

**Population dynamics of the sea urchin
Heliocidaris erythrogramma on the east coast of
Tasmania**

by

Hugh Gregory Pederson

B. App. Sc (Hons) University of South Australia

Submitted in fulfilment of the requirements for the
Degree of Doctor of Philosophy.

University of Tasmania (December, 2003)

Declarations

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Acknowledgments

Firstly, I would like to thank my supervisor Craig Johnson for his support and guidance in recent years. The contribution you have made to my future career in marine science is greatly appreciated!

To my partner Jane for the effort and sacrifices you have made for me over the past few years, without you this would have been impossible. Thankyou for your support and understanding, sense of humour and patience, your smile and laugh and most off all your friendship.

To my family who have given me the support throughout my university degrees to get me to this stage. Leaving my home state and the three of you was the toughest decision to make at such a young age, and in the same situation I would not do again. Thankyou for the phone calls, frequent visits and the enjoyable times when we are back home.

To my extended family, Tony and Vicki Hamilton, thank you for your support and understanding which has been outstanding over the past six years and I will not forget the countless things you have done for Jane and I since we met.

To me this project can be separated into two distinct halves, and without Joe Valentine I would not have been able to finish the enjoyable part, fieldwork! The contribution that you have made to my project and ultimately to my future in marine science has been endless. The effort you put in over the three years of field work was beyond the call of most people, the hundreds of hours spent underwater counting urchins, drilling

holes in urchins, injecting urchins and fishing for calamari will not be forgotten. Not only has your help been valued but your friendship treasured, thanks Valo!

There are two other people from the marine lab that have been two of the greatest friends and work mates I could have hoped for. To Jeff Ross and Regina Magierowski thank you for your help and friendship over the past four years, the times spent in the field in the early days at Alum Cliffs, Cunningham and Saltwater River and the drinking sessions over the past few years.

The university marine lab has seen many great people since I started my PhD and there are some that I would like to thank for their help including Piers Dunstan, Tim Karlov, Toby Patterson, Dirk Welsford, Jaccinta Innes and Scott Ling.

The project would not have been possible without the help of the staff within the School of Zoology most importantly Adam Stephens, Richard Holmes and Simon Talbot.

Abstract

Formation of sea urchin ‘barrens’ has been documented widely in temperate regions of both northern and southern hemispheres. While the phenomenon has been reported worldwide, the mechanism(s) underpinning barren ground formation are poorly understood. Elucidating the mechanism(s) of barrens formation is important, not the least reason being because it may provide options for management to minimise the establishment and or spread of urchin barrens. One potential mechanism is through increases in urchin population density as a result of reduced predation mortality because of exploitation of predators. We examined whether fishing of rock lobster (*Jasus edwardsii*) and fish predators on rocky reefs in Tasmania could account for population increases of the sea urchin *Heliocidaris erythrogramma* to the point where overgrazing of macroalgae may lead to urchin barrens.

Large-scale surveys (over >100 km of coastline) of abundances of urchins and putative predators revealed a significant negative relationship between urchins and lobster abundances, but not between urchins and demersal fishes. At smaller scales, both large lobsters and demersal fish are significantly more abundant inside no-take marine reserves than in equivalent adjacent habitat subject to fishing. These observations are consistent with results of small-scale experiments in which the rate of urchin mortality was ca. 23 times greater inside two marine reserves than in adjacent exploited habitats. Caging experiments also showed that predation by rock lobsters on sea urchins is highly size-specific. Juvenile lobsters are not capable of predating urchins with test diameter (TD) > 60 mm, while medium-sized lobsters preyed on urchins up to 80 mm TD, and large urchins >81 mm TD were only at significant risk

of predation mortality from large lobsters. Demersal fish were notably less important predators of urchins between 40-100 mm TD than were rock lobsters. Inside reserves, if urchins were tethered so that they could not seek shelter, then juvenile urchins were predated more frequently than larger ones. However, when tagged urchins were free to move, mortality of adult urchins was significantly higher than that of juveniles, because juveniles were able to shelter in small crevices.

I also examined the possibility that higher urchin population densities on barrens could be the result of sporadic large recruitment events. In mark-recapture experiments, three distinct urchin populations were used to construct individual-based growth models to generate size-at-age relationships. Age frequency distributions of urchin populations in algal beds and adjacent barrens habitat were estimated using this relationship and examined for the presence of dominant cohorts which may indicate prominent recruitment events. Significant differences were found in the age frequency distributions of urchin populations in barren and algal bed habitats at two separate locations, with dominant peaks in the age structures of urchins in barrens populations unmatched by those in adjacent algal beds.

Estimates of age-specific mortality rates and age frequency distributions derived for several distinct urchin populations enabled construction of matrix models of population growth. Using the empirical estimates of size-specific per capita rates of predation by lobsters on urchins, I estimate the effect of exploitation of lobsters in regulating urchin population density by comparing model projections for urchins based on lobster populations inside and outside marine reserves. The modelling suggests clearly that the reduction in biomass of legal-sized lobsters on the east coast

of Tasmania due to fishing is sufficient to account for increases in populations of *H. erythrogramma* to the point where barrens formation may occur.

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Chapter 1: General Introduction

Urchin barrens formation: mechanism underpinning community structure alteration

1.1 Introduction

The transition from rich macroalgal beds to bare rock, without visible vegetation mediated by overgrazing of urchins, has been documented widely for temperate regions in both hemispheres (Paine and Vadas, 1969; Mann and Breen, 1972; Shepherd, 1973; Lawrence, 1975; Breen and Mann, 1976; Lang and Mann, 1976; Mann, 1977; Chapman, 1981; Dean *et al.*, 1984; Harrold and Reed, 1985; Vadas *et al.*, 1986; Fletcher, 1987; Andrew, 1991; Andrew, 1993; Sanderson *et al.*, 1996). The formation of these urchin ‘barrens’ can occur over large spatial scales, affecting areas of rocky reef along 100s of kilometres of coastline (Mann, 1977; Wharton and Mann, 1981; Sanderson *et al.*, 1996; Andrew and O'Neill, 2000). However, while the phenomenon is well documented, there has been little explicit testing of the potential mechanism(s) that underpin the onset of destructive grazing of macroalgae by sea urchins.

Elucidating the mechanism(s) of barrens formation is important, not the least reason being because it may provide options for management to minimise the establishment and or spread of urchin barrens. Formation of urchin barrens is a management issue because the associated dramatic loss of primary production (Chapman, 1981) and habitat structure invokes major changes in community structure (Paine and Vadas, 1969;

Andrew and Choat, 1982; Harrold and Reed, 1985; Vadas *et al.*, 1986; Fletcher, 1987; Dayton *et al.*, 1992; Andrew and Underwood, 1993). Established hypotheses accounting for the onset of destructive grazing essentially fall into four categories, two based on changes in urchin population density and two invoking changes in urchin behaviour but not necessarily population size.

Increase in urchin population size

Significant increases in urchin population density over short temporal scales with subsequent formation of barrens may result from reduced predation mortality and or increased recruitment rates. Breen and Mann (1976a) hypothesised that destructive grazing by urchins may be density dependent in that urchins at low densities cannot efficiently graze the blades of attached plants, while at elevated urchin densities attached plants are overwhelmed by grazing pressure. Observations indicated a threshold urchin density was required before destructive grazing could occur (Breen and Mann, 1976a).

Increases in urchin population density to exceed the threshold required for barrens formation were thought to occur in response to exploitation of predators, resulting in reduced urchin mortality rates (Mann and Breen, 1972; Lowry and Pearse, 1973; Estes and Palmisano, 1974; Wharton and Mann, 1981; Tegner and Levin, 1983; Watt *et al.*, 2000; Estes and Duggins, 1995; Estes *et al.*, 1998). Following the initial hypothesis, that barrens can be formed if urchin predators are harvested, there is now strong evidence for the idea from overfishing of otters around the northern Pacific rim (Lowry and Pearse, 1973; Estes and Palmisano, 1974; Duggins, 1980; Dean *et al.*, 2000; Estes *et al.*, 1998; Watt *et al.*, 2000), finfish (Vadas and Steneck, 1995; Shears and Babcock, 2002), and

rock lobsters (Tegner and Levin, 1983; Mayfield and Branch, 2000; Shears and Babcock, 2002). Notably, the initial hypotheses about the importance of fishing lobsters and demersal fish in Nova Scotia have not been adequately tested (see (Chapman and Johnson, 1990; Elner and Vadas, 1990) for reviews).

The ability to attack and manipulate prey usually increases as a function of body size (Pollock, 1979; Griffiths and Seiderer, 1980; Tegner and Levin, 1983; Mayfield *et al.*, 2001). Continued harvesting of predator populations protected by a legal minimum size typically reduces the abundance of larger sized individuals, truncating the size spectrum (Edgar and Barrett, 1999). Thus, reduced abundance of large legal-sized predators through fishing could result in a reduced predation mortality and shift in size structure of prey towards larger individuals, even with continued high rates of recruitment of the predator.

Occasional large recruitment events have also been suggested as a possible mechanism to increase population density of urchins, and have been associated with infrequent, local oceanographic events. A positive temperature anomaly on the Atlantic coast of Canada reflected a change in the prevailing current patterns which has been hypothesised to underpin mass settlement of *Strongylocentrotus droebachiensis* (Hart and Scheibling, 1988). This hypothesis is limited to ideas about predation, since it assumes that massive recruitment events satiate predators. These hypotheses have not been tested.

Behavioural change

Two alternative mechanisms relate barren formation to changes in urchin feeding behaviour. Both assume that the urchin population is sufficiently large to cause barrens if urchins began to graze destructively. Bernstein *et al.* (1981) describes a system where urchin barren formation is precipitated by urchins forming feeding aggregations, which they argue will form in the absence of fish predators which otherwise cause aggregations to disperse (Bernstein *et al.*, 1981). However, this idea has been criticised by (Elner and Vadas, 1990) on the basis of a lack of explicit evidence and critical tests.

Destructive grazing of kelp beds is also thought to occur in response to the availability of drift algae, on which many urchins usually feed while secured in their shelters (Lawrence, 1975; Harrold and Reed, 1985; Rodriguez and Farina, 2001). Harrold, (1985) suggested that urchins leave their crevices and begin feeding in the open on attached algae when drift material becomes scarce. This model is supported by observations of urchins switching from feeding on attached plants in the open to feeding cryptically on drift, with concomitant recovery of attached plants, following the incursion of a large amount of drift material to the study site (Harrold and Reed, 1985).

Australian perspective

Shepherd's discovery of urchin barrens in eastern Victoria in 1973 was the first recorded evidence of the phenomenon in Australian waters (Shepherd, 1973). Since then, urchin barrens have been reported widely in other temperate regions of Australia (Fletcher, 1987; Andrew and Underwood, 1989; Underwood *et al.*, 1991; Andrew and Underwood, 1992), including in Tasmania (Sanderson *et al.*, 1996). The appearance of urchin barrens

on rocky reefs along the east coast of Tasmania is of particular concern as the region supports lucrative wild abalone and rock lobster fisheries.

Two species of sea urchin form barrens habitat on the east coast of Tasmania, the native urchin *Heliocidaris erythrogramma*, and a recent invader from mainland Australia, *Centrostephanus rodgersii*. While the two species co-occur along the east coast of Tasmania, dense populations of *C. rodgersii* occur largely on the exposed coast, while persistently high population densities of the native urchin and associated barrens habitat are restricted to relatively sheltered locations. Anecdotal evidence, largely from the oral histories of divers, indicates that prominent barrens have been evident only for the past 3-4 decades. This correlates with a period of increased fishing actively on the east coast. For example, it is estimated that biomass of legal sized rock lobster (*Jasus edwardsii*) on the east coast is between 2 and 8% of the virgin stock (Frusher, 1997). Reductions of this kind may have influenced urchin population structure and density over the long period of exploitation.

Thesis outline

Although identified as a species capable of forming large areas of barrens habitat on sheltered coastlines, there is little research on the population dynamics of *H. erythrogramma* and how dynamics might be influenced by predators. The broad aim of the present research was to investigate putative mechanisms that may account for urchin population densities at levels sufficient for formation of barrens habitat. In addressing the broad aim of the project several specific areas were investigated, namely patterns in the abundance of predators and prey, the relative importance of predator types and sizes

as urchin predators, population age structures in barrens and adjacent algal bed habitats, and predicted effects of fishing urchin predators on urchin population dynamics.

In chapter 2, a broad-scale spatially hierarchical survey of the east coast of Tasmania over spatial scales of 10^2 - 10^5 m, identifies the distribution patterns of potential urchin predators and their relative importance in describing patterns of urchin density.

Chapter 3 reports on a series of manipulative experiments conducted to examine specific mechanisms that may explain the patterns evident from the broad-scale survey. An important element of this work was several types of tethering experiments used to compare urchin mortality inside marine reserves (habitats with elevated urchin predator abundance) with mortality in adjacent areas of similar habitat open to fishing (where predator abundances are notably lower). The relative importance of predatory demersal fish and rock lobsters as predators of *H. erythrogramma* was then examined in a large-scale manipulative experiment. Experiments were conducted to determine the effect of urchin and rock lobster (*J. edwardsii*) size on urchin mortality. From these experiments we identify size-specific predation mortality rates as a function of urchin test diameter.

In chapter 4 I describe the growth patterns of three urchin populations from the Mercury Passage on the east coast of Tasmania. The construction of size-at-age relationships was important in determining the progression of individuals into successive age classes and the respective mortality rates of each life history stage. Development of an age-at-size 'key' allowed cohort analysis to ascertain whether unusual recruitment events could

account for differences in urchin population structure and density in algal beds and adjacent barren habitats. Oceanographic data were examined to determine whether patterns in annual recruitment events may be explained by factors such as sea surface temperature.

In many species, the means to determine age rapidly is a valuable tool in assessing population structures. In sea urchins 'natural' growth lines in the test plates have been proposed as possible chronometers in determining the age of individuals. However, reliable rapid assessment of age using 'natural' growth lines is dependent upon the periodicity of line deposition and its variance with age and body size. Thus, validation of natural growth lines using other means of tagging test plates must be conducted before natural growth lines can be used to accurately determine population age structure. In chapter 5 I examine natural growth lines in *H. erythrogramma* and compared them with fluorescent markers of known age to ascertain whether natural markings can be used as a rapid and reliable method to age this species in Tasmania.

Finally, we use the empirical data on urchin population structure and predation rates on urchins to construct a simple population model to examine the effect of predators on urchin populations. We examine whether fishing of legal-sized rock lobster to their present level on the east coast of Tasmania could account for increased population densities of *H. erythrogramma* sufficient to form barrens habitat.

The reader should note that the chapters have been written as manuscripts for publication, consequently repetition in the introductions of several chapters was unavoidable.

Chapter 2

Broad-scale relationships between sea urchins (*Heliocidaris erythrogramma*) and their putative predators in south eastern Tasmania

2.1 Abstract

Over-exploitation of commercially lucrative species, on multiple trophic levels, has resulted in significant alteration in the structure of marine ecosystems. Until recently the impacts of exploitation were often measured in terms of declines in target species and not the indirect effects on ecosystem functions. Transformation of reef community structure from one dominated by dense stands of macroalgae to urchin barrens may be an indirect effect of over-exploitation, since decreased urchin predator abundance has been linked to expansion in urchin population size.

Broad-scale negative relationships between putative predators and their urchin prey along 200 km of the east coast of Tasmania, incorporating a network of no-take marine reserves, suggest urchin population size may be regulated by total predator abundance, of which the southern rock lobster (*Jasus edwardsii*) appears to dominate the relationship. Furthermore, rock lobsters were found to be three times more abundant inside marine reserves compared to adjacent habitats subject to exploitation where lobsters at the minimum legal size (MLS) were scarce and lobsters >120 mm (CL) were almost completely absent. Reef associated demersal fishes were less important in shaping the relationship across broad spatial scales compared to lobsters

however, on smaller scales fish become relatively more important in discriminating between predator assemblages supporting significantly different urchin densities.

Inside no-take marine reserves where predators are more abundant, mean urchin size was significantly greater and population density significantly lower compared to urchin populations in adjacent habitats subject to predator exploitation. Significant differences in urchin size frequency distributions of populations in these two habitats was also apparent which we attribute to size specific predation by large predators inside the no-take reserves. On smaller spatial scales outside of no-take reserves urchin population density was significantly higher in urchin barrens habitat compared to adjacent vegetated sites suggesting urchin barren formation may result from elevated urchin population density.

2.2 Introduction

For centuries temperate marine ecosystems have been exploited at many trophic levels (Jackson *et al.*, 2001). In several cases fisheries have operated, at ostensibly sustainable levels, before sudden collapse (Kalvass and Hendrix, 1997). In the majority of cases, ecosystem-level mechanisms influencing fishery dynamics are not fully understood. Dramatic reductions in the abundance of the American lobster (*Homarus americanus*) in eastern Canada (Breen and Mann, 1976; Wharton and Mann, 1981) and the closure of the commercial red abalone (*Haliotis rufescens*) fishery in central and southern California (Karpov *et al.*, 1998), suggest that impacts of over-exploitation are not only restricted to target species, but that there may be significant flow-on effects to non-target species (Karpov *et al.*, 2001). Heavy exploitation of particular reef species can lead to shifts in community structure vastly

altered from the original state by affecting ecosystem processes such as competition and predation (Tegner and Levin, 1982; Tegner and Dayton 2000; Ebert, 2001).

Phase shifts in the structure of temperate rocky reef assemblages from diverse algal beds to sea urchin barrens largely devoid of macroalgae have been documented worldwide (North and Pearse, 1970; Mann and Breen, 1972; Shepherd, 1973; Mann, 1977; Wharton and Mann, 1981; Lawrence, 1975; Schiel and Foster, 1986; Fletcher and Underwood, 1987; Andrew, 1988; Andrew and Underwood, 1989). With loss of the algae, primary productivity can be reduced by 100-fold (Chapman, 1981), with undoubted flow-on effects to secondary production. While the phenomenon of sea urchin barrens is widely acknowledged, the mechanism(s) that underpin destructive grazing by urchins are less clear. Numerous hypotheses have been established accounting for the onset of barren formation which fall into two broad categories, changes in urchin population density (Mann and Breen, 1972; Lowry and Pearse, 1973; Estes and Palmisano, 1974; Breen and Mann, 1976; Wharton and Mann, 1981; Tegner and Levin, 1983; Hart and Scheibling, 1988) and alteration of urchin behaviour but not population size (Lawrence, 1975; Bernstein *et al.*, 1981; Harrold and Reed, 1985; Elner and Vadas, 1990). One long-standing hypothesis is that overfishing of predators allows urchin populations to expand to the point where destructive grazing and barrens formation commences (Mann and Breen, 1972; Mann, 1977; Breen and Mann, 1976; Wharton and Mann, 1981).

The advent of no-take marine reserves inside of which the average density, biomass, and size of individuals, and species diversity are known to be significantly greater compared to adjacent reference sites subject to exploitation (review by Halpen and

Warner, 2002), provides a unique opportunity to examine the relationship between elevated abundances of predators and their urchin prey. The objective of this research was to determine the relationship between urchin predators and their prey at various spatial scales along the southeast coast of Tasmania utilising the current network of established no-take marine reserves to determine if fishing of urchin predators has significant impacts on urchin population structures.

2.3 Methods

2.3.1 Survey sites

Descriptive surveys of putative urchin predator abundance (rock lobster and predatory reef fish) and sea urchin (*Heliocidaris erythrogramma*) density were conducted in three regions along the east coast of Tasmania between February and December 1999 (Figure 2.1). All three regions contain marine reserves with some level of protection from harvesting of lobsters or fish or both, while fishing continues outside the reserves (exploited habitats).

The Bicheno region to the north supports both commercial and recreational fishing on an exposed coastline, while to the south the Mercury Passage region is more sheltered and is also commercially and recreationally fished. The survey area in the Derwent Estuary is of similar exposure to the Mercury Passage, however sites outside the Crayfish Point reserve are subject to recreational fishing only. Protected areas at Bicheno (Governor Island) and Mercury Passage (Maria Island) prohibit all fishing, while only rock lobsters are protected within the Crayfish Point reserve.

Within each region the marine protected area and three adjacent unprotected reference sites characterised by dense stands of macroalgae were surveyed. In the Mercury Passage region, two sites within the Maria Island Marine Reserve were surveyed and, in addition to the three reference sites supporting macroalgae outside the reserve, two sites characterised by sea urchin barrens at Lords Bluff and Stapleton Point were surveyed during Apr-May 2000.

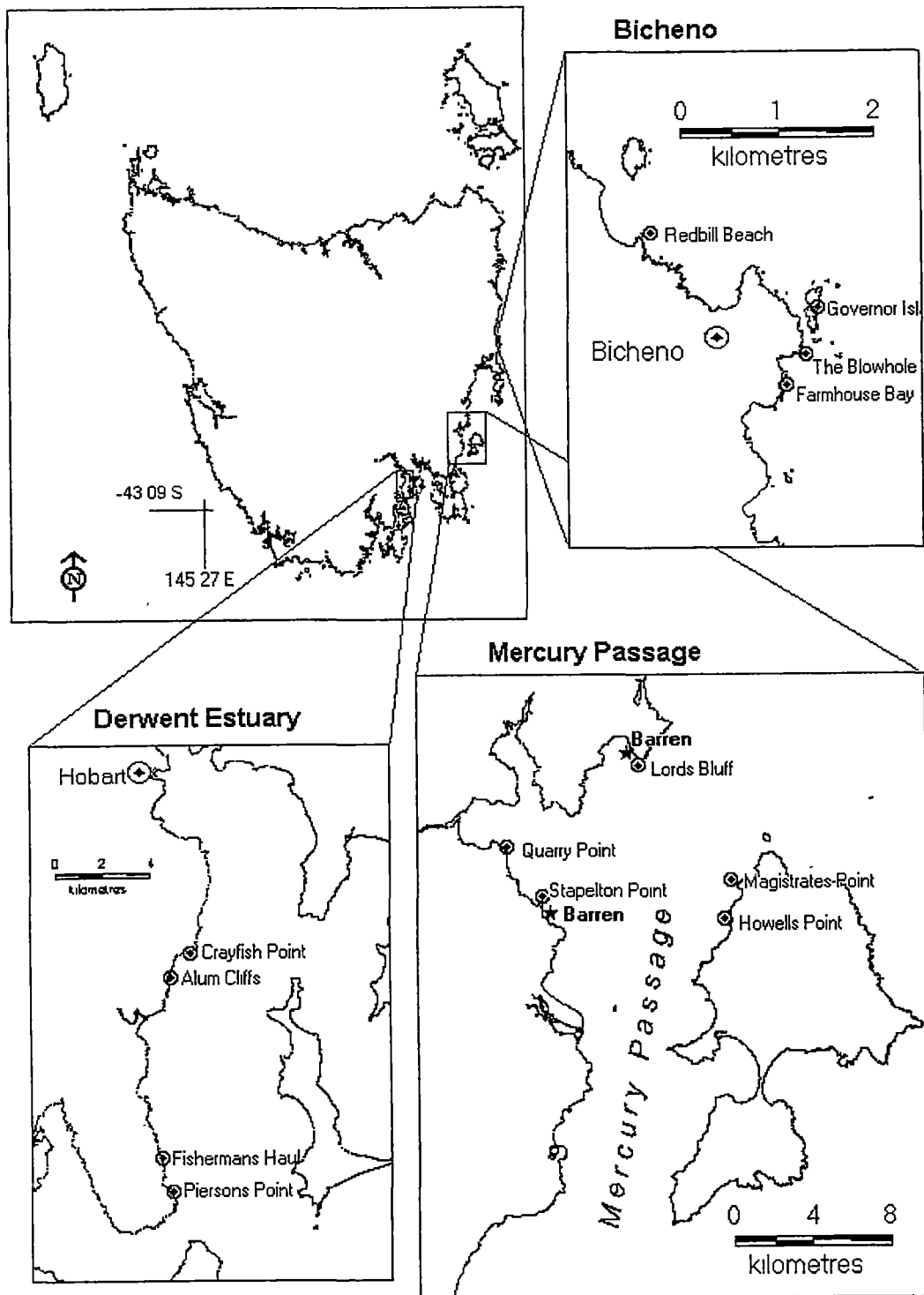


Figure 2.1 Location of sites surveyed within the three regions along the southeast coast of Tasmania. Urchin barrens (★) are located adjacent to established algal beds at Lords Bluff and Stapelton Point (Mercury Passage).

2.3.2 Survey techniques

Abundances of potential sea urchin predators were estimated by underwater visual censuses along belt transects. Demersal fish were surveyed by divers swimming a 50 m transect and recording the number of each species found within 5 m either side of the transect. Species recorded were *Notolabrus tetricus* (blue-throat wrasse), *Notolabrus fucicola* (purple wrasse), *Acanthaluteres vittiger* (toothbrush leatherjacket), *Meuschenia australis* (brown-striped leatherjacket) and *Meuschenia freycineti* (six-spined leatherjacket). Individuals smaller than ca. 100 mm total length were omitted from the count due to their cryptic nature in the presence of divers. Surveys were always conducted with underwater visibility >5 m, and between 10:00-16:00 hrs to minimise bias from diurnal behaviour of fish at dawn and dusk.

The decapod species *Plagusia chabrus* (red bait crab) and *Jasus edwardsii* (southern rock lobster) were counted by divers in a 2 m strip either side of the 50 m transect used to survey demersal fish. The abundance of lobsters in three size classes was estimated; sub-legal (small) 90-105 mm carapace length (CL); minimum legal size (medium), between 105 and 120 mm, and mature adults (large) >120 mm.

Individuals were classed by visual observation with the same diver surveying all sites within the study. At each site, 10 randomly positioned transects were surveyed within a depth range of 7 to 10 m.

Estimates of *H. erythrogramma* densities and size structure were obtained from censusing all urchins in a 16 m² quadrat located at a random distance along each of the 50 m transects previously described. All individuals were collected from the quadrat and measurements of the test diameter (TD) made to the nearest millimetre using knife-edge vernier callipers.

2.3.3 Statistical Analysis

Broad scale patterns in the abundance of putative predators and urchins were analysed using quantile regression (Buchinsky, 1998) to determine the theoretical upper bounds to the distribution using the *R* statistical package. The difference between exploited and non-exploited predator assemblages within each region was analysed using non-parametric multivariate ANOVA (NPMANOVA¹; Anderson, 2001) and the relative importance of each predator 'group' in differentiating between exploited and non-exploited habitats assessed using SIMPER analysis in the PRIMER[®] software package.

Differences in lobster abundance and the ratio of individuals in each size class between exploited and non-exploited habitats were analysed using log-linear modeling and ANOVA, while the comparison of urchin population density and size frequency distribution between the reserve and non-reserve habitats, was made using non-parametric ANOVA and Kolmogorov-Smirnov techniques in the statistical package SAS[®].

Pair-wise comparison of treatment groups in the lobster abundance ANOVAs were conducted using the Ryan-Einot-Gabriel-Welsch (Day and Quinn, 1989) multiple range comparison test to minimize Type I error. Significant differences are reported following necessary adjustment to alpha when $P < 0.05$.

¹ Data were non-standardised, fourth-root transformed based on Bray-Curtis dissimilarities.

2.4 Results

2.4.1 Broad-scale patterns of abundance of urchins and their predators

Pooling all data across all regions revealed a clear triangular relationship, with a negative slope on the upper surface, in the abundance of total predators and sea urchins (Figure 2.2a). Quantile regression (90th quantile) indicated that the negative slope of the ceiling of the distribution is highly significant. The relationship is heavily weighted in the lower left corner indicating that if predator density is low urchin density can be quite variable, when predator abundance exceeds 20 individuals per 200 m² urchin density is restricted below approximately 1 individual per m². There are no situations where high abundances of predators were found with high densities of urchins.

The distribution of the relationship between total lobster abundance and urchin density resembles a similar pattern as for total predators and urchin density (Figure 2.2b). Urchin density is variable when very few lobsters are present, but at high lobster abundance there are always fewer urchins. In contrast, there is no clear relationship between total fish predators and urchins (Figure 2.2c). This suggests that fish are relatively less important than are lobsters in describing the overall pattern between total predator abundance and urchin density at a broad spatial scale.

In separating the effect of total lobster abundance on urchin density, lobster abundance data were separated into size classes. Small lobsters were found in relatively high abundances at both the reserve and non-reserve sites (Figure 2.2d). The relationship between medium sized lobster abundance and urchin density

showed a similar pattern as small lobsters however lobsters above minimum legal size were relatively rare at non-reserve sites (Figure 2.2 e,f).

