

Proximity to rocky reefs alters the balance between positive and negative effects on seagrass fauna

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ABSTRACT: Proximity to habitat margins can alter the balance between positive and negative forces on species abundance. Based on this idea we examined abundance patterns of herbivorous gastropods in seagrasses adjacent to rocky reefs. We tested whether the balance between the intensity of predation (negative effect) and recruitment of new individuals (positive effect) changes with increasing distance from reefs. Abundances of gastropods varied with distance to reefs, but the direction of changes in abundance was taxon-specific: some taxa decreased in abundance with increasing distance from reefs (e.g. *Pyrene bidentata*), while others showed the opposite pattern (e.g. *Cantharidus lepidus*). Predators were more abundant on reefs and in immediately adjacent seagrasses, relative to seagrass meadow interiors. Predation intensity on 2 species with opposite patterns of abundance with proximity to reefs (*P. bidentata* and *C. lepidus*) was consistently higher in seagrasses near reef edges than in seagrass interiors, and *C. lepidus* was more susceptible to predation than *P. bidentata*. Recruitment of *P. bidentata* was higher in seagrasses adjacent to reefs relative to seagrass interiors, whereas recruitment of *C. lepidus* did not vary with distance from reefs. Dispersal of *P. bidentata* individuals from reefs probably explains the greater recruitment of *P. bidentata* at seagrass edges relative to interiors; this compensates for losses due to predation, thereby enabling high abundance in seagrasses adjacent to reefs despite suffering greater predation at this distance relative to the interiors of the seagrass meadows. In contrast, losses of *C. lepidus* due to predation reduced its abundance in seagrasses adjacent to reefs, while recruitment was invariant, so this species was most abundant in seagrass meadow interiors. Thus, proximity to habitat margins affected abundance patterns by influencing mortality (predation) and replenishment (recruitment) of populations. This balance was dependent on species identity, and led to contrasting patterns of abundance among species with proximity to habitat interfaces.

KEY WORDS: Cross-habitat exchanges · Gastropods · Habitat connectivity · Predation · Supply-side processes · Edge effects · Habitat linkages · Rocky reefs

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INTRODUCTION

A major focus in ecology is to predict how different processes act simultaneously to determine the abundance and distribution of species. Understanding the balance between processes that enhance growth or add new individuals ('bottom-up' and 'supply-side'

processes) and those that limit growth or cause mortality ('top-down' processes) is particularly important (Menge 2000). Studies of the relative balance between these forces have mostly been restricted to single, relatively uniform habitats. Habitats are, however, usually connected within landscapes, and the balance between positive and negative forces on abundances

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of species may vary where distinct habitats are spatially linked, such as at edges (Kareiva & Wennergren 1995).

Edges between juxtaposed habitats can influence the type and intensity of interactions between species and thus affect ecological patterns (Cadenasso et al. 2003). The movement of organisms from one habitat to another is an important ecological process because it can lead to differences in the abundance of an organism between habitat margins and interiors. For example, incursions of predators from their shelters into surrounding habitats can diminish prey abundances near habitat margins (e.g. Bell et al. 1991, Eggleston et al. 1999, Fagan et al. 1999, Langlois et al. 2005, Galvan et al. 2008), while cross-edge movements of individuals, especially propagules, can increase abundances (Puliam 1988).

When rates of these processes vary with proximity to habitat edges, prey species may vary in abundance accordingly (e.g. Langlois et al. 2005). Responses can also vary with the characteristics of the habitat. For example, vulnerability to predation can vary with the architecture of the dominant habitat (Heck & Crowder 1991, Fagan et al. 1999, Rand et al. 2006), which is illustrated by the superiority of forests to open habitats in providing protection for small birds against predators (Rodriguez et al. 2001). Further, species with different traits, such as vulnerability to predation or ability to disperse, can show contrasting responses to key processes. For example, differences in the morphological traits (e.g. thickness) of mollusc shells can affect their predator's handling time and ability to consume prey (Quensen & Woodruff 1997, Seitz et al. 2001). Each of these influences (proximity to edge, habitat architecture, and species traits) can interact to change the relative influence of positive and negative forces on abundance.

Seagrasses are key habitats along temperate and tropical coasts of the world (Hemminga & Duarte 2000), where they are frequently distributed as mosaics interspersed with other habitats, such as rocky reefs, coral reefs, mangroves and unvegetated sediments. In particular, reef–seagrass landscapes are common elements of temperate (e.g. Australasia, Wernberg et al. 2006) and tropical latitudes (e.g. the Caribbean region and Florida, Valentine et al. 2008; the Indo-Pacific region, Dorenbosch et al. 2005). In these systems, many trophic interactions occur across 2 or more habitats. For example, predation on epifauna may be most intense in seagrasses adjacent to reefs, as a result of the foraging of reef-associated consumers (Valentine et al. 2008). Seagrass meadows may also be recipients of materials advected from reefs (e.g. propagules, nutrients, detached vegetation). These flows strongly affect both ecological and abiotic pro-

cesses in seagrass meadows. For example, movement of propagules leads to high diversity and biomass of epiphytic algae on seagrasses near reefs (Van Elven et al. 2004), and the accumulation of detached reef algae influences food webs in seagrass meadows (Wernberg et al. 2006).

