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Thomas Wernberg · Mathew A. Vanderklift
Jason How · Paul S. Lavery

Export of detached macroalgae from reefs to adjacent seagrass beds

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Abstract Trophic linkages across habitats are thought to be strong when areas of different productivity are juxtaposed. Reefs dominated by macroalgae are commonly juxtaposed to less productive seagrass beds. We tested if macroalgae detached from 12 rocky reefs in south-western Australia were exported to adjacent seagrass beds and consumed by seagrass-associated fauna. We also assessed the extent of linkages by testing for patterns in biomass and consumption of reef algae, and density of herbivorous fish with increasing distance away from reefs.Detached reef algae were found in seagrass beds adjacent to all reefs. The biomass varied among reefs and with distance from reef, but detached reef algae within the seagrass beds comprised up to 23% (mean 3.6% ± 0.7 SE) of attached algae growing on an equivalent area of reef. Maximum accumulations were found immediately adjacent to reefs (0 m) and at the furthest distance away (> 300 m). Kelp (*Ecklonia radiata*) dominated the attached and detached algae, and up to 77% of the biomass of *E. radiata* tethered in seagrass beds were consumed over 5 days (mean 11.7% ± 0.5 SE). There were more herbivorous fish at 0 m than at > 300 m away from reefs, and consumption of tethered kelp was typically highest at 0 m, but was in some cases highest at > 300 m.Our study documents that, over hundreds of kilometres of coastline, macroalgae are exported from reefs to adjacent seagrass beds where they are consumed by seagrass-associated fauna. While reef algae in seagrass beds may be a patchy resource at a single time, at landscape scales and over longer time periods, the supply will be relatively predictable. We therefore suggest that detached reef algae form a significant trophic link between reefs and seagrass beds, and that this trophic link extends to distances of at least hundreds of metres away from individual reefs.

Keywords Connectivity · Food webs · Fish herbivory · Habitat linkages · Spatial subsidy

Introduction

Many food webs include components that encompass multiple habitats, implying spatial and trophic linkages between these habitats. Trophic linkages between spatially discrete habitats can occur due to movement of food resources (e.g. nutrients, detritus and prey) and movement of consumers (Polis et al. 1997). These cross-habitat linkages can have important ecological consequences, especially by increasing productivity in the recipient area. In some cases this maintains higher populations of consumers than would otherwise be supported (e.g. Bustamante et al. 1995).

Some of the best evidence for cross-habitat linkages comes from ecotones between terrestrial and aquatic habitats (e.g. Polis and Hurd 1995, 1996; Nakano and Murakami 2001). However, similar linkages should be important wherever juxtaposition of discrete habitats favours the exchange of food resources or consumers. The strength of linkages between habitats depends on the magnitude of exchange and linkages should, therefore, be particularly strong where habitats with differences in in situ productivity are juxtaposed (e.g. Polis and Hurd 1995, 1996).

Reef and seagrass habitats are juxtaposed in many areas of the world. In warmer waters, such as the Caribbean and Indo-Pacific, coral reefs are often found adjacent to seagrass beds, and strong linkages have been observed between these habitats. For example, reef-associated consumers forage in adjacent seagrass meadows, often exerting a strong influence on commu-

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T. Wernberg (✉) · M. A. Vanderklift · J. How · P. S. Lavery
Centre for Ecosystem Management, Edith Cowan University,
6027 Joondalup, WA, Australia
E-mail: wernberg@graduate.uwa.edu.au
Tel.: + 61-8-63045703
Fax: + 61-8-63045509

M. A. Vanderklift
CSIRO Marine Research,
Private Bag No. 5, 6913 Wembley, WA, Australia

nity structure in the meadows (e.g. Randall 1965; Eggleston et al. 1988). In turn, the consumers bring organic matter and nutrients back to the reefs, where they can increase productivity (Meyer and Schultz 1985).

