replacement of subtidal canopy-forming macroalgae (e.g., kelp forests) with species of lower structural and/or ecological value (e.g., filamentous turf-forming algae; Fig. 1.2; Connell 2007b). Whilst these regime shifts can occur as a result of acute human impacts (e.g., direct harvesting of species and pollution; Walker & Kendrick 1998, Jackson et al. 2001), there remains a less complete understanding of the causal mechanisms and consequences of „chronic‟ stressors such as diffuse nutrient and sediment inputs (e.g., Carpenter et al. 1998, Bowen & Valiela 2001). In nearshore aquatic systems, this lack of information has been confounded by the relatively recent history of scientific investigation (see review on the early years of subtidal research; Shepherd 2007) and the inherent technical limitations of conducting subtidal investigations.

Figure 1.2 The replacement of canopy-forming algae (e.g., kelp-dominated landscapes pictured on the top) by structurally simple and less productive habitats comprising turf-forming algae (e.g., turf-dominated landscapes pictured on the bottom) have been linked to changes in land management. The relative vulnerability of systems to such switches may be understood by identifying changes in the ratio of donor (e.g., land) to recipient (e.g., sea) subsidies. (Figure reproduced from, Gorman et al. 2009).

Turf-forming algae (hereafter, „turfs") are natural to rocky reef habitats and represent initial colonisers of disturbed space (e.g., Diaz-Pulido & McCook 2002, Irving & Connell 2006b). Under natural conditions, the re-establishment of canopy-formers precludes the persistence of turfs (Connell 2003, Wernberg & Connell 2008). This cycle appears to be facilitated by patterns of annual senescence displayed by turfs (i.e., June – August in the southern Hemisphere; Russell B.D. et al. unpublished data), which coincide with the peak recruitment phase of canopy-forming laminarian and fucoid algal species (Novaczek 1984, Hotchkiss 1999). The mechanism, by which turfs are able to disrupt community equilibrium to prevent the recovery of forests, is likely to relate to the novel environmental conditions that characterise human-dominated coastlines (Carpenter et al. 1998, Cloern 2001). The continuous discharge of terrestrial materials into coastal waters adjacent to urban catchments (e.g., sewage effluent; Valiela et al. 1997, Lapointe et al. 2004) can provide a continuous source of otherwise limiting nutrients that facilitate the persistence of such „weedy" algal opportunists (Worm et al. 1999).

Whist persistent turf-dominated gaps may be initially small and inconsequential (e.g., 3 - 6 m^2; Kennelly 1987b), the continuous failure of canopies to recover over time may enable these gaps to coalesce to form expansive areas of turfed landscape (see, Gorgula & Connell 2004). The mechanisms involved in gap persistence, therefore, appear to represent important precursors to gap expansion that can ultimately change the structure of subtidal landscapes. Over longer periods (e.g., several decades), it is possible to observe the wholesale loss of diverse macroalgal forests in favour of turfed landscapes that may be sustained for decades (e.g., Eriksson et al. 2002, Connell et al. 2008).

1.2 Spatial subsidies

Understanding the processes by which materials flow between spatially linked habitats is a vital consideration for landscape ecologists (Polis & Hurd 1996, Polis et al. 1997). Because natural spatial subsidies involve the transfer of energy, materials and often organisms across habitat boundaries (predominantly from productive to less productive habitats) human activities that modify such subsidies can drive substantial change to „recipient" ecosystems. The consequences of altered subsidies are also likely to be exacerbated where humans introduce foreign or naturally limiting resources (e.g., nutrients and sediments) because their effects are thought to be greater where there is a large ratio in resource magnitude between the donor and recipient system (Marczak et al. 2007). In this context, there is emerging concern that systems with naturally low resource availability are disproportionately vulnerable to human enhancement of these same resources (e.g., input of nutrients to nutrient poor coasts; Connell & Irving 2008). Understanding how human modification of land-to-sea subsidies can affect recipient nearshore systems is vital given that human pressure on marine resources will continue to increase (Tappin 2002).

Across the globe there has been increasing recognition of the detrimental effects that intensive land use has on marine environments (e.g., Zann 1995, Bowen & Valiela 2001, Seitzinger et al. 2005). These concerns have compelled some governments to implement regulatory controls on activities that have the potential to degrade coastal water quality (e.g., licensing for industrial and agricultural discharges; Environmental Protection Act, 1984). Whilst this control of point-source pollution (e.g., sewage effluent) can have positive, albeit variable outcomes for subtidal assemblages (e.g., Underwood & Chapman 1996, Pitt et al. 2009), non-point pollution (e.g., urban and agricultural runoff) remains a considerable and growing cause of concern (see, Carpenter et al. 1998). The difficulties involved in identifying and quantifying non-point discharge, means that it is often more useful to investigate its cumulative effects using a landscape-scale approach (see, Wiens et al. 1993); the scale at which most coastlines are managed. One way to assess the effects of human coastal development on nearshore environments is to examine the links between land use, water quality, and the composition and structure of subtidal communities (Fig. 1.3).

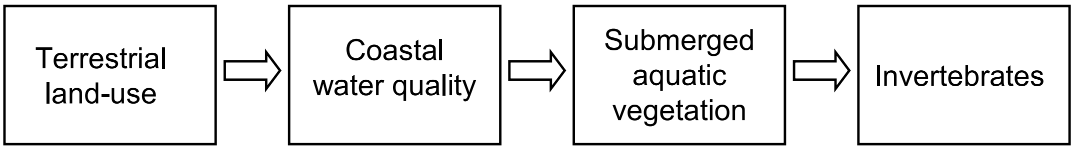

Figure 1.3 Flow diagram outlining a „landscape-scale" approach to investigating links between land use, coastal water quality and biological parameters. Given that subsidies of terrestrially derived materials such as nitrogen can have considerable effects within recipient ecosystems, it is vital to understanding how human activities can mediate the transfer of energy and materials at scales large enough to be relevant to management.

1.3 Recovery of regime-shifted landscapes?

Understanding processes of recovery within disturbed landscapes requires knowledge of the complex suite of interacting factors that govern resilience (Palumbi et al. 2008). Appreciation of the interactions between human induced stressors (nutrients and sediments) and ecosystem processes (e.g., disturbance-recovery cycles, herbivory, etc.) will facilitate the development of models that more accurately predict conditions where human activities can transform acute disturbances into chronic stress (see, Nystrom et al. 2000). Whilst turfs are generally ephemeral, human inputs can facilitate their persistence and expansion, which reduces rates of canopy recovery and ultimately affects forest resilience (review, Airoldi 2003). Rehabilitation efforts require consideration of the biotic and abiotic conditions that contribute to the phenomenon whereby forests fail to recover along increasingly human-dominated coastlines. Only by gaining this information can we hope to identify the circumstances in which regime shifts can be reversed.

Whilst there is evidence that turfs and their associated sediments can inhibit the recruitment of canopy formers (Kennelly 1987a), there remains no quantitative evidence that the removal of turfs will result in increased rates of canopy recovery. In the absence of this information models that seek to understand the processes of canopy recovery, as mediated by water quality, tend to be elusive and the potential for future restoration efforts remain uncertain. Added to this uncertainty, is the lack of understanding about the effect of regime shifts on subtidal trophic dynamics. This field of research is being increasingly seen as necessary for the development of theories that link changes to natural systems with human inputs of limiting resources (Polis & Strong 1996). Studies need to focus on the mechanisms by which changes to the food resource-base of subtidal habitats can affect the diet and relative abundance of herbivores, which in turn strongly influence the organisation and function of ecological systems (Connell & Vanderklift 2007). One way in which this can be effectively done is by combining information on habitat composition (e.g., mapping) with that of animal nutrition (using techniques for diet analysis such as stable isotope analysis) and ultimately relating these to measures of community abundance and diversity.

1.4 Stable Isotope Analysis as a tool for ecologists

Over the past few decades, the application of Stable Isotope Analysis (SIA) has grown from a technique used almost exclusively in the field of geology, into one used widely within the biological sciences (review, Peterson & Fry 1987). SIA makes use of the inherent variation in the ratio of heavy to light stable isotopes of common elements such as carbon, nitrogen, hydrogen and sulphur. The isotopic value (often termed „isotopic signature") is expressed in terms of δ notation (e.g., carbon: $\delta\ ^{13}C$ or nitrogen: $\delta\ ^{15}N$) and is calculated as the difference in parts per mille (‰; equation 1) from standard reference material (e.g., PeeDee belemnite limestone carbonate for carbon; air for nitrogen) where X is the ‰ value for the element of interest and R is the corresponding ratio of heavy to light isotopes in a sample (i.e., $^{13}C/^{12}C$ or $^{15}N/^{14}N$). Isotopic determinations are done using an ion ratio mass spectrometer, after conversion of a sample into gaseous form (for a detailed description see, Peterson & Fry 1987).

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 10^3 \qquad \text{(Equation 1)}$$

An important consideration for SIA techniques is that of isotopic discrimination or „fractionation" (Peterson & Fry 1987). Whilst many chemical and biochemical reactions can alter the ratio of heavy to light isotopes, the magnitude of change is typically quite small (i.e., 0.04%, 0.11%); for the heavy isotopes of nitrogen and carbon respectively (Peterson & Fry 1987) and is only of concern when conducting dietary analysis (see, Chapter 4).

Stable isotope analysis as an environmental tracer

Stable Isotope Analysis (SIA) presents an excellent tool for investigating process information and energy flow within aquatic systems (Michener & Schell 1994). The technique has been widely used for studying the flow of energy and materials between adjacent ecosystems (e.g., Polis & Hurd 1996, Anderson & Polis 1998, Schindler & Lubetkin 2004) and also, as a means of delineating sources of human-derived pollution across numerous ecological systems (e.g., Vandover et al. 1992, McClelland et al. 1997, Monna et al. 1997). Nitrogen isotopic values ($\delta^{15}N$) have proven particularly useful indicators of anthropogenic nutrient uptake by submerged aquatic vegetation (e.g., sewage and agricultural fertiliser; Gartner et al. 2002, Costanzo et al. 2003, Savage & Elmgren 2004). This application compares the $\delta^{15}N$ values of vegetation with those of human nitrogen sources (i.e., sewage effluent: +10 ‰ - +20 ‰; and agricultural fertilisers -4 ‰ - +4 ‰; Heaton 1986) and naturally occurring nitrogen sources (e.g., organic nitrogen; +4 ‰ - +9 ‰; Heaton 1986). The ability to delineate sources of human pollution and trace its incorporation into aquatic vegetation highlights the potential of SIA techniques as a means of investigating the causes and consequences of nutrient-driven regime shifts along temperate rocky coastlines.

Stable isotope analysis to infer the diet of animal consumers

A comprehensive understanding of the consequences of human-induced regime shifts warrants knowledge of the manner in which human perturbations can alter trophic dynamics (Polis & Strong 1996). Traditionally, trophic interactions were examined by direct observations of resource-use by consumers or by gut contents analysis (review, Hyslop 1980). These methods have significant limitations that may bias inferences, as materials ingested are not necessarily a reflection of those assimilated (Michener & Schell 1994) and differential assimilation rates of dietary components can lead to differing representations within an organisms digestive tract (e.g., Gee 1989, Day & Cook 1995).

Stable Isotope Analysis (SIA) is an effective means of dietary inference that has considerable advantages over conventional methods (Peterson et al. 1985, Gannes et al. 1997). SIA is particularly effective for assessing the nutritional importance of potential food sources in systems where direct dietary analysis is problematic owing to spatial and or temporal patterns of distribution (Melville & Connolly 2003, Connolly et al. 2005b). Dietary calculations are based on the observation that the isotopic value (or signature) of a consumer will reflect that of its food source with minimal or predictable fractionation (see, Tieszen et al. 1983, Peterson & Fry 1987). The dietary application of SIA techniques typically rely on the ratio of isotopic carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) owing to their predictable trophic discrimination (DeNiro & Epstein 1978, 1981). Comparing $\delta^{13}C$ and $\delta^{15}N$ values of animal tissue with those of isotopically distinct categories of primary producers enables calculations of the relative nutritional importance of each food source. The proportional contribution of food sources can be estimated using either mass balance equations or mixing models (Phillips 2001, Phillips & Gregg 2001).

1.5 Studying Australia's southern seas

South Australia has a coastally constrained population with > 80 % of the total inhabitants (~ 1.6 million) residing in the city of Adelaide or within the five regional town centres (ABS 2006). Coastline geomorphology includes beach-dune systems, cliffs, rocky headlands and two large inverse estuaries (i.e., Gulf St Vincent and Spencer Gulf). Excluding the upper parts of the two gulfs, the coastline is open to intense wave exposure, predominantly during the Austral winter (June – August), from Southern Ocean swells (Hemer & Bye 1999). Coastal waters are transitionally warm to cold temperate, with mean sea surface temperatures varying from ~ 13ºC in winter to ~ 23ºC in summer (Bryars & Havenhand 2006). Compared to other temperate regions, South Australia‟s coastal waters are considered nutrient poor (Rochford 1980), a likely consequence of negligible riverine inputs (DWLBC 2005) and the absence of major upwelling (Lewis 1981). Despite this, human activities over the last two centuries have substantially altered nutrient export throughout much of Australia‟s coastal zone (for background see, Flannery 1994, Connell 2007b).

Southern Australia‟s rocky subtidal landscapes are dominated by forests of canopy-forming macroalgae, of which the most common and widespread components are kelps (e.g., *Ecklonia radiata*; Goodsell et al. 2004) and fucalean species (e.g., the genera Cystoseiraceae and Sargassaceae; Wernberg & Connell 2008). Forested landscapes cover > 90 % of rocky substratum and vary from mono-specific to highly mixed communities (Connell & Irving 2008). Turf-forming algae generally comprise a relatively small component of habitat along natural or pristine coastlines (< 7 %; Connell & Irving 2008) but may increase their relative covers along urban coastlines (up to 60 %; Gorgula & Connell 2004). Another feature of southern coasts is the conspicuous absence of „urchin barrens‟, a common subtidal landscape along Australia‟s east coast (Andrew 1993). Within forest landscapes, the most abundant species of invertebrate herbivores are urchins (e.g., *Heliocidaris erythrogramma*; Vanderklift & Kendrick 2004) and Turbinid gastropods (e.g., *Turbo torquatus*; Wernberg et al. 2008). Whilst these invertebrates may reach considerable densities at some locations (see, Russell & Connell 2005), they are typically far less abundant than comparable locations at similar latitudes (e.g., eastern Australia; Fowler-Walker & Connell 2002 and New Zealand, Choat & Schiel 1982) and appear not to display the behavioural adaptations needed to create „barrens habitat‟ (Connell 2007a).

Despite South Australia‟s relatively small population and low levels of resource exploitation, there is evidence for nutrient-driven regime shifts along its developed coastlines (Gorgula & Connell 2004, Fernandes et al. 2009). This evidence centres on historical losses of seagrass meadows and kelp forests along the metropolitan coastline (reviews, Neverauskas 1987, Connell et al. 2008). Much of this degradation is believed to be the consequence of terrestrial inputs of treated sewage effluent, stormwater runoff and light industrial discharge (Wilkinson et al. 2003, Wilkinson et al. 2004). South Australia‟s „clumped‟ demography; means that these „developed‟ coastlines are interspersed amongst „undeveloped‟ alternative coastlines (i.e., native vegetation and low-level agriculture) which represents a unique „natural experiment‟ in which to study the effects of expanding human populations on coastal ecosystems (cf. Europe, where undeveloped „controls‟ are almost completely lacking; Airoldi, L. pers. comm.).

1.6 Scope and outline of the thesis

This thesis summarises my doctoral research into the effects of land use and declining water quality on the structure and function of subtidal rocky communities along the southern coastline of Australia. Specifically, I examined the effects of modified subsidies of nitrogen (land-to-sea) on the relative covers of turf-forming algae, and the mechanism by which changes to the phenology of turfs can reduce the resilience of disturbed canopy-forming forests. I then investigated how apparent change in the structure of subtidal communities (i.e., from forested to turfed landscapes) can affect the quantity and quality of ambient food resources to invertebrate consumers. The specific aims of my research were:

1. To identify and predict the effects of nitrogen subsidies from terrestrial catchments on nearshore canopy-forming algal communities (i.e., kelp forests).

2. To investigate the mechanisms whereby nutrients, persistent turf covers and sediments can affect the resilience of canopy-forming algal communities.

3. To examine the consequences of human-derived habitat change on the diet and densities of invertebrate herbivores (consumers).

4. To investigate the permanence of regime-shifted landscapes and assess the potential for their effective rehabilitation.

The thesis follows a logical order linking altered coastal water quality to habitat-loss (the observation); the factors that facilitate habitat-change (the mechanism); the subsequent effects on higher trophic levels (the consequences), and the potential for rehabilitation (management implications). Whilst each chapter is written in the form of separate scientific paper that can be reflected on independently (i.e., differing slightly in style and presentation), the body of work builds naturally for a comprehensive analysis of human-mediated changes to the resilience of subtidal forests along the southern Australian coastline.

Studying southern seas… University of Adelaide research station on West Island, South Australia, with research vessel „Odax" moored against the jetty. Photograph taken by the author during a prolonged stay in 2007.

CHAPTER TWO

CHAPTER TWO:

Land-to-sea connectivity: linking human-derived terrestrial subsidies to subtidal habitat change on open rocky coasts

CHAPTER TWO

Land-sea connectivity: linking human modification of subsidies to altered subtidal habitats

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Statement of Authorship

In this paper Sean D. Connell and I supplied funding and developed the experimental design. Bayden D. Russell contributed to the development of ideas and helped with field sampling. I collected, processed and analysed the nitrogen samples, developed and ran the algal transplant experiment and analysed the habitat data. Additionally, I developed and analysed the subsidy cf. effect size models and wrote the accepted manuscript.

I certify that the statement of contribution is accurate

Daniel Gorman (Candidate)

Signed *Date* 10/12/09

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis

Associate Professor Sean D. Connell

Signed *Date* 10/12/09

Dr Bayden D. Russell

Signed *Date* 10/12/09

Preamble

Chapter 2 examines the link between land use and altered subtidal habitats resulting from the modification of land-to-sea nitrogen subsidies. The effect of land use on coastal nitrogen concentrations and the composition of subtidal algal habitats were investigated across South Australia. The Chapter is a reproduction of a co-authored article published in the journal: *Ecological Applications*, and as such is written in plural using American English. The paper is written for a global audience with a focus on management implications as per the style of the journal. It is included with the permission of the Ecological Society of America. The article can be cited as:

Gorman D., Russell B.D. and Connell S.D. (2009) Land-sea connectivity: linking human modification of subsidies to altered subtidal habitats. *Ecological Applications* 19:1114-1126

2.1 Introduction

Recognition that disparate habitats are often energetically and dynamically linked by spatial subsidies has been an important contribution to ecological theory that seeks to integrate phenomena across scales and systems (Turner 1989, Oelschaeger 1991). Natural subsidies (i.e., fluxes of energy, materials or organisms from productive to less productive habitats) are ubiquitous among ecological landscapes and exert strong influences on the community dynamics of receiving systems (Polis et al. 1997). While natural subsides are considered fundamental to the maintenance of ecological systems (Polis & Hurd 1996, Connolly et al. 2005a), there has been comparatively less recognition of the central influence that human modification of landscapes has on rates of subsidy between spatially linked systems, many of which are under increasing pressure from human development. Human activities liberate large amounts of materials that are otherwise limiting within natural systems (e.g., nutrients and sediments), which are invariably exported to adjacent „recipient" systems.

Aquatic systems are susceptible to increased subsidies of nutrients, and links from land to rivers, lakes and estuaries have been well established (McClelland et al. 1997, Carpenter et al. 2001, Gillanders & Kingsford 2002, Vander Zanden & Sanzone 2004). There has, however, been substantially less recognition of such landscape-scale effects in open coastal habitats, possibly because the effects of nutrients are insidious compared to more conspicuous drivers of habitat change (e.g., fishing, population outbreaks, and invasive species). While there is increasing concern that human export of nutrients (particularly nitrogen; Seitzinger et al. 2005) can alter the magnitude of cross-habitat subsidies to drive change in recipient systems, such links are seldom made in coastal environments where nitrogen limitation (Howarth & Marino 2006) means that such inputs could rival climate change in their environmental effects (Vitousek et al. 1997a). A more comprehensive understanding of the land-to-sea connection is relevant to managing ecological sustainability of increasingly human-dominated coasts (Kay & Alder 2005).

Human activities such as urbanisation, industrial and agricultural production have altered the natural nutrient cycle, increasing concentrations of nitrogen within the biosphere (Tilman et al. 2001, Rabalais 2002). The degree to which these enhanced resources affect natural systems is contingent on both their ambient and historical concentrations and the capacity of the system to assimilate these additional nutrients. Subsidies have strong effects where the ratio of the subsidised resource between donor and recipient system is large (Marczak et al. 2007). In this context, there is emerging concern that systems of naturally low resources are disproportionately vulnerable to human enhancement of these same resources (e.g., input of nutrients to nutrient poor coasts; Connell & Irving 2008). The transfer of nitrogen across ecosystem boundaries is considered one of the more important forms of natural subsidy, owing to its strong influence on both biological and abiotic characteristics of recipient systems (Polis et al. 1997). In this way, the addition of nitrogen from human activities along increasingly developed coastlines has the potential to drive serious and perhaps irreversible change to subtidal habitats (Connell et al. 2008).

Undesirable habitat change is often characterized by shifts from perennial species with structurally complex communities to opportunistic species with simple and less diverse elements (Tilman et al. 2001, Hughes et al. 2005). On temperate coasts, the subtidal equivalent centres on the replacement of canopy-forming algae (e.g., kelps) by turf-forming algae (e.g., Australia, Connell et al. 2008, Baltic Sea, Worm et al. 1999, North Sea, Eriksson et al. 2002 and Mediterranean Sea, Rodriguez-Prieto & Polo 1996). The driver of such shifts appears to be the ability of turfs, which are generally ephemeral and opportunistic, to persist under conditions of elevated nutrients (Worm et al. 2000a) and subsequently inhibit the recruitment of canopies (Airoldi 2003). In this regard, we propose that regime shifts (i.e., from canopies to turfs) are more likely on coasts with greater disparity in nitrogen concentration between human inputs (i.e., nitrogen enriched donor) and recipient waters (i.e., nitrogen poor recipient). If this theory is valid, then variation in subsidy ratios (donor-recipient) should correlate to variation in the frequency and extent of substratum occupied by turf-forming algae.

The use of catchment-scale observations to assess land-to-sea linkages provides a framework to assess human driven changes at scales relevant to practical management and ecological application. This landscape-scale perspective focuses on the collective abiotic environment rather than individual sources of pollution and their small scale dynamics (e.g., the diversity of pollutants and their hourly-weekly-monthly variation). It also brings into focus longer-term issues such as the effects of historical land use (Lotze et al. 2006) and the degree of habitat degradation across one of the most intensely and historically developed zones of human habitation; the coastal zone. South Australia represents an exceptional opportunity to investigate land-to-sea subsidies as a product of past, current and future human activity because major coastal use has been very recent and well documented. Coastal occupation (1.2 million people) has occurred since European colonisation (1836), with accelerated coastal development since early 1980"s. Regime shifts (canopy-to-turf) are quantitatively understood (i.e., past environments recognized; Connell et al. 2008), spatially restricted (i.e., spatial „controls" are possible) and can be studied with reference to replicate catchments of natural vegetation (i.e., „controls" for urban runoff); a possibility that is not available on the vast majority of the globes coastlines (Airoldi & Beck 2007).

This research examined land-to-sea linkages by relating variation in donor-recipient subsidies to variation in subtidal habitat. The first step identified variation in donor-recipient ratios of dissolved inorganic nitrogen (DIN) among catchment-types. While nutrient assays provide useful information of short term DIN concentrations, they tend to fluctuate widely across short timescales and hence do not provide a time integrated assessment of available nitrogen. In contrast, nitrogen isotope values of rapidly growing algal indicator species (e.g., *Ulva australis*) provide an assessment of the available nitrogen pool over weeks (Aguiar et al. 2003, Teichberg et al. 2007) and can be used to identify it"s source (i.e., wastewater, agricultural products or atmospheric deposition; Cole et al. 2004). This technique has been successfully applied to identify linkages between terrestrial catchments and estuarine habitats (e.g., McClelland & Valiela 1998, Valiela et al. 2000, Bowen et al. 2007) but not on open rocky coasts. The second step, therefore, assessed links between elevated subsidies derived from human sources of nitrogen (i.e., sewage effluent, fertilizer) using stable isotope values of an algal indicator (Peterson & Fry 1987, Costanzo et al. 2001). The third step assessed whether there was a relationship between the donor-recipient ratios and the relative covers of habitats, particularly as predicted from knowledge of nutrient driven regime shifts (i.e., replacement of canopy-forming with turf-forming algae). If we reveal these parameters to be related, such information can be used to improve interpretations of past habitat change and predictions of the consequences of future coastal development.

2.2 Methods

Catchment-types

This study was done in South Australia, a region that comprises multiple catchments of urban activity (i.e., residential and industrial) interspersed among catchments of agricultural activity (i.e., livestock grazing) and nature conservation (i.e., natural forests with no development). Within developed catchments (urban and agricultural), sources of land-derived nutrients include fertilisers, animal wastes, sewage effluent and discharges from factories and refineries. In urban catchments, the delivery of human-derived nutrients to coastal systems tends to be continuous and pervasive, contrasting with agricultural and natural catchments which are pulse driven by winter precipitation patterns (June – September; annual average: ~ 447 mm). The population sizes in urban catchments were estimated at 4000, 12,000, 26,000 and 150,000 people, and ranged from 6 – 60 people in agricultural catchments and 0 people in natural catchments. We selected a subset of four replicate catchments of each catchment-type (i.e., urban, agricultural and natural) based on accessibility and population density (Table S1, Appendix B). Estimates of variation among the three catchment-types, therefore, were based on a hierarchical design in which the four replicate catchments (termed „Sites"; *n* = 4 sites per catchment-type) where nested within catchment-type.

Links between catchment-use and coastal nitrogen

Catchment related variation in dissolved inorganic nitrogen concentration was estimated in coastal seas during rainfall events when rainfall was heavy (90.8 mm monthly total) and light (59.2 mm monthly total) during the Austral winter of 2005. On the first rainfall event (90.8 mm), we assessed whether differences in nutrient concentration could be detected among catchments when rainfall was heavy (sampling ~ 50 m from the input of surface runoff). On the second rainfall event (59.2 mm), we tested whether catchment related patterns observed under heavy rainfall could also be detected under light rainfall, again sampling ~ 50 m from terrestrial input. On this second occasion, additional sampling was done 500 m away from input to assess the extent of influence under light rainfall (i.e., 50 cf. 500 m), and repeated 1000 m offshore to estimate background variation where the effects of terrestrial discharge are considered substantially less or even undetectable (Gaston et al. 2006). Samples were obtained at 1-2 m depth using sterile 25 ml syringes before being filtered through 0.45 μm glass fibre filters. Filtered samples were frozen *in situ* and transported to the laboratory where they were analysed for dissolved inorganic nitrogen (DIN; nitrite + nitrate + ammonium) using a Lachat QuickChem 8500 Flow Injection Analyser (Hach, Colorado, U.S.A.). Nutrient concentrations (reported as mg L^{-1}) were validated against natural seawater certified reference material.

Links between catchment-use and benthic use of nitogen

Catchment related variation in nitrogen sources was assessed using changes in nitrogen stable isotope values of benthic algae (i.e., change in values of transplants), which provide a sensitive and time-integrated assessment of the source of *in situ* nitrogen (Gartner et al. 2002). Within each catchment-type we transplanted *Ulva australis* (Areschoug) with typical marine isotopic values (i.e., mean ± SE; $\delta^{13}C$; -20.7 ± 0.3 ‰ and $\delta^{15}N$; 5.9 ± 0.5 ‰) from an off-shore island characterised by nutrient-poor waters (West Island, Russell & Connell 2005). This transplantation from a standard source allows for clearer interpretation of any change in isotopic values caused by uptake of human-derived sources of nutrients without the confounding influence of natural spatial variation (Costanzo et al. 2001). Transplants comprising of replicate algal fronds (n = 3) were placed within transparent chambers (*n* = 3 per replicate site; noting that storm related loss of chambers reduced replication from *n* = 5 at each site), that were anchored to rocky substratum at depths of 5 - 10 m (> 100 m apart) within each replicate catchments (*n* = 4 per catchment-type). Transplant sites were located < 500 m from land (i.e., within the land - sea interface) and were chosen based on similarities in reef topography, wave exposure and pre-existing algal community structure. Transplant chambers were constructed from perforated transparent plastic tubes with mesh sealing the ends to facilitate sufficient water flow. Transplants were collected after ~ 60 days (recognising that the catchment related differences may reflect values of ambient sources over shorter time-scales), stored on ice for transport to the laboratory, rinsed in deionised water, cleaned of visible epiphytes and dried at 60°C (24 h.) before being ground to a powder. Samples were then acid washed using 3M HCl to remove carbonates, re-dried to a constant weight, (60°C for 48 h.), placed in tin capsules and analyzed on an Isoprime isotope-ratio mass spectrometer. The ratios of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ for all samples were calculated as the relative per mille (‰) difference between the sample and the recognized international standard (air for nitrogen; PeeDee Belemnite limestone carbonate for carbon). Precision of the mass spectrometer using the values from duplicate samples, was 0.3 ‰ for $\delta^{15}N$ and 0.1 ‰ for $\delta^{13}C$. In addition, we report the concentrations of nitrogen and carbon in algal tissue via spectroscopic analysis.

Links between catchment-use and habitat structure

If humans modify coastal conditions to cause loss of canopy-forming algae in favour of turf-forming algae (i.e., models of Benedetti-Cecchi et al. 2001, Eriksson et al. 2002, Connell et al. 2008) we predict that patches of turf-forming algae would be larger and occupy proportionally more space (and patches of canopy-forming algae smaller and occupy less space) adjacent to catchments of increasing human-domination. To test this prediction, we sampled the percentage cover of all canopy-forming algae (i.e., *Ecklonia radiata*, *Cystophora* spp., *Sargassum* spp.) and thin filamentous, turf-forming algae (commonly *Feldmannia* spp.) in early summer of 2005. This sampling was done adjacent to each catchment-type (i.e., within 500 m from the entrance of terrestrial sources of input, and therby covering a 1 km area in which elevated nutrient concentrations were identified, Table 1). These canopy-forming species act as foundation species to entire subtidal communities on these southern coasts (review, Connell 2007a) and their extent and patch sizes within and among catchemnts are described (Results: Figs 3 and 4).

The relative sizes (diameter) of patches of canopy and turf-forming algae were quantified among catchments using replicate 1 × 100 m transects (*n* = 4 per site) separated by 50 - 100 m. At a 1 m^2 scale, habitat was conservatively identified as canopy-forming algae where at least one individual canopy-forming alga was present (i.e., 25 % cover of 1 m^2). We classified habitat at this scale (i.e., 1 m^2) because the presence of canopy-forming algae is negatively related to turf-forming algae this scale (Irving & Connell 2006b). Transects were oriented normal to the shoreline and started as close to mean low water as the prevailing conditions would allow. The distance along each transect at which the type of habitat changed was recorded, providing information on the relative size of each patch of habitat and the proportion of rock occupied under each transect (see similar methodology; Dayton et al. 1992, Goodsell et al. 2004). The seaward extent of rocky substratum at most sites varied between ~ 80 – 150 m, and sampling either stoped at the seaward edge of rock or at 100 m where rock extended past this point. For each habitat quantified, the percentage of the total recorded habitat was calculated (minus any sandy substratum).

Strength of subsidy-habitat associations

We assessed the capacity for differences in the magnitude of subsidy (i.e., donor-recipient ratio) and population size (number of people per catchment) to predict apparent change in subtidal habitat. For each catchment, the magnitude of subsidy (i.e., donor-recipient ratio) was estimated by calculating the ratio between DIN in donor waters (i.e., samples taken < 50 m away from nutrient input in heavy rainfall) and recipient waters. Recipient waters were estimated for two temporal periods (i.e., pre-European or „historical‟ and „contemporary‟). It is not possible to obtain historical records, so we used natural catchments to represent the historical state of uncleared terrestrial forests (i.e., the average of all samples taken in natural catchments < 50 m away from nutrient input in heavy rainfall). This use of „space‟ as a surrogate for „time‟ was also applied to estimates of „contemporary‟ (i.e., background) concentrations among catchment-types. To acquire background estimates that were less affected by pulses of nutrient discharge, we sampled seawater from the adjacent catchment at 1000 m seaward of discharge during light rainfall. These two types of sampling enabled us to test which estimates best correlated with habitat change in this system.

Our estimate of habitat change is based on the model of nutrient-driven expansion of covers of turf-forming algae at the expense of the cover of canopy-forming algae (described in, Connell et al. 2008). Habitat change is estimated, therefore, by calculating the proportional difference between percentage cover of canopies in natural catchments (i.e., as mean cover among all natural catchments) and percentage cover of canopies in each transect (n = 4 transects per catchment) in each catchment of agricultural and urban use (n = 4 catchments per catchment-type).

Analysis of data

Analysis of Variance was used to test for differences in measured variables (i.e., DIN, δ^{15}N, percentage cover of habitat) among catchment-types and was based on a hierarchical design in which the four replicate catchments (termed „Sites"; n = 4 sites per catchment-type) were nested within catchment-type (treated as fixed factor). Kolmogorov-Smirnov tests were used to test for differences in the size frequency distributions of turf-forming and canopy-forming algae between catchment-types. Pearson"s product-moment correlation was used to assess the most strongly correlated variables with habitat structure.

