

# Limited evidence for ecosystem-level change on reefs exposed to *Haliotis rubra* ('blacklip abalone') exploitation

JOSEPH P. VALENTINE,\* DAVID B. TARBATH, STEWART D. FRUSHER,  
CRAIG N. MUNDY AND COLIN D. BUXTON

*Marine Research Laboratories, Tasmanian Aquaculture and Fisheries Institute, University of Tasmania, Hobart, Tasmania 7001, Australia*

**Abstract** It is increasingly recognized that fisheries must take the broader ecosystem into account for sustainable management of marine systems, requiring an understanding of the interaction between fished species and other organisms. This study uses a correlative approach to investigate potential interactions between benthic organisms and *Haliotis rubra*, a dominant herbivore that is the subject of a large and valuable commercial fishery in south-eastern Australia. Specific emphasis was placed on understanding associations between *H. rubra* and understorey organisms, because particular understorey algae (crustose coralline algae) provide critical habitat for *H. rubra* larval recruitment and juvenile ecology. Broad-scale surveys along the 6–8 m depth contour (the depth range where *H. rubra* fishing activity is intense) were conducted across four regions (separated by  $10^4$ – $10^5$  m), including at least 10 sites (separated by  $10^2$ – $10^3$  m) within each region. Positive correlations between *H. rubra* and crustose coralline algae were found, while negative correlations were observed between *H. rubra* and sessile invertebrates and understorey algae. While significant, these associations were weak and *H. rubra* abundance generally only explained a small proportion of the variability in the abundance of understorey organisms ( $r^2$  0.02–0.30). *H. rubra* abundance also had a minor influence on community-level understorey patterns in comparison with differences in community structure attributable to regional variation. Patterns of *H. rubra* abundance and benthic community structure were also examined in relation to depth at a restricted number of sites. At sites where differences in understorey groups were evident, *H. rubra* abundance also varied significantly, highlighting the issue of confounding when contrasting patterns of understorey abundance using a correlative approach. Further manipulative experiments are required to confirm causal relationships; however, the available correlative evidence suggests limited ecosystem effects of *H. rubra* depletion at the scale of individual reefs.

**Key words:** abalone, correlation, crustose coralline algae, ecosystem management, understorey.

## INTRODUCTION

Marine ecosystems are in serious decline worldwide, largely caused by the effects of over-harvesting, pollution and climate change (Hughes *et al.* 2005). Dramatic shifts in community structure, known as phase or regime shifts have been documented in a variety of habitats including coral reefs, kelp forests and pelagic systems (Hughes 1994; Hughes *et al.* 2005). The consequences of ecosystem phase shifts can be severe. For example, the combined effects of overfishing, hurricane damage and disease have destroyed most corals on many Caribbean reefs, with coral cover declining from more than 50% in the 1970s to less than 5% in the 1990s (Hughes 1994). The occurrence of such

phase shifts and the existence of 'alternative stable states' have major implications for management of marine systems, because recovery often follows a different trajectory from that observed during the decline and some marine systems have changed to the point where recovery to the former state is no longer possible (Collie *et al.* 2004; Schröda *et al.* 2005). Loss of resilience through human actions can also make ecosystems vulnerable to changes that could previously be absorbed (Folke *et al.* 2004).

Over-harvesting of herbivores is recognized as one of the main factors contributing to changes in community structure in marine systems globally (Burkepile & Hay 2006). The effect of over-harvesting will be largely dependent on the relative role of consumers (top-down) *versus* resources (bottom-up) in controlling community structure (Burkepile & Hay 2006). Understanding the potential effects of herbivore removal via fishing activities requires critical investigation of the role of herbivores as a structuring influence on marine communities.

\*Corresponding author. Present address: Aquenal Pty Ltd, 244 Summerleas Rd, Kingston, Tasmania 7050, Australia (Email: jvalentine@aquenal.com.au)

Accepted for publication October 2009.

Assessing the influence of herbivores on community structure is also increasingly recognized as an important question from a fisheries management perspective. Ecologically sustainable development of marine resources requires an ecosystem-based approach to planning and management, as a result of the extensive interactions that occur between target species and other organisms (Jennings & Kaiser 1998; Pikitch *et al.* 2004) and the impacts on ecosystem function that can occur following the loss of a functional group associated with fishing activities (Pinnegar *et al.* 2000). Assessing the ecological role of a fished species represents a fundamental stage in an ecosystem-based management approach.

*Haliotis rubra* ('blacklip abalone') is the dominant herbivore in subtidal habitats on exposed coastlines of Tasmania, Australia and the focus of the world's largest abalone wild fishery (>2500 t per annum). While not confirmed, it is widely held that *H. rubra* activity contributes to the dominance of crustose coralline algae in understory communities (C. Mundy, pers. comm., 2007). Anecdotal evidence from some commercial abalone divers indicates that a shift from crustose coralline algal dominance (so called 'pink rock') to a community dominated by sessile invertebrates and foliose algae ('brown rock') is associated with depletion of *H. rubra* from reefs. On some Tasmanian reefs there is evidence that *H. rubra* numbers have been heavily depleted, with annual catches representing only 4% of the long-term average catch (Tarbath *et al.* 2004). If *H. rubra* play a key role in the maintenance of crustose coralline algae, then substantial reductions in biomass and numbers of abalone through fishing may lead to changes in ecosystem structure and function. Additional impetus for understanding '*H. rubra* – ecosystem' interactions is the fact that the majority of abalone (*Haliotis* spp.) fisheries around the world have collapsed or are in serious decline (Shepherd *et al.* 2000), raising the possibility that altered ecosystem function may have occurred as a result of removal of this key herbivore.

Reduced cover of crustose coralline algae has implications both for natural processes and for the long-term persistence of abalone populations, as other life history stages of abalone and invertebrates also rely significantly on crustose coralline algae. For example, the recent recruitment failure of black abalone in California has been linked with changes in crustose coralline algal abundance following mass mortality of black abalone populations (Miner *et al.* 2006). Larval abalone are known to preferentially metamorphose and subsequently feed on crustose coralline algae or associated bacteria and diatoms until they reach approximately 15 mm in length (Shepherd 1973; Saito 1981; Shepherd & Turner 1985; Tarr *et al.* 1996; Daume *et al.* 1999). Shell pigmentation (pink colouration) associated with this feeding activity also aids

camouflage and provides protection from predators during this critical early life history phase.

If understory community structure is determined by factors other than *H. rubra* grazing, fishing is unlikely to have a major effect on ecosystem structure. In this scenario, the ecological impact of *H. rubra* removal may be limited to pre-emption of space that might otherwise be colonized by foliose algae, as has been shown for the intertidal abalone *Haliotis roei* in Western Australia (Scheibling 1994).

Given the potential role of herbivores as a structuring influence for understory communities, and the dramatic ecosystem-level effects of large-scale herbivore removal in other systems (e.g. phase shifts on coral reefs; Bellwood *et al.* 2004), it is particularly important that the influence of *H. rubra* on understory community structure is investigated. This is crucial in order to assess the potential ecosystem effects of depletion of *H. rubra* from temperate reefs. While an experimental approach is required to ultimately determine the effect of *H. rubra* removal on the reef ecosystem, a necessary prerequisite to experimental manipulations is the use of correlative studies to identify taxa that could be potentially influenced by *H. rubra* abundance (Jenkins 2004).

The broad aim of this research was to use a correlative approach to investigate the influence of *H. rubra* on community structure and explore evidence for the existence of a phase shift following removal of *H. rubra* via fishing activities. The study examined the potential effects of *H. rubra* depletion on ecosystem structure and explored evidence for the dependence of particular understory organisms on the presence of *H. rubra*.

