Effect of predator–prey and competitive interactions on size at emergence in the black-lip abalone *Haliotis rubra* in a Tasmanian MPA

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ABSTRACT: Following more than a decade of protection from fishing activity, the direct and indirect effects of fishing on benthic community structure are becoming apparent inside no-take marine protected areas (MPAs) on Tasmania's east coast. Gradual increases in the abundance and average size of putative abalone predators inside the no-take Maria Island Marine Reserve (MIMR) have coincided with increases in the minimum size of the emergent abalone *Haliotis rubra*. This suggests that the threat of predation may influence the structuring of abalone populations. The abundance of emergent abalone was negatively associated with predator abundance, especially the rock lobster *Jasus edwardsii*, inside the MPA and in adjacent fished areas. Abalone leave cryptic habitat at smaller sizes in fished areas compared to abalone inside the MPA. Although the patterns in abalone size at emergence (SAE) were strongly correlated with rock lobster abundance and average size, the abundance of other predators (demersal predatory fish and crabs) or competitors (sea urchins) did not influence the patterns in abalone SAE. However, predation mortality in isolation could not account for the differences we observed in abalone size frequency distributions between MPA and adjacent fished locations. We suggest that a combination of factors including predation, intra and interspecific competitive interactions are responsible for patterns in abalone SAE.

KEY WORDS: Abalone · Size at emergence · SAE · Predator–prey interactions · Behaviour · Marine protected areas · MPAs · *Haliotis rubra*

INTRODUCTION

Historically, research on the effects of fishing has been focussed on determining the impact of removing target species from marine ecosystems, with most studies limited to examining changes in biomass and size structure. However, after several decades of exploitation, the indirect effects of fishing on non-target species and ecosystems are being observed in a range of temperate ecosystems (Babcock et al. 1999, Mayfield & Branch 2000, Tegner & Dayton 2000, Karpov et al. 2001, Rogers-Bennett & Pearse 2001, Shears & Babcock 2003 and reviewed by Tegner & Dayton 2000). Among the most prominent indirect effects of fishing are changes to predator–prey relationships (Estes & Palmisano 1974, Simenstad et al. 1978, Tegner

& Dayton 1981, Cowen 1983, Tegner & Levin 1983, Vadas & Steneck 1995, Tegner & Dayton 2000) and competitive interactions among species (Tarr et al. 1996, Karpov et al. 2001). In many cases assessing both the direct and indirect effects of fishing has only been possible via the advent of marine protected areas (MPAs) in which fishing is prohibited (no-take MPAs). The effectiveness of MPAs to increase the abundance, average size and biomass of exploited species (Edgar & Barrett 1999, McClanahan & Arthur 2001, Russ & Alcala 2003, Willis et al. 2003), reverse trophic cascades and restore ecosystems towards pre-fishing states is now well recognised (Shears & Babcock 2003).

Following a decade of protection from exploitation, changes in the abundance, average size and diversity of species have been observed in no-take MPAs along

Tasmania's east coast (Edgar & Barrett 1999, Buxton et al. 2006). The most notable changes have occurred in the largest no-take reserve at Maria Island where populations of 2 commercially important species, the rock lobster *Jasus edwardsii* and black-lip abalone *Haliotis rubra*, have undergone significant change compared to adjacent fished locations (Edgar & Barrett 1999, Buxton et al. 2006). In the absence of fishing, the average size and relative abundance of rock lobsters increased significantly inside the MPA. In contrast, emergent abalone populations have undergone an unexpected decline in relative abundance inside the MPA, attributable to a decline in smaller size classes (Buxton et al. 2006). This observed decline was attributed to one of several different factors: an increase in predation mortality of small individuals as predator abundances increased in the absence of fishing; a change in the emergence behaviour of juvenile abalone inside the MPA in response to non-lethal interaction with the increased number and size of predators inside the MPA; intraspecific competition for resources (food and space) as the average size of adult emergent abalone increased; or interspecific competition with sea urchins.

Although factors such as competitive interactions between abalone and sea urchins (Shepherd 1973, Andrew & Underwood 1992, Karpov et al. 2001) and predation of juvenile abalone (Shepherd 1998, Mayfield & Branch 2000, Rogers-Bennett & Pearse 2001, Shepherd & Clarkson 2001, Day & Branch 2002) have been examined, very little information exists on the mechanisms contributing to emergence behavior. Using results from a survey of abalone populations at several sites inside the MPA and adjacent fished locations, we compare patterns of abalone size at emergence (SAE) with the abundance of predators and competitors to determine the possible mechanisms leading to the observed changes in emergent abalone populations.

