

Long-term trends in invertebrate–habitat relationships under protected and fished conditions

Timothy J. Alexander · Craig R. Johnson ·
Malcolm Haddon · Neville S. Barrett · Graham J. Edgar

Received: 2 March 2014 / Accepted: 14 May 2014 / Published online: 27 May 2014
© Springer-Verlag Berlin Heidelberg 2014

Abstract Few studies examine the long-term effects of changing predator size and abundance on the habitat associations of resident organisms despite that this knowledge is critical to understand the ecosystem effects of fishing. Marine reserves offer the opportunity to determine ecosystem-level effects of manipulated predator densities, while parallel monitoring of adjacent fished areas allows separating these effects from regional-scale change. Relationships between two measures of benthic habitat structure (reef architecture and topographic complexity) and key invertebrate species were followed over 17 years at fished and protected subtidal rocky reefs associated with two southern Australian marine reserves. Two commercially harvested species, the southern rock lobster (*Jasus edwardsii*) and blacklip abalone (*Haliotis rubra*) were initially weakly associated with habitat structure across all fished and

protected sites. The strength of association with habitat for both species increased markedly at protected sites 2 years after marine reserve declaration, and then gradually weakened over subsequent years. The increasing size of rock lobster within reserves apparently reduced their dependency on reef shelters as refuges from predation. Rising predation by fish and rock lobster in the reserves corresponded with weakening invertebrate–habitat relationships for *H. rubra* and sea urchins (*Heliocidaris erythrogramma*). These results emphasise that animal–habitat relationships are not necessarily stable through time and highlight the value of marine reserves as reference sites. Our work shows that fishery closures to enhance populations of commercially important and keystone species should be in areas with a range of habitat features to accommodate shifting ecological requirements with ontogenesis.

Communicated by F. Bulleri.

T. J. Alexander (✉) · C. R. Johnson · N. S. Barrett · G. J. Edgar
Institute of Marine and Antarctic Studies, University of Tasmania,
Private Bay 49, Tasmania 7001, Australia
e-mail: tjalexander001@gmail.com

T. J. Alexander
Division of Aquatic Ecology and Evolution, Institute of Ecology
and Evolution, University of Bern, Baltzerstrasse 6, 3012 Bern,
Switzerland

T. J. Alexander
Department of Fish Ecology and Evolution, Centre of Ecology,
Evolution and Biogeochemistry, EAWAG Swiss Federal
Institute of Aquatic Science and Technology, Seestrasse 79,
6047 Kastanienbaum, Switzerland

M. Haddon
CSIRO Marine and Atmospheric Research, Castray Esplanade,
Hobart Tasmania 7000, Australia

Introduction

Ecological theory suggests that an increase in predation pressure will strengthen the relationship between habitat structure and prey for species that utilise physical refuges to avoid predators (see references in Sih et al. 1985; Anderson 2001). This pattern can be caused by a behavioural response whereby prey species seek or remain in refuges in the presence of elevated predation risk (Parker and Shulman 1986; Shears and Babcock 2002; Pederson et al. 2008), or by differential predation success where prey animals are more readily removed from areas that lack physical complexity (Connell and Jones 1991). This leaves only individuals associated with structural features or refuges that are either inaccessible or where the time and energy required to access and capture them is not worthwhile from the predator's perspective. The expression of this pattern

can depend on whether the prey species possess supplementary anti-predation mechanisms (e.g. spines in sea urchins), and the availability of appropriately scaled reef features in the local region (Eggleston et al. 1997).

In subtidal reef habitat with high predation pressure, scaling between animal body size and available reef shelter can influence both the abundance and size structure of prey species (Wahle and Steneck 1992; Beck 1995). For example, the sea urchin *Paracentrotus lividus* exhibits crevice dwelling behaviour in response to intense fish predation in a Mediterranean marine reserve, with small urchins most able to benefit from naturally available refuges resulting in higher numbers of smaller animals at protected sites (Sala and Zabala 1996). Similarly, while predation by rock lobsters was most intense on the smallest size class of tethered urchins in New Zealand, there was no difference in the density of cryptic juvenile urchins between reserve and fished sites (Shears and Babcock 2002), suggesting that predation on urchins of this size is reduced when they are permitted to seek shelter (Pederson and Johnson 2006). Hereu et al. (2005) similarly identified that predation on sea urchins decreased with greater structural complexity, although the benefit provided by structure decreased with increasing size of the sea urchin.

Two structural features of a reef surface that influence the structure of subtidal communities are topographic complexity (spatial variability in the height of the reef surface) and substratum architecture (presence/absence or density of specific architectural features of the reef). Complexity in the topography of the reef surface is likely to influence organisation of the species assemblage through processes such as shading (Adams 2001; Drolet et al. 2004a; Bernaford and Vasquez 2008), hydrodynamics (McShane et al. 1988; Koehl 2007) or through provision of transient refuges where the complexity of the reef surface can limit the visual range of hunting predators (Caley and St John 1996). Measuring substratum architecture involves developing an explicit definition of a reef feature (e.g. hole, crevice and overhang) that is expected to reduce the probability of success of a predatory attack (permanent refuges; sensu Caley and St John 1996). Given the diversity of predatory attack strategies and prey defence mechanisms, it is neither possible nor sensible to derive a single definition of 'architecture' that applies to all predator–prey interactions in an ecosystem, let alone between systems; however, some consistencies are evident. For example, a reef feature such as a thin crevice (deeper than it is wide) can shelter juvenile abalone (Shepherd 1986), shrimp (Caillaux and Stotz 2003) or the soft body of an ophiuroid (Drolet et al. 2004b). Identification and enumeration of these features can help to describe and predict spatial variation in the abundance of some benthic marine species (Roberts and Ormond 1987; Friedlander and Parrish 1998; Alexander et al. 2009).

Establishment of marine reserves can be regarded as large-scale manipulative experiments, particularly for site-attached species, allowing investigation of the impacts of natural and anthropogenic predation on species–habitat relationships and community structure. Commercial fisheries often target higher carnivores (Pauly et al. 1998), and consequently, these species most commonly exhibit the greatest benefit from protection within no-take marine reserves (Babcock et al. 1999; Edgar and Barrett 1999; Guidetti 2006). Indirect effects of fishing/protection can cause trophic cascades as a result of increased predation in marine reserves (Pinnegar et al. 2000), although the expression of these effects varies with local physical conditions such as exposure (Micheli et al. 2005) and habitat (Garcia-Charton et al. 2000). The presence of reef shelter can moderate the effects of fish predation (Eggleston et al. 1997; Caillaux and Stotz 2003; Hereu et al. 2005), and a secondary influence of marine reserves on nontarget invertebrate species is now widely accepted (McClanahan and Shafir 1990; Sala and Zabala 1996; Shears and Babcock 2002; Guidetti 2006); however, the interacting expression of these patterns for invertebrates over long time periods has not been documented.