## METHODS

### Study sites

Surveys focused on four areas of the Tasmanian coastline including St Helens, Bicheno and Dunalley on the east coast and the Actaeons region on the south-east coast. The east coast regions were chosen because it is well documented that numerous reefs in the region have experienced significant declines in *H. rubra* abundance. In contrast the Actaeons area has many reefs that have remained productive throughout the history of the fishery. The focus of the study was the 6–8 m depth range on exposed coastlines, as this is typically where *H. rubra* fishing activity takes place. The influence of depth on *H. rubra* abundance and benthic community structure was investigated for the Dunalley region, where a shallower depth range (2–3 m) was also included at a restricted number of sites.

Field surveys were conducted between 5 May and 3 August 2006. At least 10 reefs were sampled in each region (Fig. 1). As data describing *H. rubra* abundance and/or fishing history at the scale of individual reefs were not available, a correlative approach was used, necessitating surveys

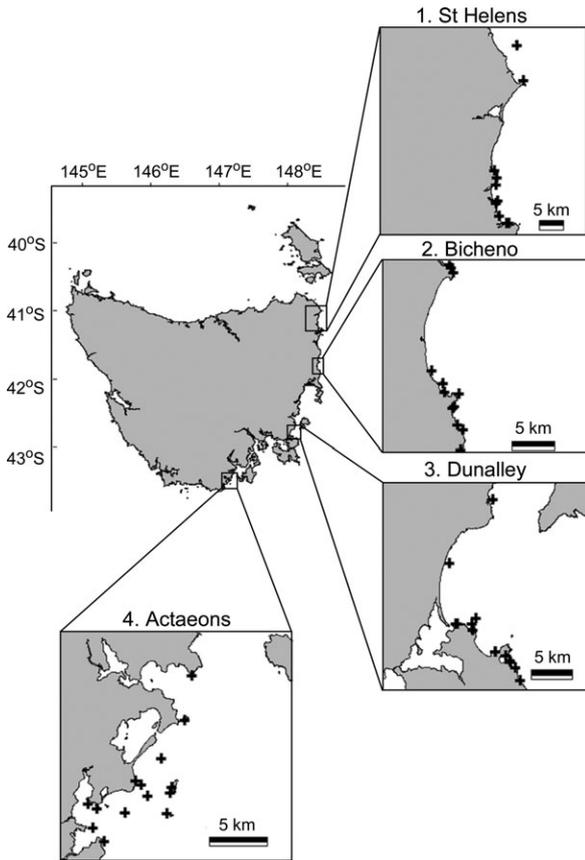


Fig. 1. Map showing location of four study regions and survey sites (+).

of reefs with contrasting abalone densities. Survey reefs were selected following interviews with commercial abalone divers who have extensive knowledge of abalone populations in the study region. Input from commercial divers ensured survey reefs encompassed the broadest range of abalone densities available. Where possible reefs inside marine-protected areas were also included in the survey; however, abalone density on these reefs was not always higher than nearby fished areas.

### Survey protocol

At each survey site a 100-m transect was deployed from the boat along the 6–8 m depth contour. Five 20 m<sup>2</sup> quadrats were positioned at 20-m intervals along the transect and in each quadrat the number of *H. rubra* and other large mobile grazers (e.g. sea urchins) was recorded. Total *H. rubra* abundance was split into two separate categories of ‘cryptic’ and ‘emergent’ based on the location of individual animals. Cryptic *H. rubra* were defined as those hidden in cracks and crevices, while emergent *H. rubra* occupied exposed reef surfaces. Abundance of canopy-forming algae in each quadrat was also estimated by classifying cover of different species according to the following categories: 1 = 0–10%; 2 = 11–30%; 3 = 31–50%; 4 = 51–75%; 5 = 76–100%.

Abundance of understory organisms (including algae and sessile invertebrates) was assessed in terms of percentage

cover. Percentage cover was estimated with a 0.25 m<sup>2</sup> ‘sub-quadrat’ using a point intercept method. The subquadrat was divided with a grid of 49 evenly spaced intersections and was laid flat on the reef during algal assessment. Algae occurring under each intercept and one corner of the subquadrat were recorded, to give a total of 50 intersections per subquadrat. Five randomly positioned subquadrats were assessed in this way for each 20 m<sup>2</sup> quadrat. Organisms were identified *in situ* to the highest taxonomic resolution possible. For canopy algae identification to species level was possible; however, it was necessary to allocate other species to species complexes or guilds (e.g. crustose coralline algae, foliose red algae, sessile invertebrates).

### Analysis

Relationships between *H. rubra* categories (total, emergent, cryptic) and the dominant benthic groups were explored using scatter plots and linear regression. For individual taxa, Spearman rank correlations were also used to identify taxa that were most strongly correlated with total *H. rubra* abundance at the regional level. While abundance of other grazers (sea urchins, gastropods) was very low, at four sites in the St Helens region the sea urchin *Centrostephanus rodgersii* was abundant in some quadrats. Because this grazer can have a major influence on algal community structure (Fletcher 1987), quadrats where *C. rodgersii* was abundant were excluded from regression analyses.

Analysis of variance (ANOVA) was used to compare *H. rubra* abundance and cover of dominant understory groups in relation to depth for the Dunalley region. *H. rubra* abundance was analysed by a two-way Model III ANOVA, while a three-factor Model III-nested ANOVA was used for cover data. Both analyses included depth (fixed factor, two levels) and site (random factor, five levels). The nested ANOVA included the effect of segment nested within all combinations of depth\*site as a random factor. Before these univariate tests, transformations to stabilize variances were determined from the relationship between group standard deviations and means (Draper & Smith 1981). Transformations were expressed in terms of the untransformed variate, *Y*.

Multivariate patterns in understory community structure among sites were examined using non-metric multidimensional scaling (MDS), an unconstrained ordination method that allows overall patterns and potential differences in relative within-group dispersions to be visualized. The nMDS routine in primer (Clarke 1993) was used for these analyses. A constrained ordination method was also used to visualize multivariate patterns with respect to particular hypotheses. Constrained ordinations were conducted using the canonical analysis of principal coordinates (CAP) method in accordance with Anderson and Willis (2003). This method is a traditional canonical discriminant or canonical correlation analysis (depending on whether the hypothesis involves group differences or continuous predictors) on a subset of coordinate axes from a metric MDS (Anderson & Willis 2003; Willis & Anderson 2003). Separate CAP analyses were conducted to visualize the relationship between multivariate variation in understory community structure and (i) *H. rubra* density; and (ii) spatial variability at the ‘regional’ level. The canonical correlations in each case were tested

using a permutation method, involving 4999 permutations of the raw data. All multivariate analyses were based on Bray–Curtis similarity matrices derived from average percentage cover data at each site. Data were 4th root transformed to reduce the influence of dominant species.

