Vol. 340: 235–243, 2007

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published June 18

# Proximity to reef influences density of small predatory fishes, while type of seagrass influences intensity of their predation on crabs

**Mathew A. Vanderklift[1,2,*], Jason How[2], Thomas Wernberg[2], Lachlan D. MacArthur[2], Kenneth L. Heck Jr.[3], John F. Valentine[3]**

[1]CSIRO Marine and Atmospheric Research, Private Bag 5, Wembley, Western Australia 6913, Australia
[2]Centre for Ecosystem Management, Edith Cowan University, 100 Joondalup Drive, Joondalup, Western Australia 6027, Australia
[3]Dauphin Island Sea Lab and University of South Alabama, 101 Bienville Boulevard, Dauphin Island, Alabama 36528-0369, USA

ABSTRACT: The magnitude of the influence that predators exert on their prey is partly determined by factors that influence the density and behaviour of predators, and partly by factors that influence the survival of prey in the presence of predators. We tested whether the presence of reefs influences the density of small predatory fishes inhabiting seagrass meadows, and the intensity of predation by these fishes on tethered crabs, by taking measurements at increasing distances from 10 rocky reefs at 2 locations separated by several hundred km. We also tested whether these variables were influenced by type of seagrass by comparing patterns yielded in meadows dominated by *Amphibolis* spp. and *Posidonia sinuosa*, 2 seagrasses with different morphological and architectural characteristics. The densities of small predatory fishes declined rapidly with increasing distance from reefs, with significantly lower densities 30 m from reefs than immediately adjacent to reefs. Densities >300 m from reefs were generally not significantly different to densities 30 m from reefs. However, the survival of tethered crabs showed no consistent trend associated with distance from reefs. Type of seagrass was not a significant influence on the density of small predatory fishes, but did influence the survival of tethered crabs: those in *Amphibolis* spp. meadows were 3.1× more likely to be eaten than those in *P. sinuosa* meadows. These patterns were consistent between locations. Our results suggest that over landscape scales (hundreds of metres) reefs are an important influence on abundance of small predatory fishes, but not on the intensity of predation on crabs. Differences in the intensity of predation between the 2 seagrass species are likely due to their dissimilar morphological and architectural characteristics.

KEY WORDS: Connectivity · Food webs · Habitat linkages · Seagrass morphology · Shelter · Wrasse

*Resale or republication not permitted without written consent of the publisher*

## INTRODUCTION

Trophic interactions that link discrete habitats can exert a profound influence on the abundance and distribution of organisms (Polis et al. 1997). 'Bottom-up' influences generated by movements of nutrients or detritus can increase primary production and abundances of consumers in a wide variety of habitats (e.g. Polis & Hurd 1995, Wallace et al. 1997, Kitchell et al. 1999). 'Top-down' influences exerted by consumers that forage across multiple habitats can also be strong. Polis et al. (1997) proposed that the magnitude of the influence of consumers moving into a habitat to feed will depend on the interaction between consumer immigration and prey productivity. Following this prediction, the effects of cross-habitat foraging by consumers might be expected to be highest at ecotones bordering favoured shelter habitat, as consumers might forage most intensively in the vicinity of their shelter.

Subtidal reefs, both coral and rock, are habitats that often harbour high densities of consumers, and densi-

---

*Email: mat.vanderklift@csiro.au

© Inter-Research 2007 · www.int-res.com

ties of consumers in adjacent habitats often decline with increasing distance from reefs (e.g. Dorenbosch et al. 2005, Wernberg et al. 2006, Valentine et al. 2007). Many reef-associated consumers show distinct patterns of movement to seek prey in adjacent habitats (e.g. Jernakoff 1987, Burke 1995). Experimental studies have often shown that the intensity of predation and herbivory matches these trends in consumer density, with intensity declining with increasing distance from reefs (e.g. Shulman 1985, Valentine et al. 2007). Prey densities often show the opposite trend, increasing with distance from reefs, a pattern consistent with a 'top-down' influence by predators (e.g. Posey & Ambrose 1994, Langlois et al. 2005). Experiments have sometimes shown that prey densities near reefs increase when predators are excluded (e.g. Posey & Ambrose 1994, Langlois et al. 2006), but not always, indicating that other influences might often be more important (e.g. Jones et al. 1992, Barros 2005).

The influence of predators is typically reduced when shelter is available for prey species. Seagrass meadows provide shelter, and a number of studies have found lower mortality of prey in seagrass compared with unvegetated habitats (see review by Heck et al. 2003). There is likely to be variation in the shelter provided by different seagrass beds; Orth et al. (1984) predicted that shoot density and plant morphology should be important influences on the value of seagrass as shelter from predators. Higher densities of seagrass do seem to provide better shelter, as measured by survival of prey (e.g. Hovel & Lipcius 2001; see also review by Orth et al. 1984). The influence of plant morphology is less well understood, as there have been few studies contrasting the value of shelter in seagrasses with different morphology. Some studies have indicated higher survival of prey in complex habitats, while others have not (see review by Heck & Orth 2006). Potentially, variations in plant morphology could influence the gradients in predation that occur with distance from reefs by influencing the intensity of interactions between predators and their prey.

We tested the general predictions that (1) the density of small predatory fishes, and (2) predation intensity (measured as mortality of tethered crabs), in seagrass will decrease with increasing distance from reefs. We tested these predictions for 2 different types of seagrass with markedly different morphologies: *Posidonia sinuosa*, which has simple strap-like leaves extending from underground rhizomes, and *Amphibolis* spp. (*A. griffithii* and *A. antarctica*), which have thin lignified stems that support clusters of small leaves. We also tested for the spatial consistency of patterns among reefs separated by hundreds of metres to kilometres, and among locations separated by hundreds of kilometres.

## MATERIALS AND METHODS

**Study area.** The study was conducted at 2 locations on the lower west coast of Australia: Marmion Lagoon (31° 49.4′ S, 115° 44.0′ E) and Jurien Bay (30° 17.3′ S, 115° 02.5′ E). This region is characterised by series of aeolianite limestone ridges that run parallel to the coast at distances ranging from 1 to 10 km offshore, forming chains of rocky reefs and islands (Searle & Semeniuk 1985): around these reefs are extensive seagrass meadows, dominated by *Posidonia* and *Amphibolis*. The study was conducted in the austral summer, between January and April 2004.