2.3 Results

Links between catchment-use and coastal nitrogen

Dissolved inorganic nitrogen (DIN) concentrations of recipient coastal waters followed a predictable pattern related to intensity of catchment use (Table 2.1). DIN concentrations of waters adjacent to urban catchments (< 50 m from input of surface runoff) were greater than agricultural and natural catchments regardless of rainfall event (Table 2.2a). During heavy rainfall, DIN concentrations of waters adjacent to agricultural catchments were greater than natural catchments, but they did not differ during light rainfall (Table 2.2a, significant Catchment × Rainfall interaction term, SNK-tests). Depending on intensity of rainfall, the ratio of donor-to-recipient DIN was between 40:1 and 192:1 in urban catchments, between 5:1 and 12:1 in agricultural catchments, and between 1:1 and 3:1 in natural catchments.

Elevated DIN concentrations extended to at least 500 m away from point of input (i.e., along the sampled coastal strip of > 1 km), but showed a general decrease in concentration by 3.6 times in urban and 2.5 times in agricultural catchments compared to 50 m samples. The significant „Catchment-type" term (Table 2.2b) detected DIN concentrations to be greater within urban than agricultural and natural catchments (SNK test: urban > agricultural = natural) across both short and long distances (i.e., 50 and 500 m, respectively). DIN decreased with distance from input among all catchment-types (Table 2.2b, SNK tests).

Table 2.1 Dissolved inorganic nitrogen (DIN) concentrations of terrestrial runoff (i.e., donor DIN) and their proportional relationship to recipient waters (i.e., donor: recipient ratio; where recipient is scaled to 1).

Catchment	$mg \cdot L^{-1}$ (mean ± SE)	Donor : 1
(a) Urban		
Heavy rainfall (< 50 m)	0.814 ± 0.148	42.8 ± 7.8
Light rainfall (< 50 m)	0.303 ± 0.037	16.0 ± 2.0
Light rainfall (> 500 m)	0.091 ± 0.021	4.8 ± 1.1
(b) Agricultural		
Heavy rainfall (< 50 m)	0.126 ± 0.019	6.7 ± 1.0
Light rainfall (< 50 m)	0.051 ± 0.004	2.7 ± 0.2
Light rainfall (> 500 m)	0.021 ± 0.003	1.1 ± 0.2
(c) Natural		
Heavy rainfall (< 50 m)	0.002 ± 0.001	0.1 ± 0.0
Light rainfall (< 50 m)	0.039 ± 0.001	2.1 ± 0.1
Light rainfall (> 500 m)	0.023 ± 0.003	1.2 ± 0.1

Notes: Data are presented for each catchment type (i.e., urban, agricultural and natural catchments), at different rainfall intensities and distances from terrestrial runoff. Values are means ± SE.

Table 2.2 Results of three-factor ANOVA testing for catchment related differences in dissolved inorganic nitrogen concentrations (DIN) of coastal waters (a) close to point sources of terrestrial runoff (< 50 m) during heavy and light rainfall, and (b) close to (< 50 m) and far from point sources of terrestrial run off (> 500 m) during light rainfall.

Treatment	*df*	MS	*F*	*P*
(a) DIN concentrations (< 50 m) sampled during heavy and light rainfall				
Catchment-type	2	242.202	29.32	***
Site (Catchment-type)	9	8.261	30.59	***
Rainfall	1	21.860	5.13	*
Catchment-type × Rainfall	2	79.939	18.76	***
Rainfall × Site (Catchment-type)	9	4.262	15.78	***
Residual	216	0.270		
(b) DIN concentrations at < 50 and > 500 m sampled during light rainfall				
Catchment-type	2	0.468	8.28	**
Site (Catchment-type)	9	0.057	15.81	***
Distance	1	0.303	6.96	*
Catchment × Distance	2	0.143	3.29	NS
Distance × Site (Catchment-type)	9	0.044	12.19	***
Residual	216	0.004		

Notes: Consistency of pattern among catchments is assessed between (a) rainfall events (i.e., temporal consistency) and (b) across distances (i.e., spatial consistency). Data were $\ln(x + 1)$-transformed to meet the assumptions of heterogeneity of variance. SNK (Student-Newman-Keuls) tests on significant catchment × rainfall term in panel (a) showed, for heavy, urban > agriculture > natural catchments; and for light rain: urban > agriculture = natural catchments. SNK tests on significant main effects terms in panel (b) showed for catchment type, urban > agriculture = natural catchments; for distance, close > far. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, not significant.

Links between catchment-use and benthic use of nitrogen

Enrichment of nitrogen isotope values ($\delta^{15}N$) of transplanted *Ulva australis* (i.e., increase relative to original value) was greater within urban catchments than agricultural and natural catchments (Fig 2.1a; $_{\text{ANOVA:}}$ $F_{2,9} = 5.87$, $P < 0.05$: SNK-test; urban > agricultural = natural). The isotopic values of algae transplanted to urban catchments (Fig. 2.1b) were indicative of assimilation of a large proportion of sewage-derived nitrogen (e.g., Gartner et al. 2002). As the $\delta^{15}N$ values provide an integrated measure of sources of available nitrogen over weeks (Cole et al. 2004), the values obtained for transplants in urban catchments show that sewage derived nitrogen was assimilated by algae during extended periods following translocation. There was a slight, but non-significant shift in $\delta^{13}C$ values between natural catchment and the two developed catchment-types (Fig 2.1b; $_{\text{ANOVA:}}$ $F_{3,37} = 0.33$, $P > 0.05$).

Tissue % N values of transplanted algae had a positive correlation to both $\delta^{15}N$ stable isotope values (Pearson‟s correlation: $r = 0.661$, $P < 0.05$) and DIN concentrations of recipient waters ($r = 0.658$, $P < 0.05$) across all sites ($n = 12$ sites; i.e., 3 catchment-types, 4 replicate transplants per site). Across all catchment-types the ratio of donor to recipient (contemporary) concentrations of DIN was positively correlated with both tissue % N values (Fig. 2.2a) and $\delta^{15}N$ (Fig. 2.2b) of transplanted algae ($P < 0.05$ and $P < 0.001$, respectively). Urban catchments were associated with the greatest subsidy, tissue % N and $\delta^{15}N$.

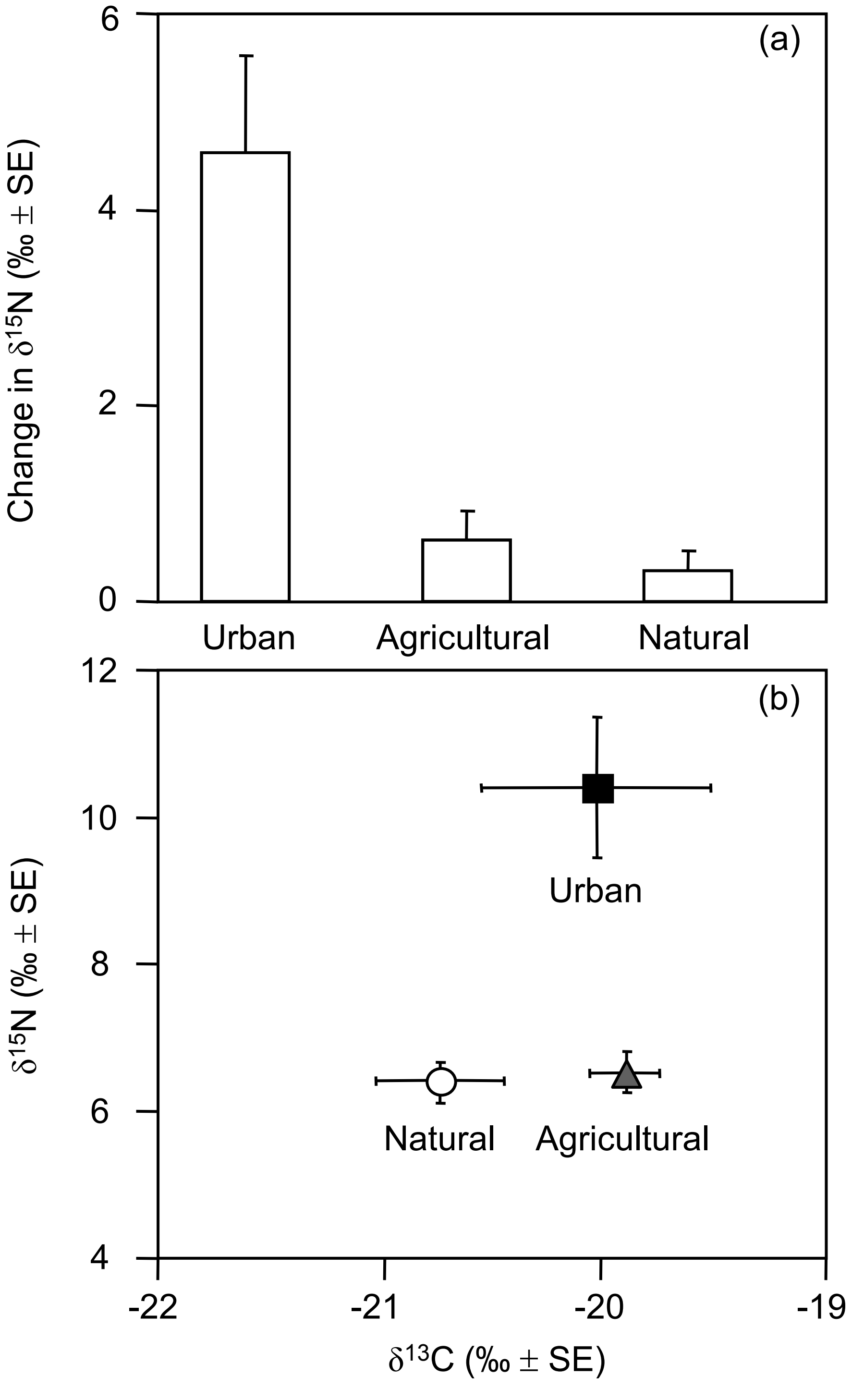

Figure 2.1 (a) Change in mean tissue δ^{15}N for *Ulva australis* transplanted (~ 60 days) among catchment-types (*n* = 3 transplants per catchment, nested within four replicate catchments per catchment-type) and (b) dual isotope plot of δ^{13}C and δ^{15}N values for algal transplants.

Links between catchment-use and habitat structure

Patches of canopy-forming algae were up to 40 m in diameter (ø) within agricultural and natural catchments, but typically less than 10 m ø within urban catchments (Fig. 2.3). The size frequency distribution of patches of canopy-forming algae in urban catchments differed from both agricultural ($K_{d\ 93,110} = 0.359$, $P < 0.05$) and natural catchments ($K_{d\ 93,117} = 0.209$, $P < 0.05$), but the distributions between agricultural and natural catchments did not differ ($K_{d\ 110,117} = 0.181$, $P > 0.05$). Turf-forming algae, the major occupiers of space in the absence of canopies (93.3 ± 6.0 % of canopy gaps across all observations: $n = 44$ transects), were typically small (< 5 m ø) within agricultural and natural catchments, but reached > 10m ø within urban catchments (Fig. 2.3). Comparison of size frequency distribution of patches of turf-forming algae detected urban catchments to differ from natural catchments ($K_{d\ 24,85} = 0.28$, $P < 0.05$), but not agricultural catchments ($K_{d\ 40,85} = 0.257$, $P > 0.05$). As a percentage of substratum per transect, canopy-forming algae was least extensive adjacent to urban catchments than agricultural and natural catchments (Fig. 2.4a; Table 2.3a). This pattern was contrasted by the percentage covers of turf-forming algae, which were more extensive in urban catchments than agricultural and natural catchments (Fig 2.4b; Table 2.3b).

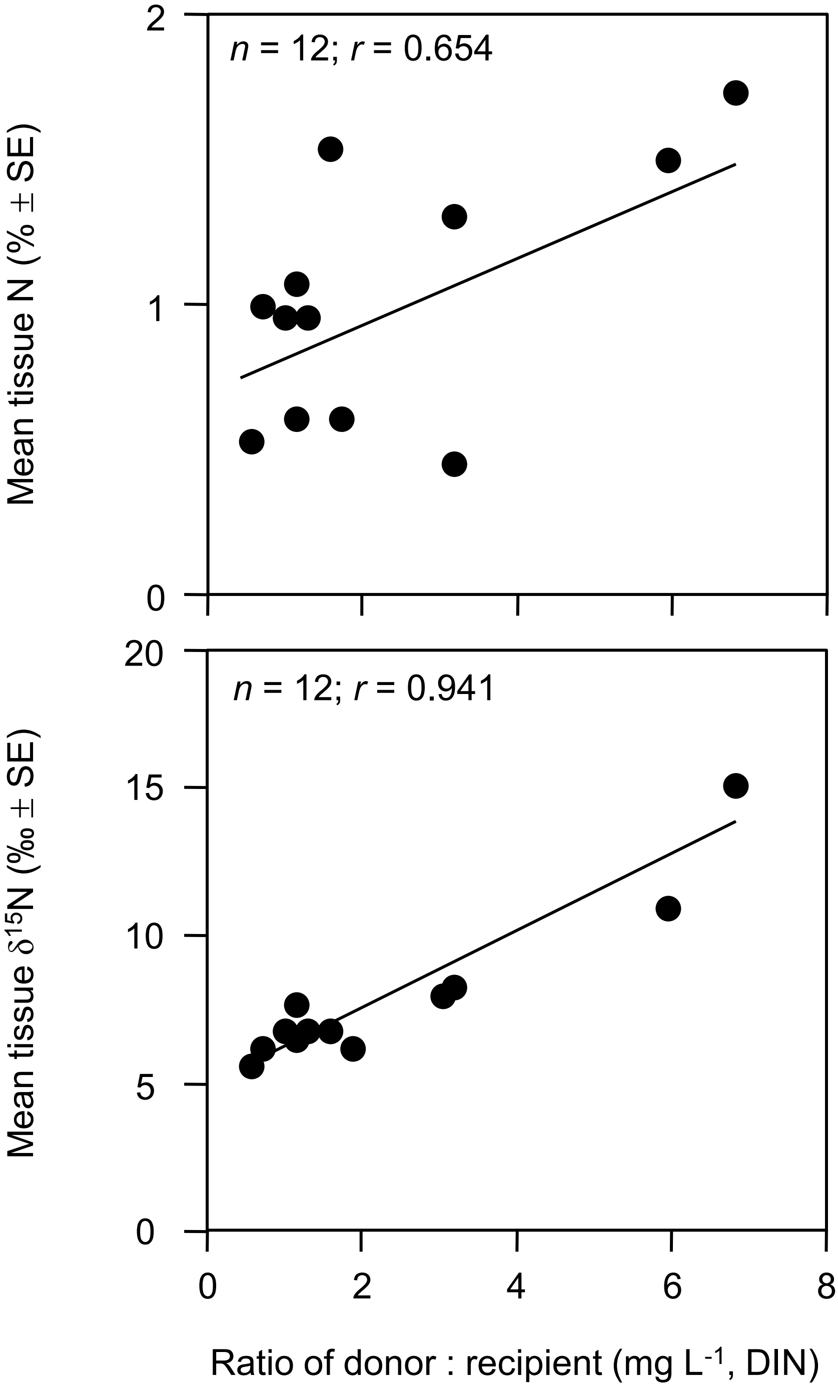

Figure 2.2 The relationship between subsidy (i.e., ratio of donor-recipient DIN concentrations) and (a) tissue % N concentrations and (b) $\delta^{15}N$ values of *Ulva australis* transplanted to alternate catchment types.

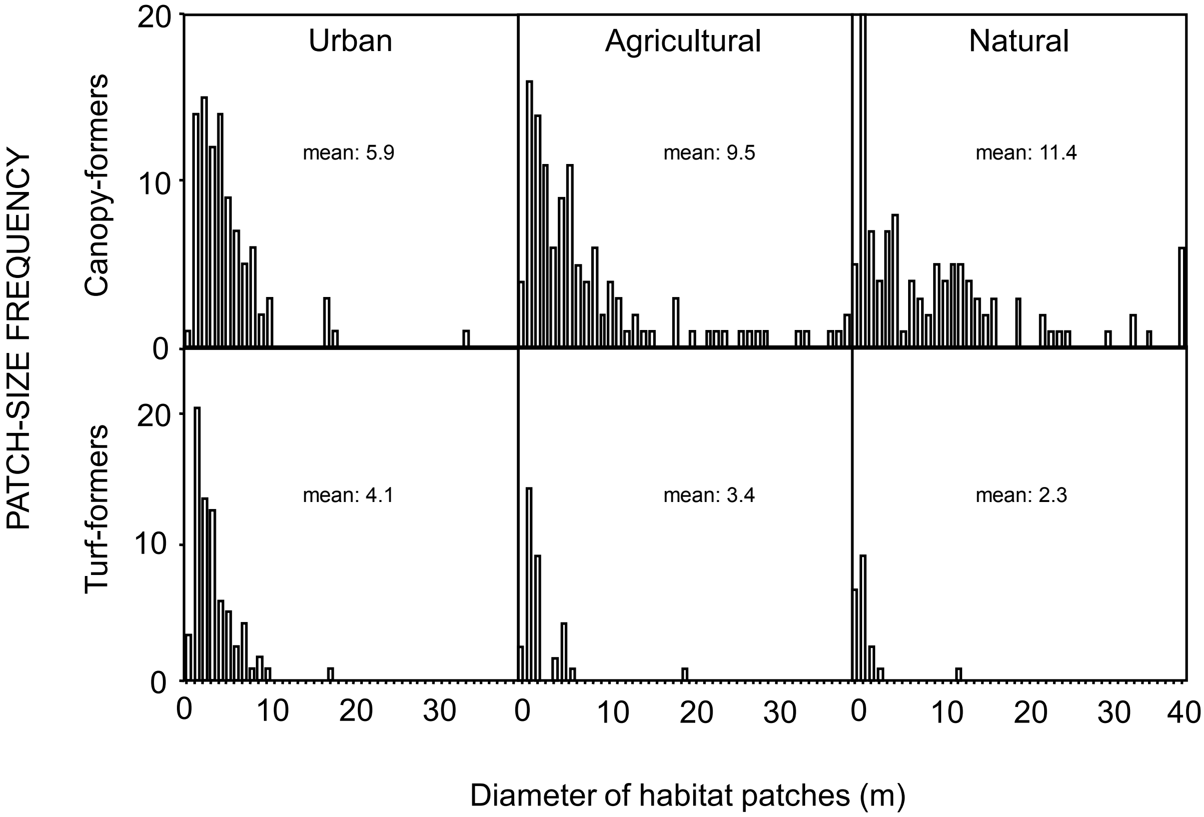

Figure 2.3 Size (patch diameter) frequency distribution of patches of habitat-forming algae among catchment-types ($n = 4$ transects per catchment, subsamples of four replicate catchments nested within three catchment-types).

Table 2.3 Two-factor ANOVA testing for differences in (a) canopy-forming and (b) turf-forming algal communities among sites and catchments

Treatment	*df*	MS	*F*	*P*
(a) Canopy-forming algae				
Catchment	2	4291.6374	25.27	***
Site (Catchment)	9	169.8330	2.81	*
Residual	36	60.4037		
(b) Turf-forming algae				
Catchment	2	1327.8783	17.27	***
Site (Catchment)	9	76.8814	2.43	*
Residual	36	31.6424		

Notes: Data were arcsine-transformed percentages. SNK test on canopy-forming algae: urban < agriculture = natural. SNK test on turf-forming algae: urban > agriculture = natural. * $P < 0.05$; *** $P < 0.001$.

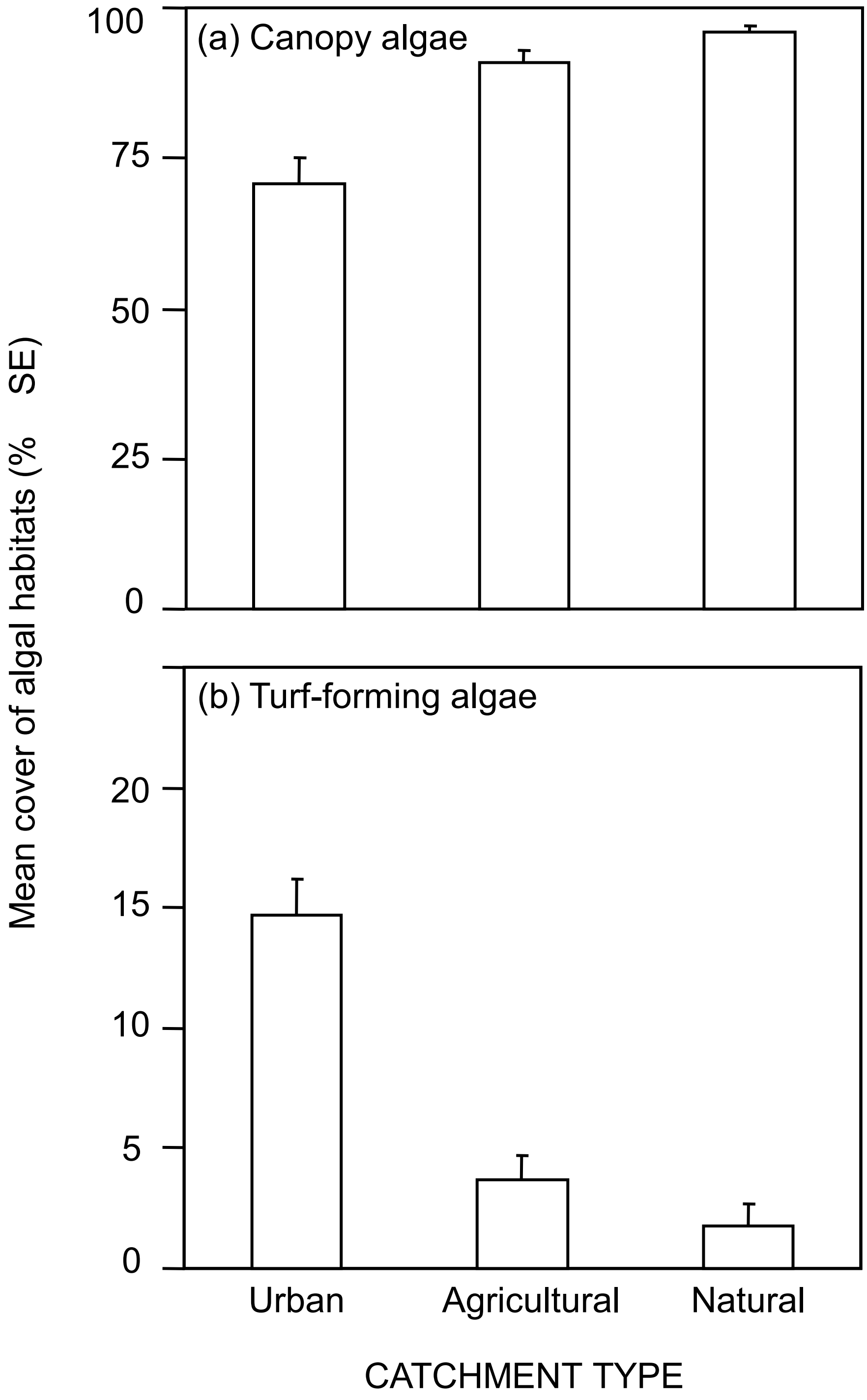

Figure 2.4 Percentage-cover of (a) canopy-forming algae and (b) turf-forming algae among catchment-types ($n = 4$ transects per catchment, subsamples of four replicate catchments nested within three catchment-types).

Strength of subsidy-habitat associations

The correlation between the size of subsidy (i.e., donor-recipient ratio) and our estimate of habitat change was strong (Fig. 2.5; $r = 0.786$, $P < 0.001$). These data not only indicate that urban catchments (larger subsidies) have a greater influence on habitat structure than agricultural catchments (smaller subsidies), but they also reveal this relationship to hold well within each catchment-type. An important realization was that these relationships are stronger when the size of subsidy (i.e., donor-recipient ratio) is based on historical estimates (Fig. 2.6a; $r = 0.891$, $P < 0.005$; $n = 8$ catchments) rather than contemporary estimates of the DIN concentration of recipient waters (Fig. 2.6b; $r = 0.849$, $P < 0.01$; $n = 8$ catchments). These results provide important insights into the usefulness of these ratio‟s when it is realised that they are a better predictor of our proxy of habitat change than DIN concentration alone (Fig. 2.6c; $r = 0.798$, $P < 0.05$; $n = 8$ catchments), which is currently the principal means of assessing coastal eutrophication. Population size correlated well with habitat change across all catchments (Fig. 2.6d; $r = 0.883$, $P < 0.005$; $n = 8$ catchments), but it is noteworthy that this association becomes less strong with increasing population size (i.e., the urban catchments).

In many instances, ecologists will need to contrast environmental affects among urban catchments, and our small sample size ($n = 4$ urban catchments) reveals that very small urban populations (i.e., ~ 4000 people) may create subsidies and impacts that are similar to populations many times their size (i.e., ~ 26,000 people). Such comparisons among urban catchments appear to be better related to estimates of the magnitude of subsidy (donor- recipient subsidies) (Figs. 2.5 and 2.6).

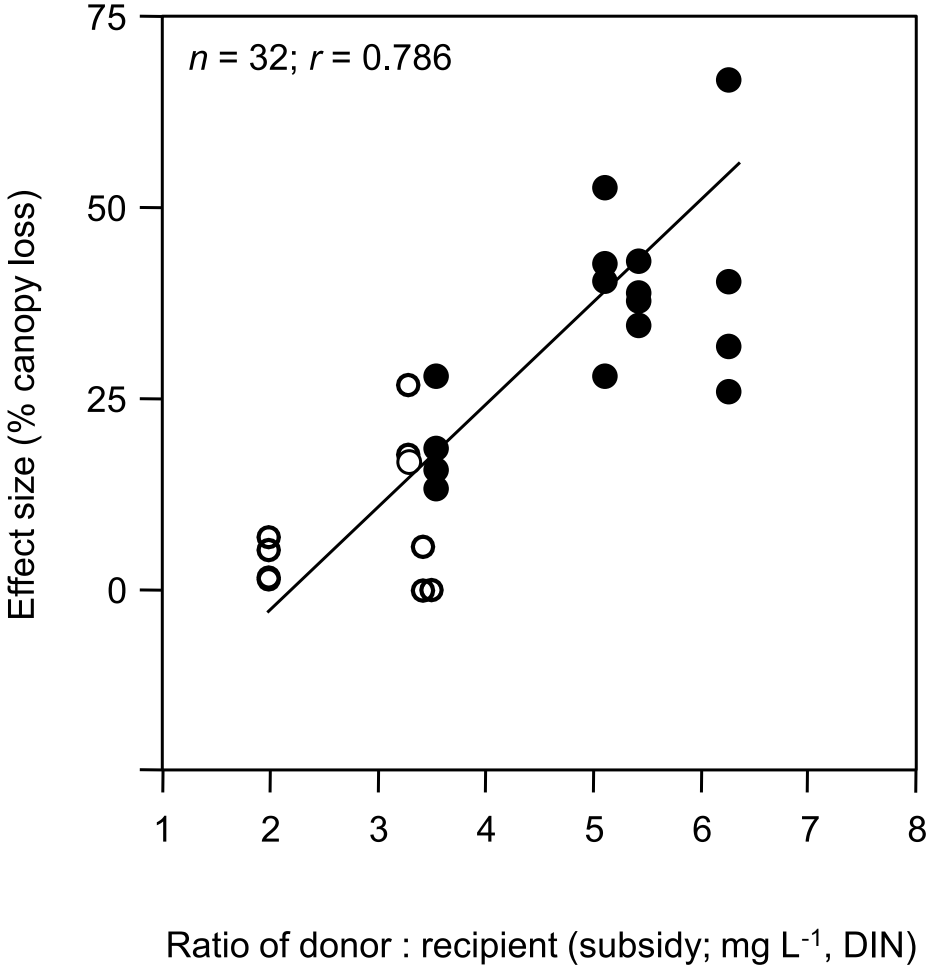

Figure 2.5 The potential of catchment related nitrogen subsidy to predict apparent habitat change (i.e., canopy loss; effect size) among replicate transects (*n* = 4 per replicate catchment). Open circles, agricultural catchments, closed circles, urban catchments. The subsidy (i.e., ratio of donor-recipient DIN concentrations) is based on historical estimates of nutrients in recipient waters (see, Fig. 2.6 for comparison).

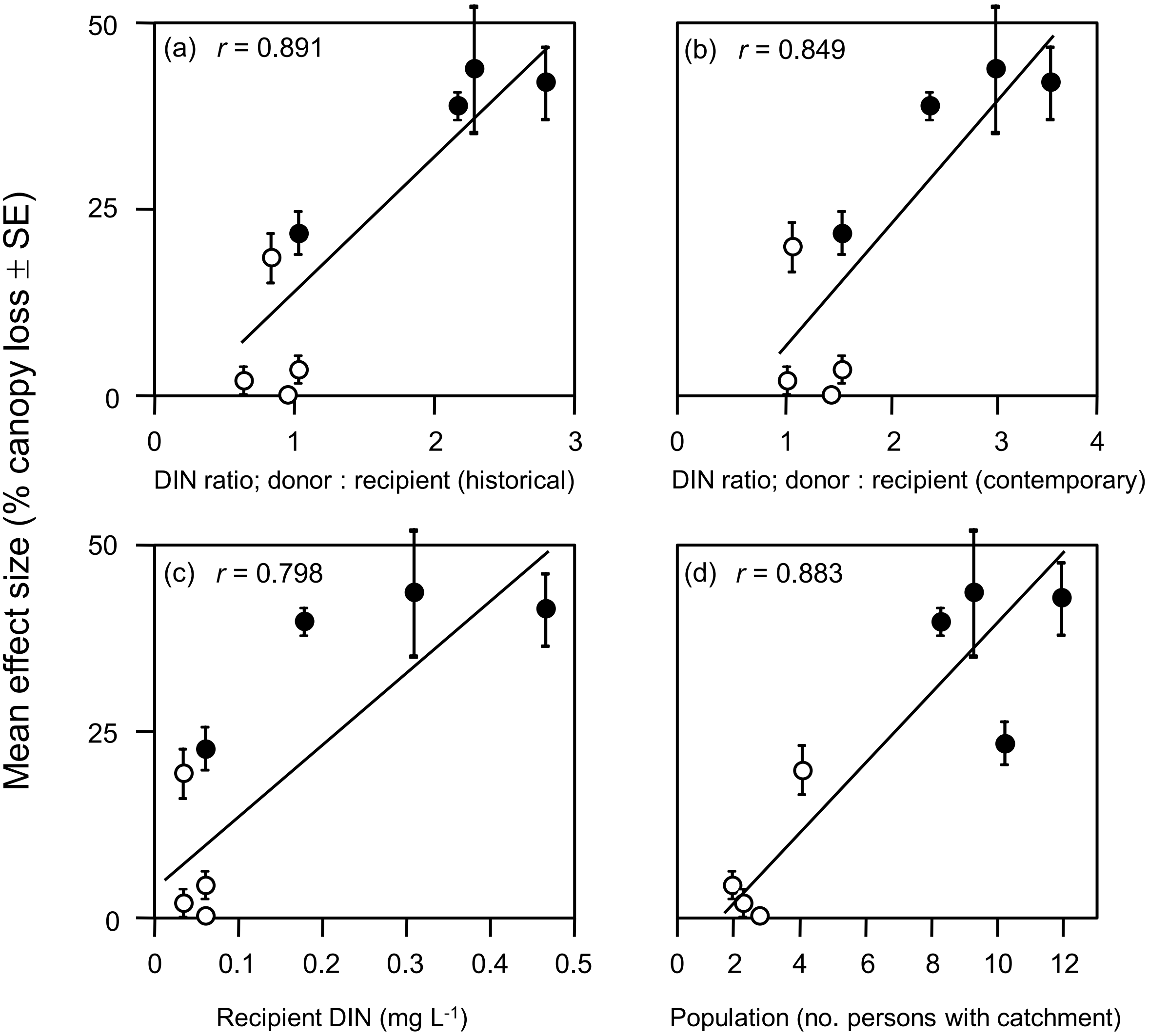

Figure 2.6 The potential of catchment related nitrogen and population size to predict apparent habitat change (mean effect size). The magnitude of subsidy (ratio of donor-recipient DIN) is more strongly related to effect size when based on (a) historical estimates of nutrients in recipient waters than (b) contemporary estimates, or (c) concentrations of DIN. Population size (d) is well correlated across the range of population sizes, but this relationship appears weak among urban catchments. All nitrogen data and population values are ln(x + 1) transformed, except for (c) absolute concentrations of DIN.

2.4 Discussion

Land-to-sea linkages among alternate catchment-types

We provide evidence that link human activities to the magnitude of land-to-sea subsidies at a landscape scale, and then linked this variation to its predicted consequences in kelp forest ecology. This evidence was based on (1) greater dissolved inorganic nitrogen (DIN) loads of coastal waters adjacent to urban catchments when compared to less developed catchments, (2) the delineation of sewage-derived nitrogen as a relatively persistent component of the DIN pool utilized by subtidal algae, and (3) the strength of the relationship between magnitude of subsidy (and size of human population) and the relative proportion of perennial habitats (canopy-forming algae) compared to ephemeral habitats (turf-forming algae).

Terrestrial subsidies of nitrogen to subtidal systems in this study are likely to arrive in rainfall driven pulses (sensu, Anderson et al. 2008), notwithstanding the more or less continuous subsidy from sewage effluent in urban catchments. In our system, heavy rainfall can deliver pulsed concentrations of DIN to urban coasts that are up to 400 times greater than less developed catchments. While we acknowledge that estimates based on DIN may slightly underestimate absolute loads of bio-available nitrogen (c.f., TDN which produces overestimates; Seitzinger et al. 2002), our results provide a robust test of the differences among alternative catchment types. Given the limiting nature of nitrogen within coastal ecosystems (Howarth & Marino 2006), and that the effect of spatial subsidies may be proportional to the ratio between donor and recipient systems (Marczak et al. 2007), it can be anticipated that habitat change would be greater within urban catchments.