MATERIALS AND METHODS

Site selection. The population structures of benthic invertebrates and demersal fish species were surveyed at 10 sites in Mercury Passage on Tasmania's east coast between May and July 2005 (Fig. 1). The sites surveyed were representative of those used in the long-term monitoring of the effectiveness of the no-take Maria Island Marine Reserve (MIMR) established in 1991 (Edgar & Barrett 1997). Study sites were located on medium profile rocky reefs at a depth of 5 m, were similar in exposure to prevailing weather conditions and supported communities of large brown macroalgae and understorey algal species typical of
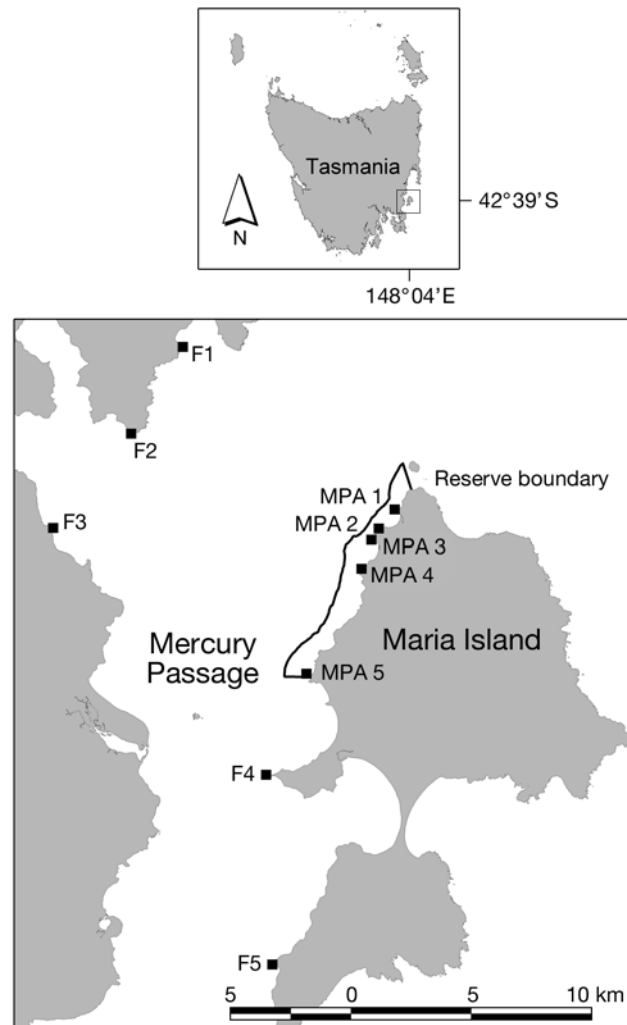

Fig. 1. Survey sites within Mercury Passage. Abalone size at emergence (SAE) surveys were conducted in fished habitats at 5 sites open to fishing (F1, F2, F3, F4 and F5) and 5 sites with similar macroalgal communities, reef topography and exposure to prevailing weather within the Maria Island marine protected area (MPA) (MPA1, MPA2, MPA3, MPA4 and MPA5)

moderately exposed coastlines in southeastern Tasmania (Edgar 1984). Five of the sites were located inside the MPA with a minimum separation of 0.8 km between sites, which is greater than the inter-annual movement of rock lobsters inside the MPA (Buxton et al. 2006), to ensure estimates of rock lobster abundance were independent of each other. Five sites were located adjacent to the MPA where commercial and recreational rock lobster and abalone fisheries continue to operate (hereafter referred to as fished sites).

Survey techniques. Benthic invertebrates and demersal fishes were surveyed using underwater visual census techniques described by Edgar & Barrett (1997). At each site, four 50 m transects were deployed

randomly along the 5 m depth contour, and the abundance and size structure of the rock lobster *Jasus edwardsii* and emergent black-lip abalone *Haliotis rubra* were recorded by divers searching a 1 m strip parallel to each transect. Within the same search area the abundance of the sea urchin *Heliocidaris erythrogramma* and crab *Plagusia chabrus* were also recorded. Abalone SAE estimates were obtained by 2 divers searching habitat 5 m on either side of the transect and restricted between the 3 and 7 m depth contours. Emergent abalone were defined as individuals not hidden from the divers' view in deep crevices but exposed to predators, whereas cryptic individuals were hidden from the divers' view in crevices and under boulders. Estimates of cryptic abalone size structures were obtained by lifting and searching underneath small boulders (ca. 0.5 to 0.75 m diameter) in the area in which emergent individuals were measured. To remove observer-induced biases in the classification of cryptic and emergent abalone, the same divers were used to survey all sites in the study. A minimum of 200 abalone (cryptic and emergent combined) were classified and measured *in situ* at each site using knife-edge calipers. To ensure that accurate estimates of SAE could be calculated, a minimum of 75 cryptic individuals were recorded in each sample where possible.