We tested whether proximity to reefs influences the abundance patterns of herbivorous gastropods (<25 mm total body whorl) in seagrass meadows by affecting the intensity of, and balance between, 'top-down' (predation) and 'supply-side' (recruitment) processes. Specifically, we predicted that (1) abundance of gastropods changes with proximity to rocky reefs, (2) predation by reef-associated consumers (fishes and decapod crustaceans) is highest in seagrasses adjacent to reefs and (3) proximity to reefs can affect the supply of new individuals. Because rates of ecological processes in seagrass systems can be strongly influenced by the architecture of the seagrass (Heck & Orth 2006), we determined the effect of 2 seagrasses with contrasting physiognomy (*Posidonia* versus *Amphibolis*) on these patterns and processes as well as whether patterns were spatially consistent between 2 different locations. This study was then based on surveys and experiments designed to test a set of specific hypotheses that involves both effects of individual factors (how patterns and processes change with proximity to reefs) and interactions (e.g. whether patterns and processes at different proximity to reefs were consistent between 2 seagrass species of contrasting physiognomy), as well as random effects across space (to test for generality of effects across 2 locations and among multiple reefs within each location). Hypotheses were tested with generalized linear models, in particular orthogonal mixed-effects ANOVA (Underwood 1997) that partitions the variability associated with each of the experimental factors (e.g. distance, seagrass types).

Gastropods are appropriate model species since they are an important part of the diet of predators (Edgar 1990a,b, MacArthur & Hyndes 2007), and food limitation is not a major factor influencing the patterns of distribution of these grazers due to the abundance of food in these systems, e.g. epiphytes and periphyton (Jernakoff & Nielsen 1998).

MATERIALS AND METHODS

Study area. The study was carried out on rocky reefs and in adjoining seagrass meadows at 2 locations ~250 km apart in southwestern Australia: Marmion (31° 50' S) and Jurien Bay (30° 18' S). In this area, the coast is characterized by sequences of limestone reefs parallel to the shore at distances ranging from <1 to 10 km offshore. Seagrass meadows consisting of *Posi-*

donia spp. and *Amphibolis* spp. are interspersed among these reefs along more than 1500 km of coastline. We selected 6 reefs, each separated by >400 m, within each location: 3 adjacent to meadows dominated by *Posidonia* (predominantly *P. sinuosa*) and 3 adjacent to *Amphibolis* (principally *A. griffithii*) (Fig. S1 in the supplement at www.int-res.com/articles/suppl/m405p175_app.pdf). Reefs adjacent to either *Posidonia* or *Amphibolis* meadows were, in all cases, interspersed at each location, i.e. reefs adjacent to either *Posidonia* or *Amphibolis* were not clumped within a particular area of each location, and were selected after our previous work in the study area (Wernberg et al. 2006, Vanderklift et al. 2007). In the study area, reefs are predominantly covered by macroalgae, primarily the small (<1.5 m), canopy-forming kelp *Ecklonia radiata*, and frondose fucallean algae, mostly of the genera *Sargassum* and *Scytothalia*. Patches of small (generally <25 cm) foliose red algae are interspersed between the larger stands of canopy-forming algae (see Wernberg et al. 2003 for a detailed description of floral assemblages). All reefs had similar vertical relief. Depths of the seagrass meadows ranged between 2 and 6 m immediately adjacent to reefs, and between 3 and 9 m at the farthest distances from the reefs. All surveyed reefs were <1 km from the adjacent shore of the nearest island (Fig. S1).

The strap-like leaves of *Posidonia* are generally uniform from base to tip, while *Amphibolis* has erect stems with small leaves arranged in terminal clusters, forming a denser canopy. Shoot densities for *Posidonia* tend to be higher than those of *Amphibolis*, while aboveground biomass (including epiphytes) is higher for *Amphibolis* (Jernakoff & Nielsen 1998).

Abundance of gastropods. At each of the 12 selected reef-seagrass landscapes, a SCUBA diver hand-picked all aboveground vegetation within 5 replicate 25 × 25 cm quadrats haphazardly laid out at 5 distances relative to the reef-seagrass edge: on the reef itself, at 0 m (first seagrass patch immediately adjacent to the reef) and 10, 50 and >300 m (first seagrass patch beyond the 300 m mark) distance away from the reef (Fig. S2 in the supplement). On reefs, collections were from haphazardly selected patches of red macroalgae, which typically host large densities of gastropods in the study area (for further details see Tuya et al. 2008). In seagrass meadows, samples were collected from monospecific stands. Each sample was washed in fresh water, and passed through a 1 mm mesh sieve. Vegetation was dried for 24 h at 70°C and then weighed (grams); the number and biomass of leaf clusters and stems, as well as the biomass of large epiphytes, was previously counted for *Amphibolis* spp. samples. These structural elements are the most relevant factors accounting for the spatial abundance patterns of sea-

grass-inhabiting gastropods in the study area (Jernakoff & Nielsen 1998), though a wide range of seagrass structural elements can affect the magnitude of ecological effects within seagrass meadows, such as predation intensity (Heck & Crowder 1991). All gastropod individuals were identified to the lowest possible taxonomic level. Surveys were repeated twice on each reef, once each during the austral summer/autumn of 2006 and 2007, to determine whether patterns were consistent when measured at different times. ANCOVA was used to partition variation in the abundance (per quadrat, i.e. 625 cm²) of each of the 8 most abundant taxa (which accounted for >90% of all individuals), separately for each survey (Fig. S3 in the supplement shows a schematic representation of the design); vegetation biomass (dry weight per quadrat) was included as a covariate to adjust (i.e. control) for differences in the amount of vegetation among samples. Each ANCOVA model incorporated the factors: (1) 'Location' (random factor), (2) 'Seagrass' (fixed factor and orthogonal to 'Location'), (3) 'Reef' (random factor nested within 'Location × Seagrass') and (4) 'Distance' (fixed factor orthogonal to all previous factors). In all cases, data were ln(x + 1) transformed to stabilize variances. Heteroscedasticity, however, remained after transformation in almost all cases (Cochran's C-test, $p < 0.05$), and so statistical significance was conservatively set at $\alpha = 0.01$. Pairwise Student-Newman-Keuls (SNK) tests were used to resolve differences in abundance among distances for each taxon. Potential differences in the biomass of each seagrass, as well as in the number of clusters and stems of *Amphibolis* spp., with varying proximity to reefs were tested for each survey by a 3-way ANOVA. The model incorporated the factors 'Location' (random factor), 'Reef' (random factor nested within 'Location') and 'Distance' (fixed factor orthogonal to the previous factors). The broad approach follows that used in other studies of connectivity between adjacent subtidal habitats (e.g. Langlois et al. 2005, Valentine et al. 2008, Vanderklift et al. 2007), and calculations of *F*-ratios in all cases followed Underwood (1997).