Numerous studies have shown the importance of wastewater as a source of human-derived nitrogen entering estuarine systems based on % N and $\delta^{15}N$ values of submerged aquatic vegetation (e.g., McClelland & Valiela 1998, Costanzo et al. 2003) but this has not been demonstrated in open coastal systems. In this study, the magnitude of enrichment observed in algal transplants within urban catchments was large (enrichment by ~ 4.5 ‰, to approach mean values of 10.4 ‰), similar to changes reported for the same species exposed to secondary treated effluent in both field and laboratory experiments (Gartner et al. 2002). This level of enrichment in algal tissue provides a direct link to sewage-derived sources of DIN, as seen in estuarine systems (McClelland & Valiela 1998), and we suggest that it similarly represents a strong and continuous source of nitrogen from urban catchments to recipient systems on open rocky coasts. It follows then that this release of material, which is often substantial, increases the magnitude of land-to-sea subsidy, particularly within coastal seas of naturally low nutrient status.

The magnitude of human-derived subsidy may be proportional to the population size of humans, but in some circumstances poor wastewater treatment (e.g., old and leaking septic systems) may provide contingent conditions. Septic systems are a major source of nitrogen in groundwater (Valiela et al. 1997), and are often used in catchments with small population sizes because of the scales of economy involved with expensive tertiary treatment. δ^{15}N values of marine plants increase in proportion to inputs of wastewater (Cole et al. 2005), which may explain our observation that the values associated with small urban catchments with aged and leaking septic systems (10.9 ± 0.8 ‰; ~ 4,000 people in Second Valley) approached values in catchments that export greater volumes of tertiary treated water (14.8 ± 0.6 ‰; > 150,000 people in Onkaparinga). As populations expand into undeveloped coast, there is an increasing need to understand how catchment management (e.g., retainment or rehabilitation of terrestrial vegetation) may counter increased N delivery of septic tanks. We suggest, therefore, that the effectiveness of wastewater treatment coupled with ambient and historical concentrations of nutrients within catchments (i.e., size of disparity between donor-recipient resources) may create substantial variance in associations between size of human population and size of subsidy from local through regional scales.

South Australia has highly seasonal rainfall and few permanent natural sources of terrestrial input to coastal systems (e.g., rivers) resulting in little export of terrestrial-derived nutrients to coastal systems outside rainfall events. It is no surprise, then, that we found donor : recipient subsidy (i.e., DIN concentration) during rainfall events to be a good predictor of the condition of subtidal habitats in our system. In regions of relatively constant natural (e.g., the large river systems of North America) or human inputs (e.g., wastewater of large populations), however, the load of nutrients within discreet rainfall events is likely to be minor compared to the annual terrestrial export to marine systems. In such cases, the total nutrient load being exported may be a better predictor of subsidy than concentration of nutrients.

While we acknowledge that agricultural development can constitute a significant source of land to sea nutrients (e.g., Costanzo et al. 2003), the lack of change in isotope values of transplants in these catchments (i.e., neither depletion, suggestive of the use of fertilizers, or enrichment, indicative of animal wastes; Heaton 1986) suggest that these activities, at their current level of intensity (i.e., mostly sparse populations of livestock with some intensive viticulture), do not constitute an important source of nitrogen to this particular coastal system.

Habitat-alternation and variation in its susceptibility

Increasing shoreline development has been associated with increasing availability of water column nitrogen which drives the replacement of longer-lived and slow-growing habitats (e.g., seagrass and large macroalgae) with opportunistic and fast-growing and smaller macroalgae (Duarte 1995). In rocky subtidal systems, nutrient-driven changes to habitat centre on the replacement of canopy-forming algae (e.g., kelp) with filamentous turfs (review, Connell 2007b). Turfs lack the capacity to store nutrients and are normally ephemeral, but are able to persist under the continual elevation of nitrogen (Connell et al. in review). The persistence of dense covers of turf creates positive feedbacks, trapping sediment and preventing the recruitment of canopy-forming algae (Airoldi 2003). Persistent turfs may initially occur through local loss of kelp in small patches (e.g., storm-driven clearings of < 3 - 6 m^2; Kennelly 1987b) which increase in size over time to coalesce into larger patches when adjacent to urban coast (Gorgula & Connell 2004). Over longer periods (e.g., several decades), it is possible to observe the wholesale loss of perennials in favour of opportunistic adjacent to developed coast (Eriksson et al. 2002, Connell et al. 2008). Such habitat alteration is considered to be quite general to developed coastlines (Worm et al. 1999, Airoldi 2003, Connell 2007b), observed as a shift from highly productive and structurally complex habitats to less productive and complex habitats, representing a fundamental shift in ecological function (e.g., habitat provision) and export of energy (Vitousek et al. 1997b).

We provide indirect evidence to support the idea that habitat-alternation is more likely where there is a greater disparity between donor (amount of enhanced subsidy) and receiver resources (ambient and historical). Understanding such donor-recipient ratios (Marczak et al. 2007) would also assist efforts to integrate cross-scale (e.g., local-regional-biogeographic) variation in coastal responses to development (Connell & Irving 2008). This effort may identify localities of probable habitat-shifts from the global set of coastlines with large human populations. For example, biogeographic variation in productivity (Rochford 1980, Russell et al. 2005) may explain regional anomalies where the role of wastewater outfalls are often deemphasised around Australia"s largest city (e.g., Sydney, on a coast of higher productivity; Chapman et al. 1995), but their role is considered profound around a small coastal city at a similar latitude (e.g., Adelaide, on coast of lower productivity; Connell et al. 2008). By achieving this understanding across successively larger scales, ecologists may assist the appropriate scale-dependent perspectives needed by management. Such knowledge may not only provide practical advice to authorities that decide local environmental policy, but it may also allow for better regional and biogeographic policy under governance of state or national institutions. Until now, it has been hard to understand why managers of small coastal populations should have legitimate concerns for nutrient pollution when those of much larger population centres and their more intensely researched coastlines fail to share the same concerns. Donor : recipient ratios have the capacity to reconcile such differences by recognising that while certain water-quality guidelines may be appropriate for some regions and their managers (e.g., eastern Australia with similarly high donor-to-recipient concentrations), they may be inappropriately liberal for other regions and managers (e.g., southern Australia with lower N delivery, but substantially lower recipient concentrations).

Managing connected land-to-seascapes

Humans are embarking on the final phase of coastal development of the world"s temperate coastlines. Whilst land-river and land-lake connections have long been recognized (Carpenter et al. 1998), the land-to-sea connections have received comparatively little attention along human-dominated coastlines (Cloern 2001). Land-to-sea connections have primarily focused on changes in estuaries and bays (reviews, Rabalais 2002, Bowen et al. 2007), showing strong links between catchment related nitrogen and shifts in abundance of submerged aquatic vegetation from slow-growing seagrasses and large macroalgae to fast-growing macroalgae (e.g., Duarte 1995, Deegan et al. 2002). Our present work appears to be the only available assessment that specifically links variation in human-use of land with variation in such regime shifts on open coastlines. In this regard, it also represents a departure from the traditional explanations of kelp deforestation that centre on top-down impacts on ecosystem drivers; i.e., trophic-cascades that cause populations of sea urchins to increase via the decline in their predators (Steneck et al. 2002). In fact, the ecological study of open coasts has been largely preoccupied with understanding the ecological effects of what humans remove from the sea (e.g., effects of fishing on trophic cascades) rather than what humans add to the sea (e.g., effects of nutrients and sediments). The reality is that alteration of both producers (e.g., nutrient driven change) and consumers (e.g., extraction of consumers) require attention to the synergies they may create (review, Connell 2007b).

Some regions may be more susceptible to nutrient-driven habitat alteration where the consumers of greater productivity (e.g., herbivores of ephemeral algae; Worm et al. 2000a, Korpinen et al. 2007b, Russell & Connell 2007) are reduced by the direct or indirect effects of harvesting (Bellwood et al. 2004). Where such synergies occur, knowledge of these interactions may contribute to the justification of Marine Protected Areas (MPA"s) because they have jurisdiction over the governance of sea-based extraction (i.e., fishing-driven declines of consumers that counter the effects of pollution), albeit not land-based addition of pollutants (i.e., catchment-use). Marine Protected Areas appear to have less ecological justification on coasts which lack functional groups of herbivores which can counter the effects of nutrient enhancement (e.g., South Australia) and for which top-down effects are weak (Connell & Irving

2008). In these cases, MPA‟s alone will be insufficient to maintain habitats and more innovative management that recognises solutions for both land-based and sea-based challenges is required (e.g., recycling land-based water).

The recent recognition of land-to-sea connectivity along climate affected coasts (i.e., drying and drought prone coasts) has caused implementation of solutions for the sea (policy on reducing discharge) that can also act as solutions for the land (policy on establishing new sources of water that do not rely entirely on rainfall). For example, new cross-government acceptance of nutrient driven habitat loss (i.e., Connell et al. 2008) has motivated policy initiatives that aim to recycle nearly 45 % of Adelaide‟s wastewater and save supplies of drinking water. Wastewater treatment plants can be upgraded to produce recycled water (for residential and industrial zones, recreational parks and agriculture) so that most of the nutrient rich discharge (nearly three billion litres per annum in Adelaide) can be used more effectively to manage the land (reduce reliance on rainfall) and sea (reduce nutrient pollution), and their connection.

In conclusion, our research demonstrates a landscape-scale approach that can provide information needed to integrate land-to-sea dynamics of ecological change at scales relevant to their governance and practical management. We provided direct evidence that human-mediated subsides from land-to-sea can alter the flow of energy to subtidal systems. Our indirect evidence (i.e., relationship between magnitude of subsidy and apparent habitat alteration) suggests that the human enhancement of subsidies across the terrestrial to marine boundary may bring greater ecological change to coastal populations that do not manage large increases of land (donor) to sea (recipient) subsidies of limiting resources. On many coasts this change may be prevented, or even reversed, where ecologists assist managers recognise the land-to-sea connection and thereby enable joint solutions to the challenges of land-based and sea-based sustainability.

“Each succeeding generation of biologists has markedly different expectations of what is natural, because they study increasingly altered systems that bear less and less resemblance to the former, pre-exploitation versions.”

Paul Dayton 1998

CHAPTER THREE

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Nutrient-driven changes to turf phenology and its implications for forest resilience

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Nutrient-driven changes to turf phenology and its implications for forest resilience

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2009

Statement of Authorship

In this paper, Sean D. Connell and I acquired funding and developed the experimental design. I conducted the field work (forest clearances), measured benthic response (turf covers and sediment dynamics), conducted the statistical analysis and wrote the draft manuscript. Bayden D. Russell contributed to the development of ideas and helped with field sampling.

I certify that the statement of contribution is accurate

Daniel Gorman (Candidate)

Signed *Date* 10/12/09

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis

Associate Professor Sean D. Connell

Signed *Date* 10/12/09

Dr Bayden D. Russell

Signed *Date* 10/12/09

Preamble

Chapter 3 provides an examination of the causes of regime shift within subtidal rocky reef ecosystems. Specifically, the work examines the relationship between increased nitrogen inputs along urban coasts, the persistence of turfs that accumulate sediments and reductions in canopy recruitment. The Chapter takes the form of a co-authored article written in plural. The unpublished work can be cited as:

Gorman D., Connell S.D. and Russell B.D. Nutrient-driven changes to turf phenology and its implications for forest resilience

3.1 Introduction

Humans represent integral components of natural ecosystems as their activities continue to modify ecological processes (Jackson 2001). By modifying processes that govern the recruitment and survival of species that form the foundation of entire ecosystems (e.g., kelp forests and coral reefs) human activities represent powerful drivers of environmental change (Vitousek et al. 1997b). The human-mediated supply of limiting resources such as nutrients can profoundly change the structure and function of numerous terrestrial and aquatic ecosystems (e.g., extent of bottom-up cf. top-down forcing; Loreau et al. 2001, Airoldi et al. 2008). Whilst the generic drivers and consequences of such anthropogenic forcing have been widely reviewed (e.g., reviews on nutrient liberation, Vitousek et al. 1997a, Tilman et al. 2001), our understanding of the mechanisms that hasten or resist change are notoriously difficult to clarify (Scheffer et al. 2001).

Canopy-forming communities that characterise temperate coasts (e.g., kelp forests) are remarkably productive and phyletically complex systems that are naturally resilient to disturbance (Dayton et al. 1992, Steneck et al. 2002). There is increasing concern, however, that the cumulative effects of human impacts along developed coastlines are reducing their ecological resilience (Folke et al. 2004). Indeed, the intensification of human activities and their associated inputs (e.g., nutrients and sediments) are believed to represent major factors contributing to the global decline of subtidal canopy-forming communities (e.g., Australia, Connell et al. 2008, Baltic Sea, Worm et al. 1999, North Sea, Eriksson et al. 2002 and Mediterranean Sea, Rodriguez-Prieto & Polo 1996). Where forests fail to recover, subtidal landscapes can shift to low diversity, filamentous turf-forming algal systems of relatively low productivity and simple topography (reviews, Duarte 1995, Connell 2007b). Whilst the initial replacement of forests by turfed landscapes may be driven by acute disturbance (e.g., Dayton et al. 1992, Edwards & Estes 2006) the persistence and expansion of these degraded habitats is a likely symptom of human changes to environmental conditions (reviews, Steneck et al. 2004, Connell 2007b, Krause-Jensen et al. 2008).

Whilst the links between eutrophication and changes to aquatic communities are becoming clearer (reviews, Cloern 2001, Rabalais 2002) less is known about the factors that reduce ecological resilience and make ecosystems susceptible to regime shift (Scheffer et al. 2001). The incidence of regime shifts occurring in the wake of disturbance is thought to relate to the formation of alternate „stable‟ states that are facilitated (via human activities) through the persistence of competitively inferior communities (e.g., filamentous turf-forming algae). Whilst turf-dominated habitats can persist as alternate „natural‟ states (e.g., through facilitation by herbivores; Irving & Witman 2009) these are generally uncommon in systems where top-down regulation is weak (e.g., southern Australia; Connell 2007b). Here, models that seek to explain the failure of subtidal forests to recover from disturbance tend to assume that algal opportunists themselves are able to alter the process of natural succession (Vadas et al. 1992, Scheibling & Gagnon 2006). The problem with this explanation is that algal colonisers tend to represent successional components that are excluded upon re-establishment of climax communities (Eston & Bussab 1990). Indeed, whilst turfs can temporarily inhibit the recruitment of canopy-formers (Kennelly 1987a, Edwards 1998, Russell & Connell 2005) canopies almost certainly recover within disturbed patches along „natural‟ coastlines (Wernberg & Connell 2008). This cycle appears to be governed by the annual winter senescence of turfs (i.e., June – August in the southern Hemisphere; Russell B.D. et al. unpublished data), which coincide with the peak recruitment phase of canopy-forming laminarian and fucoid algal species (Novaczek 1984, Hotchkiss 1999).

Across the globe, the many instances of canopy-forming communities failing to recover from disturbance, despite no perceivable changes in top-down pressure (e.g., consequences of overfishing and runaway herbivory; Connell 2007b) has galvanised concern regarding the potential influence of land-derived human inputs on processes that govern forest recruitment and resilience. Concerns centre on the belief that declining water quality (elevated nutrient concentrations) can benefit weedy species (Korpinen et al. 2007a) and thereby alter the competitive interactions that underlie natural succession (Lotze et al. 2000). Here, we propose that the continuous discharge of nutrients along developed coastlines (e.g., sewage effluent; Chapter 2) may initiate a switch in the phenology of turfs, enabling them to persist as perennial covers that can disrupt community equilibrium by inhibiting the recruitment of canopy-formers (Kennelly 1987a). Often too, the inhibitory capacity of turfs can be exacerbated where human activities simultaneously increase rates of sedimentation (i.e., urban coastlines; Fernandes et al. 2008). This is because of the positive feedbacks between turfs and sediments (see, Airoldi & Virgilio 1998) that can interfere with spore settlement and the subsequent development of canopy recruits (Moss et al. 1973, Devinny & Volse 1978). The synergy between turfs and sediments is likely to have substantial consequences for forest resilience, especially, when their effects coincide with the timing of canopy recruitment.

Our model which suggests that nutrient-driven changes to turf phenology can influence the recovery of canopies into disturbed areas (through reduced rates of recruitment) is dependent on two critically untested assumptions. The first, being that elevated nutrient concentrations can sustain turf covers beyond their natural winter decline, so as to constitute a factor contributing to recruitment failure. To test this assumption we measured the response of turfs to experimental nutrient enrichment both in the presence and absence of canopy covers (i.e., replicating disturbance and the mediating effect of canopy scour). The second assumption is that the environmental conditions characterising human-dominated coastlines (i.e., nutrients and sediments) are sufficient to facilitate such changes in turf phenology, with consequent effects on canopy recovery. To test this, we compared relative rates of canopy recruitment (i.e., covers) into experimentally disturbed plots across a spectrum of human impacted landscapes; predicting that recovery would be less (and turf development greater) on more heavily impacted coastlines (i.e., preparing the conditions for long-term decline of forested landscapes). Support for our model, not only has the potential to explain historical and future habitat-shifts on human-dominated coasts (Eriksson et al. 2002, Connell et al. 2008), but provides a better account of the frequent and extensive areas of turfed habitat observed along coastlines with greater nutrient discharge (Chapter 2). In this context, we tested the generality of our model by examining the relationship between coastal nitrogen concentrations and contemporary covers of forested cf. turfed landscape across hundreds of kilometres of temperate coastline.

3.2 Methods

Persistence of turfs under elevated nutrients

West Island (35°36‟S, 138°35‟E; Fig 3.1a), a coastal locality of low water nutrient concentrations (Gorgula & Connell 2004) was used to test whether sustained nutrient enrichment could maintain covers of turfs throughout periods of natural senescence (i.e., winter; Russell B.D. et al. unpublished data). The experiment examined the ability of turfs to persist as perennial covers using a crossed design that involved a manipulation of nutrient concentrations (ambient cf. elevated) and a test of the mediating effect of canopy covers (present cf. absent). Treatments were applied at random to 20 experimental reefs ($n = 5$, for each treatment combination) that were set on sand (~ 5 m depth) at least 10 m away from natural rocky reef. Experimental reef modules comprised of a cubic metal frame (60 cm^3) fitted with concrete paving stones (for a description see, Russell & Connell 2007). The upper concrete stone created a platform for the addition of boulders (~ 8 placed in the centre of each unit) that were collected intertidally (i.e., devoid of marine life and pre-existing algal covers) and thus acted as blank substratum for turf development. Canopy treatments were surrounded with boulders covered by established *Ecklonia radiata* individuals (densities of 9 - 11 individuals per m^2, maintained to match natural densities on adjacent reef; Russell et al. 2005). Whilst we acknowledge that the use of these boulders and their pre-existing algal assemblages (i.e., understory encrusting algae in addition to *E. radiata*) may influence natural succession (through direct propagule supply), we view this procedure as a valid test of our main hypothesis, being the influence of nutrients on relative covers of algal turf.

Nutrients were supplied as 12 g of Osmocote Plus® slow-release fertiliser pellets (6 month release: 15, 5, 10; N–P–K) contained within four nylon mesh bags (1 mm mesh size) that were attached to each reef module (see, Russell & Connell 2005). Worm et al. (2000b) recommended this slow-release approach as an effective means of enriching *in situ* water column nutrient concentrations, especially in subtidal experiments. Whilst we acknowledge the unintended potential for phosphorous and potassium to stimulate the growth of turfs (which we did not test), our primary objective was to elevate the concentration of dissolved inorganic nitrogen (i.e., the most important nutrient for algal growth; Pedersen & Borum 1996; Chapter 2) in the vicinity of reef modules. Each bag was ~ 2 cm in diameter and positioned slightly below the top surface of the central boulder so as not to interfere with water movement. Fertiliser addition successfully increased water column dissolved inorganic nitrogen concentrations around reefs (mean ± SE; „elevated‟: 0.035 ± 0.001 mg/L cf. „ambient‟: 0.019 ± 0.003 mg/L) to be within the range of those observed adjacent to urban runoff (Chapter 2). Turf covers within the centre of reefs were quantified seasonally using a 10 × 10 cm quadrat comprising of 25 points (see, Drummond & Connell 2005). The experiment was maintained over a 16 month period that encompassed six seasonal cycles (summer, autumn, winter and spring; see Appendix B, Table S2).

Recovery of canopy-forming algae

To test whether the environmental conditions that characterise developed coastlines, can reduce rates of forest recovery, we replicated storm-driven disturbance across a spectrum of human impacted landscapes. Our aim was to investigate variation in the successful recruitment of canopy-forming species (kelps and fucoids) driven by contemporary variation in nutrient concentrations, turf covers and sediment dynamics. Disturbance was created during the Austral autumn-winter of 2007 and the design incorporated two spatial scales that differed in their relative degree of human impact: (1) a „catchment-scale‟ investigation that incorporated replicate sites (*n* = 3) nested within urban, agricultural and natural catchments (Fig. 3.1a; see Chapter 2 for description of catchment-types), and (2) a „local-scale‟ investigation that incorporated replicate reefs (*n* = 3) nested within locations of „degraded‟ and „healthy‟ subtidal habitat, interspersed along an urban coastline (Fig 3.1b). Degraded sites were selected *a priori* from locations known anecdotally to have undergone substantial losses of macroalgal forest (e.g., > 60 %; Connell et al. 2008). Healthy sites were characterised by continuous stands of canopy-forming algae (*Cystophora* spp., *Ecklonia radiata* and *Sargassum* spp.) reaching ~ 40 m in diameter, whereas degraded sites comprised of small remnant forest stands (~ 1–12 m diameter) interspersed amongst turf-dominated landscapes.

Disturbance was replicated by clearing covers of canopy-forming algae during April (i.e., prior to winter in the Southern Hemisphere) so as to coincide with the natural cycle of storm-driven forest disturbance (see, Kennelly 1987b). Clearances involved the physical removal of all canopy-forming individuals (kelps and fucoids; > 5 cm in height) from experimental plots 1m^2 (i.e., a typical size of storm-driven forest disturbance; Wernberg & Connell 2008). Replicate clearance plots (*n* = 5) were created at each site/reef, within treatments and spatial scales. Relative covers of turf and canopy-forming algal recruits that colonised plots (i.e., *Cystophora* spp., *Ecklonia radiata* and *Sargassum* spp.) were quantified four months later, at the end of winter (i.e., August). The timing of experimental disturbance thus coincided with the peak recruitment phase of the majority of canopy-forming species (e.g., *Ecklonia radiata*; Novaczek 1984) and the period of winter senescence by turf-forming species (Russell B.D. et al. unpublished data). Percentage covers of turf and canopy-forming recruits were quantified from the centre of experimental plots using a randomly positioned 20 × 20 cm quadrat comprising of 25 intersect points (see, Drummond & Connell 2005).

Sediment deposition was quantified using replicate sediment traps (*n* = 5, per site) constructed from cylindrical polypropylene piping (170 mm height × 50 mm diameter) to produce an aspect ratio > 3 (as recommended by; Håkanson et al. 1989). At each sampling location, traps were attached vertically to rocky substratum and left for a period of 30 days before being capped and retrieved. In recognition of the close association between nutrients and sediments that may be independent of sediment deposition *per se* (Airoldi & Virgilio 1998), we additionally compared the standing weights of accumulated sediment between treatments for the local-scale component of the study. Weights of accumulated sediment within clearance plots were measured upon termination of the experiment by collecting all loose material within a 10 × 10 cm quadrat using a vacuum that emptied into a sealed polyethylene bag. In the laboratory, all collected sediments were filtered through Whatman® grade 1 qualitative filter papers using distilled water. The filters and retained filtrate were dried to a constant weight (60°C for 48 h.) and sediment dry-weights reported for deposition ($\text{mg} \cdot \text{cm}^2 \cdot \text{d}^{-1}$) and accumulation ($\text{mg} \cdot \text{cm}^2$).

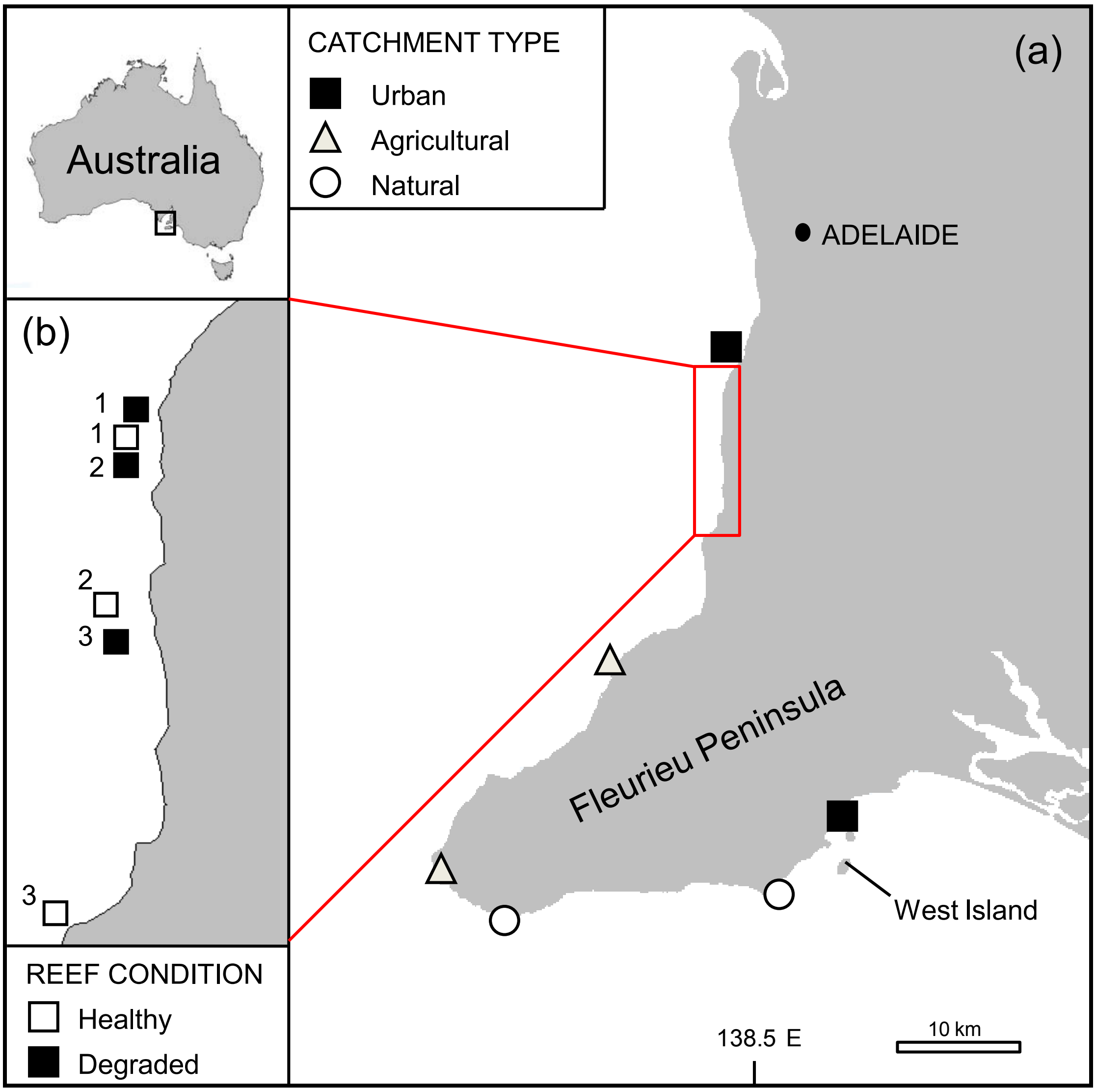

Figure 3.1 Map showing study sites along the southern Australian coastline; (a) catchment-scale investigation, including the location of West Island (the site of the nutrient enrichment experiment), and (b) replicate sites use for the local-scale investigation of recovery dynamics along an urban coastline.

Coastal eutrophication and subtidal landscapes

To test the generality of our model that water quality can drive shifts from forested to turfed landscapes we investigated the relationship between habitat covers and coastal water Dissolved Inorganic Nitrogen (DIN) concentrations across 700 kms of South Australian coastline (Fig. 3.2). Sampling was done at 22 sites during the Austral winter of 2008 so as to coincide with the period, during which, turf covers should be naturally low within disturbed patches (Russell B.D. et al. unpublished data). Whilst the results of Chapter 2 highlighted correlations between DIN and canopy loss (i.e., effect size) here we were more interested in quantifying covers of turfed habitat which may provide insights into the conditions that can cause forest decline.

Covers of turfed and forested habitat were quantified along replicate 100 m transects (*n* = 4, per site) that ran perpendicular to the shoreline and were separated by < 50 m. Changes in habitat were recorded at a 1 m scale (see, Goodsell et al. 2004) to provide relative estimates of cover (minus sandy or bare substratum) for these contrasting habitats. Coastal DIN concentrations were assessed by conducting nutrient analysis on replicate water samples (*n* = 10) collected at each location. Samples were obtained at 1-2 m depth using sterile 25 ml syringes before being filtered through 0.45 µm glass fibre filters. Filtered samples were frozen *in situ* and transported to the laboratory where they were analysed for DIN (nitrite + nitrate + ammonium) using a Lachat QuickChem 8500 Flow Injection Analyser (Hach, Colorado, U.S.A.). DIN concentrations (reported as mg/L) were validated against natural seawater certified reference material.

Analysis of data

Repeated measures Analysis of Variance (ANOVA) was used to analyse data from the nutrient elevation experiment. Analysis treated „time‟ (repeated monthly sampling of each reef) as a repeated factor; „nutrients‟ and „canopy‟ as fixed and orthogonal (2 levels of each). Factorial ANOVA was used to test for variaton in turf and recruit covers and sediment dynamics among treatments (catchment and local-scale). Analysis incorporated a hierarchical design in which replicate „sites‟ (random factor) were nested within the variable of interest i.e., catchment or reef condition (fixed). Pearson"s product-moment correlation was used to assess the relationship between coastal DIN concentrations and habitat covers.

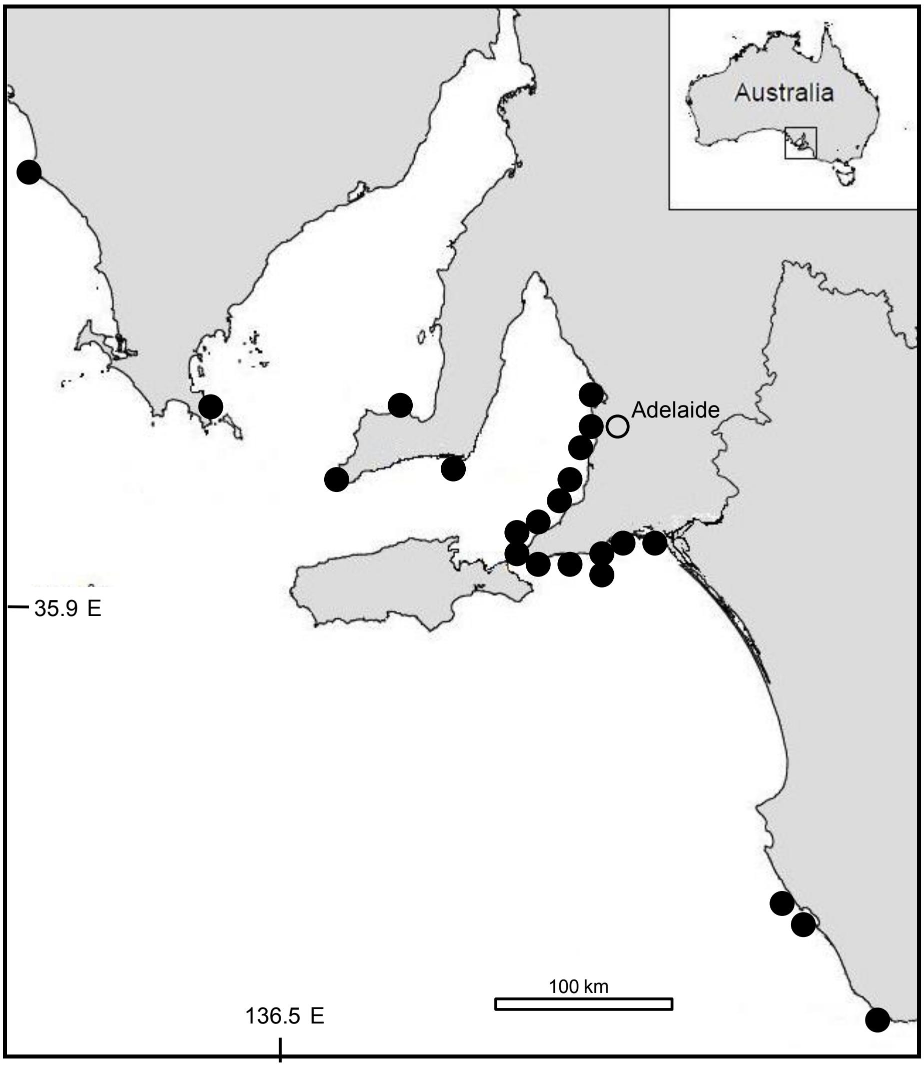

Figure 3.2 Map showing locations used to test the generality of the model that water quality (measured as dissolved inorganic nitrogen) can influence the relative covers of subtidal habitat.

3.3 Results

Persistence of turfs under elevated nutrients

The lack of a significant interaction between „season" (i.e., the repeated measure) and the orthogonal factors „nutrients" and „canopies" (Table 3.1; „season × nutrients × canopy" term) enabled interpretation of the individual effects of these factors across seasons. On nutrient elevated reefs where canopies were absent, turfs persisted throughout winter months (June to August) to have greater covers than those exposed to ambient nutrient concentrations (Fig. 3.3a; Appendix, Table S2). This contrasted the patterns observed during summer, autumn (the 1st only) and spring where no differences in covers were apparent between nutrient elevated and ambient treatments (Table S2). It must be noted that covers differed during the second autumn, which we propose may represent the onset of the natural cycle of turf senescence. Variation in the phenology of turfs was also evident in the presence of existing canopy covers (*Ecklonia radiata*) despite greater temporal fluctuations (Fig. 3.3.b). Throughout most of the year (four of the six seasons sampled) covers were greater on nutrient elevated reefs compared to ambient reefs (Table S2).