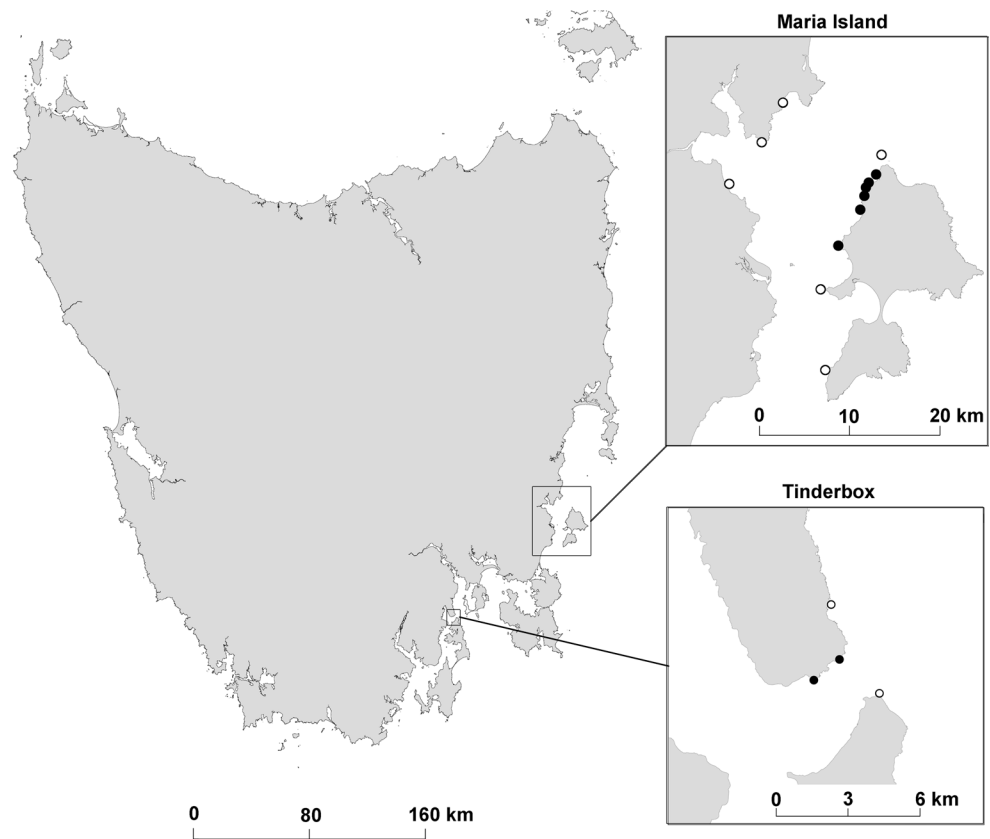
This study examines relationships between reef habitat structure and key macroinvertebrate species through time at protected and fished sites. We aim to determine whether the changing community structure resulting from protection from fishing alters habitat associations of commercially valuable and abundant invertebrate taxa. Abundances of southern rock lobster *Jasus edwardsii*, blacklip abalone *Haliotis rubra* and the purple sea urchin *Heliocidaris erythrogramma* were obtained from a long-term (17 years) ecological monitoring programme at two marine reserves in south-eastern Tasmania, Australia. Data collected at adjacent areas exposed to fishing pressure allowed separating the effects of the marine reserve from regional fluctuations such as strong recruitment years (Booth et al. 2001) or regional ocean temperature change (Ling et al. 2009; Johnson et al. 2011).

Methods

Study region

Our study focused on two no-take marine reserves located on the east and south-east coast of Tasmania, Australia (Fig. 1). Maria Island and Tinderbox marine reserves were declared in September 1991 but were not effectively enforced for the first 12 months, and some fishing probably occurred during this period (Edgar and Barrett 1997). Since establishment, biomass of large fishes has increased by an order of magnitude in these reserve sites (Edgar et al.

Fig. 1 Location of study sites in Tasmania, southern Australia. Site markers with *solid circles* were located within reserves; *open circles* indicate fished sites



2009), including a 100-fold increase in abundance of the carnivorous fish species bastard trumpeter *Latridopsis forsteri* during the first 6 years, and an increase in mean size of blue-throated wrasse *Notolabrus tetricus* (Edgar and Barrett 1999). *N. tetricus* along with the purple wrasse *Notolabrus fucicola* feeds on juveniles of the commercially important *J. edwardsii* (Mills et al. 2008) and abalone (Shepherd and Clarkson 2001), among other invertebrates (Metcalf et al. 2008). *J. edwardsii* is the dominant benthic predator on Tasmanian rocky reefs (Pederson and Johnson 2006; Ling et al. 2009) and has greatly increased in number and size in Tasmanian marine reserves (Barrett et al. 2009; Edgar et al. 2009). Increased predation, particularly by lobsters, has apparently affected herbivorous invertebrates, altering the behaviour, abundance and size structure of *H. rubra* and *H. erythrogramma* (Johnson et al. 2004; Pederson and Johnson 2006; Pederson et al. 2008; Barrett et al. 2009).

Mobile invertebrates

Populations of mobile invertebrates were censused annually in autumn at 16 fixed-position sites in and around Maria Island and Tinderbox marine reserves between 1992 and 2008 (excluding 1998 and 2003), as described by Edgar and Barrett (1997). Six sites were located within

the Maria Island marine reserve and two sites in the Tinderbox marine reserve. Data from the two reserves were considered together on the basis that Barrett et al. (2009) reported similar magnitude of changes in the abundance of rock lobster, abalone and sea urchins between the two marine reserves since protection from fishing. Reef structure measurements were also similar between the marine reserves. Surveyed sites were distributed haphazardly ca. 1 km apart across both reserves. An equivalent number of ‘control’ sites open to harvesting and in close proximity to the protected areas were also monitored. The abundance of noncryptic mobile invertebrates with a maximum dimension >20 mm was counted in a 1 × 200 m transect along the 5-m-depth contour at each site. All animals observed within cracks and crevices on the transect were counted; however, there was no attempt to overturn boulders.

Three species were selected for detailed investigation. The sea urchin *H. erythrogramma* possesses functional importance as a dominant herbivore on the east coast of Tasmanian (Sanderson et al. 1996), with the ability to create small sea urchin barrens on sheltered and semi-sheltered reefs (Johnson et al. 2004; Pederson and Johnson 2008). The species is the basis of a small fishery in the region (DEH 2005). The southern rock lobster *J. edwardsii* and blacklip abalone *H. rubra* are the two most valuable wild-caught species in Tasmania, generating fisheries

valued in 2010–11 at \$60 and \$97 million Australian dollars, respectively (Skirtun et al. 2012).