The abundance of the dominant predatory demersal fish, including the labrids *Pictilabrus laticlavius*, *Pseudolabrus psittaculus*, *Notolabrus fucicola*, *N. tetricus*, *Dotalabrus aurntiacus*; the monocanthids *Acanthaluteres vittiger*, *Meuschenia australis*, *Meuschenia freycineti*; the latrid *Latridopsis forsteri*; and the Cheilodactylids *Cheilodactylus nigripes* and *C. spectabilis*, were recorded by divers surveying a 5 m wide strip immediately above the reef along both sides of each transect. Due to the low abundances of several species, data were pooled into a group (hereafter called demersal fish) for comparison in statistical tests.

Statistical analysis. The relationship between abalone shell length and the state of emergence (cryptic or emergent) was determined using logistic regression, as the technique is most suited when the dependent variable (emergence) is binomially distributed as a function of the parameters of the independent variable (Hosmer & Lemeshow 2000). Abalone SAE was estimated using a probit regression model that assumes that the percent response (emergence) is related to the log of the independent variable (shell length) as a cumulative normal distribution (Finney 1971). The percentage of abalone emergent can be estimated using the log of shell lengths from the cumulative normal distribution with the most reliable comparisons among sites made using the fiftieth percentile.

Relationships between abalone SAE and the abundance of putative abalone predators and competitors were defined using a multiple step-wise (addition) regression and fitted using ordinary least squares. The most parsimonious model was reached when the lowest Akaike Information Criterion (AIC) value and highest adjusted R^2 values were obtained and a normal Quantile-Quantile (Q-Q) plot of residuals followed a 45° line. All analyses were undertaken using the SAS statistical software package (version 9.1, SAS Institute).

Abalone size frequency distributions were compared between MPA and fished populations using a randomisation procedure with the Kolmogorov-Smirnov test statistic (D). Data were pooled across sites within each treatment and the test statistic calculated (D_{obs}). Size frequency data from the 2 distributions were then pooled and randomly reallocated back to each original distribution and the test statistic recalculated (D_{rand}). The procedure was repeated 1000 times and the test of significant difference between the 2 distributions made by comparing the value of D_{obs} to the distribution of D_{rand} values obtained by the randomisation procedure. Significant differences were identified when less than 25 of the D_{rand} values obtained from the randomisation procedure exceeded the value of D_{obs}, following the procedure described by Haddon (2001). To ensure that meaningful comparisons between the population structures could be made, without the bias of absolute abundances, the size frequency distribution from the MPA population was rescaled to match the scale of the fished population. Rescaling was achieved by calculating a common slope and intercept of the linear relationship between frequency and shell length, between 10 and 104 mm shell lengths (smallest individuals sampled and the midpoint between the 2 sizes at emergence estimates, respectively), for each population. The common slope and intercept were then used to calculate the rescaled relative frequencies of each size class (2 mm bins) of the MPA population. The rescaled MPA population was then plotted against the unchanged fished population to allow relative comparisons between the population structures to be made.

RESULTS

Patterns in abalone SAE and population size structure

Estimates of abalone SAE varied considerably at both MPA and fished locations (Fig. 2, Table 1), but was consistently larger inside the MPA. When the data from sites within each treatment were pooled, abalone SAE in the MPA was significantly greater than at adjacent fished sites (117.8 and 87.6 mm, respectively, p < 0.001).
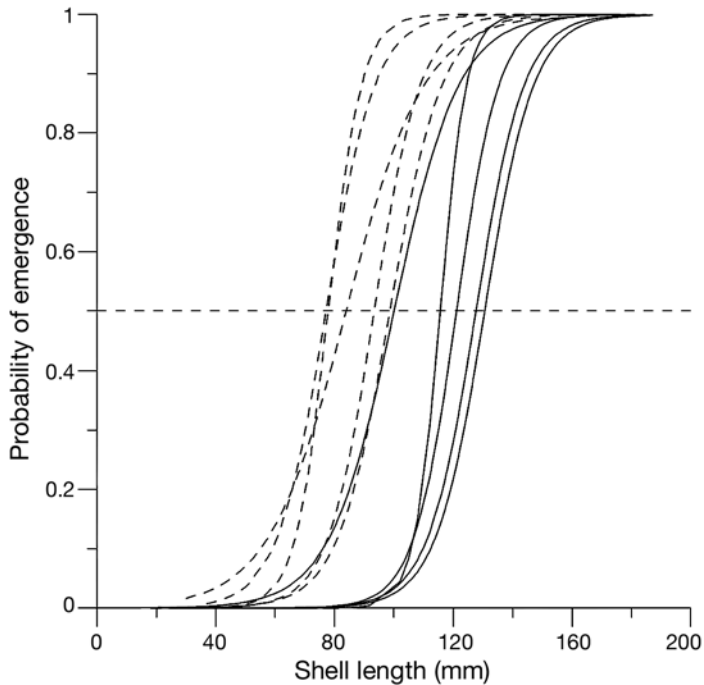
Fig. 2. *Haliotis rubra*. Size at emergence (SAE) of abalone at 10 sites within Mercury Passage. Individual plots represent the probability of abalone being emergent at any given shell length (mm). (——) SAE estimates for sites inside the marine protected area (MPA); (----) abalone populations at adjacent sites open to fishing; horizontal dashed line: 0.5 probability of abalone being emergent at the corresponding shell length