Recovery of canopy-forming algae

Within urban catchments, turfs in experimental gaps persisted through winter to have greater covers than those within agricultural and natural catchments (Fig. 3.4a; Table 3.2a). This contrasted the comparatively uniform and low (< 3 %) covers estimated under canopies across catchment types at the same time (ANOVA: between catchments, $F_{2, 6} = 1.45$, $P = 0.283$). Patterns of recruitment by canopy-forming species (*Cystophora* spp., *Ecklonia radiata*, and *Sargassum* spp.) contrasted with that of turfs, having substantially reduced covers within urban catchments compared to agricultural and natural catchments (Fig. 3.4b; Table 3.2b). Again, this contrasts with the uniform cover of recruits under extant canopies across catchments (ANOVA: $F_{2, 6} = 3.36$, $P = 0.104$). Dry weights of deposited sediment did not differ among catchment types (ANOVA: $F_{2, 9} = 0.69$, $P = 0.526$), but showed considerable variability among sites within catchments, ranging from 173 - 233 $\text{mg}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$ (ANOVA: $F_{9, 24} = 3.92$, $P = 0.004$)

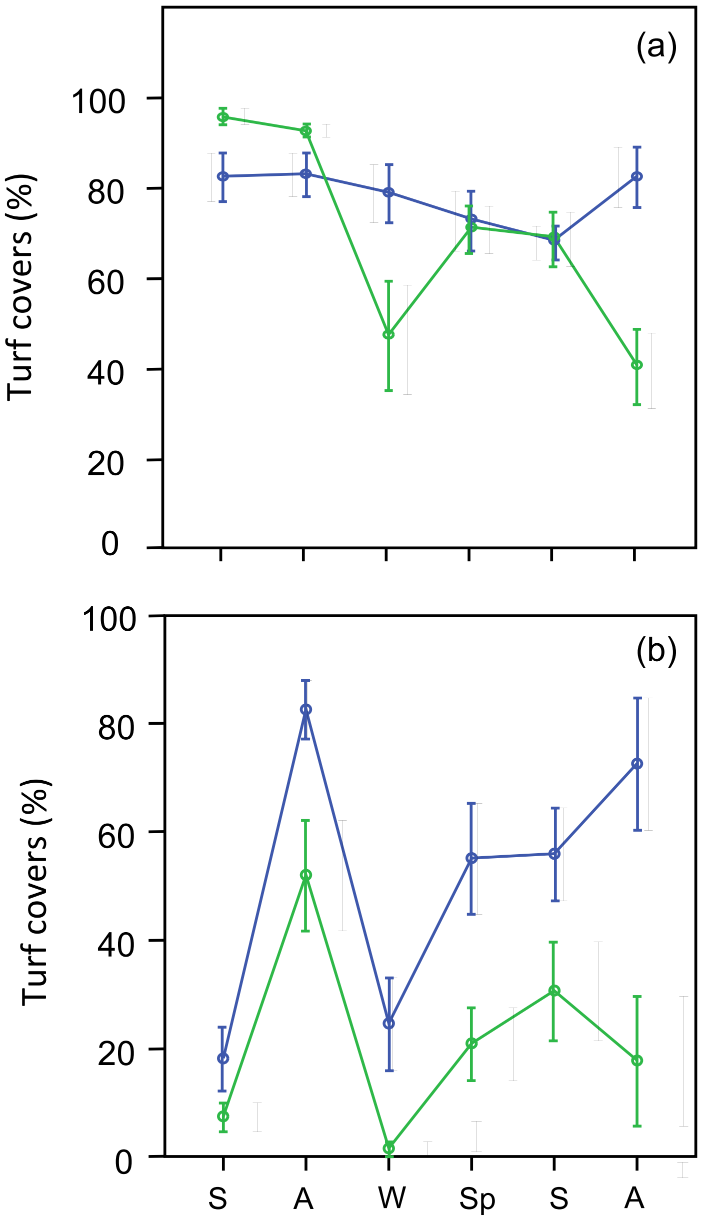

Figure 3.3 Seasonal patterns of turf cover on experimental reefs under conditions of experimental nutrient enrichment (blue lines) and ambient conditions (green lines), maintained orthogonally with treatments of *Ecklonia radiata* canopy (a) absent and (b) present. Data are mean (± SE) estimates of turf cover derived from replicate reefs allocated to each treatment combination. S = summer, A = autumn, W = winter, Sp = spring.

Table 3.1 Results of repeated measures ANOVA testing for variation in turf covers across seasons (period (time) and between orthogonal treatments comprising manipulations of nutrient concentration (i.e., ambient cf. elevated) and existing *Ecklonia radiata* canopy (present cf. absent). Where, *df* denotes degrees of freedom; MS mean square, *F*-ratio and *P* probability.

Source	*df*	MS	*F*	*P*
Season	5	8135.04	20.32	***
Season × nutrients	5	2336.46	5.84	***
Season × canopy	5	4253.60	10.62	***
Season × nutrients × canopy	5	804.14	2.01	NS
Residual	80	400.43		

Notes: Significance is denoted as: * $P < 0.05$, *** $P < 0.001$. See, Table S2, Appendix B for individual Student-Newman-Keuls (SNK) test comparisons on significant „Time × nutrients × canopy" term.

At a local-scale, the development of turfs within experimental clearance plots was strongly related to contemporary reef condition, with greater covers on degraded reefs compared to healthy reefs (Fig. 3.5a; Table 3.3a). It is worthy of notice, that comparisons of mean turf covers between degraded and healthy reefs (> 60 %) are far in excess of those between urban and alternative catchments (~ 35 %). Covers of canopy-forming recruits showed no patterns related to reef condition (Fig. 3.5b; Table 3.3b); as did dry weights of deposited sediments (Fig. 3.6a; Table 3.4a). These trends contrasted patterns of accumulated sediments, which were greater on degraded reefs than they were on healthy reefs (Fig. 3.6b; Table 3.4b). There were strong positive correlations between sediment accumulation and turf covers (Pearson"s correlation, $r = 0.83$, $P = 0.040$) but not sediment deposition ($r = 0.44$, $P = 0.379$).

Coastal eutrophication and subtidal landscapes

Dissolved Inorganic Nitrogen (DIN) concentrations of coastal waters were effective predictors of subtidal habitat across the southern Australian coastline. Areal covers of turfed habitat showed strong positive correlations with DIN (Fig. 3.7a; Pearson"s correlation, $r = 0.56$, $P = 0.007$). This contrasted the negative relationship between DIN and areal covers of macroalgal forest (Fig. 3.7b; $r = -0.65$, $P = 0.001$).

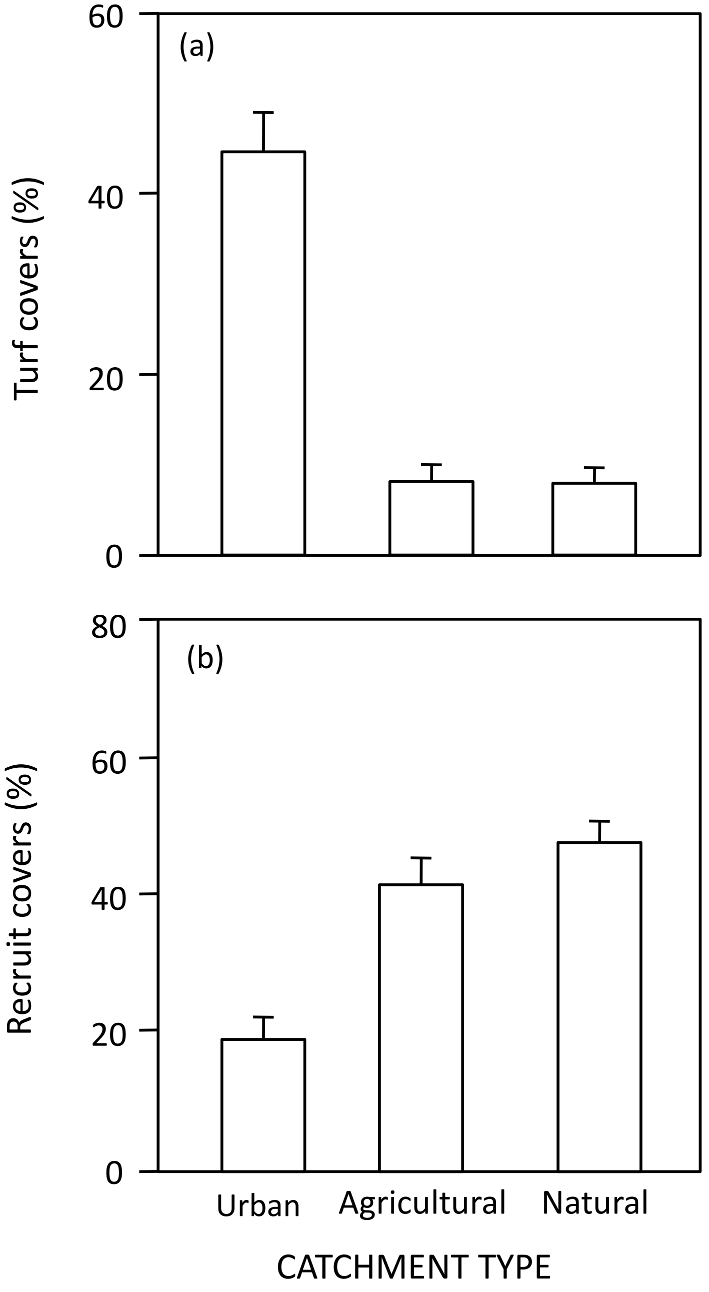

Figure 3.4 Catchment-scale variation in disturbance-recovery processes, as evidenced by contrasting covers of (a) turf, and (b) canopy recruits, quantified within 1m^2 experimental plots at the end of the Austral winter (August). Data are mean covers (+ SE).

Table 3.2 Results of nested ANOVAs testing for catchment-scale differences in winter (August) covers of (a) turfs and (b) canopy-forming algal recruits within experimental canopy clearance plots. Where *df* denotes degrees of freedom; MS mean square, *F*-ratio and *P* probability.

Source	*df*	MS	*F*	*P*	MS	*F*	*P*
		(a) Turf covers (%)			(b) Recruit covers (%)		
Catchment	2	13623.26	13.85	**	1206.41	5.21	*
Site (Catchment)	6	984.00	6.50	***	231.56	2.57	*
Residual	99	151.37			89.96		

Notes: Data were arcsine-transformed percentages. „Catchment" was treated as a fixed and orthogonal factor with three levels (urban, agricultural and natural) and „Site" as a random factor with three replicates nested within „Catchment". Significance is denoted as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Student-Newman-Keuls (SNK) on significant „Catchment" terms; turf covers in (a): Urban > Agriculture = Natural catchments; canopy recruitment (b): Urban < Agriculture = Natural catchments.

Table 3.3 Results of nested ANOVAs testing for local-scale differences in winter (August) covers of (a) turfs and (b) canopy-forming algal recruits within experimental canopy clearance plots on subtidal reefs along an urban coastline. Where *df* denotes degrees of freedom; MS mean square, *F*-ratio and *P* probability.

Source	*df*	MS	*F*	*P*	MS	*F*	*P*
		(a) Turf covers (%)			(b) Recruit covers (%)		
Condition	1	24800.40	13.79	*	91.98	2.66	NS
Reef (Condition)	4	1799.07	7.78	***	34.61	3.28	*
Residual	84	231.16			10.55		

Notes: „Condition" was treated as fixed and orthogonal factor with two levels (Healthy cf. Damaged); and „Sites" ($n = 3$), a random factor nested within „Condition". Significance is denoted as: * $P < 0.05$; ** $P < 0.01$. Student-Newman-Keuls (SNK) comparison for significant „Condition" term for turf covers (a): Degraded > Healthy.

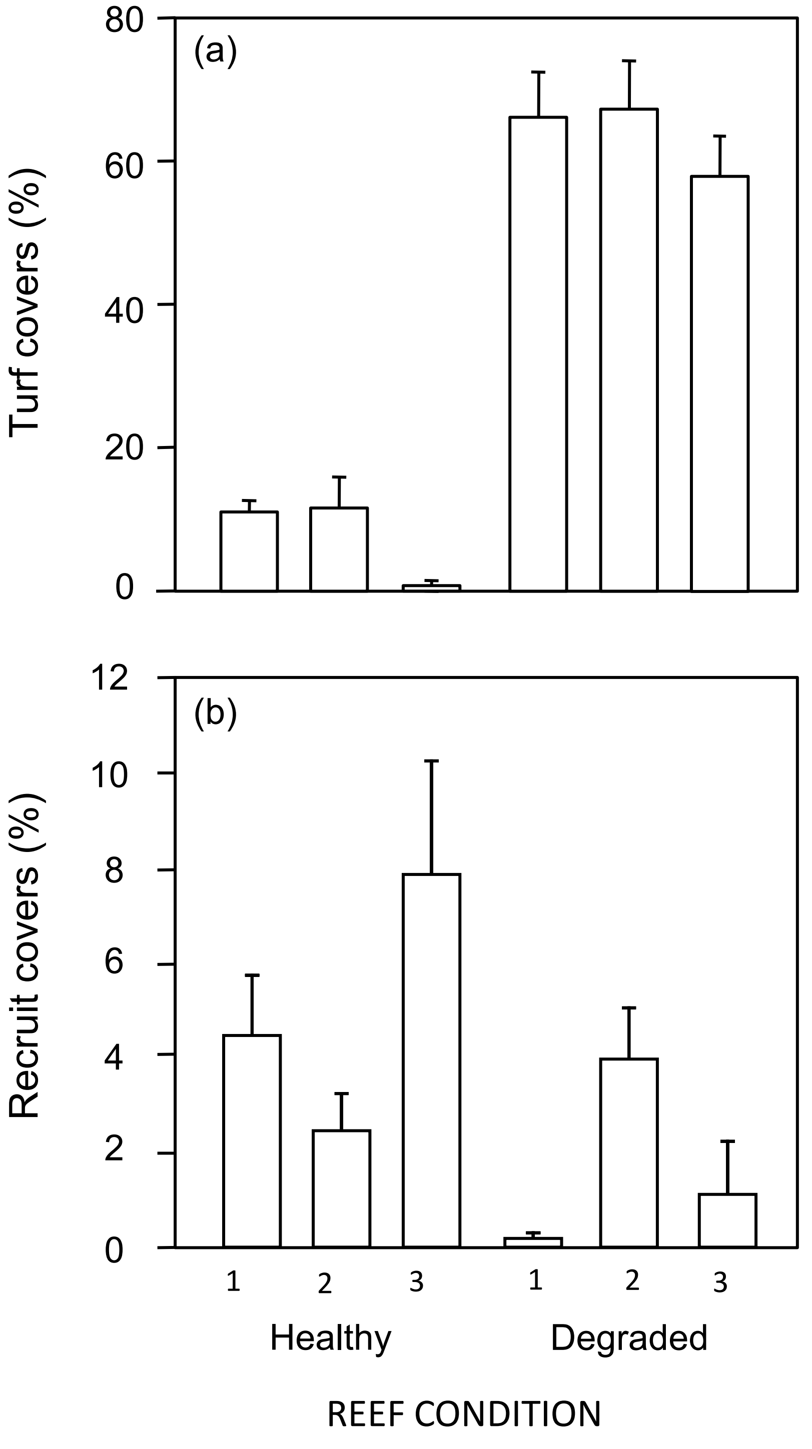

Figure 3.5 Local-scale variation in disturbance-recovery processes, as evidenced by contrasting covers of (a) turf, and (b) canopy recruits, quantified within 1m^2 experimental plots at the end of the Austral winter (August). Data are mean covers (+ SE).

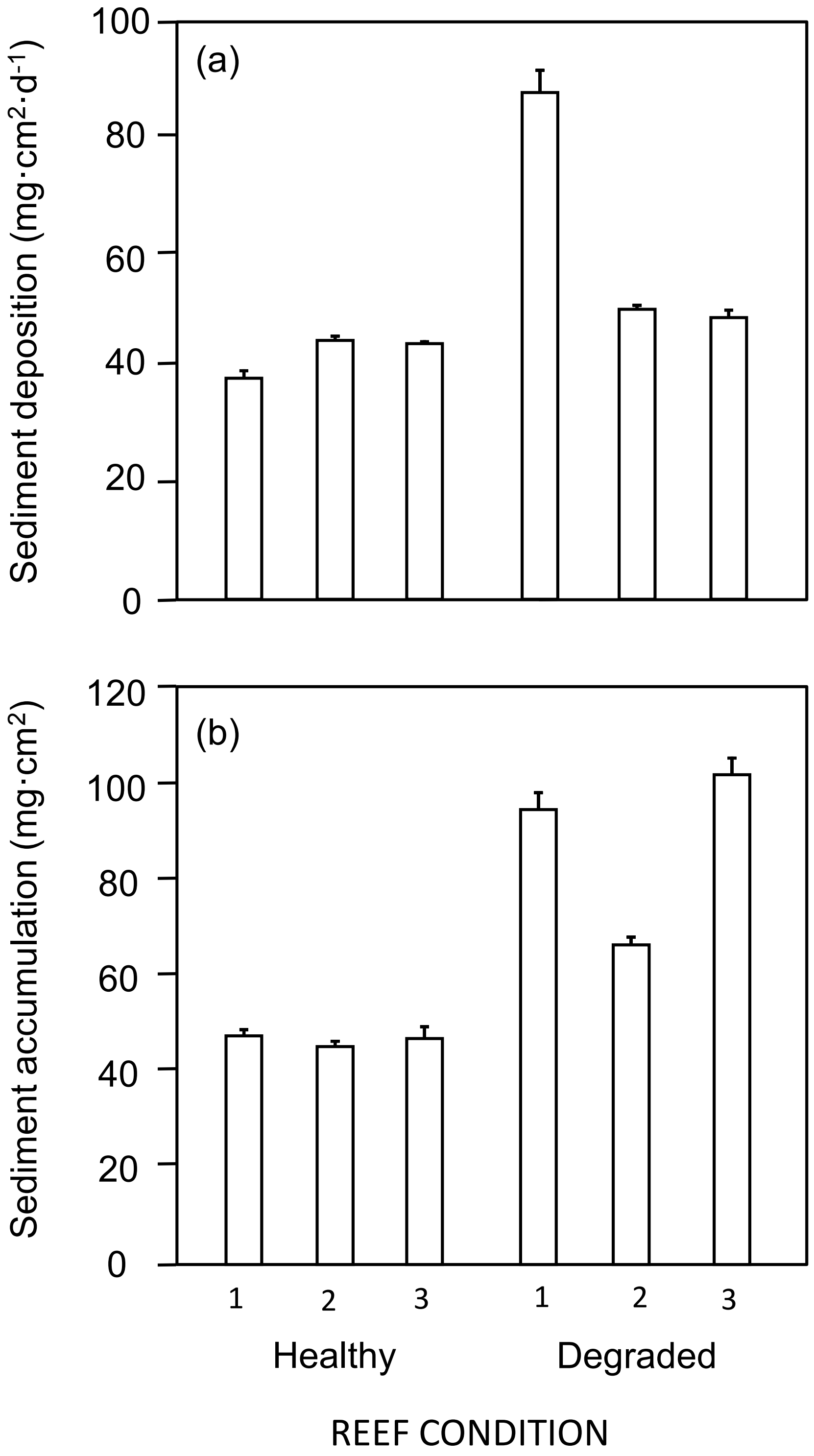

Figure 3.6 Local-scale patterns of sediment dynamics estimated at three replicate sites selected along the Adelaide metropolitan coastline, nested with „reef condition" (a) deposition, and (b) accumulation, measured as g · per m^2. Data are means (+ SE).

Table 3.4 Results of nested ANOVAs testing for local-scale differences in the sedimentation dynamics of subtidal reefs. Parameters investigated were (a) sediment deposition, and (b) sediment accumulation. *df* degrees of freedom, *MS* mean square, *F*-ratio, *P* probability.

Source	*df*	MS	*F*	*P*	MS	*F*	*P*
		(a) Deposition			(b) Accumulation		
Condition	1	2998.00	2.35	NS	12905.18	14.42	*
Site (Condition)	4	1277.33	78.48	***	895.05	28.96	***
Residual	24	16.28			30.91		

Notes: „Condition" was treated as fixed and orthogonal factor with two levels (Healthy cf. Damaged); and „Sites" ($n = 3$), a random factor nested within „Condition". Significance is denoted as: NS, not significant $P > 0.05$, * $P < 0.05$; *** $P < 0.001$. Student-Newman-Keuls (SNK) comparison for significant „Condition" term in (b): Degraded > Healthy

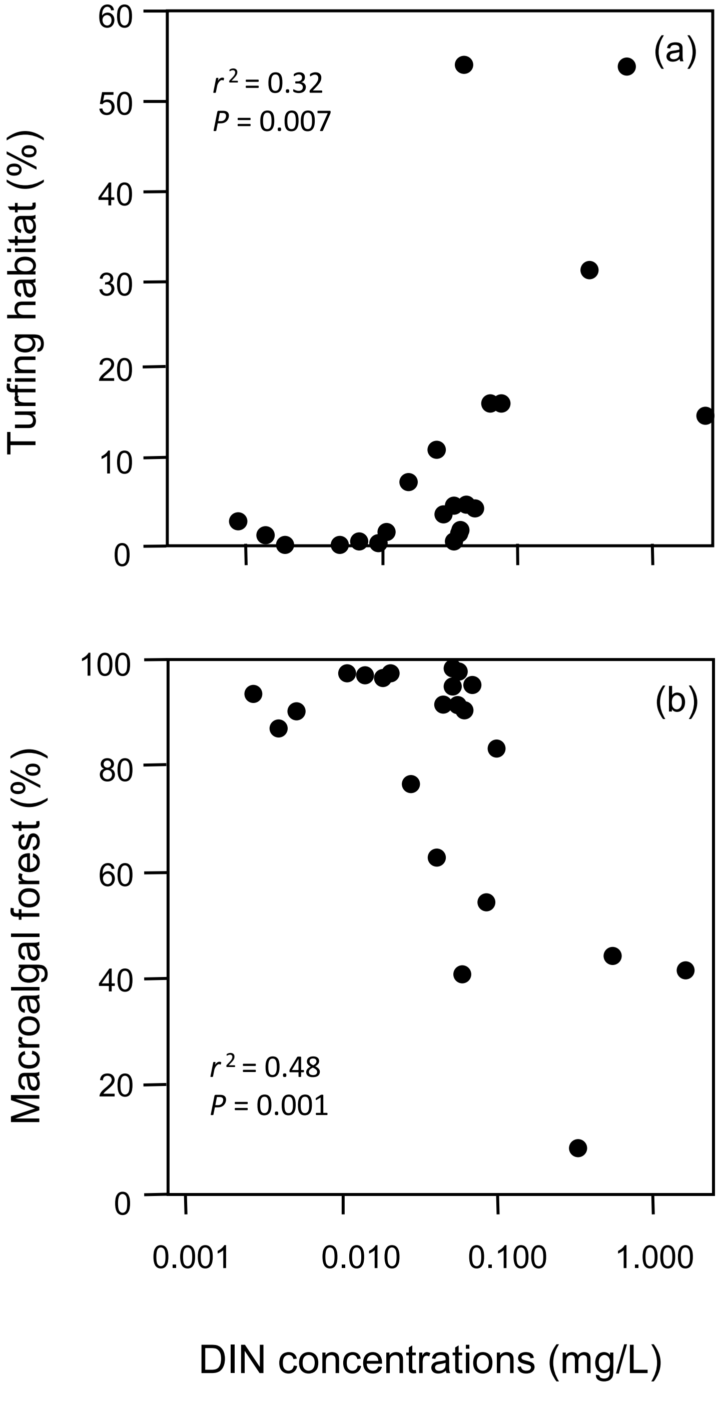

Figure 3.7 Relationship between coastal water Dissolved Inorganic Nitrogen (DIN) concentrations and areal covers of (a) turfed habitat and (b) macroalgal forest estimated at 22 coastal locations along the southern Australian coastline. X-axis values (log-scale) are mean estimates of DIN derived from replicate water samples (*n* = 10) collected from each site. Y-axis values are mean covers of habitat derived from (*n* = 4) 100 m transects.

3.4 Discussion

Some of the most pervasive forms of human impact within aquatic ecosystems result from the ubiquitous release of nutrients (Carpenter et al. 1998, Cloern 2001). A key finding of this study was that sustained nutrients can maintain turfs throughout periods of natural senescence (i.e., winter). Turf covers on nutrient elevated reefs displayed greater stability (over two consecutive annual cycles, i.e., 16 months) than those exposed to ambient nutrients. Whilst treatments had negligible effect during summer, nutrient elevation maintained dense covers of turf during winter (never less than 60 %), contrasting patterns of natural seasonal decline seen under ambient conditions (mean estimates as low as 25 %). Whilst these covers are greater than estimates of turfs derived from natural rocky reef (< 7 %; Connell & Irving 2008), variation between artificial structures and natural rock is expected (Connell & Glasby 1999), and our comparison serves more to demonstrate the relative effect of nutrient enrichment on turf phenology. Overall, the results confirm that nutrients can facilitate the persistence of turfs into the winter recruitment phase of canopy-forming species (Novaczek 1984) thereby preparing the conditions for canopy inhabitation (Devinny & Volse 1978, Airoldi 1998).

The ability of canopies to regulate the growth of opportunistic species represents an important function underlying the resilience of rocky reef ecosystems (Edwards 1998, Eriksson et al. 2007). Whilst canopy-formers generally maintain dominance on subtidal reefs by regulating the growth of turfs (Irving & Connell 2006a, Russell & Connell 2007), elevated nutrients may alter these competitive interactions (Lotze et al. 2000). Our data show that canopies (*Ecklonia radiata*) appear less able to suppress the development of turfs under conditions of nutrient enrichment. The suggestion here is that the enhanced growth potential of turfs may negate the influence of canopy scour as a mediating influence of the effects of eutrophication (Kennelly 1989). The implications of this are likely to be considerable along urban coastlines, where remaining forests tend to be fragmented and the relatively high perimeter: area ratios of turfed habitats (owing to their large size; Chapter 2) further reduce the ability of canopies to maintain turf-free substratum (Emmerson & Collings 1998).

It is becoming clear that human activities in coastal catchments can affect the health of adjoining subtidal habitats (e.g., Nystrom et al. 2000, Benedetti-Cecchi et al. 2001, Fabricius et al. 2005, Chapter 2). Our data show that conditions typical of developed coastlines (i.e., elevated nutrients and sediments) are sufficient to induce change in the phenology of turfs that can alter disturbance-recovery cycles (see, Bulleri & Benedetti-Cecchi 2006). Turf covers within urban catchments were substantially greater than those within less developed catchments (i.e., > 40 % urban, cf. < 10 %; for agricultural and natural catchments). This, at a time when canopy-formers typically re-colonise gaps (winter) is likely to have substantial implications for forest resilience. Indeed, the persistence of turfed habitats along nutrient impacted coastlines has been associated with the intergenerational loss of canopy-forming forests (Jackson 2001, Steneck et al. 2002, Connell 2007b). Our data provide a mechanism to explain this observation, showing that canopy recruitment is lower along impacted urban coastlines where covers of turf and weights of accumulated sediments are greatest. The processes that control gap persistence may therefore represent important precursors to gap expansion that can ultimately change habitat configuration (e.g., Eriksson et al. 2002, Connell et al. 2008).

Expansion or contraction of subtidal habitats is often dependent on the mechanisms driving re-colonisation of disturbed patches (Bulleri & Benedetti-Cecchi 2006). Dense and persistent covers of turfs maintained by nutrient enriched coastal waters (Carpenter et al. 1998) have the potential to cause the repeated failure of canopy recruitment. Over longer periods (e.g., several decades), it is possible to observe wholesale shifts from forested communities to turfed landscapes (Steneck et al. 2002, Hughes et al. 2005). Many of the regime shifts documented along temperate coastlines were probably driven more by processes involved in gap expansion (repeated failure of canopies to recover from disturbance), rather than those involved in gap creation (i.e., storm driven disturbance that defoliates canopies; Connell 2007a). It appears therefore, that nutrient-driven habitat-loss need not be the consequence of competitive interactions between alternate communities (i.e., forests cf. turfed landscapes), but may result from the continuous failure of dominant assemblage to recover from disturbance (see, Rogers & Miller 2006).

Dramatic ecosystem change can often be driven by synergistic processes (amplifying feedbacks) that can be disconnected from the ultimate cause of decline (Brook et al. 2008). The highly variable patterns of canopy recruitment observed at a local-scale (i.e., reefs separated by kms) suggest that that the physical factors causing habitat degradation are not simple, but rather complex interactions. It is unlikely that changes to turf phenology alone drive forest decline (see, Kennelly 1987a), as it is often the sediments trapped by turf that are the actual inhibitors of spore settlement (Neushul et al. 1976, Devinny & Volse 1978). Synergies between turfs and sediments (i.e., turfs that trap sediments and sediments that enhance turf growth; see, Airoldi 1998) are likely to have greater implications for forest recovery than these factors would on their own. Indeed, experimentally increasing rates of sedimentation has been shown to increase the growth of turfs above that observed under conditions of elevated nutrients alone (Gorgula & Connell 2004). Our correlations between turf covers and sediment accumulation (N.B. not sediment deposition *per se*) attest to the strong associations between these factors that are independent of depositional environment. Whilst turfs-sediment complexes are present year-round, nutrient elevation is likely to promote positive associations that will further reduce forest recovery. Overall, the mechanism driving forest decline may be disconnected from the ultimate cause (elevated nutrients), but instead, involve synergies between sediments and turfs that can act as an impediment to forest recovery.

The gradual degradation of forested landscapes is likely to involve multiple small-scale disturbances that initially appear unconnected, yet may have cumulative effects over time (McCook et al. 2001). Whist persistent turf-dominated gaps may be initially small and inconsequential (e.g., 3 - 6 m^2; Kennelly 1987b) continuous recruitment failure may enable these gaps to coalesce into expansive turfed landscapes (see, Chapter 2). Along urban coasts, the recalcitrance of turfs operating in concert with other factors that reduced resilience (i.e., sediments, reduced propagule supply and reduced canopy scour) may represent important precursors to regime shift. Over generational time-scales it may be possible to observe the wholesale replacement of perennial communities in favour of turfed landscapes sustained by poor water quality and reduced propagule supply (Eriksson et al. 2002, Connell et al. 2008). Our correlations between coastal nitrogen concentrations and subtidal habitat across hundreds of kilometres may be the manifestation of such processes that have gone on unnoticed for decades (i.e., contemporary patterns based on historical losses). Further, it appears from the nature of these relationships (see, Fig 3.7) that subtidal ecosystems may be initially resilient to low levels of nutrient enrichment, but that greater changes to habitat composition can be anticipated as the amount of terrestrial subsidy increases. This function may represent a threshold response, whereby recovery of degraded landscapes is difficult or impossible unless the factors reducing resilience are removed (see, Scheffer et al. 2001).

In conclusion, humans are integral components of natural ecosystems as their activities continue to modify ecological processes (Jackson 2001, Micheli et al. 2005). Whilst the link between human activities and loss of marine resources appears obvious, ecologists continue to be surprised by the unpredictable outcomes of increasing human pressures (Paine et al. 1998). Regime shifts, characterised by permanent changes to community structure and function may be the synergistic outcome of multiple interacting stressors (Hughes et al. 2005, Brook et al. 2008). Furthermore, ecosystem degradation may involve a series of small localised impacts, apparently unconnected in time and space, which go unnoticed until wholesale ecological change has occurred (Folke et al. 2004, Contamin & Ellison 2009). What is particularly worrying about this type of habitat loss is that it may go on largely unnoticed due to the „shifting baseline" syndrome (sensu, Dayton et al. 1998). The failure to recognise historical losses may result in further degradation as measures will not be implemented to remove the chronic stress from the system. Understanding the complex interactions between multiple human stressors and mechanisms that reduce the resilience of natural ecosystems is vital, not only to forecast the consequences of increasing pressure from human activities, but also to provide insights into the potential for rehabilitating degraded landscapes.

“If you are what you eat and you don't know what you're eating, do you know who you are?” Claude Fischler, 2004

Human-driven alteration of subtidal habitat is likely to affect the diet of ecologically important consumers such as the Purple Sea Urchin (*Heliocidaris erythrogramma*). Photograph taken by the author during a fieldtrip in 2008.

CHAPTER FOUR:

Habitat loss and shifts in the diet of subtidal consumers

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Habitat loss and shifts in the diet of subtidal consumers

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Oecologia 2009, submitted paper

Statement of Authorship

In this paper I obtained funding, developed the experimental design, conducted the fieldwork, analysed the results and wrote the manuscript. Sean D. Connell provided insightful criticism that improved the manuscript.