Abundance of predators. Potential predators (fish, octopus and decapod crustaceans, mainly the western rock lobster *Panulirus cygnus*) were censused on each reef during daytime hours in austral summer/autumn 2007. Fish were also counted in adjacent seagrass meadows at 2 distances relative to the reef-seagrass edge: 50 and >300 m (*P. cygnus* is nocturnal and was not present in seagrasses during the day). Abundances were recorded by a SCUBA diver within three 25 × 4 m transects (100 m²) oriented parallel to the edge of the reefs, with one side in contact with the adjacent seagrass meadow in the case of reef censuses. Patterns of abundance of predatory fish (all known and suspected

predators of gastropods, Table S1 in the supplement) and the 5 most abundant fish species (those accounting for >85% of all individuals) were examined with ANOVA (same model and transformations as outlined before for the abundance of the most abundant gastropod taxa) and SNK tests were used to resolve differences in abundance among distances.

Predation on gastropods in seagrasses. The relative intensity of predation was assessed by measuring the survival of tethered adults of 2 species of gastropods: *Pyrene bidentata* (9 to 15 mm) and *Cantharidus lepidus* (7 to 12 mm total body whorl) (Fig. S4 in the supplement). We selected these 2 species because both are consumed by rock lobsters (Edgar 1990a,b) and fishes (MacArthur & Hyndes 2007), and each displayed a opposite pattern of abundance with proximity to reefs (see Results). Although tethering can increase mortality rates, such experiments can still be used to compare relative mortality rates among different animals, or treatments, as long as the tether bias is constant among groups to be compared (see Peterson & Black 1994 for a review). Artifacts as a result of tethering were probably minimized because (1) tethers were sufficiently long (~50 to 60 cm) to allow individuals to move and shelter within the seagrass canopy, and (2) laboratory tests (5 individuals of each species in five 15 × 10 × 7 cm aquaria) yielded no mortality and no escapes from tethers after 7 d. Gastropods were tethered with a loop of monofilament line attached to the shell with cyanoacrylate glue (Fig. S4). The other end of the line was attached to a metal stake hammered into the substrate. Five individuals of each species were deployed in seagrasses 0 and >300 m away from each of 8 reefs, with 2 reefs within each location adjacent to *Amphibolis* and *Posidonia* meadows. Tethers (between 20 and 30 cm apart) were retrieved after 5 d (the duration was selected based on pilot and similar studies) and the gastropods scored as alive or consumed; based on the results of the laboratory experiments, empty 'loops' were taken as evidence of predation. Differences in consumption between species among locations, distances, seagrasses and reefs were analyzed with multiple logistic regression. We were most interested in testing whether coefficients for each of the factors, and interactions between factors, were significant, so we focused on the significance of the deviances using a χ^2 test (Hosmer & Lemeshow 2000).

Prey selectivity by rock lobsters. We tested for differences in consumption of *Pyrene bidentata* and *Cantharidus lepidus* by rock lobsters (46 to 78 mm carapace length), by multi-choice experiments in indoor aquaria (60 × 40 × 40 cm) supplied with running seawater. Six rock lobsters (1 per aquarium) were offered 10 adult individuals (10 to 16 mm of total body

whorl) of each gastropod species after 48 h of starvation. All aquaria lacked any structure where prey could shelter. We recorded consumption after another 48 h, and differences in survival of the 2 species of gastropods and consumption rates of individual rock lobsters were tested with logistic regression.

Recruitment patterns of gastropods in seagrasses. Artificial seaweed units (ASUs, 165 cm³ of volume; Fig. S5 in our supplement, Rule & Smith 2007) were used to test whether proximity to reefs (0 versus >300 m) altered the recruitment patterns of gastropods in seagrass meadows. We selected 4 reefs (a subset of those reefs where gastropod collections took place) in Marmion, with 2 reefs adjacent to *Amphibolis* and 2 reefs adjacent *Posidonia* meadows. Two ASUs were attached to each of 3 metal stakes 5 to 10 cm above the bottom for each distance; this height was chosen as a compromise between deploying the collectors within the seagrass canopy and minimising the influence of sediments, which we were unable to quantify. ASUs were collected after 4 wk in June 2007 by sealing them in separate resealable plastic bags. This is the period when recruitment of many species of molluscs, including *Pyrene bidentata* and *Cantharidus lepidus*, occurs in the study region (Edgar 1990a). In the laboratory, each collector was washed over a sieve with 0.5 mm mesh in fresh water. All gastropods were identified, counted and measured (total body whorl) to the nearest millimeter. We analyzed 5 ASUs per distance to maintain a balanced design (some ASUs were lost). Patterns of recruit abundance were examined using 3-way ANOVA, incorporating the factors: 'Seagrass' (fixed factor), 'Reef' (random factor nested within 'Seagrass') and 'Distance' (fixed factor orthogonal to the previous factors). Data were $\ln(x + 1)$ transformed.

