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# Predation of the sea urchin *Heliocidaris erythrogramma* by rock lobsters (*Jasus edwardsii*) in no-take marine reserves

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## Abstract

The formation of sea urchin ‘barrens’ on shallow temperate rocky reefs is well documented. However there has been much conjecture about the underlying mechanisms leading to sea urchin barrens, and relatively little experimentation to test these ideas critically. 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. Tethered juvenile and adult sea urchins experienced much higher rates of mortality inside no-take marine reserves where sea urchin predators were abundant compared to adjacent fished areas where predators were fewer. Mortality of tagged (but not tethered) sea urchins was also notably higher in marine reserves than in adjacent areas open to fishing. When a range of sizes of sea urchins was exposed to three sizes of rock lobsters in a caging experiment, juvenile sea urchins were eaten more frequently than larger sea urchins by all sizes of rock lobster, but only the largest rock lobsters (> 120 mm CL) were able to consume large adult sea urchins. Tagging (but not tethering) juvenile and adult sea urchins in two separate marine reserves indicated that adult sea urchins experience higher predation mortality than juveniles, probably because juveniles can shelter in cryptic microhabitat more effectively. In a field experiment in which exposure of sea urchins to rock lobster (*Jasus edwardsii*) and demersal reef fish predators was manipulated, rock lobsters were shown to be more important than fish as predators of adult sea urchins in a marine reserve. We conclude that predators, and particularly rock lobsters, exert significant predation mortality on *H. erythrogramma* in Tasmanian marine reserves, and that adult sea urchins are more vulnerable than smaller cryptic individuals. Fishing of rock lobsters is likely to reduce an important component of mortality in *H. erythrogramma* populations. © 2006 Elsevier B.V. All rights reserved.

**Keywords:** Demersal fish; Marine reserves; Predation mortality; Rock lobsters; Sea urchins; Size-specific mortality

## 1. Introduction

The influence of herbivores, and sea urchins in particular, in structuring shallow temperate subtidal reef

systems is well documented (Shepherd, 1973; Lawrence, 1975; Breen and Mann, 1976; Chapman, 1981; Andrew and Choat, 1982; Choat and Schiel, 1982; Duggins, 1983; Dean et al., 1984; Harrold and Reed, 1985; Fletcher, 1987; Vadas et al., 1986; Chapman and Johnson, 1990; Andrew, 1991, 1994). Sea urchins are important members of subtidal reef communities because some species can overgraze fleshy macroalgae to create ‘barrens’ habitat and, unlike most other herbivores, their populations can persist after overgrazing

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(Johnson and Mann, 1982). Although barrens formation has been reported in many systems, the mechanisms underpinning the phenomenon are poorly understood. Several hypotheses have been proposed, which focus on either change in sea urchin grazing behaviour or increases in their density. A behavioural shift whereby cryptic individuals emerge to destructively graze attached plants may result from either decreased predator abundance (Bernstein et al., 1981; but see Vadas et al., 1986; Elnor and Vadas, 1990) or decreased availability of drift algae (Harrold and Reed, 1985). Alternatively, increases in sea urchin population density and subsequent barrens formation can potentially arise from massive recruitment events (Hart and Scheibling, 1988), or decreases in predator abundance (Estes and Palmisano, 1974; Duggins, 1980; Wharton and Mann, 1981; Vadas and Steneck, 1995; Steneck, 1997). Because of links with fishing activity, most research concerned with the instigation of barrens has focused on control of sea urchin populations by predators subject to fishing.

The importance of predators structuring sea urchin populations has been long argued, with relatively little unequivocal evidence except in the case of the sea otter (*Enhydra lutris*) as a key predator of sea urchins at some sites in the northeastern Pacific (Estes and Duggins, 1995; Estes et al., 1998). However, after several decades of speculation and correlative evidence (Mann and Breen, 1972; Breen, 1974; Breen and Mann, 1976; Bernstein et al., 1981; Wharton and Mann, 1981; Miller, 1985), stronger evidence is now emerging to suggest that, at least in some systems, teleost fish (Vadas and Steneck, 1995; Shears and Babcock, 2002) and rock lobsters (*Jasus* species; Mayfield and Branch, 2000; Mayfield et al., 2001; Shears and Babcock, 2002) can play an important role in regulating sea urchin populations, and that the regulatory effect is influenced by fishing of these predators.

In the absence of manipulative field experiments, correlations in the abundances of sea urchins and predators across broad spatial scales have been used to infer mechanistic relationships (Estes and Palmisano, 1974; Mann, 1977; Wharton and Mann, 1981; Vadas and Steneck, 1995; Steneck, 1997) but these observations are not a critical test. The combination of broad correlative patterns and carefully controlled manipulative experiments at small scales, as explicit tests of hypotheses, is an effective approach to overcome the shortcomings of correlative patterns and single experiments at small spatial scales (Diamond, 1986; Schmitt and Osenberg, 1996; Ross et al., 2003). Even more effective is a combination of experiments at multiple spatial scales. The opportunity for such manipulations

has been achieved by using marine reserves as realistically large spatial scale manipulations of predator density (Babcock et al., 1999; McClanahan, 2000), combined with small-scale manipulations that provide additional insights into mechanisms operating within those scales (McClanahan and Muthiga, 1989; Shears and Babcock, 2002). This combination may be particularly important where predators are functionally absent from ecosystems (reviewed by Tegner and Dayton, 2000).

In the present study, we employ a variety of methods using a suite of manipulative experiments to examine the possible processes underpinning a broad scale negative correlation evident between *Helicoidaris erythrogramma* and rock lobsters (*Jasus edwardsii*) on the east coast of Tasmania (Johnson et al., 2004). In this paper we examine whether potential predators in marine reserves and adjacent areas open to fishing consume (1) tethered sea urchins prevented from seeking shelter and (2) tagged but untethered sea urchins able to behave normally and seek shelter; (3) whether predation rates on sea urchins are higher inside marine reserves than in adjacent fished areas where there are fewer putative predators; (4) the size-specific nature of predation by southern rock lobsters (*J. edwardsii*) on *H. erythrogramma*; and (5) we assess the relative importance of rock lobster and demersal fishes as predators of *H. erythrogramma* in a marine reserve.

## 2. Methods

### 2.1. Study sites

Manipulative experiments were conducted in two regions on the east coast of Tasmania where there are marine reserves and adjacent fished areas where sea urchin predators but not sea urchins have been exploited (Fig. 1). Study sites within each region were located on medium profile rocky reefs at 6–8 m depth. Within regions, reefs used in comparisons were similar in exposure to prevailing weather conditions, supported similar communities of large brown macroalgae and understorey guilds typical of moderately exposed coastlines in southeastern Tasmania (Edgar, 1984), but differed in their abundances of sea urchins and predators (Table 1). The two reserves studied were the Maria Island Marine Reserve within Mercury Passage (established in 1991) and the Crayfish Point Marine Reserve (established in 1971) within the Derwent Estuary. Both support higher abundances of putative sea urchin predators (rock lobster and reef-associated fish) compared to adjacent fished areas (Edgar and Barrett, 1999; Pederson, 2003). Despite the wide spread distribution of *H.*