**Fish assemblage.** We censused fishes in seagrass meadows adjacent to 6 reefs in Jurien Bay and 4 reefs in Marmion Lagoon. All reefs had high vertical relief and all were adjacent to extensive seagrass meadows. To allow an explicit test of the effect of type of seagrass, half of the reefs selected in each location (i.e. 3 reefs in Jurien Bay and 2 reefs in Marmion Lagoon) were adjacent to meadows of *Amphibolis* spp. (primarily *A. griffithii*, with some *A. antarctica*), and half were adjacent to meadows of *Posidonia* spp. (primarily *P. sinuosa*, with some *P. australis*). We tested for the effect of proximity to reef by taking measurements at 3 distances relative to each reef: 0 m (immediately adjacent to the reef), 30 m and >300 m. The furthest distance ranged from 300 to 1100 m away from reef, sampling the first continuous meadow beyond 300 m. Depths of the seagrass meadows at each reef ranged between 1.5 and 8 m immediately adjacent to reefs and 4 and 9 m at the furthest distances from the reefs. At each distance at each reef, we counted individuals of each species of fish observed in two 25 × 5 m transects oriented approximately parallel to the reef edge. This was repeated during daylight hours on 3 days, yielding a total of 6 replicate transects.

We analysed patterns in the abundance of wrasses (family Labridae, an abundant and ubiquitous family of fishes in this region, all of which are predators), known and suspected predators of crabs (including wrasses), and dominant species of predators (arbitrarily determined as species for which >150 individuals were recorded and that occurred in >40 transects) by mixed effects ANOVA, testing for differences between types of seagrass (fixed effect with 2 levels), between locations (random effect with 2 levels), among reefs (nested within location and type of seagrass, 3 levels for each combination at Jurien Bay, 2 levels for each combination at Marmion Lagoon) and among distances (fixed factor, 3 levels). Data were first tested for heteroscedasticity using Cochran's test, and for normality using normal probability plots, and were log-transformed if necessary. Transformation stabilised variance and improved normality in all cases.

**Relative predation intensity.** The relative intensity of predation was assessed by measuring the survival of tethered crabs placed in the seagrass for 24 h. We used brachyuran crabs (the grapsid *Cyclograpsus audouinii* and the menippid *Ozius truncatus*) collected from the shore. While the use of prey that are out of their normal habitat might reduce the robustness of inferences, it was necessary to use them as crabs were extremely scarce in the seagrass (see also Heck & Wilson 1987). Although more characteristic of hard-bottom habitats, these species can be found in seagrass, e.g. Kirkman et al. (1991). Other brachyuran crabs of similar size are characteristic of seagrass beds in south-western Australia (e.g. Kirkman et al. 1991, Orth et al. 2006), and so tests of models using these species should yield relevant inferences. Crabs were measured (carapace width, mm) and tethered by tying a loop of monofilament line around the carapace, and then attaching the loop to the carapace with cyanoacrylate glue. The other end of the monofilament line (ca. 20 cm long) was tied to a metal stake, which was pushed into the sediment. At least 3 tethered crabs were deployed on each of 2 days at 5 distances (0, 10, 20, 30 and >300 m) from each reef. We retrieved the tethers after 24 h and scored the crabs as alive or eaten (empty loop of line, or loop with fragment of carapace remaining) or uncertain (entire line missing or cut). The carapace widths of crabs ranged from 6 to 42 mm (mean: 17.4 mm). To test for the possibility that crabs might be able to escape from the tethers, which would confound our estimates of survival, we placed 10 tethered individuals of each species in separate 15 l tanks for 3 d. None escaped from their tethers, so our assessment of empty loops of line as indicators of predation is likely to be robust.

For analysis, we pooled results from the different days, removed uncertain observations, and randomly removed other observations to achieve a constant sample size (n = 5 tethered crabs per distance per reef). We analysed these data with multiple logistic regression, testing for the effects of carapace width, type of seagrass (*Amphibolis* vs. *Posidonia*), location (Jurien Bay vs. Marmion Lagoon), distance from reef (0, 10, 20, 30 and >300 m from each reef), and reef (nested in the seagrass × location interaction). We were most interested in testing whether coefficients for each of the factors, and interactions between factors, were significant (and therefore a rejection of the $H_0$ that a coefficient was zero) so we focussed on the significance of the deviances, tested using a $\chi^2$ test (Hosmer & Lemeshow 2000).

Because of the possibility that differences in survival between types of seagrass could be due to some artefact associated with the tethering, specifically differences in the degree of entanglement that might reduce the ability of crabs to escape (Peterson & Black 1994), instead of real differences in predation pressure, we conducted a test for the presence of such artefacts. For this study, we deployed 2 replicate cages of 1.5 × 1.5 m (2.25 $m^2$) constructed of black polyethylene mesh (2″ stretched) in meadows of each type of seagrass (*Posidonia sinuosa* and *Amphibolis* spp.). Five tethered crabs were placed in each cage, and in 2 uncaged plots in each type of seagrass. The cages were intended to protect crabs from predators so that the degree of entanglement of individual crabs could be assessed; however, the cages did not successfully exclude predators, as only 50% of crabs inside cages remained after 24 h, with the others showing evidence of predation. We scored all surviving crabs in caged and uncaged plots as either tangled or untangled, and tested for differences between *P. sinuosa* and *Amphibolis* spp. using logistic regression.

## RESULTS

### Fish abundance

A total of 28 species of fishes were classified as known or suspected predators of crabs (Table 1). Abundance of these predators varied significantly among distances, but the nature of differences was not consistent at all reefs (significant 'reef × distance' interaction in Table 2a). Student-Newman-Keuls (SNK) tests indicated that abundance at 0 m (overall mean number of individuals 125 $m^{-2}$ ± SE; 17.8 ± 2.1) was always significantly higher than abundance at >300 m, and usually significantly higher than at 30 m (8 out of 10 reefs, see also Fig. 1). Differences in abundance between 30 and >300 m were irregular, although abundance overall was higher at 30 m (6.7 ± 2.8) than >300 m (3.7 ± 1.2). There was no difference in abundances of these fishes between types of seagrass (Table 2a).