RESULTS

Distribution of gastropods

For most gastropod species, abundance increased with vegetation biomass (Tables 1 & 2), particularly for the most abundant taxa (e.g. *Pyrene bidentata* and *Phasianella* spp.). We observed contrasting patterns of abundance among taxa of herbivorous gastropods in seagrass meadows with varying proximity to reefs. Some taxa decreased in abundance with increasing distance from reefs (*Pyrene bidentata*, Fig. 1A; *Phasianella* spp., Fig. 1B); the magnitude, but not the direction, of these differences varied from reef to reef ('Reef [Location × Seagrass] × Distance', $p < 0.01$; Tables 1 & 2). For these 2 taxa, abundances were higher in seagrasses immediately adjacent to reefs (0 m) relative to seagrass interiors (>300 m away from

structural elements of each seagrass species that did not vary with proximity to reefs ('Distance', $p > 0.10$ in all cases; Tables S2 & S3 in the supplement). Since the biomass of each seagrass species was then irrespective of proximity to reefs, the assumption of independence of the covariate (vegetation biomass) and the treatment effects was valid.

Distribution of predators

Predatory fish were, in general, more abundant on reefs than in adjacent seagrass meadows (Fig. 2), although the magnitude of these differences varied from reef to reef ('Reef [Location \times Seagrass] \times Distance', $p < 0.01$; Table 3). In most cases, fish abun-

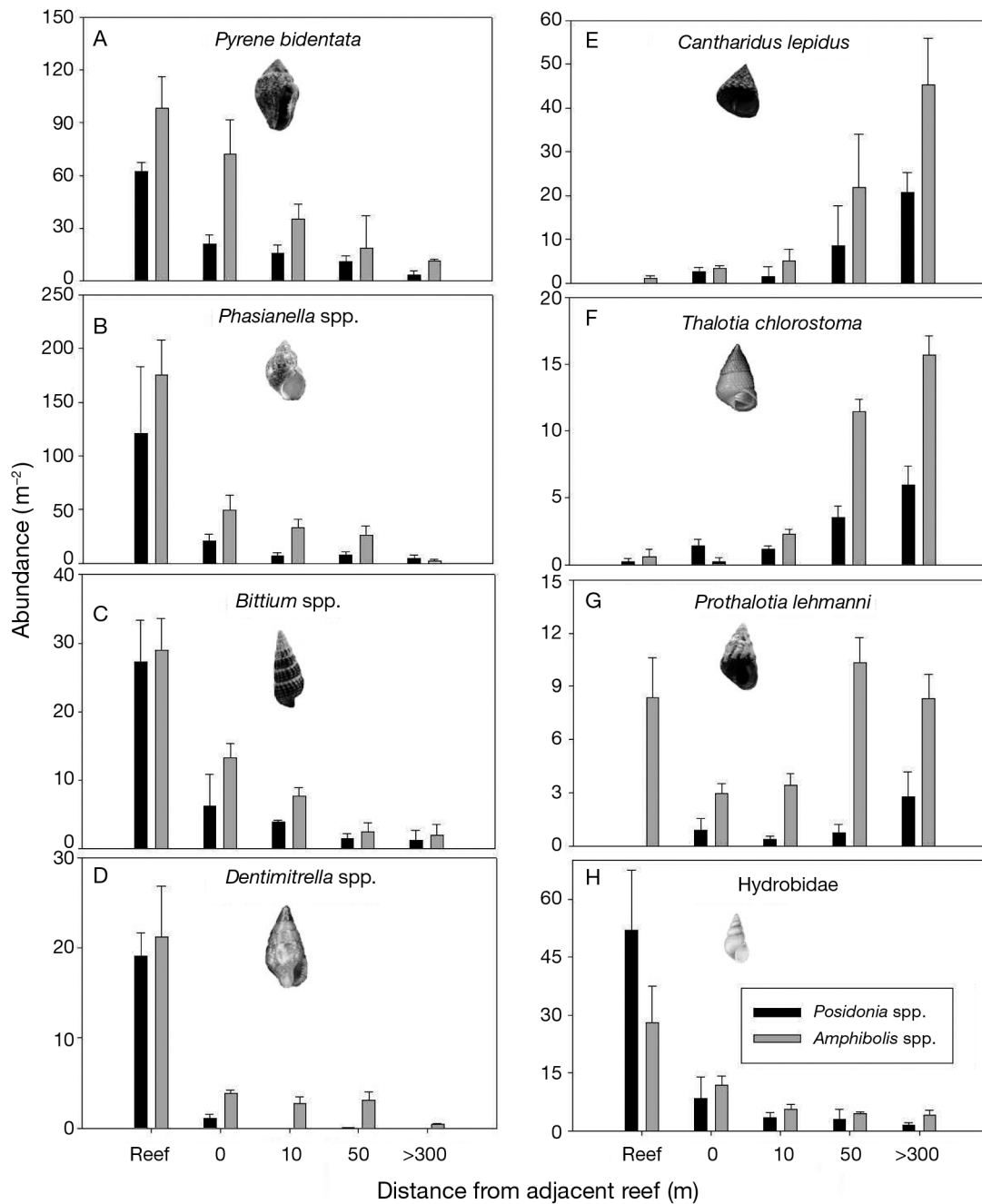


Fig. 1. Abundances (mean + SE, n = 60) of gastropods on reefs and at various distances in adjacent seagrass meadows dominated by either *Amphibolis* or *Posidonia* (data pooled through all random variability: locations, reefs within each location and surveys)