In temperate waters, such as southern Australia and the Mediterranean Sea, rocky reefs dominated by macroalgae commonly occur adjacent to seagrass beds. Primary productivity of temperate macroalgae is typically 2–4 times higher than that of seagrasses (Mann 1973; Cambridge and Hocking 1997; Cebrian 2004). In addition, the export of primary production from beds of macroalgae is generally higher than from other macrophyte communities, including seagrass beds, where most of the unconsumed primary production tends to accumulate in situ (Cebrian 1999). Macroalgae are frequently detached from reefs during periods of high wave action (Kennelly 1987; Seymour et al. 1989), and much of this detached biomass ultimately ends up in the surf zone or as wrack on beaches (see review by Kirkman and Kendrick 1997). The export of detached macroalgae from reefs, and the proximity of seagrass beds to the reefs, suggests that a significant proportion of the detached reef algae must pass through, and potentially remain in, the seagrass beds. As algae are generally more nutritious and more easily assimilated (Klumpp et al. 1989), and sometimes are preferred over seagrass as a food resource by herbivores (Robertson and Lucas 1983; Gambi et al. 2000), detached reef algae might contribute substantially to seagrass food webs.

In this study we tested if macroalgae detached from rocky reefs in south-western Australia are exported to adjacent seagrass beds. We predicted that the biomass of detached reef algae would decrease with increasing distance from reefs. We also tested whether detached reef algae were consumed in the seagrass beds, and for patterns in the abundance and distribution of one group of consumers, herbivorous fish. We tested for the generality of patterns at twelve reefs separated by up to 200 km.

In temperate Australia, the seagrass genera *Posidonia* and *Amphibolis* are the major meadow-formers (Kirkman and Walker 1989). *Posidonia* has a simple strap-like morphology, whereas *Amphibolis* has a more complex morphology of thin lignified stems that support clusters of small leaves. These differences in shoot and canopy structure may cause differences in how easily detached macroalgae are entangled and retained within the seagrass canopy. We therefore tested the prediction that the more complex canopy of *Amphibolis* would retain a higher biomass of detached reef algae than the comparatively simple canopy of *Posidonia*.

Materials and methods

Study area

This study focussed on two locations in south-western Australia—Marmion Lagoon (31°49.4 S, 115°44.0 E) and Jurien Bay (30°17.3 S, 115°02.5 E), 20 and 250 km north of Perth, respectively. In this region, a characteristic feature of the coastline is a series of aeolianite limestone reefs parallel to the coast at distances ranging from 1 to 10 km offshore (Searle and Semeniuk 1985). Extensive seagrass meadows occur around these reefs, and this juxtaposition of reef and seagrass habitat occurs along more than 1,500 km of coastline in south-western Australia (Kirkman and Walker 1989).

Nearshore hydrodynamics in the region are dominated by wind-generated seas and oceanic swell, as the region is microtidal. Winter is characterised by south-westerly swells (Searle and Semeniuk 1985) which as often as 30 times per year can generate wave heights in excess of 4 m (Lemm et al. 1999), sufficient to detach macroalgae from reefs (Thomsen et al. 2004). Large swell events also occur occasionally during summer, but this season is predominantly characterised by one of the most predictable wind patterns in the world—strong offshore winds in the morning and strong onshore sea breezes in the afternoon (Masselink and Pattiaratchi 2001). The sea breezes, which also occur in lower frequency during winter, are capable of generating seas in excess of 2 m wave height in a few hours. The combination of the diurnally changing wind directions superimposed on the swell and diffraction/refraction around the ubiquitous reef structures produces complex nearshore circulation patterns.

The reef flora in both locations is dominated by a canopy of the small (< 2 m) kelp *Ecklonia radiata* and a diverse assemblage of associated foliose algae (Kendrick 1999; Wernberg et al. 2003). The seagrass meadows adjacent to the reefs are dominated by four species:

Table 1 Results of ANOVA testing the effects of location (fixed factor) and reef within location (nested random factor) on the biomass (g fw m^{-2}) of attached macroalgae

		All macroalgae			Kelp		
Source of variation	df	*MS*	*F*	*P*	*MS*	*F*	*P*
Location	1	1639333	0.10	0.703	32429900	5.68	**0.038**
Reef(location)	10	17112300	3.56	**0.001**	5712448	1.34	0.237
Residual	48	4805956					

Untransformed data passed tests of equal variances (Cochrans C-test, $P > 0.05$) and normality (visual inspection of residuals). $P < 0.05$ highlighted in bold