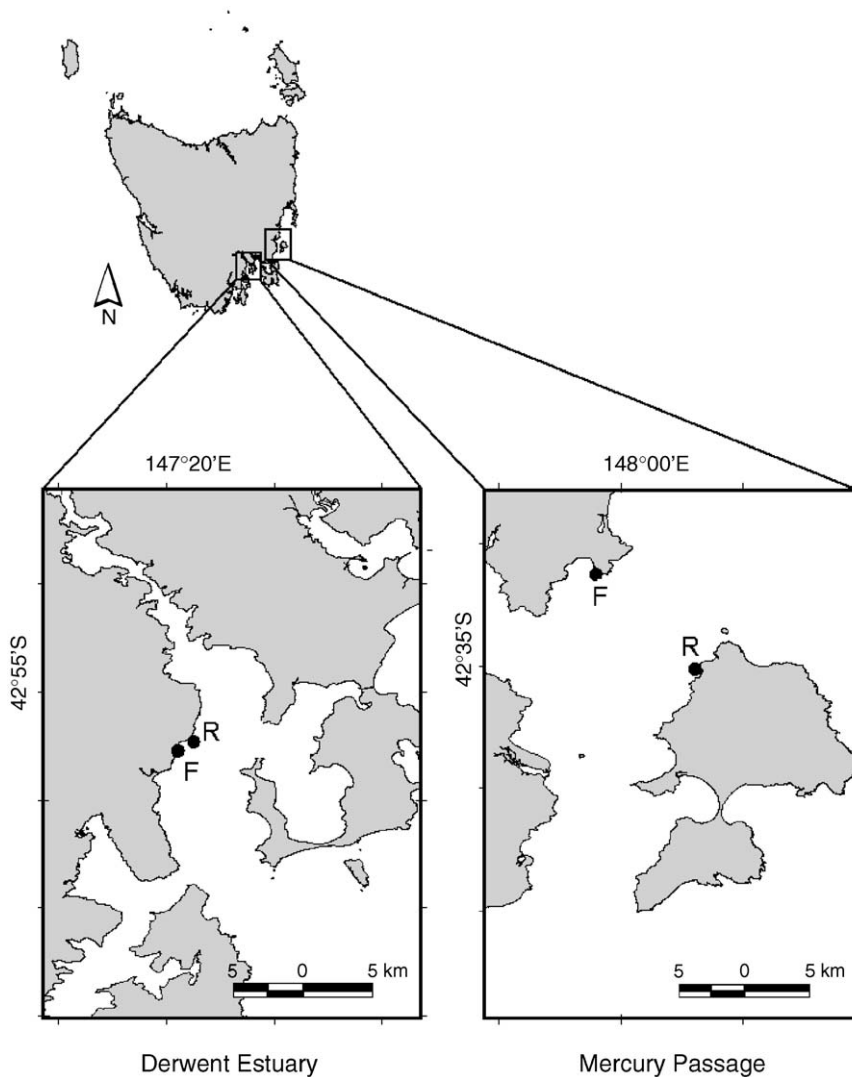


Fig. 1. Locations where manipulative experiments were conducted inside marine reserves (R) and adjacent fished areas (F) in the Derwent Estuary and Mercury Passage.

*erythrogramma* barrens throughout southeastern Tasmania (Sanderson et al., 1996), sea urchin barrens habitat were not present at any of the sites described in this study.

## 2.2. Tethering experiment

High survivorship of sea urchins on reefs may indicate either that *H. erythrogramma* has few natural predators or, alternatively, that potential predation is high but sea urchins are able to avoid predation, for example by seeking shelter. To distinguish between these possibilities, sea urchins were tethered in the open and prevented from seeking shelter. The use of tethering experiments to estimate absolute rates of predation between habitats has been criticised because of artefacts of tethering, which may

not be consistent between treatments or habitats (Peterson and Black, 1994). However, in the current study we use tethering only to determine relative measures of potential predation at different sites in comparable habitat (i.e. dense macroalgal beds).

Mortality of tethered sea urchins was examined in both regions on the east coast of Tasmania between October 2000 and January 2001. Within each region two areas of rocky reef were selected, one supporting a high density of predators and low density of sea urchins (no-take reserve) and an adjacent area open to fishing with relatively few predators and relatively more sea urchins (Table 1). Within each area two 20 m transects, separated by approximately 50 m, were deployed randomly at a depth of 6–8 m. Along each transect were placed 40 tethered sea urchins

Table 1

Summary of abundances of putative sea urchin predators and the sea urchin *Heliocidaris erythrogramma* at experimental sites prior to conducting manipulative experiments

		Mercury Passage		Derwent Estuary			
		Fished <i>n</i> =30	Reserve <i>n</i> =20	Fished <i>n</i> =30	Reserve <i>n</i> =10		
<i>Jasus edwardsii</i> (rock lobster)	2000	1.4 (0.5)	*	9.3 (1.4)	9.7 (1.6)	*	25.7 (2.5)
	2005	2.7 (1.0)	*	26.2 (1.7)			
<i>Plagusia chabrus</i> (red bait crab)		0.4 (0.2)		0.8 (0.3)	0.7 (0.2)		0.8 (0.3)
<i>Notolabrus tetricus</i> (blue-throat wrasse)		2.0 (0.4)	*	4.6 (0.5)	4.0 (0.4)	*	1.3 (0.5)
<i>Notolabrus fucicola</i> (purple wrasse)		0.8 (0.2)		1.3 (0.3)	1.1 (0.3)		0.0 (0)
<i>Pictilabrus laticlavus</i> (senator wrasse)		0.2 (0.1)		0.7 (0.2)	0.3 (0.1)		0.0 (0)
Monocanthids (leatherjackets)		1.8 (0.4)		1.2 (0.3)	0.3 (0.1)	*	1.4 (0.2)
<i>Latridopsis forsteri</i> (bastard trumpeter)		0.03 (0.03)	*	0.4 (0.2)	0.3 (0.2)		0.6 (0.2)
<i>Cheilodactylus spectabilis</i> (banded morwong)		0.1 (0.1)		0.4 (0.2)	0.1 (0.1)		0 (0)
<i>Heliocidaris erythrogramma</i> (purple sea urchin)		1.4 (0.3)		0.8 (0.1)	1.5 (0.3)		0.12 (0.1)

Data are mean densities ( $\pm$ S.E.) from *n* replicate transects and were estimated as individuals per 500 m<sup>2</sup> for fish, per 200 m<sup>2</sup> for decapod crustaceans and per m<sup>2</sup> for sea urchins from *n* replicate quadrats. The surveys were undertaken in 2000, but densities of rock lobsters in Mercury Passage were re-surveyed in 2005. \*Denotes significant difference in mean abundance between reserve and fished areas ( $\alpha=0.05$  using Kruskal–Wallis non-parametric ANOVA).

comprising 20 juveniles (test diameter 20–60 mm) and 20 adults (test diameter 65–100 mm). Within each region, all animals were collected nearby the experimental area.

Sea urchins were tethered using a modification of the method described by Ebert (1965). Two holes were made in the test using a 1.25 mm 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. Monofilament line (100 mm  $\times$  0.45 mm diameter) was threaded through the needle, the hypodermic then removed, and the monofilament attached to a fine stainless steel wire trace (200 mm) using size No. 4 leader sleeves. Each tether was identified individually by numbered flagging tape attached to the free end of the wire trace. To prevent sea urchins from seeking shelter a small weight comprising several links of 12 mm galvanised steel chain was attached to the free end of the wire trace. Pilot trials indicated that in the absence of predators sea urchins did not experience elevated mortality as a result of tagging.