I certify that the statement of contribution is accurate

Daniel Gorman (Candidate)

Signed *Date* 10/12/09

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis

Associate Professor Sean D. Connell

Signed *Date* 10/12/09

Preamble

Chapter 4 examines the potential consequences of subtidal regime shift for primary consumers (i.e., herbivores) across the coastline of South Australia. Stable isotope analysis was used to compare the diets of benthic herbivores (urchins and gastropods) between healthy and degraded locations. The aim was to examine whether shifts from forested to turfed landscapes could alter the relative dietary contributions and/or nutritional value of ambient food resources to consumers. Relationships between diet and consumer densities were also investigated in order to determine the suitability of regime shifted landscapes to invertebrate taxa. The Chapter takes the form of a co-authored article, and as such is written in plural. The manuscript is currently in review with the journal, *Oecologia*. The unpublished manuscript can be cited as:

Gorman, D. & Connell, S.D. (in review) Diet shifts on human-impacted coastlines: consequences of subtidal habitat change. *Oecologia*

4.1 Introduction

The replacement of diverse and structurally complex plant communities by structurally simple weedy assemblages is a recognised consequence of coastal development across the globe (Scheffer & Carpenter 2003, Steele 2004, Airoldi & Beck 2007, Chapter 2). Along temperate coasts, these regime shifts have been evidenced by the widespread replacement of canopy-forming forests (kelps and foliose species) by low-relief turfed landscapes (e.g., Australia, Connell et al. 2008, North Sea, Eriksson et al. 2002 and Mediterranean, Rodriguez-Prieto & Polo 1996). This degradation has been linked to the recent and intensified use of coastal resources by humans, and to the subsequent alteration of environmental conditions resulting from eutrophication, sedimentation and pollution, which can reduce the resilience of nearshore habitats to disturbance (Tilman et al. 2001, Hughes et al. 2005, Lotze et al. 2006, Chapter 3). The associated loss of structural complexity (i.e., habitat refuge) and ecological function (i.e., food resources) can profoundly impact on the ability of ecosystems to provide services to animal and human populations (Loreau et al. 2001, Balmford et al. 2002, Hooper et al. 2005).

Whilst human activities may have profound implications for submerged aquatic vegetation (Duarte 1995, Deegan et al. 2002), the consequences for higher trophic-level consumers are often more difficult to predict (Folke et al. 2002, Russell & Connell 2005). Subtidal grazing herbivores (e.g., abalone, turbinid gastropods and urchins) represent some of the most conspicuous and ecologically important consumers within temperate rocky-reef ecosystems (Andrew 1993, Fowler-Walker & Connell 2002, Wernberg et al. 2008). These benthic consumers rely primarily on autochthonous food resources (i.e., those generated locally; Steinarsdottir et al. 2009) and hence their diet is likely to be affected by changes in the spatial configuration of subtidal habitats (i.e., relative algal covers) over scales of 10‟s of meters. From this, it follows that the replacement of forested communities by turfed landscapes along urban coasts (e.g., Gorgula & Connell 2004; Chapter 2) will affect the relative contribution of these algal food sources to the diet of resident consumers. Investigating dietary shifts may represent an excellent trophic indicator of the consequences of human derived regime shifts for primary consumers and possibly entire food webs.

Alteration of algal habitats may have implications for the energetic requirements of consumers, especially if a high value food source is replaced by one of relative poor quality (Duffy & Paul 1992). The replacement of canopy-forming species by turfing assemblages may represent an overall reduction in ambient food quality (i.e., as inferred by tissue nitrogen content; Norderhaug et al. 2003, Russell & Connell 2007). Whilst mobile consumers are unlikely to be affected by nutritional constraints imposed by autochthonous (*in situ*) food quality (i.e., they can move to preferable habitats; Connolly et al. 2005b), this factor may have substantial implications for sessile or slow-moving herbivores (Steinarsdottir et al. 2009). As consumers require food of a sufficient nutritional value to sustain growth and routine metabolic functions (Hatcher 1994), the replacement of high quality forested communities may have substantial implications for the suitability of regime-shifted landscapes. In essence, the replacement of canopy-forming forests by turfed landscapes may represent a nutritional stress for resident consumers necessitating changes in behaviour and or feeding strategies according to resource availability (Jennings et al. 1997, Frost et al. 2006).

The quantity (relative availability) and quality of food resources can be a strong determinant of animal population dynamics (Pyke et al. 1977, Jennings et al. 1997, Shima et al. 2008). Consumers are able to respond to changes in food availability by altering their metabolism, modifying rates of consumption and changing their behaviour (Holling 1959, Frost et al. 2006). Consumers differing in their nutritional requirements are likely to be affected, to varying degrees, by shifts in ambient food quality. Those able to contend with low nutrient diets may be able to persist within altered landscapes, and thereby gain almost exclusive access to a nutrient-poor food resource (Higashi et al. 1992). Others, with less flexible metabolic or behavioural adaptations may be forced to leave a degraded patch and migrate to an adjacent area of higher food quality (e.g., Kareiva 1983, Ettinger-Epstein & Kingsford 2008). Variation in food resources can thus drive considerable variability in relative abundances of consumers among habitat patches (Chapman & Underwood 2008), a trend that may have dire consequences for the trophic functioning of entire food webs (Pinnegar et al. 2000).

Stable Isotope Analysis (SIA) is an effective means of investigating trophic dynamics within terrestrial and aquatic food webs (Peterson & Fry 1987). Over the last few decades, applications of SIA have been used increasingly to study relationships between consumers and their food sources (Hobson & Welch 1992, Gannes et al. 1997). SIA is particularly effective for assessing the nutritional importance of potential food sources in systems where direct dietary analysis is problematic owing to spatial and or temporal patterns of distribution (Melville & Connolly 2003, Connolly et al. 2005b). Dietary applications of SIA typically rely on comparisons of the isotopic carbon and nitrogen ratios ($\delta^{13}C$ and $\delta^{15}N$) of a consumer and its potential food sources. These elements are most commonly used because the $\delta^{13}C$ composition of consumer tissue does not generally differ from that of its food source (DeNiro & Epstein 1978) and its $\delta^{15}N$ composition typically varies in a relatively consistent and predictable way (DeNiro & Epstein 1981). $\delta^{13}C$ and $\delta^{15}N$ values can therefore be used to determine the relative nutritional reliance of a consumer on isotopically distinct categories of primary producer.

In recent years, stable isotope mixing models have been recognised as an effective means of inferring complex trophic interactions (Phillips & Gregg 2001, Vander Zanden & Rasmussen 2001). Mixing models utilise the inherent variability in isotopic values of potential food sources, to produce a mixing polygon that can be used to estimate the relative contribution of a single source or combination of food sources. The widespread application of mixing models across diverse ecological systems (see, Phillips & Gregg 2003) has enhanced our understanding of numerous trophic relationships (e.g., Polis & Hurd 1996, Connolly et al. 2005b, Crawley et al. 2009). Despite these successes, conventional models retain inherent statistical limitations, the foremost being output (generally described by a range of feasible solutions) that is not robust to post-hoc statistical testing (Inger et al. 2008). The recent advent of Bayesian mixing models opens the potential for a range of statistical applications not previously possible. Advantages of a Bayesian approach include the ability to incorporate sources of error from observed measurements (e.g., uncertainty in isotopic discrimination values) and the computation of output that has a fully defined statistical distribution (Jackson et al. 2008). Stable isotope mixing models thus present a promising tool for identifying shifts in the diet of herbivores as a consequence of human-induced habitat change.

We investigated the likely consequences of human-induced regime shifts for common benthic herbivores across the temperate coastline of southern Australian. Specifically, we tested whether (1) variation in areal covers of forested and turfed habitats can influence the relative dietary contributions of these food resources to herbivorous consumers, (2) whether these shifts have nutritional implications for consumers, and (3) whether habitat and diet can predict the observed densities of consumers along pristine (i.e., healthy) and degraded coastlines. We used four lines of evidence to achieve these aims: analysis of consumer and producer tissue stable isotopic values ($\delta^{13}C$ and $\delta^{15}N$), tissue carbon and nitrogen values (% C and % N), estimates of habitat covers and consumer densities. In order to examine the relationships between consumer diet and biological parameters (habitat covers and consumer densities); we used the Bayesian mixing model, „siar‟ (Stable Isotope Analysis in R; Parnell & Jackson 2008) to obtain robust statistical output that would enable post-hoc testing.

4.2 Methods

Study sites

This study was done across 700 km of temperate Australian coastline during 2008, and incorporated multiple locations of „degraded‟ subtidal habitat, interspersed among locations of pristine or „healthy‟ subtidal habitat (Fig. 4.1). Sampling employed a hierarchical design that comprised of replicate sites (n = 4) nested within the two „coastline types‟ (hereafter, „degraded‟ and „healthy‟). The selection of degraded sites was done *a priori* from urban locations known anecdotally to have undergone substantial losses of macroalgal forest (e.g., > 60 % when compared to historical covers; Connell et al. 2008). Additional constraints for degraded site selection were; close proximity to discharges of treated effluent (sewage) and coastal water Dissolved Inorganic Nitrogen (DIN) concentrations in excess of 0.05 mg/L (i.e., exceeding national ecosystem guidelines; ANZECC 1992). Preliminary analysis of DIN concentrations at these sites (data from Chapter 3) confirmed the distinction between degraded (mean ± SE: 0.78 ± 0.15 mg/L) and healthy sites (mean ± SE: 0.01 ± 0.001 mg/L; ANOVA: $F_{1, 6} = 6.11$; $P = 0.048$), giving further weight to our classification of coastline types. Healthy sites were similarly chosen *a priori*, based on their proximity to expansive areas of natural coastal vegetation (> 200 hectares), absence of any human development and occurrence of extensive covers of macroalgal forest (Connell & Irving 2008).

Sample collection and isotopic analysis

Invertebrate herbivores and their potential algal food sources ($n = 3$, replicate samples per site) were collected from subtidal rocky reefs (5 - 10 m depth) at distances < 500 m from land at all replicate sites using SCUBA. Collections at degraded sites had the additional constraint of being done < 500 m from the discharge point of treated sewage effluent. Species selection was contingent on distribution and feeding mode (i.e., benthic grazers) and included; the Purple Sea Urchin *Heliocidaris erythrogramma* (Valenciennes, 1846), the Blacklip abalone, *Haliotis rubra* (Leach, 1814) and the turbinid gastropod, *Turbo torquatus* (Gmelin, 1791). The mean size of collected individuals did not differ between healthy and degraded sites (ANOVA: $P > 0.05$ for all species). Across all sites, the mean shell width (mm ± standard error) of gastropod consumers were; *H. rubra* (99 ± 5) and *T. torquatus* (48 ± 3); and the mean test diameter of *H. erythrogramma* (79 ± 3).

Urchins and gastropods are able to utilise a wide range of food resources including, canopy-forming macroalgae (e.g., kelps and fucoids), encrusting and articulated corallines and filamentous turf-forming algae. Potential algal food sources were chosen based on descriptions of ingested algal material for each of the three herbivores (i.e., *H. rubra*, Guest et al. 2008, *T. torquatus*, Clarkson & Shepherd 1985, Worthington & Fairweather 1989, Wernberg et al. 2008 and *H. erythrogramma*, Vanderklift et al. 2006, Vanderklift & Wernberg 2008). Results from these studies suggested that > 90 % of ingested material within the gut of these consumers could be grouped into five potential categories. We conducted dietary analysis using the most widespread and representative genera from these five most plausible algal food categories; (1) „encrusting corallines‟ (i.e., *Sporolithon* spp.), (2) „articulated corallines‟ (*Amphiroa* spp.), (3) „filamentous turfs‟ (i.e., *Feldmannia* sp., see Roberts & Connell 2008) (4) „foliose reds‟ from the family Plocamiaceae, (i.e., *Plocamium* spp.) and (5) canopy-forming macroalgae (*Ecklonia radiata* and *Cystophora* spp.), which were subsequently pooled together as their isotopic values did not differ (ANOVA: $F_{1,32}$ $P = 0.777$ & $P = 0.341$; for δ^{13}C and δ^{15}N respectively).

Algal samples were cleaned of visible epiphytes, rinsed with distilled water, dried (60ºC for 24 h), before being acid washed (3M HCl) to remove any carbonates. Animal samples comprised of extracted muscle tissue, from the foot (gastropods) or Aristotle‟s lantern (urchin) taken from similarly sized individuals that were dried and acid washed. After acid washing, all samples were re-dryed to a constant weight (60°C for 48 h), placed in tin capsules and analysed on an Isoprime isotope-ratio mass spectrometer (Isoprime, Manchester, UK). The ratios of ^{13}C/^{12}C and ^{15}N/^{14}N for all samples were calculated as the relative per mille (‰) differrences between the sample and conventional standards (PeeDee Belemnite limestone carbonate for carbon; air for nitrogen). Precision of the mass spectrometer, using the values from duplicate samples, was 0.2 ‰ for ^{13}C and 0.1 ‰ for ^{15}N.

Sample analysis also generated values for nitrogen and carbon content (%) that enabled calculation of algal carbon to nitrogen ratios (C:N); a common measure of relative nutritional quality (Niell 1976). Using C:N values we developed a proxy for ambient „food quality‟ (Fq) at each site, as a function of the sum of the carbon to nitrogen (C:N) „value‟ of each individual algal food source (Vi) multiplied by its proportional areal cover (Pi). The equation for this proxy: $Fq = \sum (Vi \times Pi)$ was used to investigate whether a shift from healthy to degraded landscapes could represent an overall reduction in the nutritional value of locally available (i.e., *in situ*) food sources.

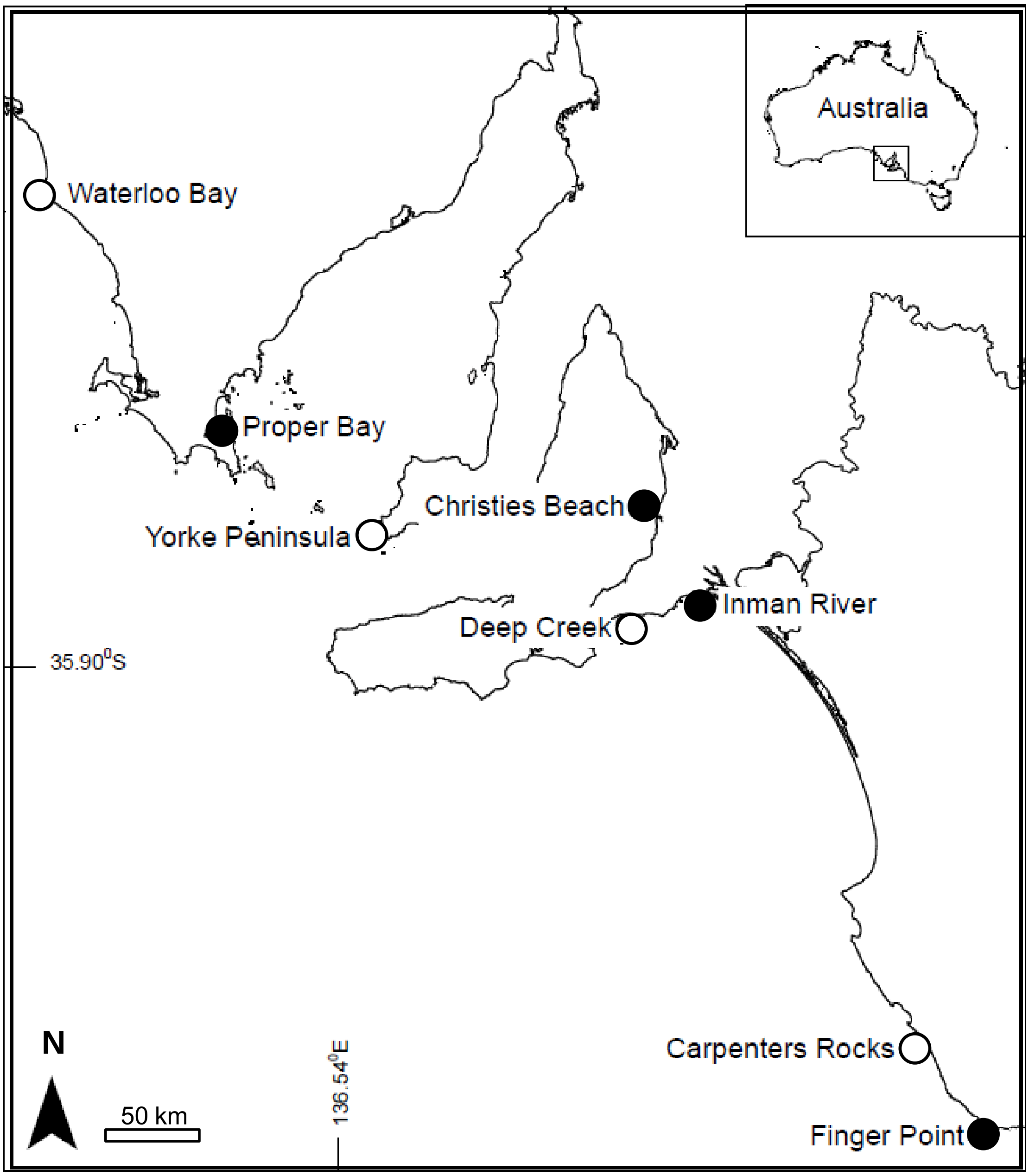

Figure 4.1 Map of study region outlining the hierarchical design that incorporated replicate „degraded" (●) and „healthy" ○) sites (n = 4, per „coastline type") interspersed across the temperate coastline of South Australia.

Dietary modelling

Dietary modelling was done using the Bayesian mixing model „SIAR" (Stable Isotope Analysis in R) available as a free download for use in the R environment and accessible from http://cran.r-project.org/web/packages/siar/index.html. The package generates estimates of the proportions of different food sources that contribute to the diet of an animal consumer. The model calculates feasible combinations of food source (based on their isotopic values) that can replicate the observed „target" values of a consumer species. The model assumes that each target value comes from a Gaussian distribution with an unknown mean and standard deviation (Parnell & Jackson 2009). The structure of the mean is a weighted combination of the isotopic values of potential food sources. The weights are made up of dietary proportions (which are given a Dirichlet prior distribution) given for the different food sources (Parnell & Jackson 2009). The standard deviation is divided up between the uncertainty around the fractionation corrections and the natural variability between target individuals.

Modelling was done for each herbivore at each replicate site within coastline type (total sites, *n* = 8). Employing this approach takes into account the inherent spatial variability of isotopic values among sites (see, Melville & Connolly 2003) and is likely to yield more accurate results than an approach that uses a single treatment mean across replicate sites. Models were run using the isotopic values ($\delta^{13}C$ and $\delta^{15}N$) of all 3 replicate consumer samples (simultaneously) at each site and the mean (± SE) of each algal food source (5 producer categories; see previous). We ran the standard model for a single group, with the following parameters; iterations: 200,000; „burn in": 50,000; „thinning" by 15 (see, Parnell & Jackson 2008). Results were reported as the distribution (95 % CI), mode and mean of feasible solutions.

The usefulness of mixing models as a means of inferring diet is dependent on correctly prescribing isotopic discrimination between a consumer and its food sources (reviews, McCutchan et al. 2003, Caut et al. 2009). We corrected the mean isotopic values of all producers (at each site) to account for isotopic discrimination. We improved the accuracy of these inferences by (1) using consumers that are exclusively herbivorous (i.e., a single trophic-level discrimination; Post 2002), (2) the use where possible of previously reported species or tissue specific discrimination values (Vanderklift & Ponsard 2003) and (3) by correcting based on the isotopic values (and the unique mixing polygon) of each individual site rather than means across coastline type.

For each herbivore, we ran repeated models using 0.1 ‰ increments within the range of previously reported correction values for the genera/taxonomic class that gave feasible solutions that were within the polygon created by producer isotopic values (Vanderklift & Ponsard 2003, Villinski et al. 2004, Guest et al. 2008, Hill & McQuaid 2008, Won et al. 2008, Steinarsdottir et al. 2009). Correction factors used for $\delta^{15}N$ ranged from 1.6 – 2.0 ‰ along degraded coastlines and 0.6 – 1.3 ‰ along healthy coastlines. $\delta^{13}C$ correction factors ranged from 0.4 – 0.7 ‰ for degraded coastlines and 0.5 – 0.9 ‰ along healthy coastlines. For each consumer we selected 10 replicate dietary solutions derived from correction factors that were consistent across sites within coastline type; and which were closest to those previously reported (see above). Whilst we acknowledge that this approach introduces variation into estimates of dietary contribution, we suggest that this is less than the error generated using a „single" but incorrect or inappropriate fractionation correction factor (see, Melville & Connolly 2003).

Herbivore densities and habitat covers

To test the prediction that the diet of subtidal herbivores can be influenced by the relative availability of algal food sources, we estimated covers of algal habitat using replicate 100 m transects (n = 4, per site) that ran perpendicular to the shoreline and were separated by < 50 m. Changes in algal species were recorded at a 1 m^2 scale to provide estimates of relative covers as a percentage of total substratum (see similar methodology; Goodsell et al. 2004, Irving & Connell 2006b). Areal covers of algal species (minus sandy or bare substrate) were subsequently pooled into the five food source categories (see, sample collection and isotopic analysis section). To investigate the relationship between habitat covers, diet and relative densities of consumers, we estimated densities of the three benthic invertebrate species (see, sample collection and isotopic analysis section) adjacent to areas of habitat sampling and isotope sample collection. Densities of all herbivores (> 20 mm diameter) were estimated using randomly positioned 1 × 5 m belt transects (*n* = 8, replicates per site) at depths between 5 – 10 m.

Analysis of data

Analysis of Variance (ANOVA) was used to test for differences in all measured variables (i.e., habitat covers, stable isotope values, % N, food quality [*Fq*] and herbivore densities) as well as estimated dietary contributions of algal food. For each analysis „coastline" (i.e., healthy cf. degraded) was treated as a fixed factor and replicate „site" as a random factor nested within „coastline". Analysis of Covariance (ANCOVA) was used to test for heterogeneity of the slopes describing the relationships between habitat covers, consumer diet and consumer densities between coastline types. Where no heterogeneity of slope was evident between degraded and healthy coastlines we were able to pool data and test for significant correlations using Pearson"s correlation coefficient (*r*). Pearson"s correlations were also used to investigate relationships between habitat cover and dissolved inorganic nitrogen concentrations, and those between algal % N and consumer δ^{15}N.

4.3 Results

Habitat covers and nitrogen concentrations

Areal covers of canopy-forming and turf-forming algae displayed predictable patterns related to coastline type (Fig. 4.2). Canopy covers along degraded coastlines were significantly less than those of healthy coastlines ($_{\text{ANOVA:}}$ healthy cf. degraded, $F_{1, 24} = 43.38$; $P < 0.001$). Furthermore, degraded coastlines displayed greater variation in canopy covers among sites than those of healthy coastlines ($_{\text{ANOVA:}}$ sites [coastline], $F_{6, 24} = 9.00$; $P < 0.001$; Student-Newman-Keuls [SNK] tests). Compared to healthy coastlines, the degree of apparent canopy-loss along degraded coastlines ranged from 52 % to 90 %. The pattern displayed by turfed landscapes contrasted that of forests with degraded coastlines having consistently greater covers than healthy coastlines ($_{\text{ANOVA:}}$ $F_{1, 24} = 15.01$; $P = 0.008$). Here again, there was considerable variability among degraded sites compared to the relative uniformity of healthy sites ($_{\text{ANOVA:}}$ $F_{6, 24} = 7.43$; $P < 0.001$; SNK tests). Analysis revealed no patterns between covers of coralline algae (both articulated and encrusting) and foliose red algae between coastlines (Fig. 4.2; ANOVA: $P > 0.05$ for all). Across all sites, concentrations of Dissolved Inorganic Nitrogen (DIN) were negatively correlated with forest cover (Pearson‟s correlation, $r = -0.77$; $P = 0.026$) but positively related to covers of turfed habitat ($r = 0.71$; $P = 0.049$). Water column DIN showed no correlations with covers of foliose red, articulated and coralline algae ($P > 0.05$ for all)

Isotope analysis

Nitrogen isotope values ($\delta^{15}N$) of benthic consumers differed among species (ANOVA: $F_{2, 12} = 7.16$; $P = 0.007$) with those of *Heliocidaris erythrogramma* generally depleted when compared to *Haliotis rubra* and *Turbo torquatus* (Fig. 4.3; Table 4.1). There were no corresponding differences in carbon isotope values ($\delta^{13}C$) among species (ANOVA: $F_{2, 12} = 3.19$; $P = 0.077$). Comparing $\delta^{15}N$ values of individual species between coastline types revealed no significant variation because of the large differences among sites within coastline type (Appendix B, Table S3). $\delta^{13}C$ values of *H. rubra* were generally enriched along degraded coastlines when compared to healthy coastlines, a trend not seen for *H. erythrogramma* and *T. torquatus*, again as a result of the considerable variation among sites (Table S3).

Tissue % N varied between the three consumer species with *H. erythrogramma* having significantly lower values than *H. rubra* and *T. torquatus* (ANOVA: $F_{2, 12} = 15.06$; $P = 0.001$). The mean tissue nitrogen content (% N) of *H. rubra* and *T. torquatus* from healthy coastlines was greater than that from degraded coastlines (Table 4.1; Table S3). No similar pattern was evident for *H. erythrogramma*.

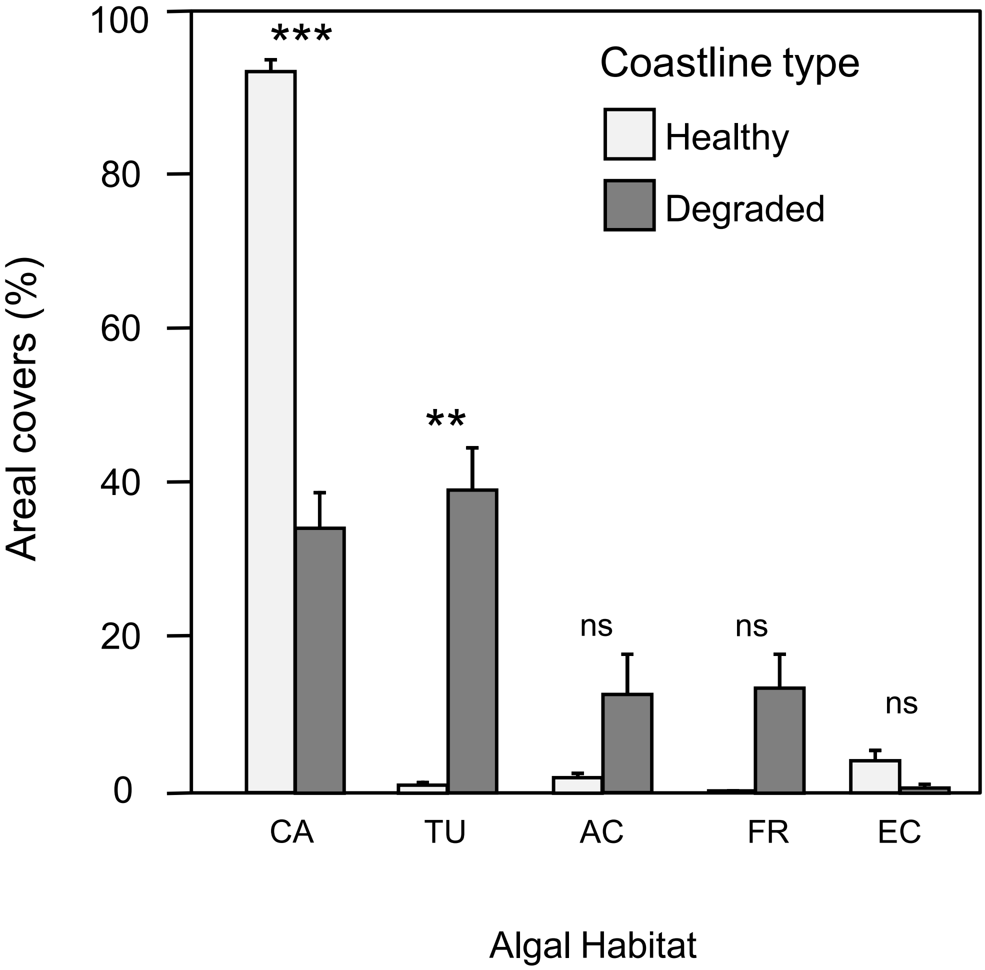

Figure 4.2 Areal covers of algal habitat estimated using replicate 100 m transects (n = 4) at replicate sites (n = 4) nested within coastline type. CA = canopy-forming algae, TU = turf-forming algae, AC = articulate coralline algae, FR = foliose red algae, and EC = encrusting coralline algae. Values are mean ± standard error. Significance for coastline effect is denoted as, ns = not significant ** = $P < 0.01$; *** = $P < 0.001$.

Carbon isotope values ($\delta^{13}C$) of algal producers differed among taxa (Fig. 4.3; Table 4.1; ANOVA: $F_{4,110} = 32.35$; $P < 0.001$; Student-Newman-Keuls [SNK] tests: FR < TU = AC = MA < EC, see Fig 4.2 for codes). No corresponding variation was apparent for nitrogen isotope $\delta^{15}N$ values (ANOVA: $F_{4,110} = 1.54$; $P = 0.196$). In general, the most representative genera of red foliose algae sampled (i.e., *Plocamium* spp.) displayed the most depleted $\delta^{13}C$ values whereas encrusting corallines (*Sporolithon* spp.) were the most enriched (Fig. 4.3). Isotope values of individual algal producers ($\delta^{13}C$ and $\delta^{15}N$) did not vary among coastline types but displayed considerable variability among sites within coastlines (Appendix B; Table S3).

Across coastlines, the tissue nitrogen content (N %) of algal turf was significantly less than all other algal food categories (ANOVA: $F_{4,110} = 10.12$; $P < 0.001$; SNK-tests: TU < AC = EC = MA = FR). Foliose red algae was the only algal group to display significant variation in N % between coastline types (degraded coasts > healthy coasts), although the large variation among sites for articulated and encrusting coralline algae probably masked a similar main effect for these taxa (Table S3). Macroalgae and turfs displayed no variation in N % values among sites or between coastline types.

Our proxy for ambient food quality (*Fq*) revealed greater values (i.e., nutritionally poorer) along degraded coastlines (mean ± SE: 22.4 ± 1.0) than it did for healthy coastlines (mean ± SE: 15.9 ± 1.1; ANOVA: $F_{1,30} = 40.04$; $P = 0.001$). There were strong correlations between the tissue % N values of canopy-forming macroalgae and the $\delta^{15}N$ values of all three consumers (Pearson's correlations, $r = 0.82$, 0.63 & 0.96; respectively for *H. rubra*, *H. erythrogramma* and *T. torquatus*, $P < 0.05$ for all). There was also a positive, although weaker relationship between tissue % N for articulated coralline algae and $\delta^{15}N$ values of *H. rubra* ($r = 0.80$; $P = 0.02$).

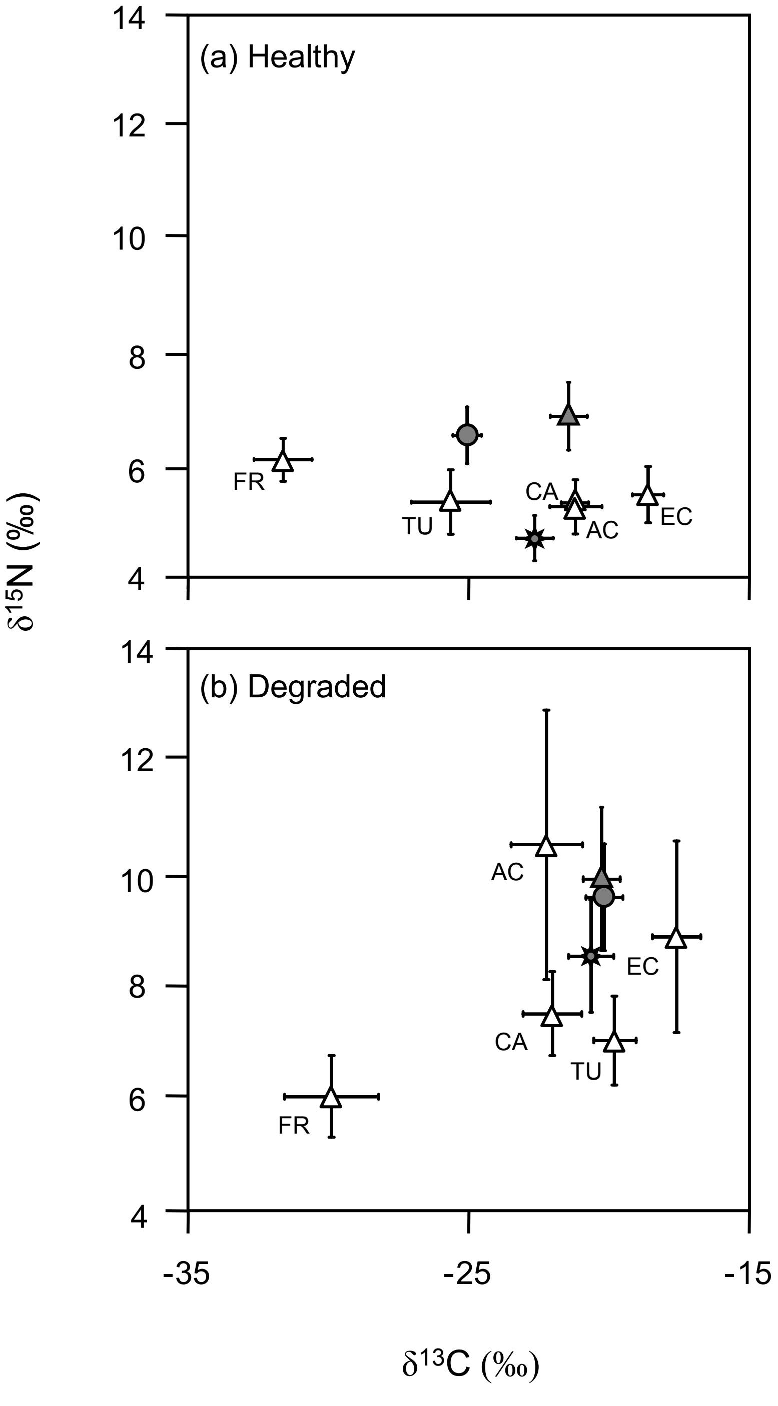

Figure 4.3 Two-element stable isotope plots giving tissue values for algal producers (△) and herbivorous consumers across (a) healthy and (b) degraded coastlines. AC = articulate coralline algae, EC = encrusting coralline algae, TU = turfs, CA = Canopy-forming macroalgae, FR = foliose red algae; and herbivores (pre-correction); *Haliotis rubra* (●), *Heliocidaris erythrogramma* (✸) and *Turbo torquatus* (▲). Data are means derived from (*n* = 12) samples per catchment type ± standard error (for producers only).