Wrasses (family Labridae) comprised 44% of the total number of individual fish. The abundance of wrasses varied significantly among distances (Table 2b, Fig. 1). Wrasses were significantly more abundant at 0 m (14.9 ± 2.0) than at 30 m (2.8 ± 1.1) and >300 m (0.6 ± 0.1), indicating that overall the abundance of wrasses declined rapidly within a short distance from the reef edge. There was also significant variation among reefs, but not between locations or between types of seagrass (Table 2b).

The western king wrasse *Coris auricularis* was the most abundant species recorded (548 individuals), and was recorded adjacent to all reefs, but was rarely recorded away from reefs. There was a significant interaction between distance and reef (Table 3a): SNK tests indicated that at 9 of the 10 reefs abundance was significantly higher at 0 m than at 30 and >300 m.

Table 1. Species of small predatory fish (n = 28) recorded during this study, with the reference from which evidence for consumption of crabs was taken, and total abundance recorded for each distance from reef, pooled over all reefs surveyed. Species which probably consume crabs, but for which dietary data could not be found, are listed as 'Suspected' predators

| Species | Family | 0 m | 30 m | 300 m | Source |
|---|---|---|---|---|---|
| *Apogon victoriae* | Apogonidae | 55 | 7 | 93 | Linke et al. (2001) |
| *Apogon rueppellii* | Apogonidae | 1 | 23 | 78 | R. K. Howard (unpubl. data) |
| *Anoplocapros robustus* | Aracanidae | 2 | 0 | 1 | Suspected |
| *Pseudocaranx dentex* | Carangidae | 17 | 0 | 0 | Edgar & Shaw (1995) |
| *Cheilodactylus gibbosus* | Cheilodactylidae | 2 | 0 | 0 | www.fishbase.org |
| *Dactylophora nigricans* | Cheilodactylidae | 0 | 1 | 0 | www.fishbase.org |
| *Cheilodactylus rubrolabiatus* | Cheilodactylidae | 1 | 0 | 0 | www.fishbase.org |
| *Enoplosus armatus* | Enoplosidae | 7 | 1 | 1 | R. K. Howard (unpubl. data) |
| *Plectorhinchus flavomaculatus* | Haemulidae | 58 | 0 | 0 | R. K. Howard (unpubl. data) |
| *Choerodon rubescens* | Labridae | 3 | 0 | 0 | Lek (2004) |
| *Austrolabrus maculatus* | Labridae | 1 | 0 | 0 | www.fishbase.org |
| *Halichoeres brownfieldi* | Labridae | 227 | 110 | 22 | Edgar & Shaw (1995) |
| *Notolabrus parilus* | Labridae | 134 | 11 | 13 | MacArthur & Hyndes (2007) |
| *Thalassoma lutescens* | Labridae | 12 | 0 | 0 | www.fishbase.org |
| *Thalassoma lunare* | Labridae | 18 | 0 | 0 | www.fishbase.org |
| *Pseudolabrus biserialis* | Labridae | 2 | 0 | 0 | www.fishbase.org |
| *Thalassoma septemfasciata* | Labridae | 1 | 0 | 0 | Suspected |
| *Coris auricularis* | Labridae | 498 | 47 | 3 | Suspected |
| *Schuetta woodwardii* | Monodactylidae | 0 | 0 | 1 | R. K. Howard (unpubl. data) |
| *Parupeneus signatus* | Mullidae | 13 | 0 | 0 | Suspected |
| *Upeneichthys vlamingii* | Mullidae | 8 | 1 | 0 | Suspected |
| *Parupeneus chrysopleuron* | Mullidae | 2 | 0 | 0 | www.fishbase.org |
| *Haletta semifasciata* | Odacidae | 0 | 6 | 1 | MacArthur & Hyndes (2007) |
| *Pempheris klunzingeri* | Pempheridae | 2 | 0 | 0 | R. K. Howard (unpubl. data) |
| *Pelsartia humeralis* | Teraponidae | 0 | 41 | 2 | R. K. Howard (unpubl. data) |
| *Pelates sexlineatus* | Teraponidae | 0 | 150 | 0 | Edgar & Shaw (1995) |
| *Torguigener pleurogramma* | Tetraodontidae | 0 | 6 | 3 | Suspected |
| *Urolophus* sp. | Urolophidae | 0 | 0 | 3 | Platell et al. (1998) |

Overall there tended to be more *C. auricularis* at 0 m (8.3 ± 1.6) than at 30 m (0.8 ± 0.7) and >300 m (0.1 ± 0.04). There were no significant differences between locations or between types of seagrass (Table 3a).

Brownfield's wrasse *Halichoeres brownfieldi* was the second most abundant species (359 individuals), and was also recorded adjacent to all reefs. *H. brownfieldi* yielded the most constant abundances, and yielded no statistically significant spatial patterns (Table 3b). There were more individuals at 0 m (3.8 ± 1.0) than at 30 m (1.8 ± 0.7) and >300 m (0.4 ± 0.1), but this was not a statistically significant pattern. *H. brownfieldi* was regularly recorded at the farthest distance, occurring at >300 m at 8 of the 10 reefs.

The brown-spotted wrasse *Notolabrus parilus* was the most ubiquitous species, recorded in 37% of transects, and was the third most abundant species recorded (158 individuals). Like *Coris auricularis*, a significant interaction between distance and reef indicated that differences among distances were not consistent for all reefs (Table 3c), although overall more individuals were recorded at 0 m (2.2 ± 0.2) than at 30 m (0.2 ± 0.1) and >300 m (0.2 ± 0.1). At 9 of the 10 reefs, SNK tests indicated that abundance of *N. parilus* at 0 m was higher than abundance at 30 and >300 m. Differences in abundance between 30 and >300 m were not consistent among reefs. There were no significant differences between locations or between types of seagrass (Table 3c).