Mortality was assessed over a 14-day period by relocating tethers and recording the state of the attached sea urchin. Tethers with no sea urchin attached were recorded as mortality events. All tethers were accounted for at the end of the experiment.

### 2.3. Size-specific predation of sea urchins by rock lobsters

Size-specific predation by rock lobsters was examined in a caging experiment conducted in Mercury Passage outside the marine reserve in January 2001. Cages were constructed from a steel frame (1 m  $\times$  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 mesh skirt bordered by 8 mm chain to prevent rock 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 sea urchins from each of the three size classes (20–60 mm, 61–80 and 81–100 mm test diameter) were placed in each cage, and cages were left overnight to ensure no animals could escape from the cages. A single rock lobster (*J. edwardsii*) of a designated size class was then added to each ‘treatment’ cage while ‘control’ cages did not contain rock lobsters. There were 3 replicate control cages, and 3 replicate treatment cages of each size class of rock lobster. Size classes of rock lobsters were denoted as juvenile (J; carapace length (CL) < 100 mm), adult class 1 (A1; CL 110 mm), and adult class 2 (A2; CL > 120 mm). On the east coast of Tasmania male *J. edwardsii* do not feed during their annual moult in November and December, with feeding rates of the rock lobsters thought to increase in the post moult period. The experiment was established early in January 2001 using post moult male rock lobsters to ensure that rock lobsters would be feeding.

### 2.4. Tagging experiment — sea urchins marked but not tethered

Since sea urchins are normally cryptic within reef habitat, the effect of seeking refuge on the likelihood of predation mortality needed to be considered. Thus, tagged but untethered sea urchins were placed on the same transects described in the tethering experiment to determine whether refuge is significant in reducing

predation mortality. The experiment was conducted in both regions simultaneously during February 2001.

The method used to tag sea urchins was identical to that for tethering the sea urchins (above) except that no weight was attached to the free end of the wire tag. Sixty tagged sea urchins were placed randomly on each of the four transects in each region, comprising 30 juvenile (test diameter 20–60 mm) and 30 adult (test diameter 65–100 mm) sea urchins. Tagged animals were placed in positions to ensure that individuals could seek shelter in crevices. Sea urchin mortality was assessed weekly for one month by relocating tags and recording the condition of the attached sea urchin. Recovered tags that were not attached to an intact sea urchin or fragment of sea urchin test were considered to be mortalities since our pilot studies found that >90% of tags were retained by sea urchins held for one month in an aquarium. Unrecovered tags were not considered to be mortalities and were excluded from analyses.

### 2.5. Relative effects of fish and rock lobsters as predators of sea urchins

To partition sea urchin predation mortality among reef-associated fishes and rock lobsters a caging experiment

was conducted within the Maria Island Marine Reserve between March and May 2001. Treatments were designed to examine all possible combinations of the presence (+) and absence (–) of rock lobsters (L) and demersal fish (F), (Fig. 2). Three replicate cages of each of the four treatments and three replicate unmanipulated control plots were positioned randomly at ca. 8 m depth on the rocky reef at Magistrates Point (42° 34' S, 148° 03' E). Cages were constructed from flexible 8 mm mesh, and measured 3 × 3 m with sides 1.5 m tall. The top of the sides was floated while the cages were weighted to the reef using 12 mm galvanised chain. Unmanipulated controls (+L+F) consisted of 8 mm galvanised chain laid on the bottom to delineate experimental plots (measuring 3 × 3 m).

Comparison of sea urchin mortality in the partial cages (+L+F) with that in the unmanipulated control (+L+F) 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 × 1 m) were cut in two opposing sides of the cage to allow free movement of both rock lobsters and fish through the cage (Fig. 2). Roofs were not fitted to these partial cages, allowing further access of fish.

Fish were allowed to gain access to sea urchins in the –L+F treatment using an open topped cage that excluded

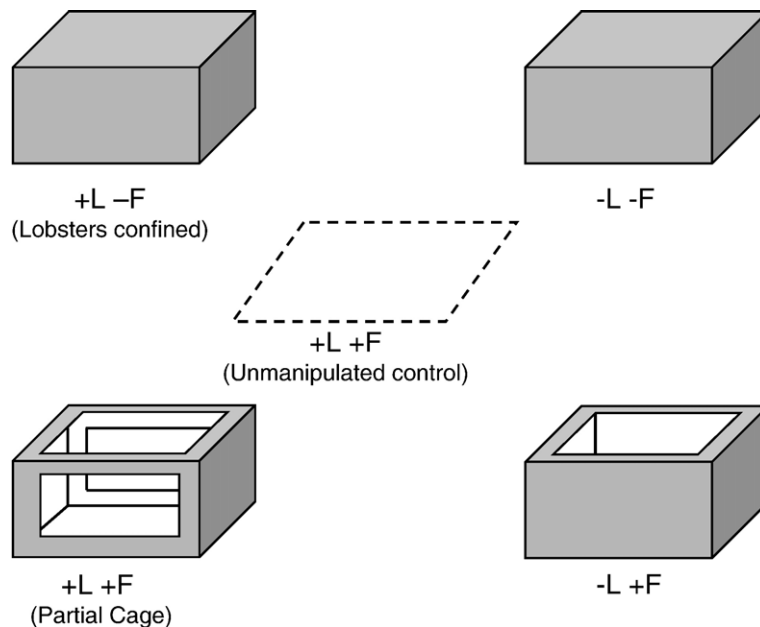


Fig. 2. Schematic of the experimental design used to assess relative importance of rock lobsters (*Jasus edwardsii*) and demersal fishes as predators of sea urchins in the Maria Island Marine Reserve. Treatments represent all combinations of the presence (+) and absence (–) of rock lobsters (L) and fishes (F). Rock lobsters were confined within +L–F cages, whereas both rock lobsters and fish were prevented from entering –L–F cages by using completely enclosed cages. An inward folding mesh skirt (150 mm) around the top of cages successfully prevented rock lobsters from entering –L+F cages. Partial cages (+L+F) with open tops and holes in opposing sidewalls to allow access by both rock lobsters and fish, were used as cage controls. Unmanipulated controls (+L+F) were delineated using 8 mm galvanised chain laid on the sea floor (measuring 3 × 3 m).

rock lobsters by an inward folding skirt at the top of the cage. Both rock lobsters and fish were excluded from experimental areas (-L-F) using cages with enclosed roofs. Cages with closed roofs were also used for the +L-F treatment.

Experimental plots (including experimental controls) were cleared of all sea urchins and rock lobsters prior to starting the experiment. Each experimental plot was then stocked with a total of fifteen sea urchins from the surrounding reef to give an overall sea urchin density of 1.7 individuals  $m^{-2}$ . Five sea urchins were selected from each of the three size classes, viz. juvenile (J) 40–60 mm, small adult (A1) 61–80 mm, and adult (A2) 81–100 mm. Two rock lobsters ( $CL > 120$  mm) were placed into cages with closed roofs (+L-F) resulting in a density of 0.22 rock lobsters  $m^{-2}$ , almost 5 times greater than the mean density of all sizes of rock lobsters (Table 1), and ca. 6 times higher than the mean density of large rock lobsters ( $CL > 110$  mm) at the site (Pederson, 2003). We elevated rock lobster densities inside containment cages for two reasons. First, this ensured that treatments remained in effect in the event of a single lobster escaping from a cage between weekly observations. Second, rock lobster densities in the reserve, and particularly of larger animals, had been increasing rapidly prior to the experiment (Edgar and Barrett, 1999) and we anticipated this trend would continue. Indeed, recent surveys in 2005 indicate that densities of rock lobsters in the reserve are ca. 0.13 individuals  $m^{-2}$  (Table 1) and closely approaching those used in containment cages in the experiment.

