

Facilitation of molluscan assemblages in mangroves by the fucalean alga *Hormosira banksii*

Melanie J. Bishop^{1,3,*}, Tara Morgan¹, Melinda A. Coleman², Brendan P. Kelaher¹,
Lyndle K. Hardstaff¹, Robert W. Evenden¹

¹Department of Environmental Sciences and Institute for Water and Environmental Resource Management, University of Technology Sydney, PO Box 123, Broadway, Sydney, New South Wales 2007, Australia

²Centre for Marine Bio-Innovation, University of New South Wales, Sydney, New South Wales 2052, Australia

³Present address: Department of Biological Sciences, Macquarie University, North Ryde, Sydney, New South Wales 2109, Australia

ABSTRACT: The fucalean macroalga *Hormosira banksii* facilitates diverse rocky intertidal communities. Along the east coast of Australia, the alga can also persist in mangroves as a free-living form trapped amongst pneumatophores. We investigated (1) whether the alga has an effect on molluscan species richness and abundance in mangroves similar to that on rocky shores, and (2) whether, in mangroves, the source (phenotypically distinct estuarine or rocky shore populations) of *H. banksii* influences the outcome of its interspecific interactions. Sampling of 3 rocky shore and 3 mangrove sites along the east coast of Australia revealed that patches of *H. banksii* consistently supported a greater species richness of molluscs than adjacent substratum. Whereas the alga increased the abundance of molluscs in the mangrove forest, it had no effect or decreased molluscan abundance on the rocky shore. Transplant of *H. banksii* from rocky shores and estuarine tidal flats into the mangrove indicated that the source of the algae influenced the magnitude of effects. Although all algae enhanced molluscan abundance and species richness, estuarine *H. banksii*, which had larger vesicles and a longer thallus, supported more molluscs of more species than rocky shore *H. banksii*. These results support the growing consensus that the influence of foundation species at the community level is dependent on environmental conditions. As human activities place increasing pressure on coastal ecosystems, it will be important to understand the mechanisms and conditions that determine community-level effects of foundation species so that biodiversity may be conserved.

KEY WORDS: Facilitation · Foundation species · Macroalgae · Mangroves · Molluscs · Rocky shore

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INTRODUCTION

Many ecological communities are defined by the structural or functional attributes of a single foundation species (Dayton 1972). For example, seagrasses modify flow, predation intensity and availability of substratum, thereby facilitating dense and diverse faunal communities (Orth et al. 1984, Summerson & Peterson 1984); trees shade the forest floor, altering light and moisture regimes; and corals form structurally complex reefs, which enhance habitat for other species (Stachowicz 2001). The dynamics of communities shaped

by these foundation species are relatively fragile and susceptible to switching between alternative stable states following even small perturbations (Dudgeon & Petraitis 2005). It is important to understand the mechanisms and conditions that determine community-level effects of foundation species so that biodiversity may be conserved in the face of local and global change.

The influence of foundation species on associated taxa may change from positive to negative depending on environmental conditions (Stachowicz 2001, Crain & Bertness 2006). Prominent ecological models predict

*Email: mbishop@bio.mq.edu.au

that positive interactions will be particularly prevalent in environments of high physical stress and high consumer pressure, and that competitive interactions will dominate more benign environments (reviewed by Bruno et al. 2003). Consequently, a reduction in environmental stress may diminish the benefits derived from a formerly positive interaction, changing the net outcome to neutral or even negative (e.g. Crain 2008). Costs and benefits of interactions may also shift according to spatial or temporal variability in the morphology of a foundation species (e.g. Hacker & Steneck 1990, Levin & Hay 1996). The challenge, therefore, is to develop an understanding of how variability in environmental conditions, as well as key morphological characteristics of the participants, causes shifts in the outcome of interactions.

The fucalean macroalga *Hormosira banksii* serves as a foundation species on rocky intertidal shores of Australia and New Zealand. The extensive monotypic stands formed by the alga at mid-tidal elevations directly and indirectly influence abundances of other algae and invertebrates through environmental amelioration and habitat provision (Keough & Quinn 1998, Underwood 1999, Lilley & Schiel 2006, Schiel & Lilley 2007). Experimental removal of *H. banksii* results in the loss or marked decline of up to 45% of associated species (Lilley & Schiel 2006) and reduction in cover by trampling has similar deleterious effects (e.g. Keough & Quinn 1998, Schiel & Taylor 1999, Schiel & Lilley 2007). Although experimental considerations of the ecological role of *H. banksii* have been confined to the rocky shore, the alga also proliferates as a free-living form in mangrove forests (King 1981, King & Wheeler 1985). Fronds and fragments of *H. banksii* float and, following detachment during storms, wash ashore in significant quantities (McKenzie & Bellgrove 2008). Whereas on exposed sandy beaches *H. banksii* wrack represents an ephemeral resource, in mangroves *H. banksii* becomes trapped among pneumatophores, survives and, in some instances, reproduces (McKenzie & Bellgrove 2008), leading to persistent free-living populations.

The persistence of *Hormosira banksii* in mangrove forests raises the question of whether it plays an ecological role in determining small-scale variability in diversity in this habitat similar to that on rocky shores. There is growing evidence that structural complexity may not be as important in structuring populations of gastropods in mangroves as on intertidal rocky shores (Crowe 1996, Beck 1998, Bishop et al. 2007). Further, because *H. banksii* may be washed into mangrove forests from estuarine or coastal rocky shores, it raises the question of how phenotype influences the outcome of interspecific interactions involving this habitat-forming species. Across its broad geographic range,

H. banksii, which is characterized by a distinctive thallus of branched chains of spherical to elongate vesicles (Womersley 1987), shows considerable morphological variation (Osborn 1948, Womersley 1987). Whereas vesicles from rocky shore *H. banksii* are elongate in shape, those from estuarine plants are roughly spherical, with a volume 3 to 10 times that of vesicles from plants in more exposed locations (Osborn 1948, Womersley 1987, Ralph et al. 1998, Macinnis-Ng et al. 2005).