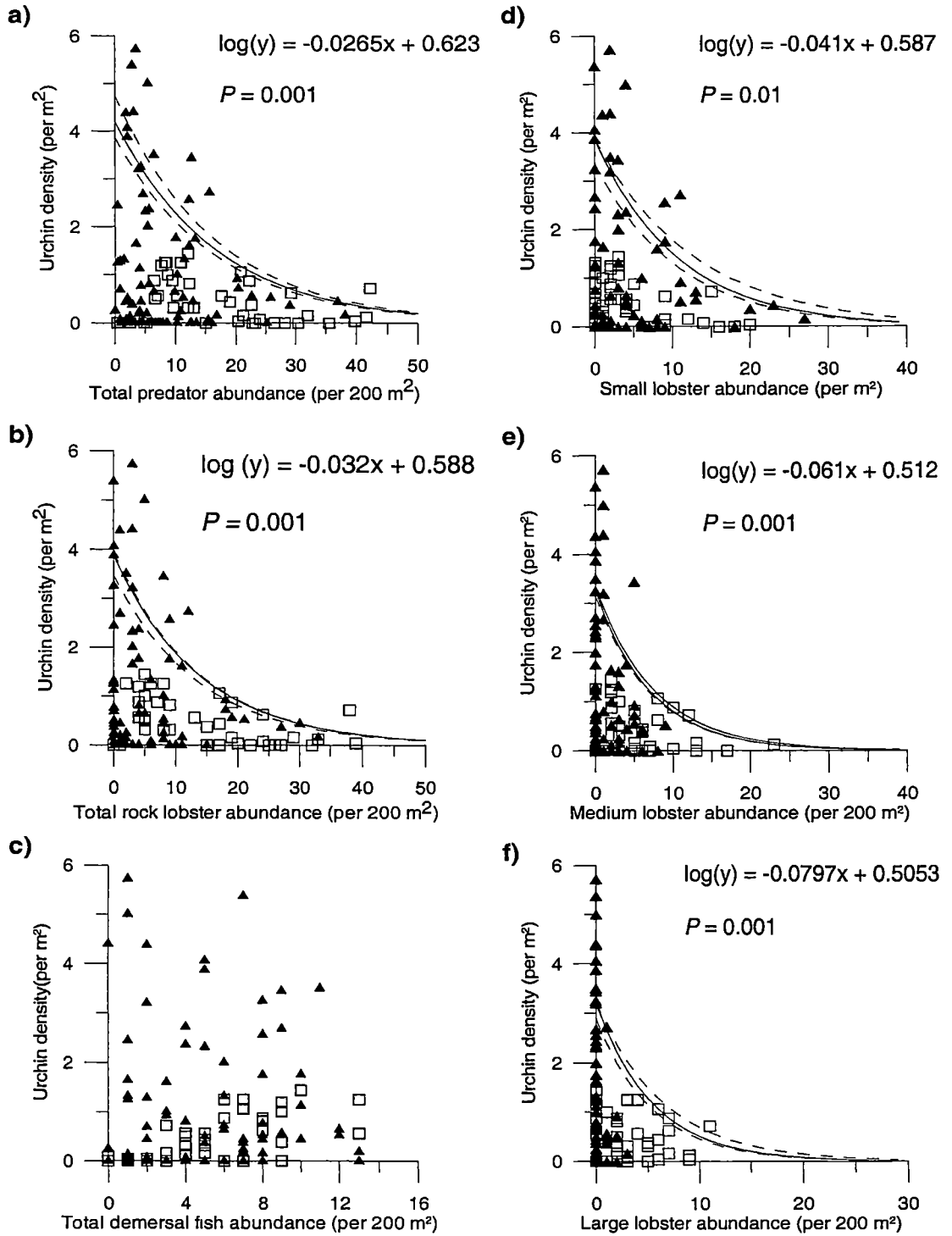


Figure 2.2 Relationships between urchin density and predators across all regions, with upper limits plotted from quantile regression (90th quantile, 70% confidence limits). Relationships are shown between urchin density and (a) all predators; (b) total lobsters; (c) total demersal fish predators; (d) small lobsters (sub-legal, 90-105 mm CL); (e) medium lobsters (minimum legal size, 105-110 mm CL); and (f) large lobsters (>120 mm CL). Each data point is from a 16 m² quadrat (for urchins) associated within a 200 m² (lobster) or 500 m² (fish) survey area at non-reserve (▲) and reserve sites (◻).

2.4.2 Spatial variation of predator assemblages

Analysing the structure of predator assemblages when data were pooled within each level of reserve (reserve and non-reserve) and across all the regions, using non-parametric multivariate analysis of variance (NPMANOVA), revealed significant differences in predator assemblage between reserve and non-reserve sites ($F_{1,128} = 3.22$, $P = 0.023$). Non-reserve sites displayed a higher within-group dissimilarity than reserve sites suggesting predator assemblages become heterogeneously distributed when exploited, compared to homogeneously distributed predators assemblages at protected sites. To interpret the complex nature of spatial variation in predator assemblages between reserve and non-reserve sites the data were separated into individuals regions for further analysis.

2.4.2.1 Derwent Estuary

Significant differences between predator assemblages from reserve and non-reserve sites were found, when data were pooled across sites within each level of reserve (NPMANOVA; $F_{1,38} = 6.49$, $P = 0.002$). Analysis of the percentage of similarity (SIMPER) between predator assemblages at reserve and non-reserve sites found total lobster abundance to be the major factor discriminating between the two levels of reserve accounting for over 23% of the dissimilarity between the two levels of reserve. Total lobster and leatherjacket abundance were higher inside the reserve compared to non-reserve sites, all other species were found in higher abundance outside the reserve.

When the data were separated into individual sites a significant difference was found between each non-reserve site and the reserve ($F_{3,36} = 11.99$, $P < 0.001$)². However, SIMPER analysis found no consistent pattern in the dominant species discriminating between reserve and non-reserve sites.

2.4.2.2 Mercury Passage

Significant differences in predator assemblages were found between reserve and non-reserve sites when data were pooled across each level of reserve (NPMANOVA; $F_{1,48} = 7.30$, $P < 0.001$). Non-reserve sites were found to have a greater within-group dissimilarity than the reserve sites indicating predator assemblages were more spatially variable when exploited.

The SIMPER technique indicated total lobster abundance accounted for approximately 40% of the difference in predator assemblages between reserve and non-reserve sites. The average abundance of all species were higher inside the reserve compared to outside the reserve except for leatherjackets which accounted for 17% of the difference between reserve and non-reserve sites. When combined demersal fish account for approximately 49% of the dissimilarity between the reserve and non-reserve sites, decapod crustaceans accounted for approximately 46%. Although demersal fish account for a greater percentage of dissimilarity five species comprise the group compared to only two species of crustaceans.

Using SIMPER analysis total lobster abundance was the major group separating predator assemblages inside the reserve from each non-reserve site within the

² Adjusted alpha for pair-wise comparisons = 0.0017.

Mercury Passage. Compared to some of the exploited sites, lobsters were 30 times more abundant inside the reserve. However, demersal fishes were found to be relatively less important in discriminating between reserve and non-reserve sites than average lobster abundance. The order of importance within the fish species was not consistent in pair wise comparisons made between reserve and non-reserve sites.

2.4.2.3 Bicheno

Contrary to results from the other two regions in which predator assemblages in reserve and non-reserve sites were highly significantly different, only slight significant differences between predators assemblages were found in the Bicheno region ($F_{1,38} = 3.18$, $P = 0.043$). SIMPER analysis found total lobsters abundance to be the major factor discriminating reserve from non-reserve sites with the average lobster abundance inside the reserve three to five times higher than the exploited sites and accounted for between 25% and 30% of the dissimilarity between habitats. Of the other species surveyed only purple wrasses were found in greater numbers inside the reserve compared to non-reserve sites.

2.4.3 Broad scale patterns in lobster abundance

Log-linear modelling of average lobster abundance data revealed significant differences between regions along the east coast. The most parsimonious model included three main effect terms, region, reserve and lobster size since the three way interaction of region*reserve*size was not significant in model fit. When pooled across all other factors the Derwent Estuary was found to have two to three times more lobsters compared to both the Bicheno and Mercury Passage regions where lobsters were in similar abundance.

The abundance of sub-legal size lobsters (small, 90-105 mm CL) was three times higher than large lobsters (>120 mm CL) when pooled across all regions and both levels of reserve. The average abundance of minimum legally sized lobsters was ca. 2.25 times the average abundance of large lobsters across all regions and levels of reserve. The ratio of small to medium sized lobsters is close to 1:1 with a slight but non-significant trend towards small lobsters.

Analysis of the lobster abundance data using a three way ANOVA model indicated significant region*reserve and region*size interactions ($F_{2,372} = 7.84$, $P < 0.001$ and $F_{4,372} = 9.12$, $P < 0.001$ respectively, Figure 2.3). To interpret the effect of protection (reserve) and location (region) in determining average lobsters abundance the data were separated into the three separate regions.

2.4.3.1 Derwent Estuary

Small lobsters were significantly more abundant inside the reserve than medium and large size lobsters, which were found in similar abundance (Figure 2.3a). Sites outside the reserve had significantly fewer large lobsters compared to either small or medium size individuals, which were found in similar abundance. Lobsters in each size class were found in significantly higher abundance inside the reserve compared to non-reserve sites.

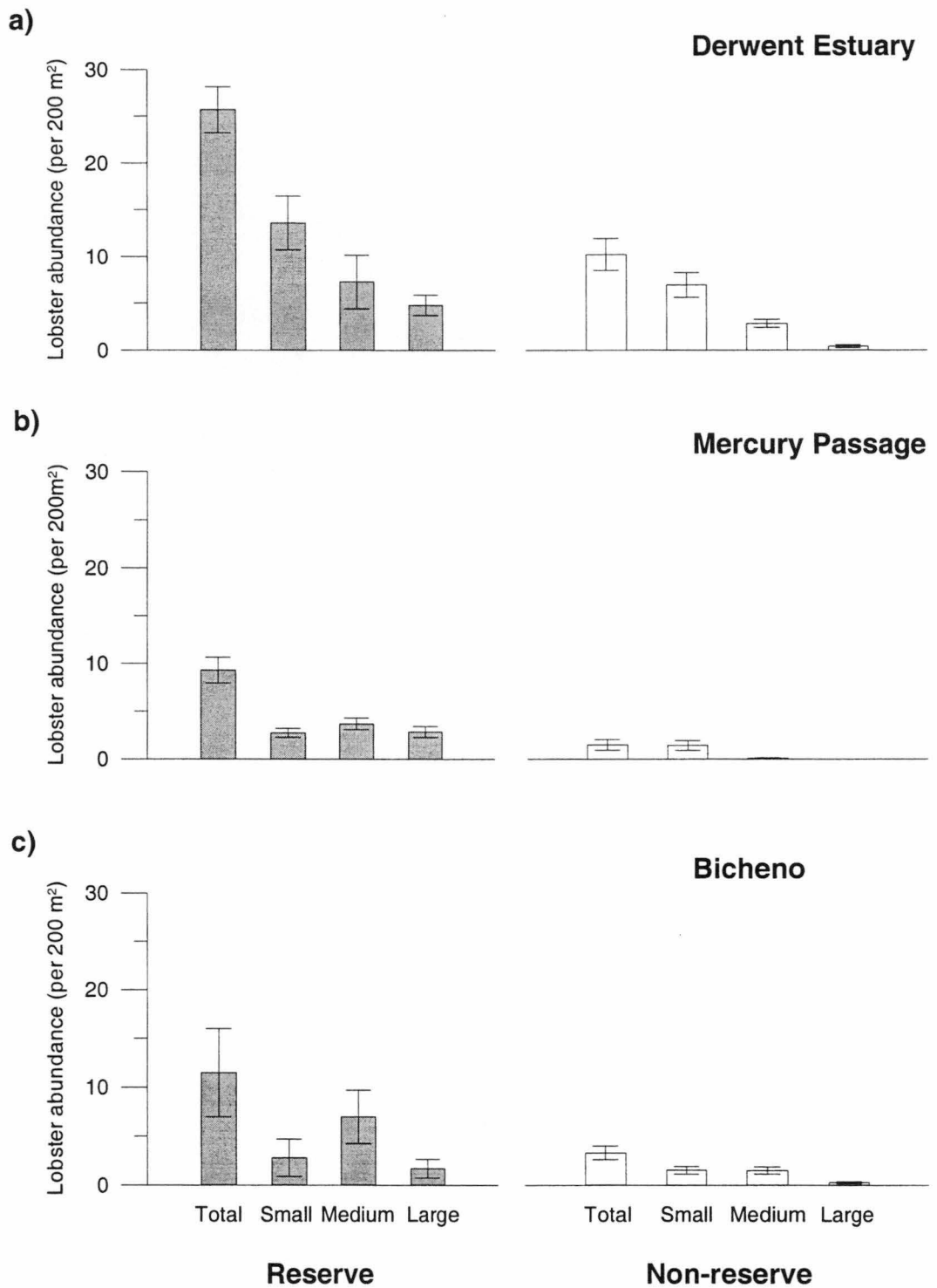


Figure 2.3 Average abundance of small, medium and large lobsters (per 200 m² ± SE) pooled across sites within each level of reserves within a) Derwent Estuary, b) Mercury Passage, and c) Bicheno.

2.4.3.2 Mercury Passage

Pooled across both levels of reserve, no significant difference existed between the abundance of lobsters within the three size classes (Figure 2.3b), while protection

from exploitation was found to significantly increase the abundance of lobsters in all three size classes.

2.4.3.3 Bicheno

Significantly more medium sized lobsters were found inside the reserve compared to either small or large individuals (Figure 2.3c). In comparison the ratio of lobster abundance between the three sizes classes at sites outside the reserve was not significantly different. The abundance of medium sized lobsters was higher inside the reserve than at non-reserve sites. However, both small and large sized lobsters were at similar abundance inside and outside of the reserve.

2.4.4 Urchin population structure –the effect of reserves and spatial scale

Comparison of urchin size frequency distributions, on data pooled across all sites within each level of reserve across all three regions, indicated a significant difference between reserve and non-reserve sites (Figure 2.4, $N=1992$, 1762-nonreserve, 230-reserve, $P < 0.001$). Non-parametric analysis of variance found urchins inside reserves have larger mean test diameters compared to urchins at non-reserves sites (81.7 and 76.6 mm TD respectively, $F_{1,1990} = 30.38$, $P < 0.001$).

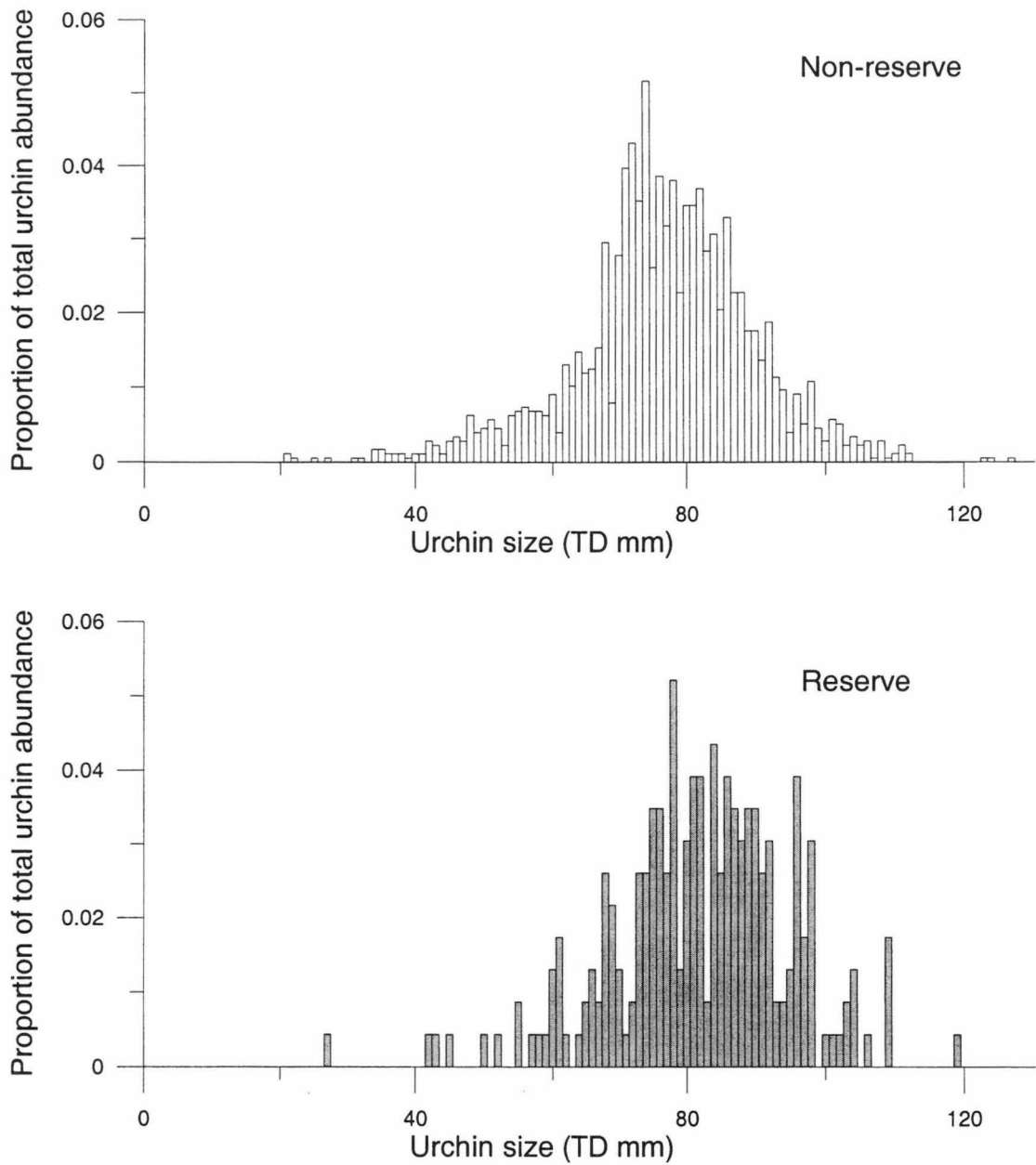


Figure 2.4 Urchin size frequency distributions, pooled across regions within each level of reserve (reserve and non-reserve). Urchin size frequencies represent the proportion of total urchin abundance, with distributions found to be significantly different (Kolmogorov-Smirnov test $N = 1992$; 1762-nonreserve, 230-reserve, $P = 0.0001$).

The broad scale pattern in urchin density was examined using a 1-way Model III ANOVA with reserve(region) as a random factor, which found no significant difference in urchin density between the 13 sites. However, the variance explained

by each source of the model is of greater biological interest. Results from the analysis show at large spatial scales very little variance in urchin density is explained (Table 2.1). On progressively small scales the amount of variance in urchin density increases with approximately 30% at a scale of 10^3 m (distance between reserve and non-reserve sites). On the scale between replicate transects (50 m), over 65% of the variance in urchin density across all sites within the three regions is explained.

Table 2.1 Variance components of urchin density data pooled across sites with each level of reserve and across regions.

Source	Mean Square	ω
Region	4390.76	4.07
Res(Region)	1767.20	28.95
Error	332.11	67.10

Interpreting the biological effect of urchin predator abundance in determining urchin population density on broad spatial scales is complex given the greatest variance in urchin density is explained on the smaller spatial scales. Therefore the data were separated by region and reanalysed.

2.4.4.1 Derwent Estuary

Preliminary analysis of the data found heterogeneity in relationship of group standard deviation and group means and were log transformed to stabilise variance before analysis using 1-way ANOVA. Significant differences in urchin density were found between the four sites ($F_{3,36} = 8.25$, $P < 0.001$), with a Ryan-Einot-Gabriel-Welsch multiple range test detecting significantly lower urchin density inside the Crayfish Point reserve, where predator abundance is elevated, compared with the non-reserve sites. The three non-reserve sites were not significantly different in their urchin density.

Due to the low number of urchins found in the reserve interpretation of any differences in mean urchin test diameter and the distribution of urchin size frequencies is difficult. However, when the analysis is performed no difference in mean urchin test diameters or the distribution of urchin size frequencies between reserve and adjacent exploited sites is found (Figure 2.5a, $P = 0.099$, $N = 1126$).

2.4.4.2 Mercury Passage

Significant differences in urchin population density were found when data were pooled across sites within each level of reserve ($F_{4,45} = 4.59$, $P < 0.01$). Analysis of the data separated by site within each level of reserve (Ryan-Einot-Gabriel-Welsch Multiple Range Test) indicated urchin density at Quarry Point was similar to the algal habitat at Stapleton Point but significantly higher compared to Lords Bluff, Magistrates Point (reserve), and Howells Point (reserve).

Analysis of the data pooled across sites within each level of reserve found the distribution of urchin size frequencies inside the reserve was significantly different compared to the adjacent exploited sites outside the reserve (Figure 2.5b, $P < 0.001$, $N = 851$), with urchins inside the reserve having significantly larger mean test diameters (reserve mean = 84 mm and non-reserve mean = 80 mm, $F_{1,850} = 6.07$, $P = 0.014$).

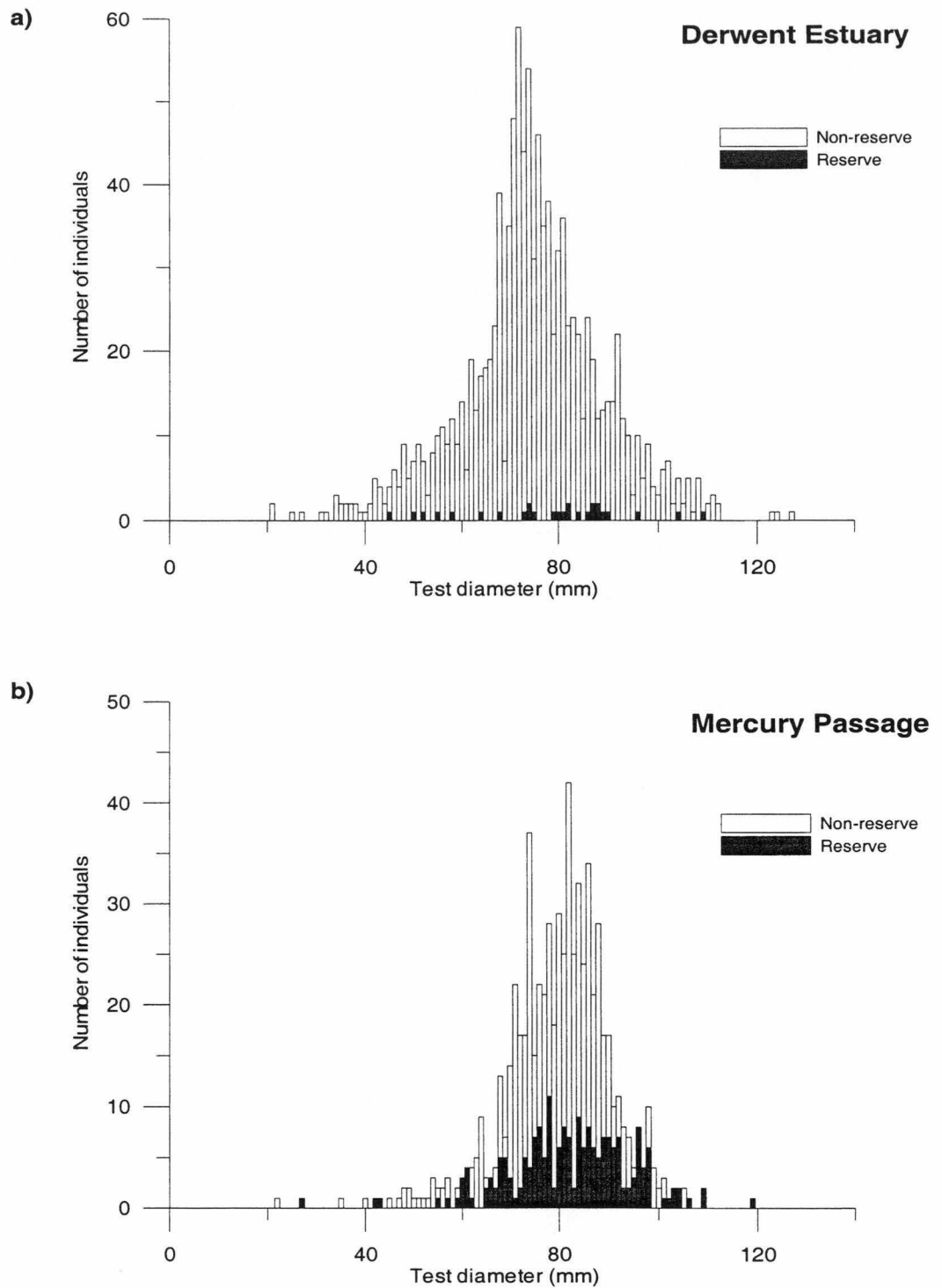


Figure 2.5 Urchin size frequency distributions for reserve and non-reserve sites in the a) the Derwent Estuary were not significantly different (Kolmogorov-Smirnov test $\text{Prob} > K_{sa} = 0.099$), and the b) Mercury Passage where distributions were significantly different (Kolmogorov-Smirnov test $\text{Prob} > K_{sa} = 0.0002$).

2.4.4.3 Bicheno

The abundance of urchins across all sites in the Bicheno region was not sufficient to conduct a meaningful analysis (15 individuals in 640 m² surveyed).

2.4.5 Sea urchins and predators in algal beds and adjacent urchin barrens habitat (outside reserves)

The broad picture to emerge from the Mercury Passage was that the average density of urchins was significantly higher on barrens compared to adjacent algal habitats, and barren sites, in general, support a greater abundance of predators (Figure 2.6). Total predator abundance within barren habitats appears to be dominated by the demersal fish, in particular wrasse and leatherjacket species. Although higher in barren habitats than the adjacent algal beds, no relationship between total predator abundance and urchin density could be identified.

Whilst demersal fish were relatively abundant in both habitat types, lobsters were scarce; those individuals located within the barren habitat were found to be below the legal catch size (pers. obs.). Total lobster abundance was relatively less important in discriminating between the predator assemblages on barrens and algal beds than demersal fish species accounting for a minor percentage (6%) of the dissimilarity between the two habitats.

When pooled across sites within habitat type (barren and algal beds), urchin size frequency distributions and average individual size were significantly different (Figure 2.7). Intermediate sized urchins (60-70 mm test diameter) appear to be underrepresented in the algal bed habitat in comparison to the barren habitat in which

the size class dominates the size frequency distribution. Juvenile urchins below 60 mm TD were rare in both habitat types.

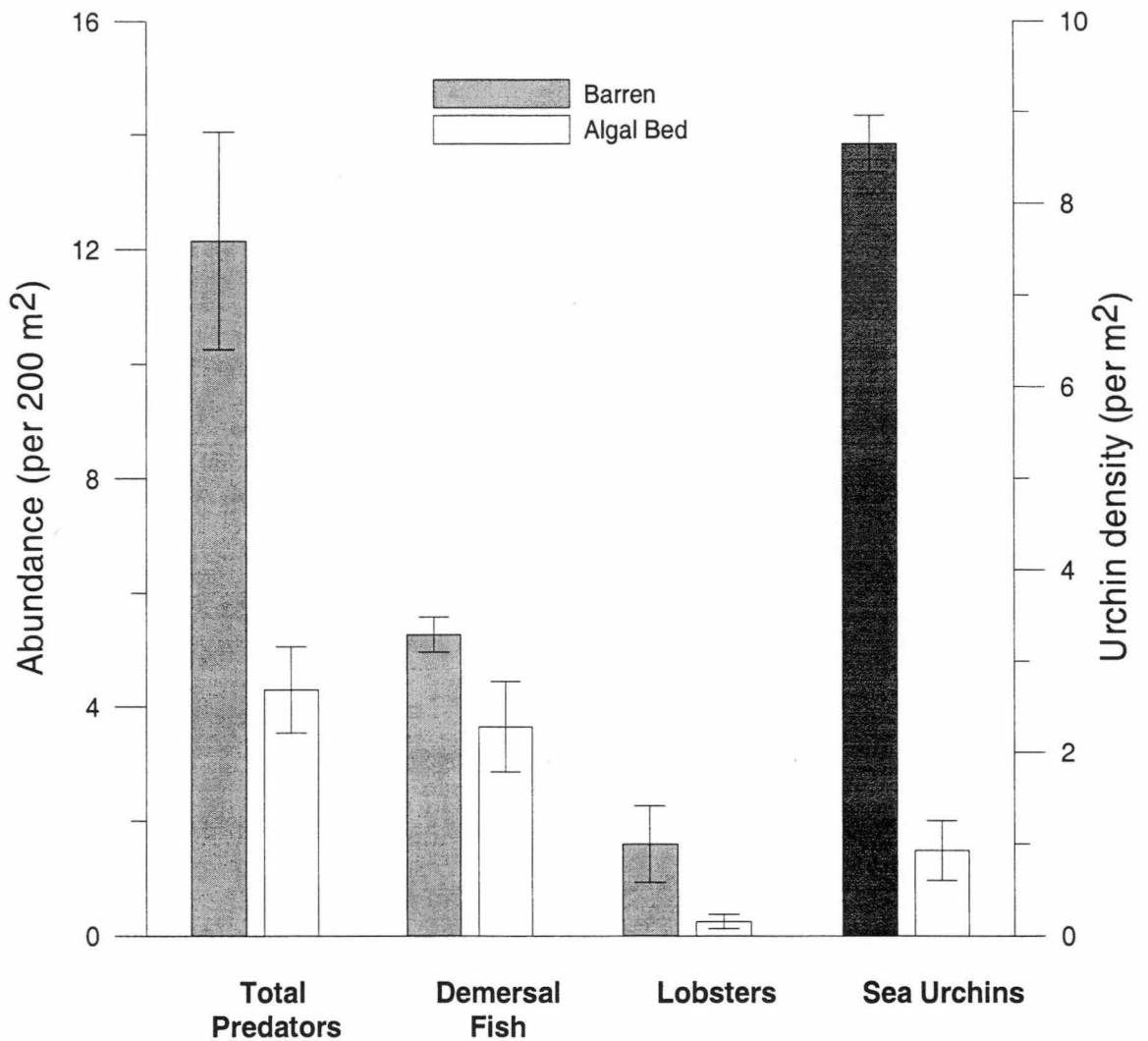


Figure 2.6 Average abundance of total predators (lobsters and demersal fish combined), demersal fish, rock lobsters and urchin density across two barren and two algal bed habitats (\pm SE). Total predators $F_{1,38} = 14.79$, $P < 0.001$; Demersal fish $F_{1,38} = 18.03$, $P < 0.001$; Lobsters $F_{1,38} = 3.97$, $P = 0.054$; Urchin density $F_{1,38} = 94.03$, $P < 0.001$.