Posidonia sinuosa, *P. australis*, *Amphibolis antarctica* and *A. griffithii.*

Export of macroalgae from reefs to adjacent seagrass habitats

To test for patterns in the biomass of detached reef algae, we selected six reefs in each location that all broke the surface. All reefs were several hundred metres across at the widest point. Reefs within locations were generally separated by at least 1 km, the only exception being Whitfords Rock (Marmion Lagoon), for which we sampled opposite ends of the same reef (approximately 300 m apart) as these were dominated by different seagrass species. Reefs were selected so that the adjacent areas were dominated by either *Posidonia* (three reefs) or *Amphibolis* (three reefs). The direction of sampling followed the distribution of seagrasses. This was usually, but not always, towards the shore. Sampling was done at depths ranging from 1.5 to 8 m on reefs and in seagrass beds near reefs, and 4–9 m in seagrass beds at the furthest distance away from reefs. Reefs were sampled between 3 and 13 March 2004 in Jurien Bay and between 26 March and 14 April 2004 in Marmion Lagoon.

At each reef, we collected detached reef algae (macroalgae that had an obvious reef origin) from five distances relative to the reef: on the reef itself, 0 m (i.e. immediately adjacent to the reef), 10 m, 50 m and >300 m away into the adjacent seagrass beds. The furthest distance ranged from 300 to 1,100 m away from reef, sampling the first continuous meadow beyond the 300 m mark. At each distance, all loose-laying reef algae within ten haphazardly positioned 1 m^2 quadrats were collected by hand. The loose-laying algae were dominated by species clearly originating from the reefs and it was possible to distinguish these from algae growing epiphytically on seagrasses, based on our previous experience (Vanderklift and Lavery 2000; Lavery and Vanderklift 2002; Wernberg et al. 2003). Macroalgae attached to the reefs were quantified by handpicking all erect macroalgae (>5 cm) within five 0.25 m^2 quadrats on each reef. All algae were subsequently sorted into four groups: kelp (*E. radiata*), other brown algae, red algae and green algae, and were then weighed (fresh weight).

Consumption of reef algae in adjacent seagrass habitats

To test for patterns in the consumption of reef-derived algae in seagrass beds, we used tethered pieces of *E. radiata*. We chose this species because of its dominance in both the attached and detached algae, and because it is known to be consumed by a variety of herbivores (Robertson and Lucas 1983; Steinberg 1995; Moran and Clements 2002; Hill et al. 2003). For this component of the study we selected four reefs in each location, two adjacent to *Posidonia* meadows and two adjacent to *Amphibolis* meadows. Pieces of kelp (10–15 g fresh weight) were attached with clothes-pegs to thin steel rods pushed into the sand, and left for 5 days. Each piece of kelp was blotted with paper tissue and weighed (fresh weight) before and after deployment. Consumption was calculated as the relative change in biomass (% loss). At each reef we deployed eight replicate tethers at each of the same distances as those used in the survey of drift biomass, with the exception that we did not deploy tethers on the reef itself. Treatments to separate autogenic changes in biomass were not included as preliminary in situ tests showed these to be negligible (mean loss 1.57% ± 0.29 SE, $n=32$) and undetectable ($t_{(30,0.05)}=0.23$; $P=0.82$), when herbivores were excluded.

Abundance of herbivorous fish

We quantified the abundances of herbivorous fish along transects adjacent to reefs (0 m) and far away from reefs (>300 m) at the same sites as the tethering experiments. At each reef a diver experienced with identification of the local fish fauna swam two 25×5 m^2 belt transects on three separate days, yielding six replicates incorporating both spatial and temporal variability.

Statistical model

The significance of patterns in biomass of detached reef algae, abundance of herbivorous fishes, and consumption of tethered kelp were tested using mixed effects ANOVA, with the main effects of location (fixed factor, two levels), seagrass canopy type (fixed factor, two levels), reef (nested within location and seagrass type, three levels for each combination) and distance (fixed factor, five levels for detached reef algae, two levels for abundance of herbivorous fish, four levels for consumption). Linear regression was done to test relationships between variables using mean values. Patterns in the biomass of attached macroalgae on the reef were tested with a nested ANOVA, with the main effects of location (fixed factor, two levels) and reef (nested within location, six levels per location). We had no expectations of differences between locations, but included this factor to increase the spatial replication and thus the generality of our findings.