### Survival of tethered crabs

Survival of tethered crabs varied inconsistently among different combinations of type of seagrass, location and distance from reef (see significant 'seagrass × location × distance' interaction in Table 4, and patterns in Fig. 2). Despite this variation, some overall trends could be distinguished. On average, survival of tethered crabs was significantly lower in *Amphibolis* spp. than in *Posidonia sinuosa* meadows (Table 4), with an odds ratio of 3.1; this indicated that, when placed in *Amphibolis* spp., tethered crabs were 3.1× more likely to be eaten. There was no difference in the degree of entanglement between *P. sinuosa* and *Amphibolis* spp. (deviance = 0.049, p > 0.8), indicating that these

Table 2. Results of mixed effects ANOVA for effect of type of seagrass (fixed factor), location (random factor), reef within location and type of seagrass (nested random factor) and distance (fixed factor) on abundance of (a) small predatory fish and (b) wrasses. **Bold:** statistical significance at $p < 0.05$. All data log $(x + 1)$ transformed

| Source of variation | df | MS | *F* | p |
|---|---|---|---|---|
| **(a) Small predatory fish (including wrasses)** | | | | |
| Seagrass | 1 | 0.06 | 0.08 | 0.82 |
| Location | 1 | 17.45 | 4.88 | 0.07 |
| Seagrass × Location | 1 | 0.68 | 0.19 | 0.68 |
| Reef (Seagrass × Location) | 6 | 3.57 | 3.92 | **0.001** |
| Distance | 2 | 48.84 | 50.10 | **0.02** |
| Seagrass × Distance | 2 | 4.25 | 5.10 | 0.16 |
| Location × Distance | 2 | 0.97 | 0.48 | 0.63 |
| Seagrass × Location × Distance | 2 | 0.83 | 0.41 | 0.67 |
| Reef (Seagrass × Location) × Distance | 12 | 2.03 | 2.22 | **0.01** |
| Error | 150 | 0.91 | | |
| **(b) Wrasses only** | | | | |
| Seagrass | 1 | 4.54 | 3.15 | 0.33 |
| Location | 1 | 7.57 | 4.53 | 0.08 |
| Seagrass × Location | 1 | 1.44 | 0.86 | 0.39 |
| Reef (Seagrass × Location) | 6 | 1.67 | 2.46 | **0.03** |
| Distance | 2 | 68.30 | 120.50 | **0.01** |
| Seagrass × Distance | 2 | 0.94 | 2.79 | 0.26 |
| Location × Distance | 2 | 0.57 | 0.55 | 0.59 |
| Seagrass × Docation × Distance | 2 | 0.34 | 0.33 | 0.72 |
| Reef (Seagrass × Location) × Distance | 12 | 1.03 | 1.51 | 0.13 |
| Error | 150 | 0.68 | | |

differences were unlikely to be due to an experimental artefact.

Survival was significantly lower at Jurien Bay than at Marmion Lagoon (Table 4), with an odds ratio of 1.9, i.e. tethered crabs were 1.9× times more likely to be eaten at Jurien Bay than at Marmion Lagoon. Survival was also significantly different among reefs (Table 4): survival at Wreck Rock tended to be higher than other *Amphibolis* spp. meadows, while survival at Fisherman Islands tended to be lower than other *Posidonia sinuosa* meadows. Proximity to reef had no apparent overall influence on survival. The carapace width of tethered crabs also had no apparent influence on survival.

## DISCUSSION

The density of small predatory fish inhabiting seagrass meadows was strongly related to proximity to reef, but not to type of seagrass. In contrast, the survival of tethered crabs showed no consistent pattern related to proximity to reef, but differed between types of seagrass. We therefore found no simple relationship between density of small predatory fishes and predation intensity.