Reef structure measurements

Two descriptors of rocky reef habitat structure, topographic complexity and reef architecture, were measured at all long-term monitoring sites. Topographic complexity was calculated on a profile of consecutive water depth measurements using a dive computer under calm sea-state conditions at 1 m intervals along the 200 m of reef investigated at each site. Topographic complexity was calculated as the sum of the squared differences in depth between consecutive observations along a transect, with the square root of the sum total taken to linearise the final values. This metric was introduced by McCormick (1994) in a study where it differentiated between schematic profiles and displayed the highest number of significant correlations with fish species amongst nine metrics tested. The advantage of this measurement over the conceptually similar, and more commonly used, chain-and-tape rugosity measure is that it incorporates information on the spatial arrangement of substratum heights (McCormick 1994), with the squared operator giving particular emphasis to large height changes over a short horizontal distance. This has ecological relevance as many reef species tend to aggregate around large ledges and drop-offs (Leum and Choat 1980), features that are often associated with deeply undercut horizontal caves on granite and sandstone reefs around Tasmania (TJA, pers. obs.).

Measurement of reef architecture involved counting the density small reef features presumed to provide refuge from predation for vulnerable species (see methods in Alexander et al. 2009). Briefly, reef features were considered to comprise a refuge where (1) three planes of the substratum meet with at least one of these planes forming an angle of $<90^\circ$; (2) two planes of the substratum meet at an angle of 45° or less; and (3) the refuge must be deeper than the minimum dimension of its entrance. Small refuges are features with the minimum dimension of their aperture between 1 and 5 cm. Refuge counts used in the analysis were averaged from eight 1×5 m surveys randomly distributed within each 200 m site. This measure is linked to the combined abundance of the benthic invertebrate assemblage in this region (Alexander et al. 2009).

Statistical analysis

Analyses aimed to determine whether the rate of temporal change in invertebrate–habitat relationships differs between fished and protected locations. The fact that newly protected communities in marine reserves are in a state of flux, while populations at fished locations remain relatively stable, increases the likelihood of finding differences

between protected and fished locations. Randomisation tests were therefore necessary to determine whether the increasing/decreasing relationships to reef structure are truly linked to the reef structure at the sites or whether the same relationship could also be found if the reef structure values were randomly re-organised among the sites. Changing strength of invertebrate–habitat relationships through time was therefore assessed using a three-stage analysis. Initially, the relationships between the abundance of each target species and reef structure metrics at each time step was determined using linear regression models in R version 2.9.2 (R Development Core Team 2009). The size of the R^2 value from each regression was used to represent the relative strength of reef structure metrics in describing variation in the abundance of the key species among sites. Separate regression models were created for sites inside and adjacent to the marine reserve in each year. The second stage of the analysis involved the construction of the linear regression model: $R^2 \sim \text{Time} + \text{Reserve} + \text{Time} \times \text{Reserve}$, where R^2 is the proportion of variance explained by reef structure for each year (i.e. the R^2 value derived from the regression models between the response variable and reef habitat structure metric); ‘Time’ is the number of years since the declaration of the reserve; and ‘Reserve’ is a categorical factor reflecting whether the test was carried out on data from inside or external to the marine reserve.

We test the null hypothesis that protection from fishing did not affect relationships between invertebrates and reef structure by examining the significance of the Reserve \times Time interaction term in the above model. A significant interaction term indicates that change through time in the strength of the invertebrate–habitat relationship is different between protected and fished sites. Invertebrate populations at Tinderbox and Maria Island marine reserves are changing in response to protection from fishing while populations at fished control sites are relatively stable (Edgar and Barrett 1999; Barrett et al. 2009; Edgar et al. 2009). Since the reef structure is static through time, relationships to reef structure will not change whilst the invertebrate abundance at these sites also remains constant. On the other hand, habitat associations for populations in flux, such as those at marine reserve sites, will almost certainly increase or decrease through time. To accommodate this elevated likelihood of finding a significant interaction term, the values for each reef structure metric were randomly reassigned between sites and the first two stages of the analysis carried out between the randomised structure metrics and the true abundances of each of the three species. This process was repeated 1,000 times. The F -statistic for the interaction model based on the true data was then compared with the distribution of F -statistics from the randomisation tests. The interaction term was deemed significant if

less than 5 % of randomised tests produced an F -statistic greater than that the value for the real data.

Results

All three species tested showed gradually weakening relationships to habitat structure at protected sites through time relative to fished sites. The two highly targeted commercial species, *J. edwardsii* and *H. rubra*, were weakly associated with habitat structure at protected sites immediately after declaration of the marine reserves (linear regression of *J. edwardsii* ~ Topographic complexity, for protected sites in 1992: $F = 0.11$, $p = 0.75$, $R^2 = 0.02$; *H. rubra* ~ Topographic complexity, for protected sites in 1992: $F = 0.21$, $p = 1.83$, $R^2 = 0.03$; Figs 2, 3, 4). However, these species both experienced a rapid strengthening of their relationship to habitat structure in the second year of protection. The strongest trends occurred for *J. edwardsii*, which exhibited a highly significant, positive relationship with

reef topographic complexity in the early years after protection (linear regression of *J. edwardsii* ~ Topographic complexity, for protected sites in 1993: slope = 4.1, $F = 54.1$, $p < 0.001$, $R^2 = 0.9$; 1994: slope = 4.9, $F = 16.7$, $p < 0.01$, $R^2 = 0.74$; Fig. 2). An increase in the density of this species in the marine reserves over time, however, particularly at sites with low and medium values of this habitat metric, weakened the relationship until it was no longer significant after 1999 surveys (linear regression of R^2 ~ Time, for protected sites: slope = -0.03 , $F = 8.6$, $p < 0.05$, $R^2 = 0.40$; Fig. 3). Running the analyses excluding the 1992 outlier dramatically increased the significance and doubled the R^2 of this regression (linear regression of R^2 ~ Time, for protected sites excluding 1992: slope = -0.05 , $F = 45.9$, $p < 0.001$, $R^2 = 0.80$). The relationship between *J. edwardsii* and topographic complexity at fished sites was highly variable between years and showed no significant directional change over time (linear regression of R^2 ~ Time, for fished sites: $F = 0.34$, $p = 0.34$, $R^2 = 0.07$; Fig. 3). The difference between fished and protected sites in the slope of