## RESULTS

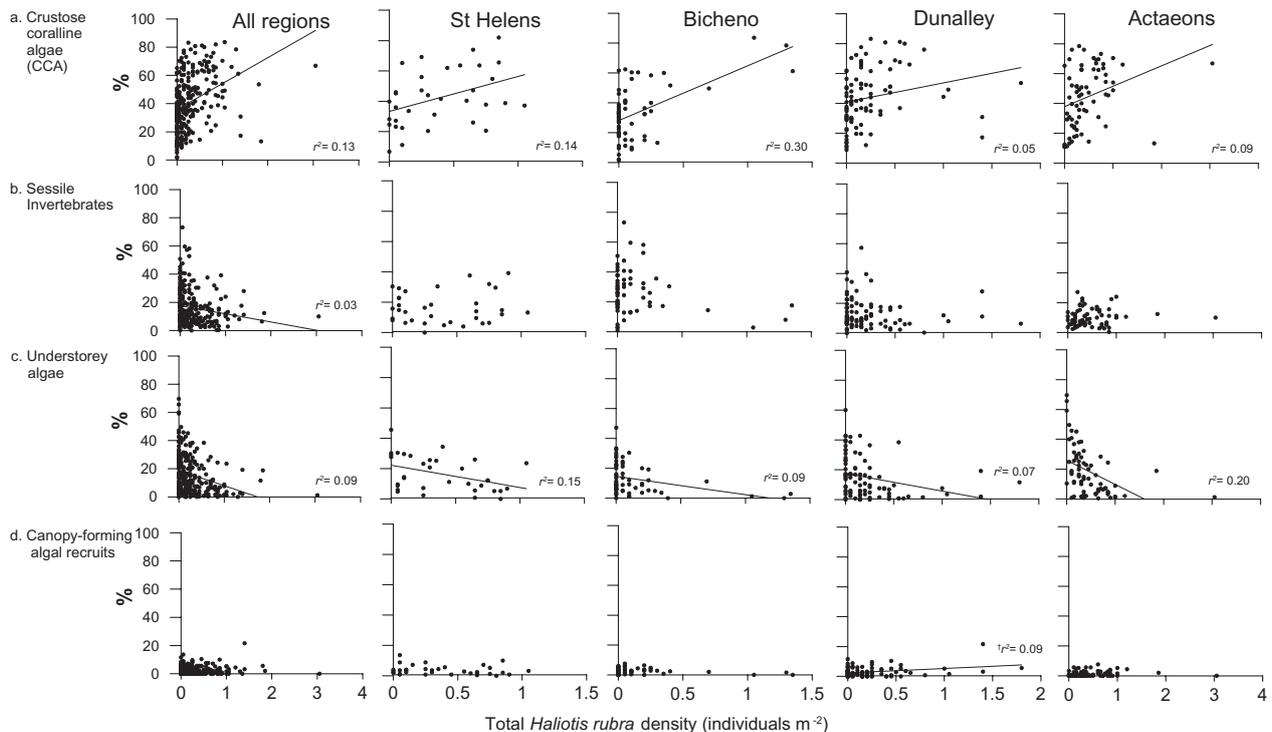
### Correlations between abalone and understory organisms

Significant correlations between total *H. rubra* abundance and understory organisms were observed for data collected at the ‘quadrat’ level, although for some understory groups, the nature of the relationship varied among regions (Fig. 2). Although significant in a number of cases, correlations were typically weak for all understory groups. The strongest correlation observed was between total *H. rubra* abundance and crustose coralline algae at Bicheno, with an  $r^2$  value of just 0.30. Significant associations between total *H. rubra* abundance and particular benthic groups appear to be driven largely by the abundance of emergent *H. rubra*, as observed patterns were consistent between the ‘total abundance’ and ‘emergent’ categories (Appendix SI). Relationships between cryptic *H. rubra* abundance and cover of understory organisms were weak or non-existent (Appendix SII).

Crustose coralline algal cover was positively correlated with total *H. rubra* abundance for all survey regions. A feature of all correlations was the high level of variability and corresponding low  $r^2$  values. While there was a general trend of higher crustose coralline algal cover associated with *H. rubra* density, there were many instances where high crustose coralline algal cover was observed at low *H. rubra* densities.

Sessile invertebrates were negatively correlated with total *H. rubra* abundance when data were pooled across all regions ( $r^2 = 0.03$ ), but when regions were considered in isolation no significant relationships were evident (Fig. 2). In contrast, significant negative correlations were evident in all regions for understory algae. While significant, these correlations were again weak. The ‘triangular’ nature of this relationship suggests that while other factors influence understory algal abundance, *H. rubra* abundance sets an ‘upper limit’ to their abundance (a so-called ‘factor ceiling distribution’; Thompson *et al.* 1996). Cover of understory algae varied substantially when *H. rubra* density was low, but high values were only observed in the presence of low *H. rubra* densities. When *H. rubra* density was high, only low cover of understory algae was observed (Fig. 2).

Spearman rank correlations confirmed the positive correlation detected in the linear regression analyses, with a significant positive correlation between *H. rubra* and crustose coralline algae across all regions



**Fig. 2.** Relationship between total *Haliotis rubra* abundance and understory organisms. Significant regression lines ( $\alpha = 0.05$ ) and corresponding  $r^2$  values are shown. Note different scales on the x-axis. †Relationship influenced by outlier with strong leverage.

**Table 1.** Spearman rank correlations of algal and invertebrate groups, derived from regional-level data

Variable	St Helens ( <i>n</i> = 50)		Bicheno ( <i>n</i> = 60)		Dunalley ( <i>n</i> = 90)		Actaeons ( <i>n</i> = 55)	
	S Rank	<i>P</i>	S Rank	<i>P</i>	S Rank	<i>P</i>	S Rank	<i>P</i>
Encrusting algae								
NCERA	-0.235	0.1004	0.0461	0.7265	0.1901	0.1293	0.1606	0.2414
CCA	0.3525	<b>0.0121</b>	0.3706	<b>0.0036</b>	0.3683	<b>0.0025</b>	0.4836	<b>0.0002</b>
Geniculate coralline algae	-0.0849	0.5577	-0.3005	<b>0.0197</b>	-0.2868	<b>0.0205</b>	0.14	0.308
Foliose understory algae								
<i>Carpoglossum confluens</i>	-0.1189	0.4108	NA	NA	-0.2475	<b>0.0468</b>	-0.0198	0.8861
<i>Carpomitra costata</i>	-0.1475	0.3067	0.1401	0.2858	0.1206	0.3384	-0.1374	0.317
<i>Caulerpa flexilis</i>	-0.1512	0.2947	-0.287	<b>0.0262</b>	-0.1047	0.4066	-0.4569	<b>0.0005</b>
<i>Caulerpa rhizome</i>	NA	NA	-0.1241	0.345	NA	NA	-0.0545	0.6926
<i>Colpomenia</i> spp.	-0.269	0.0589	NA	NA	NA	NA	NA	NA
Filamentous red	-0.1494	0.3004	-0.0232	0.8604	0.2411	<b>0.053</b>	-0.0104	0.9401
Foliose red algae	-0.2254	0.1156	-0.4295	<b>0.0006</b>	-0.2929	<b>0.0179</b>	-0.6188	<b>&lt;0.0001</b>
Filamentous green	NA	NA	-0.2166	0.0964	-0.1346	0.2849	0.276	<b>0.0414</b>
<i>Halopteris</i> spp.	0.2238	0.1183	0.3022	<b>0.019</b>	-0.3975	<b>0.001</b>	NA	NA
Red recruits	-0.0794	0.5836	-0.0722	0.5838	0.2105	0.0924	-0.029	0.8338
<i>Sonderapelta</i> spp.	0.1026	0.4782	0.0835	0.526	-0.3892	<b>0.0014</b>	-0.2632	0.0522
<i>Xiphophora gladiata</i>	NA	NA	-0.0634	0.6301	0.1451	0.2488	-0.2996	<b>0.0263</b>
<i>Zonaria</i> spp.	0.3048	<b>0.0314</b>	0.3162	<b>0.0138</b>	-0.1067	0.3978	0.2277	0.0945
Canopy-forming algal recruits								
<i>Ecklonia radiata</i>	-0.1666	0.2475	-0.1286	0.3275	-0.1558	0.2151	-0.1369	0.319
<i>Cystophora moniliformis</i>	NA	NA	NA	NA	-0.2369	0.0574	NA	NA
<i>Cystophora retroflexa</i>	NA	NA	NA	NA	-0.1341	0.287	0.1031	0.4539
<i>Phyllospora comosa</i>	-0.16	0.2671	0.2922	<b>0.0235</b>	-0.1974	0.115	0.108	0.4326
<i>Sargassum decipiens</i>	NA	NA	NA	NA	-0.1013	0.4219	NA	NA
<i>Sargassum</i> spp. recruit	-0.1847	0.1991	0.0444	0.7362	-0.0148	0.9071	0.0982	0.4755
Invertebrates								
Barnacles	-0.0932	0.5197	-0.1241	0.345	0.1312	0.2976	NA	NA
<i>Bugularia dissimilis</i>	-0.128	0.3759	-0.0434	0.742	-0.3404	<b>0.0055</b>	-0.257	0.0582
Colonial Ascidian	NA	NA	-0.016	0.9032	NA	NA	0.1867	0.1724
Encrusting bryozoa	0.148	0.3049	-0.0586	0.6563	0.0677	0.5922	0.3606	<b>0.0068</b>
Erect sponge	-0.2785	0.0502	0.0465	0.724	-0.1346	0.2849	-0.0644	0.6403
Encrusting mussels	NA	NA	-0.0686	0.6024	NA	NA	NA	NA
Encrusting sponge	0.0917	0.5264	-0.0312	0.8127	-0.0275	0.8279	-0.0953	0.4888
<i>Orthoscuticella phoeniceum</i>	-0.2271	0.1127	-0.0598	0.65	-0.3012	<b>0.0148</b>	-0.0713	0.6051
Solitary Ascidian	0.3083	<b>0.0294</b>	-0.0019	0.9884	0.0005	0.9969	0.265	<b>0.0505</b>