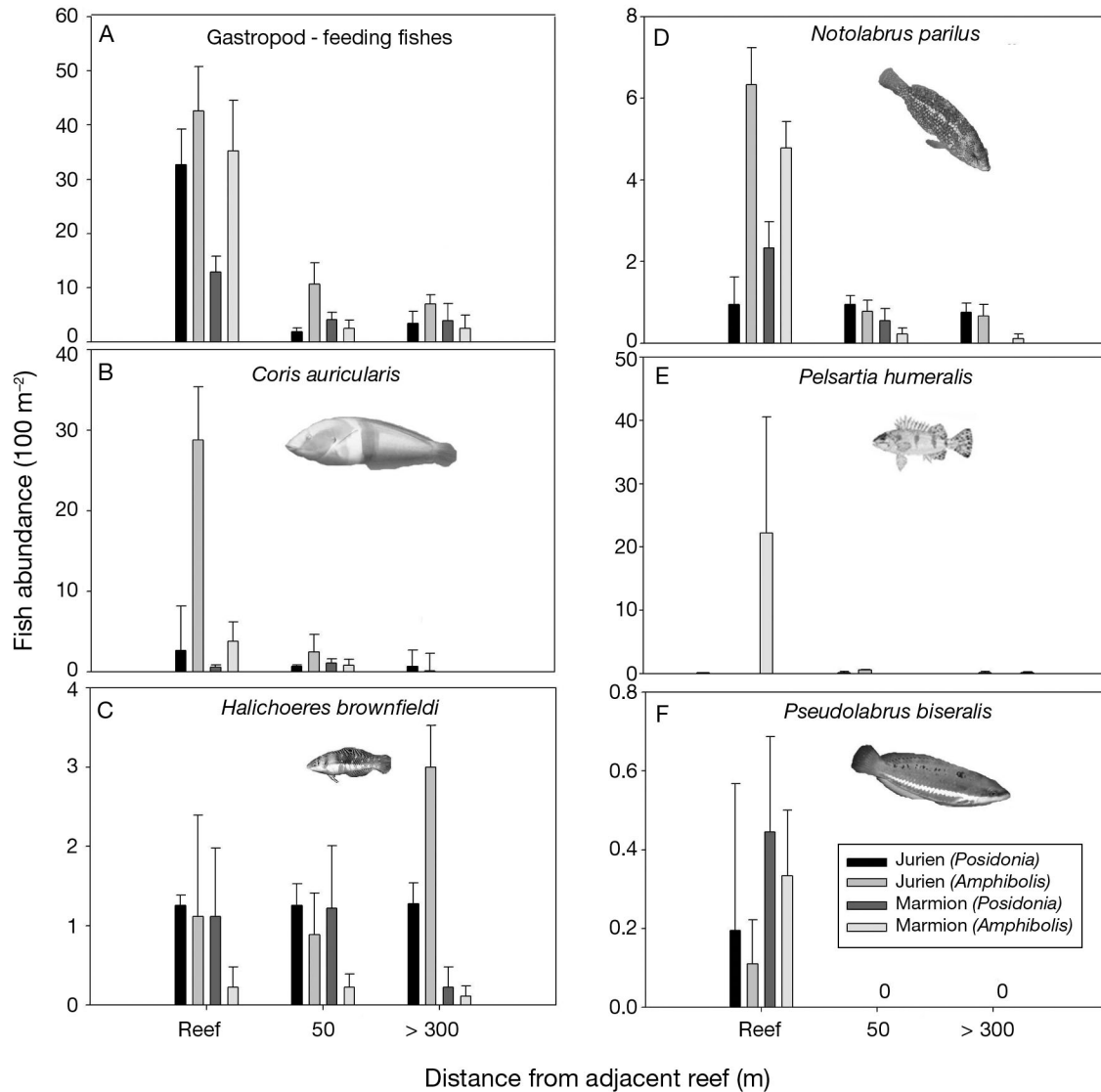


Fig. 2. Abundances (mean + SE, n = 9) of predatory fishes on reefs and at various distances in adjacent seagrass meadows dominated by either *Amphibolis* or *Posidonia* (data pooled through all random variability: locations and reefs within each location)

Table 3. Results of ANOVA (*F*-ratios) testing the effects of 'Location' (Lo), 'Seagrass' (Sg), 'Reef' and 'Distance' (Di) on the abundance of predatory fishes. ***p* < 0.01, *0.01 < *p* < 0.05

	df	MS denominator term	Predatory fishes	<i>Coris auricularis</i>	<i>Halichoeres brownfieldi</i>	<i>Notolabrus parilus</i>	<i>Pelsartia humeralis</i>	<i>Pseudolabrus biserialis</i>
Location	1	Reef (Lo × Sg)	7.87*	8.22**	4.34	4.46	0.65	0
Seagrass	1	Reef (Lo × Sg)	0.08	0.36	0.25	12.39*	6.18	0.64
Reef (Lo × Sg)	8	Residual	3.43**	8.98**	1.08	1.43	0.4	8.00**
Distance	2	Reef (Lo × Sg) × Di	66.80**	13.47**	1.69	67.46**	1	3.50*
Lo × Sg	1	Reef (Lo × Sg)	2.19	0.07	0.62	0.92	0.18	0.28
Lo × Di	2	Reef (Lo × Sg) × Di	1.62	10.29**	4.35*	1.18	1.17	0
Sg × Di	2	Reef (Lo × Sg) × Di	7.04	0.24	0.37	7.51**	0.67	0.64
Reef (Lo × Sg) × Di	16	Residual	2.04*	6.84**	0.74	1.66	1	8.00**
Lo × Sg × Di	2	Reef (Lo × Sg) × Di	0.08	0.02	0.4	0.04	1.41	0.28
Residual	72							

dance was higher on reefs relative to seagrass meadows at both distances surveyed (i.e. both 50 and >300 m distances, Table S4). *Halichoeres brownfieldi*