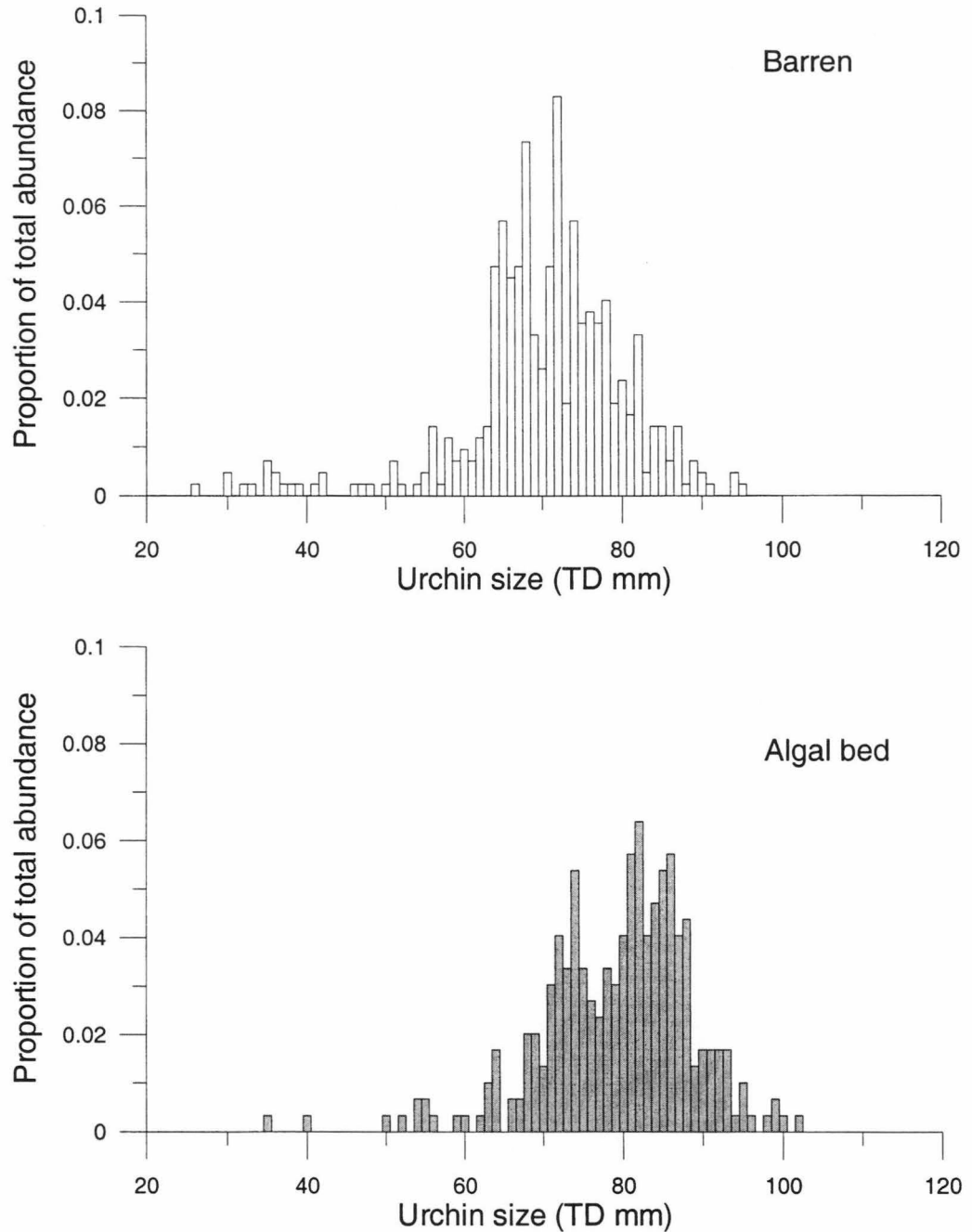


Figure 2.7 Urchin size frequency distributions from barren and algal bed sites (pooled within habitat type across locations). Test diameter frequencies are represented as proportions of total urchin abundance within each habitat type. Distributions were found to be significantly different using the Kolmogorov-Smirnov test ($\text{Prob} > K_{sa} = 0.001$). Urchins on barrens had significantly smaller mean test diameters compared to urchins in adjacent algal beds (69.9 mm on barrens and 84.9 mm in algal habitats; $F_{1,717} = 142.45$, $P < 0.001$ using NP-ANOVA).

2.5 Discussion

Over-exploitation of marine resources has resulted in significant shifts in the community composition of subtidal ecosystems and species extinction (Dayton *et al.*, 1995; Tegner *et al.*, 1996; Dayton *et al.*, 1998; Pauly *et al.*, 1998; Sala *et al.*, 1998; Steneck, 1998). Prohibition of exploitation via the establishment of marine protected areas (MPAs) can result in marked changes to the abundance of target and non-target species over varying temporal scales (Babcock *et al.*, 1999; Edgar and Barrett, 1997; Edgar and Barrett, 1999; Wallace, 1999; McClanahan, 2000; Karpov *et al.*, 2001; Rogers-Bennett and Pearse, 2001; Shears and Babcock, 2002), reviewed by (Halpen and Warner, 2002). The potential benefits of marine reserve establishment, as fisheries management tools, have been demonstrated for reef fishes (Bennett and Attwood, 1991; Polunin and Roberts, 1993; Roberts and Polunin, 1993; Russ and Alcala, 1996; Cole *et al.*, 2000; McClanahan, 2000; Paddack and Estes, 2000; Babcock *et al.*, 1999) and to a lesser extent in lobsters (Davis and Dodrill, 1989; Edgar and Barrett, 1997; Edgar and Barrett, 1999; Kelly *et al.*, 2000).

2.5.1 Broad-scale patterns of urchin and predator abundance and size structure

Establishment of four marine reserves on the east of Tasmania in 1991 resulted in significant changes in the population structure and abundance of both demersal fishes and rock lobsters (Edgar and Barrett, 1997; Edgar and Barrett, 1999). Significant increase in abundance and average size of rock lobsters were particularly noticeable in the largest reserve at Maria Island located within the Mercury Passage (Edgar and Barrett, 1999). However, the significant increase in lobster abundance recorded within Maria Island Reserve over a seven-year period has not been matched by a

significant reduction in urchin density. The general pattern in the distribution of total putative urchin predator abundance and urchin density found in this study, which represents a single point in time, does indicate a significant negative relationship exists. Habitats supporting relatively high abundances of putative predators such as *J. edwardsii*, *N. tetricus* and *N. fucicola* also support low densities of *H.*

erythrogramma. It is evident that as predator abundance decreases average urchin density increases but is highly variable. When predator abundance is significantly reduced by exploitation the average urchin density is no longer dependent upon predator abundance, rather factors such as habitat suitability, resources availability and physical factors may become more important in determining urchin density.

In separating lobsters and demersal fish, there was a clear relationship between urchin density and lobster abundance but not between urchins and demersal fish abundance. The observed independence of abundances of urchins and demersal fish at the broad spatial scale across regions does not necessarily infer that the same pattern will not hold at smaller spatial scales. Studies conducted across small spatial scales have shown the mortality of juvenile urchins to significantly decrease as a function of predatory fish abundance (Andrew and Choat, 1982; Shears and Babcock, 2002).

Another broad-scale effect of reserve to emerge is the relative reduction in the ratio of small to large sized lobsters between exploited and protected habitats. The smaller ratio of small to large sized lobsters inside the reserve compared to non-reserve sites may be a result of the competitive exclusion of small lobsters by larger conspecifics from preferred crevice space when total lobster abundance is elevated

by protection. However, under estimation of juvenile lobster abundance may occur when population density is elevated due to the formation of dense aggregations of the size class and aggregations that may be missed in surveying broad spatial scales (MacDiarmid, 1993). Independent of population density, adult lobsters are normally solitary and evenly dispersed through the habitat resulting in accurate representation in population surveys (Zimmer-Faust and Spanier, 1986).

2.5.1.1 Size structure and density of urchin populations

The direct effect of protection from exploitation has on increasing the abundance and average size of urchins has been demonstrated for urchin species with the establishment of marine protected areas (Rogers-Bennett *et al.*, 1995; Tuya *et al.*, 2000). The difference in urchin size frequency between the reserve and non-reserve sites in the current study is unlikely to reflect protection from fishing of the urchin directly since the local fishery targets soft sediment habitats rather than rocky reefs, and more likely to reflect differences is urchin mortality due to elevated predator density and average size inside the reserve.

When pooled across all sites within each level of reserve, across all regions, significant differences in predator assemblages were found between non-reserve and reserve, with non-reserve found to have greater within group dissimilarities compared to reserve sites of the predator assemblages present. Exploitation of urchin predators appears to increase the patchiness of the individuals within the habitat on similar scales to the patchiness in urchin abundance. Partitioning variance in urchin density to all the sources of error in the 1-way Model III ANOVA, resulted in over 65% of variance in urchin density explained on the smallest of spatial scale, which

supports the idea that distribution of urchins may be directly related to the distribution of predators.

2.5.2 Localised patterns of urchin and predator abundance

2.5.2.1 Derwent Estuary

The effect of protection in increasing the average abundance of urchin predators compared to adjacent exploited habitats was not consistent across all the species surveyed. Lobsters were more abundant inside the reserve compared to adjacent exploited sites, and *N. tetricus* and *N. fucicola* were found in higher abundance outside the reserve. The higher abundance of *N. tetricus* and *N. fucicola* at non-reserve sites, compared to the reserve, may be in response to the availability of preferred prey. Male *N. tetricus* were observed predating juvenile urchins at sites where urchin abundance was high. The lack of small and medium sized urchins inside the reserve may be responsible for the absence of demersal fish such as *N. tetricus* and *N. fucicola*.

The high abundance of lobsters supported within the reserve appear to predate on attached shellfish such as the blue mussel (*Mytilus edulis*) and the Pacific oyster (*Crassostrea gigas*) and rarely on urchins due to their low availability (pers. obs). The abundance of urchins inside the reserve was found to be significantly lower compared to non-reserve sites where urchin density was relatively high, however the average urchin size and frequency distributions could not be separated. We attribute the low density of urchins inside the reserve to high levels of predation mortality since lobster abundance inside the reserve was ca. 2.5 times greater compared to adjacent exploited habitats. Furthermore urchins inside the reserve have been exposed to high predator abundance and predation mortality through 30 years of

lobster fishing prohibition. The lack of significant difference in mean urchin test diameter and between the frequency distributions is likely to be affected by the low sample size ($n = 27$ reserve, $n = 1099$ non-reserve).

Pooled across all size classes the Derwent Estuary has significantly more lobsters compared to the other two regions, almost three times more than the Mercury Passage and twice that of Bicheno. The high lobster abundance in this region is primarily accounted for by the Crayfish Point reserve in which the lobster abundance has been elevated through 30 years of fishing protection (Zeigler, 2001), and the absence of commercial exploitation in habitats outside the reserve.

2.5.2.2 Mercury Passage

Whilst urchin density was found to be similar between reserve and non-reserve sites within the Mercury Passage, significant differences were found in the distribution of test diameter frequencies. Smaller mean urchin test diameters at non-reserve sites may be in response to the lack of predation pressure exerted on the medium-sized urchins due to low numbers of large putative urchin predators. Predator assemblages within the reserve are distinguishable from adjacent exploited sites primarily by the abundance of medium and large sized lobsters. Extended periods of lobster exploitation in the Mercury Passage region has resulted in lobsters greater than the minimum legal size to be rare in habitats outside of the reserve (Edgar and Barrett, 1997; Edgar and Barrett, 1999). If urchin predation mortality is size specific then the lack of large predators in exploited habitats may account for the size frequency distribution and mean urchin size to be skewed towards smaller sized urchins. Size specific predation by lobster is thought to account for bi-modal size frequency

distributions of some prey species (Griffiths and Seiderer, 1980) and has also been suggested to occur in urchin populations in the presence of predatory fish (Andrew and Choat, 1982).

2.5.2.3 Bicheno

As observed in the other two regions predator assemblages within the Bicheno region were significantly different in exploited habitats compared to the reserve. However, predator assemblages were more spatially variable inside the reserve compared to the adjacent exploited habitats. One possible cause of the greater patchiness of predators inside the reserve is the large variation in habitat in the 7-10 m depth range inside the reserve. Large expanses of flat rock within this depth range did not allow for an even distribution of decapod predators. Lobsters and crabs were found aggregated around the rare boulders and crevices that break up the large expanses of flat rock (pers. obs.) In contrast the only suitable adjacent reference sites (non-reserve), were not characterised by large expanses of flat rock allowing for those decapod predators that were present to be less aggregated.

The lack of suitable crevice space inside the reserve within the surveyed depth range may have been responsible for the lack of urchins located during the survey, the number of urchins found within the region across all sites was however very low. Consequently the abundance, mean size and size frequency distributions were not analysed to determine if patterns existed between the reserve and non-reserve sites. The lack of urchins located within the surveyed depth, within this region, may be due to many factors however it has been noted *H. erythrogramma* prefers sheltered to moderately exposed coastlines (Edgar, 2000); the Bicheno region experiences

infrequent heavy ocean swells which may prevent the urchin from establishing in high abundance. The species is found on exposed coastlines in moderate densities at depths greater than 15 m, depths that were not covered during these surveys.

2.5.3 Urchins barrens and adjacent algal beds outside of reserves

Results from the surveys indicate the average abundance of all predator species surveyed was significantly higher on barrens habitat compared to the adjacent algal beds. This result is contradictory to the notion that formation of barren habitat is a response to increased urchin density via decreased predation mortality. Theory suggests the opposite is a more likely situation where the predator abundances are greater in established algal beds with low urchin abundance (Mann and Breen, 1972; Lowry and Pearse, 1973; Estes and Palmisano, 1974; Breen and Mann, 1976).

Examination of the data (Figure 2.6) indicates demersal reef fish are the group of predators responsible for significant differences in predator assemblages between the two habitats. Average abundance of demersal reef fish was greater on barren areas and appears to be dominated by the presence of *N. tetricus*. Lobster abundance inside the kelp beds was on average lower compared to the barrens habitat, again a situation contradictory to common theory. The presence of lobsters in the barrens habitat was however restricted to samples from the Stapleton Point barren site, with small lobsters found on six of the ten transects. In surveying the four sites no lobsters were located above the minimum legal size limit. The absence of adult lobsters (>110 mm) may reflect the intense commercial and recreational fishing pressure within the Mercury Passage region.

The significantly higher urchin density in barrens habitat compared to adjacent algal beds does however support the hypothesis that elevated urchin density is responsible for the formation of barren grounds.

2.6 Conclusions

The broad-scale negative relationship between predator abundance and urchin density is dominated by the southern rock lobster *Jasus edwardsii*, while demersal fish were found to be relatively less important in describing the pattern in urchin density across the broad-scale of the southeast coast of Tasmania. On smaller spatial scales fish become relatively more important in discriminating between predator assemblages in habitats supporting significantly different urchin densities.

Lobster abundance was the major factor distinguishing between predator assemblages between reserve and non-reserve sites within each region. The effect of protection from exploitation was evident in average lobster abundance, in particular individuals above minimum legal catch size. The impact of increased average lobster sizes within the reserve on urchin populations is speculative, however the average size and size frequency of urchins inside the Maria Island reserve suggests a size-specific relationship exists.

Chapter 3

Predation on sea urchins (*Heliocidaris erythrogramma*) in kelp beds in Tasmania

3.1 Abstract

The formation of sea urchin ‘barrens’ on shallow temperate rocky reefs is well documented. Since they were first reported there has been much conjecture as to the possible mechanism(s) leading to urchin barrens, but there has been relatively little experimentation to critically test these ideas. One hypothesis that has provoked considerable discussion is that urchin population density is regulated by predation, and that a decline in the number of urchin predators can lead to urchin barrens. We conducted a series of manipulative experiments to determine whether predation mortality is an important mechanism structuring populations of the sea urchin *Heliocidaris erythrogramma* in Tasmania. Tethering both juvenile and adult urchins so that they were exposed to predation revealed that predation mortality is significantly greater inside no-take marine reserves compared to adjacent exploited habitats. When a range of sizes of urchins were exposed to three sizes of lobsters in a caging experiment, juvenile urchins were eaten more frequently than larger urchins by all sizes of lobster, while only the largest lobsters (>120mm CL) were able to consume large adult urchins. Tagging (but not tethering) juvenile and adult urchins in a marine reserve indicated that large adult urchins are at greater risk of predation mortality compared to juveniles, ostensibly because juveniles seek shelter in small crevices. In an experiment in which accessibility of rock lobster (*Jasus edwardsii*) and demersal reef-associated fish to urchins was systematically controlled, lobsters were shown to be relatively more important than fish as predators of adult urchins in

kelp beds in the marine reserves. We conclude that predators, and particularly rock lobsters, exert significant predation mortality on *H. erythrogramma* in kelp beds in marine reserves in Tasmania, and that adult urchins are more vulnerable than smaller juveniles.

3.2 Introduction

The structuring of shallow temperate subtidal reef systems by herbivores, and sea urchins in particular, is well documented (Shepherd, 1973; Lawrence, 1975; Breen and Mann, 1976b; Chapman, 1981; Andrew and Choat, 1982; Choat and Schiel, 1982; Duggins, 1983; Dean *et al.*, 1984; Harrold and Reed, 1985; Fletcher, 1987b; Vadas *et al.*, 1986; Chapman and Johnson, 1990; Andrew, 1991; Andrew, 1994). Sea urchins are important because their overgrazing can facilitate transition from diverse macroalgal beds to ‘barren grounds’ devoid of macroalgae and, unlike most other herbivores, their populations can persist after overgrazing (Johnson and Mann, 1982). While the phenomenon has been reported worldwide, the mechanism(s) underpinning barren ground formation are poorly understood. At least four hypotheses have been forwarded, which focus on either changes in urchin behaviour but not in population size, or increases in population density, or both. A shift in urchin behaviour from individuals feeding on drift algae and remaining cryptic, to emerging to form aggregations and graze destructively on attached plants, may result from decreased predator abundance (Bernstein *et al.*, 1981, but see Vadas *et al.*, 1986; Elner and Vadas, 1990) or decreased availability of drift algae (Harrold and Reed, 1985). Alternatively, changes in urchin population density and subsequent barren formation can potentially arise from massive recruitment events (Hart and Scheibling, 1988), or decreases in predator abundance (hypothesised by Mann and

Breen, 1972; Breen and Mann, 1976a; Wharton and Mann, 1981; Andrew and Choat, 1982). Because of links with fishing activity, most research concerned with the instigation of barrens has focused on predatory control of urchin populations.

Several guilds of predators have been identified as predators of urchins in temperate waters, including crustaceans, finfish and marine mammals (Breen and Mann, 1976a; Wharton and Mann, 1981; Andrew and MacDiarmid, 1991; Mann *et al.*, 1984; Cowen, 1983; Bernstein *et al.*, 1981; Estes and Palmisano, 1974; Tegner and Levin, 1983; Tegner and Dayton, 1981; Estes *et al.*, 1998; Dean *et al.*, 2000; Watt *et al.*, 2000; Mayfield and Branch, 2000; Shears and Babcock, 2002). However, while the keystone role of the sea otter (*Enhydra lutris*) as a predator of *Strongylocentrotus* species in the northeast Pacific is well established (Lowry and Pearse, 1973; Estes and Palmisano, 1974; Duggins, 1980; Estes *et al.*, 1998; Dean *et al.*, 2000; Watt *et al.*, 2000) the exact role of predators in controlling urchin abundances and, ultimately, the likelihood of barrens formation in other systems, is not so clear. Not only is the identity of the predator an important factor in determining predation mortality for particular prey, but so is the relative size of predators to the urchin prey (Pollock, 1979; Tegner and Dayton, 1981; Tegner and Levin, 1983; Zoutendyk, 1988; Griffiths and Seiderer, 1980; Mayfield *et al.*, 2001). Large predators are more likely to capture, handle and crush larger urchins (Tegner and Levin, 1983; Tegner and Dayton, 1981; McClanahan and Muthiga, 1989; Mayfield *et al.*, 2001).

The advent of no-take marine reserves provides important opportunities to critically test ideas about interactions between urchins and their putative predators in cases where predators are subject to fishing outside of reserved areas. In a recent review of

studies of 80 marine reserves, Halpern and Warner (2002) concluded that the average density, biomass, size of individuals and species diversity inside no-take reserves was higher than in reference sites subject to exploitation. The greatest difference between protected and exploited reference sites was in the biomass of exploited species which, on average, was 192% higher in reserves. This reflects that heavily targeted species can respond significantly to the cessation of exploitation once the main factor limiting population abundance is removed (Polacheck, 1990; Carr and Reed, 1993; Rowley, 1994).

In the absence of manipulative experiments, correlative patterns in urchin and predator abundances across broad spatial scales have been used to infer mechanistic relationships (Estes and Palmisano, 1974; Mann, 1977; Duggins, 1980; Wharton and Mann, 1981; Estes and Duggins, 1995; Babcock *et al.*, 1999; Mayfield and Branch, 2000). In a broad-scale survey covering a 200 km section of the east coast of Tasmania, the density of *Heliocidaris erythrogramma* was negatively associated with the density of total putative predators, including the commercially exploited southern rock lobster *Jasus edwardsii* but not demersal reef-associated fishes (Chapter 2). In the present study we undertake a suit of manipulative experiments, three of which involve manipulations in marine reserves, to estimate the impact of predators on *H. erythrogramma* in southeast Tasmania. We test whether potential and actual predation in unfished areas is likely to be an important source of urchin mortality, whether predation mortality rates vary with predator density and the relative size of predator and prey, and whether the commercially exploited rock lobster (*Jasus edwardsii*) is likely to be an important predator of this urchin.

3.3 Methods

Because appraisal of the effects of predators on urchins should, at very least, consider predation rates, size-specific predation and the relative importance of different predator guilds, several experiments are required. Multi-method approaches to single issues are powerful because they can overcome the shortcomings of single experiments (Diamond, 1986; Schmitt and Osenberg, 1996; Lodge *et al.*, 1998, Ruiz *et al.*, 1999, Ross *et al.*, 2003). Here we employ manipulative experiments to identify the processes underpinning the broad scale negative correlation between *Heliocidaris erythrogramma* and reef associated predators on the east coast of Tasmania, with a particular focus on rock lobsters given their specific broad-scale negative correlation with the urchins (Chapter 2).

3.3.1 Tethering experiment

Low predation mortality of urchins in reef habitat may indicate either that *H. erythrogramma* have few natural predators or, alternatively, that potential predation is high but urchins are able to avoid predation, e.g. by seeking shelter. To distinguish between these possibilities, urchins were tethered in the open and prevented from seeking shelter.

Mortality of tethered urchins was examined in two regions on the east coast of Tasmania, viz Mercury Passage (October - November 2000) and in the Derwent Estuary (December 2000 - January 2001). Within each region two areas were selected, one supporting a high density of predators (no-take reserve) and an adjacent area open to fishing with a relatively low predator density. The Maria Island Marine Reserve (42° 35' S, 148° 03' E) within the Mercury Passage and the Crayfish Point

Reserve (42° 95' S, 147° 35' E) within the Derwent Estuary were utilised as areas supporting relatively high densities of urchin predators. Within each area, two 20 m transects were deployed randomly approximately 50 m apart on rocky reef. Along each transect were placed 50-tethered urchins comprising 25 juveniles (test diameter 20-60 mm) and 25 adults (test diameter 65-100 mm). Within each region, all animals were taken from a non-experimental area nearby to the experimental area.

Urchins were tethered using a modification of the method described by Ebert (1965). Two holes were made in the test using a 1.25mm hypodermic needle attached to a pneumatic drill. The needle passed through the test close to the maximum ambital radius between the oral and aboral surfaces through an interambulacral plate, and exited the test on the aboral surface. Through the needle was passed 100 mm of 0.45 mm diameter monofilament line. The monofilament line was attached to a very fine stainless steel wire trace 200 mm in length (through a small loop at one end of the trace). The two ends of the monofilament loop were then secured by crimping with size No.4 brass leader sleeves. Each tether was identified individually by numbered coloured flagging tape attached to the free end of the wire trace. To prevent urchins from seeking shelter a small weight comprised of several links of 12 mm galvanised steel chain was attached to the free end of the wire trace.

Mortality was assessed twice over a fortnight period (7 and 14 days) by locating tethers and recording the state of the urchin attached. Tethers found with no urchin attached were recorded as mortalities.

3.3.2 Tagging experiment – urchins marked but not tethered

Since urchins are normally cryptic within reef habitat the effect of seeking refuge in reducing the likelihood of predation mortality could not be examined in the tethering experiment. Tagged urchins, allowed to access refuge within the reef habitat, were placed at the same sites described in the tethering experiment to determine if refuge was significant in reducing predation mortality.

The method used to tag urchins was identical to that for tethering the urchins (above) except that the free end of the wire tag was had no weight attached. Using the same transects as the previous experiment 60-tagged urchins were placed at random distances on each transect comprising 30 juvenile (test diameter 20-60 mm) and 30 adult (test diameter 65-100 mm) urchins. At the randomly located positions tagged urchins were placed into the nearest suitable crevice within the substrate to ensure that individuals could seek shelter.

3.3.3 Size-dependent predation by lobsters

Size-specific predation by lobsters was examined in a caging experiment conducted at Lords Bluff in the Mercury Passage (42° 31' S, 147° 59' E) in January 2001.

Cages were constructed from a steel frame measuring 1 m x 1 m at the base and 0.5 m high covered in 5 mm plastic mesh. Secured around the inside bottom edge of each cage was a flexible 150 mm skirt boarded by 8 mm chain to prevent lobsters escaping from the cages during the experimental period.

Each cage was placed on a suitable patch of reef so that the steel frame of the cage was resting on relatively flat substratum. Five urchins from each of three size classes (20-60 mm, 61-80 and 81-100 mm) were placed in each cage. Cages were left

overnight to ensure no animals could escape from the cages. A single post-moult lobster (*Jasus edwardsii*) of a designated size class was then added to each cage. There were three replicate cages of each size class of lobster, and size classes were denoted as juvenile (J₁; carapace length (CL) 90-105 mm), adult class 1 (A₁; CL 105-110 mm), and adult class 2 (A₂; CL >120 mm). On the east coast of Tasmania male *J. edwardsii* undergo an annual moult during November and December and feeding rates of the lobsters are thought to increase in the post moult period. The experiment was established early in January 2001 using post moult male lobsters to ensure that lobsters would be feeding.

Mortality of urchins was assessed daily for one week then again after 14 days upon which the total number of urchins in each size class remaining in each cage was recorded. Predated urchins found during the experimental period were removed from cages but not replaced.

3.3.4 Relative importance of fish and lobsters - large caging experiment

A caging experiment was conducted within the Maria Island Marine Reserve at Magistrates Point (42° 34' S, 148° 03' E) between March and May 2001. Three replicates of all possible combinations of the presence and absence of rock lobsters and demersal fish, and unmanipulated controls, were allocated randomly to 15 experimental plots each 3 m x 3 m.

For all treatments except the unmanipulated control plots, the experiment used flexible mesh cages with a base measuring 3 m x 3 m and sides 1.5 m tall. Cages were constructed of netting mesh (8 mm) anchored to the reef by a skirt of 12 mm galvanised chain. A 150 mm inward folding skirt (of the same mesh) boarded by 8

mm chain prevented animals from entering or leaving the cages at the substratum interface. Each cage had a similar inward folding skirt (but without the chain) on the top of the cage to prevent lobsters and urchins from escaping the cages. Treatments requiring the exclusion of either lobsters and/or fish from the experiment plot, and the containment of lobsters inside cages, had a mesh roof attached to the top of the cages (of similar material to the walls). Fish inclusion treatments allowed individuals free access to the substrate but did not confine them to the experimental plots.

To control for the effect of caging on urchin mortality, a partial cage treatment was included which allowed both lobsters and fish access to the experimental plot.

Comparison of urchin mortality in partial cages with the unmanipulated control plots was used to assess the effect of caging. Partial cages were identical in construction to those used for the other treatments except that large holes (ca. 2 m x 1 m) were cut in two opposing sides of the cage to allow free movement of both lobsters and fish through the cage. Roofs were not fitted to these partial cages, allowing further access of fish.

Experimental plots were cleared of all urchins and lobsters prior to starting the experiment. Each experimental plot was then stocked with a total of fifteen urchins to give an overall urchin density of $1.7 \text{ individuals m}^{-2}$, which is the mean density at the site (see Chapter 2). Five urchins were selected from each of three size classes, juvenile (J_1) 40-60 mm, adult class 1 (A_1) 61-80 mm and adult class 2 (A_2) 81-100 mm. Two adult lobsters ($CL > 120 \text{ mm}$) were placed into the appropriate treatment cages to ensure the presence of at least one lobster inside the cage at all times which resulted in a density of $0.22 \text{ lobsters m}^{-2}$. The mean background density of lobsters at

the site was ca. 6 times lower than the density inside experimental cages (Barrett pers. comm.). Unmanipulated plots (control plots) were exposed to background densities of demersal fish and 0.037 rock lobsters m⁻².

Urchins were allowed to acclimate to the experimental plots for 24 hours before the addition of lobsters. The number of urchins from each size class was recorded after the acclimation period, and all individuals were accounted for. Urchin mortality in experimental plots was assessed weekly over a two-month period.

3.3.5 Size frequency distributions of urchin populations within the Mercury Passage

Size structure of five urchin populations within the Mercury Passage, three from fished habitats (Quarry Point 42° 34' S, 147° 54' E; Stapleton Point algal bed 42° 35' S, 147° 55' E; Lords Bluff algal bed 42° 31' S, 147° 59' E), and two from within the Maria Island Maria Reserve (Magistrates Point 42° 34' S, 148° 03' E; Howells Point 42° 36' S, 148° 02' E) were estimated from 10 randomly placed 16m² quadrats (Chapter 2). The test diameter (TD) of each individual was measured to the nearest millimetre using knife-edge callipers. Test diameter measurements of all urchins across the fished sites were pooled to generate a size frequency distribution to which a similar distribution generated by pooling the urchin sizes from the protected sites was compared.

3.3.6 Data Analysis

Urchin mortality from the tethering and tagging experiments was analysed using logistic modeling to determine the significance of different overall mortality rate among experimental treatments.

Size-specific predation by the lobster *Jasus edwardsii* in the small-scale caging experiment was examined using both a split-plot ANOVA to compare mean urchin losses, and a logistic model to compare mortality rates pooled across replicates of identical lobster ‘treatments’. For the ANOVA’s, the relationship between standard deviation and means of treatment groups was used to determine the appropriate transformation to stabilise variances, and transformed data were checked for both normality (using normal probability plots) and homoscedasticity. Transformations are expressed in terms of the untransformed variable, Y.