Here we test the null hypothesis that *Hormosira banksii* will play a role in facilitating assemblages of mobile molluscs in mangrove forests similar to that on rocky shores. To assess the role that morphology plays in determining the outcome of interspecific interactions, we transplanted *H. banksii* from different rocky shore and estuarine locations into a mangrove forest and compared molluscan colonization. As increasing human visitation of rocky shores continues to put increasing pressure on their *H. banksii* populations (Keough & Quinn 1998, Schiel & Lilley 2007), it will be important to know how these changes subsequently influence the biodiversity of mangrove forests, which receive *H. banksii* from these donor sites.

MATERIALS AND METHODS

The present study encompassed several types of data collection and analysis: (1) mensurative sampling on rocky shores and in mangroves, testing the hypothesis that in each habitat, densities and diversities of molluscs will be greater inside than outside patches of *Hormosira banksii*; (2) a manipulative experiment investigating whether, in mangrove forests, differences in molluscan assemblages between patches with and without *H. banksii* are indeed attributable to the alga, and not a covariable; and (3) a transplant experiment investigating the importance of *H. banksii* phenotype in determining the alga's affect on molluscan assemblages of mangroves.

The mensurative sampling was conducted on the mid-shore (mean low water [MLW] + 0.6 to 0.8 m) of 3 rocky shores and in 3 mangrove forests along the coast of New South Wales, Australia, where *Hormosira banksii* forms patches several meters in diameter of >90% canopy cover (Table 1). On the rocky shores, *H. banksii* was directly attached to the primary substratum whereas in the mangrove forests the alga was free-living, trapped amongst pneumatophores of *Avicennia marina*.

The 2 experiments were conducted within the Quibray Bay mangrove forest (34° 01' 29' S, 151° 10' 45' E) within the Towra Point Aquatic Reserve, Botany Bay, Sydney. This site, listed under the 1984 Ramsar

Table 1. *Hormosira banksii*. Morphological measurements (means \pm 1 SE) of the alga sampled at 6 sites along the east coast of Australia. n = 60 thalli

Site	Habitat	Latitude	Longitude	Thallus length (cm)	Vesicle length (L) (mm)	Vesicle diameter (D) (mm)	L:D ratio
Pearl Beach	Rocky shore	33°33'S	151°19'E	21.8 \pm 0.4	10.2 \pm 0.1	7.2 \pm 0.1	1.48 \pm 0.02
Long Reef	Rocky shore	33°45'S	151°19'E	12.2 \pm 0.5	9.5 \pm 0.2	7.1 \pm 0.2	1.37 \pm 0.02
Bellambi	Rocky shore	34°22'S	150°55'E	17.2 \pm 0.6	9.1 \pm 0.1	6.0 \pm 0.1	1.59 \pm 0.03
Salamander Bay	Mangrove	32°44'S	152°06'E	28.3 \pm 1.3	20.4 \pm 0.3	17.2 \pm 0.3	1.20 \pm 0.01
Towra Point	Mangrove	33°59'S	151°12'E	17.2 \pm 0.6	10.2 \pm 0.1	9.4 \pm 0.1	1.13 \pm 0.01
Narooma	Mangrove	36°13'S	150°08'E	20.4 \pm 0.8	18.5 \pm 0.5	16.9 \pm 0.4	1.10 \pm 0.01

Convention on Wetlands of International Importance, is a major breeding, feeding and roosting site for 34 migratory bird species, some of which are listed as endangered, and supports more than 230 species of fish (NPWS 2001). Although sheltered from wave action, the prevailing summertime northeast winds deposit large amounts of wrack, dislodged from nearby rocky shores and seagrass beds, onto the Quibray Bay intertidal mudflat and the mangrove forest immediately behind.

Mensurative sampling of rocky shores and mangrove forests. At each of the 3 rocky shore and 3 mangrove sites (Table 1) we compared assemblages of epifaunal molluscs between patches with >90% canopy cover of *Hormosira banksii* and adjacent bare patches lacking the alga, but of similar primary substratum and tidal elevation. In each of the habitats, the bare patches were free of other species of canopy-forming algae and beds of habitat-forming molluscs such as oysters and mussels. In the mangrove forests, patches with and without *H. banksii* contained a similar density of *Avicennia marina* pneumatophores, which also contribute to structural complexity.

All epifaunal molluscs >2 mm in shell height were identified and enumerated within twenty 0.5 \times 0.5 m quadrats haphazardly placed in each of the 2 patch types. Within the quadrats with *Hormosira banksii*, we first searched the algal thalli for canopy molluscs, and then moved the algae aside to count the molluscs on the primary substratum below. Canopy and primary molluscs were pooled in analyses because many of the species encountered are able to occupy both microhabitats. Consequently, many of those recorded in the canopy at the time of sampling may also spend a portion of their time on the primary substratum below.

To assess whether spatial variability in the role of the alga is correlated to spatial variability in its phenotype, we quantified the morphology of *Hormosira banksii* in each of the quadrats in which it was present. Within each quadrat, 3 *H. banksii* thalli (arising from a single holdfast on the rocky shore or free-living in the mangrove forest) were haphazardly selected for measure-

ment. For each alga, we measured the length (to the nearest cm) from the holdfast (or, in the case of mangrove *H. banksii* which is frequently free-living, the oldest basal tissue) to the apical growing tip and the length and diameter (to the nearest mm) of 10 healthy, non-branching vesicles in the middle of a branch. Quantification of these variables allowed algal morphology at our study sites to be directly compared to previous assessments of *H. banksii* morphology by Ralph et al. (1998) and Macinnis-Ng et al. (2005). Furthermore, as the vesicles of *H. banksii* are the primary point of molluscan attachment, quantification of their size and number (estimated by length of *H. banksii*) was ecologically relevant.