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

### 2.6. Size–frequency distributions of sea urchin populations within Mercury Passage

The size–structure of five sea urchin populations from areas open and closed to exploitation of rock lobster and demersal fish in Mercury Passage was compared. Sea urchins were collected randomly from rocky reefs at three locations open to harvesting (Quarry Point 42° 34' S, 147° 54' E; Stapleton Point 42° 35' S, 147° 55' E; Lords Bluff 42° 31' S, 147° 59' E), and from two locations within the Maria Island Marine Reserve closed to fishing (Magistrates Point 42° 34' S, 148° 03' E; Howells Point 42° 36' S, 148° 02' E). At each of the

five locations all sea urchins were collected from 10 randomly placed 16- $m^2$  quadrats (mid 2000) and the test diameter (TD) of each individual measured to the nearest millimetre using knife-edge callipers.

### 2.7. Data analysis

Sea urchin mortality from the tethering and tagging experiments was analysed using logistic modelling in which a generalised linear model (GLM) was applied to the binomially distributed response variable (mortality) using a log-link function (Hosmer and Lemeshow, 2000; Quinn and Keough, 2002). Logistic models were able to determine the significance of any differences in overall mortality in fished and unfished areas and, more importantly, to estimate the relative likelihood of mortality in unfished and fished areas. Fully saturated logistic models were constructed using the four main effect terms (region, reserve, sea urchin size and transect) and all possible interactions. Parsimonious models were obtained using a stepwise removal of terms from the fully saturated model until a significant decrease in the model fit ( $\chi^2$ ) was observed.

Size-specific predation by the rock lobster *J. edwardsii* in the small-scale caging experiment was examined using both a split-plot ANOVA to compare mean losses of sea urchins among treatments, and logistic modelling to compare the likelihood of mortality of different sizes of sea urchins in the presence of particular sizes of lobsters. In developing the logistic models data were pooled across replicates of identical rock lobster ‘treatments’ to provide adequate sample sizes for the procedure.

The relative importance of rock lobsters and demersal fish as sea urchin predators was assessed using both a three-way ANOVA and logistic modelling. The ANOVA included fixed main effects of fish and rock lobsters (each with 2 levels: presence and absence), and sea urchin size (3 levels: small, medium and large), and compared mean numbers of surviving sea urchins among treatments. The logistic model compared the likelihood of survival of sea urchins in the different treatments, and again data were pooled across replicates of the same treatment. Data from both caging experiments used to construct logistic models followed binomial distributions with the response variable, survival, recorded as a proportion of the total test sample.

Sea urchin population size structures in the Maria Island Reserve and adjacent fished areas were estimated by pooling data across locations in each level of ‘reserve status’. Pooling in this way was necessary given that the

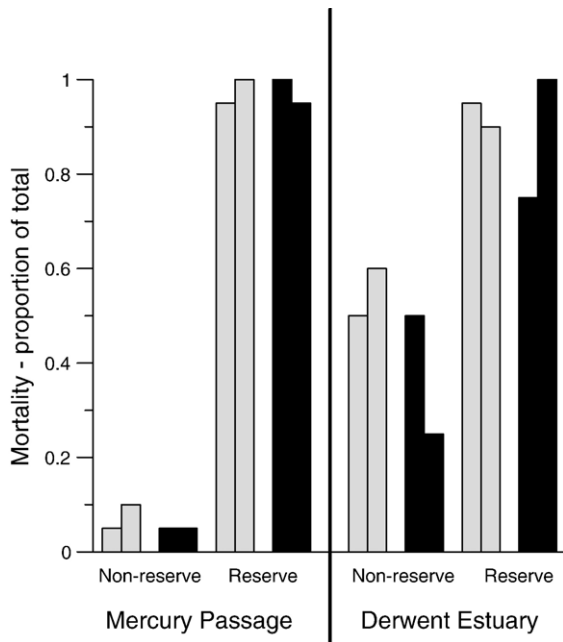


Fig. 3. Mortality of two size classes of tethered sea urchins (*Heliocidaris erythrogramma*) after 14 days exposure to predators in marine reserves and fished sites in both regions. All tethers (20 of each size class of sea urchin on each transect; total  $N=320$  sea urchins) were accounted for. Each bar represents a single transect. Lightly shaded bars indicate juvenile sea urchins (40–60 mm test diameter) while solid bars indicate adult sea urchins (65–80 mm test diameter).

small sample sizes prevented meaningful comparisons between locations within reserve and non-reserve areas. The two size structures were compared using the Kolmogorov–Smirnov test.

For all parametric ANOVAs, 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,  $Y$  (Draper and Smith, 1981). We compared means of treatment groups after ANOVA using the Ryan–Gabriel–Elliot–Welsh procedure ('Ryan's test') which controls for type I error (Day and Quinn, 1989). The statistical package SAS© V6.12 was used for all analyses.

### 3. Results

#### 3.1. Mortality of tethered sea urchins

When sea urchins were tethered and unable to escape to shelter, the likelihood of sea urchin mortality was

notably higher inside the marine reserves where predators were abundant compared to adjacent exploited habitats (Fig. 3). In analysing the complete data set with a logistic model, the full model failed to converge the 4-way interaction term, and so separate analyses were undertaken for each region.

For Mercury Passage the most parsimonious model included the effect of reserve ( $\chi^2=165.4703$ ,  $df=1$ ,  $p=0.0001$ ), but not the other main effects (transect and sea urchin size) or interaction terms. This model indicated that the chance of sea urchin mortality inside the reserve was significantly higher than that of adjacent fished areas ( $\chi^2=54.7997$ ,  $df=1$ ,  $p=0.0001$ ). There was

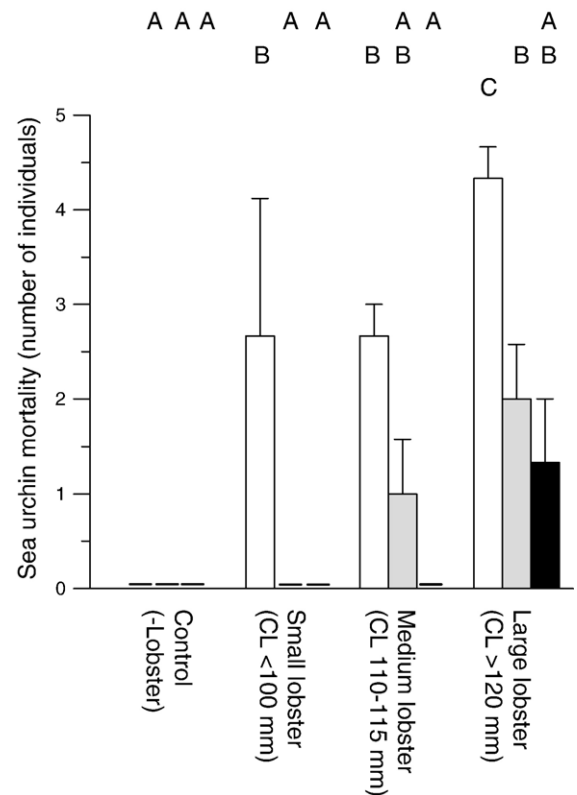


Fig. 4. Size-specific predation by rock lobsters (*Jasus edwardsii*) on three size classes of sea urchins (*Heliocidaris erythrogramma*) in cages. Sea urchin mortality shows the number of mortalities in each size class after 17 days of exposure to rock lobster predation. Data are means ( $\pm$  S.E.) of  $n=3$  replicates of each treatment. There were initially 5 sea urchins in each size class with a single rock lobster of a designated size class in each 'treatment' cage while 'control' cages did not contain rock lobsters. Open bars = juvenile sea urchins (test diameter 40–60 mm); lightly shaded bars = small adult (A1) sea urchins (test diameter=61–80 mm); and solid bars = large adult (A2) sea urchins (test diameter 81–100 mm). CL = carapace length (CL) of rock lobsters. Letters above individual treatments represent groupings assigned by Ryan's multiple range test (REGW). Dashed horizontal lines represent mean response values of zero.