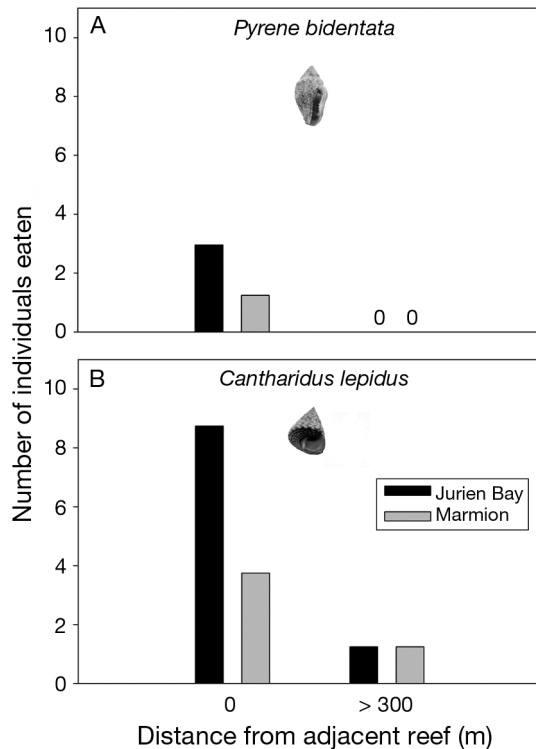


Fig. 3. Relative intensity of predation (number of tethered gastropods eaten during 5 days, $n = 20$) on *P. bidentata* and *C. lepidus* in seagrass meadows at various distances from adjacent reefs

Table 4. Results of logistic regression testing for differences in survival of tethered gastropods. All lower-level interactions were highly nonsignificant ($p > 0.8$)

Source of variation	df	Deviance	p
Species (Sp, <i>Pyrene bidentata</i> vs. <i>Cantharidus lepidus</i>)	1	6.34	0.012
Seagrass (Sg)	1	0.08	0.782
Sp \times Sg	1	0.28	0.599
Location (Lo)	1	1.94	0.163
Sp \times Lo	1	0.004	0.950
Sg \times Lo	1	2.60	0.107
Sp \times Sg \times Lo	1	0.25	0.619
Reef (Sg \times Lo)	4	6.29	0.178
Sp \times Reef (Sg \times Lo)	4	7.08	0.132
Distance (Di)	1	11.65	0.0006
Sp \times Di	1	0.71	0.400
Sg \times Di	1	4.47	0.034
Lo \times Di	1	0.006	0.938
Residual	128	56.86	1.000

was the only exception to this general pattern (Fig. 2C), being equally abundant on reefs and in seagrass meadows. *Pelsartia humeralis* was only present in appreciable numbers at one reef (Fig. 2E; 'Distance', $p > 0.2$; Table 3). Abundance of *Noto labrus parilus* decreased with increasing distance from reefs, but the decrease was more pronounced in *Amphibolis* meadows (Fig. 2D; 'Seagrass \times Distance', $p < 0.01$; Table 3), due to the higher abundance of this species on reefs bordering *Amphibolis* meadows. On the whole, the total abundance of predatory fishes was greater at Jurien Bay compared with Marmion; this pattern was primarily driven by *Coris auricularis*, the most abundant predatory fish overall (Fig. 2A,B, respectively; 'Location', $p < 0.05$; Table 3). Similarly, rock lobsters were more abundant in Jurien Bay (1.54 ± 0.23 individuals [ind.] 100 m^{-2} , mean \pm SE) relative to Marmion, where no individuals were observed in the transects.

Predation on gastropods

Predation intensity on tethered gastropods was greater in seagrasses at 0 m than at >300 m away from reefs for both species of gastropods (Fig. 3A,B; 'Distance', $p < 0.01$; Table 4), with an odds ratio of 7.6 (i.e. tethered gastropods were 7.6 times more likely to be consumed at 0 m than at >300 m). Predation on *Cantharidus lepidus* (Fig. 3B) was higher than on *Pyrene bidentata* (Fig. 3A) ('Species', $p < 0.01$; Table 4), with an odds ratio of 4.5 (*C. lepidus* was 4.5 times more likely to be consumed than *P. bidentata*). This was reflected in the laboratory experiments, in which *C. lepidus* was 4.7 times more likely to be consumed than was *P. bidentata* by rock lobsters ($df = 1$, Deviance = 16.08, $p < 0.001$), though variation in predation by individual lobsters was evident ($df = 5$, Deviance = 33.17, $p < 0.001$).

Recruitment of gastropods

Abundance of recruits of *Pyrene bidentata* in ASUs was higher in seagrasses at 0 m than at >300 m away from reefs (Fig. 4A; 'Distance', $p < 0.01$; Table 5), with ~90% of individuals in the size range of 2 to 4 mm (Fig. 4A inset). In contrast, the abundance of recruits of *Cantharidus lepidus* (all individuals were 2 to 4 mm, Fig. 4B inset) did not show consistent differences with distance from reefs (Fig. 4B; 'Distance', $p > 0.1$; Table 5), but showed inconsistent patterns from reef to reef ('Reef [Seagrass] \times Distance', $p < 0.01$; Table 5; pairwise comparisons indicated greater abundance far away from reefs at only one reef).

DISCUSSION

The present study demonstrates that ecological processes near habitat margins where seagrasses and reefs are juxtaposed can strongly influence the patterns of abundance of seagrass fauna. We documented a shift in the intensity of, and in the balance between, positive (recruitment) and negative (predation) effects on abundance from reef–seagrass edges to seagrass interiors. The balance was different between 2 gastropod species, and culminated in contrasting distributions with increasing distance from habitat edges. Importantly, the patterns in abundance that are the outcome of these competing processes were consistent in the 2 years that surveys were conducted. Most of these results, nonetheless, were obtained in just one season (austral summer/autumn), so we cannot rule

Table 5. Results of ANOVA (F -ratios) testing the effects of 'Seagrass' (Sg), 'Reef' and 'Distance' (Di) on the abundance of recruits of gastropods in artificial seaweed units. Data were $\ln(x + 1)$ transformed. ** $p < 0.01$, * $0.01 < p < 0.05$

	df	MS denominator term	<i>Pyrene bidentata</i>	<i>Cantharidus lepidus</i>
Seagrass	1	Reef (Sg)	18.94	8.44
Reef (Sg)	2	Residual	0.21	4.21*
Distance	1	Reef (Sg) \times Di	130.26**	0.15
Sg \times Di	1	Reef (Sg) \times Di	20.57*	0.33
Reef (Sg) \times Di	2	Residual	0.21	8.50**
Residual	32			