Where taxa were not recorded in a particular region the notation 'NA' applies. Significant *P*-values ( $\alpha = 0.05$ ) are shown in boldface. CCA, crustose coralline algae; NCERA, non-coralline encrusting red algae (includes the algal genera *Peyssonnelia* and *Hildenbrandia*).

(Table 1). Significant correlations were rarely consistent between regions for individual taxa, with the exception of foliose red algae that was negatively correlated with *H. rubra* abundance for three of the four survey regions. Other significant correlations were evident but were only in particular regions (e.g. *Zonaria* spp. was positively correlated with *H. rubra* at St Helens and Bicheno).

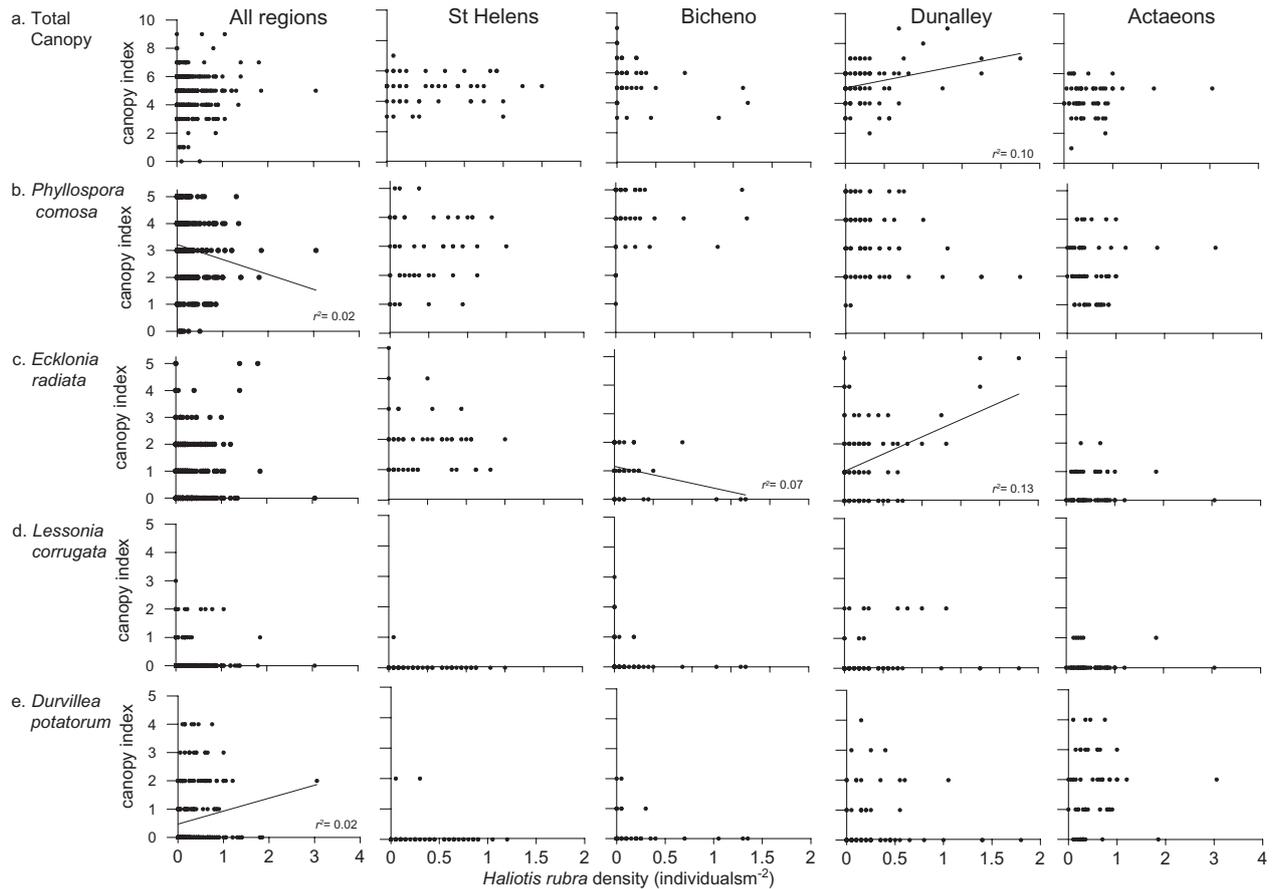
### Correlations between abalone and canopy-forming algae

Very few significant associations were identified between *H. rubra* and the various canopy-forming algal species encountered in the study (Fig. 3). The

associations that were observed were weak and not consistent between regions.

### Influence of depth on abundance of abalone and understory organisms

Important insights into the influence of depth on patterns of *H. rubra* abundance and understory community structure were provided by the Dunalley survey reefs (Fig. 4). Depth-related patterns were site specific, with the exception of the 'canopy-forming algal recruit' category, indicated by a significant Depth\*Site interaction in the ANOVA models (Table 2). For some of the understory groups, differences attributable to depth were evident at the same sites where differences in *H. rubra* abundance were found. For example, crustose



**Fig. 3.** Relationship between total *Haliotis rubra* abundance and canopy-forming algae. Significant regression lines ( $\alpha = 0.05$ ) and corresponding  $r^2$  values are shown. Note different scales on the x-axis.

coralline algal cover was significantly higher in the shallow depth zone at sites s1, s3 and s5. *H. rubra* abundance was also higher for these same sites, although statistically significant differences were only evident for sites s1 and s5. Similar patterns were evident for understory algae. For 'sessile invertebrates' and 'canopy-forming algal recruits' strong depth-related patterns were not apparent. These patterns highlight the potential for confounding when examining correlations between *H. rubra* and benthic community structure. In this particular example, differences in crustose coralline algal abundance among depths could be related to *H. rubra* abundance; however, these differences were clearly confounded by depth and could also be explained by the physical environment that also varies with depth.