no evidence that sea urchin size or position of the transect influenced the mortality of sea urchins tethered in the open.

Results were more complex for a similar experiment conducted in the Derwent Estuary, and the full model indicated that the 3-way interaction reserve\*size\*transect was significant ( $\chi^2=8.1614$ ,  $df=1$ ,  $p=0.004$ ). To interpret this, separate analyses were undertaken for reserve and fished areas. In the reserve, the 2-way interaction of size\*transect was significant in the fit of the model ( $\chi^2=5.6837$ ,  $df=1$ ,  $p=0.0171$ ). This model indicated that mortality of juvenile sea urchins inside the reserve was significantly greater than that of adult sea urchins, but that the effect was spatially variable at the scale of the 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 sea urchins in this area did not depend on either sea urchin size or the location of tethered animals on the reef.

### 3.2. Size-specific predation of sea urchins by rock lobsters

We examined the significance of overall effects with ANOVA (using a split-plot design to account for the non-independence of different sea urchin size classes within cages), while estimates of likelihoods of mortality were obtained using logistic modelling.

The split-plot ANOVA indicated significant effects of rock lobster size ( $F_{3, 8}=11.02$ ,  $p=0.003$ ) and sea urchin size on sea urchin mortality ( $F_{2, 16}=18.42$ ,  $p=0.0001$ ), whereas the interaction of rock lobster size\*sea urchin size was not significant ( $F_{6, 16}=2.22$ ,  $p=0.095$ ). The consistent pattern was that large sea urchins were eaten only by large rock lobsters, whereas all sizes of rock lobsters preyed heavily on small sea urchins (Fig. 4). This pattern is explored in more detail in the logistic models.

The full logistic model revealed no significant interactions and, in keeping with the results of the overall ANOVA, the parsimonious model required inclusion of only the effects of sea urchin size and rock lobster size. The reduced model indicated that the chance of mortality of juvenile sea urchins was ca. 35 times greater than that of large adult (A2) sea urchins ( $\chi^2=24.25$ ,  $df=1$ ,  $p=0.0001$ ), whereas the likelihood of sea urchin mortality in the A1 size class was not significantly different to that in the A2 size class ( $\chi^2=2.45$ ,  $df=1$ ,  $p=0.1175$ ).

To examine the relationship between the likelihood of predation and size of rock lobster, we analysed each size class of sea urchin separately (Table 2). This showed that the predicted likelihood of mortality of juvenile sea

Table 2

Estimated likelihood of sea urchin (*Heliocidaris erythrogramma*) predation mortality in the presence of different sized rock lobster (*Jasus edwardsii*) compared to mortality in the absence of rock lobsters

Sea urchin size (TD mm)	Rock lobster size (CL mm)		
	Small (<100)	Medium (110)	Large (>120)
J1 juvenile (40–60)	$8 \times 10^{11}$	$8 \times 10^{11}$	$6.5 \times 10^{12}$
A1 adult (61–80)	NS	$3.4 \times 10^{11}$	$9 \times 10^{12}$
A2 adult (81–100)	NS	NS	$1.3 \times 10^{12}$

Note that medium-sized rock lobsters (carapace length 110 mm) represent the minimum legal size of male rock lobsters in the fishery. TD = test diameter; CL = carapace length; NS = predation mortality not significantly different to mortality in the absence of rock lobsters.

urchins in the presence of large rock lobsters was >8 times that in the presence of medium or small rock lobsters (Table 2). The likelihood of mortality of juvenile sea urchins in the presence of either small or medium rock lobsters was not distinguishable. The likelihood of mortality of smaller A1 adult sea urchins was 27 times greater in the presence of large rock lobsters compared with medium rock lobsters, however juvenile rock lobsters (<100 mm CL) were not able to successfully consume sea urchins >61 mm TD. The ability of rock lobsters to capture and consume *H. erythrogramma* >81 mm TD is limited to those individuals considerably larger than the minimum legal exploitable size of 110 mm CL (i.e. rock lobster >120 mm CL).

### 3.3. Mortality of tagged sea urchins

Consistent with the results of the tethering experiment, in both regions the mortality of sea urchins that were tagged but not tethered was greater in habitats with abundant predators (marine reserves) than in adjacent fished areas which supported fewer predators (Fig. 5). However, the effect of increased predator abundance on sea urchin mortality was slightly greater in the Derwent Estuary than in Mercury Passage. Differences in mortalities between regions, habitats (i.e. reserved vs. fished areas) and sea urchin size classes were examined using logistic modelling.

The most parsimonious logistic model included 3 of the 4 main effects, namely reserve, sea urchin 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 sea urchin mortality.

The logistic model indicated that the likelihood of mortality of juvenile sea urchins was significantly less than adults, with the chance of mortality of adult sea urchins 2.3 times that of the juveniles ( $\chi^2=4.2720$ ,  $df=1$ ,  $p=0.039$ ). The model also indicated that sea urchin mortality inside the reserve was significantly

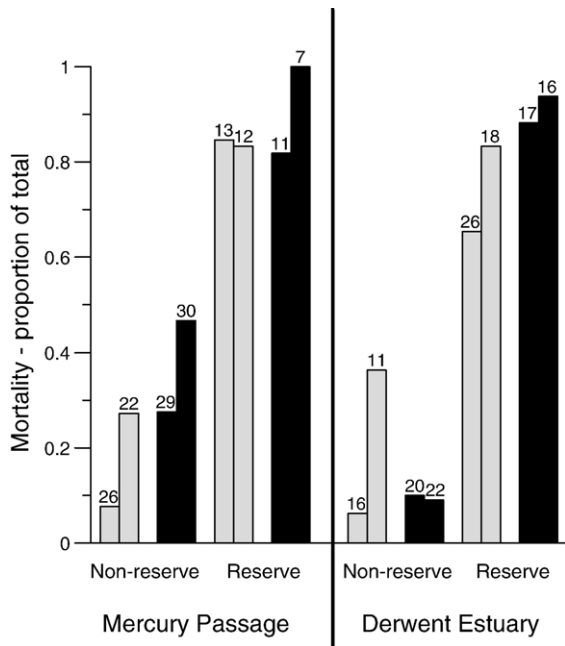


Fig. 5. Mortality of two size classes of tagged (but not tethered) sea urchins (*Heliocidaris erythrogramma*) after 28 days exposure to predators in marine reserves and fished sites in both regions. The total number of tag returns for each transect/size class combination is displayed above each bar, with each bar representing a single transect (30 animals of each size class were initially deployed on each transect). Proportion mortality is expressed in terms of the total number of tags recovered (not the total initially deployed). Lightly shaded bars indicate juvenile sea urchins (40–60 mm test diameter) while solid bars indicate adult sea urchins (65–80 mm test diameter).