The size frequency distributions of abalone populations from inside the MPA were significantly different from those in adjacent fished locations (D_{obs} = 0.389, p < 0.0001) with abalone larger than 140 mm accounting for the greatest difference in the size frequency distributions (Fig. 3). In the MPA a smaller fraction of the population was between the SAE and the minimum legal size of 136 mm compared to the fished sites (16 and 55%, respectively). In contrast, the proportion of the population above the minimum legally exploitable size was much greater in the MPA than at fished sites (55 and 18%, respectively). Despite the observed differences between emergent individuals, the proportion of each population remaining cryptic was similar (27% fished and 29% MPA).

When the size frequency distribution of the MPA population was rescaled relative to the fished population to remove biases in absolute abundance, there was no evidence that predation mortality had significantly reduced the proportion of abalone below the SAE estimate inside the MPA (Fig. 4). Instead, the relative differences between the rescaled frequency distributions indicated the fished and MPA populations were similar in structure up to the minimum legally

exploitable size of 136 mm (D_{obs} = 0.039, p = 0.43), after which there was a clear effect of protection on abalone size structure (D_{obs} = 0.389, p < 0.0001).

Relationships with predators and competitors

The most parsimonious multiple regression model explaining the patterns in abalone SAE included the individual terms of rock lobster *Jasus edwardsii* abundance, mean size of rock lobsters (carapace length) and the interaction between rock lobster and sea urchin abundance (Table 2). The individual terms of the crab *Plagusia chabrus*, predatory demersal fish, emergent abalone, emergent abalone >140 mm and sea urchin *Heliocidaris erythrogramma* abundance were not related to abalone SAE and not significant components in the most parsimonious model (Fig. 5).

DISCUSSION

Abalone are amongst the most exploited of all temperate inshore fisheries. Although a large volume of literature on abalone biology and abalone fisheries exists, there is a paucity of information on the indirect effects of fishing on abalone populations, specifically behaviour of abalone and the stimuli responsible for emergence behaviour. The present study found significant variation across small spatial scales (10^3 m) in the

Table 1. *Haliotis rubra*. Abalone size at emergence (SAE) estimates (±95% CI) at 5 sites open to fishing and 5 sites inside the Maria Island no-take marine protected area (MPA). SAE estimates represent the shell length when there is a probability of 0.5 that an individual will be emergent. Estimates of SAE for MPA and fished populations were calculated on data pooled across sites within each treatment

Site	SAE (mm)	% of sample < SAE	N
Fished			
1	77.2 (72.6–81.1)	15.7	185
2	77.9 (73.1–82.1)	21.6	194
3	93.4 (91.4–95.2)	29.3	259
4	83.9 (80.2–87.1)	25.7	222
5	98.7 (94.6–102.5)	45.9	211
Pooled	87.6 (86.8–88.4)	27.6	1071
MPA			
1	121.1 (118.5–124.3)	27.1	259
2	127.6 (124.4–130.4)	24.6	183
3	130.6 (128.5–132.4)	39.4	259
4	115.6 (110.9–119.0)	29.4	238
5	100.1 (96.8–102.9)	30.8	234
Pooled	117.8 (117.1–118.5)	30.2	1173

size at which abalone emerge from cryptic habitat, which correlated with both the abundance and mean size of the rock lobster *Jasus edwardsii*. Lobsters are predators of other benthic invertebrates including sea urchins (Shears & Babcock 2002, Pederson & Johnson 2006) and juvenile abalone (Tarr et al. 1996, Mayfield et al. 2001) in temperate ecosystems.

In contrast the patterns in abalone SAE were not dependent upon the density of the most common crab *Plagusia chabrus* or a suite of predatory demersal fishes including the labrids *Notalabrus tetricus* and *Pictilabrus laticlavius,* which are predators of juvenile abalone elsewhere in temperate Australia (Shepherd & Turner 1985, Shepherd & Clarkson 2001). This result is not surprising given that the abundance of both *N. tetricus* and *P. laticlavius* have not responded to the effect of protection inside the MPA (Barrett et al. 2007).