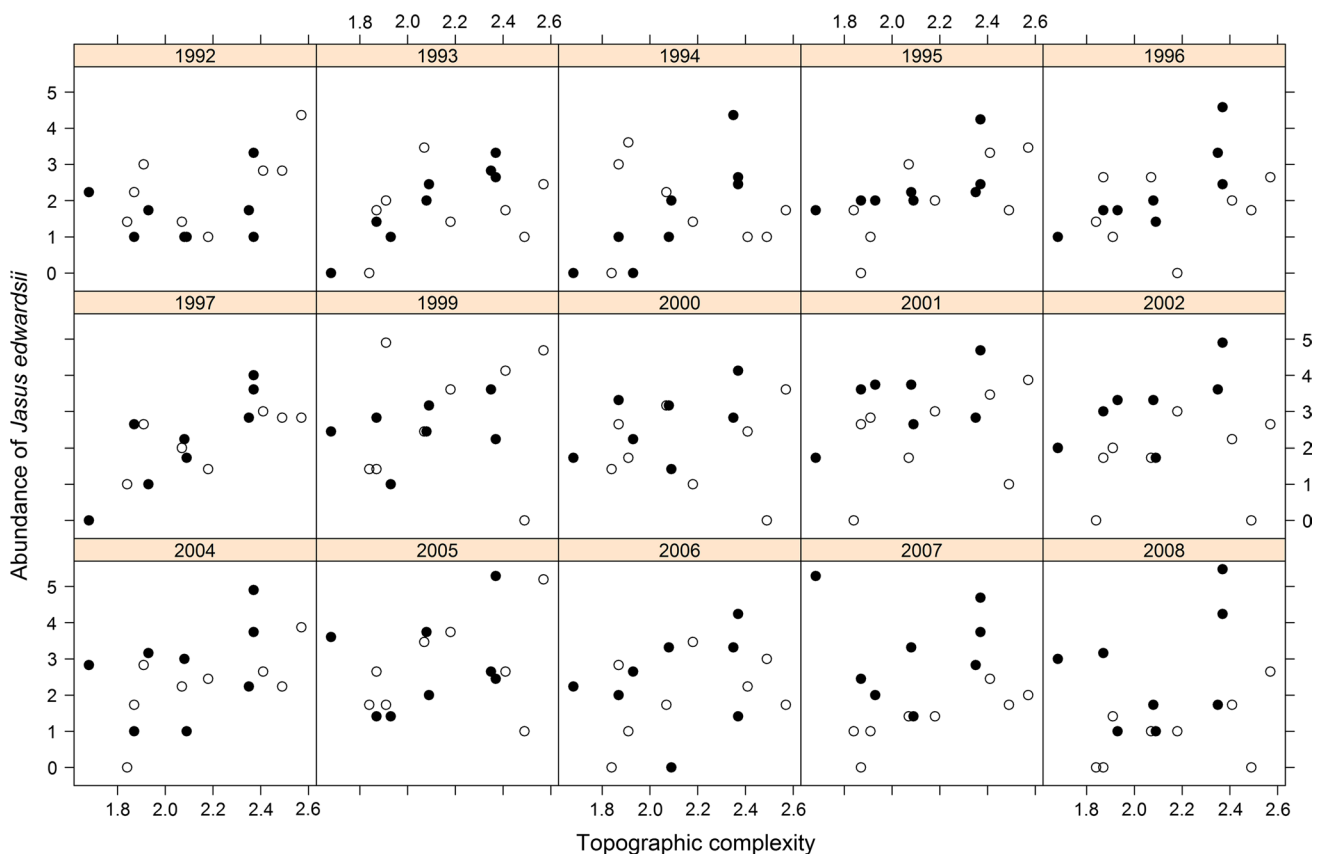


Fig. 2 Scatterplots of annual data demonstrate the sudden increase, then gradually weakening relationship between abundance of *J. edwardsii* (per 200 m², square root transformed) and reef topographic complexity at protected sites (solid circles). The same relationship at fished sites (open circles) remained weak and variable through time. Particularly, high abundances of *J. edwardsii* were recorded at one

protected site in several years. These data were truncated from the plots to facilitate trend visualisation in the remaining data. The topographic complexity of the excluded site was 2.37, and the abundance of *J. edwardsii* in 1999 was 9.43, in 2000 was 6.86, in 2001 was 7.75, and in 2002 was 6.93

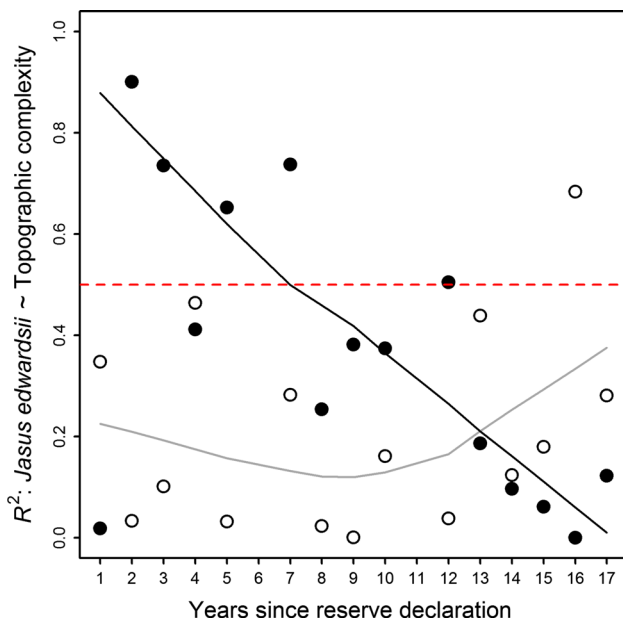


Fig. 3 Steadily decreasing R^2 values for linear regressions between the abundance of rock lobster *J. edwardsii* and reef topographic complexity at protected sites (solid circles). R^2 values at fished sites (open circles) remain relatively constant through time. *J. edwardsii* was positively related to topographic complexity in all annual regressions. The dashed red line shows the $p = 0.05$ significance level for a regression test within an individual year. Solid lines are LOWESS trend lines

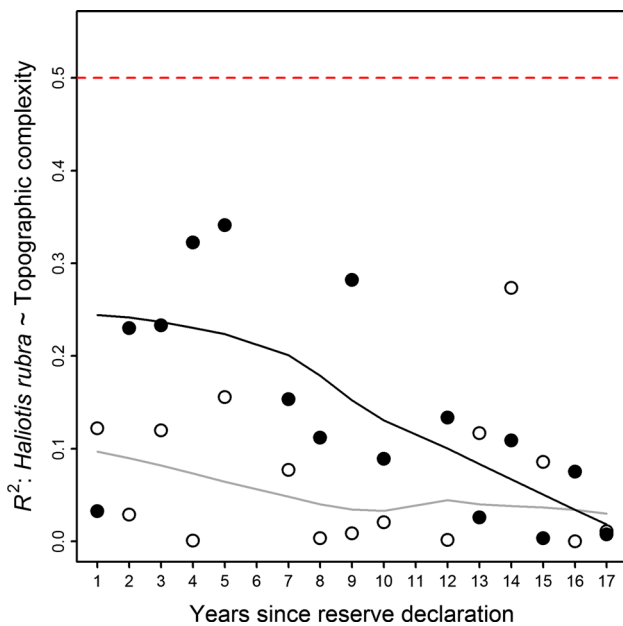


Fig. 4 Weakening negative relationship between abundance of blacklip abalone *H. rubra* and reef topographic complexity at protected sites (solid circles), while the same relationship at fished sites (open circles) remained low and variable through time. The dashed red line shows the $p = 0.05$ significance level for a regression test within an individual year. Solid lines are LOWESS trend lines

this relationship was confirmed by the fact that the F -statistic for the $R^2 \sim \text{Time} \times \text{Reserve}$ interaction term was larger than 97.5 % of F -statistics based on models where the values of topographic complexity were repeatedly re-assigned for each site (Table 1).