Table 4.1 Mean (± SE) stable isotope ($\delta^{15}N$ and $\delta^{13}C$) and % N values for invertebrate herbivore and algal producer tissue collected from degraded and healthy coasts (*n* = 3, replicate samples from each of four replicate sites within coastline type).

Sample	**Healthy**			**Degraded**		
	$\delta^{15}N$ ‰	**$\delta^{13}C$ ‰**	**% N**	**$\delta^{15}N$ ‰**	**$\delta^{13}C$ ‰**	**% N**
Invertebrate herbivore						
Haliotis rubra	6.6 ± 0.3	-25.3 ± 0.5	15.9 ± 0.6	9.6 ± 0.8	-20.2 ± 0.6	11.9 ± 0.6
Heliocidaris erythrogramma	4.8 ± 0.3	-22.8 ± 0.6	6.7 ± 0.5	8.3 ± 1.0	-20.4 ± 0.7	5.3 ± 0.5
Turbo torquatus	7.0 ± 0.5	-21.7 ± 0.9	17.5 ± 1.4	9.7 ± 1.2	-20.3 ± 0.6	13.5 ± 0.8
Algal producer						
Articulated corallines	5.2 ± 0.5	-21.3 ± 0.9	2.6 ± 0.4	10.4 ± 2.4	-22.2 ± 1.3	4.3 ± 0.4
Encrusting corallines	5.4 ± 0.5	-18.7 ± 0.6	3.6 ± 0.5	8.8 ± 1.7	-17.6 ± 0.9	2.7 ± 0.5
Canopy-forming algae	5.3 ± 0.4	-21.3 ± 0.5	2.0 ± 0.2	7.4 ± 0.7	-22.0 ± 1.0	2.2 ± 0.2
Red foliose algae	6.1 ± 0.4	-31.7 ± 1.0	4.6 ± 0.3	5.9 ± 0.7	-29.8 ± 1.7	2.4 ± 0.3
Turf-forming algae	5.3 ± 0.6	-25.7 ± 1.4	1.9 ± 0.3	6.9 ± 0.8	-19.8 ± 0.8	1.4 ± 0.3

Shifts in consumer diet

Dietary modelling revealed variation in the relative importance of algal food sources between consumer species and coastline types (Fig. 4.4). The relative contribution of turfs to the diet of the all three consumers was consistently greater along degraded coastlines when compared to healthy coastlines (Table 4.2). Contrastingly, there was a significant decrease in the relative contribution of articulated coralline algae to the diet of *H. rubra* (i.e., 60 % less along degraded coastlines; $_{\text{ANOVA:}}$ $F_{1,\ 72} = 14.65$; $P = 0.009$) along with a similar, albeit marginally non-significant difference for the other two consumer species (owing to large variation among sites within coastline types). Similarly, contributions of foliose red algae to the diet of *H. rubra* appeared comparatively less along degraded, when compared to healthy coasts, but this was marginally non-significant at α 0.05. The relative dietary contributions of canopy-forming and encrusting coralline algae did not differ between healthy and degraded coastlines for any of the consumer species.

In general, coralline algae (encrusting and articulated) dominated the diet of *Heliocidaris erythrogramma* and *Turbo torquatus* along healthy coastlines, with lesser contributions from, turfs, foliose and canopy-forming algae (Fig. 4.4b & c). This pattern contrasted that of degraded coasts, where turfs were one of the principle dietary components at the apparent expense of articulated coralline algae. Indeed, dietary contributions of turf were negatively correlated with those of articulated coralline algae for all species of consumer (Pearson‟s correlation: $P < 0.05$ for all). The diet of *Haliotis rubra* along healthy coastlines differed somewhat to the other herbivores (Fig. 4.4a), being dominated by articulated corallines and foliose reds, with lesser and equal contributions of turfs, canopy-forming and encrusting coralline algae. Again, this pattern contrasted that observed for degraded coasts, where turfs became an important dietary component and the contribution of articulated corallines and foliose red algae was comparatively less.

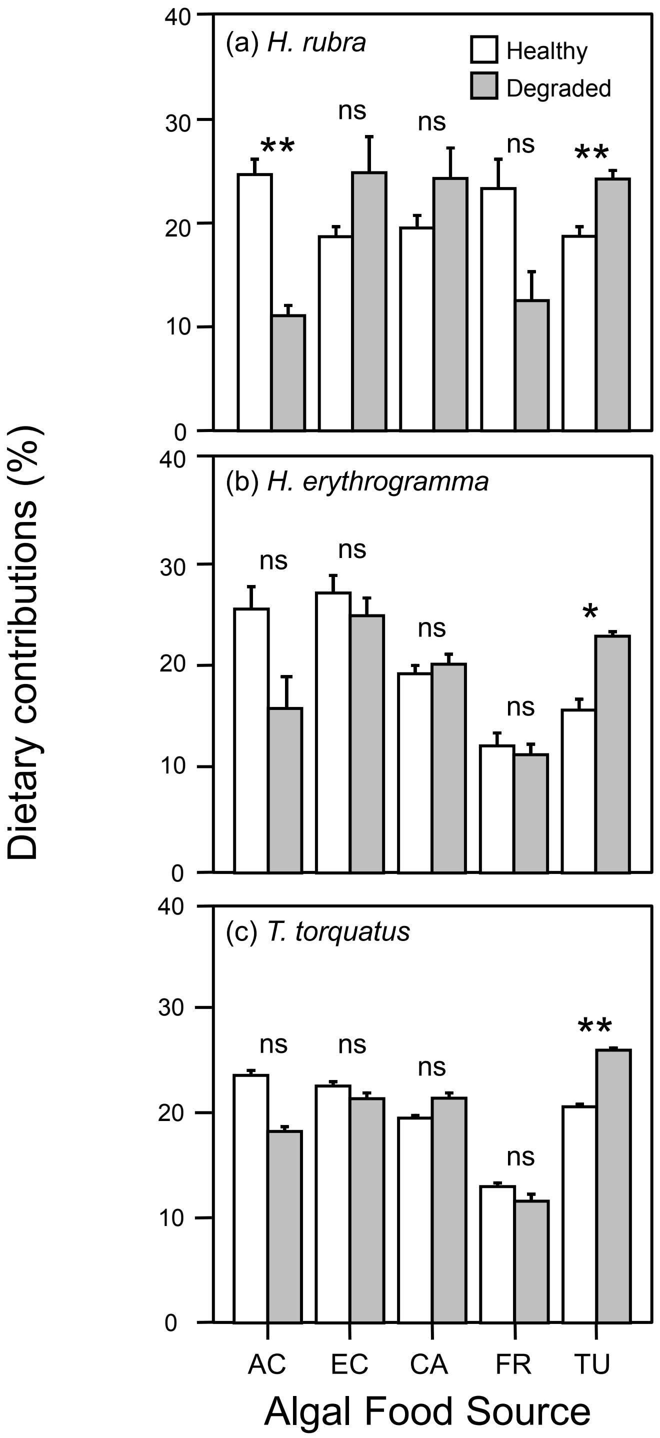

Figure 4.4 Relative dietary contributions of algal food sources to the nutrition of (a) *Haliotis rubra*, (b) *Heliocidaris erythrogramma*, and (c) *Turbo torquatus* sampled from replicate healthy and degraded coastlines as determined using the Bayesian mixing model siar. AC = articulate coralline algae, EC = encrusting coralline algae, CA = canopy-forming algae, FR = foliose red algae, and TU = turfs. Values are percentage means for dietary contribution (+ SE). Significance for coastline effect is denoted as, ns = not significant * = $P < 0.05$; ** = $P < 0.01$.

Table 4.2 Results of ANOVAs testing for differences in the relative contribution of turfs to the diet of (a) *Haliotis rubra* (b) *Heliocidaris erythrogramma*, and (c) *Turbo torquatus* sampled from replicate sites ($n = 4$) within healthy and degraded coastlines.

Treatment	*df*	MS	*F*
(a) *H. rubra*			
Coastline	1	4245.67	14.65 **
Site (coastline)	6	289.76	2130.60 ***
Residual	72		
(b) *H. erythrogramma*			
Coastline	1	1437.36	6.10 *
Site (coastline)	6	235.57	172.64 ***
Residual	72		
(c) *T. torquatus*			
Coastline	1	394.72	21.16 **
Site (coastline)	6	18.66	111.16 ***
Residual	72		

Notes: Data were ln ($x + 1$) transformed to meet the assumptions of homogeneity of variance. SNK (Student-Newman-Keuls) tests on „coastline‟ term for all three consumer species showed that „degraded‟ > „healthy‟. Significance is denoted as: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

The potential for areal covers of turfed habitat to predict the relative dietary contributions of turfs differed between herbivores (Fig. 4.5). Whilst an effect of coastline type was evident for all three species (ANCOVA: „healthy‟ cf. „degraded‟, $P > 0.05$ for all), testing for homogeneity of slopes, revealed no heterogeneity across coastline types (ANCOVA: on „covers × coastline‟ interaction term: $P > 0.05$ for all species). Subsequent pooling of values across coastline types, revealed positive relationships between turf covers and diet, for *Haliotis rubra* and *Turbo torquatus* (Fig. 4.5a & c; Pearson‟s correlation, $r = 0.71$; $P = 0.049$ & $r = 0.91$; $P = 0.002$; respectively). Despite a similar and apparently positive trend for *Heliocidaris erythrogramma*, correlations between turf covers and diet were marginally non-significant (Fig 4.5b; $r = 0.65$; $P = 0.081$).

Densities of benthic herbivores differed between coastline types and among sites (Fig. 4.6; Table 4.3). *Heliocidaris erythrogramma* occurred in greater abundance on degraded coastlines compared to healthy coastlines, whereas an opposite trend was apparent for *Haliotis rubra* and *Turbo torquatus*. Further, the contribution of turf to consumer diet represented a good predictor of consumer densities, albeit in contrasting directions (Fig. 4.7). Testing for homogeneity of slopes describing the relationship between diet and densities revealed no heterogeneity between coastline types (ANCOVA: „coastline × diet‟, interaction term $P > 0.05$ for all species). Pooling data, showed that densities of *T. torquatus* were negatively related to the dietary contribution of turf (Fig. 4.7c; Pearson‟s correlation, $r = -0.92$; $P = 0.001$). *H. rubra* displayed a similar negative trend, however, correlations were non-significant at a critical value of $\alpha = 0.05$ (Fig. 4.7a; $r = -0.52$; $P = 0.182$). These trends contrasted with the significant positive relationship between the contribution of turf to diet and densities of *H. erythrogramma* (Fig. 4.7b; $r = 0.71$; $P = 0.047$).

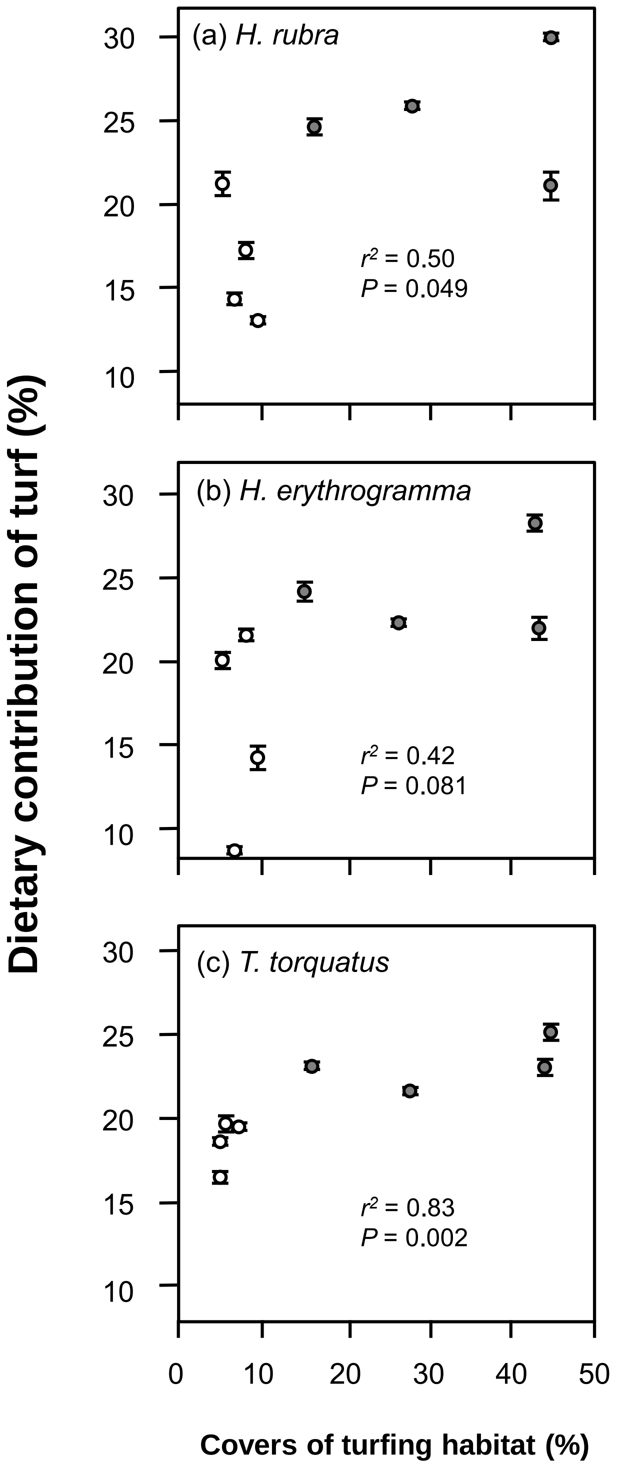

Figure 4.5 Relationship between areal covers of turfed habitat and the relative contribution of turfs to the diet of (a) *Haliotis rubra*, (b) *Heliocidaris erythrogramma* and (c) *Turbo torquatus* across replicate sites (*n* = 8) spanning 700 kms of southern Australian coastline. Coastline types: healthy (○) and degraded (●). X-axis values are arcsine percent-transformed averages of turf cover derived from (*n* = 4) 100 m transects. Y-axis values are averages (± SE) of the dietary contributions of turf derived from isotope modelling.

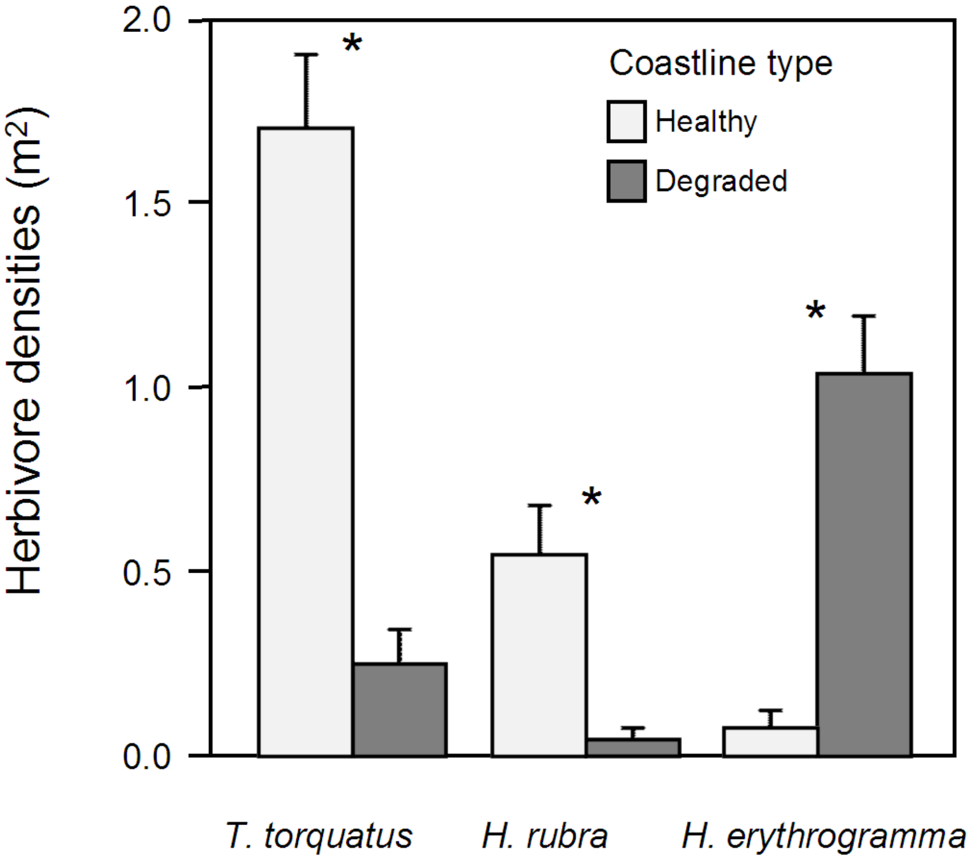

Figure 4.6 Densities of herbivorous consumers (*Turbo torquatus*, *Haliotis rubra* and *Heliocidaris erythrogramma*) estimated using replicate 1 × 5 m belt transects (n = 8) at replicate sites (n = 4) nested within coastline type. Values are mean + standard error. Significance for coastline effect is denoted as, * = $P < 0.05$.

Table 4.3 Results of ANOVA testing for differences in the densities of (a) *Heliocidaris erythrogramma*; (b) *Haliotis rubra* and (c) *Turbo torquatus* sampled using 1 × 5 m ($n = 8$) transects at replicate sites ($n = 4$) nested within healthy and degraded coastlines.

Treatment	*df*	MS	*F*
(a) *H. erythrogramma*			
Coastline	1	14.63	8.89 *
Site (coastline)	6	1.65	5.73 ***
Residual	56		
(b) *H. rubra*			
Coastline	1	4.05	6.37 *
Site (coastline)	6	0.64	2.42 *
Residual	56		
(c) *T. torquatus*			
Coastline	1	33.64	10.56 *
Site (coastline)	6	3.18	6.07 ***
Residual	56		

Notes: Data were ln ($x + 1$) transformed to meet the assumptions of homogeneity of variance. Significance is denoted as: * = $P < 0.05$; *** = $P < 0.001$.

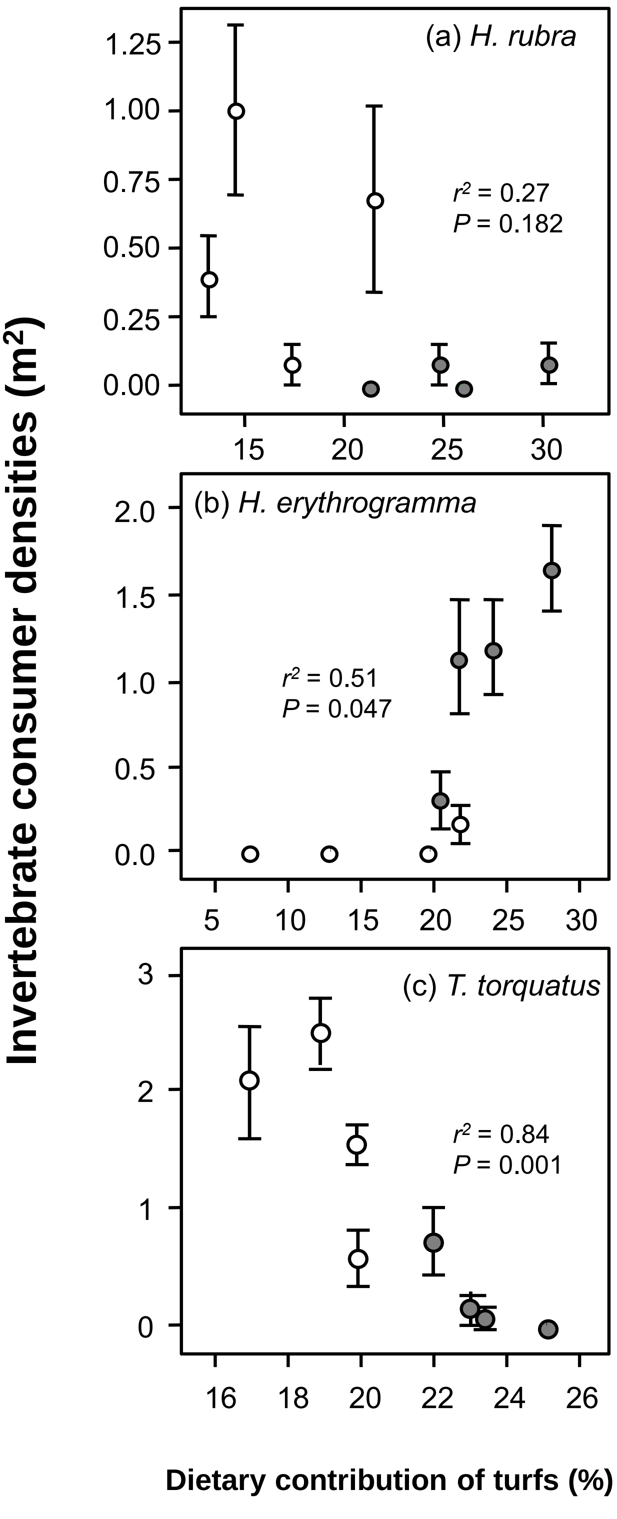

Figure 4.7 Relationships between the relative dietary contribution of turfs and densities for (a) *Haliotis rubra* (b) *Heliocidaris erythrogramma* and (c) *Turbo torquatus* determined from replicate sites ($n = 4$) nested within coastline types: healthy (○) and degraded (●). X-axis values are arcsine percent-transformed averages of turf cover derived from ($n = 4$) 100 m transects. Y-axis values are mean $\ln(x+1)$ transformed herbivore densities (± SE) estimated from replicate 1 × 5 m belt transects ($n = 8$).

4.4 Discussion

Human disturbance can alter the food web dynamics of nearshore ecosystems (Estes & Duggins 1995, Pinnegar et al. 2000, Benedetti-Cecchi et al. 2001). We show that the replacement of subtidal forests by turfed landscapes may have marked consequences for the diet of herbivorous consumers along temperate coasts. We base our evidence on the relationship between covers of turfed habitat and the relative contribution of turf-forming algae to the diet of common benthic invertebrates. Whilst we acknowledge that such dietary shifts ultimately reflect habitat associations, our proxy for ambient food quality (i.e., proportional covers of algal producers as a function of their C:N ratios) suggests that changes in the relative cover of algal species may have additional implications for the nutritional value of autochthonous food resources. Replacement of high value canopy-forming, encrusting and foliose algal species (high % N) by low value turfs (low % N) may contribute to the observed variation in consumer abundance seen between coastlines dominated by turfed verses canopy-forming landscapes.

Stable isotope values

Stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) of both algae and invertebrates were within the range of those reported elsewhere in southern Australia (Hyndes & Lavery 2005, Vanderklift et al. 2006, Guest et al. 2008). Whilst the variability in isotope values among sites obscured significant affects of coastline for most taxa, there was a general enrichment in isotope values (principally, $\delta^{15}N$) for both producers and consumers collected from degraded sites. Enrichment in producer and consumer $\delta^{15}N$ values is often attributed to long term exposure to, and subsequent uptake of sewage-derived nitrogen (Costanzo et al. 2001, Pitt et al. 2009 Chapter 2). As consumers graze on enriched algal food sources they incorporate the enriched $\delta^{15}N$ signature into their tissue and thereby transfer it to successive trophic levels (Cabana & Rasmussen 1996, Carlier et al. 2008). Whilst the degree of enrichment seen in our study was moderate and quite variable (cf., Gartner et al. 2002; Chapter 2) we view this as evidence for the incorporation of human-derived nitrogen into higher trophic levels within rocky reef food webs. Our data thus confers with previous studies that highlight the pervasiveness of wastewater inputs (via terrestrial subsidies) within nearshore ecosystems (e.g., estuaries, McClelland et al. 1997, and sandy beach systems, Schlacher & Connolly 2009).

Shifts in consumer diet

The loss of subtidal macrophyte communities can affect invertebrate assemblages by reducing habitat complexity (i.e., Connolly 1995, Ettinger-Epstein & Kingsford 2008) and by modifying the availability and or quality of food resources (e.g., Pyke et al. 1977, White 1984, Spalinger & Hobbs 1992). Regime shifts that drive changes in the resource-base of rocky reef systems are likely to be reflected by changes in the diet of resident consumers (Steinarsdottir et al. 2009). Indeed, our data demonstrates that turfs comprise a greater component of consumer diet along degraded coastlines where turfed landscapes have replaced extensive areas of macroalgal forest (Connell et al. 2008). The observation that producer isotope values ($\delta^{13}C$ and $\delta^{15}N$) did not vary between coastlines (or varied only slightly) lends weight to the model that habitat configuration *per se* does indeed contribute to variation in consumer diet, and that the patterns derived from dietary modelling are real and not just an artefact of variation in isotope values. The failure to detect any variation in the dietary contribution of canopy-forming algae is a likely consequence of the large overall covers of forest even at degraded locations (i.e., never less than 35 %), variation in estimated contributions among sites, and the fact that kelps often represent an allochthonous resource, consumed as drift rather than via active grazing (Vanderklift & Kendrick 2005). Another point of note was the apparent (though not uniformly significant) decrease in the relative contribution of articulated corallines to the diet of consumers along degraded coastlines. Although coralline algae are unlikely to constitute a crucial nutritional resource for benthic invertebrates (but see, Clarkson & Shepherd 1985), their often facilitative interactions with canopies (i.e., canopies can prevent overgrowth by turfs; Irving & Connell 2006b) suggest they are likely to occur and be consumed to a greater degree (incidentally through grazing) wherever forested landscapes dominate. Whilst removal of coralline species from diet models may alter overall dietary inferences, this is unlikely to obscure contrasts between the relative importance of turfs between healthy and degraded coastlines.

Our correlations between consumer diet and environmental data suggest that regime shifts can alter the food resource-base of generalist herbivores, a phenomenon that is seldom recognised because of a preoccupation with habitat change *per se*. As with all isotope mixing models, the potential for Bayesian approaches to accurately infer dietary associations requires correct assignation of discrimination correction values between a consumer and its food source (Caut et al. 2008, 2009). This can often be confounded by variation in the magnitude of $\delta^{15}N$ discrimination between an animal and its diet, owing to differences in the nitrogen content of potential food sources (review, Vanderklift & Ponsard 2003). We revealed a significant correlation between tissue % N of canopy-forming algae and the $\delta^{15}N$ values of all three species of consumer. We conclude from this that trophic fractionation may be greater along degraded coastlines because of the high tissue nitrogen content of algal food sources, driven by terrestrial nitrogen inputs (Chapter 2). This may explain why marginally greater discrimination correction values were required for modelling of consumer diets along degraded coastlines. Whilst we acknowledge the limitations of mixing models as a means of inferring exact trophic relationships, our comparison serves to show relative differences in consumer diet between coastlines as a function of habitat cover and associated food availability.

Consequences of habitat alteration

Changes to ambient food quality associated with regime shifts may have nutritional implications for invertebrate consumers (Hemmi & Jormalainen 2002). The work presented here is novel and suggests that shifts from forested to turfed landscapes may represent a reduction in the nitrogen content of *in situ* food resources. Compared to coralline and canopy-forming algal species turfs had comparatively lower tissue nitrogen content (% N), which meant that our proxy for ambient food quality within regime shifted landscapes was less than that of forested landscapes. Whilst mobile consumers are unlikely to be affected by such nutritional constraints (i.e., they can move to preferable habitats), this factor is likely to have consequences for sessile or slow-moving herbivores (Connolly et al. 2005a, Steinarsdottir et al. 2009). Our data show that tissue % N values of both *Haliotis rubra* and *Turbo torquatus* were greater along healthy coastlines than degraded coastlines where their dietary reliance on turfs was greater. Previous work suggests that invertebrate herbivores require food with a

C:N ratio of no more than 17:1 in order to sustain growth and maintain routine metabolic function (Hatcher 1994). Our data suggests that the combined nutritional value of available food resources within degraded landscapes (~ 22:1) exceeds this threshold and may therefore have implications for growth, reproduction and survival of resident consumers (Cruz-Rivera & Hay 2000a). Although we do not speculate on aspects of food selectivity or palatability, our data suggests that the replacement of forested communities by turfed landscapes may represent a nutritional stress to consumers (Jennings et al. 1997).

The response of herbivores to nutrient limitation can be varied and include changes to metabolism, altered rates of consumption and behavioural adaptation (Cruz-Rivera & Hay 2000a, Frost et al. 2006). Variation in the ability of consumers to contend with nutritional stress is thus likely to have marked consequences for relative species abundance (Pyke et al. 1977, Edgar & Aoki 1993, Lyons & Scheibling 2007). We showed that densities of *Haliotis rubra* and *Turbo torquatus* were negatively associated with dietary contributions of turf. This may correspond to the ability of these taxa to contend with the conditions (both nutritionally and structurally) that characterise degraded subtidal landscapes (Duffy & Hay 1991). When faced with shifts to comparatively simple habitats (e.g., via storm events that denude canopies; Connell 2007a) these relatively mobile benthic consumers (Shepherd 1973, Ettinger-Epstein & Kingsford 2008) are likely to move to adjacent areas that provide improved food and shelter (Kareiva 1982, Pyke 1984). This can result in considerable variation in abundance among discrete habitat patches over short time scales (i.e., weeks – months; Benedetti-Cecchi et al. 2001). There is also evidence that the distances over which these herbivores are able to forage in search of food (up to 30 meters for *T. torquatus*; Ettinger-Epstein & Kingsford 2008) can exceed the largest patches of turfed habitat along urbanised coastlines (Chapter 2), and it is therefore not improbable that they would emigrate from a localised patch of degraded habitat.

Whilst some species may be negatively affected by regime shifts, others may be able to increase in relative abundance by capitalising on exclusive access to a nutrient-poor food resource (Higashi et al. 1992, Gamito & Furtado 2009). We show that unlike gastropods, densities of *Heliocidaris erythrogramma* were positively related to turfs both as a habitat and food source. Whilst we acknowledge that urchin densities are often negatively correlated with certain gastropod taxa, in particular abalone (Andrew & Underwood 1992) the scale over which our surveys were done (~ 40 m^2) should account for this „small-scale spatial segregation" (see, Fowler-Walker & Connell 2002, Fowler-Walker et al. 2005) and we suggest that the overall patterns of abundance are most likely related to habitat suitability. The comparatively greater abundances of *H. erythrogramma* along degraded coastlines suggest that this species and perhaps urchins in general may be better able to contend with a nutrient-poor resource-base. In addition, urchins have been shown to derive a substantial proportion of their nutrition from drift algae (Minor & Scheibling 1997, Vanderklift & Kendrick 2005), which may contribute to their persistence within degraded habitats. Although the nitrogen content of drift algae has been shown to be less than that of live kelp (Basch & Tegner 2007), drifting food resources as suggested by Vanderklift and Wernberg (2008) may represent a spatial subsidy and one that supplements the poor nutritional quality of turfs.

Whilst behavioural and metabolic traits may influence invertebrate assemblages over the short term, patterns of recruitment and reproduction determine community structure over generational time-scales (Keough & Downes 1982, Connolly et al. 2001, Menge et al. 2003). The fecundity, reproductive effort and growth of benthic herbivores are strongly influenced by food quantity and quality (Minor & Scheibling 1997, Kawamura et al. 1998). Improvements to food quality have been shown to increase reproductive output, which may in turn lead to an accelerated rate of population growth (Hemmi & Jormalainen 2002). Contrastingly, decreased herbivore density may be the result of declines in reproductive output resulting from poor quality food resources and/or reduced larval settlement owing to the absence of preferential habitat queues (Elkin & Marshall 2007, Hayakawa et al. 2008, Huggett et al. 2008). Overall, we suggest that the observed variation the relative densities of urchins and gastropods is likely to be the combined result of short term behavioural adaptations (movement from areas of canopy-loss) and longer term patterns of recruitment and larval supply driven by changes to the resource base of nearshore rocky systems.

Changes to the relative composition and abundance of herbivores can have consequences for the structure of subtidal habitats (Andrew 1993) and on trophic cascades believed to regulate the potential for nutrient driven regime shifts (Connell 2007b). Alteration of invertebrate community structure, driven by shifts in food availability, may initiate positive feedbacks that can have implications for the stability (and resilience) of remaining forested habitats (Steneck et al. 2002). Changes to the food resource base of regime-shifted landscapes may initiate intensification of grazing activities, which can have profound effects for subtidal forests (Mann 1977, Harrold & Reed 1985, Watanabe & Harrold 1991). Such compensatory feeding has also been shown to enable sedentary species to circumvent the effects of low nutritional quality and thereby minimise movement among host habitats (Cruz-Rivera & Hay 2000b). The ability of urchins to switch from a drift feeding to benthic feeding mode (Vanderklift et al. 2009) may have implications for the relative importance of top-down regulation of forest communities.

Conclusions

Loss of ecological function is a recognised consequence of human impacts within nearshore ecosystems (review, Hooper et al. 2005). Whilst it is becoming increasingly clear that human disturbance can cause shifts from structurally complex plant communities to simpler and nutritionally depauperate ones (Connell et al. 2008; Chapters 2 & 3), less attention has been given to the consequences of such shifts on higher trophic levels (i.e., animal consumers). Despite an appeal for improved awareness of the nutritional links between consumers and their food resources within marine systems (Cruz-Rivera & Hay 2000a), there has been little advancement in our understanding of the trophic consequences of diet shifts or nutritional compensation for benthic consumers. The apparent links between habitat structure, ambient food quality, herbivore diet and relative densities presented in this study represent new insights into consequences of regime shifts for rocky-reef systems. Given the central importance of subtidal landscapes as both a source of nutrition and refuge to countless animal consumers, it is vital that we understand the causes and effects of human-induced ecological change. Recognising how shifts in food quality can affect consumers may aid understanding of the consequences of habitat-loss for numerous food webs and on the provision of ecosystem services to human populations.