### Community-level patterns

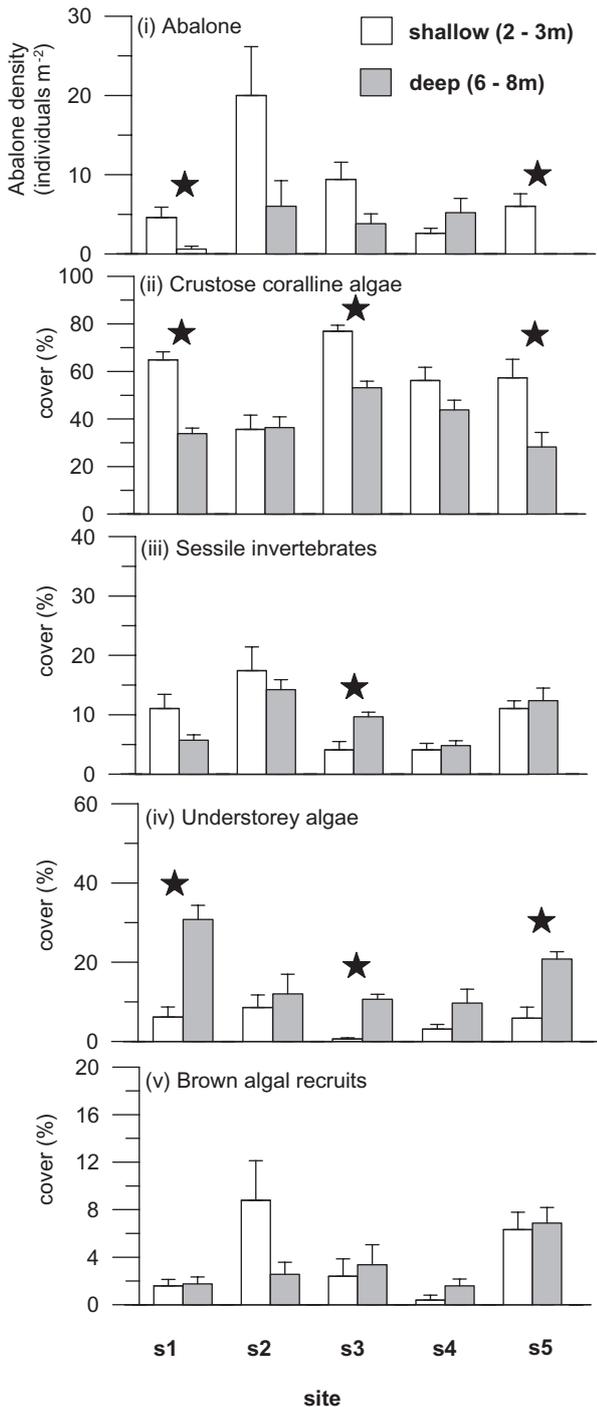
Multidimensional scaling analysis reflected regional differences in understory community structure, with Actaeons sites generally distinct from the three east coast regions (Fig. 5a). The bubble plot (Fig. 5b) also

tended to show sites with high *H. rubra* density forming a distinct group, but this grouping could also be attributable to regional differences in understory community structure. CAP analyses showed a significant correlation between understory assemblage composition and both 'Region' and '*H. rubra* density'; however, regional correlations were much stronger than those attributable to *H. rubra* density (Table 3). The four regions separated clearly in the canonical axis for 'region' (Fig. 6a), shown by the high-squared canonical coefficient. The canonical axis for '*H. rubra* density' showed some clustering of sites consistent with *H. rubra* density as a structuring influence, although there were a number of instances of overlap between sites with contrasting densities (Fig. 6b).

## DISCUSSION

### Evidence for *Haliotis rubra* as a structuring influence on subtidal reef communities

The correlative evidence arising from the present work provides limited evidence for ecosystem change



**Fig. 4.** Influence of depth on patterns of (i) *Haliotis rubra* abundance and (ii–v) understorey cover for the Dunalley region. *H. rubra* abundance represents mean (+SE) abundance across five randomly positioned 20 m<sup>2</sup> quadrats at each site. Cover of understorey organisms represents mean (+SE) percentage cover across quadrats ( $n = 5$ ) determined from five randomly positioned 0.25 m<sup>2</sup> subquadrats within each 20 m<sup>2</sup> quadrat. Symbol (★) indicates site where a significant difference between depths was evident ( $\alpha = 0.05$ ).

associated with *H. rubra* depletion. The most consistent pattern across regions was the existence of a weak positive correlation between total *H. rubra* abundance and crustose coralline algae, and a weak negative correlation between total *H. rubra* abundance and understorey algae. The rare and inconsistent patterns observed between *H. rubra* abundance, other understorey groups (sessile invertebrates and canopy-forming algal recruits) and canopy-forming algae provide further evidence of a weak structuring role. Although multivariate analyses showed a significant correlation with *H. rubra* density, stronger correlations were observed based on regional differences in understorey community structure.

There are a range of possible reasons that may account for the observed weak correlations between *H. rubra* and understorey organisms. *H. rubra* activity may indeed have only a minor influence on understorey community structure. This would be expected if *H. rubra* feed on drift algae and display limited movement patterns around a 'homesite' or 'scar'. While this mode of behaviour explains the limited structuring influence of *H. roei* on algal communities in Western Australia (Scheibling 1994), similar evidence for *H. rubra* is lacking. Although *H. rubra* is thought to be a generalist herbivore, feeding mainly on drift algae (Shepherd 1973), detailed studies incorporating movement and feeding behaviour across broad spatial and temporal scales are vital to better understand ecological interactions between *H. rubra* and benthic communities. Recent work conducted in a sheltered bay on the east coast of Tasmania has shown limited movement by blacklip *H. rubra* (Lansdell 2006), with more than 80% of animals moving less than 30 cm per day. The generality of this recent work requires further investigation.

It remains possible that *H. rubra* activity influences community structure outside the immediate homesite; however, the ability to detect these potential effects will depend on the density and distribution of *H. rubra* and the scale of influence of individual animals. Because of the inherent patchy nature of subtidal reefs at small scales (e.g. Kennelly 1987; Fowler-Walker & Connell 2002) these relatively small-scale effects would have been difficult to detect in the present survey, which was designed to detect 'reef-scale' differences in community structure. Clearly the scale of any potential influence of individual *H. rubra* is a question that must be addressed in future research. If *H. rubra* activity can be shown to structure understorey communities, the underlying mechanisms require further investigation. While the correlations observed in the present study are consistent with grazing effects (i.e. positive correlations between *H. rubra* and crustose coralline algae, negative correlation with understorey algae), the structuring mechanism of *H. rubra* is not necessarily restricted to grazing, as mucus produc-

**Table 2.** Influence of depth on (a) abundance of understorey organisms and (b) *Haliotis rubra*

	Source of variation							
	Depth		Site		Depth*site		Segment (Depth*site)	
	<i>F</i> (d.f. = 1, 4)	<i>P</i>	<i>F</i> (d.f. = 4, 40)	<i>P</i>	<i>F</i> (d.f. = 4, 40)	<i>P</i>	<i>F</i> (d.f. = 40, 200)	<i>P</i>
a. Benthic groups								
Crustose coralline algae (no transformation)	10.31	<b>0.033</b>	9.94	<b>&lt;0.001</b>	3.79	<b>0.011</b>	2.10	<b>&lt;0.001</b>
Sessile invertebrates ( $\sqrt{Y}$ )	0.01	0.917	12.32	<b>&lt;0.001</b>	4.43	<b>0.0047</b>	1.18	0.2331
Understorey algae [ $\ln(Y+0.1)$ ]	13.93	<b>0.020</b>	4.08	<b>0.007</b>	2.64	<b>0.048</b>	2.22	<b>&lt;0.001</b>
Canopy-forming algal recruits <sup>†</sup> [ $\ln(Y+0.1)$ ]	0.70	0.407	3.13	0.148	2.26	0.079	1.91	<b>0.002</b>
b. Abalone								
Abalone [ $\ln(Y+0.1)$ ]	5.98	0.071	5.06	<b>0.002</b>	3.93	<b>0.009</b>		

Results describe the overall ANOVA examining the effect of different depths (2–3 m vs. 6–8 m) on understorey and *Haliotis rubra* abundance. Significant *P*-values ( $\alpha = 0.05$ ) are shown in boldface. Transformations are expressed in terms of the untransformed variable, *Y*. <sup>†</sup>Transformation improved data structure considerably but did not achieve normality and homoscedasticity.