The strengthening negative relationship between *H. rubra* and topographic complexity in the second year of protection was caused by an increase in abundance at less complex sites and a decrease in abundance at sites with higher complexity. In the years that followed, a decrease in abundance of *H. rubra* at protected sites with low topographic complexity caused a steady decrease in the strength of the negative, but nonsignificant, relationship between this species and habitat structure (linear regression $R^2 \sim \text{Time}$, at protected sites; slope = -0.01 , $F = 7.32$, $p < 0.05$, $R^2 = 0.36$; Fig. 4). The relationship between *H. rubra* and topographic complexity remained stable at fished sites throughout the survey period (linear regression of $R^2 \sim \text{Time}$, at fished sites: $F = 0.02$, $p = 0.89$, $R^2 = 0.002$). Comparison with models on randomised reef structure

Table 1 Influence of protection on the strength of the relationship between reef structure and invertebrates

Invertebrates	Topographic complex- Reef architecture			
	ity		ity	
	Fished	Protected	Fished	Protected
<i>Jasus edwardsii</i>				
Slope: $R^2 \sim \text{Time}$	0.010	-0.035^*	-0.011	-0.001
$F_{\text{real}}: \text{Time} \times \text{Reserve}$	8.3		1.4	
$F_{\text{random}} > F_{\text{real}}$	2.5 %		25.6 %	
<i>Haliotis rubra</i>				
Slope: $R^2 \sim \text{Time}$	-0.001	-0.013^*	0.011	0.001
$F_{\text{real}}: \text{Time} \times \text{Reserve}$	3.8		0.4	
$F_{\text{random}} > F_{\text{real}}$	9.9 %		51.1 %	
<i>Heliocidaris erythrogramma</i>				
Slope: $R^2 \sim \text{Time}$	0.0001	0.002	0.005	-0.021^{**}
$F_{\text{real}}: \text{Time} \times \text{Reserve}$	0.6		17.4	
$F_{\text{random}} > F_{\text{real}}$	45.5 %		3.6 %	

‘Slope’ represents the slope coefficient of a linear regression between R -squared values (for invertebrate–habitat relationships at each yearly survey) and the number of years since reserve declaration with fished and protected sites tested separately. Trends were summarised by F_{real} , which is the F -statistic for the interaction term of the regression model: $R^2 \sim \text{Time} + \text{Reserve} + \text{Time} \times \text{Reserve}$, where the R^2 is derived from the relationship between reef structure and biological response at each year. $F_{\text{random}} > F_{\text{real}}$ represents the significance of the interaction term indicated by proportion of the regression models on 1,000 sets of randomised reef structure data with F -statistics for the interaction term greater than that of the regression model based on the reef structure data as collected

* Significant influence of time on the R^2 for the invertebrate–habitat relationship at $p < 0.05$; ** $p < 0.01$

data indicated that the original calculated F -statistic for the Time \times Reserve interaction was greater than 90.1 % of F -statistics (Table 1). When data for the first year of protection were excluded from the regression of $R^2 \sim$ Time for protected sites, the significance and fit of the relationship increased dramatically (linear regression of $R^2 \sim$ Time, at protected sites excluding 1992: slope = -0.02 , $F = 23.3$, $p < 0.001$, $R^2 = 0.66$).

The results of this study indicate that the greatest loss of sea urchins in the marine reserve occurred at sites with high reef architecture, which weakened the *H. erythrogramma*–reef architecture relationship through time at protected sites (linear regression of $R^2 \sim$ Time, for protected sites: slope = -0.02 , $F = 15.8$, $p < 0.01$, $R^2 = 0.55$; Table 1). The decline in the strength of this relationship was greatest for the first 7 years of protection when R^2 values decreased steadily from 0.42 in 1992 to 0.01 in 1999, after which it varied but remained less than 0.2 (Fig. 5). Comparatively, the relationship between *H. erythrogramma* and reef architecture remained stable at fished sites throughout the survey period (linear regression of $R^2 \sim$ Time, at fished sites: $F = 2.27$, $p = 0.16$, $R^2 = 0.15$). The $R^2 \sim$ Time \times Reserve interaction term was larger than that of 96.4 % of randomised models, indicating that these trends were unlikely to have been caused by chance (Table 1).

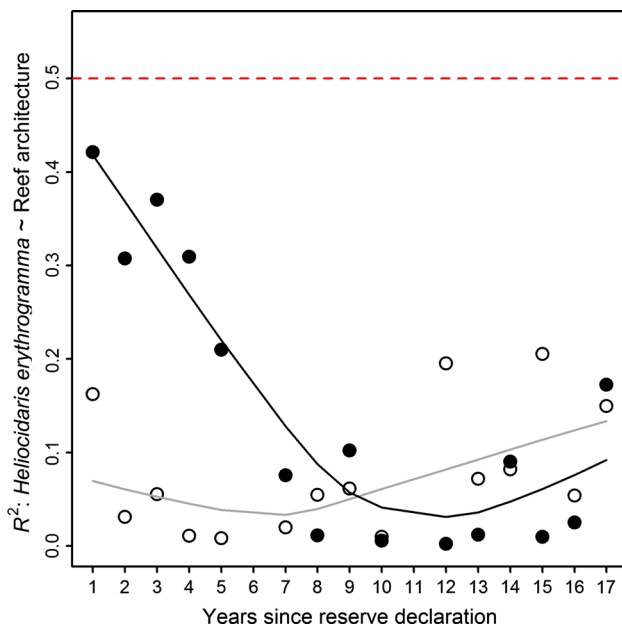


Fig. 5 Decreasing R^2 values for linear regressions between the abundance of sea urchin *H. erythrogramma* and reef architecture at protected sites (solid circles) for the first decade of protection. The same relationship at fished sites (open circles) remained weak and variable. *H. erythrogramma* was positively related to reef architecture in all annual regressions. The dashed red line shows the $p = 0.05$ significance level for a regression test within an individual year. Solid lines are LOWESS trend lines

Discussion

With the declaration of the Tasmanian marine reserves in 1991, several invertebrate predators (predominantly fishes) increased in abundance and size in response to release from fishing pressure (Edgar and Barrett 1999). In the face of this increasing predation, structurally complex habitats presumably provided refuge for the small lobsters, realising the rapid strengthening of the lobster–habitat relationship after only 2 years of protection. The rapidity of this increase was probably enhanced as lobsters grew into size-classes more likely to be observed by visual census, and as divers became more experienced in the survey techniques (Edgar and Stuart-Smith 2009).

The strong relationship of smaller *J. edwardsii* to habitat structure in the initial years of protection reflects the fact that many lobster species shelter among the structural features of rocky and coral reefs (Barshaw and Spanier 1994), particularly during the early stages of their life history (Wahle and Steneck 1992; Weiss et al. 2008). Juvenile *J. edwardsii* closely associate with reef features (Booth 2001; Booth and Ayers 2005); however, the closeness of their relationship to these features decreases with increasing carapace length (Edmunds 1995). The mean size of rock lobsters in Maria Island marine reserve increased relative to fished areas over the first 10 years of protection (Barrett et al. 2009). Presumably, the physical size and strength of larger *J. edwardsii* deterred successful attacks by some predator species, reducing the dependency of larger animals on reef structure and allowing protected sites with lower topographic complexity to support greater numbers of larger animals. This corresponds with observations of this species in New Zealand (Freeman 2008), and our own experience at long-protected sites where very large individuals of *J. edwardsii* are often observed to openly forage on exposed surfaces during the day.