Differences in urchin population size structure and mean urchin size in fished and protected habitats were analysed using Kolomogorov-Smirnov and non-parametric ANOVA techniques.

The relative importance of rock lobsters and demersal fish as urchin predators was assessed using both a three-way ANOVA and logistic model. The ANOVA included fixed main effects of fish (2 levels: presence and absence), rock lobsters (2 levels: presence and absence), and urchin size (3 levels: small, medium and large), and compared mean numbers of surviving urchins among treatments. The logistic model compared survival of urchins pooled across replicates of the same treatment. We compared means of treatment groups after ANOVA using the Ryan-Gabriel-Elliot-Welsh procedure (‘Ryan’s test’) for multiple range tests (Day and Quinn, 1989).

The statistical package SAS[®] was used for all analyses.

3.4 Results

3.4.1 Tethering experiments

When urchins were tethered and unable to escape into shelters the likelihood of urchin mortality was significantly higher inside the marine reserves compared with adjacent exploited habitats (Figure 3.1). In analysing the complete data set with a logistic model, the full model failed to converge the 4-way interaction term, and so derivation of parameter estimates was problematic. Accordingly separate analyses were undertaken for each region.

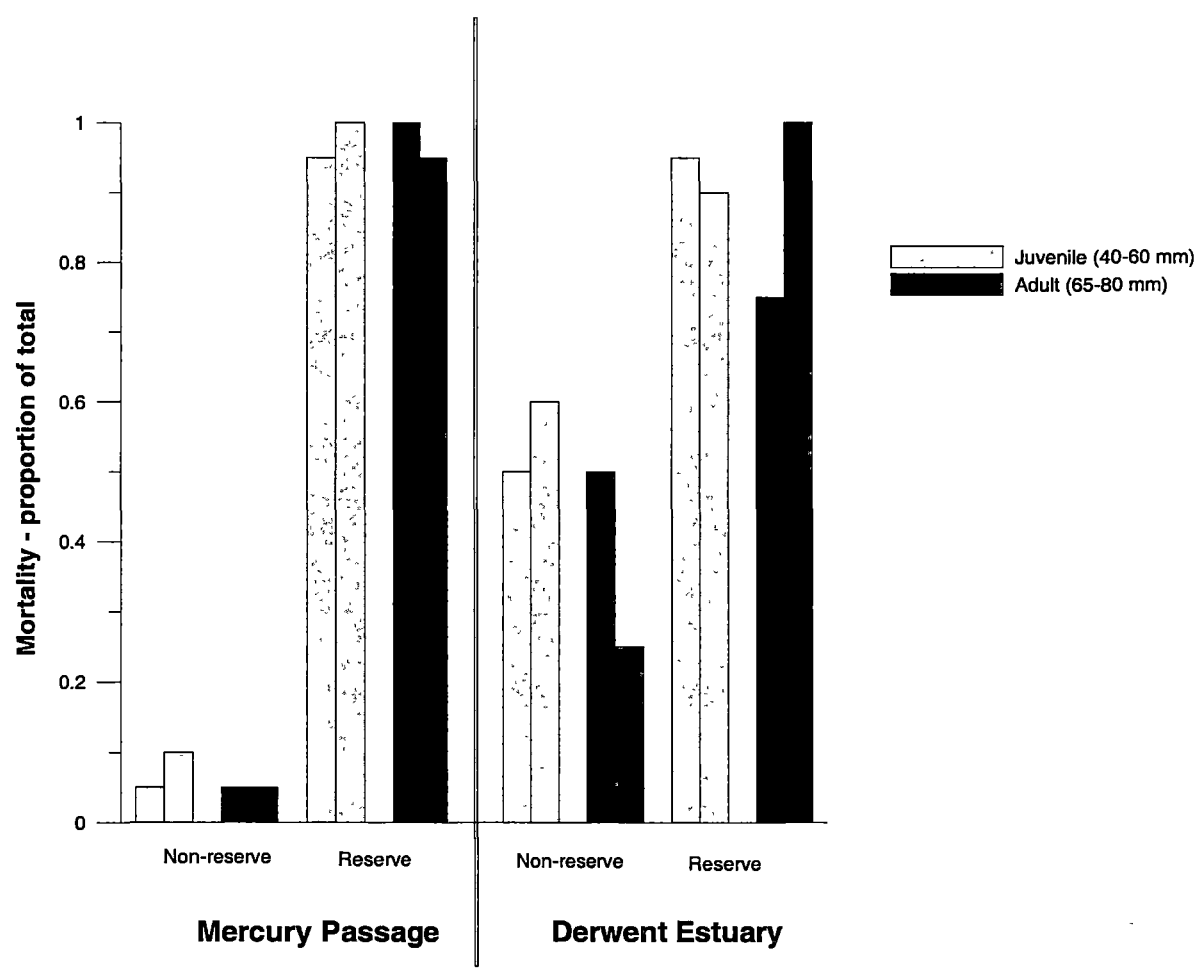


Figure 3.1 Comparison of mortality of tethered urchins between regions, between reserve and non-reserve sites, and among urchin size classes (sizes are test diameters). All 25 tethered urchins from each size class on each transect were recovered. Each bar represents a single transect.

For the Mercury Passage the most parsimonious model included the effect of reserve ($\chi^2 = 165.4703$, $df = 1$, $P = 0.0001$), while all other main effects and interaction terms could be removed without significantly affecting the fit of the model. This model predicted that the chance of urchin mortality inside the reserve is ca. 610 times that of adjacent fished areas ($\chi^2 = 54.7997$, $df = 1$, $P = 0.0001$). There was no evidence that urchin size or position of the transect influenced the mortality of urchins tethered in the open.

Results were more complex for a similar experiment conducted in the Derwent Estuary, for which the full model identified that the 3-way interaction of reserve*size*transect as significant ($\chi^2 = 8.1614$, $df = 1$, $P = 0.004$). To interpret this, separate analyses were undertaken for reserve and non-reserve areas. In the reserve, the 2-way interaction of size*transect was significant in the fit of the model ($\chi^2 = 5.6837$, $df = 1$, $P = 0.0171$). The model predicted that mortality of juvenile urchins inside the reserve was ca. 2×10^{11} greater than that of adult urchins, but that the effect is spatially variable at the scale of separation of transects (ca. 50 m).

For the adjacent unprotected habitat where predators were less numerous the full model was not significant ($P > 0.1$) indicating that mortality of urchins in this area does not depend on either urchin size or the location on the reef.

3.4.2 Size-specific predation of urchins by rock lobsters

We examined the overall effects with ANOVA using a split-plot design (to account for the non-independence of the different size classes within cages). Estimates of likelihoods of mortality were obtained using logistic modeling.

The split-plot ANOVA indicates significant effects of lobster size ($F_{3,8} = 11.02$, $P = 0.003$) and urchin size on urchin mortality ($F_{2,16} = 18.42$, $P = 0.0001$), while the interaction of lobster size*urchin size was not significant ($F_{6,16} = 2.22$, $P = 0.095$).

The consistent pattern was that large urchins were eaten only by large lobsters, while all sizes of lobsters preyed heavily on small urchins (Figure 3.2). This pattern is explored in more detail through logistic modeling.

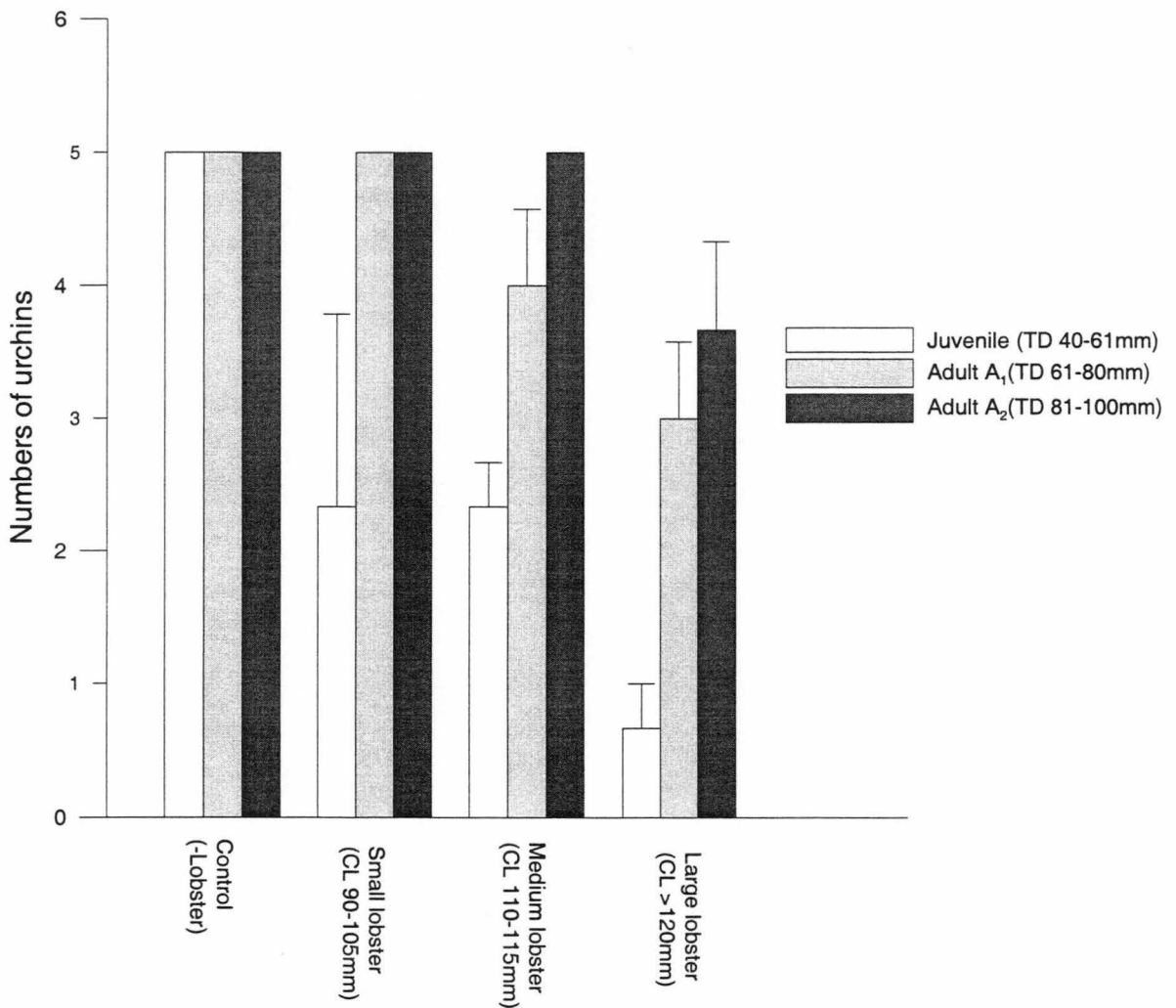


Figure 3.2 Size-specific predation by lobsters (*Jasus edwardsii*) on the sea urchin *Heliocidaris erythrogramma* (urchin sizes are test diameters). Urchin survival is plotted as individuals remaining in each size class after 17 days of exposure to lobster predation. There were initially 5 urchins in each size class in each cage. Data are means (\pm SE) of $n=3$ replicate cages of each treatment.

The full logistic model revealed no significant interactions and, in keeping with the results of the overall ANOVA, the parsimonious model required inclusion only of the

effects of urchin and lobster size. The reduced model predicts that the chance of mortality in the juvenile (J_1) size class is ca. 35 times greater than that in the large A_2 urchin size class ($\chi^2 = 24.25$, $df = 1$, $P = 0.0001$), while the chance of urchin mortality in the A_1 size class is not significantly different to that in the A_2 size class ($\chi^2 = 2.45$, $df = 1$, $P = 0.1175$).

To examine the relationship of increased predation ability within increasing size of lobster, the data were split into separate urchin size classes for analysis (Table 3.1).

Table 3.1. Approximate likelihood of urchin predation mortality due to lobsters of different size compared to the absence of lobsters. (Note that medium-sized lobsters (carapace length 105-110mm) represents the minimum legal size in the fishery).

Urchin size	Lobster size (CL mm)		
	Small (90-105)	Medium (105-110)	Large (> 120)
J_1 juvenile (40-60 mm)	8×10^{11}	8×10^{11}	6.5×10^{12}
A_1 adult (61-80 mm)	NS	3.4×10^{11}	9×10^{12}
A_2 adult (81-100 mm)	NS	NS	1.3×10^{12}

In breaking down the analysis into separate urchin size classes the model predicts the likelihood of mortality of juvenile urchins in the presence of large lobsters to be >8 times that in the presence of medium or small lobsters (Table 3.1). The likelihood of mortality of juvenile urchins in the presence of either small or medium lobsters were not distinguishable. The likelihood of A_1 adult urchin mortality is 27 times greater in the presence of large lobsters compared with medium lobsters, however juvenile lobsters (90-105 mm CL) were not able to successfully consume urchins > 61 mm TD. The ability of lobsters to handle urchin prey greater than >81 mm is limited to those individuals considerably larger than the minimum legal exploitable size (> 120 mm CL).

3.4.3 Tagging experiment

In both regions, urchin mortality was greater in habitats with more abundant predators (reserves) than in adjacent fished areas (with fewer predators; Figure 3.3). However, the effect of increased predator abundance on urchin mortality was greater in the Derwent Estuary than in the Mercury Passage. Differences in mortalities between regions, habitats (i.e. reserve vs. non-reserve) and urchin size classes were examined using logistic modelling.

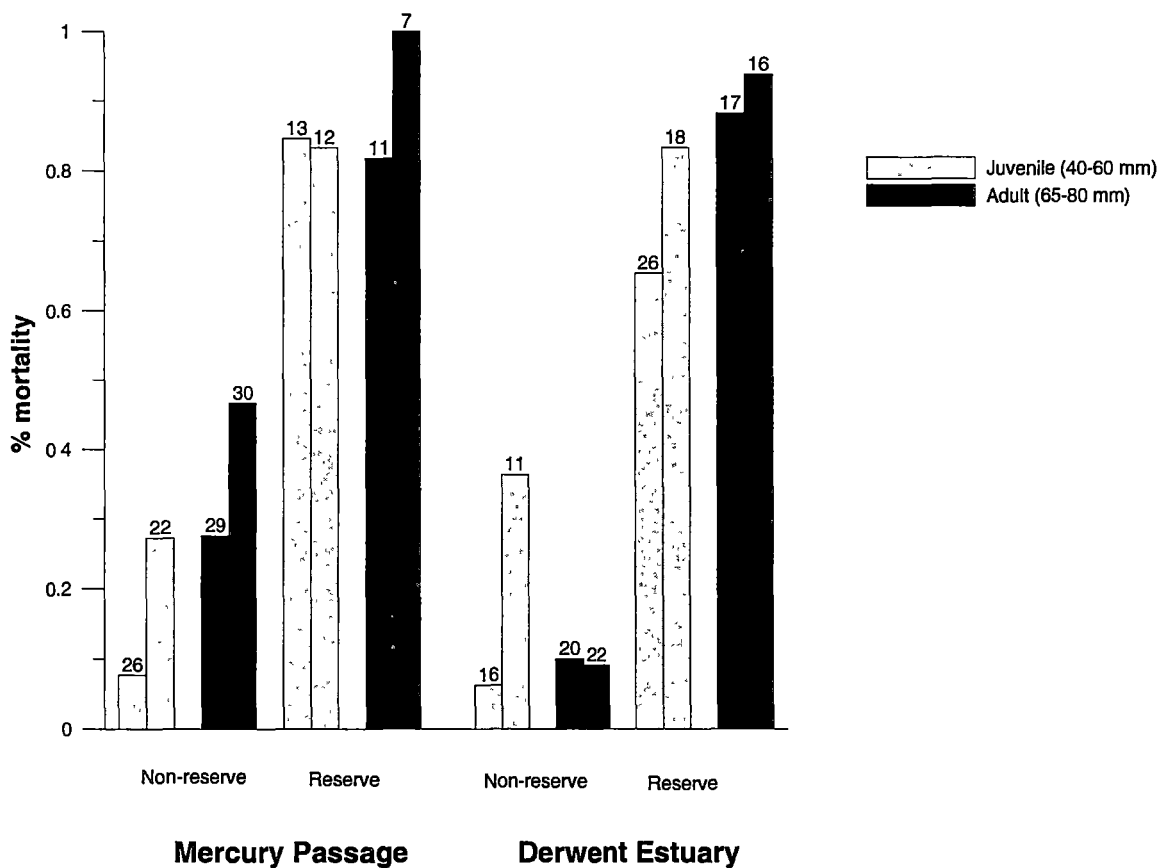


Figure 3.3 Comparison of mortality of tagged urchins between regions, between reserve and non-reserve sites, and among urchin size classes (urchin sizes are test diameters). The total number of tag returns for each transect/size class combination is displayed above each bar. 30 animals were initially deployed of each size class on each transect. Each bar represents a single transect.

The most parsimonious logistic model includes 3 of the 4 main effects of ‘reserve’, ‘size’ and ‘transect’. ‘Region’ was not significant in the model fit, indicating that

spatial variability at the scale of region, i.e. between the Derwent Estuary and Mercury Passage, was not significant in describing urchin mortality.

The logistic model predicts that the likelihood of mortality of juvenile urchins is significantly less than adults, with the chance of mortality of adult urchin 2.3 times that of the juveniles ($\chi^2 = 4.2720$, $df = 1$, $P = 0.039$). The model also predicts that urchin mortality inside the reserve is significantly greater than in adjacent fished areas by a factor of ca. 23 times ($\chi^2 = 84.8912$, $df = 1$, $P = 0.0001$). Interestingly, the logistic model also identified significant differences between replicate transects within site-treatment combinations ($\chi^2 = 8.3625$, $df = 1$, $P = 0.0038$), indicating significant spatial variation in urchin predation mortality at a scale of ca. 50 m.

Since we had an *a priori* interest in the difference between habitats (reserve vs. non-reserve) and not between regions we analysed each region independently to examine the biological effect of fishing. For the Mercury Passage the parsimonious logistic model included the main effects of reserve, size and transect, but interaction terms were not significant. The model predicts that the likelihood of urchin mortality inside the reserve is ca. 24 times greater than in adjacent fished habitats ($\chi^2 = 34.1367$, $df = 1$, $P = 0.0001$), that the chance of adult urchin mortality is ca. 3 times greater than that of juveniles ($\chi^2 = 5.1542$, $df = 1$, $P = 0.0232$), and that there is significant spatial variability in mortality between transects ($\chi^2 = 5.2931$, $df = 1$, $P = 0.0214$).

Results for the Derwent Estuary were slightly different. The most parsimonious model included the main effects of reserve and size, and two-way interaction term of reserve*size which was significant in the model fit ($\chi^2 = 4.6083$, $df = 1$, $P = 0.032$).

While ‘size’ was not significant as a main effect ($\chi^2 = 0.8048, df = 1, P = 0.3697$) it was included in the model because of the significance of the interaction term. This analysis estimated that mortality of adult urchins inside the reserve is ca. 8 times greater than that outside the reserve ($\chi^2 = 4.3610, df = 1, P = 0.0368$), while the likelihood of overall urchin mortality inside the reserve is 95 times that of adjacent fished areas. In the Derwent Estuary, mortality patterns on the different transects were not significantly different.

3.4.4 Relative effects of fish and lobsters – large caging experiment

3.4.4.1 Artefacts of caging- control plot vs. partial cage

We first compare mortality in the unmanipulated control plots with that in the partial cages to examine potential artefacts associated with cages. Split-plot ANOVA (main effects of cage treatment and urchin size) indicated that the presence of the cage did not significantly influence urchin mortality ($F_{1,12} = 1.33, P = 0.273$), however there was an effect of urchin size ($F_{2,12} = 13.00, P = 0.001$), but no evidence of interaction ($F_{2,12} = 1.07, P = 0.385$)(also see Figure. 3.4). Similarly, comparing these two treatments using a logistic model indicated an identical overall outcome, namely that the effect of ‘cage’ treatment was not significant. On this basis, we assume that the cages did not influence urchin mortality, and the control plots were removed from the primary analysis.

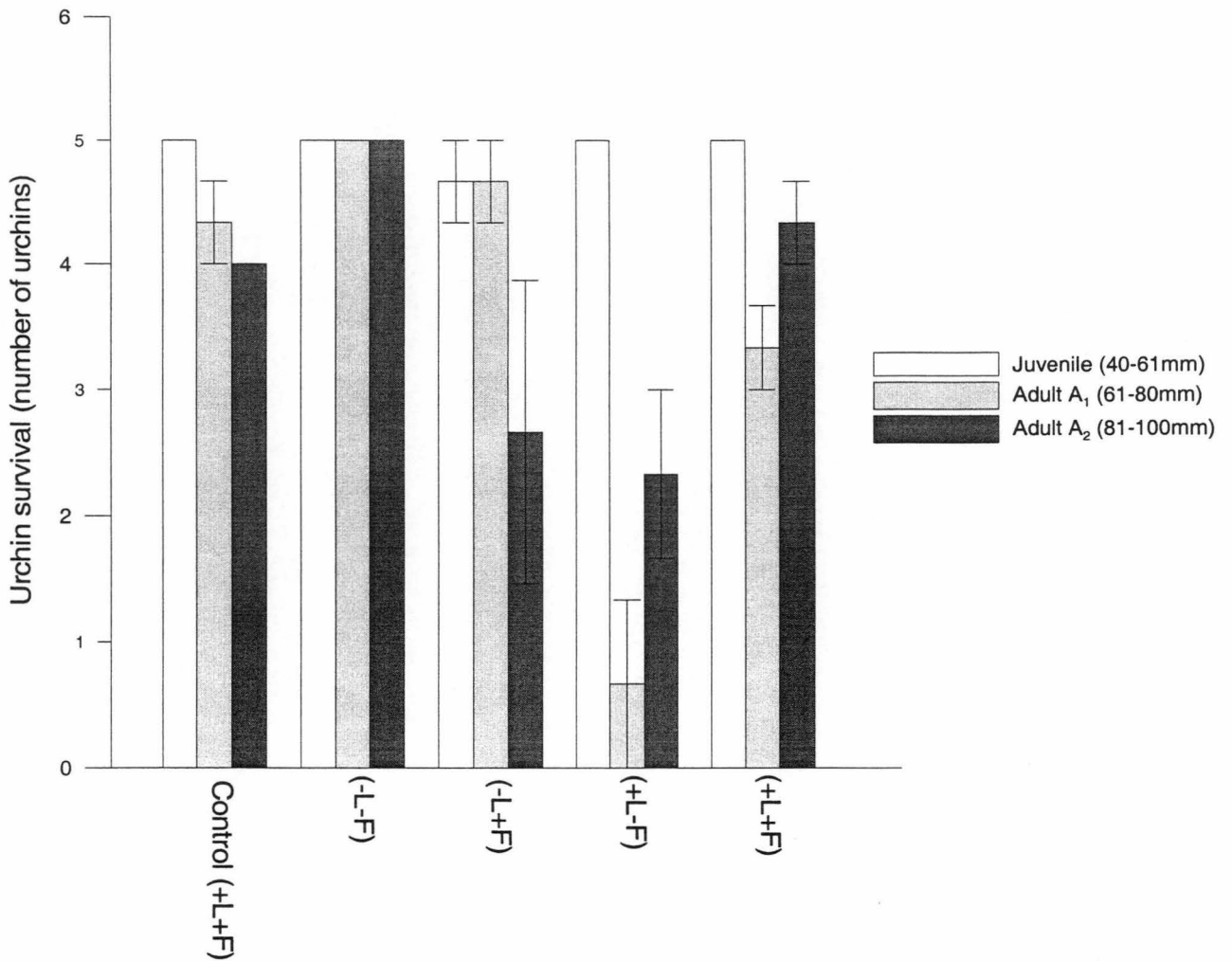


Figure 3.4. Relative importance of reef fish (F) and lobsters (L) as predators of the urchin *Heliocidaris erythrogramma*. Urchin survival is plotted as the number of urchins of each of the three size classes (sizes are test diameters) remaining after 8 weeks of exposure to various predators, which was manipulated using various designs of cages each measuring 3x3x1 m. There were initially 5 urchins of each size class in each experimental plot. Control (+L+F) = no manipulation of natural densities of urchins and lobsters in the plot area and no cage structure; (-L-F) = complete exclusion of both predator types using an enclosed cage; (-L+F) = exclusion of lobsters while allowing access by fish using a cage with no roof; (+L-F) = lobster inclusion with fish excluded using an enclosed cage; and (+L+F) both predators have access to urchins in a partial cage. Data are means (\pm SE) of $n=3$ independent replicates of each treatment.

Analysis of the effects of presence and absence of fish and lobsters (3-way

ANOVA), indicated a significant lobster*urchin size interaction ($F_{2,24} = 10.92$, $P =$

0.004). Multiple range comparisons (REGW) indicated that the mortality of juvenile

urchins was very low and not-significantly different across treatments, while small

adult (A₁) urchins suffered the highest mortality, although this was not significantly different to mortality of the largest (A₂) urchins. The highest mortality was observed in the presence of lobsters alone (Figure 3.4).

These data were also analysed using a logistic model to estimate the likelihood of urchin mortality under particular treatments. The model predicts that urchin mortality is ca. 7-times more likely in the presence of lobsters compared to when lobsters are absent, pooling across all urchin size classes and the presence and absence of fish ($\chi^2 = 5.5281$, $df = 1$, $P = 0.019$). Similar to the result from the ANOVA, the logistic model indicated that urchin mortality is not influenced by the presence or absence of fish pooled across all levels of lobster and urchin size ($\chi^2 = 1.6453$, $df = 1$, $P = 0.198$). Large (adult A₂) urchins were 7×10^{11} times more likely to be consumed in the experiment than were juveniles ($\chi^2 = 556.1988$, $df = 1$, $P = 0.0001$), while Adult A₁ urchins were ca. 4-times more likely to be consumed than their larger A₂ counterparts ($\chi^2 = 5.0572$, $df = 1$, $P = 0.025$).

To interpret the significant lobster*fish*urchin size interaction term in the overall logistic model, separate logistic analyses were undertaken on each urchin size class (excepting the juveniles, for which mortality was too low to enable meaningful analysis). The logistic model estimates that in the presence of lobsters, the likelihood of mortality of A₁ urchins is ca. 7-times that when lobsters are absent ($\chi^2 = 25.7704$, $df = 1$, $P = 0.0001$). When pooled across all levels of lobster, the effect of fish was significant ($\chi^2 = 6.2879$, $df = 1$, $P = 0.012$) with the model predicting that urchin mortality is 13-times more likely in the absence of fish ($\chi^2 = 7.5023$, $df = 1$, $P = 0.006$) (see Discussion section).

Examination of mortality of A₁ urchins (Figure 3.4) reveals that the exclusion of fish and prevention of lobsters from leaving the experimental plots in the +lobster –fish treatment, leads to increased mortality compared to the +lobster +fish treatment where the partial cage does not prevent lobsters from leaving the experimental plot. In the +lobster –fish treatment, the density of lobsters is fixed at one per 4.5 m², while in the +lobster +fish treatment, legal-sized lobsters will occur at the background density which is on average, 1 per 27 m².

For the largest urchins, a logistic model indicates that the two main effect terms are not significant in the fit of the model (lobster $\chi^2 = 0.7417$, df = 1, $P = 0.39$; fish $\chi^2 = 0.0831$, df = 1, $P = 0.77$). However, the lobster*fish interaction term was significant ($\chi^2 = 17.4684$, df = 1, $P = 0.001$) since A₂ urchin mortality was significantly greater in the presence of lobsters alone (+lobsters –fish) compared with the presence of both lobsters and fish (+lobsters +fish).

3.4.5 Effect of predation mortality on urchin population size structure

Within the Mercury Passage, the mean size and size frequency distributions of urchins inside and outside the reserve were significantly different. While the tails of the size distributions were similar, the size spectrum in the reserve was much flatter than in fished areas where urchins were more abundant (Figure 3.5).