Results

Biomass of attached and detached reef algae

The total biomass of attached algae was not significantly different between Marmion Lagoon and Jurien Bay (overall mean 3.44 kg fw m^{-2} ± 0.51 SE, Table 1), but there were significant differences from reef to reef within locations (Table 1, Fig. 1). Unlike the total biomass of

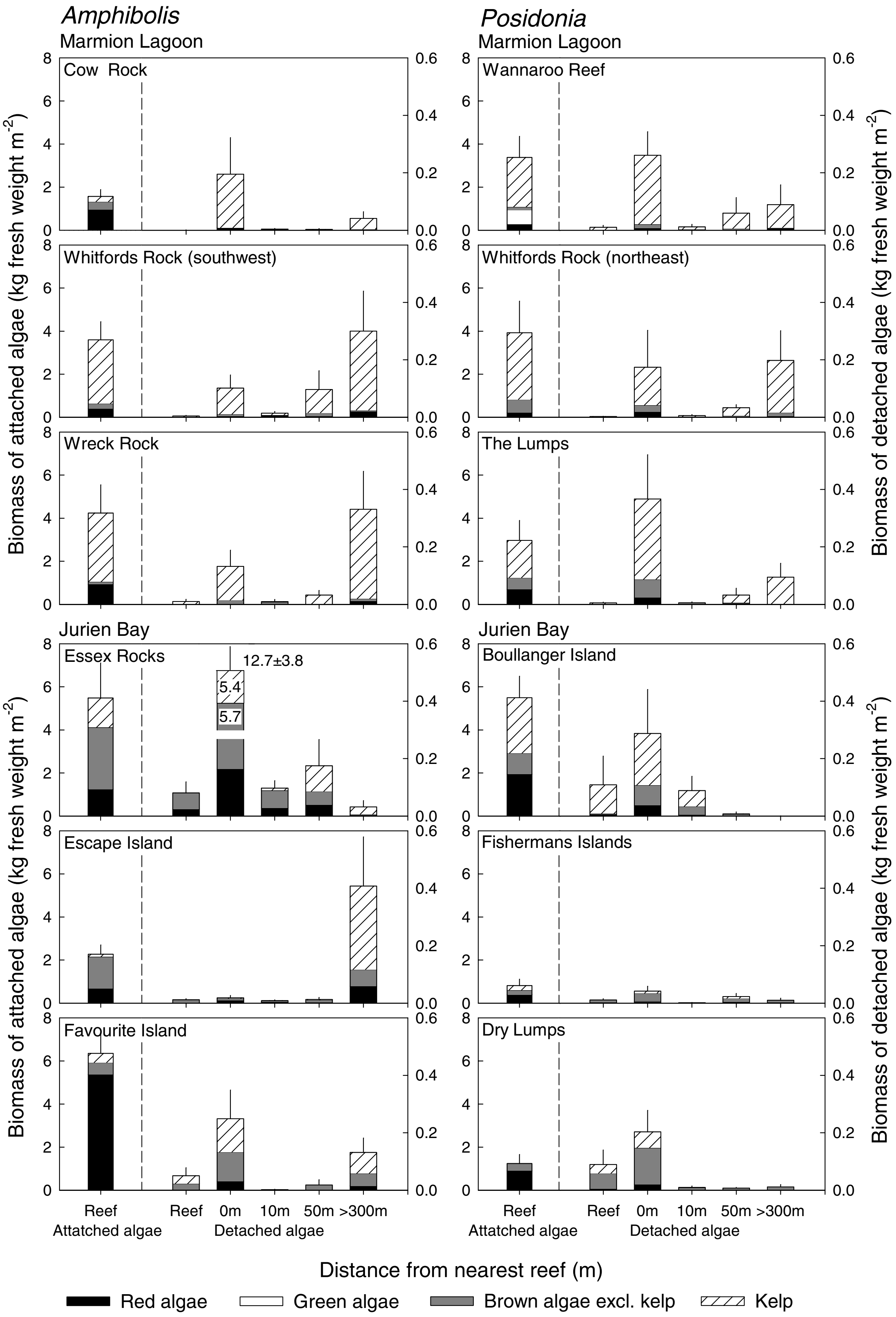

Fig. 1 Mean biomass (± SE) of attached ($n = 5$) and detached ($n = 10$) reef algae in Marmion Lagoon and Jurien Bay