**Table 3.** Results of canonical analysis of principal coordinates examining the effects of 'Region' and *Haliotis rubra* density on understorey assemblages

Factor	<i>m</i>	%Var	Allocation success (%)				Total	$\delta^2$	<i>P</i>
			Group 1	Group 2	Group 3	Group 4			
Region	9	85.3	90.9 (Actaeons)	61.5 (Dunalley)	83.3 (Bicheno)	100.0 (St Helens)	82.6	0.90	0.0002
<i>H. rubra</i> density	12	95.1						0.55	0.003

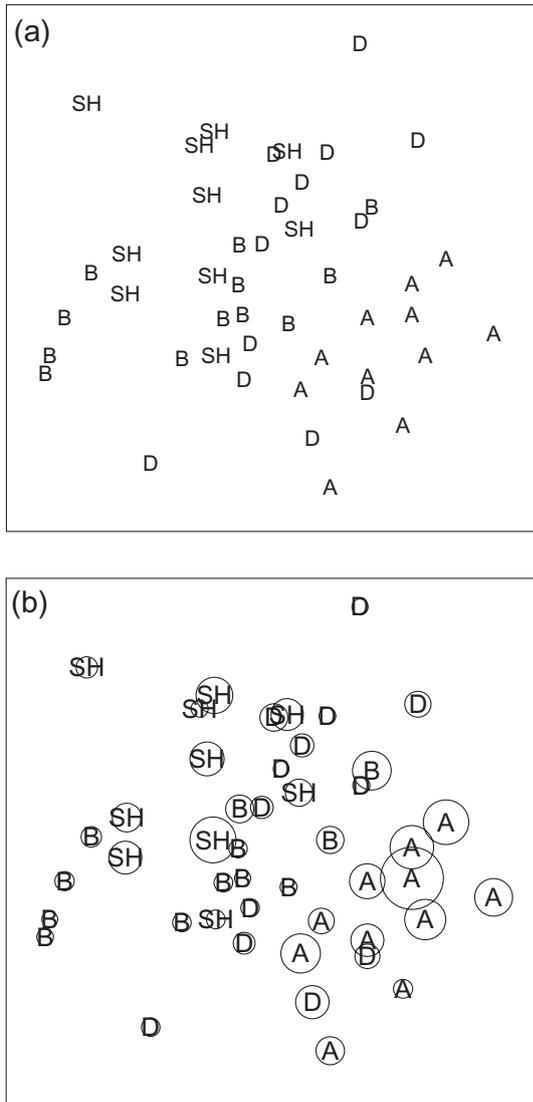
%Var, percentage variation explained by the first *m* principal coordinate axes; allocation success, percentage of points correctly allocated into each group;  $\delta^2$ , squared canonical correlation.

tion (Johnson & Strathmann 1989; Searcy-Bernal *et al.* 1992) and bulldozing (Dayton 1971; Hawkins 1983) by grazing molluscs also have the potential to modify benthic communities.

Environmental and habitat conditions are also a major consideration when interpreting the results of the current study. The current survey focused on the 6–8 m depth range on exposed coastlines because of its relevance to the *H. rubra* fishery. The possibility exists that *H. rubra* may play a more important structuring role in habitats that were not considered in the present study. For example, stronger correlations might exist for deeper water *H. rubra* populations, for sheltered sites, or in other biogeographic regions. Whether or not *H. rubra* activity influences understorey community structure, the present study clearly shows that factors other than *H. rubra* grazing contribute to variation in benthic community structure.

### Factors effecting abundance of understorey organisms

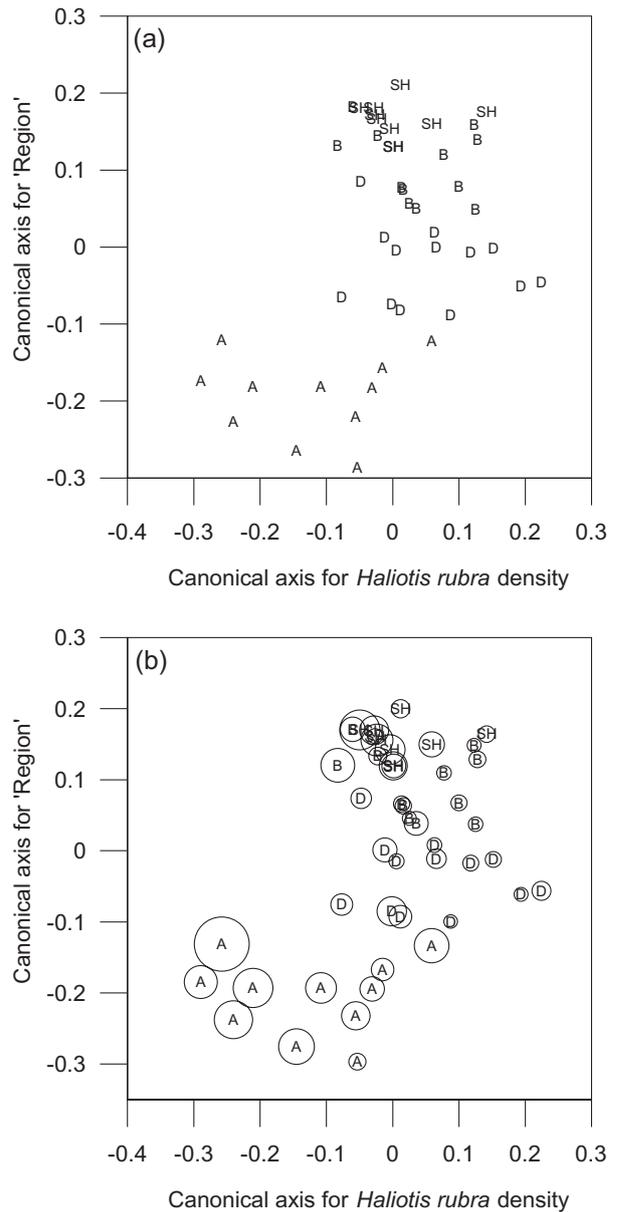
A range of factors have been reported to influence the distribution and abundance of understorey organisms. Herbivory is most commonly identified as the source of disturbance that maintains dominance of encrusting algal communities, preventing fouling by turf-forming algae (Steneck 1986). In benthic marine systems, most studies of plant–herbivore interactions have focused on the grazing influence of sea urchins, which can have a dramatic impact on benthic community structure (e.g. Chapman 1981; Johnson & Mann 1993; Scheibling *et al.* 1999; Bulleri *et al.* 2002; Tuya *et al.* 2004). In the present study density of grazers other than *H. rubra* were generally very low and could not account for the high cover of crustose coralline algae that was frequently observed in the absence of high *H. rubra* densities.



**Fig. 5.** Multidimensional scaling (MDS) plots based on mean understorey community composition at each site (4th root transformation, Bray–Curtis similarity; stress = 0.2). (a) MDS indicating individual sites; (b) MDS indicating individual sites superimposed with a bubble plot representing average *Haliotis rubra* density at each site. A, Actaeons; B, Bicheno; D, Dunalley; SH, St Helens.

Canopy-forming algae can also influence understorey community structure through several physical mechanisms including shading, prevention of sediment accumulation and the scour effect associated with algal fronds abrading the substratum (Kennelly 1987; Melville & Connell 2001). Each of these mechanisms can maintain dominance of crustose coralline algae by inhibiting the establishment of foliose algae and invertebrates. Both the canopy species composition (Irving *et al.* 2004; Irving & Connell 2006) and plant density (Kendrick *et al.* 1999) have also been shown to influence understorey community structure.

doi:10.1111/j.1442-9993.2009.02088.x



**Fig. 6.** (a) Two-dimensional scatter plot of the canonical axes for *Haliotis rubra* density and 'Region', based on understorey community composition at each site (4th root transformation, Bray–Curtis similarity). (b) Canonical axes plot superimposed with a bubble plot representing average *H. rubra* density at each site. A, Actaeons; B, Bicheno; D, Dunalley; SH, St Helens.