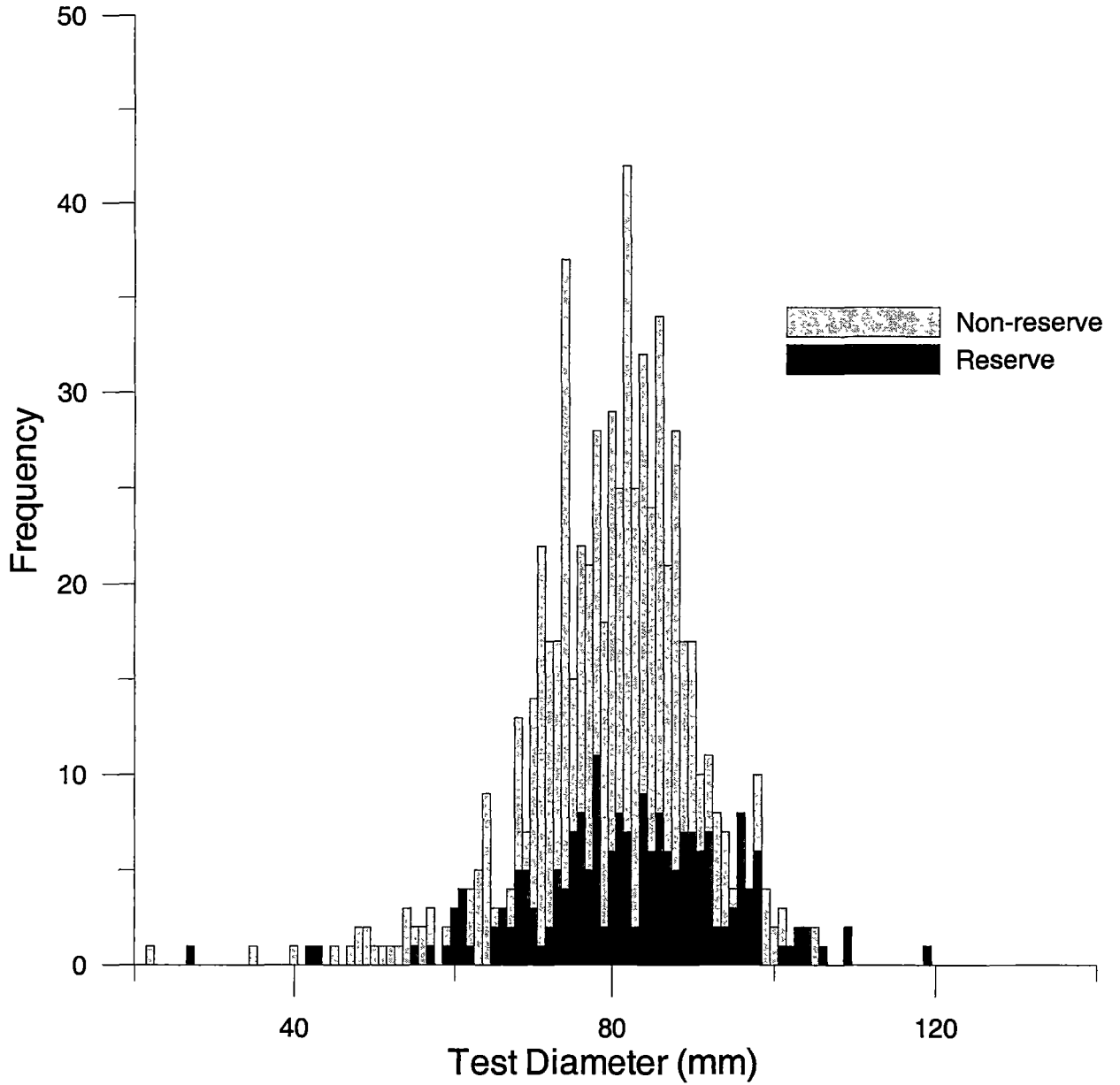


Figure 3.5 Size frequency distributions of urchin populations within the Mercury Passage on the east coast of Tasmania. The size frequency distributions are significantly different (Kolmogorov-Smirnov test, $P = 0.002$), with significant difference between the mean size of urchins in the two habitat types. Reserve sites mean size = 82 mm TD, non-reserve sites mean size = 80 mm TD. (NP-ANOVA, $F_{1, 580} = 6.066$, $P = 0.014$).

3.5 Discussion

Because of the scale at which urchin barrens can develop (Mann, 1977; Wharton and Mann, 1981; Estes and Duggins, 1995; Sanderson *et al.*, 1996; Andrew and O'Neill, 2000), the high stability of urchin barrens in the absence of urchin epizootics, and the pronounced loss of physical structure, biodiversity and productivity associated with barrens formation, then the phenomenon of urchin barrens can present significant challenges for managers of coastal systems. In this context, determining the mechanisms that regulate urchin populations is of vital importance.

The importance of predators in structuring urchin populations has been long argued, but there is relatively little unequivocal evidence exists except in the case of the sea otter (*Enhydra lutris*) as predators of urchins at some sites in the northeast Pacific (Lowry and Pearse, 1973; Estes and Palmisano, 1974; Duggins, 1980; Estes *et al.*, 1998; Dean *et al.*, 2000; Watt *et al.*, 2000). However, more recently a stronger case is emerging to demonstrate that, at least in some systems, scale fish (Vadas and Steneck, 1995; Shears and Babcock, 2002) and rock lobsters (*Jasus* species; Mayfield and Branch, 2000; Shears and Babcock, 2002) can play an important role in regulating urchin populations, and that the regulatory effect is influenced by fishing of the predators. The declaration of marine protected areas (MPAs) has provided important opportunities to test explicitly the effect of predator abundance on urchin mortality rates.

3.5.1 Significance of urchin predators inside marine reserves

The establishment of marine protected areas in temperate regions has realised significant shifts in community structure, including increases in the size of

populations and individuals of harvested species, and the indirect ‘flow-on’ effects of changes to harvested species (Davis, 1981; McClanahan and Mangi, 2000; Cole *et al.*, 1990; Russ and Alcala, 1996; Babcock *et al.*, 1999; Edgar and Barrett, 1999; Wallace, 1999; Kelly *et al.*, 2000; Paddock and Estes, 2000; reviewed by Halpen and Warner, 2002). Increases in the abundance of predators such as rock lobsters and demersal fish in protected areas are well documented and have been implicated in the reduction urchin population densities in reserve areas (Babcock *et al.*, 1999; Edgar and Barrett, 1999; McClanahan and Mangi, 2000; Shears and Babcock, 2002). Tethering experiments typically indicate that urchin mortality is 2-7 times greater inside marine reserves, where predator abundance is higher, than in adjacent fished habitat (McClanahan and Muthiga, 1989; McClanahan and Shafir, 1990; Sala and Zabala, 1996; McClanahan *et al.*, 1999; McClanahan, 2000; Shears and Babcock, 2002). Our results indicated a much greater difference (>600 fold) in mortality rates inside and outside reserves. This is likely to reflect that in our experiment urchins unable to seek refuge when tethered. Accordingly, these results should be interpreted as an assay of potential predation. Since differences in predator densities inside and outside reserves are nothing like 600 fold, our results suggest non-linear interactions between predators and urchin prey

From the results of the tethering, tagging and large cages we would expect a significantly lower urchin density inside no-take marine reserves compared with adjacent fished habitats. However, sufficient time may not have passed since declaration of the reserves to detect significant broad-scale change in urchin population density. The size frequency distributions of urchin populations within the Maria Island Marine reserve and adjacent non-reserve sites already show significant

differences. With further protection from exploitation the difference in both urchin density and size frequency may become more pronounced if size-selective predation is occurring and both the abundance and mean size of predators continues to increase.

3.5.2 Size-specific predation

Size selective predation has been proposed as a possible mechanism by which prey population size frequencies can be transformed from normal to bimodal distributions (Pollock, 1979; Griffiths and Seiderer, 1980; Tegner and Dayton, 1981; Tegner and Levin, 1983; Mayfield *et al.*, 2001). In examining the importance of size-specific predation in altering size frequency distributions, the two key factors of predator accessibility to different sized urchins within the substrate and the relationship between predation ability and predator size need to be addressed. In the current study, when urchins were tethered so that they could not seek shelter, juveniles were as vulnerable to predation as were adults. In contrast, in the size-selection experiment with lobsters, juveniles were clearly eaten at a higher rate than larger urchins, while small and medium-sized lobsters did not eat urchins larger than 80 and 100 mm test diameter respectively. Dissimilar to both of these results, when urchins and predators were not restrained in any way, survival of juvenile urchins in the tagging and large cage experiments was greater than that of adult urchins.

How do we reconcile these ostensibly conflicting results? When tethered, juvenile urchins were eaten in equal numbers to adults only when predation mortality was low (ca. 0%) or under very high predation (close to 100%). The former situation occurred when urchin predators were effectively absent, while the latter suggested that some

experiments were run too long to be able to differentiate predation on different size classes. The pattern in which juveniles were eaten in notably greater numbers than adults was evident only when levels of predation (Derwent Estuary non-reserve site) permitted survival of ca. 60% of the urchins. Differential predation on juvenile urchins was also clear results in the lobster caging experiment, where only juvenile urchins were eaten readily by all size classes of lobsters examined. In both of these experiments the urchins could not seek shelter and so were easily accessible to predators. The contrast in these results with those from both the tagging and large caging experiment, where adults were eaten in higher numbers than juveniles, can be reconciled in that juveniles seek deeper refuge within the substrate than do adults, and so are better protected from larger predators than are the more exposed larger urchins.

The high mortality rate of small adult urchins (61-80 mm) in the large caging experiment reflects their inability to escape predation by seeking deep refuge within the substrate, and compared to larger adults (81-100 mm) are more easily preyed upon by large predators. In protected habitats in which large predators are abundant the higher mortality rate of small adult urchins could result in reduced numbers of intermediate sized urchins and alteration of population size structure as seen in the comparison of size frequency distributions in fished and protected habitats within the Mercury Passage (Figure 3.5). In areas where predators are abundant intermediate size classes of *Strongylocentrotus franciscanus* experience a higher predation mortality rate than juveniles as they lose their ability to stay cryptic and may be sufficient to explain non-normal population size structures (Tegner and Levin, 1983).

Although the tethering, tagging and large caging experiments identified urchin size to be significant in determining predation-related mortality, the effect of predator size on urchin mortality could not be assessed using these experiment designs. In the size specific predation experiment where the physical capability of the southern rock lobster to predate different sized urchins was assessed, the results conclusively show an increased ability to attack larger prey items as a function of increasing lobster size. Of the three size classes, large adult lobsters are 8-times more effective at consuming juvenile urchins and the only lobster size class to significantly predate on the largest of urchins. Small lobsters (CL 90-105 mm) were not able to consume urchins above 60 mm TD. In a similar study Mayfield *et al.* (2001) found small *Jasus lalandii* were not capable of consuming juvenile urchins, however the predation ability of lobsters was found to increase as a function of carapace length. Andrew and MacDiarmid (1991) had earlier found small individuals of *J. edwardsii* were capable of consuming juvenile urchins, but not adults, a result similar to the findings in the current study.

Comparisons of fished and protected areas in Tasmania reveals that commercial exploitation of rock lobsters significantly reduces the number of legal-sized lobsters (Edgar and Barrett, 1999). We anticipate that because areas open to lobster exploitation experience reduced abundances of large lobsters, that mortality of large urchins would decrease, restricting urchin predation mortality to the smaller urchin size classes, which are those most effective at finding refuge from predation. Cryptic behaviour of juvenile urchins, coupled with the reduced predation of large adult urchins, could intensify predation of small adult (61-80 mm) urchins and result in a bimodal size frequency distribution. Through time the distribution could become

more pronounced as the number of large urchins increases due to low levels of predation mortality with consistent levels of urchin recruitment and lobster exploitation.

3.5.1 Relative importance of lobsters and fish as urchin predators

The importance of urchin predators such as the sea otter (*Enhydra lutris*) in structuring urchin populations in the northeast Pacific is well documented (Lowry and Pearse, 1973; Estes and Palmisano, 1974; Duggins, 1980; Dean *et al.*, 2000; Estes *et al.*, 1998; Watt *et al.*, 2000). In comparison little unequivocal evidence existed for the importance of scale fish and rock lobsters in structuring urchin populations until recently (Vadas and Steneck, 1995; Mayfield and Branch, 2000; Shears and Babcock, 2002). While a stronger experimental approach to these issues is welcome after several decades of speculation and correlative evidence (Mann and Breen, 1972; Breen, 1974; Breen and Mann, 1976b; Bernstein *et al.*, 1981; Wharton and Mann, 1981; Miller, 1985a), more extensive experiments are necessary to determine the generality of these results, and in particular the assess the relative importance of fishes and lobsters as urchins predators.

In temperate reef systems in New Zealand, fish have been found to be relatively more important as predators of some size classes of the urchin *Evechinus chloroticus* than are lobsters (Shears and Babcock, 2002). While fish are more effective in predating juvenile *E. chloroticus* than are lobsters, the relative importance is reversed as urchin size increases, with lobsters playing a greater role in determining adult urchin predation mortality. The combined results of the experiment examining size-specific predation by lobsters, and the large caging experiment partitioning predation mortality between lobsters and fishes, suggest that legal-sized lobsters have a greater

effect on urchin mortality than do fish. This reflects our observations made during the tethering and tagging experiments where lobsters were often seen attacking urchins, even during the day. While we observed male blue-throat wrasse (*Notolabrus tetricus*) to prey on juvenile urchins placed along the transect lines in the tagging and tethering experiments, there was virtually no mortality of juvenile urchins over the 8 week period of the larger scale experiment in the Maria Island reserve, despite large populations of *N. tetricus* in the reserve. These results combined with our previous work showing negative correlations at large spatial scales between lobsters and urchins, but not between fish and urchins (Chapter 2), lead us to conclude that in unfished areas lobsters are more important than fish as predators of *H. erythrogramma*. This is contrast to other temperate systems where evidence suggests that fish are more important predators of urchins than are lobsters (Andrew and Choat, 1982; Vadas and Steneck, 1995; Sala and Zabala, 1996; Babcock *et al.*, 1999; Shears and Babcock, 2002).

The statistically significant interaction between lobsters and fish, found in the large-scale caging experiment, is not likely to represent a biologically meaningful effect. The +lobsters -fish treatment requires lobsters to be completely contained inside a cage at a density of 0.22 m^{-2} . Direct comparison with the +lobster +fish (partial cage) is problematic since lobsters (and fish) in the partial cage are free to move into and out of the experimental area. Here, legal-sized lobsters are at a background density of ca. 0.037 m^{-2} , nearly 6 times less than in the enclosed cages. Containment of lobsters inside the cage (the +lobster –fish treatment) will realise a greater encounter rate between lobsters and urchins than in the +lobster +fish treatment, which ultimately is likely to lead to increased urchin predation.

3.6 Conclusions

Urchin mortality is far greater inside marine reserves where predator abundance is elevated compared with adjacent fished habitat. Decrease in predation mortality outside reserves is disproportionate to decreases in predator numbers, because predators are smaller, predation is size specific, and small urchins are better at seeking shelter.

Our results suggest urchin mortality to be highly size specific with the effect of both predator and prey size important in determining predation mortality. Urchin mortality was found to increase as a function of increasing lobster size. In heavily lobster-exploited habitats the inability of sub-exploitation sized lobsters to predate large adult urchin (>80 mm TD) could result in significant changes in population size frequency distributions through time.

We can also conclude that the southern rock lobster (*Jasus edwardsii*) is more important in structuring populations of *Heliocidaris erythrogramma* than demersal fish. Combination of these factors indicates populations of *Heliocidaris erythrogramma*, on the east coast of Tasmania, could be influenced by the abundance and average size of the southern rock lobster *Jasus edwardsii*.

Chapter 4

Individual-based growth models for three distinct populations of the sea urchin *Heliocidaris erythrogramma*: Evidence of spatial variability in urchin recruitment.

4.1 Abstract

Rapid elevation in urchin population density in response to fluctuations in larval supply has been proposed as a possible mechanism in the formation of urchin barrens habitat. Despite the development of the hypothesis as a plausible mechanism in the formation of barrens habitat, explicit testing is wanting. If the idea is valid, then urchin populations inhabiting barren sites would be more likely to have age distributions dominated by distinct modes than urchin populations at low densities in adjacent vegetated sites. Examination of population age structures to identify the presence of dominant peaks requires specific knowledge of the relationship between size and age.

The development of barrens habitat by the urchin *Heliocidaris erythrogramma* in relatively small patches (10^2 - 10^3 m) on the east coast of Tasmania allows for direct comparisons of population age structures in barren and adjacent vegetated algal habitats. In the present study we present empirically derived fitted growth models based on tag-recapture of individuals for three distinct populations of *H. erythrogramma*. Population age structures generated from the fitted growth models revealed dominant peaks to exist in urchin populations in barrens habitat which were

absent in adjacent algal habitat populations. The presence of the peaks in the age structure of the urchin populations in barrens habitat suggests that infrequent fluctuations in larval supply of this lecithotrophic species occur on small spatial scales (10^2 m) and may be responsible for elevating urchin population density.

4.2 Introduction

Distinctive phase shifts in community structure from luxurious kelp beds to habitats devoid of erect macroalgae occur in temperate regions worldwide as a result of overgrazing by sea urchins (North and Pearse, 1970; Mann and Breen, 1972; Shepherd, 1973; Lawrence, 1975; Breen and Mann, 1976a; Breen and Mann, 1976b; Lang and Mann, 1976; Mann, 1977; Wharton and Mann, 1981; Fletcher, 1987; Andrew and Underwood, 1989). Destructive overgrazing of nearshore seagrass habitats by sea urchin populations has also been observed (Camp *et al.*, 1973; Valentine and Heck, 1991; Heck and Valentine, 1995; Rose *et al.*, 1999). While the phenomenon is well described, the underlying mechanism(s) leading to formation of sea urchin barrens is not so clear, but there are several hypotheses (Mann and Breen, 1972; Lowry and Pearse, 1973; Estes and Palmisano, 1974; Lawrence, 1975; Breen and Mann, 1976a; Bernstein *et al.*, 1981; Wharton and Mann, 1981; Harrold and Reed, 1985; Hart and Scheibling, 1988; Elner and Vadas, 1990). One suggestion links overgrazing to increases in urchin population density in response to fluctuations in the supply of urchin larvae and, subsequently, recruitment. There is limited correlative evidence that occasional spectacular recruitment events may rapidly elevate urchin population density (Hart and Scheibling, 1988; Camp *et al.*, 1973) with concomitant changes in grazing pressure. Certainly the pattern of occasional prodigious settlement events, of the order of once per decade or longer, has been

reported for broadcast spawning echinoderms with planktotrophic larvae (reviewed by Ebert, 1983). Once barrens have formed, ongoing recruitment at lower levels can be sufficient to maintain grazing pressure and prevent the reestablishment of algal cover (Miller, 1985b; Scheibling, 1986; Tegner and Dayton, 1981; Wharton and Mann, 1981).

If a sharp rise in urchin population density from a recruitment peak at a particular site were responsible for overgrazing of macroalgae and the eventual formation of barrens habitat, then distinct differences in population structure should be evident when compared to urchin populations in adjacent algal beds. If a massive recruitment event is a major contributing cause, then urchin populations inhabiting barren sites are more likely to have age distributions dominated by distinct modes than are urchins at low densities in adjacent vegetated sites. However, despite a wealth of studies of growth and survivorship in both temperate and tropical urchins (Ebert, 1968; Gage and Tyler, 1985; Levitan, 1988; Kenner, 1992; Ebert and Russell, 1993; Minor and Schiebling, 1997; McShane and Anderson, 1997; Russell *et al.*, 1998; Meidel and Scheibling, 1999; Lamare and Mladenov, 2000; Russell and Meredith, 2000), this idea has not been examined carefully. In the present study we construct an age-at-size relationship for a temperate sea urchin (*Heliocidaris erythrogramma*), and use this information to estimate age frequency distributions which we examine for evidence of large recruitment events.

Among echinoids, *H. erythrogramma* is one of only three species with a lecithotrophic planktonic larval phase, and of the three species the only one known to form barrens habitat. The lecithotrophic larvae develop rapidly and reach settlement

within 5 days under favourable conditions (Smith, 1997; Emlet, 1995) potentially restricting the dispersal of propagules to relatively small distances from the adult spawning population and resulting in small-scale patchiness in settlement patterns. The formation of patchy barrens habitat across relatively small spatial scales, which arises on the east coast of Tasmania, may be a function of the short larval duration and limited dispersal of the lecithotrophic planktonic larvae of *H. erythrogramma*. This pattern provides a unique opportunity to examine urchin population structures in barrens habitat and adjacent vegetated sites for possible large recruitment events.

4.3 Methods

4.3.1 Study sites, tagging and recovery

Populations of *H. erythrogramma* were tagged with tetracycline during January and February 1999 at three sites in the Mercury Passage on Tasmania's east coast (Figure 4.1). The three sites were chosen based on similarity of physical habitat characteristics and were distinguished from one another by the abundance of macroalgae. The tagging site at Lords Bluff was located in an urchin barren, the site in Chinamans Bay was a fringe algal community in an area of incipient urchin barren, while at Four Mile Point there was a dense cover of macroalgae.

Within the Mercury Passage urchin barrens appear on various spatial scales and most commonly immediately adjacent to an established macroalgal bed. The tagging site located on the urchin barren at Lords Bluff (Figure 4.1) is immediately adjacent to a macroalgal community (Lords Bluff algal bed) which is used for direct comparison of urchin age frequency distributions. The urchin barren at Stapleton Point is also

characterised by its immediate proximity to a macroalgal bed (Stapleton Point algal bed).

Approximately 400 individuals were tagged at each of the three tagging sites by removing all urchins from an experimental plot measuring approximately 10 m x 6 m depending upon the urchin density. Experimental plots were located on the 5m-depth contour at each site.

Test dimensions of each urchin were measured to the nearest millimetre using knife-edge vernier callipers before injecting urchins with tetracycline (Kobayashi and Taki, 1969) at a concentration of 10 g l^{-1} in seawater, using a small-gauge hypodermic needle (adapted from Ebert, 1977). To ensure all urchins received a standard dose of the tetracycline solution (0.006 ml.g^{-1}), test diameter (TD) measurements were used to estimate body weight (W) from a pre-determined function ($W = 3.49 \cdot \text{TD} - 154.14$, $n = 40$, $R^2 = 0.93$). Tagged urchins were returned to experimental plots soon after receiving injections. Mortality from handling was assessed 72 hours post tagging by searching experimental plots for fresh mortalities, and was less than 5% of tagged individuals.

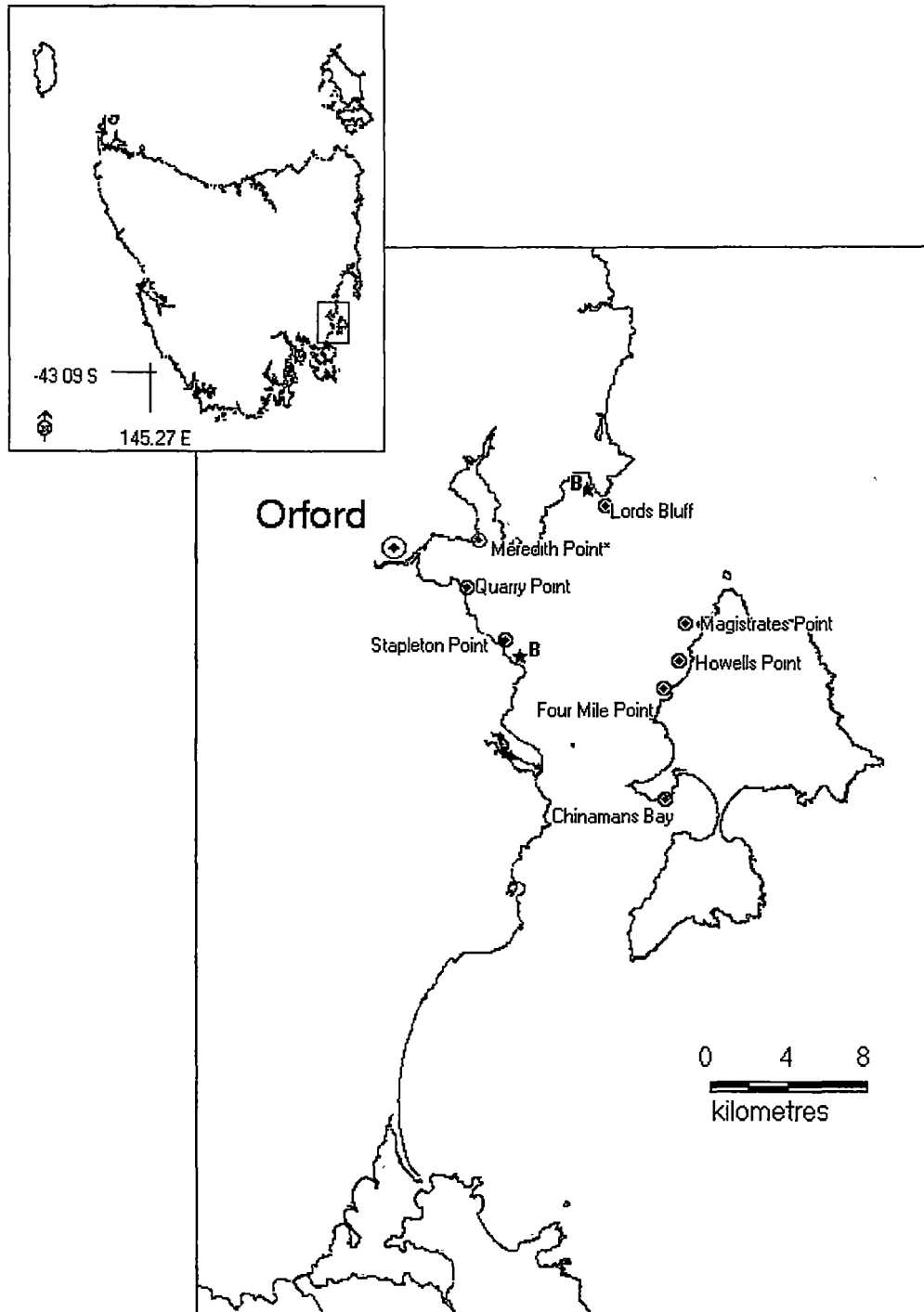


Figure 4.1 Location of tetracycline tagging sites within the Mercury Passage on the east coast of Tasmania. Tagged urchin populations were located at Lords Bluff (urchin barren site), Four Mile Point and Chinamans Bay. Paired sites for direct comparison between populations and urchin barrens habitat (★B) and adjacent algal beds were located near the Lords Bluff tagging and Stapleton Point. Size frequency data was collected from urchin populations in established algal beds at Magistrates Point and Howells Point to determine spatial variation in urchin recruitment* Experimental site used by Sanderson et al. (1996) to study growth of *H. erythrogramma* (Meredith Point).

Experimental plots were sampled three times between February 1999 and February 2001 (12, 14 and 24 months post tagging). Examination of samples from the 12 month sampling revealed a high tag return rate, enabling another sampling two months later (14 months post tagging) and allowing approximately half of the original number of tagged urchins to remain for a further 10 months to complete two years post-tagging (Table 4.1). Recaptured urchins were sampled haphazardly in the experimental plots and then frozen prior to dissection in the laboratory. On the final sampling in early February 2001 all remaining urchins were removed from within the plots and a 1m perimeter around the plots, to leave the experimental areas devoid of urchins.

Table 4.1 Summary of tag returns across the three sampling periods from the three tagging sites. After correcting, data for animals collected 12 and 14 months after tagging were pooled and considered representative of the population surviving to 1 year post tagging.

Site/ Time	Number of tagged urchins (t)	Number of urchins collected	Number of positive tag returns	Relative recovery rate (%)
<i>Four Mile Point</i>				
0 months	355			
12 months		83	51	61
14 months		72	39	54
24 months		230	57	25
Overall recovery rate (%)	42			
<i>Lords Bluff</i>				
0 months	431			
12 months		115	71	62
14 months		98	65	66
24 months		288	92	32
Overall recovery rate (%)	53			
<i>Chinaman s Bay</i>				
0 months	416			
12 months		100	74	74
14 months		99	54	55
24 months		233	100	43
Overall recovery rate (%)	55			

4.3.2 Determining size-at-age

The diameter and height of the test was measured prior to dissection. On dissection, half of the test and the entire Aristotle's lantern were placed into a solution of 5% sodium hypochlorite. The calcified material remaining after 24 hours was rinsed thoroughly with freshwater before being air-dried for 48 hours. Demipyramids (hereafter referred to as jaws) and test plates from the prepared samples were exposed to ultraviolet light and examined for the presence of the tetracycline tag.

A small sample of urchins ($n = 30$) was collected from areas adjacent to the three experimental sites during February 2000 and prepared for ultraviolet examination. These samples were controls for the presence of 'natural' or background fluorescence in jaws and test plates. Of the ninety 'control' urchins collected, none showed any sign of fluorescence in either test plates or jaws. We interpret the absence of background fluorescence to indicate that the marks detected in experimental animals are a result of the tagging process and not environmental contamination.

Growth increments (ΔJ) were measured on one half of a jaw to the nearest 50 μm with an ocular micrometer under 20x magnification. Measurements were made from the inside edge of the fluorescent band to the aboral surface. Jaw length at tagging (J_t) and jaw length at time of sampling ($J_{t+\Delta t}$) were measured to the nearest 0.5 mm using knife-edge vernier callipers.

Growth parameters of tagged populations were estimated by fitting the generalised Richards function (Ebert *et al.*, 1999) to data obtained from the one and two year post-tagging animals by minimizing the squared differences between the observed

growth increments (ΔJ) and the expected growth increments (sums of squared error SSE) using Equation 1. The generalised Richards function is written as:

$$J_t = J_\infty (1 - be^{-Kt})^{-n} \quad (\text{Eq. 1})$$

where J_t is jaw length at time (t), J_∞ is the infinite jaw length (when growth is 0), K is the growth rate constant, b is $(J_\infty - J_0/J_\infty)$, J_0 is the jaw length at recruitment to the population, and n is the shape parameter. When $n = -1$ the Richards function becomes known as the Brody-Bertalanffy Growth Function (BBGF). Data from the three populations were fitted to both the generalised Richards function and the BBGF for comparison of model suitability in determining a size-at-age relationship.

Because growth models were constructed from growth increments measured in the jaws of tagged urchins and the population size frequency distribution was determined from diameters, the relationship between jaw length and test diameter at tagging (t) was established. The relationship was established by \log_e transforming jaw length (J) and test diameter (D) measurements at the time of sampling ($t + \Delta t$) and determining the constants α and β using a geometric mean (GM) functional regression (Ricker, 1973). Test diameters of each urchin were then calculated at the time of tagging (D_t). The allometric relationship between jaw length (J) and test diameter (D) can be expressed as:

$$J = \alpha D^\beta \quad (\text{Eq. 2})$$

Because our samples did not include recently settled urchins, we estimated size at settlement (time $t = 0$) from urchins recruited to artificial collectors deployed in November 2000 and sampled each month until May 2001 to ensure detection of recent settlement (this period covered the adult spawning period). The collectors

were 15 x 15 cm sections of artificial turf secured to concrete blocks of similar dimensions placed in a random arrangement at Lords Bluff. Artificial turf has been used successfully for this purpose by Lambert and Harris (2000). Juvenile urchins were located on the collectors 6 months after being deployed. The test diameter of individuals was measured to the nearest 0.05 mm using an ocular micrometer prior to dissection. Individuals were identified as *H. erythrogramma* using the pore structure of the interior surface of test plates (Baker, 1982). Following dissection jaw length was measured using an ocular micrometer to the nearest 0.05 mm to gain an estimate of jaw length at the time of recruitment to the population (J_0).