While patterns in abalone SAE correlate with the abundance and mean size of rock lobsters, size-specific predation of small abalone could not account for the differences in SAE estimates between fished sites and the MPA. For this to have occurred there would have had to have been a distinguishable gap in the size frequency distribution immediately below the SAE inside the MPA. This was not the case. Our results indicate the structure and relative abundance of abalone below the minimum legally exploitable size (136 mm) inside the MPA were similar to those in the adjacent fished areas. Instead, mortality appears to have acted uniformly across a wide range of size classes and reduced the absolute abundance of small abalone inside the MPA compared to the adjacent fished sites.

The clear indirect effect of lobster fishing on abalone populations was to change the SAE. Outside the MPA, in the presence of lower numbers and smaller sized lobsters, more than half of the individuals below the minimum legal size were emergent (55%). This fraction was greatly reduced inside the MPA (16%), where individuals greater
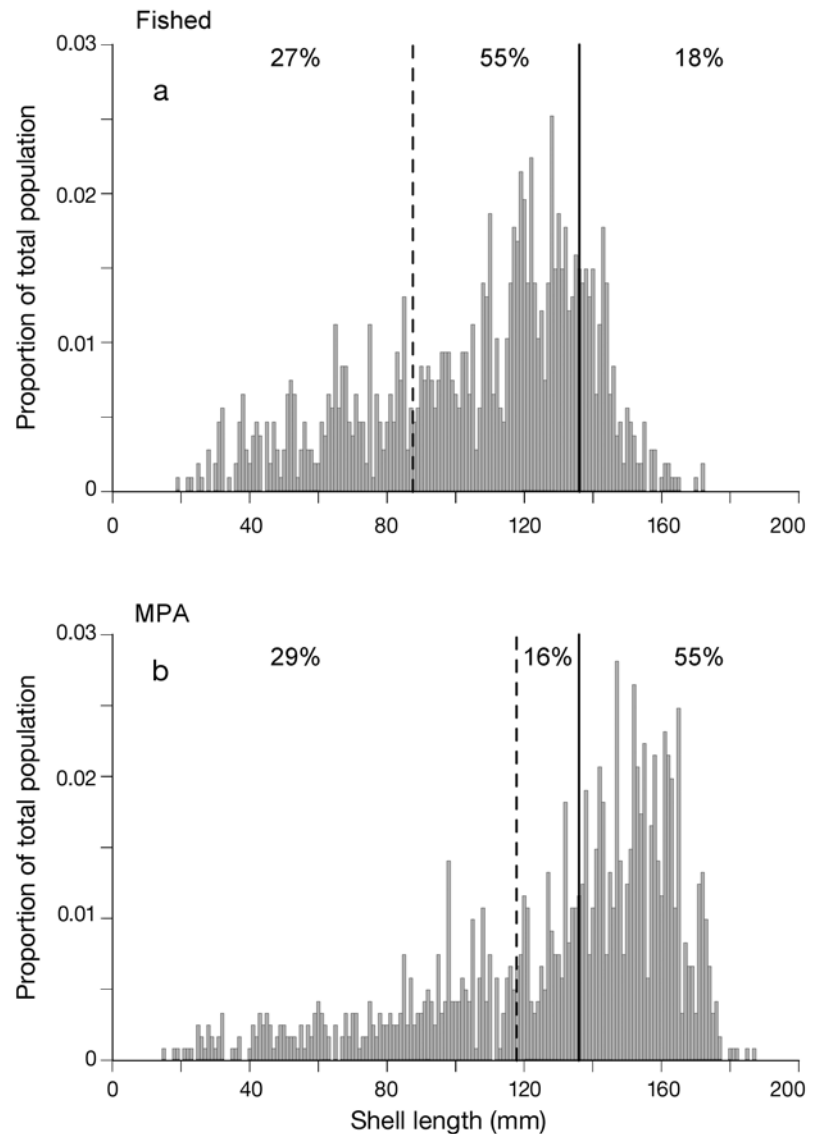

Fig. 3. *Haliotis rubra*. Size frequency distributions of abalone in populations at fished sites (a) within Mercury Passage and (b) inside the marine protected area (MPA). Distributions were constructed by pooling size data across 5 sites within each treatment (N = 1071 fished, N = 1209 MPA). Distributions of abalone sizes were significantly different (D_{obs} = 0.389, p < 0.0001), with the maximum divergence between distributions at shell lengths of 140 mm. Dashed vertical lines: size at emergence (SAE) estimates for data pooled across sites within each treatment; solid vertical lines: minimum legally exploitable size for abalone in the region (136 mm)

Table 2. The most parsimonious multiple regression model explaining patterns in abalone size at emergence (SAE) (dependent variable). AIC: Akaike Information Criterion