In the absence of a macroalgal canopy and grazers, some authors have shown that crustose coralline algae are capable of maintaining dominance by sloughing and shedding epithallial cells (Breitburg 1984; Johnson & Mann 1986), or through production of allelopathic substances (Kim *et al.* 2004).

Recent advances in understanding understorey community structure across temperate Australia have

involved understory communities occurring beneath a canopy of the common kelp *Ecklonia radiata* (Fowler-Walker & Connell 2002; Connell 2003; Irving *et al.* 2004). This work has shown that inside kelp forests, the presence of the canopy may be more important than grazers in facilitating maintenance of crustose coralline algal dominance. For example, beneath kelp canopies cover of crustose coralline algae was found to be high (>75%) on Western Australian and South Australian reefs, despite the virtual absence of grazers, while crustose coralline algal cover remained low (<10%) outside kelp canopies (Fowler-Walker & Connell 2002). The present study was not designed to contrast community structure inside and outside canopies so it is difficult to make direct comparisons with the aforementioned studies. Nonetheless, canopy-forming algal cover was generally high across all sites in the present survey (mean cover > 75%), so if the same processes hold in Tasmanian waters the apparent weak influence of *H. rubra* on understory communities should not be an unexpected result.

#### Limitations of present work and future directions

There are significant limitations when using correlative studies to infer the impact of *H. rubra* removal on ecosystem structure and function. Confounding factors represent a serious issue, as differences in understory communities attributed to differences in *H. rubra* density could also be caused by other factors (e.g. depth, exposure, regional differences in understory communities). For example, the Actaeons region had a distinct understory community but also the highest *H. rubra* density so the influence of *H. rubra* is confounded by 'region' in this particular situation. Similarly, effects of *H. rubra* on understory communities were clearly confounded by depth for the Dunalley region.

Clearly the only way to show causality is through manipulation of *H. rubra* densities. Considerations for an experimental approach to understanding effects of *H. rubra* fishing (e.g. plot size, target densities, statistical power) have been discussed previously (see Jenkins 2004); however, there remains no published work examining manipulation of *H. rubra* densities and subsequent effects on benthic communities. Experimental studies involving manipulation of *H. rubra* densities are currently underway in Tasmania and Victoria and these will enable a greater understanding of ecosystem effects on benthic community structure. The ability to generalize from these studies will be a significant issue; however, as the spatial distribution of *H. rubra* on the reef provides exceptional challenges in this regard. For example,

adult *H. rubra* populations along the Victorian coast are typically associated with crevices and caves (McShane 1999), whereas adult *H. rubra* populations on the east coast of Tasmania are generally associated with exposed reef surfaces (e.g. exposed surface of boulders). Similar differences in *H. rubra* distribution can be evident over much smaller scales (J. P. Valentine, pers. obs., 2006). The inherent variation in abalone abundance that occurs at multiple spatial scales presents major challenges when quantifying *H. rubra* abundance (e.g. McShane 1994; Officer *et al.* 2001); these same challenges also need to be considered when examining the effects of *H. rubra* depletion in future experimental studies.

#### Conclusions

The lack of a strong consistent pattern between communities with contrasting *H. rubra* densities suggests that phase shifts in benthic community structure are unlikely following depletion of *H. rubra* stocks. While there was a weak positive correlation between total *H. rubra* abundance and crustose coralline algae, there was no evidence that abalone removal results in a major shift towards an ecosystem state with low crustose coralline algal cover.

The correlative evidence indicates that herbivores are not a major structuring force on the reefs studied, suggesting that bottom-up forces may be more important than top-down forces in controlling marine communities in the study region. Previous work has shown that human influences on habitat-forming macroalgae vary depending on latitude, the primary producers involved, and ecosystem productivity (Burkpile & Hay 2006). While examination of the influence of ecosystem productivity on benthic community structure was not considered in this study, bottom-up forces in temperate systems are typically more important in controlling communities in high productivity systems (Burkpile & Hay 2006). Thus, the apparently weak effects of *H. rubra* are likely to reflect the more dominant role of bottom-up forces in structuring communities in the study region.

While the results from this study may be of some relief to managers of subtidal reefs in the region, a number of questions must be addressed to adequately understand impacts of *H. rubra* depletion. Experimental studies are clearly required in habitats with varying physical characteristics and the scale of influence of individual *H. rubra* must also be critically examined. Understanding the influence *H. rubra* removal across varying environmental gradients is also a particularly important question, given that the relative influence of herbivores as a structuring influence on marine benthic communities has

also been shown to vary according to environmental gradients, such as wave exposure (Shears *et al.* 2008). A major challenge for management will be to identify environmental and physical characteristics that can be used to identify reef systems that may be at most risk of ecosystem change following depletion of *H. rubra* stocks.

## ACKNOWLEDGEMENTS

This research was supported by a Fisheries Research and Development Corporation grant. We thank Dane Jones, Justin Hulls and Chris Jarvis for assistance with diving operations.