4.3.3 Comparing age-frequency distributions

A predicted age-at-size relationship was used to generate age frequency distributions for 7 other sites across the Mercury Passage. Five of these sites, Quarry Point, Stapleton Point, Lords Bluff (algal bed), Howell's Point and Magistrate's Point represent habitats with high algal abundance. Construction of age frequency distributions for these high algal abundance sites used the growth model constructed from tagged urchins at Four Mile Point and assumes the growth rate of urchins to be similar across the five sites. Age frequency distributions of urchin populations in the five high algal abundance habitats were compared using the Kolmogorov-Smirnov test. To prevent compounding of Type I errors, adjustment was made using the Dunn-Sidak adjustment. Measures of kurtosis and skewness were estimated for each population age frequency distribution to allow comparison to be made between the sampled populations.

To determine whether localised large recruitment events could account for elevated population densities and eventual barren formation, comparison of age frequency distributions between barren and adjacent algal bed habitats was conducted. Two barren habitats were sampled in the Mercury Passage at Lords Bluff and Stapleton Point and age frequency distributions constructed using the growth model developed for urchins tagged on barrens at Lords Bluff and assumes the growth rate of urchins in the two barrens populations to be similar. The broader survey of the barrens habitat at Lords Bluff encompassed the area around the experimental tagging plot and covered the same area (ca. 160 m²) as sites supporting high algal abundance. Age frequency distributions of adjacent urchin populations were compared using the Kolmogorov-Smirnov test.

Analysis of residual sums of squares (ARSS) found no significant difference between the two growth models used to generate the age frequency distributions for the two habitat types. However, when the data were pooled the fitted growth model did not adequately describe growth for urchins in the barren habitat populations where urchins do not grow as large as their counterparts in adjacent algal habitats. We justify generating the age frequency distributions for the barren and vegetated urchin populations using separate growth models since the parameter estimates derived in each model more accurately describe urchin growth in each habitat. Notwithstanding, we emphasise that use of either the pooled data growth model or separate growth models to generate the age frequency distributions of the two habitats results in identical biological interpretations and conclusions regarding population size structuring.

Annual survival rate estimates were calculated using the parameter estimates generated by the Richards function and substituted into the formulae presented by Ebert (2001a):

$$Z = \frac{K(D_{\infty}^{-1/n} - \bar{X})}{\bar{X} - D_R^{-1/n}} \quad (\text{Eq. 3})$$

where Z is the mortality coefficient, \bar{X} is the mean of transformed test diameters ($D^{-1/n}$ where n is the shape parameter from the fitted Richards function) and D_R is the test diameter at recruitment to the population. Annual survival (p) rates were then calculated using equations 4:

$$p = e^{-Z} \quad (\text{Eq. 4})$$

In estimating survival (using equations 3 and 4) recruitment is assumed to be constant and continuous. Ebert (2001b) argues that this assumption is reasonable if the size at recruitment to the sampled population is large relative to the size at settlement. The estimated size at recruitment to the 0 year class is taken at 6 months (i.e. mid way between 0-12 months), which comes from measurements of juvenile urchins on collectors and compared to estimates of the size at settlement (Williams and Anderson, 1975), which is ca. 5 times greater than the size at settlement.

4.4 Results

Examination of the differences between predicted jaw length at time of sampling ($J_{t+\rho t}$) from the fitted growth model and actual jaw length (residuals), plotted as a function of jaw length at tagging (t), indicates a similar pattern for both 12 and 14 month sampling period (Figure 4.2). To increase the sample size of the 12 months post tagging dataset, adjustment was made to each data point in the 14 month group to account for the extra 2 months between samplings and allow the two data sets to be combined. To adjust for the extra growth period, the raw residual of each jaw length (Jt) in the 14 month data set was subtracted from the predicted jaw length (J_t) plotted using the parameters of jawlength at tagging (J_t) as a function of jaw length at sampling ($J_{t+\Delta t}$) generated from the 12 month sample. The combined datasets were then used to generate the 12 month growth functions using the Richards model.

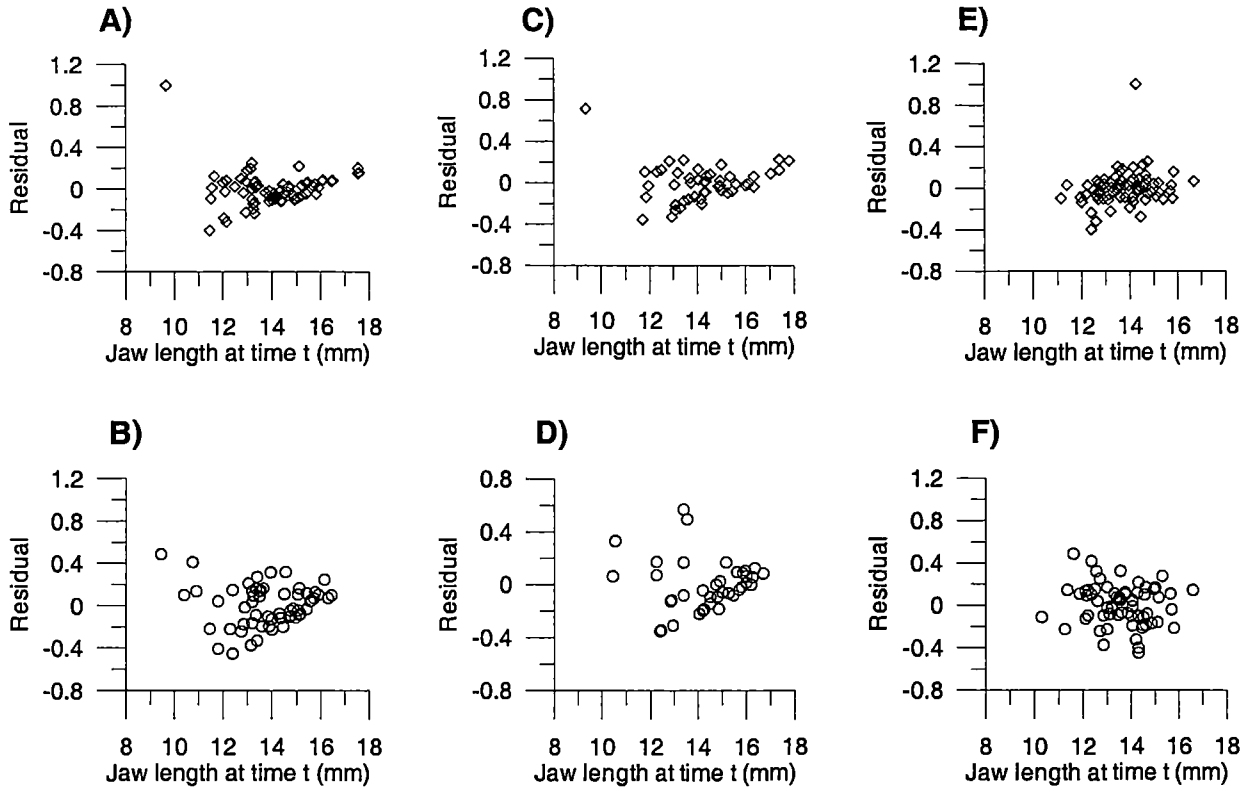


Figure 4.2 Residuals (predicted minus actual jaw length at t_{+dt}) vs. Jaw length at the time of tagging (J_t). A) Lords Bluff sampled after 12 months, B) Lords Bluff samples after 14 months, C) Four Mile Point sampled after 12 months, D) Four Mile Point samples after 14 months, E) Chinamans Bay sampled after 12 months, F) Chinamans Bay sampled after 14 months.

4.4.1 Site-specific growth functions

The use of the Richards function for the construction of growth models for the three sampled populations was based on the shape of the plot of J_{tx} as a function of J_t (Walford, 1946; Ebert, 2001b). The linear nature of the relationship between J_{tx} as a function of J_t for *H. erythrogramma* suggests that the Richards function is appropriate to describe growth (Figure 4.3).

Growth curves for each site were compared to determine whether any differences in growth of *H. erythrogramma* correlated broadly with differences in algal abundance.

4.4.1.1 Four Mile Point

Comparison of the two fitted growth functions, BBGF and Richards function, to data collected from individuals one year after tagging showed the Richards function ($n = -1.19$) to have the lowest SSE scaled by sample size (ie average magnitude of residuals) of the two models tested (Table 4.2). Fitting the Richards function to data collected two years after tagging gave a higher average magnitude of residuals compared to the model fitted to data collected after only one year of growth. Subsequent size-at-age estimates for the population at Four Mile Point were calculated using parameter estimates from the model fitted to the data collected one year after tagging ($k = 0.14$, $D = 98.10$ mm and $n = -1.19$).

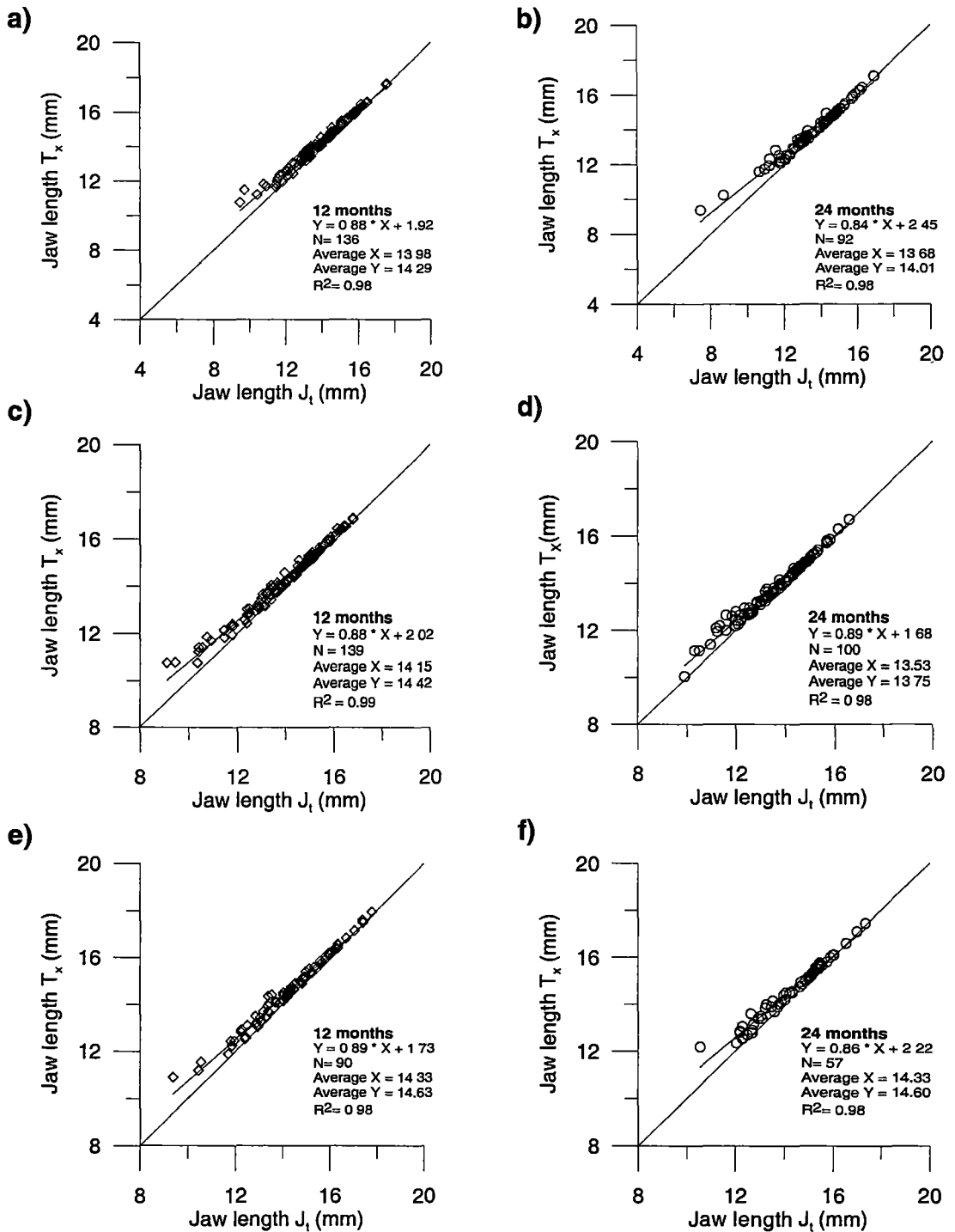


Figure 4.3 Walford plots ($J_{t+\Delta t}$ as a function of J_t) for tetracycline tagged urchins. a) Lords Bluff, samples 12 months after tagging, b) Lords Bluff samples 24 months after sampling, c) Chinamans Bay 12 months after tagging, d) Chinamans Bay samples 24 months after tagging, e) Four Mile Point 12 months after tagging, and f) Four Mile Point samples 24 months after tagging. Values falling on the 1:1 represent zero growth between the time of tagging and the time at sampling.

4.4.1.2 Lords Bluff

Comparison of the two growth functions fitted to the data collected one and two years after tagging revealed the lowest average magnitude of residuals was obtained using the Richards function, with a shape parameter of $n = -1.11$, fitted to data collected 12 months after tagging. In this case, the difference in fits for the BBGF or the Richards function was minor, however we used the Richards function because we have an estimate of size at recruitment and to reduce the error associated in estimating sea urchin age from the fitted growth model.

4.4.1.3 Chinamans Bay

In contrast to the other two tagging sites, the Richards function fitted to the data collected 12 months following tagging higher average magnitude of residuals compared to the 24-month data using the same growth function (Table 4.2).

Similarly, fitting the BBGF to the data collected 12-months after tagging resulting in a higher average magnitude of residuals compared to the model fitted to data collected 24 months after tagging. However, while the Richards model fitted to the data collected one year after tagging had a higher average magnitude of residuals, the maximum range of sizes covered in the tag returns was in the first year sample, and is therefore likely to better represent growth than the data collected in the second year post-tagging.

Note that the size-at-age relationship developed for the Chinamans Bay population has not been used in the construction of age frequency distributions for the other vegetated sites because, in supporting an intermediate algal abundance, it did not

match that of either the high algal abundance sites or barrens habitat sites examined in the broader survey.

Table 4.2 Growth model parameters for the Brody-Bertalanffy Growth Function (BBGF) and the Richards Function for the three tagging sites for samples collected 1 and 2 years after tagging, where k is the growth rate, D_{∞} is the infinite test diameter size (mm), J_{∞} is the infinite jaw length (mm), SSE are the error sums of squares, with N number of samples, and n the shape parameter specific to the Richards Function. The average magnitude of residuals is SSE scaled by N .

	Brody-Bertalanffy Growth Function (BBGF)						Richards function						average magnitude of residuals
	k	D_{∞}	J_{∞}	SSE	N	average magnitude of residuals	k	D_{∞}	J_{∞}	n	SSE	N	
Four Mile Point 1 year	0.16	97.80	17.60	5.875	90	0.065	0.14	98.10	17.70	-1.19	3.491	90	0.039
Four Mile Point 2 year	0.16	91.90	16.30	4.301	57	0.075	0.22	93.25	16.70	-1.05	2.801	57	0.049
Lords Bluff 1 year	0.21	86.90	17.00	6.228	163	0.046	0.19	87.20	17.05	-1.11	5.419	136	0.039
Lords Bluff 2 year	0.38	81.10	15.95	3.956	92	0.043	0.27	81.20	15.95	-0.97	3.799	92	0.041
Chinamans Bay 1 year	0.18	83.60	16.25	5.856	139	0.042	0.25	83.50	16.55	-1.23	4.896	139	0.035
Chinamans Bay 2 year	0.16	83.10	15.90	3.299	100	0.033	0.20	83.10	15.90	-1.20	3.133	100	0.031

4.4.2 Age frequency distributions

Age frequency distributions for populations found at each of the tagging sites were constructed from relationships of test diameter as a function of age (Figure 4.4) using model parameter estimates that minimised SSE (Table 4.2). Given the dependence of echinoid growth on resource availability, the choice of predictive age at size function was based on the similarity of algal abundance of the survey site to those of the three sites where urchins were tagged and growth functions determined. Because of its diverse algal community, the function derived for Four Mile Point tagging site was used to construct the age frequency distributions at sites with high algal cover, namely Quarry Point, Stapleton Point (algal bed), Lords Bluff (algal bed), Magistrates Point and Howells Point. The age frequency distributions of the two barren sites were constructed using the function derived for the population on barrens habitat at the Lords Bluff tagging site.

4.4.2.1 Tagged populations

The estimated age frequency distribution of tagged urchins at Four Mile Point, based on the output of the Richards model, indicates that individuals between 5 and 15 years of age dominate the distribution, with a mode at 10 years (Figure 4.5e). The distribution declines at 20 years of age with no individuals present above 25 years of age. A small number of individuals nominally at 60 years of age (grey bar) were animals whose test diameter was above the predicted (theoretical) infinite size. This can arise when jaw length and test diameters are on the asymptote of the predictive curve where accurate prediction of age is not possible. Predicted ages of 60 years are considered to be artefacts of the model and were not considered further.

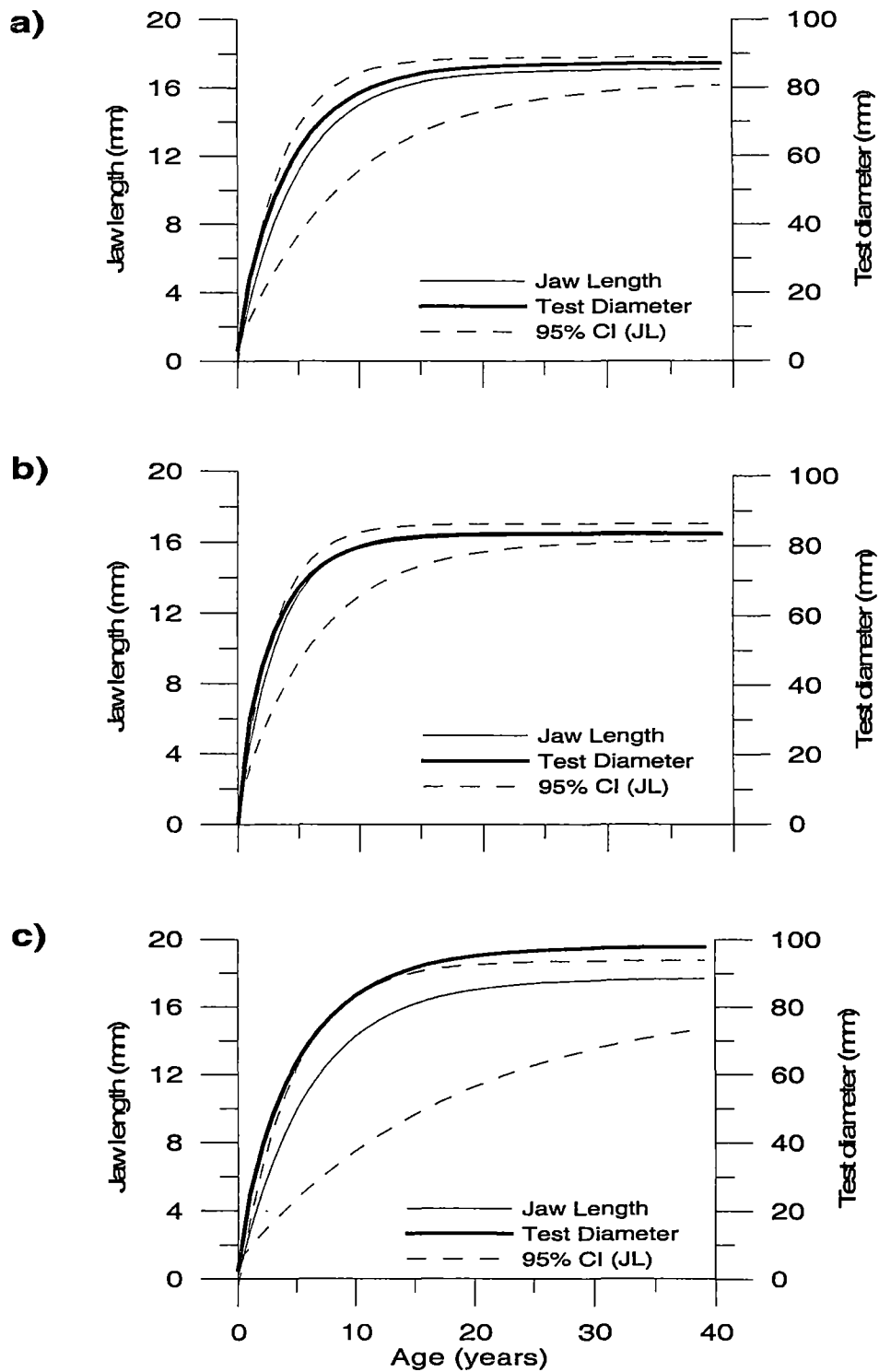


Figure 4.4 Size at age relationships for the three tagged populations using the Richards Function fitted data collected 12 months following tagging and a) Lords Bluff, functions on both test diameters and jaw lengths with 95% CI (jaw lengths), b) Chinamans Bay, functions based on test diameters and jaw lengths with 95% CI (jaw lengths), and c) Four Mile Point, functions based on test diameters and jaw lengths with 95% CI (jaw lengths).

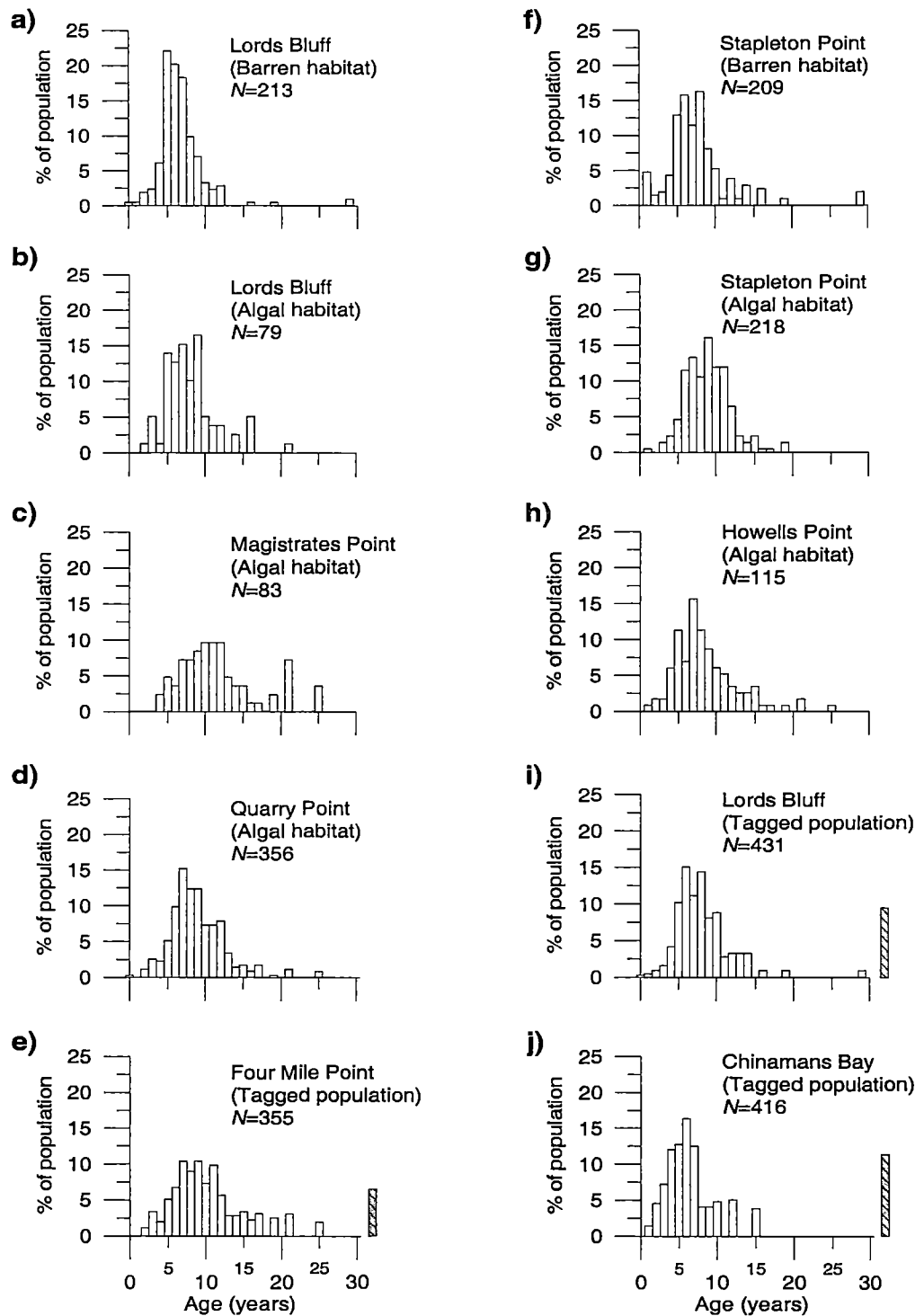


Figure 4.5 Age frequency distributions for sites within the Mercury Passage based on test diameter measurements. Distributions for d) Quarry Point, g) Stapleton Point (algal habitat), b) Lords Bluff (algal habitat), c) Magistrates Point and, h) Howells Point distributions, all supporting dense algal growth, were generated using the Four Mile Point growth model. Distributions for a) Lords Bluff and h) Stapleton Point (barren habitat) age frequency distributions were generated using the Lords Bluff growth model. Age frequency distributions of tagged urchin populations used to generate individual based growth models at i) Lords Bluff, e) Four Mile Point and, j) Chinamans Bay include the percentage of the population with test diameters larger than the predicted infinite size (grey bars).

The age frequency distribution of the tagged population at Chinamans Bay indicates that individuals between 3 and 8 years dominate the distribution. There were relatively fewer individuals in the 10-15 year age class at Chinamans Bay than at Four Mile Point, while no animals older than 15 years of age were detected. However, approximately fifty individuals (12%) were found to be larger than the theoretical infinite test diameter of 83.60 mm (grey bar, Figure 4.5j). These individuals are unlikely to be 60 years old, as predicted by the model, rather they are most likely to be closer to 20 years of age.

Similarly, the predicted infinite test diameter of urchins at Lords Bluff indicated approximately 45 individuals aged at 60 years and, for the same reasons, these animals are likely to be closer to 20 years (grey bar, Figure 4.5i). At this site urchins between 4 and 11 years old dominate the age frequency distribution with the mode at 6 years. The model predicts individuals survive up to ca. 15 years of age in reasonable abundance on barrens at Lords Bluff.

Comparing the age frequency distributions of the tagged populations indicates similar and relatively low positive skewness to be similar (Table 4.3). However, the distribution of ages in the tagged population at the Lords Bluff site is more leptokurtic (non-normal in distribution) than the other tagged populations, suggesting fewer cohorts dominate the age structure. The distribution of ages in the tagged populations at Chinamans Bay and Four Mile Point were similar in their mean age, skewness and kurtosis, while the population at Chinamans Bay showed the least variance in ages of individuals.

Table 4.3 Distribution statistics of urchin population age frequency distributions for sites within the Mercury Passage during 1999. * Sites at which urchin populations were tagged to construct individual based growth models. Estimates of skewness and kurtosis are comparisons to a normal distribution of age frequencies.

	<i>N</i>	Mean	Variance	Skewness	Kurtosis
*Four Mile Point (algal bed)	355	10.2	23.2	0.94	0.85
*Chinamans Bay (incipient barren)	416	6.4	9.7	0.98	0.84
*Lords Bluff (barren)	431	8.1	13.7	2.17	9.27
Quarry Point (algal bed)	356	9.0	13.6	1.26	3.29
Magistrates Point (algal bed)	83	11.7	26.3	0.98	0.48
Howells Point (algal bed)	115	8.6	17.4	1.29	2.42
Lords Bluff (algal bed)	79	8.1	11.9	1.21	2.21
Lords Bluff (barren)	213	6.8	10.3	3.51	21.23
Stapleton Point (algal bed)	218	8.9	8.52	0.63	1.25
Stapleton Point (barren)	209	7.8	20.1	2.30	8.52

4.4.3 Estimated population age frequency distributions throughout the Mercury Passage

The age frequency distribution of urchin populations at Lords Bluff, Quarry Point, Four Mile Point, Stapleton Point and Howells Point, all of which support high algal abundance, have a high abundance of individuals 7 years of age representing a cohort originating in 1992 (Figure 4.5b,d,e,g,h). Furthermore all these populations contain a high proportion of individuals 9 years of age. Individuals older than 20 years of age were found in low abundance at all of the sites supporting high algal abundance except Magistrates Point where ca. 10% of the population was predicted to be between 21 and 25 years of age.

Comparison of the age frequency distributions across all sites supporting high algal abundance found Magistrates Point to be significantly different compared to other sites ($P < 0.005$), which can be attributed to the greater number of older individuals, those between 10 and 12 years old, in the Magistrates Point urchin population compared to the other four populations. Excluding Magistrates Point, the age

frequency distributions of the remaining five sites were not significantly different from each other ($P > 0.005$; after Dunn-Sidak adjustment).

4.4.4 Age structures of urchins on barrens and in native algal beds

When the data were pooled across locations within each habitat type, barrens and adjacent algal beds, the age frequency distributions were significantly different ($P = 0.0001$). Analysis of the data separated by location gave a similar result with significant differences between the age frequencies of urchins in barrens habitat compared to urchin populations in adjacent algal beds at Stapleton Point and Lords Bluff ($P = 0.0001$).

At Stapleton Point the distribution of ages in the barrens habitat urchin population contained dominant cohorts between 6 and 8 years of age (Figure 4.5f), compared to cohorts between 6 to 11 years of age which dominate the urchin population in the adjacent algal bed (Figure 4.5g). The distribution of urchin age frequencies in the barrens habitat has higher a positive skewness and greater peakedness compared to the urchin population in the adjacent algal bed (Table 4.3). The descriptors of skewness and kurtosis and the age frequency distribution (Figure 4.5f) suggests the urchin population in the barrens habitat at Stapleton Point is comprised of relatively fewer cohorts of younger individuals compared to the adjacent algal bed.