The herbivorous sea urchin *H. erythrogramma* and blacklip abalone *H. rubra* were initially related to different elements of reef structure, and these relationships weakened with time following protection from fishing. Common explanations for the initial relationships with reef structure include higher food availability as crevices trap drifting algae (Shepherd 1973), higher settlement rates with topographic complexity restricting hydrodynamic flows causing greater retention of larvae (McShane et al. 1988), or the structural characteristics of the reef providing protection against predation (Eggleston et al. 1997; Grabowski 2004; Weiss et al. 2008).

Following the latter scenario, we would expect increasing association between prey species and habitat structure with the return of previously fished predators to the marine reserve sites (Sih et al. 1985). Instead we observed a weakening of prey–habitat linkages through time. One

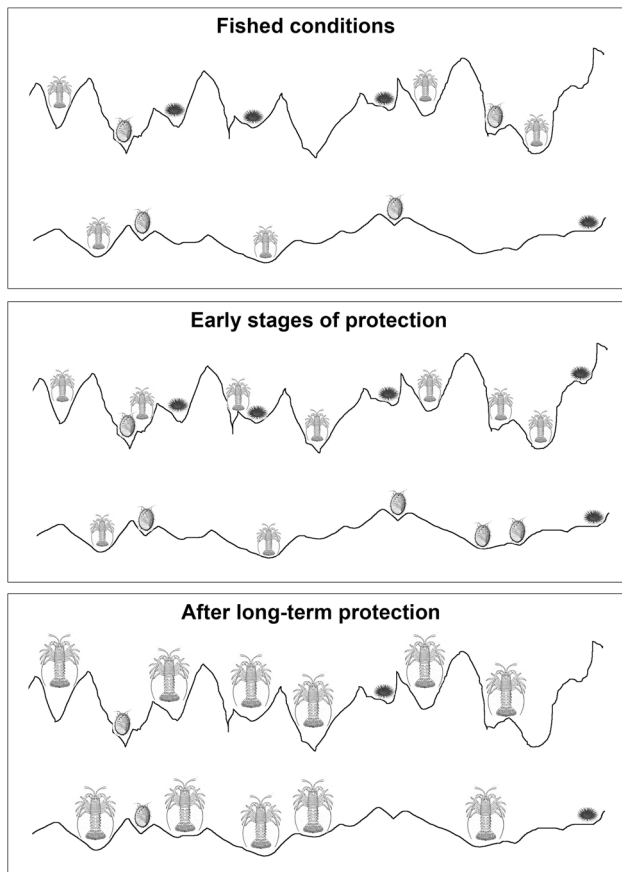


Fig. 6 Relationship between invertebrates and habitat structure under fished and protected conditions. Commercial and recreational fishing appeared to suppress the expression of natural lobster–habitat relationships. After protection, smaller rock lobsters were initially more abundant at sites with high reef structure. Lobsters then increased in size at all protected sites (Barrett et al. 2009), and particularly increased in abundance at sites with low and medium reef structure. Sea urchins and abalone both decreased in number from sites where they were initially abundant (abalone: low topographic complexity; sea urchins: abundant reef architecture)

explanation is that while reef structural features were initially sufficient to provide a buffer against the predator guild present before the reserve came into place (i.e. low numbers of small lobsters and fish), the increasing number and size of rock lobsters and demersal fishes increased their predatory capacity until they were able to overcome most benefits offered by the refuges to prey species (summarised in Fig. 6). For *J. edwardsii*, the dominant benthic predator on rocky reefs in Tasmania (Pederson and Johnson 2006), larger individuals are able to attack and consume larger sea urchins and become more effective at consuming juvenile urchins with increasing lobster carapace length (Andrew and Macdiarmid 1991; Guidetti 2004; Pederson and Johnson 2006).

Larger lobsters also presumably possess longer and stronger fore-legs, allowing them to remove urchins and

abalone from reef structural features that provide refuge against smaller lobsters. Andrew and Macdiarmid (1991) identified that the provision of shelter increased the survivorship of small sea urchins subject to predation by *J. edwardsii* in laboratory studies. The experiments of these researchers could be extended to test the ability of different sized lobsters to remove (and consume) small urchins and abalone from within different shapes and sizes of reef architectural features. Explicit, quantitative criteria could then be derived to describe specific reef features that provide spatial refuge for prey species. This information would be particularly useful in Tasmania where the increase in predator biomass, particularly rock lobsters, in marine reserves is thought to be the main contributor to the steady decline in the abundance of emergent highly valuable *H. rubra* at protected sites (Barrett et al. 2009; Babcock et al. 2010). Knowledge of particular reef features that offer refuge for *H. rubra* against *J. edwardsii* could be used to identify reef areas for closure as fisheries enhancement or insurance populations in Tasmania, allowing the persistence of healthy abalone populations in the presence of elevated rock lobster predation.

The changing relationships between mobile macroinvertebrates and their habitat presented here suggest that researchers should not assume that models developed to describe habitat associations of marine species, based on one or two temporal samples collected over a short duration, will apply equally well through time. This is particularly the case for biological communities subject to a perturbation such as the declaration of a marine reserve where species, and their relationship to the environment, can continue to change after more than a decade of protection (Shears and Babcock 2003; Russ and Alcala 2004; Edgar et al. 2009). Numerous studies of relationships between reef habitat structure and fishes and invertebrates have been undertaken in marine reserves (Lecchini et al. 2002; Friedlander et al. 2003; Willis and Anderson 2003; Garcia-Charton et al. 2004; La Mesa et al. 2004; Hereu et al. 2005; Alexander et al. 2009), and our results suggest that the temporal persistence of the relationships reported depends on whether the community has stabilised after rebuilding populations of fished species. In circumstances where the changing nature of structure–abundance relationships is driven by recovery of predator populations, models of species–habitat relationships are likely to be improved by including predation pressure as a covariate.

Our results also highlight the value of no-take marine reserves in creating ecological conditions that are absent from physically similar, nearby seascapes due to pervasive commercial and recreational fishing (Edgar et al. 2009). These unique conditions facilitate valuable research on ecological interactions, both among species and between species and their environment (see other important examples by Ling et al. 2009; Eddy et al. 2014), particularly since they more

closely reflect the ecological context under which the communities evolved (e.g. Heino et al. 2013). This knowledge can, in turn, be used to inform conservation planning and the management of commercially valuable species. In this case, the changing relationships between lobsters, abalone and reef structure after protection emphasises that habitat quality plays an important role in the trajectory of recovery for fished species (see also Alexander 2013). This suggests that reefs closed for the purposes of fisheries enhancement (as insurance populations), conservation of biodiversity, or as buffers against the effects of climate change (Ling et al. 2009), should include a range of habitat features to accommodate shifting ecological requirements of commercially important and keystone species with both increasing density and ontogenesis.