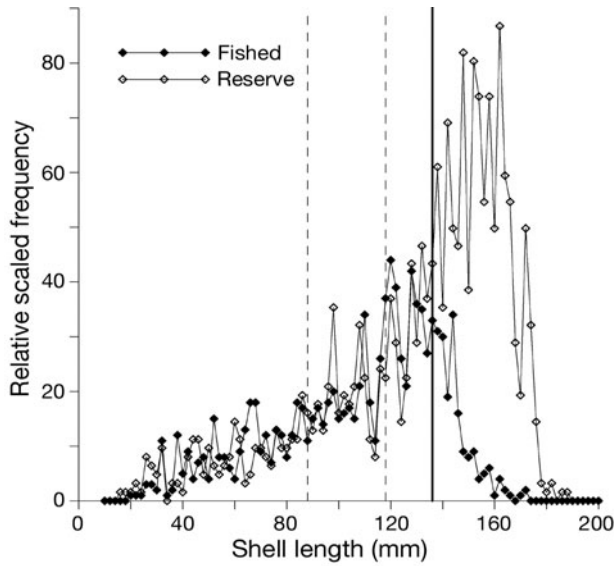| Parameters	Estimate	SE	p
Intercept	78.42	3.37	<0.001
Rock lobster abundance	3.97	0.75	<0.001
Mean rock lobster size (mm)	0.13	0.047	<0.01
Rock lobster × Sea urchin abundance	−0.013	0.003	<0.001
Multiple R^2 = 0.75, Adjusted R^2 = 0.73, $F_{3, 36}$ = 35.77, p < 0.001, AIC = 303.9			

Fig. 4. *Haliotis rubra*. Comparison of relative scaled frequency distributions for abalone populations at fished sites within Mercury Passage and the Maria Island marine protected area (MPA). The distribution from the MPA has been rescaled using a slope and intercept common to both distributions from the linear regression between frequency and shell length (between 10 and 104 mm) for each population. Dashed vertical lines: mean size at emergence (SAE) in fished and MPA populations (88 and 118, respectively); solid vertical line: minimum legally exploitable size (136 mm)

than the minimum legally exploitable size of 136 mm accounted for more than half the population compared to adjacent areas where fishing has reduced the number of exploitable individuals to less than 20% of the population.

While competitive interactions among other abalone and sea urchin species have been documented (North & Pearse 1970, Lowry & Pearse 1973, Shepherd 1973, Tegner & Levin 1982), the effect of sea urchin *Helio-cidais erythrogramma* abundance on abalone emergence behaviour was not evident over the scales and habitats we surveyed. Similarly the lack of any correlation between abalone SAE and the density of emergent abalone suggests that density-dependent inter- and intraspecific competition does not play a major role in determining abalone emergence behaviour. However, because of the problems associated with accurately quantifying the abundance of cryptic abalone in 3-dimensional substrate, we cannot rule out that emergence behaviour is linked to the abundance of cryptic abalone.

Since the abundance of rock lobsters is correlated with patterns of abalone SAE, and predation mortality cannot account for the differences between MPA and adjacent fished locations in isolation, how do we explain the patterns in abalone SAE within Mercury Passage? Although the patterns in abalone SAE corre-
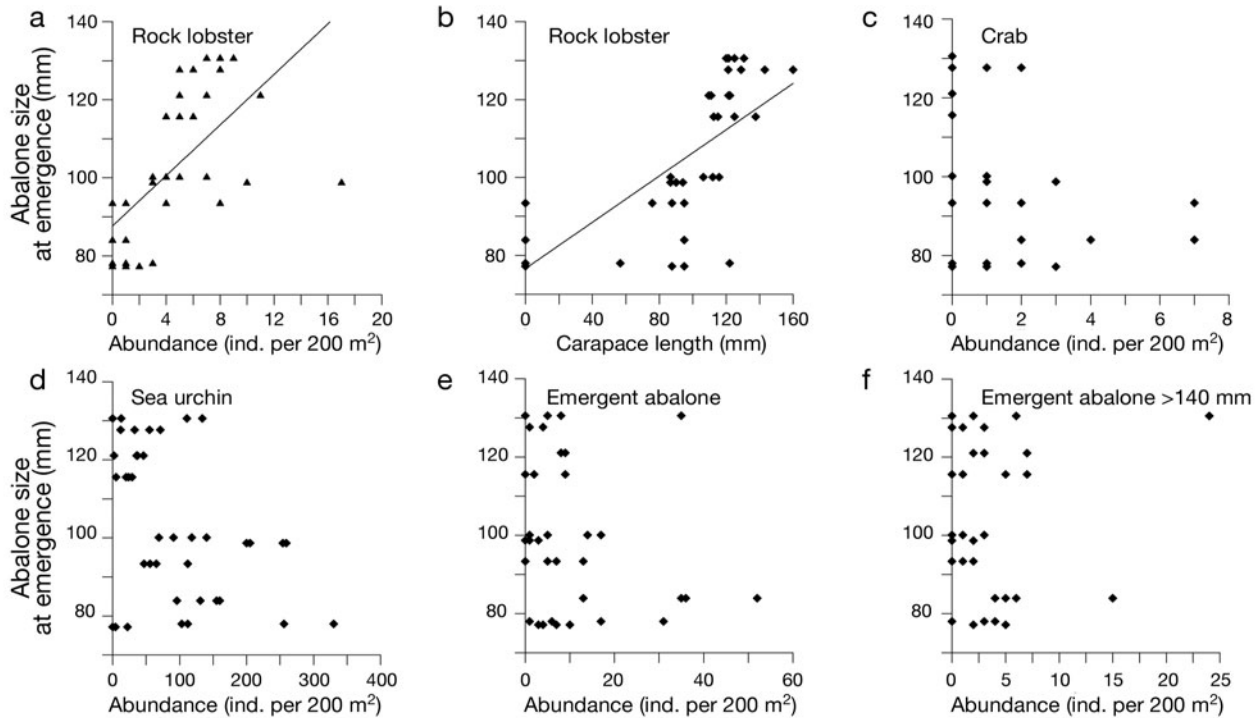