Individuals between 6 and 8 years of age dominate the age frequency distribution in the barrens habitat urchin population at Lords Bluff (Figure 4.5a), compared to individuals 5 to 9 years old which dominate the age frequency distribution of the urchin population in the adjacent algal bed (Figure 4.5b). Descriptive statistics of the

two age frequency distributions show the distribution of urchin age in the barrens habitat has a greater positive skewness and is more leptokurtic compared to the urchin population in the adjacent algal bed (Table 4.3). The descriptors suggest the urchin population in the barrens habitat is dominated by young individuals in a small number of cohorts compared to the population in the adjacent algal habitat, which has individuals spread across a greater number of cohorts.

4.4.5 Survival rates

Survival rates were calculated for the three tagged populations using parameters from the Richards growth function fitted to data from animals collected 12 months after tagging. The annual survival rate (p) of the Four Mile Point population was the highest than urchins at the other sites (Table 4.4). The populations at Lords Bluff and Chinamans Bay displayed similar rates of annual survival.

Table 4.4 Annual survival (p) rates calculated for the three tagging sites constructed on data collected one year after tagging.

Site	p
Lords Bluff	0.956
Chinamans Bay	0.954
Four Mile Point	0.966

4.5 Discussion

4.5.1 Appropriate models describing growth in *Heliocidaris erythrogramma*

Application of the Richards function to model sea urchin growth is wide spread (Ebert, 1980a; Ebert, 1980b; Ebert, 1982; Gage and Tyler, 1985; Russell, 1987; Ebert and Russell, 1992; Kenner, 1992; Ebert and Russell, 1993; Lamare and Mladenov, 2000). We examined more complex growth functions, however the linear nature of the relationship between $J_{t+\Delta t}$ and J_t suggests that the simple Richards function is appropriate to model these data (Figure 4.3). The Richards function allows inclusion of known size-at-age data, which in turn facilitates fine tuning of other model parameters.

Parameter estimates from the BBGF were, in most cases, similar to those of the Richards function, and the predicted infinite size was similar in all three population when fitted to data collected one and two years after tagging. The main difference between the two models was in the estimates of growth rate. The BBGF estimated a higher rate of growth than the Richards function at both Four Mile Point and Lords Bluff, but a slower rate at Chinamans Bay in individuals collected one year after tagging. A similar pattern occurred when fitting the BBGF to data collected two years after tagging, except at Four Mile Point where predicted growth rates were greater under the Richards function. The consistent pattern in SSE between the two sampling periods, was that growth functions constructed using data obtained one year post tagging were more precise than those constructed using data from urchins sampled two years post tagging. The original experimental design included only a single sample from the tagged populations at the end of the first year. Extension of

the sampling period to include a second season was made to compare variability in constructing the growth model on the basis of collecting data one and two years post tagging. Modeling data obtained one-year post tagging using the Richards function provided the lower SSE. These findings indicate that leaving half of the tagged populations at liberty for a second year did not significantly improve model fit. Removing all tagged animals at the end of the first year of growth after tagging would have undoubtedly improved the model fit by increasing the sample size.

4.5.2 Growth parameters of *H. erythrogramma*

Growth rate parameter estimates determined by Ebert (1982) of *H. erythrogramma* in New South Wales and Western Australia are different to those found in this study, and estimates of asymptotic size are greater at the three Tasmanian sites compared to those of the mainland. Differences in parameter estimates from the present study with those of Ebert (1982) are not unexpected given that the geographic range of this species encompasses a large spectrum of water temperatures (from subtropical to cool temperate water), and that the species is largely intertidal in the northern part of its range while it is restricted to subtidal habitats in Tasmanian waters.

In a similar study, Sanderson *et al.* (1996) constructed a growth function of *H. erythrogramma* from urchins tagged at a site within the Mercury Passage (Figure 4.1), their study estimated the growth rate constant k to be 0.20 with an infinite test diameter of 85.0 mm. Our estimates of the growth constant ($k = 0.19$) and D_{∞} (87.2 mm) at Lords Bluff are remarkably similar to the estimates of Sanderson (1996) at a nearby site (where $k = 0.20$ and $D_{\infty} = 85.0$ mm).

4.5.3 Growth of juvenile urchins

While chemical tagging of juvenile urchins is relatively straight forward, recovery of sufficient numbers of juveniles at a time in the future often poses considerable difficulties. The lack of data from juvenile urchins in fitting growth models poses particular and significant problems. For most growth functions, the shape of the lower region of the curve influences the shape of the curve describing growth of adult urchins. The usual method of growth curve construction is to concentrate on those size classes that are easily tagged and recovered and interpolate into regions of the curve that are not sufficiently sampled. Under representation of tagged juveniles may be offset by size-at-age data from other sources such as known size at the time of settlement or recruitment to the sampled population.

The lack of juvenile urchins in samples of the tagged populations could be attributed to several factors. First, the sampling effort was intensive in clearing the treatment plots at the end of the experiment of all urchins, juveniles have an advantage over adults in their ability to seek deep refuge in crevices and escape collection.

Accordingly, given the inability of divers to move larger boulders, under these circumstances it is likely that a majority of juvenile urchins are unable to be recovered from the substratum. In addition, Russell *et al.*, (1998) found that smaller individuals tended to migrate more frequently than larger individuals in a similar tagging experiment, resulting in under representation of juveniles when constructing the model. However, nothing is known about size-dependent mobility in *H. erythrogramma* to support this possibility in the current study.

4.5.4 Predicting age at size

The ability to accurately measure a live urchin's test diameter to sub-millimetre accuracy in the asymptotic region of the growth curve causes inevitable problems for both the accuracy and precision of prediction resulting in an accumulation of ages within size classes. The difference in predicted age of individuals, whose body size is less than 1 mm different, may be greater than 40 years. The problem with the accumulation of ages within size classes is not of concern in the current study as the focus is on individuals less than 20 years of age, those located on the region of the growth curve with the greatest resolving power of age-at-size.

4.5.5 Spatial variability in urchin recruitment

Analysis of urchin population age structures in vegetated habitats shows there is little variation in cohort structure across a 10^3 m spatial scale. The lack of significant difference between the sites (excluding Magistrates Point) suggests the recruitment history of these separate populations is similar.

Since the recruitment history of urchin populations inhabiting algal beds within the Mercury Passage is consistent we would expect significant differences in urchin population age structures in adjacent barrens habitat if abnormally high recruitment events facilitate barrens formation. Cohorts from 1992, 1993 and 1994 dominate the age frequency distribution at Stapleton Point accounting for roughly 45% of the population suggesting three years of strong recruitment into the population starting in the summer of 1991/1992, similarly cohorts originating in 1992 and 1993 dominate the age frequency distribution at the Lords Bluff barren site accounting for roughly 45% of the urchin population in the barrens habitat at Lords Bluff. Since the two barrens sites, which are separated by some 20 km have the same strong recruitment events beginning in late 1991 and is not present at other site colonised by algal stands

suggesting the events may have been localised. The algal bed adjacent to the barren habitat at Lords Bluff does have a high proportion of 7 year old individuals, again a cohort originating in the late 1991, however the 5 and 6-year-old cohorts are significantly smaller in size. The emerging pattern of the presence of dominant cohorts in barrens habitats that are unmatched in their magnitude in the adjacent algal bed urchin populations suggest sufficient variation in urchin recruitment at the localised scale (between habitats 10^2 m) does occur. Since the age of the dominant cohorts does not predate the anecdotal evidence that urchin barrens were formed sometime in the 1970s within the Mercury Passage, it is apparent that abnormally high recruitment events in the 1990s are not responsible for the formation of urchin barrens. However, the presence of dominant peaks in the age frequency distribution of urchin populations in barrens habitat that are absent in urchin populations in adjacent algal beds suggest there is sufficient localised variation in urchin recruitment dynamics to elevate urchin population densities on small spatial scales. Small-scale variation in urchin settlement rates in the years following barren formation may be influenced more by physical processes unique to each location than a dependence upon the presence of macroalgae (Schroeter et al., 1996).

We propose that spatial variation in urchin recruitment in the 1970s may have been similar to that described in the 1990s in which small-scale variation in urchin recruitment resulted in elevated urchin densities on barrens compared with adjacent algal beds. Unfortunately we cannot confirm this as evidence of abnormal recruitment events in the 1970s would not be apparent from age structures calculated in this study as the once dominant cohort(s) would have left the population through mortality.

4.6 Conclusion

Comparison of fitted growth functions suggests the Richards function to be appropriate in describing growth in *Heliocidaris erythrogramma*. Using data collected from samples collected one year after tagging resulted in a lower SSE and average magnitude of residuals compared to fitting the Richards function to data of individuals collected two years after tagging.

Comparison of age frequency distributions of urchin populations in algal bed habitats across the Mercury Passage found a consistent pattern of urchin recruitment, with the presence of 7 and 9 year old individuals, in most cases in moderate abundance, at five of the six sites.

The urchin population age frequency distributions of barrens habitat and adjacent algal beds were significantly different with barrens populations dominated by young individuals. In contrast urchin populations in the adjacent algal beds contained a more even distribution of individuals in cohorts up to 20 years of age. The presence of three dominant cohorts in urchin populations on barrens habitats, which are not present in urchin populations occupying adjacent algal beds, are not likely to have been responsible for the formation of the barren habitats since anecdotal evidence suggests the formation of barrens may have occurred 30 years or more prior to the study. Instead, the presence of the three dominant cohorts in the barrens populations indicates sufficient variation in urchin recruitment occurs on small spatial scales to account for localised expansion of urchin population density.

Parameter estimates of the fitted models predict slow growth rates and high annual survival suggesting *H. erythrogramma* to be a species of high longevity.

Chapter 5

Determining sea urchin age using natural growth lines: accuracy of a rapid aging technique

5.1 Abstract

Accurate and robust methods of rapidly determining the age of sea urchins are lacking. Counting natural growth bands in sea urchin ossicles has been used as a rapid method of age determination, but in many cases there has been no attempt to validate the periodicity of line deposition. In the present study we use chemically tagged sea urchins to determine the rate at which natural growth lines in the sea urchin *Heliocidaris erythrogramma* are deposited. Examination of samples from three distinct sea urchin populations revealed that only a small proportion (17-21%) of tagged sea urchins deposited one complete cycle of growth lines annually. For this subset of animals, the deposition of one cycle annually was found to be independent of sea urchin size. For a given size class from the same population, there was considerable variation in the number of growth lines laid down annually. Using natural lines in test plates of *H. erythrogramma* will significantly overestimate the age of individual sea urchins, and age frequency distributions generated using the natural growth line counts differed significantly to those generated using fitted growth models.

5.2 Introduction

The appearance of banding patterns in test fragments of sea urchins has been likened to growth rings in trees (Sumich and McCauley 1973; Gage 1991) and, accordingly, has been used to age a variety of sea urchin species (Lang and Mann 1976; Walker 1981; Wharton and Mann 1981; Nichols et al. 1985; Sime and Cranmer 1985; Gage et al. 1986; Turon et al. 1995). Natural banding appears as an alternation of light and dark bands in skeletal plates, reflecting differential structural characteristics (Pearse and Pearse 1975). However, there are several critical assumptions in using natural growth bands to indicate age, namely that the deposition rate of lines is regular (usually assumed to be annual), and independent of age and the size of the test. Thus, despite the obvious appeal of the simplicity of using growth lines to determine age, validation of the deposition rate is necessary as a first step.

Several studies using growth lines as indicators of sea urchin age did not attempt to establish the accretion rate of lines (Sumich and McCauley 1973; Lang and Mann 1976; Walker 1981; Sime 1982; Duineveld and Jenness 1984; Gage and Tyler 1985; Nichols et al. 1985; Gage et al. 1986). Validating the rate at which lines are accreted has often been attempted by correlating the number of lines with sea urchin size (Miller and Mann 1973; Crapp 1975; Turon et al. 1995). However, indirect correlative techniques are not appropriate because a significant correlation would be obtained if line deposition were episodic because large sea urchins typically have more growth lines in their ossicles compared with smaller sea urchins. A more robust approach is to compare deposition rates directly to a chemical tag laid down in the test at a known time (Kobayashi and

Taki 1969; Pearse and Pearse 1975; Ebert 1988; Gage 1991; Gage 1992; Brey et al. 1995; Robinson and MacIntyre 1997; Russell and Meredith 2000). Notably, in a recent review, Russell and Meredith (2000) concluded that the majority of validation studies using chemical tagging did not find a consistent deposition of growth lines on an annual cycle or consistency in the deposition rate across size classes.

Chemical tagging, primarily using tetracycline and to a lesser extent calcein, is now common in describing growth and estimating age in echinoderms (Gage 1991; Ebert and Russell 1992; Gage 1992; Kenner 1992; Ebert and Russell 1993; Brey et al. 1995; Robinson and MacIntyre 1997; Russell et al. 1998; Ebert et al. 1999; Lamare and Mladenov 2000; Russell and Meredith 2000). The drawback of the technique is the long time interval between tagging and recovery of individuals (usually requiring one full year of growth in the field) and the lengthy laboratory preparation. By comparison, examination of natural growth lines in test plates and the jaw structure of sea urchins is relatively rapid, and thus can potentially facilitate rapid assessment of population age structure. Moreover, sample sizes can be relatively small compared with those required for chemical tagging because all the individuals sampled are used to construct the age frequency distribution. However, validation is essential as a first step to ensure the accuracy of the age predictions from growth lines. In this paper we compare ages predicted from natural growth lines with a fitted growth model constructed from tag-recapture data for the temperate sea urchin *Heliocidaris erythrogramma* in Tasmania.

5.3 Methods

5.3.1 Study sites and tagging

In January and February 1999 approximately 400 individuals were chemically tagged at each of three sites in the Mercury Passage, Tasmania. At each site all sea urchins from an experimental plot measuring approximately 10 m x 6 m depending upon the sea urchin density were collected for tagging. Sites were at Four Mile Point (42° 37' S, 148° 01' E), Chinamans Bay (42° 40' S, 148° 02' E) and Lords Bluff (42° 31' S, 147° 59' E), and experimental plots were located on the 5m-depth contour at each site. Qualitative assessment of each site prior to tagging found attached macroalgae to be highly abundant at Four Mile Point, moderately abundant at Chinamans Bay, and almost completely absent at Lords Bluff (sea urchin barren habitat).

Test dimensions of each sea urchin were measured to the nearest millimetre using knife-edge vernier callipers before injecting sea urchins with tetracycline (Kobayashi and Taki 1969)) at a concentration of 10 gl^{-1} in seawater, using a small-gauge hypodermic needle (adapted from (Ebert 1977)). To ensure all sea urchins received a standard dose of the tetracycline solution (0.006 ml.g^{-1}), test diameter (TD) measurements were used to estimate body weight (W) from a pre-determined function (Pederson and Johnson unpub. data. $W = 3.4903.TD - 154.14$, $n = 40$, $R^2 = 0.93$). Chemically tagged sea urchins were returned to experimental plots soon after receiving injections. Mortality from handling was assessed 72 hours post tagging by searching experimental plots for fresh mortalities, and was less than 5% of tagged individuals. Two samples of tagged sea urchins were later recovered to determine the deposition rate of growth lines, 12 and 24 months post-tagging.

5.3.2 Sample preparation

Prior to dissection the test diameter of each sea urchin was measured to the nearest mm using knife-edge vernier callipers. On dissection, half of the test and the entire Aristotle's lantern were placed into a solution of 5% sodium hypochlorite. The calcified material remaining after 24 hours was rinsed thoroughly with freshwater before being air-dried for 48 hours.

Four separate ossicles were selected from each individual sea urchin. Three plates were selected from the interambulacral column for preparation, *viz.* from the oral end, mid-axis and aboral end along with one demipyramid. The mid-axis plate is located at the maximum radius of the test curvature. The oral plate was located by measuring the mid-point between the oral nerve complex and the mid-axis plate and the aboral plate located mid way between the mid-axis plate and the genital plate.

Ossicles were prepared in two stages. Plates and demipyramids were first prepared for viewing under ultraviolet light to reveal the tetracycline tags, after which they were prepared for reading natural growth lines under visible light. Measurements based on the tetracycline tag were made prior to preparing ossicles for reading the natural growth lines because the latter process requires charring the plates at high temperature, which destroys the tetracycline tag.

Test plates were sanded lightly using 400-grit and then 800-grit wet-and-dry sand paper to reveal tetracycline marks. Demipyramids were sanded lightly to remove ridges using only 800 grit paper. Ossicles were then examined under a dissecting microscope using

ultraviolet illumination. If a tetracycline tag was present the amount of calcite deposition from the growing plane to the tetracycline tag was measured to the nearest 25 μm using an optical micrometer in a dissecting microscope. Ossicles (jaws and plates) were then charred for ca. 30 minutes at 300°C in a muffle furnace until the surface of each ossicle turned light brown. Once cooled, ossicles were sanded lightly using 800 grit paper and then dipped in mineral oil to reveal the natural growth lines. Natural growth lines were easily distinguishable and counted using a dissecting microscope at 50 times magnification.

5.3.3 Sample selection and growth measurement

Individuals from the one and two year sampling periods with clear tetracycline marks on the demipyramids were sorted into 2 mm size classes based on test diameter. Individuals from each of the size classes displayed the greatest and least amount of growth on the demipyramid were included in the sample as well as the smallest and largest individual from each site with tetracycline marks on their demipyramids. Individuals not showing clear tetracycline marks on their demipyramids were excluded from the analysis.

Growth occurring between the time of tagging and time of sampling was quantified on test plates by measuring the distance between the inter-radial suture edge and the tetracycline tag. The measurements were made along an axis running from the inter-radial suture edge to the centre of the plate. Similarly growth in the demipyramid was quantified by measuring the distance between the aboral edge and the tetracycline mark along an axis running from the aboral edge to oral tip of the demipyramid.

Growth cycles consisting of one light and one dark growth line were counted from the inter-radial suture edge towards the centre of mid axis test plates only, since growth lines were not readily distinguishable in either aboral or oral plates. The number of growth cycles deposited per annum was determined by counting the number of cycles occupying the section of test plate between the inter-radial suture edge and the position of the tetracycline mark. For individuals from the two year samples the number of cycles counted between the plate edge and the position of the tetracycline was halved to determine the number deposited per annum. This resulted in half-counts being obtained in individuals depositing odd numbers of cycles over the two-year growth period. Mid-axis plates in which natural lines were not distinct were discarded and another plate prepared from the same individual until a clearly readable sample was obtained.

The total number of growth cycles appearing between the inter-radial suture edge and the centre of mid axis plates were counted and divided by the rate of cycle deposition to determine age of individual sea urchins.

5.3.4 Comparing aging techniques

Age frequency distributions generated from natural growth line counts were compared with similar distributions generated from fitted growth models (Chapter 4) using the Kolmogorov-Smirnov test for each of the three urchin populations. Mean urchin age was calculated using both aging techniques for each population and compared using non-parametric analysis of variance (NPANOVA).

5.4 Results

The deposition of natural growth lines in the mid-axis test plates of *Heliocidaris erythrogramma* is not a uniformly annual event (Figure 5.1). Analysis of covariance (ANCOVA) found no significant interaction between treatment (populations) and covariate (test diameter $F_{2,5}=1.86$, $P=0.159$). Subsequently no clear relationship between the number of cycles deposited annually in mid-axis plates and test diameter was evident among the three populations ($F_{2,3}=1.96$, $P=0.144$). High variances in the rate of deposition of growth cycles preclude using the total number of growth cycles present in mid-axis test plates for accurate prediction of sea urchin age. Notably, the deposition of one complete cycle within one year occurred in only a small percentage (13-23%) of individuals at each of the three sites (Figure 5.1).

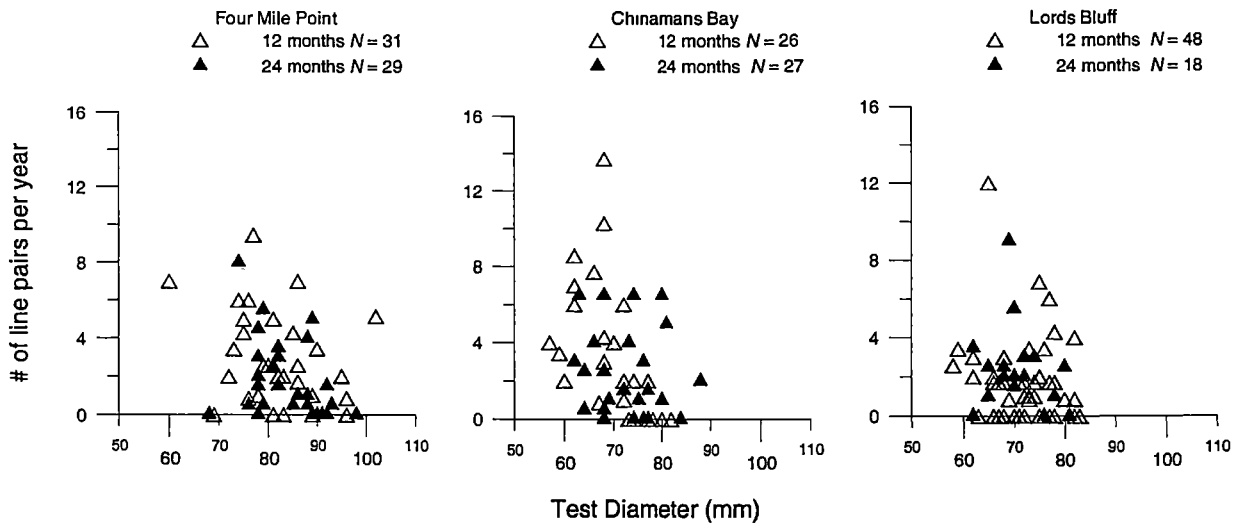


Figure 5.1 Relationship between the numbers of cycles deposited annually in mid-axis plates as a function of sea urchin test diameter at three sites in the Mercury Passage. One growth cycle consists of a single light and a single dark growth band. Data points represent individuals with clear tetracycline tags (tag success) on mid-axis test plates from the one- and two-year post-tagging samples. Tagging success (percentage of individuals with clear tetracycline tags on mid-axis plates) was 55% at Four Mile Point, 38% at Chinamans Bay and 46% at Lords Bluff.

The percentage of tagged individuals with positive tetracycline tags displayed on test plates reflects the relative portioning of resources for growth within the sea urchin. Of the 138 individuals with clear positive tags on their jaws from Chinamans Bay, only 38% had readable tags on test plates. The percentage of test plates with positive readable tags was the greatest at the Four Mile Point site. However over one half of all samples with readable jaw tags lacked the corresponding tags on their test plates.

Similarly, the number of individuals showing positive tetracycline tags on plate margins but with no visible sign of natural band deposition was not related to sea urchin size at any of the three sites. The absence of any growth between the tetracycline tag and the

plate margin (0 growth cycles occurred at a relatively high frequency, viz. 37% of individuals at Four Mile Point, 36% at Lords Bluff, and 32% at Chinamans Bay (Figure 5.1). The lack of growth displayed in the test plates was not reflected in the jaw elements of the same individuals. All tagged sea urchins recovered, including those not displaying growth on plate margins over the experimental period, displayed measurable growth on jaw elements.

Assuming a single cycle of growth lines were deposited annually, the age of each individual was calculated and compared with those estimated from fitted growth models (Richards function, Table 5.1) developed in Chapter 4. At all three sites, the mean age of individuals was significantly higher, based on this assumption and using counts of natural growth cycles, compared with the estimates of the fitted model (chapter 4).

Table 5.1 Summary of parameters estimates for fitted growth models (Richards function) of three sea urchin populations in the Mercury Passage (Chapter 4), where k is the growth rate, D_{∞} is the infinite test diameter size (mm), SSE the error sums of squares with shape parameter n constructed with N number of individuals.

Site	k	D_{∞}	SSE	n	N
Four Mile Point	0.14	98.10	3.491	-1.19	90
Chinamans Bay	0.25	83.50	4.896	-1.23	139
Lords Bluff	0.19	87.20	5.419	-1.11	136

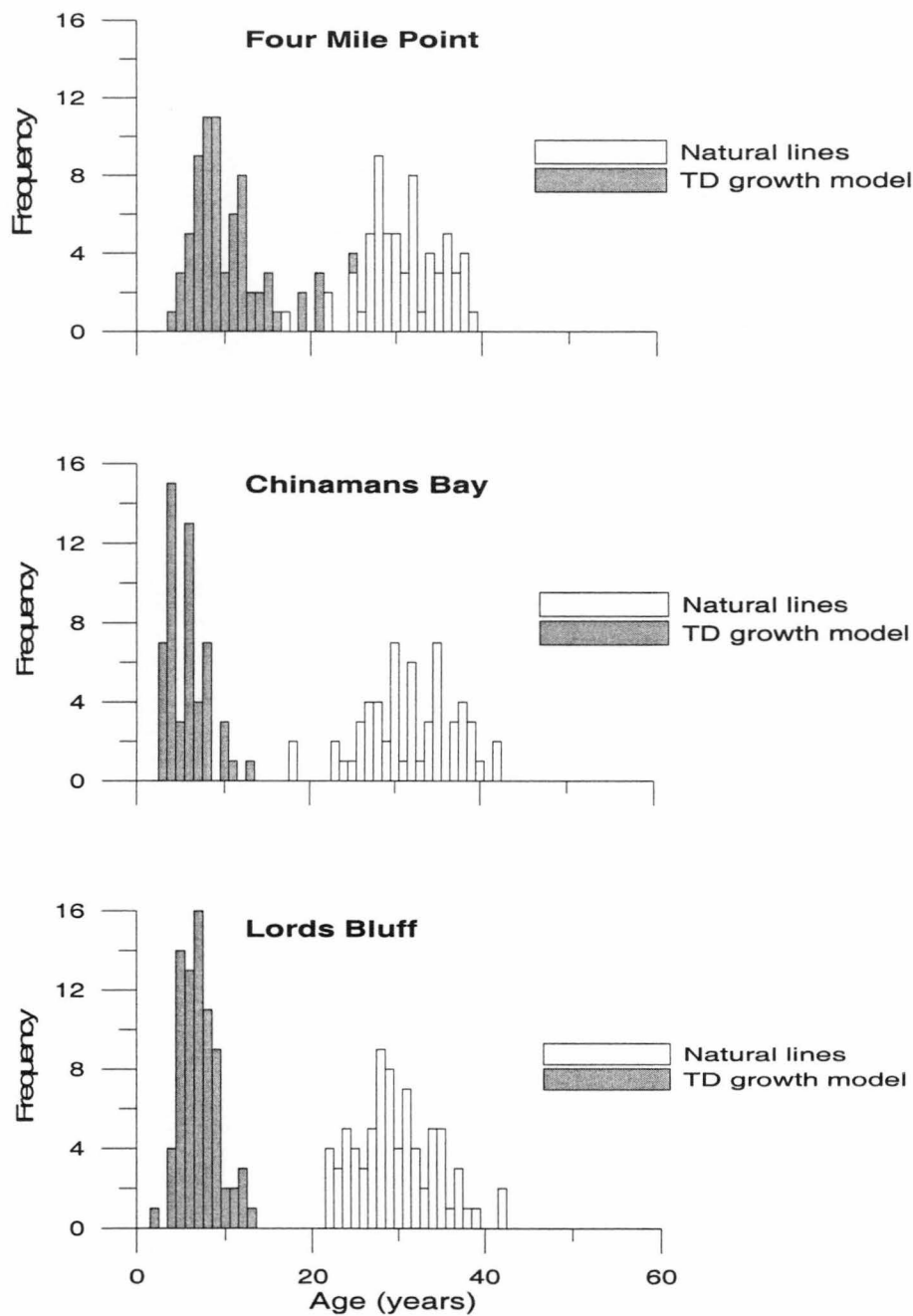


Figure 5.2 Age frequency distributions of the three tagged populations estimated from natural growth lines (white bars, assuming annual deposition occurs across all size classes) and predicted from a size-at-age growth model derived from growth of tagged sea urchins (shaded bars, Chapter 4). At all sites the two distributions were significantly different (Kolmogorov-Smirnov, $P < 0.0001$ in each case). Mean sea urchin age determined using natural growth cycle counts (assuming annual deposition) and from the individual size-at-age model (Chapter 4) were significantly different (non-parametric ANOVA) at Four Mile Point (32.86 and 12.07 $F_{1,146}=232.7$ $P=0.0001$), Chinamans Bay (31.65 and 8.63 $F_{1,112}=164.9$ $P=0.0001$) and Lords Bluff (29.71 and 7.08 $F_{1,150}$ $P=0.0001$).

5.5 Discussion

5.1 Validation of growth lines

Our results show clearly that the deposition of natural growth lines in the mid-axis test plates of *Heliocidaris erythrogramma* in Tasmania is not uniformly an annual phenomenon in any of the ages classes sampled. We are confident in our results since counting growth lines on the plates was unambiguous. Using natural growth lines and assuming annual deposition overestimates age and provides a larger spread of ages than using the size-at-age model based on growth in tagged sea urchins (Figure 5.2). Another method to rapidly assess age in *H. erythrogramma* based on counting ridges on the jaw surface similarly showed no consistent annual deposition pattern (Sanderson et al. 1996).

Considering our findings and the review of Russell and Meredith (2000), the emerging picture is that uniform annual deposition of natural growth lines across size and age classes, as occurs in the Antarctic sea urchin *Strerechinus neumayeri* (Brey et al. 1995), is the exception rather than the rule. Even the findings of Gage (1991, 1992a,b), that the deposition of natural growth lines followed an annual pattern in juvenile *Echinus esculentus* but not in adults, appears to be a unique case. The validity of using natural growth lines to determine the age of sea urchins is, at best, equivocal.

Poor concordance of band formation with an annual cycle may reflect that accurate identification of bands can decrease as a function of test diameter as the quantity of calcite deposited on plate margins decreases (Gage 1991). This can result in observer error and erroneous rejection of the hypothesis of annual periodicity. However, in our

samples the presence and absence of lines was unambiguous. Our observations of animals with clear tetracycline marks on their jaws but no evidence of any tag on their plates, and others with the tetracycline tag at the very margins of plates, indicates that the absence of any visible deposition of calcite on plates (and therefore absence of plate growth) in some individuals was real. Furthermore, *H. erythrogramma* showed no dependence of the number of bands deposited on size or age, as small sea urchins were found to deposit similar numbers of bands as adults over the one-year tagging period. Clearly, the quantity of calcite deposited in test plates is highly variable within age and/or size classes compared with that in jaw elements. Therefore, using jaw elements to study growth in *H. erythrogramma* would be preferable to the use of test plates.