Mixed-model ANOVAs with 3 factors, Habitat (2 fixed levels, rocky shore vs. mangrove), Site (3 random levels, nested within Habitat) and Microhabitat (2 fixed levels, inside vs. outside of *Hormosira banksii*; orthogonal to Habitat and Site) assessed whether there were differences in molluscan abundance and species richness between habitat patches with and without *H. banksii*, and whether these differences were consistent between rocky shore and mangrove habitats. Three-way ANOVAs with the factors of Habitat, Site and Quadrat (20 random levels: nested within Site), which used individual *H. banksii* thalli as replicates, tested for differences in frond length, vesicle length, vesicle diameter and vesicle length:diameter (L:D) ratio between rocky shore and mangrove habitats. Prior to each analysis, Cochran's *C*-test was performed and heterogeneous abundance data were $\sqrt{(x + 1)}$ transformed. Where variances remained heterogeneous even after transformation, ANOVAs were performed anyway and results were interpreted as significant at the more conservative level of $\alpha = 0.01$ (otherwise $\alpha = 0.05$). ANOVAs were followed by a *posteriori* Student-Newman-Keuls (SNK) tests to identify those treatment means that differed significantly.

Establishing the causative role of *Hormosira banksii* in modifying molluscan assemblages. We performed a manipulative field experiment to establish whether, in the mangrove forest, differences in mollus-

can assemblages between the inside and outside of *H. banksii* patches are due to the presence of the alga (as opposed to another factor, such as high pneumatophore density, with which *H. banksii* appears to be associated). On the mid-shore (~MLW + 0.8 m) of the Towra Point mangrove forest, we established 24 circular 1 m² plots within *H. banksii* patches, from which all molluscs and algae were removed. Natural densities of *H. banksii*, free of epifauna, were re-added from the surrounding mangrove forest to 12 plots haphazardly assigned to the *H. banksii* treatment, thereby establishing plots with and without *H. banksii*. At this study site, as in many mangroves in which the alga is found, *H. banksii* is free-living. Consequently, thalli were placed on the sediment surface, without attachment to pneumatophores or other hard substrata. To prevent *H. banksii* from washing into the algae-free treatments, while ensuring that all plots were handled in the same way, we erected a galvanized mesh fence around each. The 200 mm-high fences, constructed of 5 mm galvanized mesh held in place by three 450 mm long plastic stakes, had a 50 mm gap between the sediment surface and their base so that molluscs could migrate in and out of plots. A pilot study indicated that the native Towra Point *H. banksii* used in this experiment was not sufficiently buoyant to float over the tops of fences. Thus the tops of the fences were left open to predators. After 6 wk we compared the molluscan assemblages colonizing these experimental plots to those in similarly sized undisturbed patches with and without *H. banksii* (n = 12). Sampling was done within a 0.2 × 0.2 m quadrat placed haphazardly within each plot, at least 0.2 m from fences. Pilot studies indicated no effect of fencing on molluscan abundance (ANOVA: $F_{2,6} = 0.43$, p = 0.67) or assemblage structure (PERMANOVA: $F_{2,6} = 0.74$, p = 0.76). Hence, a control for fencing was not included in our experimental design.

To assess the degree to which differences among treatments represent a behavioural response of mobile molluscs to the alga, we compared emigration of the biomass-dominant *Batillaria australis* from plots with and without *Hormosira banksii*. The mud whelk *B. australis* is extremely common in southeast Australian estuaries, reaching densities as high as 2000 m⁻². Ten *B. australis*, marked with nail polish, were positioned in the center of each of the experimental plots, with and without *H. banksii*. Pilot studies indicated that the application of nail polish did not influence the survivorship or behavior of the snails. Two days and 2, 4 and 6 wk after marking, we thoroughly searched each plot for marked snails and recorded the number remaining. The positive identification of large numbers of the marked snails in *H. banksii* surrounding the cleared plots indicated that loss of marked snails from plots was due to migration and not mortality or crypsis.

The number and species richness of molluscs colonizing experimental plots was compared to undisturbed plots using a 2-way orthogonal ANOVA with the factors Treatment (2 fixed levels: experimental, undisturbed) and Patch type (2 fixed levels: *Hormosira banksii*, bare).

Effect of *Hormosira banksii* source on molluscan assemblages of mangroves. To assess whether the source of *H. banksii* accumulating in mangrove forests influences the molluscan assemblages it supports, we performed an algal transplantation experiment. We transplanted *H. banksii* from each of the previously sampled rocky shores (Green Point, Long Reef and Bellambi) and from estuarine tidal flat populations (Salamander Bay, Towra Point and Narooma; adjacent to the respective mangrove forests) into the Towra Point Nature Reserve. Although we acknowledge that large quantities of algae from the furthest locations could not possibly wash up in the Towra Point mangrove forest, they were chosen for transplantation because they encompass a large range of variability in *H. banksii* morphology. *H. banksii* was collected from each of the 6 sites over a 3 d period. Although collection of alga from rocky shores required detachment of algal holdfasts, we did not control for this in our design, as algae could not wash up into mangrove forests without such detachment occurring. Upon return to the laboratory, each alga was visually inspected and all remaining fauna removed by hand. Algae were held in aerated 17 l aquaria, illuminated by UV lights set to a 12:12 h light:dark cycle, until deployment at Towra Point on the third day.

Hormosira banksii was transplanted to a section of the Towra Point mangrove forest where it forms patches of >90% cover amongst the pneumatophores of *Avicennia marina*. At low tide we established forty-eight 0.25 m² plots, each separated by 2 to 3 m, at a tidal height of MLW + 0.8 m. All native *H. banksii* and associated molluscs were removed from each plot and one of the 6 *H. banksii* sources was haphazardly added to each (n = 8) to form 100% cover. As with the manipulative experiment described above, each plot was surrounded by a 200 mm high, 5 mm galvanized mesh fence with a gap at its base. This kept the transplanted algae in place, while allowing migration of mobile taxa.