Fig. 5. *Haliotis rubra.* Scatterplots showing the distribution of abalone size at emergence (SAE) estimates in relation to (a) rock lobster abundance ($p < 0.001$, $R^2 = 0.44$), (b) mean rock lobster carapace length ($p < 0.001$, $R^2 = 0.55$), (c) crab abundance, (d) sea urchin abundance, (e) emergent abalone abundance and (f) emergent abalone >140 mm abundance. Trend lines represent significant relationships between abalone SAE and single independent variables fitted using ordinary least squares regression

lated with the abundance and mean size of rock lobsters, the pattern may be the result of non-lethal interactions with rock lobsters. Cryptic abalone inside the MPA may encounter rock lobsters more frequently inside the MPA as rock lobster abundance increases and their foraging intensifies (N. Barrett pers. obs). The result of the increased non-lethal interaction with rock lobsters may alter the behaviour of small abalone and delay their emergence until they reach a suitable size refuge. The non-lethal interaction may be further enhanced by intraspecific competition with the large emergent abalone during competition for space and food and delay the onset of emergence. Patterns in abalone SAE are likely to be the result of a complex combination of factors including predation, intra- and interspecific competitive interactions.

While our observations apply to the Maria Island MPA, the generality of the interspecific interaction described here has yet to be tested more broadly. While clear responses to protection by both rock lobster and abalone populations have been observed within the Maria Island MPA (Edgar & Barrett 1997, 1999, Buxton et al. 2006), trends have not been as evident in 3 smaller MPAs in eastern Tasmania, where rock lobster increases were not always associated with abalone declines. The difference in response to protection within the smaller MPAs has been attributed to the differences in area under protection (ca. 1000 ha within Maria Island vs. 45 to 60 ha in the other MPAs), lack of sufficient space to place replicate survey sites within reserves (power), prominent edge effects, higher intensity of fishing effort close to boundaries and habitat differences (Buxton et al. 2006). The variation in responses highlights the need to have a series of sufficiently large MPAs, with sufficient statistical power, to effectively assess the impact of protection on population dynamics and species interactions.

LITERATURE CITED

Andrew NL, Underwood AJ (1992) Associations and abundance of sea urchins and abalone on shallow subtidal reefs in southern New South Wales. Mar Freshw Res 43: 1547–1559

Babcock RC, Kelly S, Shears NT, Walker JW, Willis TJ (1999) Changes in community structure in temperate marine reserves. Mar Ecol Prog Ser 189:125–134

Barrett NS, Edgar GJ, Buxton CD, Haddon M (2007) Changes in fish assemblages following 10 years of protection in Tasmanian marine protected areas. J Exp Mar Biol Ecol 345:141–157

Buxton C, Barrett N, Haddon M, Gardner C, Edgar GJ (2006) Evaluating the effectiveness of marine protected areas as a fisheries management tool. Report No. FRDC 1999/162. Fisheries Research and Development Corporation, Hobart

Cowen RK (1983) The effect of sheephead (*Semicossyphus pulcher*) predation on red sea urchin (*Strongylocentrotus franciscanus*) populations: an experimental analysis. Oecologia 58:249–255

Day E, Branch GM (2002) Effects of sea urchins (*Parechinus angulosus*) on recruits and juveniles of abalone (*Haliotis midae*). Ecol Monogr 72:133–149