Table 2 Results of ANOVA testing the effect of location (fixed factor), seagrass type (fixed factor), reef within location and seagrass type (nested random factor) and distance (fixed factor) on biomass (g fw m^{-2}) of detached macroalgae

Source of variation	*df*	All macroalgae			Kelp		
		MS	*F*	*P*	MS	*F*	*P*
Location	1	8.78	2.51	0.152	53.55	4.91	0.058
Seagrass	1	2.05	0.59	0.466	5.30	0.49	0.506
Reef(L × S)	8	3.50	5.67	**0.000**	10.91	3.31	**0.001**
Distance	4	21.89	11.95	**0.000**	82.65	14.67	**0.000**
L × S	1	9.18	2.62	0.144	13.76	1.26	0.294
L × D	4	3.11	1.70	0.175	8.24	1.46	0.237
S × D	4	4.11	2.24	0.087	13.17	2.34	0.076
Reef(L × S) × D	32	1.83	2.97	**0.000**	5.64	1.71	**0.010**
L × S × D	4	0.63	0.34	0.846	4.15	0.74	0.574
Residual	540	0.62			3.30		

Data were transformed (Log $x+1$) and subsequently passed tests of equal variances (Cochrans C-test, $P > 0.05$) and normality (visual inspection of residuals). $P < 0.05$ highlighted in bold

all attached algae, the biomass of attached kelp (*E. radiata*) was significantly different between the two locations, but not among reefs within location (Table 1): the biomass of attached kelp was higher in Marmion Lagoon (mean of 2.25 kg fw m^{-2} ± 0.46 SE) than Jurien Bay (mean of 0.78 kg fw m^{-2} ± 0.41 SE). Kelp also accounted for a greater proportion of the total biomass in Marmion Lagoon: 47 ± 7 % (mean ± SE) versus 16 ± 6 % in Jurien Bay.

The biomass of detached reef algae varied from reef to reef and with distance from reef, but not between locations (overall mean 0.33 kg fw m^{-2} ± 0.05 SE) or between *Posidonia* and *Amphibolis* meadows (Table 2). However, there was also a statistically significant interaction between reef and distance, indicating that the patterns of distribution of detached reef algae with distance were not consistent at all reefs (Table 2). With few exceptions though, pair-wise comparisons among distances for each reef (Table 3) showed that the biomass of detached reef algae at 0 m was significantly different from all other distances—at most reefs this was because the highest biomass of detached reef algae occurred at 0 m (Fig. 1). The biomass of detached reef algae at 0 m was always higher than on the reef and at 10 and 50 m (this difference was usually significant), and usually greater than at >300 m; the biomass at 0 m was significantly higher than at >300 m at 5 of the 12 reefs. There was generally little difference in the biomass of detached reef algae on the reef and at the 10 and 50 m distances. The biomass of detached reef algae at >300 m showed inconsistent patterns, being significantly higher than the biomass of detached reef algae at other distances at some reefs and being significantly lower at others. Importantly, this demonstrates that at some places there were substantial accumulations of detached reef algae in the seagrass meadows up to hundreds of metres from the nearest reef.

The amount of detached kelp at Marmion was typically higher than at Jurien, although this pattern was narrowly non-significant ($P < 0.06$; Table 2). Patterns with distance from reef were qualitatively similar to those for total detached reef algae, with the biomass at 0 m typically higher than other distances (Table 3). There were also substantial accumulations of detached kelp at distances >300 m from the reefs (Fig. 1).

The amount of detached reef algae present in adjacent seagrass habitats at the various distances away from the reefs generally varied between 1 and 15% (overall mean 3.6% ± 0.7 SE, maximum 23%) of the biomass of attached algae in an equivalent area on the nearest source reefs. There was no relationship between biomass of attached algae on the nearest reef and biomass of detached reef algae at any distance ($r^2 < 0.15$, $P > 0.2$). Patterns in detached kelp alone were very similar to those shown by the total detached macroalgae.