The molluscan assemblages colonizing *Hormosira banksii* transplants were sampled 1 and 2 wk following algal transplantation. To avoid any edge effects associated with the fences, molluscs were sampled within a 0.2 × 0.2 m quadrat placed in the center of each plot. The experiment was terminated at 2 wk because plots receiving Towra Point *H. banksii* had accumulated a molluscan assemblage that was statistically indistinguishable from adjacent, undisturbed plots of

H. banksii by this time (M. J. Bishop unpubl. data). Differences among treatments in the number and species richness of molluscs colonizing transplants were assessed using separate ANOVAs for each of the 2 non-independent times. The ANOVAs had 2 factors: Habitat (2 fixed levels: rocky shore, mangrove) and Site (3 random levels, nested in Habitat).

RESULTS

Mensurative sampling of rocky shores and mangrove forests

In our sampling, we encountered 43 species of molluscs (Table 2). Of these, 33 were found exclusively on rocky shores, 7 were found exclusively in mangroves and 3 were found in both habitats.

On rocky shores and in mangroves, molluscan species richness was generally greater inside than outside of *Hormosira banksii* patches (Table 3, Fig. 1). All taxa within several of the families encountered (e.g. Turbinidae) were only found within patches of *H. banksii* (Table 2). While at certain sites, some taxa were found only outside of *H. banksii* patches (e.g. *Bembicium nanum* at Narooma), this pattern was not consistent across all sites sampled.

Patterns of abundance were, by contrast, more spatially variable (Table 3, Fig. 2). At 2 of the rocky shore sites, Pearl Beach and Bellambi, there was no significant difference in the abundance of molluscs between patches of habitat with or without *Hormosira banksii*. At the third rocky shore site, Long Reef, molluscan abundances were reduced within patches of the alga. At Long Reef, a dense turf of the coralline algae *Corallina officinalis* was found beneath the *H. banksii* canopy, on which few macro-molluscs were found. In the mangrove habitat, abundances of molluscs were generally greater inside than outside of *H. banksii* patches (Table 3, Fig. 2). This pattern was not statistically significant at Salamander Bay, where abundances were very low. Although we did not quantify the population structure of molluscs in each of the habitats, we observed that all size classes

Table 2. Molluscan taxa present at 3 rocky shore (PB: Pearl Beach; LR: Long Reef; BE: Bellambi) and 3 mangrove (SB: Salamander Bay; TP: Towra Point; NA: Narooma) sites, within patches of habitat with (+) and without (-) the alga *Hormosira banksii*

Taxa	— Rocky shore —			— Mangrove —		
	PB	LR	BE	SB	TP	NA
Class Polyplacophora						
Family Ischnochitonidae						
<i>Ischnochiton australis</i>	+		+			
Family Chitonidae						
<i>Sypharochiton pelliserpentis</i>	- +	+	+			
<i>Onithochiton quercinus</i>	+					
Juvenile chiton			+			
Class Gastropoda						
Subclass Prosobranchia						
Family Fissurellidae						
<i>Montfortula rugosa</i>	+	+	+			
Family Patellidae						
<i>Cellana tramoserica</i>	- +	- +	- +			
Family Lottidae						
<i>Patelloida alticostata</i>		- +				
<i>Patelloida mimula</i>			+		+	+
<i>Patelloida mufria</i>		+				
<i>Notoacmea falmmea</i>	+					
Family Trochidae						
<i>Austrocochlea porcata</i>	- +	- +	- +	- +	+	- +
<i>Calthotia fragum</i>				+	+	
<i>Cantharidella picturata</i>	+	- +	+			
<i>Phasianotrochus eximius</i>	+					
Family Turbinidae						
<i>Phasianella australis</i>		+				
<i>Turbo militaris</i>	+					
<i>Turbo torquatus</i>	+		+			
<i>Turbo undulatus</i>	+	+	+			
Family Neritidae						
<i>Nerita atramentosa</i>	- +	- +	- +			
Family Epitoniidae						
<i>Epitonium christyi</i>		+				
Family Littorinidae						
<i>Bembicium auratum</i>				- +	- +	+
<i>Bembicium nanum</i>	- +	- +	- +		- +	-
<i>Nodilittorina acutispira</i>		- +	-			
<i>Littorina unifasciata</i>	+	- +	-			
Family Batillariidae						
<i>Batillaria australis</i>					+	+
<i>Pyrazus ebeninus</i>				- +	-	- +
Family Naticidae						
<i>Polinices sordidus</i>					+	+
Family Cymatiidae						
<i>Cabestana spengleri</i>	+					
Family Muricidae						
<i>Agnewia tritoniformis</i>	+					
<i>Cronia margariticola</i>		+				
<i>Dicathais orbita</i>	+	+	+			
<i>Morula marginalba</i>	- +	- +	- +			
Family Columbellidae						
<i>Mitrella</i> sp.	+		+			
Family Conidae						
<i>Conus papilliferus</i>			+			
Family Mitridae						
<i>Mitra glabra</i>	+					

(Table continued on next page)

Table 2 (continued)

Taxa	— Rocky shore —			— Mangrove —		
	PB	LR	BE	SB	TP	NA
Subclass Pulmonata						
Family Siphonariidae						
<i>Siphonaria denticulata</i>	- +	- +	- +			
<i>Siphonaria virgulate</i>	-					
<i>Siphonaria</i> spp. juv.		-				
Family Onchidiidae						
<i>Onchidella patelloides</i>			+			
Class Bivalvia						
Family Mytilidae						
<i>Brachiodontes rostratus</i>	+	+				
Family Ostreidae						
<i>Ostrea angasi</i>		- +	+			
<i>Saccostrea glomerata</i>				+	- +	
Family Erycinidae						
<i>Lasea australis</i>		+				

Establishing the causative role of *Hormosira banksii* in modifying molluscan assemblages

Experimental plots to which defaunated *Hormosira banksii* was added were rapidly colonized by molluscs. One week into the experiment, the plots, dominated by *Batillaria australis* (87% of total abundance), *Austrocochlea porcata* (9%) and *Bembicium auratum* (5%), contained up to 2325 molluscs m⁻². Experimental plots from which *H. banksii* had been removed were relatively free of molluscs. Full sampling of experimental and undisturbed plots 6 wk after the start of the experiment revealed similar levels of abundance and species richness of molluscs between undisturbed and manipulated plots with *H. banksii* (Fig. 3). Experimental plots from which *H. banksii* had been

were more abundant in patches of mangrove habitat with than without *H. banksii*.