Acknowledgments This research was supported by funding from the Australian Research Council. TJA was supported by an Australian Postgraduate Award and a Commonwealth Scientific and Industrial Research Organisation/University of Tasmania scholarship in Quantitative Marine Science. The manuscript was improved through constructive comments from two anonymous reviewers.

References

- Adams NL (2001) UV radiation evokes negative phototaxis and covering behavior in the sea urchin *Strongylocentrotus droebachiensis*. *Mar Ecol Prog Ser* 213:87–95
- Alexander TJ (2013) Cryptic invertebrates on subtidal rocky reefs vary with microhabitat structure and protection from fishing. *Mar Ecol Prog Ser* 481:93–104
- Alexander TJ, Barrett N, Haddon M, Edgar G (2009) Relationships between mobile macroinvertebrates and reef structure in a temperate marine reserve. *Mar Ecol Prog Ser* 389:31–44
- Anderson TW (2001) Predator responses, prey refuges, and density-dependent mortality of a marine fish. *Ecology* 82:245–257
- Andrew NL, Macdiarmid AB (1991) Interrelations between sea urchins and spiny lobsters in northeastern New Zealand. *Mar Ecol Prog Ser* 70:211–222
- 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
- Babcock RC, Shears NT, Alcala AC, Barrett NS, Edgar GJ, Lafferty KD, McClanahan TR, Russ GR (2010) Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proc Natl Acad Sci USA* 107:18256–18261
- Barrett NS, Buxton CD, Edgar GJ (2009) Changes in invertebrate and macroalgal populations within Tasmanian marine reserves in the decade following protection. *J Exp Mar Biol Ecol* 370:104–119
- Barshaw DE, Spanier E (1994) Antipredator behaviors of the Mediterranean slipper lobster, *Scyllarides latus*. *Bull Mar Sci* 55:375–382
- Beck MW (1995) Size-specific shelter limitation in stone crabs: a test of the demographic bottleneck hypothesis. *Ecology* 76:968–980
- Bernafoord JL, Vasquez M (2008) Solar radiation plays a role in habitat selection by the sea star *Pisaster ochraceus*. *Mar Ecol Prog Ser* 368:177–187. doi:10.3354/meps07598
- Booth JD (2001) Habitat preferences and behaviour of newly settled *Jasus edwardsii* (Palinuridae). *Mar Freshw Res* 52:1055–1065
- Booth JD, Ayers D (2005) Characterising shelter preferences in captive juvenile *Jasus edwardsii* (Palinuridae). *NZ J Mar Freshwat Res* 39:373–382
- Booth JD, Stotter DR, Forman JS, Bradford E (2001) Juvenile abundance both mirrors and masks a settlement pulse of the rock lobster *Jasus edwardsii*. *Mar Freshw Res* 52:1067–1075
- Caillaux LM, Stotz WB (2003) Distribution and abundance of *Rhynchocinetes typus* (Crustacea: Decapoda), in different benthic community structures in northern Chile. *J Mar Biol Assoc UK* 83:143–150
- Caley MJ, St John J (1996) Refuge availability structures assemblages of tropical reef fishes. *J Anim Ecol* 65:414–428
- Connell SD, Jones GP (1991) The influence of habitat complexity on post recruitment processes in a temperate reef fish population. *J Exp Mar Biol Ecol* 151:271–294
- DEH (2005) Assessment of the Tasmanian commercial dive fishery. Department of the Environment and Heritage, Australian Government, Australia
- Drolet D, Himmelman JH, Rochette R (2004a) Effect of light and substratum complexity on microhabitat selection and activity of the ophiuroid *Ophiopholis aculeata*. *J Exp Mar Biol Ecol* 313:139–154
- Drolet D, Himmelman JH, Rochette R (2004b) Use of refuges by the ophiuroid *Ophiopholis aculeata*: contrasting effects of substratum complexity on predation risk from two predators. *Mar Ecol Prog Ser* 284:173–183
- Eddy TD, Pitcher TJ, MacDiarmid AB, Byfield TT, Tam JC, Jones TT, Bell JJ, Gardner JPA (2014) Lobsters as keystone: only in unfished ecosystems? *Ecol Model* 275:48–72
- 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
- Edgar GJ, Stuart-Smith RD (2009) Ecological effects of marine protected areas on rocky reef communities—a continental-scale analysis. *Mar Ecol Prog Ser* 388:51–62
- Edgar GJ, Barrett NS, Stuart-Smith RD (2009) Exploited reefs protected from fishing transform over decades into conservation features otherwise absent from seascapes. *Ecol Appl* 19:1967–1974
- Edmunds M (1995) The ecology of juvenile Southern Rock Lobster *Jasus edwardsii* (Hutton 1875) (Palinuridae). Unpublished PhD thesis. Zoology, Hobart
- Eggleston DB, Lipcius RN, Grover JJ (1997) Predator and shelter-size effects on coral reef fish and spiny lobster prey. *Mar Ecol Prog Ser* 149:43–59
- Freeman DJ (2008) The ecology of spiny lobsters (*Jasus edwardsii*) on fished and unfished reefs, Auckland
- Friedlander AM, Parrish JD (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *J Exp Mar Biol Ecol* 224:1–30
- Friedlander AM, Brown EK, Jokiel PL, Smith WR, Rodgers KS (2003) Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs* 22:291–305
- Garcia-Charton JA, Williams ID, Perez-Ruzafa A, Milazzo M, Chemello R, Marcos C, Kitsos MS, Koukouras A, Riggio S (2000) Evaluating the ecological effects of Mediterranean marine protected areas: habitat, scale and the natural variability of ecosystems. *Environ Conserv* 27:159–178
- Garcia-Charton JA, Perez-Ruzafa A, Sanchez-Jerez P, Bayle-Sempere JT, Renones O, Moreno D (2004) Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. *Mar Biol* 144:161–182
- Grabowski JH (2004) Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. *Ecology* 85:995–1004