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 sea urchin predation mortality within habitat types at a scale of ca. 50 m.

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

Results of similar models for the Derwent Estuary were slightly different. The most parsimonious model

also included the main effects of reserve and sea urchin size, but in addition included the two-way interaction term of reserve\*sea urchin size ( $\chi^2=4.9142, df=1, p=0.029$ ). Although sea urchin 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

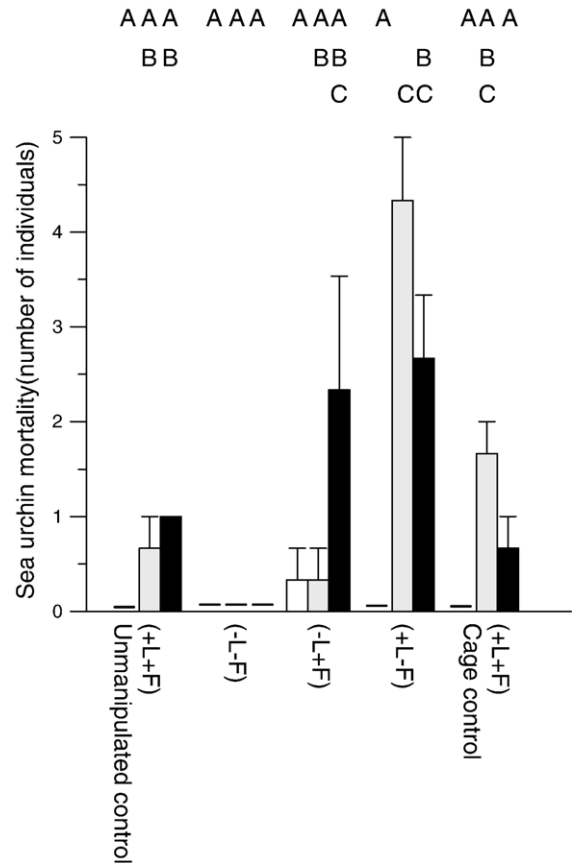


Fig. 6. Relative importance of demersal reef fish (F) and rock lobsters (*Jasus edwardsii*, L) as predators of sea urchins. Sea urchin (*Heliocidaris erythrogramma*) mortality is plotted as the number of sea urchins of each of three size classes after 8 weeks of exposure to predators. There were initially 5 sea urchins of each size class in each experimental plot. Unmanipulated control (+L+F) = no manipulation of natural densities of rock lobsters and fishes and no cage structure; (-L-F) = complete exclusion of both predators using an enclosed cage; (-L+F) = exclusion of rock lobsters while allowing access by fish using a cage with no roof; (+L-F) = rock lobster inclusion with fish excluded using an enclosed cage; and (+L+F) both predators have access to sea urchins in a partial cage (cage control). Data are means (+S.E.) of  $n=3$  independent replicates of each treatment. Open bars = juvenile sea urchins (test diameter 40–60 mm); lightly shaded bars = small adult (A1) sea urchins (test diameter=61–80 mm); and solid bars = large adult (A2) sea urchins (test diameter 81–100 mm). Letters above individual treatments represent groupings assigned by Ryan’s multiple range test (REGW). Dashed horizontal lines represent mean response values of zero.

of adult sea urchins inside the reserve is ca. 8 times greater than that outside the reserve ( $\chi^2=4.3610$ ,  $df=1$ ,  $p=0.0368$ ), whereas the likelihood of overall sea urchin

mortality inside the reserve was ca. 95 times that of adjacent fished areas. In the Derwent Estuary, mortality patterns were similar across the different transects.

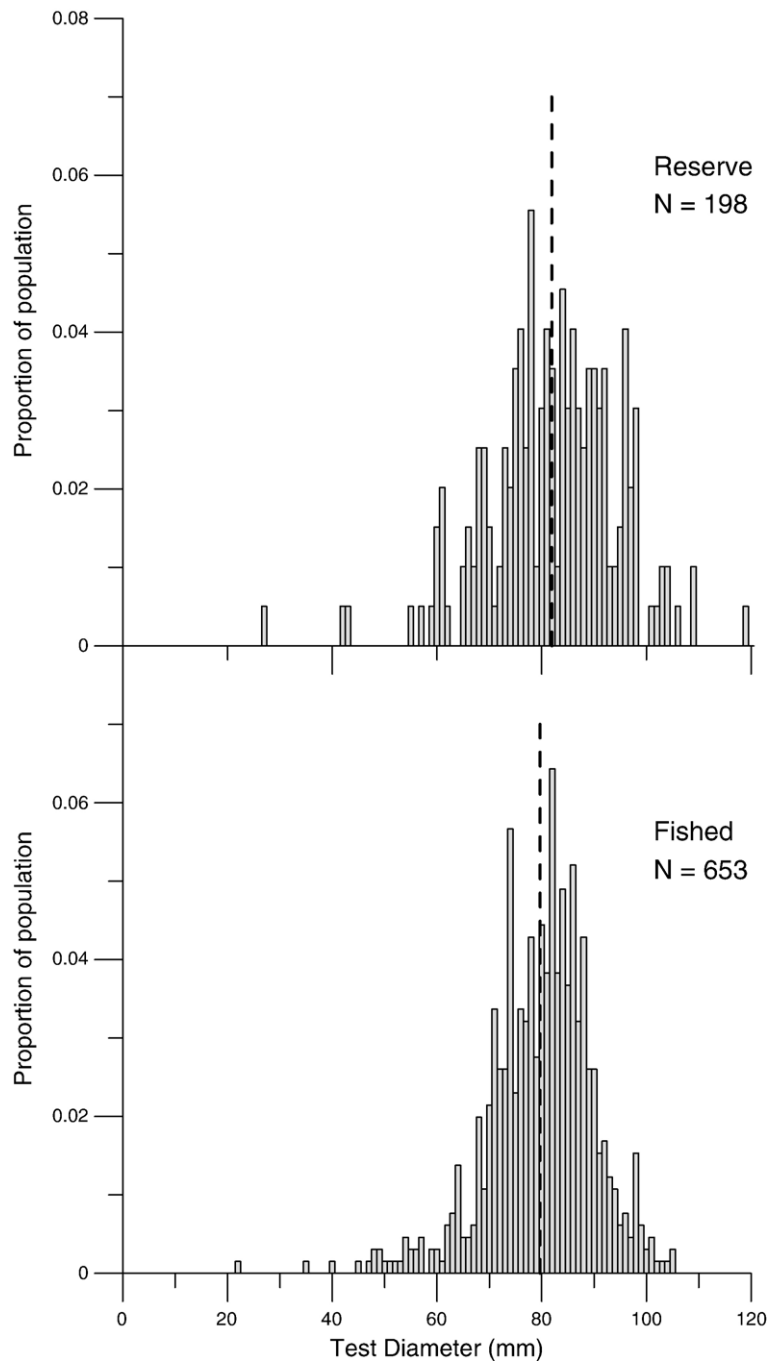


Fig. 7. Size–frequency distributions of *Heliocidaris erythrogramma* populations within Mercury Passage on the east coast of Tasmania. The size–frequency distributions of sea urchins in reserve and fished sites were significantly different (Kolmogorov–Smirnov test,  $p=0.002$ ). The size–frequency distribution of sea urchins from fished sites was more negatively skewed and more peaked than that of sea urchins from the reserve ( $Sk=-0.88$ ,  $Kur=2.59$  and  $Sk=-0.59$ ,  $Kur=1.83$  respectively). Dashed vertical lines represent mean sea urchin size in reserve and fished areas (82 and 80 mm test diameter respectively).