The frond length, vesicle length, vesicle diameter and L:D ratio of *Hormosira banksii* varied among sites and quadrats (Tables 1 & 4). Rocky shore *H. banksii* was generally characterized by shorter chains of narrower vesicles than mangrove *H. banksii* (Table 1). Their L:D ratio reflected a more cylindrical shape than the more spherical vesicles of the mangrove algae (SNK tests; Table 4). This cylindrical vesicle morphology was most pronounced at Bellambi, the southernmost of the rocky shore locations sampled. While the *H. banksii* of all 3 mangrove sites contained highly spherical vesicles, the vesicles of those at Towra Point were generally smaller than at the other 2 mangrove locations (Tables 1 & 4).

removed contained an abundance and species richness of molluscs as low as that in plots naturally free of the alga (ANOVA: $F_{1,44} = 1.44$, $p < 0.25$; Fig. 3). Consequently, ANOVA revealed a main effect of Patch type (*Hormosira* versus bare) on molluscan abundance ($F_{1,44} = 131$, $p < 0.001$) and species richness ($F_{1,44} = 97$, $p < 0.001$), that was apparent irrespective of whether the plots were experimental or undisturbed.

Following deployment of marked *Batillaria australis* into experimental plots, rapid emigration of snails from unvegetated habitat was observed (Fig. 4). Two days after experimental deployment, <10% of *B. australis* remained in plots without *Hormosira banksii*, whereas ~80% were retained in plots with the algae. The observation of large numbers of the marked snails in the undisturbed *H. banksii*

Table 3. Results of 3-factor mixed-model ANOVAs testing for spatial variation in species richness and abundance of molluscs. Habitat had 2 fixed levels: rocky shore (R) and mangrove (M). Site had 3 random levels, nested within Habitat—Rocky shore: Pearl Beach (PB), Long Reef (LR) and Bellambi (BE); Mangrove: Salamander Bay (SB), Towra Point (TP) and Narooma (NA). Patch type had 2 fixed levels: *Hormosira banksii* (H) and bare (B). Terms significant at $\alpha = 0.05$ are in **bold**. n = 20 quadrats

Source	Species richness				Abundance		
	df	MS	F	p	MS	F	p
Habitat	1	375	23.93	0.008	515	0.89	0.400
Site (Habitat)	4	16	9.65	<0.001	581	27.53	<0.001
Patch type	1	163	25.15	0.007	98	0.21	0.671
Habitat × Patch type	1	<0	0.01	0.924	1373	2.93	0.162
Patch type × Site (Habitat)	4	6	4.00	0.004	469	22.23	<0.001
Residual	228	2			21		
Transformation				-		$\sqrt{(x + 1)}$	
Cochran's test				$C = 0.21$, $p < 0.01$		$C = 0.58$, $p < 0.01$	
Student-Newman-Keuls tests				Patch type × Site (Habitat):		Patch type × Site (Habitat):	
				[R] PB: H > B; LR: H = B; BE: H > B		[R] PB: H = B; LR: H < B; BE: H = B	
				[M] SB: H > B; TP: H > B; NA: H > B		[M] SB: H = B; TP: H > B; NA: H > B	

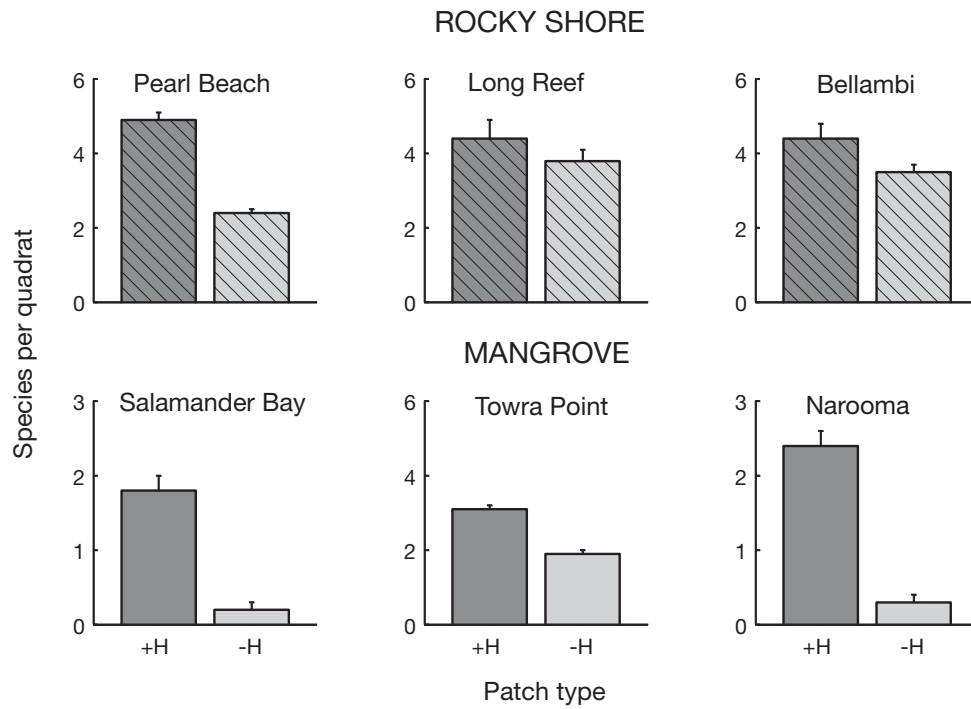


Fig. 1. Mean (+1 SE) species richness of molluscs per 0.25 m² quadrat in patches of habitat with (+H; dark grey bars) and without (-H; light grey bars) *Hormosira banksii*. n = 20