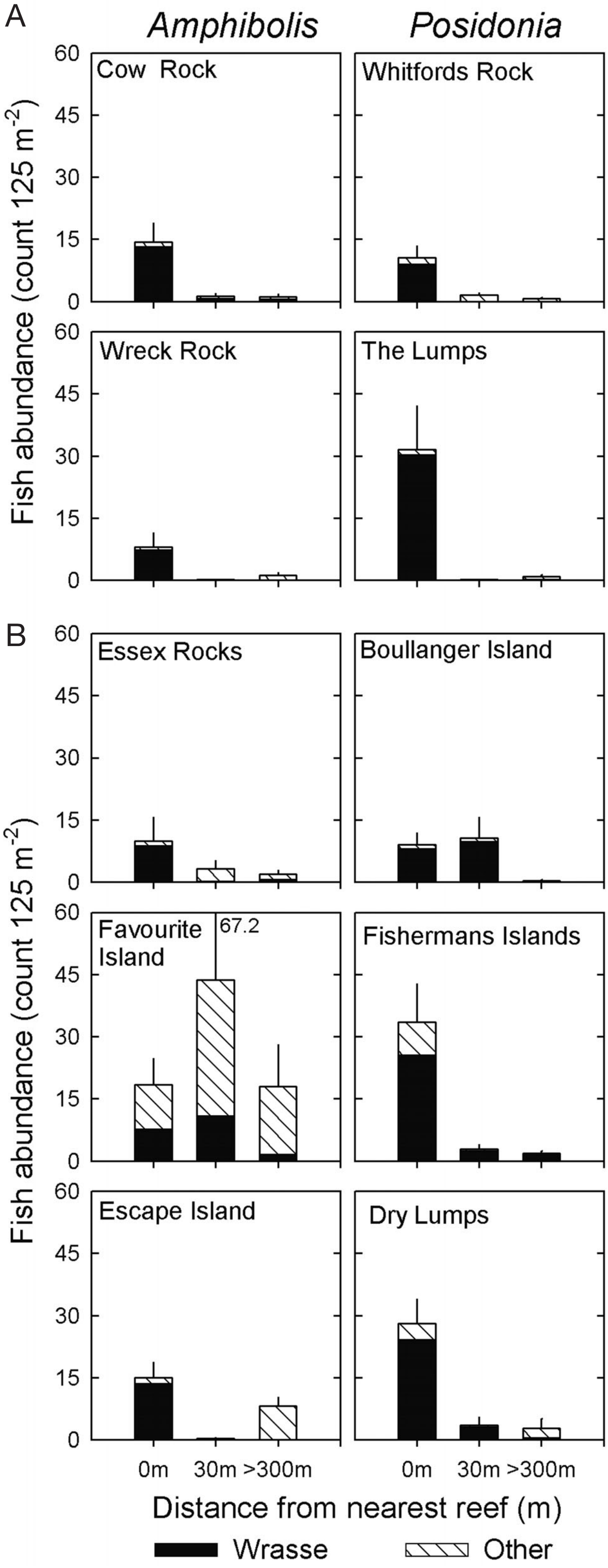

Fig. 1. Mean densities of fish that are potential predators of crabs (±SE, n = 6) in seagrass meadows adjacent to (A) 4 reefs in Marmion Lagoon and (B) 6 reefs in Jurien Bay. Other: abundance of other small predatory fishes

Table 3. Results of mixed effects ANOVA for effect of type of seagrass (fixed factor), location (fixed factor), reef within location and type of seagrass (nested random factor) and distance (fixed factor) on abundance of 3 abundant and ubiquitous species of wrasse. **Bold:** statistical significance at $p < 0.05$. All data were log $(x + 1)$ transformed

| Source of variation | df | MS | *F* | p |
|---|---|---|---|---|
| **(a) Western king wrasse *Coris auricularis*** | | | | |
| Seagrass | 1 | 1.08 | 16.58 | 0.15 |
| Location | 1 | 2.75 | 1.62 | 0.25 |
| Seagrass × Location | 1 | 0.06 | 0.04 | 0.85 |
| Reef (Seagrass × Location) | 6 | 1.70 | 3.59 | **0.002** |
| Distance | 2 | 38.96 | 48.97 | **0.02** |
| Seagrass × Distance | 2 | 2.00 | 45.43 | **0.02** |
| Location × Distance | 2 | 0.79 | 0.47 | 0.64 |
| Seagrass × Location × Distance | 2 | 0.04 | 0.02 | 0.97 |
| Reef (Seagrass × Location) × Distance | 12 | 1.70 | 3.59 | **<0.001** |
| Error | 150 | 0.47 | | |
| **(b) Brownfield's wrasse *Halichoeres brownfieldi*** | | | | |
| Seagrass | 1 | 2.08 | 0.75 | 0.54 |
| Location | 1 | 1.30 | 1.79 | 0.23 |
| Seagrass × Location | 1 | 2.75 | 3.79 | 0.10 |
| Reef (Seagrass × Location) | 6 | 0.72 | 1.09 | 0.37 |
| Distance | 2 | 5.79 | 2.74 | 0.27 |
| Seagrass × Distance | 2 | 0.22 | 0.57 | 0.63 |
| Location × Distance | 2 | 2.11 | 3.10 | 0.08 |
| Seagrass × Location × Distance | 2 | 0.39 | 0.57 | 0.58 |
| Reef (Seagrass × Location) × Distance | 12 | 0.68 | 1.02 | 0.43 |
| Error | 150 | 0.67 | | |
| **(c) Brown-spotted wrasse *Notolabrus parilus*** | | | | |
| Seagrass | 1 | 0.0003 | 0.11 | 0.80 |
| Location | 1 | 0.81 | 1.40 | 0.28 |
| Seagrass × Location | 1 | 0.002 | 0.004 | 0.95 |
| Reef (Seagrass × Location) | 6 | 0.58 | 3.88 | **0.001** |
| Distance | 2 | 15.80 | 136.30 | **0.01** |
| Seagrass × Distance | 2 | 0.31 | 3.74 | 0.21 |
| Location × Distance | 2 | 0.11 | 0.25 | 0.78 |
| Seagrass × Location × Distance | 2 | 0.08 | 0.18 | 0.83 |
| Reef (Seagrass × Location) × Distance | 12 | 0.45 | 3.05 | **<0.001** |
| Error | 150 | 0.15 | | |

## Proximity to reef influences fish density

The overall density of small predatory fish was consistently higher immediately adjacent to reefs, and declined abruptly away from reefs: there were significantly lower densities at 30 m from reefs than at 0 m. There was no consistent overall difference in density between 30 and >300 m from the reef, indicating that after the abrupt decline in density between 0 and 30 m, the density of small predatory fish remained low. These patterns were also generally reflected by two of the 3 most abundant small predatory fishes, *Coris auricularis* and *Notolabrus parilus*. The same patterns were found for herbivorous fishes by Wernberg et al. (2006) at the same study sites.

An essentially similar result was found in an area near our study locations by Howard (1989), who used gill nets placed both immediately adjacent to the limestone reefs, and at distances >25 m from the reefs. Although the species composition he reported is different (probably reflecting the different selectivities of the methods), the number of fish caught was higher at the reef edge (Howard 1989).

In tropical areas, similar patterns are present for fishes adjacent to coral reefs. In the Florida Keys (USA), the density of fish was significantly higher immediately adjacent to the reef than 30 m away (Valentine et al. 2007). Several small predatory fishes, as well as some larger piscivorous fishes, followed this same trend (Valentine et al. 2007). In contrast, a study in Zanzibar did not find that fish density declined significantly from immediately adjacent to the reef to 30 m away, although some reef-associated fishes were present adjacent to the reef that were not present away from the reef (Dorenbosch et al. 2005).

The high densities we recorded adjacent to the reefs might be due to reef-associated fishes foraging over adjacent seagrass; for example, the 3 most abundant wrasses in our study are also abundant over the reef habitat (M. A. Vanderklift unpubl. data). However, some of the species we recorded have also been recorded in seagrasses distant from reefs, e.g. *Notolabrus parilus* (Hyndes et al. 2003); for these species, the reasons for increases in density with proximity to reef are less clear.