- Guidetti P (2004) Consumers of sea urchins, *Paracentrotus lividus* and *Arbacia lixula*, in shallow Mediterranean rocky reefs. *Helgol Mar Res* 58:110–116
- Guidetti P (2006) Marine reserves reestablish lost predatory interactions and cause community changes in rocky reefs. *Ecol Appl* 16:963–976
- Heino M, Baulier L, Boukal DS, Ernande B, Johnston FD, Mollet FM, Pardoe H, Therkildsen NO, Uusi-Heikkilä S, Vainikka A, Arlinghaus R, Dankel DJ, Dunlop ES, Eikeset AM, Enberg K, Engelhard GH, Jørgensen C, Laugen AT, Matsumura S, Nusslé S, Urbach D, Whitlock R, Rijnsdorp AD, Dieckmann U (2013) Can fisheries-induced evolution shift reference points for fisheries management? *ICES J Mar Sci* 70:707–721. doi:10.1093/icesjms/fst077
- Hereu B, Zabala M, Linares C, Sala E (2005) The effects of predator abundance and habitat structural complexity on survival of juvenile sea urchins. *Mar Biol* 146:293–299. doi:10.1007/s00227-004-1439-y
- Johnson C, Valentine J, Pederson H (2004) A most unusual barrens: complex interactions between lobsters, sea urchins and algae facilitates spread of an exotic kelp in eastern Tasmania Echinoderms: Munchen. Balkema, Leiden, pp 213–220
- Johnson CR, Banks SC, Barrett NS, Cazassus F, Dunstan PK, Edgar GJ, Frusher SD, Gardner C, Haddon M, Helidoniotis F, Hill KL, Holbrook NJ, Hosie GW, Last PR, Ling SD, Melbourne-Thomas J, Miller K, Pecl GT, Richardson AJ, Ridgway KR, Rintoul SR, Ritz DA, Ross DJ, Sanderson JC, Shepherd SA, Slotwinski A, Swadling KM, Taw N (2011) Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. *J Exp Mar Biol Ecol* 400:17–32
- Koehl MAR (2007) Mini review: hydrodynamics of larval settlement into fouling communities. *Biofouling* 23:357–368
- La Mesa G, Micalizzi M, Giaccone G, Vacchi M (2004) Cryptobenthic fishes of the “Cyclopi Islands” marine reserve (central Mediterranean Sea): assemblage composition, structure and relations with habitat features. *Mar Biol* 145:233–242
- Lecchini D, Lenfant P, Planes S (2002) Variation in abundance and population dynamics of the sea-urchin *Paracentrotus lividus* on the Catalan coast (north-western Mediterranean Sea) in relation to habitat and marine reserve. *Vie Milieu* 52:111–118
- Leum LL, Choat JH (1980) Density and distribution patterns of the temperate marine fish *Cheilodactylus spectabilis* (Cheilodactylidae) in a reef environment. *Mar Biol* 57:327–337
- Ling SD, Johnson CR, Frusher SD, Ridgway KR (2009) Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. *Proc Natl Acad Sci USA* 106:22341–22345
- McClanahan TR, Shafir SH (1990) Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia* 83:362–370
- McCormick MI (1994) Comparison of field methods for measuring surface topography and their association with a tropical reef fish assemblage. *Mar Ecol Prog Ser* 112:87–96
- McShane PE, Black KP, Smith MG (1988) Recruitment processes in *Haliotis rubra* (Mollusca: Gastropoda) and regional hydrodynamics in southeastern Australia imply localized dispersal of larvae. *J Exp Mar Biol Ecol* 124:175–203
- Metcalf SJ, Dambacher JM, Hobday AJ, Lyle JM (2008) Importance of trophic simplification and aggregation error in ecosystem models. *Mar Ecol Prog Ser* 360:25–36. doi:10.3354/meps07394
- Micheli F, Benedetti-Cecchi L, Gambaccini S, Bertocci I, Borsini C, Osio GC, Roman F (2005) Cascading human impacts, marine protected areas, and the structure of Mediterranean reef assemblages. *Ecol Monogr* 75:81–102
- Mills DJ, Johnson CR, Gardner C (2008) Bias in lobster tethering experiments conducted for selecting low-predation release sites. *Mar Ecol Prog Ser* 364:1–13
- Parker KR, Shulman MJ (1986) Avoiding predation: alarm responses of Caribbean sea urchins to simulated predation on conspecific and heterospecific sea urchins. *Mar Biol* 93:201–208
- Pauly D, Christensen V, Dalsgaard J, Froese R Jr, Torres F (1998) Fishing down marine food webs. *Science* 279:860–863
- Pederson HG, Johnson CR (2006) Predation of the sea urchin *Heliocidaris erythrogramma* by rock lobsters (*Jasus edwardsii*) in no-take reserves. *J Exp Mar Biol Ecol* 336:120–134
- Pederson HG, Johnson CR (2008) Growth and age structure of sea urchins (*Heliocidaris erythrogramma*) in complex barrens and native macroalgal beds in eastern Tasmania. *ICES J Mar Sci* 65:1–11
- Pederson HG, Barrett NS, Frusher SD, Buxton CD (2008) Effect of predator–prey and competitive interactions on size at emergence in the black-lip abalone *Haliotis rubra* in a Tasmanian MPA. *Mar Ecol Prog Ser* 366:91–98
- Pinnegar JK, Polunin NVC, Francour P, Badalamenti F, Chemello R, Harmelin-Vivien ML, Hereu B, Milazzo M, Zabala M, D'Anna G, Pipitone C (2000) Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Environ Conserv* 27:179–200
- R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Roberts CM, Ormond RFG (1987) Habitat complexity and coral reef fish diversity and abundance on Red sea fringing reefs. *Mar Ecol Prog Ser* 41:1–8
- Russ GR, Alcala AC (2004) Marine reserves: long-term protection is required for full recovery of predatory fish populations. *Oecologia* 138:622–627
- Sala E, Zabala M (1996) Fish predation and the structure of the sea urchin *Paracentrotus lividus* populations in the NW Mediterranean. *Mar Ecol Prog Ser* 140:71–81
- Sanderson JC, Rossignol M, James W (1996) A pilot program to maximise Tasmania's sea urchin (*Heliocidaris erythrogramma*) resource
- Shears NT, Babcock RC (2002) Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia* 132:131–142
- Shears NT, Babcock R (2003) Continuing trophic cascade effects after 25 years of no-take marine reserve protection. *Mar Ecol Prog Ser* 246:1–16
- Shepherd SA (1973) Studies on southern Australian abalone (genus *Haliotis*) I. Ecology of five sympatric species. *Aust J Mar Freshw Res* 24:217–257
- Shepherd SA (1986) Movement of the southern Australian abalone *Haliotis laevigata* in relation to crevice abundance. *Aust J Ecol* 11:295–302
- 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
- Sih A, Crowley P, McPeck M, Petranka J, Strohmeier K (1985) Predation, competition, and prey communities: a review of field experiments. *Annu Rev Ecol Syst* 16:269–311
- Skirtun M, Sahlqvist P, Curtotti R, Hobsbawn P, ES ABAR (2012) Australian Fisheries Statistics 2011. Australian Bureau of Agricultural and Resource Economics, Canberra
- Wahle RA, Steneck RS (1992) Habitat restrictions in early benthic life: experiments on habitat selection and in situ predation with the American Lobster. *J Exp Mar Biol Ecol* 157:91–114
- Weiss HM, Lozano-Álvarez E, Briones-Fourzán P (2008) Circadian shelter occupancy patterns and predator–prey interactions of juvenile Caribbean spiny lobsters in a reef lagoon. *Mar Biol* 153:953–963
- Willis TJ, Anderson MJ (2003) Structure of cryptic reef fish assemblages: relationships with habitat characteristics and predator density. *Mar Ecol Prog Ser* 257:209–221