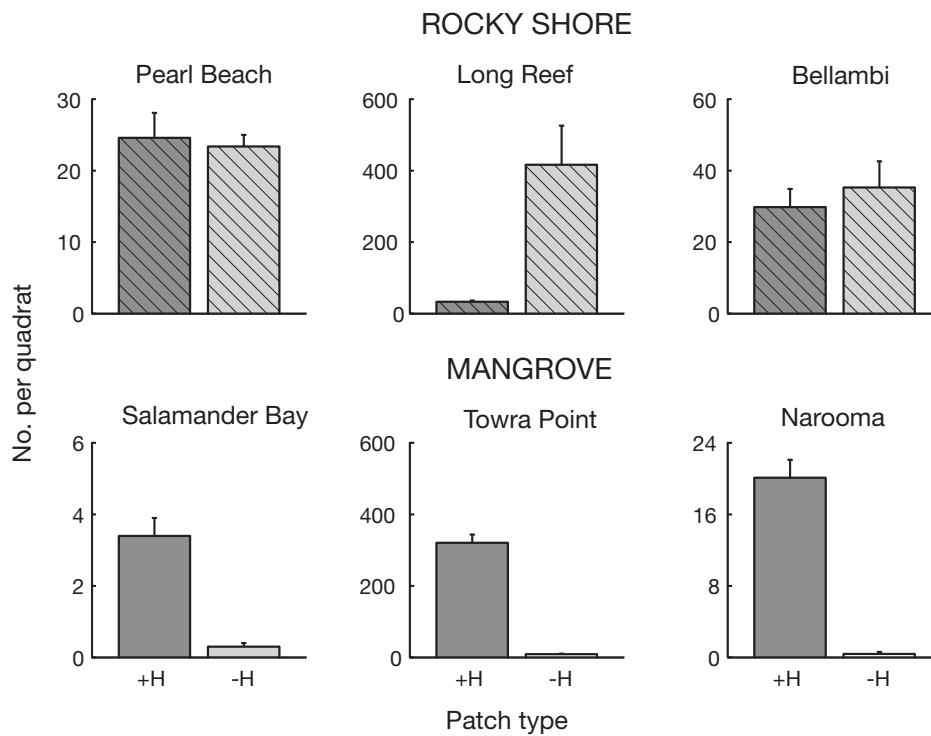


Fig. 2. Mean (+1 SE) abundance of molluscs per 0.25 m² quadrat in patches of habitat with (+H; dark grey bars) and without (-H; light grey bars) *Hormosira banksii*. n = 20

Table 4. Results of 3-factor nested ANOVAs testing for spatial variation in the vesicle length, diameter, length:diameter ratio and thallus length of *H. banksii* from rocky shore and mangrove habitats. Habitat had 2 fixed levels: rocky shore (R) and mangrove (M). Site had 3 random levels, nested within Habitat—Rocky shore: Pearl Beach (PB), Long Reef (LR) and Bellambi (BE); Mangrove: Salamander Bay (SB), Narooma (NA) and Towra Point (TP). Quadrat had 20 random levels, nested within Site. Terms significant at $\alpha = 0.05$ are in **bold**. $n = 3$ thalli. SNK: Student-Newman-Keuls tests

Source	df	Vesicle length (L)			Vesicle diameter (D)			L:D ratio			Thallus length		
		MS	F	p	MS	F	p	MS	F	p	MS	F	p
Habitat	1	4245	4.99	0.089	5216	8.30	0.045	7.18	11.51	0.027	3453	2.93	0.162
Site (Habitat)	4	3404	88.41	<0.001	628	98.78	<0.001	0.62	13.35	<0.001	1180	14.22	<0.001
Quadrat (Habitat × Site)	114	1097	3.29	<0.001	6	3.14	<0.001	0.05	1.99	<0.001	83	2.21	<0.001
Residual	240	9449			2			0.02			38		
Cochran's test SNK		C = 0.07, p < 0.05			C = 0.07, p < 0.05			C = 0.11, p < 0.01			C = 0.21, p < 0.01		
		Site: [R] PB = LR = BE; [M] SB > NA > TP			Habitat: R < M Site: [R] PB = LR = BE; [M] SB > NA > TP			Habitat: R > M Site: [R] BE > PB = LR; [M] SB = NA = TP			Site: [R] PB > BE > LR; [M] SB > NA = TP		

immediately outside of the cleared plots indicated that reduced numbers of snails in the bare plots was primarily due to emigration of the animals and not mortality. Although some emigration of snails out of the plots with *H. banksii* also occurred, 6 wk after deployment ~30% still remained, compared to none in the bare plots.

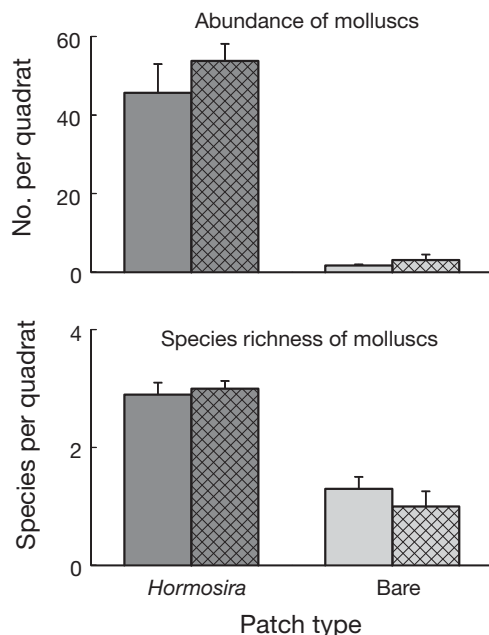


Fig. 3. Mean (± 1 SE) abundance and species richness of molluscs per 0.04 m² quadrat in plots with (dark grey bars) and without (light grey bars) *Hormosira banksii*. Plain bars denote undisturbed plots; hatched bars denote experimental plots. Molluscs colonising the plots were sampled 6 wk after defaunation. $n = 12$