“Conservation is the foresighted utilization, preservation and/or renewal of forests, waters, lands and minerals, for the greatest good of the greatest number for the longest time.” Gifford Pinchot

CHAPTER FIVE

CHAPTER FIVE:

Recovering subtidal forests in human-dominated landscapes

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Recovering subtidal forests in human-dominated landscapes

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Statement of Authorship

I developed the experimental design with the help of Sean D. Connell‟s extensive knowledge of historical patterns of habitat-loss along the Adelaide metropolitan coastline. Sean and I obtained funding for the project. I conducted all experimental components of the research, processed and analysed results and wrote the paper.

I certify that the statement of contribution is accurate

Daniel Gorman (Candidate)

Signed *Date* 10/12/09

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis

Associate Professor Sean D. Connell

Signed *Date* 10/12/09

Preamble

Chapter 5 investigates the relationship between turfs and sediments, as mediated by poor water quality, and examines their synergistic effects on forest recovery. The chapter compares canopy recovery post disturbance (experimental) between degraded and healthy reefs along the Adelaide metropolitan coastline. The chapter examines the potential for regime-shifted landscapes to be rehabilitated through the active removal of turfs and associated sediments. The chapter is a reproduction of a co-authored article published in *The Journal of Applied Ecology* and is written in plural. The article is included with the permission of the British Ecological Society and can be cited as:

Gorman, D. & Connell, S.D. (2009) Recovering subtidal forests in human-dominated landscapes. *Journal of Applied Ecology* 46 1258-1265

5.1 Introduction

The surprising failure of ecosystems to recover from human disturbance has galvanised ecologists around theories relating to restoration and conservation (Hobbs & Norton 1996, Dobson et al. 1997). Restoration of previous states or conservation of current conditions requires knowledge of the mechanisms that hasten or resist recovery, especially those that follow disturbance of sufficient size that allows alternate habitats to colonise. The failure of systems to recover can lead to regime shifts whereby early-successional and fast-growing assemblages may become permanent (Duarte et al. 2009; Chapter 3). Knowledge of the interactions between human induced stressors and natural processes are needed for the development of models that more accurately predict conditions whereby humans can transform acute disturbances into chronic stress (Nystrom et al. 2000) and identify the circumstances in which regime shifts can be reversed.

On temperate coasts, there is concern about the permanent replacement of perennial canopy-forming algae (i.e., structurally complex and highly productive habitats), with opportunistic taxa such as filamentous turf-forming algae (i.e., comparatively simple habitats; see review, Krause-Jensen et al. 2008). The replacement of canopy-forming „forests‟ with „turfing‟ landscapes, relates to the physiology of algal opportunists that enable them to persist in human-dominated landscapes (e.g., enriched nutrients; Worm et al. 1999). These types of regime shift are of global concern, particularly where the nutrient concentrations of historically oligotrophic coastal waters have been elevated by subsidies of nutrients from activities that relate to intensified land use (e.g., Australia, Connell et al. 2008, Baltic Sea, Österblom et al. 2007, North Sea, Eriksson et al. 2002 and Mediterranean Sea, Mangialajo et al. 2008). Whilst the drivers and consequences of anthropogenic forcing have been widely documented (e.g., eutrophication and overfishing; previous citations), models that account for the mechanisms that hasten or resist change are notoriously difficult to clarify (Scheffer et al. 2001).

Models that account for changes in the ability of aquatic systems to respond to disturbance (e.g., „adaptive capacity‟; Gunderson 2000) and its consequences for habitat degradation (e.g., loss of forest canopies), generally recognise modified water quality (i.e., increasing nutrient and sediment loads) and biotic interactions (i.e., increased competition) as key drivers of change (reviews, Steneck et al. 2004, Connell 2007b, Krause-Jensen et al. 2008). These models also acknowledge the mediating influence of biogeography on the relative extent to which eutrophication and overfishing can alter the abundance of species that facilitate or inhibit canopy recruitment (Connell & Irving 2008). Nevertheless, a quite general model in subtidal ecology centres on the important influence of water quality on the maintenance of interactions that facilitate forest recovery.

Models of kelp forest function recognise these communities as dynamic systems that are constantly reshaped by disturbance-recovery cycles (Dayton et al. 1992). The phenomenon whereby forests fail to recover along increasingly human-dominated coastlines relates to coastal activities that modify environmental conditions that facilitate the persistence of turfs which inhibit canopy recruitment (review, Airoldi 2003). In refining this model, current research shows that turfs are normally ephemeral, but are able to persist under conditions (i.e., experimental) and locations (i.e., urban) with sustained levels of enriched nutrients (Chapters 2 and 3). Whilst the ability of turfs and their associated sediments to inhibit the recruitment of canopy formers has been demonstrated (Kennelly 1987a), there is still no quantitative evidence that the removal of turfs can result in increased rates of canopy recovery. In the absence of this evidence, models that seek to understand the processes of canopy facilitation and inhibition, as mediated by water quality tend to be elusive, and the potential for future restoration efforts remain uncertain. The need for this information is particularly urgent for those managing landscapes in which propagule supply is likely to decline with continuing declines in canopy cover; and thereby further reduce rates of forest recovery.

Here, we redress some of these information gaps by examining the processes of canopy recovery and inhabitation using a two-step approach. First, we tested the hypothesis that rates of canopy recovery are indeed substantially less in turf-dominated habitats (hereafter „turfed landscapes‟) relative to canopy-dominated landscapes (hereafter „forested landscapes‟). Second, we tested the hypothesis that canopy recovery would be enhanced within turfed landscapes if turfs and associated sediments were removed from the spaces between remnant forests.

5.2 Methods

Location and timing of study

This study was done in the Gulf St Vincent (Fig. 5.1, South Australia) for which Connell et al. (2008) provide a historical description of urbanisation and associated loss of forests. Briefly, this coast was colonised by Europeans in 1836, and as coastal urbanisation intensified from the early 1980‟s, water quality declined along with a reduction in forest canopy covers (up to 70 %). Canopy covers were originally similar to non-urbanised coast across the broader region (i.e., ~ 100 km) and the broader biogeographic province (i.e., Flindersia; ~ 2000 km). Whilst much of the original areal covers of forest have been replaced by turfed habitat, small remnants of forests are common. Turfs are made up of taxonomically diverse, but morphologically similar groups of filamentous algae (e.g., *Feldmannia* spp., see Russell & Connell 2007, Roberts & Connell 2008). Our experiments were done on subtidal rock (4 to 10 m depth) at three forested and three degraded sites selected at random along an 18 km stretch of metropolitan coast based on previous habitat mapping (see, Connell et al. 2008). Forested landscapes were characterised by uninterrupted stands of canopy-forming algae reaching ~ 40 m diameter and commonly interspersed by small gaps of 1-3 m diameter. Turfed landscapes were characterised by carpets of uninterrupted turf-forming algae reaching ~ 20 m diameter and commonly punctuated by small remnant forests of 1-12 m diameter (Chapter 2; Fig. 2.3).

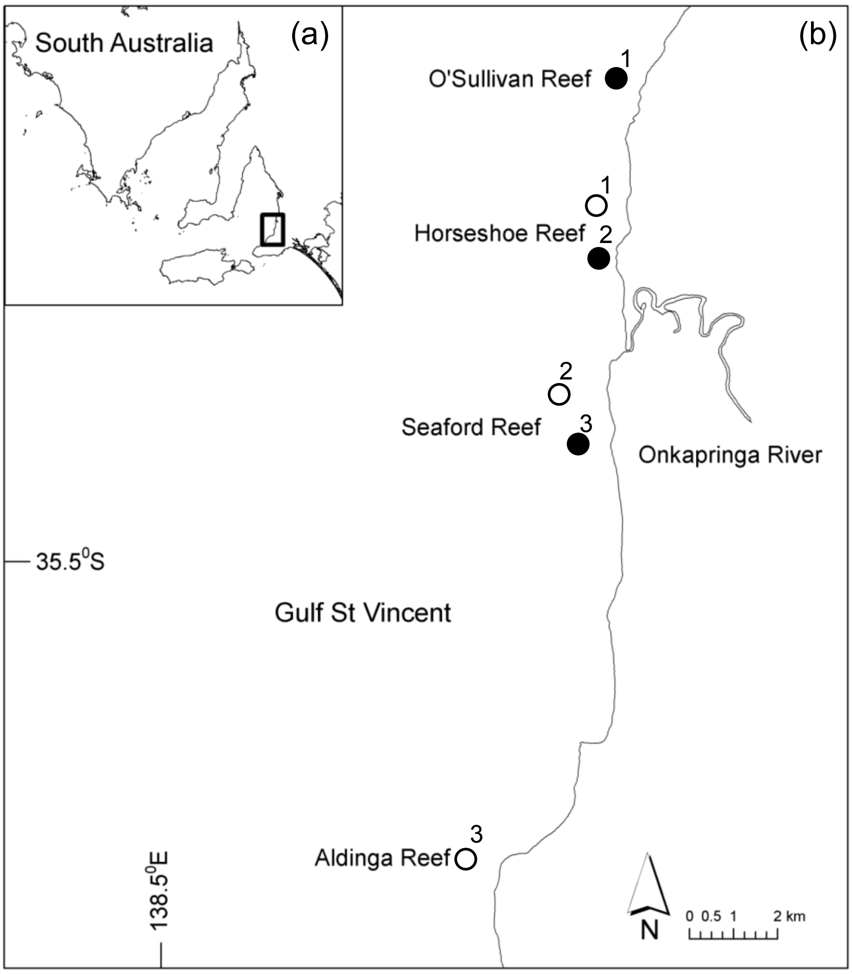

Figure 5.1 Location of experiments within (a) South Australia and (b) replicate landscapes on the Adelaide metropolitan coastline. Open circles = forested landscapes, closed circles = turfed landscapes.

Experiments spanned 12 months (2007 – 2008) and their initiation was timed to coincide with the onset of storm-driven canopy disturbance (Kennelly 1987b) and the winter sporulation period of the most common canopy-forming algal species (i.e., *Ecklonia radiata*, Novaczek 1984, Cystoseiraceae, Hotchkiss 1999 and most Sargassaceae, Womersley 1987).

Landscape-scale variation in canopy recovery

If the novel environmental conditions that characterise turfed landscapes (i.e., increased covers of turf and accumulated sediments) can indeed reduce rates of recovery, we would expect that the re-establishment of canopies would be slower in these habitats than forest landscapes where turf covers are naturally sparse. To evaluate this hypothesis we tested whether canopy recovery in the wake of experimental disturbance would be greater within forested than turfed landscapes. „Recovery" was calculated as the difference in percentage cover of canopy-forming algae between pre-clearance covers (i.e., before) and upon termination of the experiment (i.e., after). The experiment was terminated once the percentage cover of canopy-forming algae within plots did not differ from adjacent un-manipulated canopy plots in forested landscapes. This rule removed the potential influence of seasonal variation in canopy cover on estimates of recovery between landscapes (i.e., ~ 8 months for this first component of study).

Experimental disturbance was produced by clearing canopy-forming algae from replicate circular areas of 1.5 m^2; a size within the range of natural storm-driven canopy-loss (Kennelly 1987b) and which is sufficiently large to allow turfs to colonise free from canopy scour (Melville & Connell 2001, Wernberg & Connell 2008). Replicate experimental plots ($n = 6$) were created at each of three replicate sites nested within forested and turfed landscapes (Fig. 5.1). Within turfed landscapes, canopy clearings were done within remnant patches of forest (~ 5 - 12 m diameter) that had similar canopy covers to canopy-dominated landscapes (ANOVA: $F_{1, 8} = 1.39$; $P = 0.303$). Percentage covers of canopy-forming recruits (i.e., *Cystophora* spp., *Ecklonia radiata*, and *Sargassum* spp.) were quantified within experimental plots after 4 and 8 months using a 1 × 1 m quadrat comprising of 25 random intersects (see, Drummond & Connell 2005).

A characteristic of filamentous turfs is their ability to accumulate large volumes of sediment (Airoldi 2003); a characteristic that inhibits canopy recruitment (Devinny & Volse 1978). We augmented our interpretation of the effects of landscape on canopy recovery by quantifying the temporal evolution of turf covers and sediment accumulation among treatments (i.e., at 0, 4 and 8 months). Turf covers within experimental plots were estimated using (n = 3) replicate 25 × 25 cm quadrats (25 random points method ; Drummond & Connell 2005) that provided an average measure of percentage cover within each plot. Standing weights of accumulated sediment (i.e. net) were estimated by collecting loose sediment within a 10 × 10 cm quadrat using a vacuum. In the laboratory the collected sediment was filtered though Whatman® (27 cm ø) grade 1 qualitative filter papers using distilled water. The filters and retained filtrate were dried to a constant weight (60˚C for ~ 48 h.) and reported as g dry wt · cm^2.

The aim of this experiment was to test for variation in the recovery of canopies within forested and turfed landscapes. Recovery was initially compared using analysis of covariance (ANCOVA); where the main treatment was landscape type; replicate sites were nested within landscape type and turf covers were treated as a covariate. ANCOVA initially tested for heterogeneity of slopes describing the relationship between recovery and turf covers among landscape types. Where no heterogeneity in slopes was evident between forested and turfed landscapes, we were able to test for variation in recovery, after accounting for the effect of turf cover.

Can turf removal facilitate canopy recovery?

We tested the prediction that the removal of turfs and associated sediment from turfed landscapes would facilitate the recovery of forests. At each of the three turfed landscapes (Fig. 5.1) we removed turf and associated sediment from 12 replicate 1 × 1 m plots within large turf-dominated gaps (~ 10 m in diameter) using paint scrapers and wire brushes. We recognise that this procedure may alter the natural rate of forest recruitment which we have not attempted to quantify. Our intention here, was not so much to quantify absolute rates of recruitment among treatments, but to use a procedure that would quantify relative rates of recovery (as per hypothesis), and allow us to assess the applicability of such removal for restoration efforts. These experimental manipulations, as well as untouched controls ($n = 12$), were interspersed at distances < 1 m from adjacent stands of canopy within turf dominated gaps at each site. Percentage covers of canopy-forming recruits (i.e., *Cystophora* spp., *Ecklonia radiata*, and *Sargassum* spp.) were quantified after 12 months using a 1 × 1 m quadrat comprising of 25 random intersects (Drummond & Connell 2005). Recovery was estimated as the difference in percentage cover of canopy-forming algae between pre-clearance covers sampled in remnant forests (i.e., before) and the termination of the experiment (i.e., after). The experiment was terminated after approximately 12 months (April 2008), once the percentage cover of canopy-forming algae within turf removal plots did not differ from adjacent forest (~ 5 - 8 m diameter) again, to control for any potential influence of seasonal variation. ANOVA was used to compare canopy recovery among orthogonal treatments (i.e., turf removal plots cf. controls) at each replicate turfed landscape (Fig. 5.1).

5.3 Results

Landscape-scale variation in canopy recovery

Patterns of canopy recovery differed among landscapes at the end of 8 months (Fig. 5.2). Analysis of covariance (ANCOVA) detected no heterogeneity in the slope describing the relationship between recovery and turf covers between landscapes for both sampling periods ($_{\text{ANCOVA:}}$ 4 months: $F_{1, 24} = 3.58$; $P = 0.070$, and 8 months: $F_{1, 24} = 0.00$; $P = 0.986$), thereby enabling tests of the main effects (Table 5.1). Whilst the recovery of canopies did not differ after 4 months, clear differences between forested and turfed landscapes emerged after 8 months. At this time turf covers were generally less (~ 30 %) and canopy recovery significantly greater within forests compared to turfed landscapes (Fig. 5.2). After 8 months, canopy covers within forests did not differ significantly from temporal controls at the same site, whereas those at turfed sites were markedly less than the equivalent controls ($_{\text{ANOVA:}}$ $F_{1, 30} = 2.37$; $P = 0.198$; SNK-tests on interaction term; turfing: clearances < controls, forests: clearances = controls). We recognise the conservative nature of this comparison (cf. stands in remnants opposed to forested landscapes) and therefore, comparison powerfully demonstrates the validity of the hypothesis (i.e., recovery is substantially less in regime shifted landscapes).

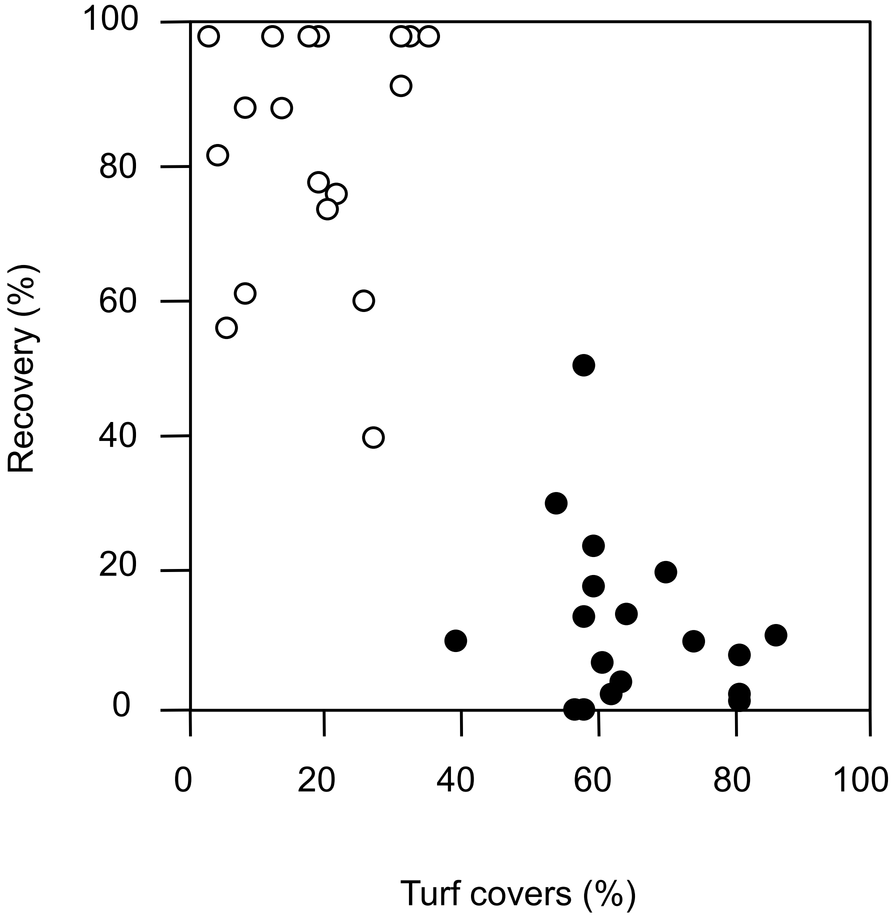

Figure 5.2 Recovery of canopy-forming algae within experimental plots of canopy clearance (*n* = 6 clearances per site) within turfed and forested landscapes (*n* = 3 sites per landscape type) after 8 months. Open circles = forested landscapes, closed circles = turfed landscapes.

Table 5.1 ANCOVA testing for differences in canopy recovery between landscape types (i.e., three turfed vs. three forested sites) after 4 and 8 months ($n = 6$ plots per site)

Treatment	*df*	MS	*F*
Canopy recovery after 4 months			
Landscape	1	0.01	0.000 $^{\mathrm{NS}}$
Site (Landscape)	4	33.92	1.70 $^{\mathrm{NS}}$
Turf covers	1	19.89	0.996 $^{\mathrm{NS}}$
Residual	29	281.13	
Canopy recovery after 8 months			
Landscape	1	4415.45	17.08 **
Site (Landscape)	4	431.40	1.82 $^{\mathrm{NS}}$
Turf covers	1	0.27	0.001 $^{\mathrm{NS}}$
Residual	29	237.02	

Notes: Data were square root ($x + 1$) transformed to meet the assumptions of heterogeneity of variance. Analysis treated „landscape‟ as fixed, „site‟ as random and nested within „landscape‟, and „turf covers‟ as a continuous covariate. Significance: NS, not significant; $P > 0.05$; ** $P < 0.01$.

Understanding variation in the capacity of forests to recover among landscape types may be improved by observations of turf development and sediment accumulation in the wake of canopy-loss. The temporal evolution of turfs and accumulated sediments within clearance plots revealed considerable variation between landscapes (Fig. 5.3a). Turf covers were initially sparse (mean: < 8 %, across all sites) and were relatively uniform under canopies within both landscape types (ANOVA: $F_{1,30} = 2.37$; $P = 0.198$). After 8 months, however, covers within turfed landscapes were ~ 3 times greater than those in forested landscapes (Fig. 5.3a; ANOVA: $F_{1,30} = 28.43$; $P = 0.006$). Similarly, while the amount of sediment under canopies (dry weight) did not vary between landscape types before clearance (ANOVA: $F_{1,30} = 0.49$; $P = 0.523$), weights measured from turfed landscapes after 8 months were ~ 10 times greater than those of forested landscapes (Fig. 5.3b; ANOVA: $F_{1,30} = 22.12$; $P = 0.009$). These patterns (Fig. 5.3 a, b) were opposite to the rate of canopy development (Fig. 5.3c).

The relationship between turfs and sediments differed between forested and turfed landscapes (Fig. 5.4; ANCOVA: „covers × landscape" interaction, $F_{1,60} = 4.37$; $P = 0.014$). In general, turfed landscapes were characterised by greater covers of turfs and greater volumes of accumulated sediments. Analysis of the relationships between turf and sediment revealed positive correlations for both turfed landscapes (Pearson"s correlation coefficient, $r = 0.757$, $P = 0.001$) and similar, albeit less strong correlations for forested landscapes ($r = 0.624$, $P = 0.001$).

Can turf removal increase rates of canopy recovery?

The removal of turfs and associated sediment from turfed landscapes resulted in greater rates of canopy recovery than non-removal plots (Fig. 5.5). Turf removal resulted in recovery that was relatively consistent across sites (mean ± SE: 89.3 % ± 2.5 %; across all sites) in contrast to control plots that displayed significant site variation, with means ranging from 11.9 % - 61.4 % (Fig. 5.5; Table 5.2, „Treatment × Site" interaction). At the end of the experiment (~ 12 months), canopy covers within turf removal plots did not differ significantly from temporal controls, and both were significantly greater than non-removal plots (ANOVA: $F_{2,75} = 13.79$; $P = 0.016$).

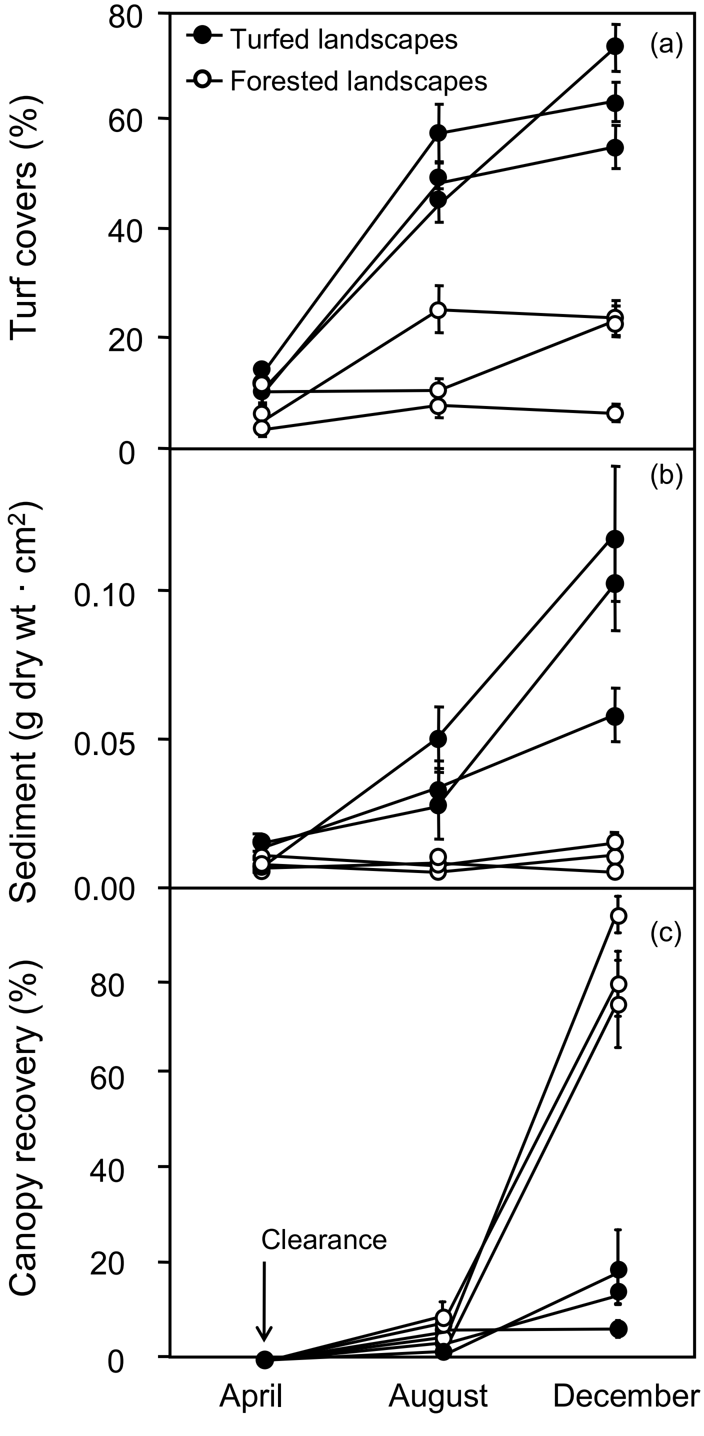

Figure 5.3 The influence of landscape-type (i.e., turfed cf. forested landscapes) on (a) the development of turfs, (b) the accumulation of sediment and (c) canopy recovery within plots of canopy clearance. Each landscape is represented by a mean ± SEM for each of three turfed and forested sites (*n* = 6 replicate plots per site).

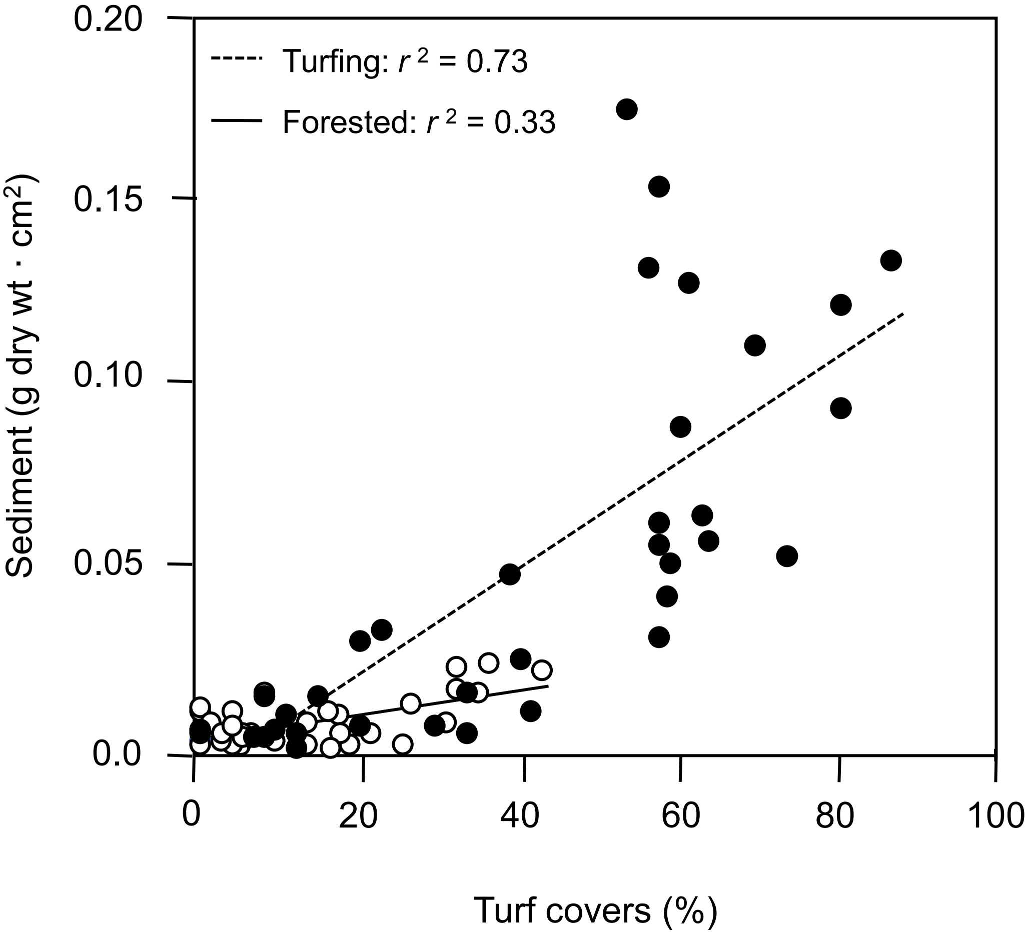

Figure 5.4 Correlation between covers of turf and accumulated sediment post-canopy loss. Open circles = forested landscapes, closed circles = turfed landscapes.

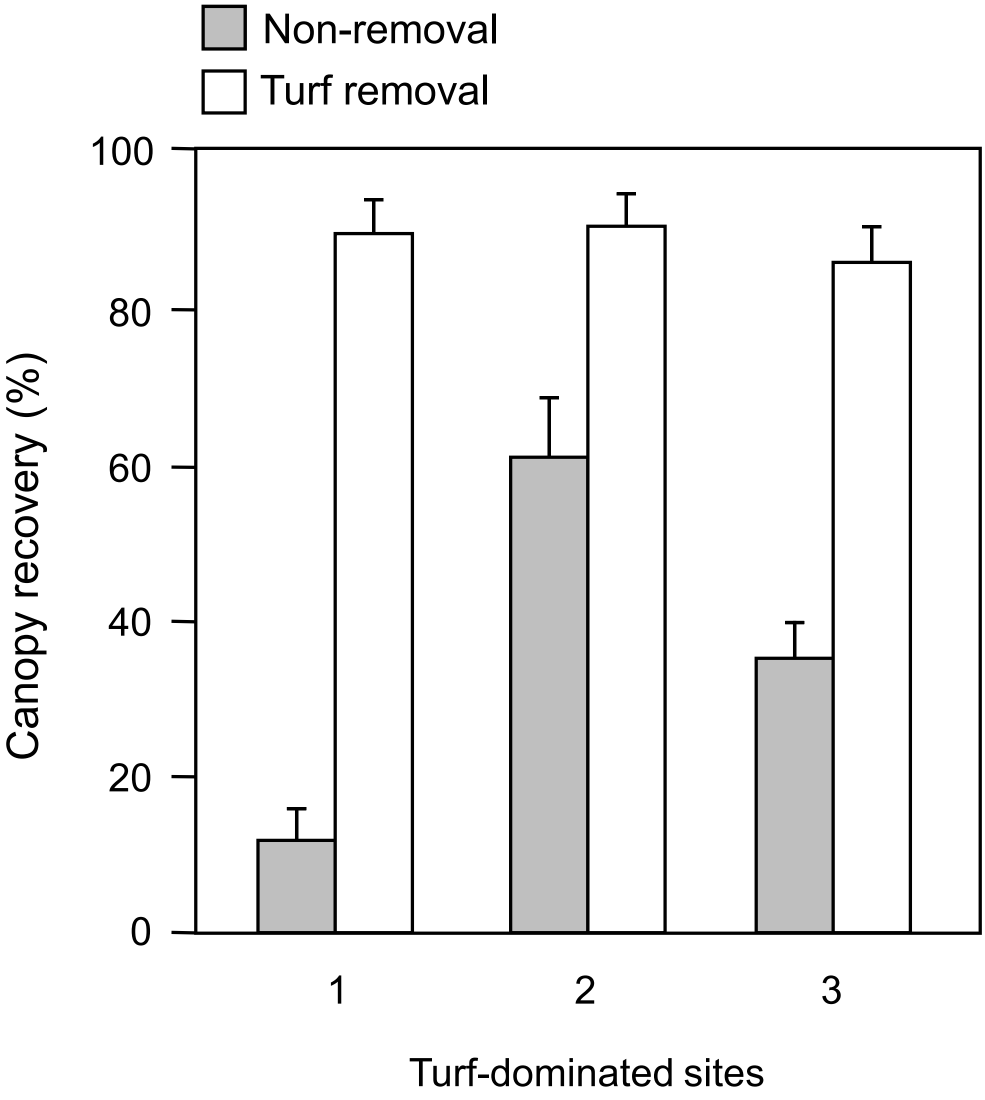

Figure 5.5 A comparison of canopy recovery between treatments from which turfs were removed (turf removal) and left untouched (non-removal) 12 months previously. Each treatment is represented by a mean ± SEM for each of three turfed sites (n = 12 replicate per treatment per site).

Table 5.2 ANOVA testing for the effect of turf on canopy recovery (turf removal vs. non-removal-treatments; *n* = 12 per treatment) among three replicate-turfed landscapes

Treatment	*df*	MS	*F*
Turf removal	1	50705.20	14.27 NS
Site	2	3862.71	1.09 NS
Turf removal × Site	2	3552.29	11.46 ***
Residual	66	309.98	

Notes: Data were arcsine-transformed percentages to meet the assumptions of heterogeneity of variance. „Treatment" was treated as fixed and „Sites" as random (*n* = 12 replicate plots per site). SNK (Student-Newman-Keuls) tests on significant interaction „Treatment × Site" term showed, for turf removals, site 1 = site 2 = site 3; and for controls, site 1 < site 3 < site 2. Significance is denoted as: NS, not significant; $P > 0.05$; *** $P < 0.001$.