Edgar GJ (1984) General features of the ecology and biogeography of Tasmanian subtidal rocky shore communities. Pap Proc R Soc Tasman 118:173–186

Edgar GJ, Barrett NS (1997) Short term monitoring of biotic change in Tasmanian marine reserves. J Exp Mar Biol Ecol 213:261–279

Edgar GJ, Barrett NS (1999) Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. J Exp Mar Biol Ecol 242:107–144

Estes JA, Palmisano JF (1974) Sea otters: their role in structuring nearshore communities. Science 185:1058–1060

Finney DJ (1971) Probit analysis. Cambridge University Press, Cambridge

Haddon M (2001) Modelling and quantitative methods in fisheries. Chapman & Hall/CRC Press, Boca Raton, FL

Hosmer DW, Lemeshow S (2000) Applied logistic regression, John Wiley & Sons, New York

Karpov KA, Tegner MJ, Rogers-Bennett L, Kalvass PE, Taniguchi IK (2001) Interactions among red abalones and sea urchins in fished and reserve sites of northern California: implications of competition to management. J Shellfish Res 20:743–753

Lowry LF, Pearse JS (1973) Abalones and sea urchins in an area inhabited by sea otters. Mar Biol 23:213–219

Mayfield S, Branch GM (2000) Interrelations among rock lobsters, sea urchins, and juvenile abalone: implications for community management. Can J Fish Aquat Sci 57: 2175–2185

Mayfield S, de Beer E, Branch GM (2001) Prey preference and the consumption of sea urchins and juvenile abalone by captive rock lobsters (*Jasus lalandii*). Mar Freshw Res 52:773–780

McClanahan TR, Arthur R (2001) The effect of marine reserves and habitat on populations of east African coral reef fishes. Ecol Appl 11:559–569

North WJ, Pearse JS (1970) Sea urchin population explosion in southern California coastal waters. Science 167:209

Pederson HG, Johnson CR (2006) Predation of the sea urchin *Heliocidaris erythrogramma* by rock lobsters (*Jasus edwardsii*) in no-take marine reserves. J Exp Mar Biol Ecol 336:120–134

Rogers-Bennett L, Pearse JS (2001) Indirect benefits of marine protected areas for juvenile abalone. Conserv Biol 15: 642–647

Russ GR, Alcala AC (2003) Marine reserves: rates and patterns of recovery and decline of predatory fish, 1983–2000. Ecol Appl 13:1553–1565

Shears NT, Babcock RC (2002) Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia 132:131–142

Shears NT, Babcock RC (2003) Continuing trophic cascade effects after 25 years of no-take marine reserve protection. Mar Ecol Prog Ser 246:1–16

Shepherd SA (1973) Competition between sea urchins and abalone. Aust Fish 32:4–7

Shepherd SA (1998) Studies on southern Australian abalone (genus *Haliotis*)—XIX: long-term juvenile mortality dynamics. J Shellfish Res 17:813–825

Shepherd SA, Clarkson PS (2001) Diet, feeding behaviour, activity and predation of the temperate blue-throated wrasse, *Notolabrus tetricus.* Mar Freshw Res 52:311–322

Shepherd SA, Turner JA (1985) Studies of southern Aus-

tralian abalone (genus *Haliotis*). VI. Habitat preference, abundance and predators of juveniles. J Exp Mar Biol Ecol 93:285–298

Simenstad CA, Estes JA, Kenyon KW (1978) Aleuts, sea otters, and alternate stable-state communities. Science 200:403–411

Tarr RJQ, Williams PVG, MacKenzie AJ (1996) Abalone, sea urchins and rock lobsters: a possible ecological shift that may affect traditional fisheries. S Afr J Mar Sci 17:319–323

Tegner MJ, Dayton PK (1981) Population structure, recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in a kelp forest. Mar Ecol Prog Ser 5:255–268

Tegner MJ, Dayton PK (2000) Ecosystem effects of fishing in kelp forest communities. ICES J Mar Res 57:579–589

Tegner MJ, Levin LA (1982) Do sea urchins and abalone compete in California kelp forest communities? In: Lawrence JM (ed) International Echinoderms Conference. Balkema, Rotterdam

Tegner MJ, Levin LA (1983) Spiny lobsters and sea urchins: analysis of a predator-prey interaction. J Exp Mar Biol Ecol 73:125–150

Vadas RL, Steneck RS (1995) Overfishing and inferences in kelp-sea urchin interactions. In: Skjodal HR, Hopkins C, Erickstad K, Leinaas H (eds) Ecology of fjords and coastal waters. Elsevier, Amsterdam, p 509–524

Willis TJ, Millar RB, Babcock RC (2003) Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. J Appl Ecol 40:214–227