Effect of *Hormosira banksii* source on molluscan assemblages of mangroves

Irrespective of *Hormosira banksii* source, its addition to experimental plots increased the abundance and species richness of molluscs as compared to nearby plots naturally devoid of the algae (Fig. 5). Nevertheless, 1 wk after transplantation, patches with estuarine *H. banksii* supported >200% more molluscs than those with the rocky shore morph (ANOVA: $F_{1,4} = 21.61$, $p < 0.01$; Fig. 5). Each of the plots supported a similar species richness of molluscs, irrespective of the source site ($F_{4,42} = 0.67$, $p > 0.6$) or source habitat ($F_{1,4} = 3.76$, $p > 0.1$) of its algae (Fig. 5).

Although the total abundance of molluscs in plots changed little between the first and second sampling, the strength of the habitat difference declined (ANOVA: $F_{1,4} = 4.93$, $p > 0.09$) and site-specific source

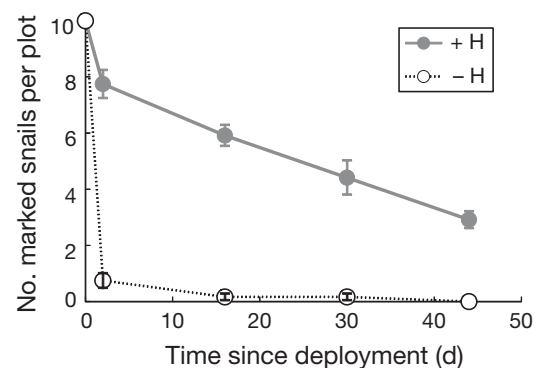


Fig. 4. *Batillaria australis*. Mean (± 1 SE) number (out of 10) of marked snails retained by experimental plots with (+H; grey circles) and without (-H; white circles) *Hormosira banksii*. $n = 12$

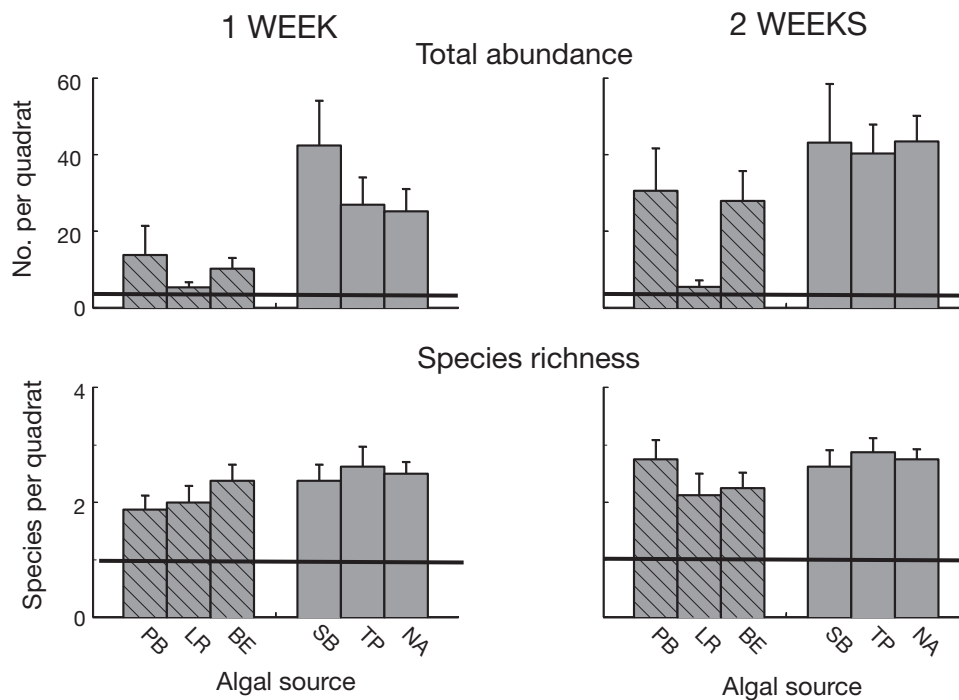


Fig. 5. Mean (+1 SE) abundance and species richness of molluscs per 0.04 m² quadrat colonizing plots with *Hormosira banksii* transplanted from rocky shore (patterned bars: Pearl Beach [PB], Long Reef [LR] and Bellambi [BE]) and estuarine (plain bars: Salamander Bay [SB], Towra Point [TP] and Narooma [NA]) sites into the Towra Point mangrove forest. Plots were sampled 1 and 2 wk following algal transplant. The horizontal black lines denote mean abundance and species richness of molluscs in plots lacking the alga. n = 8

effects became more apparent ($F_{4,42} = 2.46$, $p < 0.06$) (Fig. 5). Among the rocky shore sources, *Hormosira banksii* from Long Reef supported fewer molluscs than *H. banksii* from the other 2 locations (Fig. 5). In contrast to the weakening effect of algal source on molluscan abundance, its effect on molluscan richness strengthened. A statistically significant effect of source habitat was detected ($F_{1,4} = 9.14$, $p < 0.05$) (Fig. 5).

DISCUSSION

Previous studies have identified *Hormosira banksii* as a critical determinant of biodiversity on intertidal rocky shores (e.g. Keough & Quinn 1998, Lilley & Schiel 2006, Schiel & Lilley 2007). The present study tested whether *H. banksii* plays a similar role in mangrove forests, where it can accumulate and persist as a free-living form following dislodgement from hard substrata. Our sampling revealed that in mangrove forests, as on rocky shores, patches of *H. banksii* were generally associated with greater molluscan species richness. Whereas on the rocky shore the alga had no effect on or decreased total molluscan abundance, in the mangrove forest its small-scale effect on molluscan abundance was generally positive. Our finding that the

influence of the alga on molluscan abundances differs between rocky shores and mangroves adds to growing evidence that, at the community level, the role of foundation species may change from positive to negative depending on environmental conditions (Stachowicz 2001, Crain & Bertness 2006).