This pattern of increasing fish density with increasing proximity to reef has been reported many times and seems to be quite common in landscapes with reef and seagrass habitats in close proximity. Many coral reef residents, such as adult parrotfishes and grunts, have long been known to forage daily in adjacent seagrass meadows (Ogden 1980). Thus, energy subsidies from seagrass meadows assist in maintaining the

Table 4. Results of logistic regression testing for difference in survival of tethered crabs (primarily *Cyclograpsus audouinii* and *Ozius truncatus*). **Bold**: statistical significance at $p < 0.05$

| Source of variation | df | Deviance | p |
|---|---|---|---|
| Carapace width | 1 | 2.67 | 0.102 |
| Seagrass | 1 | 12.40 | **<0.001** |
| Location | 1 | 4.54 | **0.033** |
| Seagrass × Location | 1 | 0.74 | 0.391 |
| Reef (Seagrass × Location) | 6 | 3.39 | **0.002** |
| Distance | 4 | 1.39 | 0.236 |
| Seagrass × Distance | 4 | 1.38 | 0.236 |
| Location × Distance | 4 | 1.28 | 0.277 |
| Seagrass × Location × Distance | 4 | 3.93 | **0.003** |
| Reef (Seagrass × Location) × Distance | 24 | 0.96 | 0.519 |
| Error | 197 | 0.86 | 0.924 |

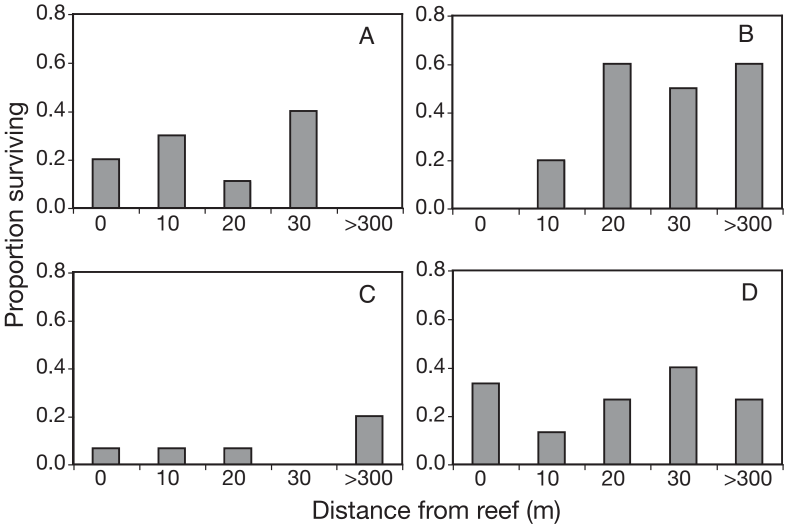

Fig. 2. (A,C) *Amphibolis* spp. and (B,D) *Posidonia sinuosa.* Proportion of tethered crabs surviving for 24 h in seagrass meadows at different distances from reefs in (A,B) Marmion Lagoon and (C,D) Jurien Bay

abundance of coral reef fishes (Valentine & Heck 2005). However, the reasons for this pattern have not been critically evaluated. Presumably, the greater structural complexity of reefs provides protection from predators, leading to enhanced survival of fish. In addition, the availability or diversity of food might be greater on and around reefs, causing fish to aggregate around these structures. Yet the relative contributions of these and other factors are unknown, and these and other hypotheses offer intriguing avenues for further research.

### Limited influence of type of seagrass on fish density

We found no differences between types of seagrass in the density of any of the main species or groups we investigated (see also Wernberg et al. 2006). Our results contrast with those of other studies, which have often found differences in abundances of fish among different types of seagrasses, e.g. Rotherham & West (2002), Hyndes et al. (2003). The lack of difference between seagrasses in our study might be due to our method: we used underwater visual census (UVC), while all the other studies used nets. Harmelin-Vivien & Francour (1992) found that UVC underestimated the abundances of a range of species which inhabited the canopy, but was a good method of estimating abundance of species which swam above the canopy. Fishes that inhabit the seagrass canopy might respond to morphological variations among seagrasses to a greater degree than fishes that swim above the canopy; our results might therefore apply to only a subset of the fish fauna, and we do not expect that the results would be consistent for the entire fish fauna inhabiting the area.

### Predation intensity not influenced by proximity to reef

Overall, we found that the intensity of predation on tethered crabs was not strongly influenced by proximity to reef, although there was an indication that this might be important in limited circumstances, e.g. *Posidonia sinuosa* meadows in Marmion Lagoon. This result contrasts with the results of studies elsewhere. For example, Valentine et al. (unpubl.) found that survival of tethered crabs increased significantly with distance from the reefs in an extensive study in the Florida Keys.

There are several potential explanations for the absence of differences in predation intensity related to proximity to reef. One is that fishes other than the species we observed to be abundant were responsible for predation. We often observed wrasses consuming tethered crabs near reefs; however, our counts showed that the density of these species declined rapidly with decreasing proximity to reef. These species might cause strong localised predation intensity immediately adjacent to reefs, while seagrass-associated species might also exert strong predation intensity in meadows far from reefs. Many of the species of fishes commonly recorded in seagrass beds along the western Australian coast, but not recorded in our study, are small predatory species that tend to remain concealed within the seagrass canopy. For example, *Cnidoglanis macrocephalus* (Plotosidae), *Gymnapistes marmoratus* (Scorpaenidae) and *Leviprora inops* (Platycephalidae) are all capable of eating crabs of the sizes used in our study, and are all cryptic species unlikely to be efficiently surveyed by UVC but which can be abundant in seagrass in south-western Australia, e.g. Edgar & Shaw (1993), Hyndes et al. (2003). These species might not have gradients in abundance related to proximity to reef, and predation by them could dampen gradients in predation intensity away from reefs.