### 3.4. Relative effects of fish and rock lobsters as predators of sea urchins — large caging experiment

#### 3.4.1. 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 sea urchin size) indicated that the presence of the cage did not significantly influence sea urchin mortality ( $F_{1, 12}=1.33$ ,  $p=0.273$ ), however there was an effect of sea urchin size ( $F_{2, 12}=13.00$ ,  $p=0.001$ ). There was no evidence of any interaction ( $F_{2, 12}=1.07$ ,  $p=0.385$ ). Similarly, comparing these two treatments using a logistic model indicated no effect of the ‘cage’ treatment. On this basis, we assume that the cages did not influence sea urchin mortality, and do not consider the unmanipulated control plots further in the primary analysis.

#### 3.4.2. Comparing mortality of sea urchins attributable to rock lobsters and fishes

Analysis of the effects of the presence and absence of fish and rock lobsters (3-way ANOVA), indicated a significant rock lobster\*fish\*sea urchin size interaction ( $F_{2, 24}=3.76$ ,  $p=0.0379$ ). Multiple range comparisons (REGW) indicated that the mortality of juvenile sea urchins was very low and not significantly different across treatments, whereas small adult (A1) sea urchins suffered the highest mortality, although this was not significantly different to mortality of the largest (A2) sea urchins. The highest mortality was observed in A1 adult sea urchins in the presence of rock lobsters and the absence of fish (Fig. 6).

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

To interpret the significant rock lobster\*fish\*sea urchin size interaction term in the overall logistic model, separate logistic analyses were undertaken on each sea urchin size class (excepting the juveniles, for which mortality was too low to enable meaningful analysis). The

logistic model estimated that in the presence of rock lobsters, the likelihood of mortality of A1 sea urchins is ca. 7 times that when rock lobsters are absent ( $\chi^2=25.7704$ ,  $df=1$ ,  $p=0.0001$ ). When pooled across all levels of rock lobster, the effect of fish was significant ( $\chi^2=6.2879$ ,  $df=1$ ,  $p=0.012$ ) with the model estimating that sea urchin mortality was 13 times more likely in the absence of fish ( $\chi^2=7.5023$ ,  $d=1$ ,  $p=0.006$ ) (see below).

For the largest sea urchins, the logistic model indicated that the two main effects were not significant in the fit of the model (rock lobster  $\chi^2=0.7417$ ,  $df=1$ ,  $p=0.39$ ; fish  $\chi^2=0.0831$ ,  $df=1$ ,  $p=0.77$ ). However, the rock lobster\*fish interaction term was significant ( $\chi^2=17.4684$ ,  $df=1$ ,  $p=0.001$ ) since mortality of large A2 sea urchins was significantly greater in the presence of rock lobsters alone (+rock lobsters – fish) than in the presence of both rock lobsters and fish (+rock lobsters + fish, cage control). Note that in the treatment ‘+rock lobster – fish’, the density of rock lobsters was fixed at 0.22 individuals  $m^{-2}$ , whereas in the +rock lobster +fish treatment, rock lobsters would have occurred at the background density which was, on average, 0.047 individuals  $m^{-2}$ .

### 3.5. Effect of predation mortality on sea urchin population size structure

Within Mercury Passage, the size–frequency distributions of sea urchins inside and outside the reserve were significantly different (Kolmogorov–Smirnov  $p=0.002$ ). When compared to a normal distribution, the size structure of the sea urchin population from fished sites was more negatively skewed and more peaked than the size structure of sea urchins from the reserve, although the mean size in the two populations was similar (Fig. 7).

## 4. Discussion

### 4.1. The significance of sea urchin predators inside marine reserves

The establishment of marine protected areas in temperate regions has revealed significant shifts in community structure, including increases in both population size and the size of individuals of harvested species (Edgar and Barrett, 1999; Wallace, 1999; Kelly et al., 2000; reviewed by Halpern and Warner, 2002), and the indirect ‘flow-on’ effects of these changes (Babcock et al., 1999; McClanahan et al., 1999). Increases in the abundance of predators such as rock lobsters and demersal fish on protected temperate reefs are well documented and have been implicated in the reduction of sea urchin densities in reserves (McClanahan and Muthiga, 1989; Babcock et al.,

1999). Tethering experiments typically indicate that sea urchin mortality is 2–7 times greater inside marine reserves where predator abundances are 2–8 times greater than in adjacent fished habitats (McClanahan and Muthiga, 1989; McClanahan and Shafir, 1990; Sala and Zabala, 1996; McClanahan et al., 1999; McClanahan, 2000; Shears and Babcock, 2002). Results of our tethering experiment indicated a 10-fold increase in sea urchin mortality rates inside the marine reserves relative to mortality in nearby areas open to fishing in comparable habitats. This is likely to reflect that in our experiment sea urchins were unable to seek refuge when tethered. Thus, while the results of tethering can be interpreted as an assay of potential predation, they do not indicate either absolute or relative estimates of actual predation. Absolute predation rates are better indicated by following the fate of tagged but untethered sea urchins. These data indicated that when sea urchins and predators were unrestricted, sea urchin mortality rates inside the marine reserves were 3–9 times greater than in adjacent areas open to fishing. These estimates are conservative given that lost tags were not included when estimating the mortality rates.

#### 4.2. Size-specific predation

Although differences in sea urchin mortality rates exist between areas protected from and open to fishing, size-specific predation will determine how sea urchin population size structures are altered under different levels of predation pressure. Size-specific predation can shift the distribution of prey population size from normal to non-normal distributions (Pollock, 1979; Griffiths and Seiderer, 1980; Tegner and Dayton, 1981; Tegner and Levin, 1983; Cole and Keuskamp, 1998) with potential flow-on effects on the demography of the prey. In examining the effect of size-specific predation on prey, the four key factors of sea urchin behaviour, predator access to different sized sea urchins, the relationship between predation ability and predator size, and the selectivity of prey by different predators need to be addressed.

##### 4.2.1. Predator access to different sized prey

In the current study, when sea 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 rock lobsters in cages, juveniles were eaten at a notably higher rate than larger sea urchins, although small- and medium-sized rock lobsters did not eat sea urchins larger than 60 and 80 mm test diameter respectively. Dissimilar to both of these results, when sea urchins and predators were not restrained in any way, survival of juvenile sea urchins in the

‘tagging’ and ‘large cage’ experiments was greater than that of adult sea urchins. These ostensibly conflicting results are reconciled by considering sea urchin behaviour. When juvenile sea urchins were unrestricted they displayed cryptic behaviour and sought refuge in crevices too small to allow access by many predators, similar to the behaviour of juvenile *Evechinus chloroticus* in New Zealand marine reserves (Shears and Babcock, 2003). When unrestricted, small adult (A1) sea urchins (61–80 mm) experience higher mortality rates than other size classes. This is because, unlike juvenile sea urchins, they are too large to seek refuge in crevices not accessible to predators, but they are too small to have developed the effective spine canopy possessed by larger adult (A2) sea urchins (81–100 mm) which effects a refuge in size.