5.4 Discussion

Recovery of canopy-forming algae was substantially less in turfed landscapes than it was in forested landscapes. Whilst covers of canopy recovered to match those of adjacent forest after 8 months in forested landscapes, those in turfed landscapes were substantially less than remnant forest stands (< 50 %). It is apparent from this, that the natural disturbances involved in gap creation (i.e., small, storm driven canopy-loss < 10 m in diameter along the Australian coast; Connell 2007) are disconnected from the human stressors that facilitate the expansion of turfed landscapes (i.e., facilitation by increased nutrient and sediment loads; Duarte 1995, Gorgula & Connell 2004, Airoldi et al. 2008). Our results support the idea that declines in forest cover need not be a synchronised event, but instead may be the consequence of declining water quality that can over many years reduce rates of canopy recovery thereby enabling gaps to expand over broad areas (see, Chapter 2). We propose that gap persistence, therefore, is an important component of gap expansion (i.e., individual gaps coalescing). Our demonstration of the inhibitory effects of turfs on canopy recovery not only provides a mechanism that underpins regime shifts along human-dominated coasts, but also provides a powerful demonstration of the potential for reversing the human-mediated conditions that enable turfs to retain space (i.e., restoration).

Natural communities are often founded on spatially heterogeneous mosaics of habitat-forming species mediated by disturbance-recovery cycles (Pickett & White 1985, Diaz-Pulido & McCook 2002). Whilst turfs are natural to subtidal landscapes even on undeveloped coastlines (e.g., Irving & Connell 2006b), human activities provide the environmental conditions that enable them to retain space throughout periods of natural senescence (i.e., winter) which, coincides with the period of canopy recruitment (Novaczek 1984, Hotchkiss 1999). This timing is crucial because the positive feedbacks between canopy and understorey (i.e., kelp – crust associations; Irving et al. 2004) are disrupted by turfs that overgrow understorey taxa upon which canopies recruit (i.e., encrusting corallines). Whilst canopies inhibit turfs (Connell 2003), turfs inhibit the recruitment of canopies (i.e., this study) and create their own positive feedbacks needed to retain space (i.e., turf-sediment associations; Airoldi 2003). In essence, each habitat (canopy cf. turf) is maintained by different feedback mechanisms that can switch to produce contrasting habitats (e.g., forested to turfed landscapes).

It is often simpler to identify the general causes of regime shifts (e.g., pollution and nutrient overloading; Rabalais 2002, Duarte et al. 2009) than to identify the factors that maintain these shifts (i.e., the mechanisms that prevent return to a pre-existing state). This is particularly true of forest dynamics (marine or terrestrial; Eriksson et al. 2002, Worrall et al. 2005) where the agents involved in gap expansion do not occur in a consistent and uniform manner that is easily attributed to a single factor or event. Humans can reduce the capacity of habitats to recover when their activities transform acute disturbance (such as storm events; Wernberg & Connell 2008) into a chronic stress that makes recovery slow or potentially impossible (see, Gorgula & Connell 2004). We propose that coastal eutrophication can work in concert with natural disturbance to facilitate the persistence of turfs in gaps, thereby creating a chronic stress that results in long-term forest decline over broader areas. Such links between declining water quality and the structure of subtidal communities have been evidenced throughout the globe (Duarte 1995, Cloern 2001, Deegan et al. 2002) and in the context of our study we refer to the 70 % reduction in forest covers that have been witnessed over the last 30 years (Connell et al. 2008).

Regime shifts from forested to turfed landscapes may be sustained for decades on rocky coasts (e.g., Eriksson et al. 2002, Connell et al. 2008) by poor water quality resulting from continuous terrestrial nutrient discharges (e.g., wastewater; Wilkinson 2005, Chapter 2). While ecologists are concerned that such regime shifts may be permanent (reviews, Scheffer & Carpenter 2003, Folke et al. 2004) we show that it may be possible to reverse the habitat degradation, particularly if done on conjunction with resilience-building policies (e.g., improving coastal water quality). The life-history and physiology of turfs are better suited to nutrient overloading (Gorgula & Connell 2004) and their sediment-trapping morphology enables them to rapidly recruit to and retain space under conditions of heavy sediment accumulation (Airoldi & Virgilio 1998). This positive association between turfs and sediment enables these habitats to better withstand the negative effects of sedimentation than their competitors (i.e., canopy recruitment is inhibited by sediment; Devinny & Volse

1978). Yet, managers of marine resources have little or no jurisdiction over land-based activities that elevate nutrient and sediment loads (e.g., catchment management). Current developments in coastal policy (i.e., marine protected areas) act primarily on extraction (what is removed from the sea) rather than addition (what is added to the sea). Understanding, therefore, how to restore habitats in systems dominated by humans provides useful information that may be realistically applied.

This study joins with the idea that restoration ecology provides a powerful tool for „speeding‟ the recovery of damaged landscapes (Dobson et al. 1997). Future restoration efforts are possible if the link between elevated coastal water nutrient concentrations and persistent covers of turfs can be interrupted. These efforts are realistic when viewed in the light of new policy initiatives that aim to increase wastewater recycling for residential and industrial use (e.g., nearly 45 % of Adelaide‟s wastewater; "Water Proofing Adelaide" policy of the South Australian Government). Initiatives that reduce coastal nutrient loading and consequently reduce the persistence and areal extent of turfed landscapes are likely to enhance forest resilience and restoration by interrupting the positive feedback between turfs and sediments (i.e., turf-sediment associations; Airoldi 2003) that inhibit recruitment and subsequently prevent the recovery of canopy-formers in the wake of disturbance.

In conclusion, humans are an integral part of the environment, and have a long and continuing history of manipulating environmental conditions that encourage unwanted regime shifts (Jackson et al. 2001). Resilience-based management provides a framework for evaluating the links between habitats and humans; linking ecological resilience to their governance (Hughes et al. 2005). Restoration and resilience-building policies are necessarily based on the ecological capacity to anticipate or reverse the trend of unwanted regime shifts; a particularly relevant but vexing challenge for ecologists. Not all components of resistance will be as fully understood as ecologists may hope for (as recognised by, Gunderson & Holling 2002), and therefore resilience-building management may need to accommodate flexible and open learning to provide the adaptability and capacity needed to enhance resilience in the face of uncertainty (Folke et al. 2004). We take significant steps to redress uncertainty about restoration policy by demonstrating that the feedbacks which maintain regime shifts need not be permanent, thereby opening opportunities for improving the resilience and restoration of subtidal systems on rocky coasts.

CHAPTER SIX

CHAPTER SIX:

General Discussion

“Humankind has not woven the web of life. We are but one thread within it. Whatever we do to the web, we do to ourselves. All things are bound together. All things connect”. Chief Seattle 1855

Chapter Six

General Discussion

Disturbance plays a vital role in determining the structure and function of natural ecosystems (Connell 1978, Petraitis & Dudgeon 2004). There is growing concern, however, that terrestrial inputs associated with coastal development (i.e., nutrients and sediments) may be reducing the ability of nearshore habitats to recover from disturbance (Palumbi et al. 2008). Across the globe this phenomenon has been well documented by the replacement of canopy-forming algal forests by comparatively depauperate turfed landscapes (e.g., Australia, Connell et al. 2008, Baltic Sea, Worm et al. 1999, North Sea, Eriksson et al. 2002 and Mediterranean Sea, Rodriguez-Prieto & Polo 1996). These regime shifts have profound consequences for the ecological function of rocky coastlines (Hughes 1994, Scheffer & Carpenter 2003, Connell et al. 2008). This thesis presents novel insights into the factors that contribute to the loss of forested communities along the southern coastline of Australia, with a specific emphasis on the interactions between nutrients, sediments and persistent turfed landscapes.

The research I have presented here links terrestrial land use (principally urban development) with altered land-to-sea nitrogen subsidies (Chapter 2) that can affect coastal water quality to facilitate the persistence and expansion of turfed landscapes (Chapter 3). I subsequently demonstrated that such changes to the configuration of subtidal landscapes (forested to turfed) can have follow-on effects for higher trophic level consumers (i.e., herbivores) possibly altering their food resource-base and relative densities (Chapter 4). Lastly, I investigated the potential for regime shifted subtidal landscapes to be rehabilitated through improved management of the land-to-sea interface (Chapter 5). In summary, the thesis documents the complex relationships between terrestrial inputs of nitrogen derived primarily from human waste (sewage), changes to the phenology of opportunistic turf-forming algae, and observable reductions in the ability of forests to recover from disturbance.

6.1 Terrestrial inputs as drivers of regime shifts

Across the globe, the supply of land-derived nutrients to coastal ecosystems has increased dramatically with predictable consequences for nearshore water quality (Carpenter et al. 1998, Seitzinger et al. 2005). Often, inappropriate or intensified land use (i.e., urbanisation and agricultural development) has been implicated as the principle driver of increases to coastal water nutrient concentrations and its subsequent effects on marine communities (Zann 1995, Bowen & Valiela 2001). The focus of Chapter 2 was to investigate the relationship between land use, coastal nitrogen concentrations and contemporary patterns of subtidal habitat structure (forested cf. turfed landscapes). My results confirmed that land use can directly influence coastal water quality, with urban catchments receiving dissolved inorganic nitrogen concentrations that were substantially greater than those measured from agricultural and natural catchments. Further, the consistency of this pattern across a range of rainfall events, attests to the fact that urban discharge represents a pervasive source of nitrogen to coastal waters.

Given the vital importance of nitrogen to coastal systems (Rabalais 2002), and the potential for nutrient elevation to promote the growth and persistence of opportunistic species (Worm et al. 1999, Bracken et al. 2007), such increases to land-to-sea nitrogen subsidies are likely to have profound implications for subtidal habitats (Cloern 2001, Deegan et al. 2002). My model of nutrient-driven habitat change was supported by observations of greater covers, frequency and size distributions of turfed landscapes adjacent to urbanised coasts. As covers of turfed habitat are typically low along natural coasts (< 7 %; Connell & Irving 2008), the large size of patches observed along urban coasts (> 10 m diameter) is evidence that processes structuring subtidal communities along developed coastlines differ to those that operate under natural conditions. It is likely, that the contemporary patterns of canopy-loss along urban coasts are the result of incremental changes to environmental conditions brought about by coastal urbanisation and its associated nutrient inputs (Wilkinson 2005). Connell et al. (2008) provide evidence that historical covers of canopy-forming algae along Adelaide‟s metropolitan coastline (circa, 1968) were not dissimilar to extant covers along undeveloped coastlines sampled more recently (2005). From the evidence, I propose that the current degraded state of Adelaide‟s coastal environments (i.e., seagrasses as well as that observed for kelp forests; Neverauskas 1987) may be due in part, to modified rates of land-to-sea nitrogen subsidy resulting from the accelerated coastal development since the late 1970"s (Wilkinson et al. 2004). Increases in nutrient discharge associated with these growing populations (e.g., wastewater) were the likely precursors of habitat change that has resulted in the extensive replacement of subtidal forest by turfed habitats.

Together my data complement previous findings that emphasise the potential for human nutrient subsidies to drive regime shifts along nutrient poor coastlines (e.g., southern Australia; Gorgula & Connell 2004, Connell 2007b). The results, placed in the context of biogeographic patterns in ambient seawater nutrient concentrations (e.g., Rochford 1980) may also help to reconcile conflicts into the effects of urban nutrient discharge across Australia and possibly the globe. For instance, the degree of habitat loss seen at some locations along Adelaide"s metropolitan coastline (e.g., up to 70 % loss of forests; Connell et al. 2008) appear disproportionately large when compared to more densely populated regions along the continent"s eastern coast (e.g., Sydney; population ~ 4.2 million). My results suggest that the degree of habitat loss may be directly related to the proportional relationship between ambient resources within a recipient system (i.e., coastal productivity) and those provided by the donor system (i.e., terrestrial discharges). Where coastal productivity is high such as Australia"s eastern coast and more so regions of the globe that experience substantial upwelling, the effects of urbanisation and associated inputs may be negligible (see, Underwood & Chapman 1996). Along oligotrophic coastlines such as those characterising southern Australia (Rochford 1980) the effects of even moderate increases in land-to-sea subsidies may have large and unpredictable effects (see, Russell et al. 2005).

Though a significant challenge, identifying and tracing the sources of terrestrial non-point nutrient inputs is a vital requirement for effective management of coastal eutrophication (Carpenter et al. 1998). The use of algal indicator species has been successfully employed to determine the influence of urban and agriculturally derived nitrogen to aquatic systems (Costanzo et al. 2001, Gartner et al. 2002). My use of an algal indicator species (*Ulva australis*) across a spectrum of coastlines differing in their degree of contemporary impact (i.e., developed cf. relatively pristine) successfully identified wastewater as a substantial component of the bioavailable nitrogen pool along urban coastlines. Indeed, the degree of $\delta^{15}N$ enrichment seen in transplanted *U. australis* (+ 4 ‰) was greater than that reported by Gartner et al. (2002) after exposure of this species to secondary-treated sewage effluent in the laboratory. The low levels of industrial development and animal husbandry within the urban catchments sampled (i.e., few alternate explanations for comparable enrichment) suggest that discharges of human wastes such as runoff (commercial, garden and hard-surface) and more importantly sewage effluent (either from existing wastewater treatment plants or septic systems) are major contributors of nitrogen to these usually oligotrophic coasts. The lack of any corresponding depletion in tissue $\delta^{15}N$ values of algae transplanted into agricultural catchments (i.e., indicative of industrial fertiliser derived nitrogen; Heaton 1986), suggest that unlike other regions of Australia (Brodie & Mitchell 2005, Fabricius 2005) and the globe (Vitousek et al. 1997a), agricultural activities at their current intensity do not constitute a significant source of terrestrial nitrogen to coastal waters within the greater Adelaide region.

6.2 Reduced resilience in macroalgal forests

The results of Chapter 2 provide evidence that increased subsidies of nitrogen from developed coastlines; when juxtaposed with nutrient poor coastal waters; can result in large-scale loss of canopy-forming forests. This work fits in with much of the global literature, albeit focused on estuaries and bays that emphasise the strong links between eutrophication and changes to submerged aquatic vegetation (reviews, Duarte 1995, Rabalais 2002). Whilst the links between nutrient loading and marine regime shifts are becoming clearer (Cloern 2001), little is known about the causal mechanisms that reduce the capacity of forests to recover from disturbance. The data I presented in Chapter 3 demonstrate that turfs are able to persist beyond their natural winter decline (June-August) under conditions of sustained nutrient elevation. This alteration of phenology can sustain dense (perhaps perennial) covers of turf throughout the peak season of canopy recruitment (i.e., winter for kelp and fucoid species; Novaczek 1984, Hotchkiss 1999) and is therefore likely to have substantial implications for forest resilience. My results help to refine models that seek to explain the links between nutrient inputs and change to macrophyte communities as facilitated by inhibition by opportunistic species (see, Kennelly 1987a, Camus 1994, Scheibling & Gagnon 2006). In refining this model, it appears that dense ephemeral „summer‟ covers of turfs observed naturally on rocky reef (Russell & Connell 2007, Wernberg & Connell 2008) are unlikely to affect forest recovery, but any environmental or anthropogenic factor that extends the persistence of these covers into periods of canopy re-colonisation are likely to negatively impact on rates of forest recovery.

The ability of canopies to regulate the growth of opportunistic species represents an important function underlying the resilience of rocky reef ecosystems (Edwards 1998, Eriksson et al. 2007). Whilst canopies can regulate the growth of turfs under natural conditions (Russell et al. 2005, Irving & Connell 2006a) there is concern that the enhanced growth rate of turfs, facilitated by nutrient inputs, may interrupt the interactions of coexistence between canopies and encrusting corallines that facilitate canopy recruitment (i.e., kelp – crust associations; see, Airoldi 2000). In Chapter 3 I presented novel data showing that canopies appear less able to regulate the growth of turfs under sustained nutrient elevation. Turfs released from the mediating control of canopy scour (Kennelly 1989) are able to overgrow encrusting corallines; the substratum on which canopy spores preferentially settle (Irving et al. 2004). The implications of this are likely to be considerable along urban coastlines where remaining forests tend to be fragmented and the relatively low perimeter: area ratios of turfed habitats (owing to their large diameter; Chapter 2) further reduce the ability of canopies to maintain turf-free substratum (Emmerson & Collings 1998).

Dramatic ecosystem change can often be driven by synergistic processes (amplifying feedbacks) that can be disconnected from the ultimate cause of decline (Brook et al. 2008). The highly variable patterns seen in disturbance-recovery processes across multiple spatial scales (i.e., local, through catchment and ultimately biogeographical; Connell & Irving 2008) suggest that the factors driving habitat degradation are not simple, but rather complex interactions. It is unlikely that changes to turf phenology alone cause forest decline (see, Kennelly 1987a), as increased rates of sedimentation are also widely acknowledged to have negative effects on nearshore benthic communities (reviews, Airoldi 2003, Fabricius 2005). My results demonstrate strong associations between turfs and accumulated sediments (Chapters 3 and 5) which, concur with similar observations across the globe (e.g., McClanahan & Obura 1997, Airoldi & Virgilio 1998, Gorostiaga et al. 1998). Persistent turfs and their accumulated sediments form a carpet-like benthic mat (Huff & Jarett 2007) that can interfere with spore attachment and the subsequent development of canopy-forming recruits (Moss et al. 1973, Devinny & Volse 1978). Indeed, I demonstrated reduced recovery (both in terms of covers and rates post disturbance) on degraded reefs characterised by dense and persistent turf covers and associated sediments. The recalcitrance of turf-sediment complexes may be the precursor to regime shift as ongoing disturbance increases their frequency within the habitat mosaic (Chapter 2) eventually enabling them to coalesce into expansive turfed landscapes (see, Gorgula & Connell 2004). Overall, the mechanism driving forest decline may be disconnected from the ultimate cause (elevated nutrients) but instead, involve synergies between sediments and turfs that can erode the resilience of forests (Eriksson et al. 2002, Yanez et al. 2008).

The gradual degradation of forested landscapes is likely to involve multiple small-scale disturbances that initially appear unconnected, yet may have cumulative effects over time (McCook et al. 2001). I identified correlations between coastal nitrogen concentrations and subtidal habitat across hundreds of kilometres of temperate coastline, which may be the consequence of nutrient-driven canopy loss that has proceeded unnoticed for decades (i.e., contemporary patterns based on historical losses). Areal covers of turfed habitats were far greater, and forests covers comparatively less, where human activities have increased coastal nitrogen concentrations. Further, it appears from the nature of these relationships that subtidal ecosystems may be initially resilient to low levels of nutrient enrichment, but as the ratio of terrestrial subsidy increases, a threshold point may be reached above which return to a pre-disturbed condition is difficult or impossible unless the factors reducing resilience are removed (see, Scheffer et al. 2001).

6.3 The effect of regime shifts on higher trophic levels

The loss of subtidal macrophyte communities can affect invertebrate assemblages by reducing habitat complexity (i.e., Connolly 1995, Ettinger-Epstein & Kingsford 2008) and by modifying the availability and or quality of food resources (e.g., Pyke et al. 1977, White 1984, Spalinger & Hobbs 1992). Regime shifts that drive change to the food resource-base of rocky reef systems are likely to have substantial implications for the diet of resident consumers (Steinarsdottir et al. 2009). My results demonstrate that turfs represent a more important component of consumer diet (all taxa) along degraded coastlines, where turfed landscapes have replaced much of the historical forest covers. Furthermore, this pattern contrasts the apparent (though not uniformly significant) reduction in the relative importance of articulated corallines and foliose red algae.

These types of diet shift are likely to have substantial nutritional implications for consumers; as compared to coralline and canopy-forming algal species (kelps and foliose) turfs had comparatively lower tissue nitrogen content (% N). Indeed, my proxy for ambient food quality of subtidal landscapes (based on the C:N ratios and areal covers of potential food sources) suggests that the overall nutritional value of degraded landscapes may be less than that required to sustain growth and maintain routine metabolic function (Hatcher 1994). From the evidence, I suggest that changes to the food resource-base (quantity and quality) of rocky reef systems driven by regime shift, may have nutritional implications for resident consumers (Jennings et al. 1997, Frost et al. 2006).

The response of herbivores to nutrient limitation can be varied and include changes to metabolism, altered rates of consumption and behavioural adaptations (Cruz-Rivera & Hay 2000a, Frost et al. 2006). Variation in the ability of grazing invertebrates (i.e., urchins and gastropods) to contend with nutrient limitation is likely to drive considerable differences in their relative abundance among habitat patches (Chapman & Underwood 2008). My observed patterns of herbivore density are a likely reflection of both behavioural and metabolic adaptations to changes in habitat quality. Densities of the abalone *Haliotis rubra* and the turbinid gastropod *Turbo torquatus* were comparatively less along degraded coastlines, suggesting that the characteristics (both structurally and nutritionally) of turfed landscapes may less suitable to these taxa. Given that consumers typically forage in a way that optimises energy intake (Pyke 1984), and that these invertebrates are able to move substantial distances (Kareiva 1983, Ettinger-Epstein & Kingsford 2008), it is not improbable that they would emigrate from a localised patch of degraded habitat. The patterns displayed by the two species of gastropod starkly contrast that observed for the urchin *Heliocidaris erythrogramma*, which displayed positive relationships with turf both as a habitat and food source. It is likely that this animal, and perhaps urchins in general, are better able to contend with a nutrient-poor resource-base (also consider the low tissue % N values for this species; ~ 5 %). The capacity for urchins to tolerate conditions of starvation (Lares & Pomory 1998) and their ability to derive a substantial proportion of their nutrition from drift algae (Minor & Scheibling 1997, Vanderklift & Kendrick 2005) are likely to give them a competitive advantage, which enables them to not only persist, but indeed proliferate along human-dominated coastlines.

The apparent links between habitat structure, ambient food quality, consumer diet and relative densities, represent novel insights into consequences of nutrient-driven change to entire foodwebs. While I do not speculate as to issues of food selectivity or the importance of structural complexity (Warfe et al. 2008) the contrasting patterns of consumer abundance among alternative landscapes serve to highlight the apparent differences in their suitability to various consumers. Whilst behavioural and metabolic traits may influence invertebrate assemblages over the short term, patterns of recruitment and reproduction determine community structure over generational time-scales (Keough & Downes 1982, Connolly et al. 2001, Menge et al. 2003). The fecundity, reproductive effort and growth of benthic herbivores are strongly influenced by food quantity and quality (Minor & Scheibling 1997, Kawamura et al. 1998) and hence variation the relative densities of urchins and gastropods is likely to be the combined result of short term behavioural adaptations (movement from areas of canopy-loss) and longer term patterns of recruitment and larval supply driven by changes to the resource base of nearshore rocky systems. Changes to the overall densities of ecologically important herbivores (e.g., urchins and gastropods) may have dire consequences on entire food chains and on the potential for human harvesting (Pinnegar et al. 2000).

6.4 Implications for the restoration of regime-shifted landscapes

My demonstration that forest recovery can be enhanced through the active removal of turfs and sediments (Chapter 5) provides encouraging evidence that regime shifts are not necessary permanent. It also suggests that habitat degradation may be actively reversed, as some of the metropolitan locations where I was able to enhance recovery have persisted in a degraded state for many years (Connell et al. 2008). Mangialajo et al. (2008) propose active transplantation of canopy-formers as a means of aiding the restoration of forested landscapes. This approach may have merit as it is likely to increase propagule supply (Worm et al. 1999) and extend the area over which canopies can maintain free substratum for canopy recruitment (Irving & Connell 2006a). Additionally, canopy transplantation is likely to facilitate the recovery of large gaps more rapidly than lateral expansion of remnant forests (Emmerson & Collings 1998).

Whilst small-scale efforts for active rehabilitation are likely to be constructive, particularly at highly degraded locations, the realisation of conservation goals requires strategies for managing whole landscapes (Margules & Pressey 2000). Catchment-scale policies that interrupt the negative feedbacks between persistent turfs and recruitment failure are likely to be more relevant to management and readily applicable (Hobbs 1997). Clearly, regulating the volume of nutrients discharged into coastal waters is the most effective means of doing this. Water recycling holds the potential for reducing the discharge of inorganic nutrients (in particular, nitrogen) into coastal waters. Within South Australia, initiatives aimed at increasing wastewater recycling capacity up to 45 %, at some localities ("Water Proofing Adelaide" policy of the South Australian Government) are likely to dramatically improve the water quality of adjacent nutrient-poor coastlines. By re-using water, we will not only safeguard domestic drinking water supplies (i.e., a particularly contentious issue in a drying continent such as Australia) but will fortify the ability of nearshore communities to withstand ongoing pressure from growing coastal communities. Finally, the intrinsic relationship between turfs and sediments mean that any concomitant efforts to reduce rates of sediment transport from catchments to the marine environment (e.g., via erosion controls) are likely to have observable benefits for coastal habitats.

Overall, the management and conservation of the world‟s marine resources require a comprehensive understanding of the distribution and intensity of human impacts (Halpern et al. 2008). The development of management initiatives that hold the potential for stopping further degradation will require in-depth knowledge of the way in which human impacts can facilitate ecosystem change (Tappin 2002). My research addresses some of the key knowledge gaps in temperate subtidal systems, showing that coastal urbanisation can be responsible for changes to nearshore water quality (via nitrogen subsidies) that can reduce the resilience of kelp forests. The response of ecosystems to human disturbance is not always linear or predictable (Folke et al. 2002). In recognition of this reality, I demonstrated the complex interaction between persistent turf covers, accumulated sediments and recruitment failure, as mediated by poor water quality. These, along with my observation of a possible threshold response of subtidal communities to coastal eutrophication, highlight the need for an integrated approach to land-to-sea management. I also point to the tremendous need for such action along nutrient poor temperate coastlines where the consequences of eutrophication may be large and unpredictable (see, Russell et al. 2005).

6.5 Future research

Whilst the results of Chapter 2 impart much needed insight into the causes and consequences of altered land-to-sea nitrogen subsidies, further work needs to be done to assess the generality of this model both spatially (i.e., across biogeographic regions) and temporally (i.e., across seasons, years and in response to changing climate). To validate the model that habitat loss may be related to the magnitude of donor to recipient subsidy, data will be required across a full spectrum of locations that differ in both donor inputs and relative productivity. In doing this, theories may be developed that can identify thresholds for water quality beyond which rapid and perhaps permanent degradation of subtidal systems can be expected. Chapter 4 highlighted the potential for regime shifts to alter the food resource base of benthic consumers. These preliminary findings open up a range of research possibilities such as; the physiological effects of altered food quality on consumers (e.g., fitness and reproductive output; Cruz-Rivera & Hay 2000a, Frost et al. 2006) and the subsequent effects of such changes on secondary consumers and detritivores (via trophic relay). Lastly, my demonstration that turf removals can increase rates of forest recovery on historically degraded coastlines (Chapter 5) points to the ample opportunities for investigating more closely the processes that govern the resilience of subtidal forested landscapes. Research should be aimed at monitoring the persistence of recovered canopies (i.e., in the current absence of definitive reductions in nutrient inputs) and at developing strategies that will facilitate management-scale recovery of degraded landscapes (i.e., transplantation, seeding, etc). These avenues of research are not only likely to enhance our understanding of the processes which govern ecosystem resilience (terrestrial as well as marine), but may help develop the capacity for resilience building policy and restoration management.

6.6 Conclusions

Across the globe coastal development has been linked to regime shifts within nearshore ecosystems (Hughes 1994, Scheffer & Carpenter 2003, Connell 2007b). In this thesis I demonstrate comparable shifts along Australia‟s southern coastline, which are the likely result of human-mediated changes to rates of land-to-sea nitrogen subsidy. Ecological theory suggests that the effects of subsidies are strongest where the ratio of subsidised resource between the donor and recipient system is large (Marczak et al. 2007). Based on the evidence, I propose that recipient systems most vulnerable to change are those where there is a large disparity between terrestrial inputs and ambient coastal productivity. The most vulnerable coastlines will require ongoing and integrated management of the land-to-sea interface to limit changes to environmental conditions that can reduce ecological resilience (Palumbi et al. 2008). Whilst ecologists are often overwhelmed by a pessimistic world-view of ecological degradation (Odenbaugh 2001, Sagoff 2003), I wish to conclude with the optimistic position that the reversal of regime shifts appear not only possible (this study), but probable, if management incorporates resilience-building policies aimed at controlling local stressors that can potentially mitigate the effects of global stressors (see, Russell et al. in press). There has never been a more pressing need to recognise the effects of human activities on spatially and energetically linked natural systems that provide such valuable but finite resources to humans.

Appendices

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Chapter 2

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Chapter 5

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Appendix B: Supplementary material

Chapter 2

Table S1 Locations and estimated population sizes (Australian Bureau of Statistics, Population Census 2006) for replicate urban, agricultural and natural sites sampled during the study.

Catchment/type	Latitude/longitude	*c*. Population (2006)
Urban		
Onkaparinga	S35.11887 E138.46494	150,000
Inman River	S35.57126 E138.61221	12, 000
Pedler Creek	S35.18224 E138.45808	26, 000
Second Valley	S35.50954 E138.21445	4, 000
Agricultural		
Blowhole Creek	S35.65649 E138.15550	9
King Head Creek	S35.60551 E138.58308	6
Fishery Creek	S35.63456 E138.11514	12
Myponga River	S35.36672 E138.38075	60
Natural		
Marrano Creek	S35.66367 E138.17893	N/A
Aaron Creek	S35.66381 E138.19993	N/A
The Deep Creek	S35.65429 E138.24546	N/A
Waitpinga Creek	S35.64568 E138.52011	N/A

Chapter 3

Table S2 Pair wise comparisons of covers of turf forming algae within experimental treatments of nutrient elevation (enriched cf. ambient) and canopy cover (present cf. absent) across seasons.

Season	Sampling duration	Canopy cover	
		Absent	Present
Summer	December – February	$N^+ < N^-$	$N^+ = N^-$
Autumn	March – May	$N^+ = N^-$	$N^+ > N^-$
Winter	June – August	$N^+ > N^-$	$N^+ = N^-$
Spring	September – November	$N^+ = N^-$	$N^+ > N^-$
Summer	December - February	$N^+ = N^-$	$N^+ > N^-$
Autumn	March – May	$N^+ > N^-$	$N^+ > N^-$

Notes: N^+ = Nutrients elevated and N^- = Ambient nutrients.

Chapter 4

Table S3 Results of nested ANOVA testing for differences in tissue isotope values (δ^{15}N and δ^{13}C) and percentage nitrogen (% N) of algal producers and benthic herbivores between coastline types (*n* = 4 replicate sites, per coastline type).

Sample	*df*	δ^{15}N		δ^{13}C		% N	
		MS	*F*	MS	*F*	MS	*F*
Articulated corallines							
Coastline	1	161.20	1.22^{NS}	5.13	0.10^{NS}	16.17	2.95^{NS}
Site (coastline)	6	132.53	405.18^{***}	53.15	205.73^{***}	5.49	5.33^{**}
Residual	16	0.33		0.26		1.03	
Encrusting corallines							
Coastline	1	65.68	0.97^{NS}	6.72	0.36^{NS}	4.51	0.60^{NS}
Site (coastline)	6	67.78	62.71^{***}	18.44	10.96^{***}	7.54	15.08^{***}
Residual	16	1.08		1.68		0.50	
Canopy-forming							
Coastline	1	49.14	5.31^{NS}	8.05	0.22^{NS}	1.64	4.06^{NS}
Site (coastline)	6	10.34	2.93^{*}	40.43	2.74^{NS}	0.37	0.63^{NS}
Residual	16	3.53		14.74		0.58	
Red foliose							
Coastline	1	0.18	0.01^{NS}	21.66	0.26^{NS}	29.70	9.49^{*}
Site (coastline)	6	13.36	20.22^{***}	82.89	131.92^{***}	3.13	20.30^{***}
Residual	16	0.66		0.63		0.15	
Turfs							
Coastline	1	15.04	0.78^{NS}	212.42	4.13^{NS}	1.40	1.12^{NS}
Site (coastline)	6	19.22	23.48^{***}	51.48	30.62^{***}	1.26	2.33^{NS}
Residual	16	0.82		1.68		0.54	
H. rubra							
Coastline	1	54.30	3.55^{NS}	157.08	10.68^{*}	61.33	12.34^{*}
Site (coastline)	6	15.31	47.40^{***}	14.71	86.30^{***}	5.25	2.64^{NS}
Residual	16	0.32		0.17		1.99	
H. erythrogramma							
Coastline	1	75.26	3.56^{NS}	35.77	2.11^{NS}	9.40	3.20^{NS}
Site (coastline)	6	21.13	27.56^{***}	16.94	68.44^{***}	2.92	1.46^{NS}
Residual	16	0.77		4.80		2.00	
T. torquatus							
Coastline	1	46.48	1.28^{NS}	12.47	0.56^{NS}	0.32	7.59^{*}
Site (coastline)	6	36.27	102.41^{***}	22.23	26.54^{***}	0.42	0.90^{NS}
Residual	16	0.35		0.84		0.47	

Notes: „Coastline" was treated as fixed and orthogonal factor with two levels (Healthy cf. Degraded). Significance is denoted as: $^{\mathrm{NS}}$ not significant $P > 0.05$, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

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SPECIAL NOTE

Diving the exposed southern coastline of Australia is a unique experience, limited to the adventurous and some say the mad. Only by persevering through the storms, cold, poor visibility and threat of sharks does one find the true essence of the Southern Ocean. The highs - ability to conduct ground breaking subtidal research, diving places few will ever visit and sharing the sea with unique creatures - are rewards that override all of the negatives. The thrill of diving this wild coastline, however, needs to be tempered with respect. I wish to make a special dedication to the late Jarrod Stehbens, a mate that I travelled much of the southern Australian coastline with, and one whose passion for the sea inspired all. Jarrod was tragically taken by a Great White Shark offshore from Adelaide on the 24th August 2005. His memorial on West Island, SA, which faces the full force of the Southern Ocean, reads words true to all who knew him
"A Great Bloke".