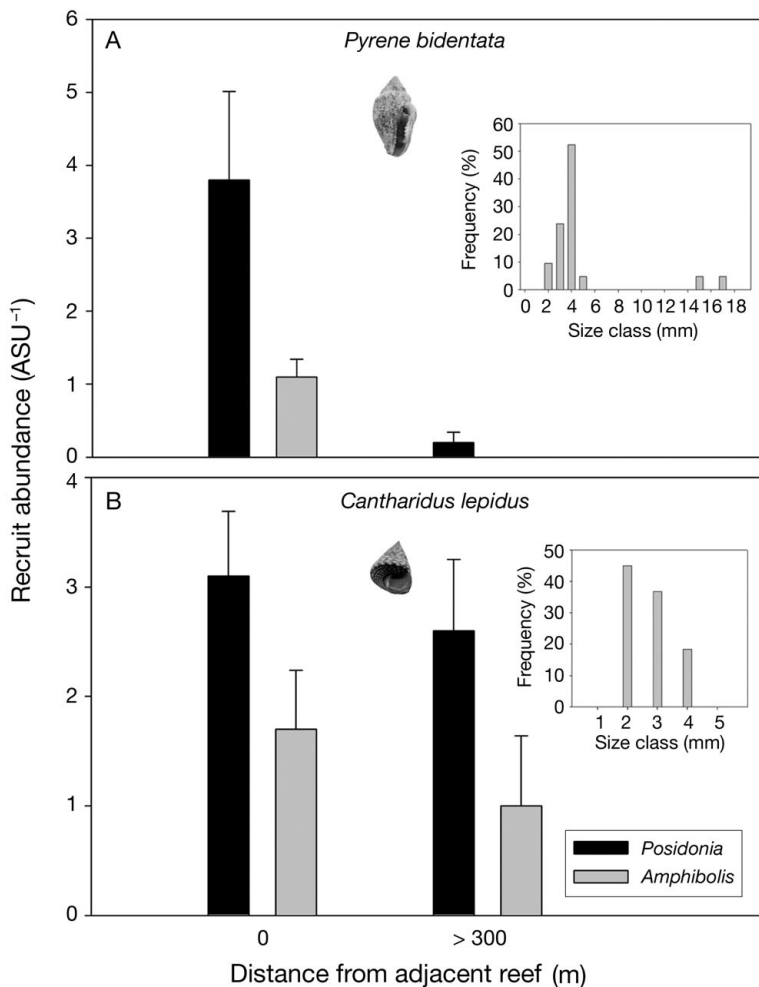


Fig. 4. Abundances (mean + SE, $n = 10$) of recruits of *Pyrene bidentata* and *Cantharidus lepidus* in artificial seaweed units (ASUs) placed in seagrass meadows at various distances from adjacent reefs dominated by either *Amphibolis* or *Posidonia*. Insets: size-class distributions (total body whorl); data pooled through reefs (random variability) as well as from the 2 types of seagrass meadows as this factor was nonsignificant (Table 5)

out that some of these outcomes can change over large time scales. Moreover, our experimental measurements (predation and recruitment patterns) were, due to logistical constraints, limited to the endpoints of the reef–seagrass landscape, so we cannot unambiguously leave out other potential factors that can affect these processes along reef–seagrass landscapes.

Proximity to reefs influences predator abundances and predation rates

Predatory fish were considerably more abundant on reefs than in seagrass meadows away from reefs, reflecting the global generality of this pattern for carnivorous fishes where reefs and seagrasses are adjacent (Dorenbosch et al. 2005, Vanderklift et al. 2007, Valentine et al. 2008). In addition to fishes, the western rock lobster *Panulirus cygnus* moves from reefs to adjacent seagrass meadows during the night to forage (Edgar 1990a,b), typically within ~50 m of the reef edge (MacArthur et al. 2008). This concentration of predators near reefs matched the spatial patterns in predation intensity on both species of gastropods used in the tethering experiments. The higher predation detected at Jurien Bay is also consistent with the higher abundance of predators (fishes and rock lobsters) at this location.

The higher abundance of predatory fishes in seagrasses adjacent to reefs, regardless of the dominant seagrass species, is similar to the finding of previous studies using similar visual techniques in the study area (Wernberg et al. 2006,

Vanderklift et al. 2007), although this outcome might differ if other techniques were implemented, because visual counts underestimate cryptic species (Hyndes et al. 2003). The spatial correspondence between abundance of predators and rates of predation on tethered prey suggests that cryptic predators are probably not important predators of gastropods. However, it is also possible that other cryptic predators, such as octopuses and other molluscs, help drive the observed abundance patterns by foraging at a higher intensity closer to reefs.

Predation by reef-associated predators may also explain gradients in abundance of fauna in soft bottoms adjacent to reefs (Langlois et al. 2005, Galvan et al. 2008). Similarly, higher predation in seagrass meadows immediately adjacent to reefs was probably due to the greater densities of predators (fishes and rock lobsters) on and near reefs. These results demonstrate the importance of proximity to edges not only for predator abundance, but also as a key influence on the strength of predation (Rand et al. 2006).

Prey identity influences predation intensity

The intensity of predation, and its effect on prey abundance, varied considerably between prey species. Selection of molluscan prey depends, among other factors, on prey morphology, which influences a predator's handling time (Seitz et al. 2001). The vulnerability of gastropods to shell-crushing predation by crustaceans decreases with an increase in shell wall thickness (Robles et al. 1990). In our study, *Cantharidus lepidus* was more frequently consumed in field and laboratory experiments than was *Pyrene bidentata*; in turn, because of its comparatively thin shell (Edgar 1990b), *C. lepidus* is one of the main gastropod prey of western rock lobsters in the study area (MacArthur et al. 2006). In contrast, rock lobsters have great difficulty breaking through the thicker shell of *P. bidentata* (Edgar 1990b), which was confirmed in our laboratory experiments. Indeed, adult *P. bidentata* have low rates of mortality and survive for several years (Edgar 1990a,b). At the moment, we cannot differentiate between the effects of predation by rock lobsters and fishes. However, it is also likely that the vulnerability of *C. lepidus* to fish predation is greater relative to that for *P. bidentata*, since fish have similar difficulties with thick-shelled prey (Palmer 1979).