##### 4.2.2. Relationship between predation ability and predator size

Although the tethering, tagging and ‘large cage’ experiments identified sea urchin size as significantly influencing predation-related mortality, the effect of predator size on sea urchin mortality could not be assessed using these designs. In the experiment assessing the capability of rock lobsters to consume different sized sea urchins, the results showed conclusively that as rock lobsters grow larger, they are able to attack and consume larger sea urchins. Of the three size classes, large adult rock lobsters (CL > 120 mm) were 8 times more effective at consuming juvenile sea urchins and were the only size class to consume large adult (A2) sea urchins. Small lobsters (CL < 100 mm) were only able to consume small sea urchins (< 60 mm TD). Similar to our results, Andrew and MacDiarmid (1991) also found that small individuals of *J. edwardsii* were capable of consuming juvenile sea urchins (*E. chloroticus* < 65 mm TD), but not adults (70–90 mm TD), while Mayfield et al. (2001) found that small *Jasus lalandii* (< 68 mm CL) were unable to either partially or completely consume sea urchins (*Parechinus angulosus* 10–61 mm TD), and that the predation ability of this species increased as a function of carapace length.

##### 4.2.3. Selectivity of prey by different predators

The clear evidence of the importance of the sea otter (*Enhydra lutris*) as a predator structuring sea urchin populations in the northeastern Pacific is relatively unique (Lowry and Pearse, 1973; Estes and Palmisano, 1974; Duggins, 1980; Estes and Duggins, 1995; Estes et al., 1998; Dean et al., 2000; Watt et al., 2000). While a broadly similar scenario invoking control of sea urchin populations by predators is emerging for other regions where mammalian predators are absent (Vadas and Steneck, 1995; Mayfield and Branch, 2000; Mayfield et al., 2001; Babcock et al.,

1999), there is relatively little unequivocal evidence to identify key predators or partition mortality among putative predators. In temperate reef systems in New Zealand, the relative importance of demersal fish and rock lobsters as predators of *E. chloroticus* has been examined and in one instance at least 45% of adult sea urchin mortality is attributed to rock lobsters (Shears and Babcock, 2002). However, partitioning mortality among different predators was problematic since the remains of at least half of large sea urchin mortalities, and the majority of smaller individuals, could not be identified or attributed to a specific predator. Similarly, Vadas and Steneck (1995) make a convincing case for the importance of predation by demersal fishes on sea urchins in the north west Atlantic, but no attempt was made to partition mortality due to predation by fishes and lobsters.

In the current study we conducted an experiment designed specifically to test differences in sea urchin mortality attributable to rock lobsters and demersal fishes. The results showed that when sea urchins were able to adopt their usual behaviour, rock lobsters were more important predators than demersal fishes. While juvenile sea urchins were immune to predation by both rock lobsters and demersal fishes, most likely by seeking refuge in crevices, the mortality of small adult (A1) sea urchins was almost entirely attributed to rock lobsters, and the mortality of large adult (A2) sea urchins to both rock lobsters and demersal fish. These results reflect our observations of sea urchin remains made during the tagging experiments where the majority of sea urchin mortalities could be attributed to rock lobsters. Unlike fish, rock lobsters remove the Aristotle's lantern but leave the test relatively undamaged, whereas predation by fishes typically results in the destruction of the test.

The weight of evidence from the suite of experiments reported here, combined with our previous work showing negative correlations between rock lobsters and sea urchins at large spatial scales, but not between fishes and sea urchins (Johnson et al., 2004), lead us to conclude that in eastern Tasmania rock lobsters are more important than fish as predators of *H. erythrogramma*. This is in contrast to other temperate systems where evidence to date suggests that fish may be important predators of sea urchins (Cowen, 1983; Vadas and Steneck, 1995).

#### 4.3. Sea urchin population structure

Exploitation of rock lobsters has significantly reduced the number of legal-sized individuals in areas open to fishing. Projections from stock assessment models estimate that the biomass of legal-sized rock lobsters (> 110 mm CL) on the east coast of Tasmania has recently been as low as 2–

8% of the virgin stock (Frusher, 1997) although legal biomass is now ostensibly rebuilding as a result of changed management practice (Frusher, pers. comm.). We therefore infer that, since areas open to rock lobster exploitation on the east coast have for several decades supported relatively few legal-sized rock lobsters, and that the majority of predation on adult sea urchins is attributed to legal-sized rock lobsters, the mortality of adult sea urchins in areas open to rock lobster exploitation has declined. Conversely, sea urchin mortality inside marine reserves, where the average size and abundance of rock lobsters has risen substantially over the last decade (Edgar and Barrett, 1999), is likely to have increased. Given our experimental results demonstrating that rock lobster predation of sea urchins is size-specific, and small adult (A1) sea urchins experience higher rates of mortality than other smaller and larger size classes, we anticipate that high levels of predation mortality will reduce the number of small adult (A1) sea urchins in a population where legal-sized rock lobsters are in high abundance. This mechanism is consistent with the different population size structures reported for reserve and fished areas within Mercury Passage where the relative proportion of small adult sea urchins was lower inside the reserve compared with sea urchin populations in adjacent exploited habitats (Fig. 7). Similarly, for several other species of sea urchins it has been inferred that when intermediate-sized sea urchins lose their ability to remain cryptic, intense predation mortality leads to non-normal population structures (Tegner and Levin, 1983; Andrew and MacDiarmid, 1991; Scheibling and Hamm, 1991; Cole and Keuskamp, 1998).

From the results of the tethering and tagging experiments we would expect a significantly lower sea urchin density inside marine reserves than adjacent habitats open to fishing of predators. This was evident within the Derwent Estuary where sea urchin densities inside the reserve were significantly lower and predators more abundant compared to adjacent fished habitats. This pattern was not as well defined within Mercury Passage where sea urchin densities inside the reserve were lower but not significantly different to those in adjacent fished areas. This may reflect that, at the time of sampling the reserve in the Derwent Estuary had been established for almost three decades while the Maria Island Reserve had been established for less than one decade. Time lags for similar effects have been documented in other temperate systems (Shears and Babcock, 2003).

## 5. Conclusions

Results from our study show that predation mortality is an important component of mortality structuring *H.*

*erythrogramma* populations. Our results show that (1) sea urchin mortality is much greater inside marine reserves, where predators are more abundant and larger, than in adjacent fished areas; (2) sea urchin mortality is highly size-specific, and both predator and prey size is important in determining predation mortality; (3) intermediate sized sea urchins (61–80 mm TD) experience higher rates of predation mortality than larger sea urchins that are immune to predation by small rock lobsters, while small sea urchins are more successful in sheltering from predators; and (4) observational and experimental evidence suggests the southern rock lobster (*J. edwardsii*) is more important in structuring post-recruitment populations of *H. erythrogramma* on the east coast of Tasmania than are demersal fish. We propose that heavy exploitation of rock lobsters, given the inability of small (sub-legal) rock lobsters to prey on large adult sea urchins, could result in significant changes in both the population size and in the size–frequency patterns of sea urchins.

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