Like previous studies (e.g. Ralph et al. 1998, Macinnis-Ng et al. 2005), we found major differences in the morphology of exposed rocky shore and sheltered estuarine populations of *Hormosira banksii*. The vesicles of estuarine populations of *H. banksii* were larger and more spherical than those of rocky shore populations, and specimens typically had a longer thallus. Yet phenotypic differences between rocky shore *H. banksii* and the estuarine algae which tends to accumulate in mangrove forests could not alone explain differences in the alga's role between habitats. Following transplant of the alga from rocky shore and estuarine sources into a single mangrove forest, *H. banksii* universally increased molluscan abundance and richness, irrespective of its source. Further studies are thus needed to determine which of the many factors that differ between rocky shores and mangrove forests—such as wave action, dominant taxa and the availability of resources—influence the alga's role.

In mangroves, the presence of *Hormosira banksii* added structure to the environment and may have biophysically modified soil-surface microhabitats and provided a new source of food for some organisms. We did not investigate the mechanism by which patches of *H. banksii* acquire more molluscs (in terms of abundance and species richness) than adjacent habitat in the mangrove forest. Nevertheless, we suspect that enhancement of the area of hard substratum available for molluscan attachment and grazing, and modification of inter- and intraspecific interactions by the introduction of complexity, may be major contributing factors. As *H. banksii* was predominantly found under the mangrove canopy, in an already shaded and moist environment, the alga's role is unlikely to have been in the amelioration of desiccation stress.

The availability of hard substrata is often considered the limiting resource for epifaunal and fouling benthic marine organisms (e.g. Connell 1961). Even in mangrove forests, where many taxa can survive on soft and hard substrata, the availability of hard surfaces appears to influence the abundance of epifaunal molluscs (see Underwood & Barrett 1990). In the transplant experiment, the magnitude by which *Hormosira banksii* enhanced molluscan abundance and richness varied according to the alga's source, and was consistent with differences in the total surface area of substratum it provided. The estuarine algae, generally of greater vesicle size and longer thallus length than the rocky shore algae, usually supported greater densities and levels of species richness of molluscs. Among the 3 rocky shore sources, the algae from Pearl Beach, which had the largest vesicle size and the longest thallus length, supported the greatest abundance of molluscs. The Long Reef algae, which supported the fewest molluscs, had the smallest surface area of the algal sources considered, possessing much shorter thalli and smaller vesicles than the other sources.

The addition of *Hormosira banksii* to plots increased not only the surface area for molluscan attachment, but also the surface area available for growth of microfilms. *Batillaria australis*, *Austrochlea porcata* and *Bembicium auratum*, the 3 dominant molluscs at our study site, are each considered generalist grazers that consume diatoms, algal spores and detritus present on tree trunks, pneumatophores, dead wood and on the mud surface (Creese & Underwood 1976, Branch & Branch 1980, McKinnon et al. 2009). These gastropods, which maintain densities as high as 2000 m⁻² on the mid-shore of mangrove forests throughout the tidal cycle, may experience intense intra- and interspecific competition for food resources (Branch & Branch 1980). The addition of hard structure has previously been observed to increase the body weight and survivorship of *Bembicium auratum* (Branch & Branch 1980),

perhaps by increasing the surface area on which microflora can grow (Branch & Branch 1980, but see Underwood & Barrett 1990). Thus the addition of *H. banksii* may have decreased the magnitude of inter- and intraspecific competition for common resources among epifaunal gastropod species.

The alga may also have influenced interactions between epifaunal gastropods and their prey. Predation is important in structuring the molluscan populations of the Towra Point mangrove forest (Bishop et al. 2008). The naticid *Polinices sordidus*, a resident species among the mangroves, and toadfish *Tetractenos glaber* are active and abundant predators of mangrove molluscs at high tide (Bishop et al. 2008). In other systems, the introduction of structural complexity has reduced the strength of predation (e.g. Crowder & Cooper 1982, Almany 2004).

Both migration of molluscs from adjacent habitat and increased production contributed to the differences in molluscan abundance between patches with and without *Hormosira banksii* within the mangrove forest. Our observation of rapid migration of molluscs from cleared plots into surrounding *H. banksii* patches clearly demonstrated attraction of molluscs to *H. banksii* patches. Although we did not directly quantify recruitment of juvenile molluscs to *H. banksii*, we observed high densities of small size classes as well as adults in the *H. banksii* patches. This suggests that molluscan productivity was greater in the *H. banksii* patches.

Our finding that, within mangrove forests, molluscan assemblages are generally more abundant and species rich inside than outside *Hormosira banksii* patches challenges the suggestion that complexity is of little importance in structuring benthic assemblages of mangroves. Whereas a multitude of studies have shown that complexity can influence the density, species richness and dispersal of molluscs on rocky shores (e.g. Kohn & Leviten 1976, Chapman & Underwood 1994, Beck 2000), support for such effects had been notably lacking in mangroves. Beck (1998) found that, in mangroves, snail density was independent of the number of structural elements. Crowe (1996) reported that dispersal of gastropods in mangrove forests was never affected by the surrounding habitat structure, despite the same gastropods sometimes responding to the same type of structure when transplanted to rocky shores (Crowe & Underwood 1999).

The present study provides evidence that *Hormosira banksii* is important in facilitating molluscan abundance and species richness in mangrove forests, and that the magnitude of this facilitation is dependent on the source of the algae. Thus, processes that alter the supply and source of *H. banksii* washing into mangrove forests will have major effects on the benthic

ecology of these habitats. As human activities place increasing pressure on coastal ecosystems, it will be important to better understand the conditions surrounding the interaction between *H. banksii* and mangrove communities. Only with such an understanding will it be possible to conserve associated biodiversity.

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