## REFERENCES

- Anderson M. J. & Willis T. J. (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology* **84**, 511–25.
- Bellwood D. R., Hughes T. P., Folke C. & Nystroem M. (2004) Confronting the coral reef crisis. *Nature* **429**, 827–33.
- Breitburg D. L. (1984) Residual effects of grazing: inhibition of competitor recruitment by encrusting coralline algae. *Ecology* **65**, 1136–43.
- Bulleri F., Bertocci I. & Micheli F. (2002) Interplay of encrusting coralline algae and sea urchins in maintaining alternative habitats. *Mar. Ecol. Prog. Ser.* **243**, 101–9.
- Burkepile D. E. & Hay M. E. (2006) Herbivore vs. nutrient control of marine primary producers: context-dependent effects. *Ecology* **87**, 3128–39.
- Chapman A. R. O. (1981) Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St. Margaret's Bay, eastern Canada. *Mar. Biol.* **62**, 307–11.
- Clarke K. R. (1993) Nonparametric multivariate analyses of change in community structure. *Aust. J. Ecol.* **18**, 117–43.
- Collie J. S., Richardson K. & Steele J. H. (2004) Regime shifts: can theory illuminate the mechanisms? *Prog. Oceanogr.* **60**, 355–85.
- Connell S. D. (2003) The monopolization of understory habitat by subtidal encrusting coralline algae: a test of the combined effects of canopy-mediated light and sedimentation. *Mar. Biol.* **142**, 1065–71.
- Daume S., Brand-Gardner S. & Woelkerling W. J. (1999) Settlement of abalone larvae (*Haliotis laevigata*) in response to non-geniculate coralline red algae (Corallinales, Rhodophyta). *J. Exp. Mar. Biol. Ecol.* **234**, 125–43.
- Dayton P. K. (1971) Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* **31**, 351–89.
- Draper N. & Smith H. (1981) *Applied Regression Analysis*. Wiley, New York.
- Fletcher W. J. (1987) Interactions among subtidal Australian sea urchins, gastropods, and algae: effects of experimental removals. *Ecol. Monogr.* **57**, 89–109.
- Folke C., Carpenter S., Walker B. *et al.* (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Syst.* **35**, 557–81.
- Fowler-Walker M. J. & Connell S. D. (2002) Opposing states of subtidal habitat across temperate Australia: consistency and predictability in kelp canopy-benthic associations. *Mar. Ecol. Prog. Ser.* **240**, 49–56.
- Hawkins S. J. (1983) Interactions of *Patella* and macroalgae with settling *Semibalanus balanoides* (L.). *J. Exp. Mar. Biol. Ecol.* **71**, 55–72.
- Hughes T. P. (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* **265**, 1547–51.
- Hughes T. P., Bellwood D. R., Folke C., Steneck R. S. & Wilson J. (2005) New paradigms for supporting the resilience of marine ecosystems. *Trends Ecol. Evol.* **20**, 380–6.
- Irving A. D. & Connell S. D. (2006) Physical disturbance by kelp abrades erect algae from the understory. *Mar. Ecol. Prog. Ser.* **324**, 127–37.
- Irving A. D., Connell S. D. & Gillanders B. M. (2004) Local complexity in patterns of canopy-benthos associations produces regional patterns across temperate Australasia. *Mar. Biol.* **144**, 361–8.
- Jenkins G. P. (2004) The ecosystem effects of abalone fishing: a review. *Mar. Freshwater Res.* **55**, 545–52.
- Jennings S. & Kaiser M. J. (1998) The effects of fishing on marine ecosystems. *Adv. Mar. Biol.* **34**, 201–352.
- Johnson C. J. & Mann K. H. (1993) Rapid succession in subtidal understory seaweeds during recovery from overgrazing by sea urchins in eastern Canada. *Bot. Mar.* **36**, 63–77.
- Johnson C. R. & Mann K. H. (1986) The crustose coralline alga, *Phymatolithon* Foslie, inhibits the overgrowth of seaweeds without relying on herbivores. *J. Exp. Mar. Biol. Ecol.* **96**, 127–46.
- Johnson L. E. & Strathmann R. R. (1989) Settling barnacle larvae avoid substrata previously occupied by a mobile predator. *J. Exp. Mar. Biol. Ecol.* **128**, 87–103.
- Kendrick G. A., Lavery P. S. & Phillips J. C. (1999) Influence of *Ecklonia radiata* kelp canopy on structure of macro-algal assemblages in Marmion Lagoon, Western Australia. *Hydrobiologia* **399**, 275–83.
- Kennelly S. J. (1987) Physical disturbances in an Australian kelp community. II. Effects on understory due to differences in kelp cover. *Mar. Ecol. Prog. Ser.* **40**, 155–65.
- Kim M., Choi J., Kang S. *et al.* (2004) Multiple allelopathic activity of the crustose coralline alga *Lithophyllum yessoense* against settlement and germination of seaweed spores. *J. Appl. Phycol.* **16**, 175–9.
- Lansdell M. J. (2006) *Movement of blacklip abalone (Haliotis rubra Leach) at small temporal and spatial scales – implications for fisheries management* (Honours Thesis). University of Tasmania, Hobart.
- McShane P. E. (1994) Estimating the abundance of abalone (*Haliotis* spp.) stocks – examples from Victoria and southern New Zealand. *Fish. Res.* **19**, 379–94.
- McShane P. E. (1999) Blacklip abalone. In: *Under Southern Seas. The Ecology of Australia's Rocky Reefs* (ed. N. L. Andrew) pp. 72–7. UNSW Press, Sydney.
- Melville A. J. & Connell S. D. (2001) Experimental effects of kelp canopies on subtidal coralline algae. *Austral Ecol.* **26**, 102–8.
- Miner C. M., Altstatt J. M., Raimondi P. T. & Minchinton T. E. (2006) Recruitment failure and shifts in community

- structure following mass mortality limit recovery prospects of black abalone. *Mar. Ecol. Prog. Ser.* **327**, 107–17.
- Officer R. A., Haddon M. & Gorfine H. K. (2001) Distance-based abundance estimation for abalone. *J. Shellfish Res.* **20**, 781–6.
- Pikitch E. K., Santora C., Babcock E. A. *et al.* (2004) Ecosystem-based fishery management. *Science* **305**, 346–7.
- Pinnegar J. K., Polunin N. V. C., Francour P. *et al.* (2000) Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Environ. Conserv.* **27**, 179–200.
- Saito K. (1981) The appearance and growth of 0-year-old Ezo Abalone. *Bull. Jap. Soc. Sci. Fish.* **47**, 1393–400.
- Scheibling R. E. (1994) Molluscan grazing and macroalgal zonation on a rocky intertidal platform at Perth, Western Australia. *Aust. J. Ecol.* **19**, 141–9.
- Scheibling R. E., Hennigar A. W. & Balch T. (1999) Destructive grazing, epiphytism, and disease: the dynamics of sea urchin – kelp interactions in Nova Scotia. *Can. J. Fish. Aquat. Sci.* **56**, 2300–14.
- Schröda A., Persson L. & De Roos A. M. (2005) Direct experimental evidence for alternative stable states: a review. *Oikos* **110**, 3–19.
- Searcy-Bernal R., Salas-Garza A. E., Flores-Aguilar R. A. & Hinojosa-Rivera P. R. (1992) Simultaneous comparison of methods for settlement and metamorphosis induction in the red abalone (*Haliotis rufescens*). *Aquaculture* **105**, 241–50.
- Shears N. T., Babcock R. C. & Salomon A. K. (2008) Context-dependent effects of fishing: variation in trophic cascades across environmental gradients. *Ecol. Appl.* **18**, 1860–73.
- Shepherd S. A. (1973) Studies on southern Australian abalone (genus *Haliotis*) I. Ecology of five sympatric species. *Aust. J. Mar. Freshwater Res.* **24**, 217–57.
- Shepherd S. A. & Turner J. A. (1985) Studies on southern Australian abalone (genus *Haliotis*) VI. Habitat preference, abundance and predators of juveniles. *J. Exp. Mar. Biol. Ecol.* **93**, 285–98.
- Shepherd S. A., Preece P. A. & White R. G. (2000) Tired nature's sweet restorer? Ecology of abalone (*Haliotis* spp.) stock enhancement in Australia. In: *Workshop on Rebuilding Abalone Stocks in British Columbia* (ed. A. Campbell) pp. 84–97. NRC Canada, Nanaimo.
- Steneck R. (1986) The ecology of coralline algal crusts: convergent patterns and adaptive strategies. *Annu. Rev. Ecol. Syst.* **17**, 273–303.
- Tarbath D. B., Mundy C. N. & Haddon M. (2004) *Tasmanian abalone fishery 2003*. Tasmanian Aquaculture and Fisheries Institute Technical Report Series, pp. 1–108.
- Tarr R. J. Q., Williams P. V. G. & Mackenzie A. J. (1996) Abalone, sea urchins and rock lobster: a possible ecological shift that may affect traditional fisheries. *S. Afr. J. Mar. Sci.* **17**, 319–23.
- Thompson J. D., Weiblen G., Thompson B. A., Alfaro S. & Legendre P. (1996) Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. *Ecology* **77**, 1698–715.
- Tuya F., Boyra A., Sanchez-Jerez P., Barbera C. & Haroun R. (2004) Can one species determine the structure of the benthic community on a temperate rocky reef? The case of the long-spined sea-urchin *Diadema antillarum* (Echinodermata: Echinoidea) in the eastern Atlantic. *Hydrobiologia* **519**, 211–14.
- Willis T. J. & Anderson M. J. (2003) Structure of cryptic reef fish assemblages: relationships with habitat characteristics and predator density. *Mar. Ecol. Prog. Ser.* **257**, 209–21.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

- Appendix SI.** Relationship between emergent *Haliotis rubra* abundance and understorey organisms. Significant regression lines ( $\alpha = 0.05$ ) and corresponding  $r^2$  values are shown. Note different scales on the  $x$ -axis
- Appendix SII.** Relationship between cryptic *Haliotis rubra* abundance and understorey organisms. Significant regression lines ( $\alpha = 0.05$ ) and corresponding  $r^2$  values are shown. Note different scales on the  $x$ -axis.
- †Relationship strongly influenced by outlier with strong leverage