Another possible explanation for the patterns we observed is that reef-associated predators forage widely away from reefs at night. We did our UVC surveys during daylight hours, but the crabs were exposed to predators for 24 h, and were thus available to nocturnal predators as well. The foraging behaviour of the fauna of these reefs is virtually unknown. In one of the few studies so far, Jernakoff (1987) found that western rock lobster *Panulirus cygnus*, which spend daylight hours sheltering in reefs, forage widely in adjacent seagrass beds at night. It is possible that other reef-associated species also forage in seagrass at night, as has been found elsewhere (e.g. Ogden & Zieman 1977, Burke 1995) — if so, this could be another mechanism by which the intensity of predation remains uniform at different distances from reefs.

### Type of seagrass influences predation intensity

Overall, survival of tethered crabs was higher in *Posidonia sinuosa* than in *Amphibolis* spp., although there was some variation within this overall trend (see significant 'seagrass × location × distance' effect in Table 4). *P. sinuosa* and *Amphibolis* spp. differ in several ways, including overall morphology, total above-ground biomass and shoot density. Each of these characteristics have been shown to influence survival of prey in experimental studies (see reviews by Orth et al. 1984, Heck & Crowder 1991, Heck & Orth 2006). We do not have site-specific estimates of shoot density or above-ground biomass, but data are available for the region to assess broad trends. In the Marmion Lagoon and Jurien Bay regions, shoot density of *P. sinuosa* is typically in the range of 700 to 1480 shoots $m^{-2}$, while shoot density of *Amphibolis griffithii* (the main species of *Amphibolis* in our study) is typically in the range of 330 to 420 stems $m^{-2}$ (Jernakoff & Nielsen 1998, P. Lavery & M. Westera unpubl. data). Overall above-ground biomass (dry weight, including epiphytes) is in the range of 249 g $m^{-2}$ for *P. sinuosa*, and 450 to 1000 g $m^{-2}$ for *A. griffithii* (Jernakoff & Nielsen 1998, P. Lavery & M. Westera unpubl. data). Shoot densities for *P. sinuosa* are therefore higher than those of *A. griffithii*, indicating a much denser structure, while above-ground biomass is typically higher for *A. griffithii*. The distribution of this biomass is also different, with much of the biomass of *A. griffithii* located in the leaf clusters that occur at the top of the canopy, while biomass of *P. sinuosa* is more evenly distributed. The high shoot density of *P. sinuosa*, coupled with the higher proportion of biomass near the sediment, could potentially hinder the ability of predators to locate and attack the prey we used.

Plant morphology is also likely to be an influence; Heck & Orth (1980) suggested that prey would survive better in plants with complex leaves than plants with simple leaves. Well-designed experiments testing the influence of plant morphology on survival of prey remain rare, and those experiments that have been done do not always support this prediction (Heck & Crowder 1991, Heck & Orth 2006). The prey we used tended to stay associated with the sediment, often buried, and did not climb into the upper canopy. This might have made them more susceptible to predators in *Amphibolis* spp. beds, where shoot density was lower and most of the biomass was located in the canopy. Use of other types of prey that inhabit the upper canopy might yield different results.

Differences between types of seagrass in the abundance of fish, or in species and size composition of fishes, might also have influenced the observation of differences in predation intensity. Although we detected no differences between *Posidonia sinuosa* and *Amphibolis* spp. using UVC, as mentioned earlier, it is possible that some species that are not efficiently surveyed by UVC could be predators of crabs; these species might differ in abundance between *Amphibolis* spp. and *P. sinuosa* meadows. In addition, Hyndes et al. (2003) found that fishes inhabiting *Amphibolis griffithii* tended to be larger than those inhabiting *P. sinuosa*, perhaps due to the larger spaces under the *A. griffithii* canopy: many of these fishes were predators, which could also tend to increase the intensity of predation in *Amphibolis* spp. beds.

Overall, our study has revealed that there are landscape-scale patterns in ecological patterns and processes in seagrass beds related to proximity to reef (for fish density) and type of seagrass (for predation intensity). The potential for differences in predation within and among seagrass habitats warrants further investigation in other regions where multiple types of seagrass occur.

*Acknowledgements.* This research was supported by the Australian Research Council, the Department of Environmental Protection (Western Australia) and Edith Cowan University. We thank K. Cook, K. Crawley and T. Daly for assistance with the research, and R. Howard, P. Lavery and M. Westera for access to unpublished data. R. Black, G. Hyndes and F. Tuya provided comments that helped us improve the manuscript.

## LITERATURE CITED

Barros F (2005) Evaluating the importance of predation on subtidal benthic assemblages in sandy habitats around rocky reefs. Acta Oecol 27:211–223

Burke NC (1995) Nocturnal foraging habitats of French and bluestriped grunts, *Haemulon flavolineatum* and *H. sciurus*, at Tobacco Caye, Belize. Environ Biol Fish 42:365–374

Dorenbosch M, Grol MGG, Nagelkerken I, van der Velde G (2005) Distribution of coral reef fishes along a coral reef-seagrass gradient: edge effects and habitat segregation. Mar Ecol Prog Ser 299:277–288

Edgar GJ, Shaw C (1993) Inter-relationships between sediments, seagrasses, benthic invertebrates and fishes in shallow marine habitats off south-western Australia. In: Wells FE, Walker DI, Kirkman H, Lethbridge R (eds) Proc 5th Int Mar Biol workshop: the marine fauna and flora of Rottnest Island, Western Australia. Western Australian Museum, Perth, p 429–442

Edgar GJ, Shaw C (1995) The production and trophic ecology of shallow-water fish assemblages in southern Australia: II. Diets of fishes and trophic relationships between fishes and benthos at Western Port, Victoria. J Exp Mar Biol Ecol 194:83–106

Harmelin-Vivien ML, Francour P (1992) Trawling or visual census? Methodological bias in the assessment of fish populations in seagrass beds. PSZN I: Mar Ecol 13:41–51

Heck KL Jr, Crowder LB (1991) Habitat structure and predator–prey interactions in vegetated aquatic systems. In: Bell SS, McCoy ED, Mushinsky HR (eds) Habitat structure: the physical arrangement of objects in space. Chapman & Hall, London, p 281–299

Heck KL Jr, Orth RJ (1980) Seagrass habitats: the role of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. In: Kennedy VS (ed) Estuarine perspectives. Academic Press, New York, p 449–464