Proximity to reefs influences the supply of recruits

Proximity to sources of recruits influences patterns in composition and abundance of biota (Witman & Day-

ton 2001). For example, proximity to reefs affects the epiphytes colonizing adjacent seagrass meadows (Van Elven et al. 2004). Artificial substrata are mainly colonized through recruitment of planktonic larvae or migration (e.g. drifting, crawling) of juveniles and adults from nearby habitats (Rule & Smith 2007). The prevailing mechanism depends on the larval ecology of each species. Most individuals of both *Pyrene bidentata* and *Cantharidus lepidus* collected in the ASUs were uniformly small, and thus were probably new recruits from the same cohort.

The larval ecology of *Pyrene bidentata* is unknown; however, larvae of pyrenid gastropods are typically nonplanktonic, developing within egg masses until they emerge as crawling juveniles (Amio 1955, Wilson 1993). *P. bidentata* can easily colonize artificial seaweed units several meters away from adjacent algal patches (Tuya et al. 2009). Dispersion of individuals from either the reef or the surrounding seagrass, both of which hosted greater abundance of *P. bidentata* than seagrass interiors, therefore probably explains the greater recruitment of *P. bidentata* at seagrass edges relative to interiors. In contrast, abundance of recruits of *Cantharidus lepidus*, which were not abundant on or near reefs (Tuya et al. 2008, present study), varied little in seagrasses with proximity to reefs. Most Australasian trochid gastropods have a short planktonic larval stage (Wilson 1993), typically ~1 wk (Edgar 2000). The spatial extent over which larvae of *C. lepidus* can disperse is thus probably greater than *P. bidentata*, a trait that probably explains the invariance of *C. lepidus* recruit abundance with proximity to reefs.

Minor effects of seagrass species on patterns and processes with proximity to reefs

The physiognomy of seagrasses can interact with different factors (e.g. predation, competition) to alter ecological patterns and the magnitude of ecological processes (Hemminga & Duarte 2000, Heck & Orth 2006). However, patterns and processes in seagrasses with proximity to reefs were, in general, consistent in direction (although for some variables varied in magnitude) between *Posidonia* and *Amphibolis* seagrass meadows, highlighting the generality of our findings across 2 types of seagrass habitats. Moreover, significant changes in the density of both seagrass species with varying proximity to reefs were not detected, so we can rule out the potential confounding effect of seagrass habitat structure on the patterns and processes outlined by the present study on seagrass with varying proximity to reefs.

High predation of tethered gastropods occurred in seagrasses near reefs for both *Posidonia* and *Amphibolis* meadows, although the magnitude of predation was

different. This outcome is similar to the consumption of crabs (Vanderklift et al. 2007) and detached kelp (Wernberg et al. 2006) in both seagrasses with varying proximity to reefs in the study area. Therefore, these results suggest a lack of interactive effects between proximity to reefs and the dominant species of seagrass as determinants of the intensity of these 'top-down' processes.

Balance between positive and negative influences depends on proximity to reefs and species identity

Dispersal of individuals of *Pyrene bidentata* from either reefs or surrounding seagrass probably explains the greater recruitment of *P. bidentata* at seagrass margins relative to interiors. This may compensate for losses due to predation, facilitating high abundance in seagrasses adjacent to reefs despite higher predation here versus in seagrass meadow interiors. In contrast, predation considerably reduced the abundance of *Cantharidus lepidus* in seagrasses adjacent to reefs, while reefs did not affect recruitment patterns, so that this species was more abundant in seagrass meadow interiors.

Historically, small herbivorous gastropods have been often considered as a homogeneous functional group in marine habitats, such as seagrass meadows; however, the relevance of species identity in the functioning of seagrass ecosystems is increasingly recognized (Duffy et al. 2001). Our study supports the notion that species identity does matter not only for the functioning of seagrass ecosystems, but it also strongly influences the patterns of abundance and distribution that emerge from the various competing processes. We documented that the intensity of linkages between seagrass meadows and reefs depends on proximity, but also is strongly connected with the identities of predators and prey. As a result, generalizations concerning the relative importance of different ecological processes, even within the same assemblage, are therefore dependent on the identities of the species, as has been reported from tropical coral reefs (Burkepile & Hay 2008). A challenge for ecologists is to quantify the traits that enable species to flourish in different circumstances.

In summary, proximity to habitat margins influenced abundance and distribution patterns of herbivorous fauna by changing the balance of forces influencing the mortality (predation) and the replenishment (recruitment) of these populations from habitat edges to interiors.

Acknowledgements. F.T. was supported by a postdoctoral research fellowship within the MEC framework Plan de Formación y Perfeccionamiento. This work was funded by an ECU Faculty Small Grant and the Strategic Research Fund for the Marine Environment. The Western Australia Department

of Fisheries kindly enabled access to an indoor tanks facility. We thank A. Abelardo, N. Alcorriz, C. Doropoulos, A. Gartner, P. Lavery and B. Toohey for their help during the field work. P. Lavery, T. Langlois, L. MacArthur and 4 anonymous reviewers provided constructive comments on previous drafts of the manuscript. The work detailed in this paper complies with the laws of Australia.

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*Editorial responsibility: Just Cebrian,
Dauphin Island, Alabama, USA*

*Submitted: April 20, 2009; Accepted: January 27, 2010
Proofs received from author(s): April 26, 2010*