5.2 Relative allocation of resources for growth

Of the individuals processed in the current study in which jaw elements demonstrated a readable tag, only about 46% showed tetracycline marks on test plates, indicating that the deposition of calcite and the incorporation of tetracycline into jaw elements is greater than in test plates. This is likely to reflect differential resource allocation within individual sea urchins (Ebert 1980). The relative importance of jaw deposition over test growth suggests that the increases in jaw length relative to test diameter may increase the efficiency of obtaining food for the same body volume. Sea urchins in food-limited populations are known to have relatively larger jaw elements compared with individuals of equivalent test size in populations where food resources are abundant (Ebert 1980; Black et al. 1982; Levitan 1991; McShane and Anderson 1997). This mechanism may allow sea urchins to optimise their grazing ability.

5.3 Mechanisms of growth line deposition

It is clear that in *H. erythrogramma* natural growth lines are laid down more frequently than annually. This raises the question of the mechanism(s) of growth line deposition. The rate of deposition of natural growth lines has been suggested to reflect food intake in *Strongylocentrotus purpuratus* (Pearse and Pearse 1975), the Antarctic sea urchin *Strechinus neumayeri* (Brey et al. 1995) and in *Paracentrotus lividus* (Turon et al. 1995). Of the three locations used in the present study, the site at Lords Bluff is the only one situated on a sea urchin barren habitat with characteristically little available attached algae. The percentage of samples showing one complete cycle to be deposited over the one-year period, and therefore validating deposition as an annual event, was the greatest at the barren site compared with the two alternate locations with greater attached food resources. The remaining individuals in the Lords Bluff population deposited on average 2 growth cycles per year compared with 3 growth cycles on average in the 'non-validating' individuals from the other two sites. However, the pattern was not consistent with a high degree of variation displayed between individuals in the same size and/ or age class at the same site. The rate of natural line deposition is not clearly related to food intake in a gross sense, although it may possibly reflect variation among individuals in feeding.

Determining the mechanisms, which underpin the rate of natural line deposition in *H. erythrogramma*, requires further investigation to resolve these issues.

General discussion:

Effects of fishing rock lobsters on sea urchin population dynamics and formation of urchin 'barrens' on the east coast of Tasmania

6.1 Introduction

Dramatic phase shifts in ecosystem structure from one dominated by macroalgae to urchin 'barrens' largely devoid of macroalgae have been documented in temperate regions worldwide (Shepherd, 1973; Lawrence, 1975; Chapman, 1981; Andrew, 1988; Shears and Babcock, 2002). Transition of these systems from the structurally complex algal dominated configuration to urchin barrens habitat results in decreases in primary production of the order of 100-fold (Chapman, 1981), and presumably there are flow-on effects for secondary production. Once established, urchin barren habitats can persist for extensive periods due to the highly plastic nature of urchin resource allocation (Johnson and Mann, 1982). This phenomenon is well documented, but there have been few explicit tests of the numerous hypotheses suggested as plausible mechanisms that underpin the onset of destructive grazing of macroalgae by sea urchins.

Because the density of sea urchins on barren grounds is usually greater than that in kelp-bed habitat in the same area, Breen and Mann (1976a) proposed that a 'threshold' urchin density is required to facilitate overgrazing of attached macroalgae. Attached kelp plants survive when urchin abundance is low but are vulnerable to overgrazing when urchin density exceeds the threshold level. This idea

raises the question as to the likely mechanism(s) facilitating increases in urchin populations. One possibility invokes the removal of top-down predatory control of urchin populations as the major inhibitor of urchin population expansion. Since the hypothesis was first generated in the early 1970's (Mann and Breen, 1972; Lowry and Pearse, 1973; Estes and Palmisano, 1974), a range of studies have identified decapod crustaceans (Tegner and Levin, 1983; Mayfield and Branch, 2000; Shears and Babcock, 2002), teleost fish (Vadas and Steneck, 1995; Babcock *et al.*, 1999; Shears and Babcock, 2002) and marine mammals (Duggins, 1980; Dean *et al.*, 2000; Estes *et al.*, 1998; Watt *et al.*, 2000) as predators likely to regulate urchin population density and size structure.

Intensive exploitation of urchin predators, in many cases over many decades or centuries, has significantly reduced the abundance and average size of urchin predators in exploited habitats (Lowry and Pearse, 1973; Estes and Palmisano, 1974; Duggins, 1980; Vadas and Steneck, 1995; Estes *et al.*, 1998; Dean *et al.*, 2000; Mayfield and Branch, 2000; Watt *et al.*, 2000; Shears and Babcock, 2002). The advent of no-take marine protected areas (MPAs), in which abundances and average size of putative predators potentially increase towards pre-fishing levels, provide a valuable opportunity to test the hypothesis that removal of top-down predatory control facilitates urchin population density expansion. Transformation of urchin barren habitats to macroalgal dominated communities as a result of increased abundances of urchin predators, and the reinstatement of top-down predatory control of urchin populations, has been recently documented inside no-take marine reserves in northeastern New Zealand (Shears and Babcock, 2003).

In the current study aspects from our previous work are used to assess the effect of fishing lobsters on the expansion of urchin populations. Simple population matrix models constructed using empirically derived estimates of age-specific mortality (Chapter 3) and urchin population age frequency distributions (Chapter 4) are used to demonstrate that the exploitation of urchin predators to be an important mechanism accounting for expansion of sea urchin (*Heliocidaris erythrogramma*) populations in south eastern Tasmania.

6.2 Model development

Matrix projection models have been widely applied in marine science as a useful means to predict population growth (see Caswell (2001) for overview). Here we use a matrix model to project urchin population growth under varying rates of urchin mortality and survival as a function of predator abundance. The structure of the model can be written as:

$$N_t = N_{a,t-1} \cdot S_{a,t-1 \rightarrow t} + R_{a,t_0} \quad (\text{Eq .1})$$

where N_t is the abundance of all individuals at time t , which is the sum of multiplying the abundance of individuals in each age class at time $t-1$ ($N_{a,t-1}$) by the probability of individuals in each age class surviving from time $t-1$ to t ($S_{a,t-1 \rightarrow t}$), plus annual recruitment into the first age class at time t_0 (R_{a,t_0}) where the time parameter t are yearly increments.

In all population projections the rate of recruitment (R) to the sampled population was set at a predefined level and therefore can be considered a constant, a similar approach to that of by Hughes (1994).

6.2.1 Model components and parameter estimates

Estimates of age-specific mortality and population age-frequency distribution were made from empirical data collected in previous manipulative experiments (Chapter 3) and surveys (Chapter 2), at sites within the Mercury Passage on the south-eastern coast of Tasmania (Figure 2.1). Within the Mercury Passage, the community structure of subtidal rocky reefs are either sea urchin dominated (barrens) or support dense stands of macroalgae (Valentine, 2003).

6.2.1.1 Population age structures

The population age frequency distribution used to simulate population trajectories was constructed from size frequency data, from a representative algal dominated habitat within the Mercury Passage region, collected during a large-scale survey of urchin populations on the east coast of Tasmania in 1999 (Chapter 2). The size frequency distribution, consisting of more than 2100 individuals, was converted to an age frequency distribution using a size-at-age relationship generated from individual-based urchin growth models (Chapter 4).

6.2.1.2 Estimating urchin mortality rates in exploited habitats

Estimates of instantaneous age-specific mortality rates for an urchin population exposed to relatively low predator abundances, typical of rocky reefs in the Mercury Passage open to fishing, were calculated from an age-frequency distribution generated in Chapter 4 (method overview by Ebert, 1999). Instantaneous age-specific mortality was estimated as a decaying exponential function (Equation 2). These mortality estimates incorporate both predation mortality and other sources of mortality.

The decaying exponential function can be written as:

$$N_t = N_0 \cdot e^{-Zt} \quad (\text{Eq. 2})$$

Where N_0 is the number of individuals in a cohort at time $t=0$, N_t is the number of individuals in the same cohort after time interval t , and Z the mortality coefficient used to estimate instantaneous mortality rates using $1 - e^{-Z}$. Note that instantaneous age-specific mortality was converted to age-specific survival (e^{-Z}) for the survival probability matrix (Eq 1)

6.2.1.3 Estimates of urchin mortality rates in predator abundant habitats

Broad-scale surveys along ca. 200km of the south eastern coastline of Tasmania found the population density of *H. erythrogramma* to be negatively associated with both abundance of rock lobsters and total putative predator abundance (Chapter 2). At smaller scales, we found that total predator abundances were significantly greater inside than outside no-take marine reserves (Chapter 2). Closer examination of the relationship shows urchin density is dependent upon the abundance of rock lobsters, in particular those above the minimum legally exploitable size (>110 mm CL), while the relationship between urchin density and demersal fish abundance was not clear. Furthermore in a large scale caging experiment, inside a no-take marine reserve, to separate the effects of lobsters and demersal fish, lobsters were found to have a significant negative effect on urchin survival while demersal fish played a minor role in determining urchin survival (Chapter 3).

Treatment plots in the large-scale caging experiment (Chapter 3) in which both lobsters and fish were allowed access to urchins inside crevices (open plots) resulted in significantly reduced urchin survival compared to treatments in which both

predators were excluded which allowed us to estimate age-specific urchins mortality rates. We considered urchin mortality inside open plots to be an estimate of predation mortality rate over 2 months, which we attribute primarily to lobsters in light of the patterns observed in the broad scale survey and the results from the manipulative experiments (Chapter 3). Annual urchin predation mortality attributed to lobsters, was estimated by projecting the 2-month mortality rate over 9-months to exclude moulting and mating periods.

Note that the estimated age-specific mortality calculated from results of the manipulative experiment consists of only predation mortality and not other sources of mortality and as such is considered to be conservative.

6.2.2 Model assumptions

Two sites within the Mercury Passage in which established urchin barrens habitat extended over several hundred meters of reef bottom (Figure 2.1), supported populations of adult urchins (>30 mm TD) at an average urchin density of 9 individuals per m^2 (Chapter 2). However, localised urchin densities of up to 50 individuals per m^2 were observed in response to drift algae at both sampling sites. We proposed that the background density of 9 individuals per m^2 is sufficient to provide enough individuals that when aggregated (ca. 50 individuals per m^2) can destructively graze attached macroalgae. Since the density of adult urchins (>30mm TD) inside algal beds adjacent to established barrens, were on average less than 3.5 m^{-2} , we conclude that the higher urchin density of 9 individuals per m^2 is the 'threshold' required to facilitate barren formation.

Due to inherent problems associated with sampling cryptic post-settlement juvenile urchins <30 mm test diameter, we use recruitment rates into the adult population (>30 mm TD) in projecting population density. Since juvenile urchins (<30 mm) are highly cryptic and not likely to be predated upon by the same predators as their larger/older conspecifics, their exclusion from the modelled population is justified. In comparing trajectories of populations exposed to different abundances of predators of adult urchins, we assume use of recruitment rates to the adult population is valid.

6.3 Results

Projection of the representative algal bed urchin population over 50 years under two different levels of predation pressure, representing areas open and closed to fishing, revealed two clearly dissimilar trajectories (Figure 6.1). After an initial phase of population expansion, the two trajectories become asymptotic and relatively stable at ca. 6 and 10 urchins.m⁻² for habitat open to, and protected from, fishing respectively.

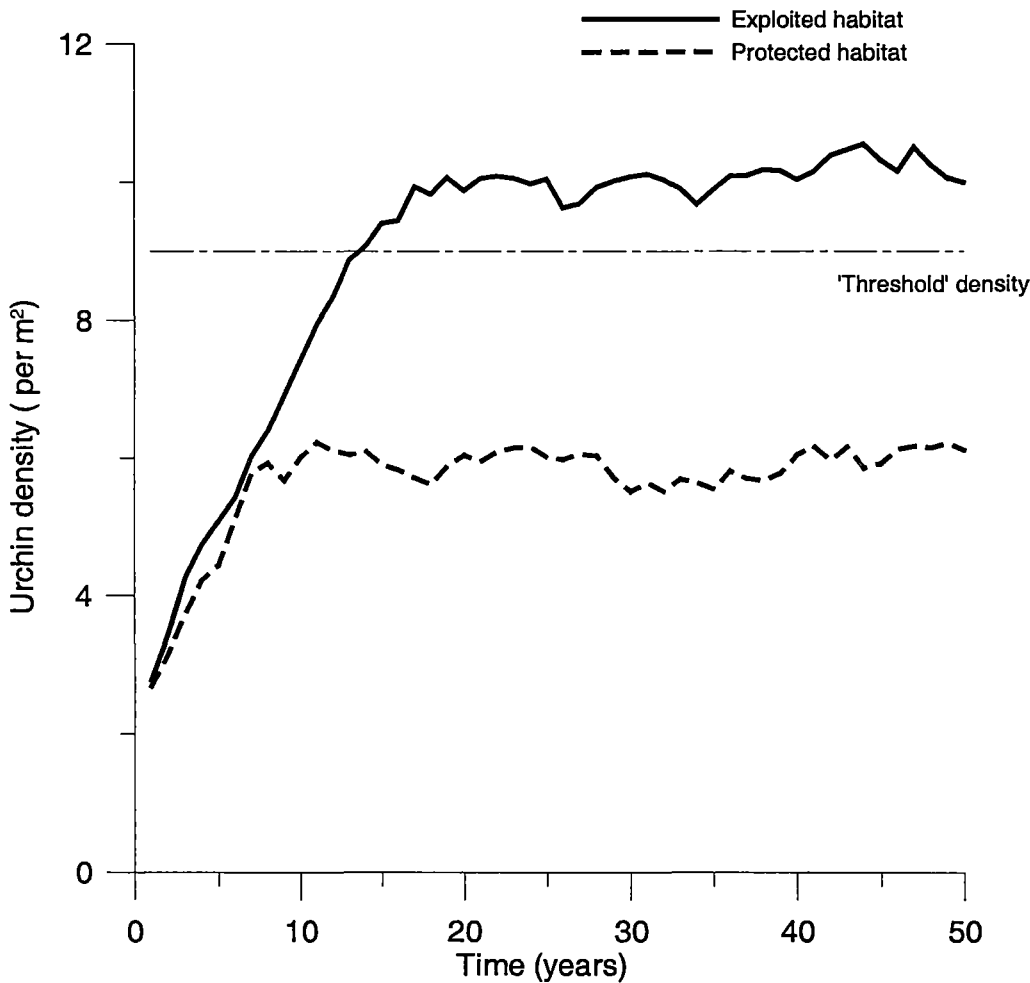


Figure 6.1 Projected urchin population density trajectories under low predation pressure (exploited habitat) and high predation pressure (protected habitat). 'Threshold' density represents the theoretical urchin density to facilitate 'barrens' formation (9 individuals.m⁻²). Recruitment rate into the sampled population was set at 0.75 individuals.m⁻².yr⁻¹.

Despite that both populations experience the same recruitment rate over a 50-year time period, high predation mortality at the level experienced inside the no-take

marine reserve, is sufficient to limit population density well below the theoretical threshold density for barrens formation. In comparison, the population trajectory exposed to low predation mortality rates, typical of areas open to fishing, stabilised at a population density above the theoretical 'threshold' that would facilitate barren formation.

To determine the recruitment rate required to push urchin population density above the threshold density of urchin barren formation, population density was projected over a 50 –year time period for a range of recruitment rates. Average population densities were calculated over the last 30 years of population projection (i.e. in the asymptotic range) across an order of magnitude change in recruitment to the adult population (TD >30 mm). The relationship between asymptotic population density and recruitment rate follows a positive linear relationship with the two population trajectories crossing the theoretical threshold at different points (Figure 6.2). To facilitate urchin barren formation under low predation mortality typical of exploited habitats, a recruitment rate of 0.75 individuals $\text{m}^{-2} \text{year}^{-1}$ is required. Under a high predation mortality rate the same urchin population requires an annual recruitment rate of 1.25 adults m^{-2} to facilitate barren formation.

For a projected urchin population, experiencing low predation rates, to remain at a stable density of 2.5 individuals m^{-2} (i.e. at the average urchin density in algal beds within the Mercury Passage) a recruitment rate to the 1+ age class (>30mm TD) of 0.22 $\text{m}^{-2} \cdot \text{year}^{-1}$ is required. This is comparable with estimates of recruitment made by Sanderson *et al.* (1996) in a nearby algal bed habitat within the Mercury Passage. To maintain an average urchin density of 0.75 individuals $\cdot \text{m}^{-2}$, equivalent to densities

inside the no-take marine reserve, an annual recruitment rate of 0.08 individuals m^{-2} to the 1+ age class is required. A 3.5 fold increase in annual recruitment is needed under low mortality rates, to elevate the population above the theoretical threshold density, while under high levels of predation mortality, an order of magnitude increase in annual recruitment will elevate the population above the theoretical threshold density.

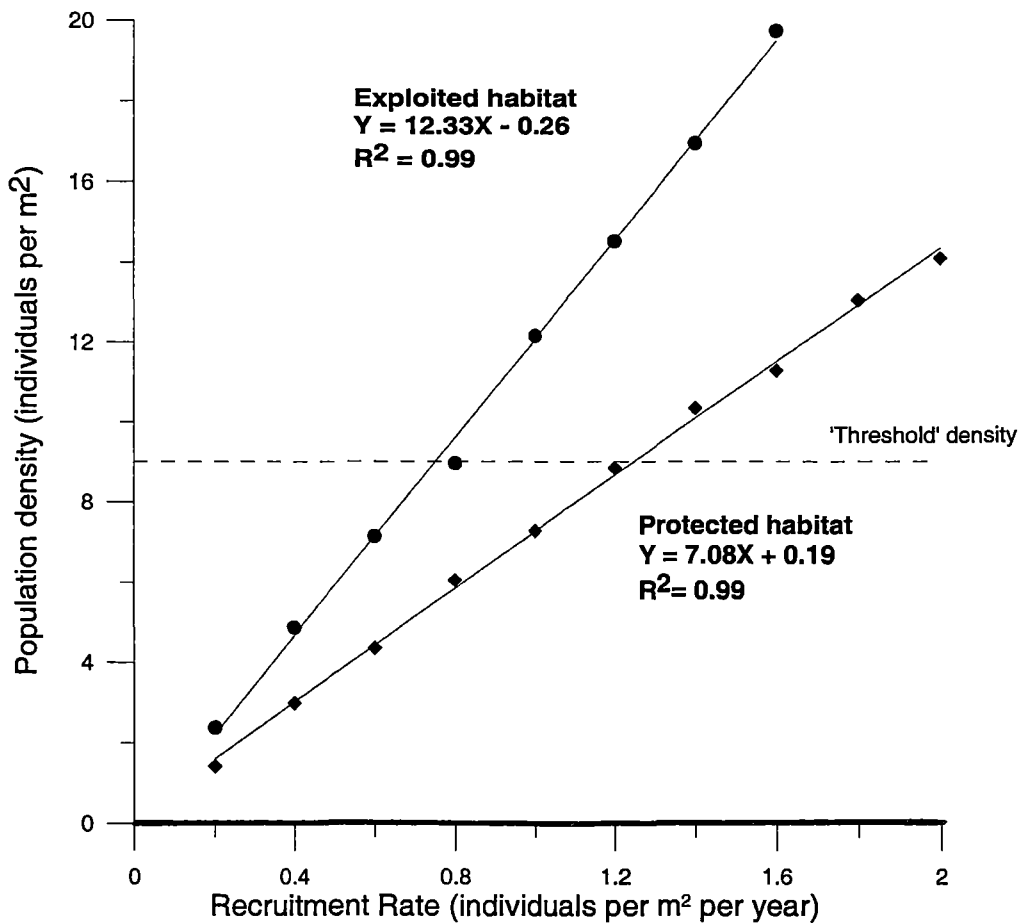


Figure 6.2 Predicted urchin population densities in fished and protected habitats as a function of annual recruitment rate into the 'sampled' population. Population density calculated as the average asymptotic density over a 30-year period.

On average, adult urchin population density will be 1.6 times greater under low predation pressure compared to the same population projected under high levels of predation mortality across an order of magnitude range in recruitment rates.

Projecting the two populations, under the same rate of adult recruitment, over a 50-year period results in significantly different age frequency distributions (Figure 6.3, Kolmogorov-Smirnov $P = 0.0001$). Younger individuals dominate the population age frequency distribution under high predation pressure (protected habitat) with very few individuals older than 10 years present. In contrast the age frequency distribution of the population under low predation pressure has a wider range of age classes with a greater proportion of individuals over 10 years compared to the population subject to high predation mortality.

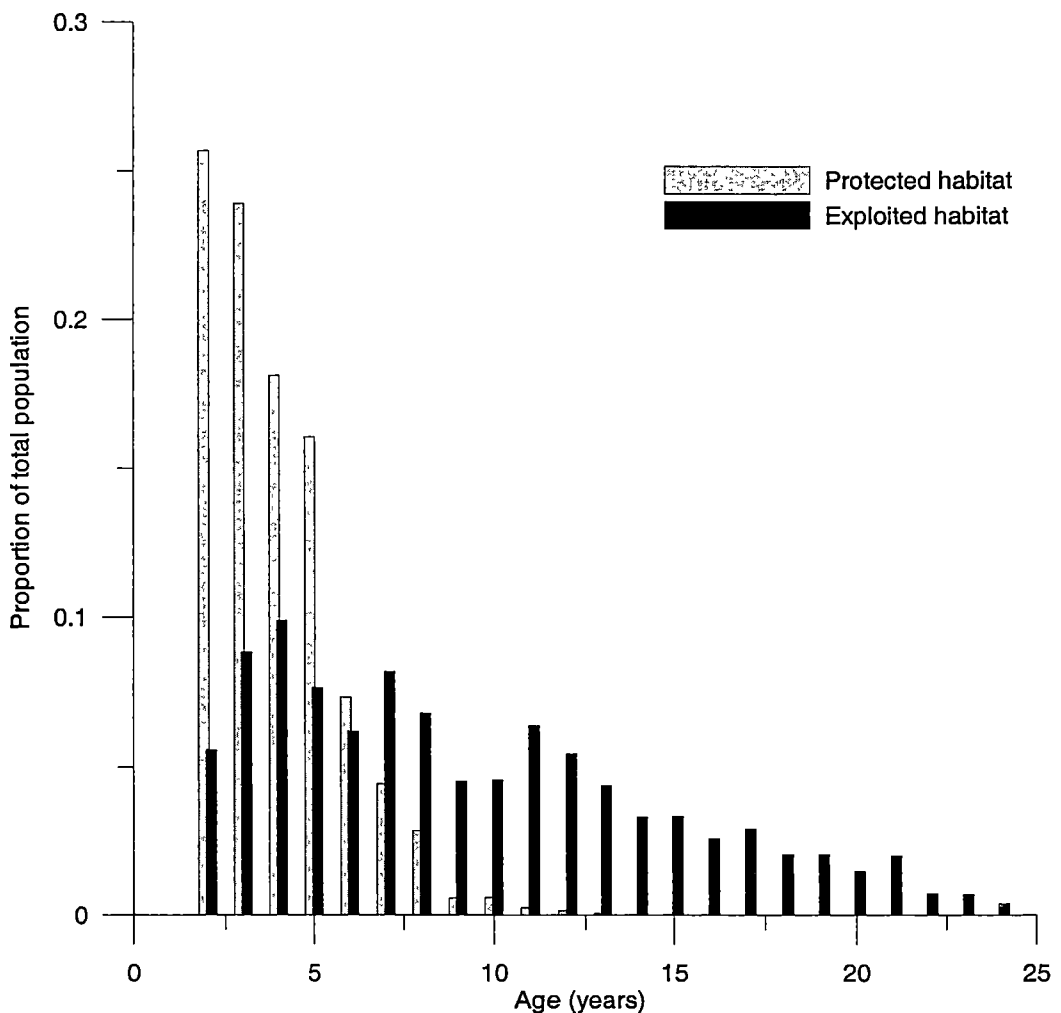


Figure 6.3 Urchin population size frequency distributions under two different predation mortality scenarios, experiencing equivalent adult recruitment rates, were significantly different after 50 years of projection (Kolmogorov Smirnov test, $\text{Prob} > K_{sa} = 0.0001$).

6.4 Discussion

Since the development of the predator control hypothesis there has been conjecture about whether, and which, predators might control urchin populations. Although predatory control has been clearly demonstrated in the case of the sea otters in the northeastern Pacific (Lowry and Pearse, 1973; Estes and Palmisano, 1974; Duggins, 1980; Estes *et al.*, 1998; Dean *et al.*, 2000; Watt *et al.*, 2000), the controlling influence of urchin predators in other systems is less certain. Relatively recently, strong evidence has emerged of top-down predatory control of urchin populations has been demonstrated in temperate ecosystems of the southern hemisphere by lobsters (Mayfield *et al.*, 1999; Shears and Babcock, 2002) and fish in the northern hemisphere (Steneck *et al.*, 1995; Vadas and Steneck, 1995). In temperate Australian waters the importance of top-down predatory control of urchin populations has not been examined.

It has been speculated that the extent of urchin barrens on the east coast of Tasmania could account for approximately 50% of inshore subtidal reef habitats along ca 200 km of coastline (Sanderson *et al.*, 1996). Within this region commercial and recreational fisheries have significantly reduced the abundance of predators of *H. erythrogramma*, including rock lobster (Edgar and Barrett, 1999), which has potentially reduced predation mortality rates in urchin populations. A clear negative correlation between total abundance of putative urchin predators and urchin density along this section of coastline (Chapter 2), and the presence of localized urchin populations at relatively high densities inside urchin barrens suggests decreased predation mortality rates due to exploitation of predators could have allowed urchin populations to expand.

6.4.1 Effects of fishing urchin predators

Close examination of the clear negative correlation between total putative urchin predator abundance and urchin density along the east coast of Tasmania is dominated by the abundance of rock lobsters (Chapter 2). Furthermore, the abundance of lobsters larger than the minimum legally exploitable size (>110 mm CL) displayed a strong negative relationship with urchin abundance. While the relationship between lobsters and urchins was clear across the broad scale of the east coast of Tasmania, the relationship between demersal fish and urchin abundance was not clear. Combined with results of a large-scale caging experiment, in which the survival of a wide range of urchin sizes (40-100 mm TD) was significantly reduced in the presence of lobster but not demersal fish, indicates lobster to be more important predators of adult urchins compared to demersal fish.

We suggest the significant reduction in legal sized lobster biomass to less than 4-8% of the virgin pre-exploitation stock on the east coast of Tasmania (Frusher, 1997) is likely to have influenced populations of *H. erythrogramma*. The reduction in lobster biomass has ultimately resulted in the size frequency of the rock lobster population to become positively skewed, dominated by a greater number of smaller individuals relative to a normal distribution of size classes. Intensive fishing has resulted in large lobsters being almost exclusively restricted to within marine “no-take” reserves (Chapter 2).

Results of an experiment to examine size specific predation showed conclusively that the predation potential of lobsters is positively related to lobster body size (Chapter 3). The larger the sea urchin, the larger must be the lobster to successfully capture and consume it (Chapter 3). Clearly, a shift in the size structure of rock lobsters

towards one dominated by juveniles will result in decreased mortality rates of large sized urchins. Our simple models suggest that the significant reduction in biomass of legal sized lobsters could be sufficient to account for differences in the age structure of the two urchin populations after 50 years, noticeably the greater proportion of older urchins in exploited habitats.

Although demersal fish appear to have minimal effect on survival of urchins 40-100 mm test diameter (chapter 3), their effect on sizes <40 mm may be significant. The impact fishes may have on structuring the urchin population in the early life history stages is not clear and requires further investigation. A significant reduction in the abundance of *Notolabrus tetricus* and other large demersal feeding fish via gill netting and live trapping may play a considerable role in shaping the density and size structure of the urchin populations, and in particular the recruitment of animals to the 1+ age class (ca. 30 mm TD).

6.4.2 Fluctuating recruitment rates as a likely mechanism in urchin population expansion

For urchin population density to expand to a level above the theoretical ‘threshold’ density to facilitate barren formation under low predation pressure, a 3.5 times increase in the estimated average recruitment to the adult population is required. In comparison, in a habitat in which predation mortality is high (inside a no-take marine reserve) an order of magnitude increase in average recruitment is required to push urchin densities above this threshold. While fluctuations in recruitment can vary (reviewed by Ebert (1983)), in some cases by orders of magnitude, the likelihood of several consecutive prodigious recruitment events are unlikely. In the advent of a single prodigious increase in larval supply urchin density would initially increase in predator abundant habitats, and after a lag phase, urchin density would begin to

decline. The same situation would not occur in a habitat in which predator abundance is significantly reduced since predation mortality is not sufficient to limit population expansion. Therefore, we propose predator abundance to be an important factor in limiting expansion of *H. erythrogramma* populations experiencing vast fluctuations in annual recruitment.

6.5 Conclusion

The correlative evidence from published work suggests that several mechanisms may operate to cause urchin barrens. Their development may occur after prolonged exploitation of urchin predators, especially if accompanied by occasional prodigious peaks in urchin recruitment. It has become clear that urchin populations under high predation pressure require significantly higher recruitment rates to elevate urchin density above threshold densities necessary to form urchin barrens. Results from the current study suggest the reduction in legal-sized lobster biomass on the east coast of Tasmania to below 8% of the virgin biomass is sufficient to account for expansion in density of *Heliocidaris erythrogramma* populations to levels exceeding the theoretical ‘threshold’ to facilitate barren formation. We do not suggest that predation and recruitment are the only processes leading to urchin barrens formation in southeastern Tasmania since high densities of urchins are found in habitats still supporting macroalgae although very rarely. Instead we propose a number of other processes outside the scope of this research in combination with predation and recruitment, cause sufficient alteration in the urchin population dynamic to cause urchin barrens to form.

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