Heck KL Jr, Orth RJ (2006) Predation in seagrass beds. In: Larkum AWD, Orth RJ, Duarte CM (eds) Seagrasses: biology, ecology and conservation. Springer, Dordrecht, p 537–550

Heck KL Jr, Wilson KA (1987) Predation rates on decapod crustaceans in latitudinally separated seagrass communities: a study of spatial and temporal variation using tethering techniques. J Exp Mar Biol Ecol 107:87–100

Heck KL Jr, Hays G, Orth RJ (2003) Critical evaluation of the nursery role hypothesis for seagrass meadows. Mar Ecol Prog Ser 253:123–136

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

Hovel KA, Lipcius RN (2001) Habitat fragmentation in a seagrass landscape: patch size and complexity control blue crab survival. Ecology 82:1814–1829

Howard RK (1989) The structure of a nearshore fish community of Western Australia: diel patterns and the habitat role of limestone reefs. Environ Biol Fish 24:93–104

Hyndes GA, Kendrick AJ, MacArthur LD, Stewart E (2003) Differences in the species- and size-composition of fish assemblages in three distinct seagrass habitats with differing plant and meadow structure. Mar Biol 142:1195–1206

Jernakoff P (1987) Foraging patterns of juvenile western rock lobsters *Panulirus cygnus* George. J Exp Mar Biol Ecol 113:125–144

Jernakoff P, Nielsen J (1998) Plant-animal associations in two species of seagrasses in Western Australia. Aquat Bot 60: 359–376

Jones GP, Ferrell DJ, Sale PF (1992) Fish feeding and dynamics of soft-sediment mollusc populations in a coral reef lagoon. Mar Ecol Prog Ser 80:175–190

Kirkman H, Humphries P, Manning R (1991) The epibenthic fauna of seagrass beds and bare sand in Princess Royal Harbour and King George Sound, Albany, south-western Australia. In: Wells FE, Walker DI, Kirkman H, Lethbridge R (eds) Proc of 3rd Int Mar Biol workshop: the marine flora and fauna of Albany, Western Australia. Western Australian Museum, Perth, p 553–563

Kitchell JF, Schindler DE, Herwig BR, Post DM, Olson MH, Oldham M (1999) Nutrient cycling at the landscape scale; the role of diel foraging migrations by geese at the Bosque del Apache National Wildlife Refuge, New Mexico. Limnol Oceanogr 44:828–836

Langlois TJ, Anderson MJ, Babcock RC (2005) Reef-associated predators influence adjacent soft-sediment communities. Ecology 86:1508–1519

Langlois TJ, Anderson MJ, Babcock RC, Kato S (2006) Marine reserves demonstrate trophic interactions across habitats. Oecologia 147:134–140

Lek E (2004) Diets of three carnivorous fish species in marine waters of the west coast of Australia. Honours thesis, Murdoch University, Perth

Linke TE, Platell ME, Potter IC (2001) Factors influencing the partitioning of food resources among six fish species in a large embayment with juxtaposing bare sand and seagrass habitats. J Exp Mar Biol Ecol 266:193–217

MacArthur LD, Hyndes GA (2007) Varying foraging strategies of Labridae in seagrass habitats: herbivory in temperate seagrass meadows? J Exp Mar Biol Ecol 340: 247–258

Ogden JC (1980) Faunal relationships in Caribbean seagrass beds. In: Phillips RC, McRoy CP (eds) Handbook of seagrass biology: an ecosystem perspective. Garland STPM Press, New York, p 173–198

Ogden JC, Zieman JC (1977) Ecological aspects of coral reef-seagrass bed contacts in the Caribbean. In: Taylor DL (ed) Proc 3rd Int Coral Reef Symp. Rosenstiel School of Marine and Atmospheric Science, Miami, FL, p 377–382

Orth RJ, Heck KL Jr, van Montfrans J (1984) Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator–prey relationships. Estuaries 7:339–350

Orth RJ, Kendrick GA, Marion SR (2006) Predation on *Posidonia australis* seeds in seagrass habitats of Rottnest Island, Western Australia: patterns and predators. Mar Ecol Prog Ser 313:105–114

Peterson CH, Black R (1994) An experimentalist's challenge: when artifacts of intervention interact with treatments. Mar Ecol Prog Ser 111:289–297

Platell ME, Potter IC, Clarke KR (1998) Resource partitioning by four species of elasmobranchs (Batoidea: Urolophidae) in coastal waters of temperate Australia. Mar Biol 131: 719–734

Polis GA, Hurd SD (1995) Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. Proc Natl Acad Sci USA 92:4382–4386

Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu Rev Ecol Syst 28: 289–316

Posey MH, Ambrose WG Jr (1994) Effects of proximity to an offshore hard-bottom reef on infaunal abundances. Mar Biol 118:745–753

Rotherham D, West RJ (2002) Do different seagrass species support distinct fish communities in south-eastern Australia? Fish Manag Ecol 9:235–248

Searle DJ, Semeniuk V (1985) The natural sectors of the inner Rottnest Shelf coast adjoining the Swan Coastal Plain. J R Soc West Aust 67:116–136

Shulman MJ (1985) Recruitment of coral reef fishes: effects of distribution of predators and shelter. Ecology 66: 1056–1066

Valentine JF, Heck KL Jr (2005) Perspective review of the impacts of overfishing on coral reef food web linkages. Coral Reefs 24:209–213

Valentine JF, Heck KL Jr, Blackmon D, Goecker ME and 6 others (2007) Food web interactions along seagrass–coral reef boundaries: effects of piscivore reductions on cross-habitat energy exchange. Mar Ecol Prog Ser 333:37–50

Wallace JB, Eggert SL, Meyer JL, Webster JR (1997) Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102–104

Wernberg T, Vanderklift MA, Lavery PS, How J (2006) Export of detached macroalgae from reefs to adjacent seagrass beds. Oecologia 147:692–701

*Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany*

*Submitted: August 16, 2006; Accepted: December 4, 2006*
*Proofs received from author(s): May 28, 2007*