The proportion of biomass of kelps was greater in the detached than in the attached assemblage in both Marmion Lagoon (88% ± 2 SE in the drift vs. 47% ± 7 SE in the attached assemblage) and Jurien Bay (44% ± 9 SE vs. 16% ± 6 SE).

Fish abundance

Five taxa of herbivorous fish were encountered in the seagrass meadows. Silver drummers (*Kyphosus sydneyanus*) yielded the highest densities, but were only encountered at two reefs, one in each location (Fig. 2). Scalyfins (*Parma* spp.) were found around all reefs except The Lumps in Marmion Lagoon where no fish were recorded over seagrass. Scalyfins were not identified to species, but were dominated by western scalyfin (*Parma mccullochi*). Herring cale (*Odax cyanomelas*), rainbow cale (*Odax acroptilus*) and fuscous rabbitfish (*Siganus fuscescens*) were only seen occasionally (Fig. 2). There were almost always more herbivorous fish at 0 m than at >300 m (The Lumps was the only exception), but analyses indicated that the magnitude of this difference varied significantly among reefs (Table 4). There were no statistically significant differences between locations, or between *Amphibolis* and *Posidonia* meadows.

Table 3 Summary of results of pair-wise comparisons (SNK-tests) of biomass at all reefs where there was a significant effect of distance

Comparison	Number of reefs	
	Detached reef algae	Detached kelp
0 m > reef	7 (58%)	4 (33%)
0 > 10 m	8 (67%)	4 (33%)
0 > 50 m	7 (58%)	4 (33%)
0 > >300 m	5 (42%)	3 (25%)
10 m > reef	1 (8%)	–
10 > >300 m	2 (17%)	–
50 > 10 m	1 (8%)	–
50 > >300 m	1 (8%)	–
>300 m > reef	3 (25%)	2 (17%)
>300 > 0 m	1 (8%)	1 (8%)
>300 > 10 m	3 (25%)	2 (17%)
>300 > 50 m	2 (25%)	1 (8%)

The numbers and percentage of significant ($P < 0.05$) comparisons

The total biomass of attached macroalgae on the reef itself was negatively related to the density of herbivorous fish at 0 m; this pattern was significant ($r^2 = 0.59$, $P = 0.03$, $n = 8$; Fig. 3).

Consumption of drift

Overall, the consumption of tethered kelp was significantly higher in Jurien Bay (mean 17.2% ± 4.6 SE) than in Marmion Lagoon (mean 6.2% ± 3.5 SE) (Table 5, Fig. 4). There were no differences in consumption of kelp between *Amphibolis* and *Posidonia* meadows. Consumption did vary with distance from reef, but not in a consistent way—consumption was significantly higher at 0 m at some reefs (Table 6), but in some cases was highest at >300 m. At most distances at most reefs, there was just less than 10% consumption of tethered kelp over the 5 days deployment (Fig. 4). However, at some distances on half of the reefs there was between 25 and 75% consumption. There was a significant positive relationship between mean consumption and the mean density of herbivorous fish at 0 m ($r^2 = 0.92$, $P < 0.001$), but not at >300 m ($r^2 = 0.16$, $P > 0.3$; Fig. 3).

Discussion

Our study documents that detached reef algae are exported to adjacent seagrass beds where they are consumed by seagrass-associated fauna. Accumulations of detached reef algae were found in seagrass beds adjacent to all reefs. In some places the biomass of detached reef algae was up to 23% (overall mean 3.6% ± 0.7 SE) of the biomass of attached algae in an equivalent area on the nearest reef. There was no simple relationship between the biomass of detached reef algae and distance from the nearest reef because maximum accumulations were found either at 0 m or >300 m away. The kelp *E. radiata* dominated the attached and the detached algae, and up to 77% (overall mean 11.7% ± 0.5 SE) of the biomass of *E. radiata* tethered in seagrass beds was consumed over a 5-day period.

The large quantities of detached algae and the high rates of consumption suggest that this might form a considerable trophic link between reefs and adjacent seagrass habitats. In some places the spatial extent of this trophic link extends more than 300 m away from the reefs. This pattern was present across the ~200 km spatial extent of our study.

Biomass of attached and detached reef algae

There were no significant overall differences between locations in biomass of either attached or detached reef

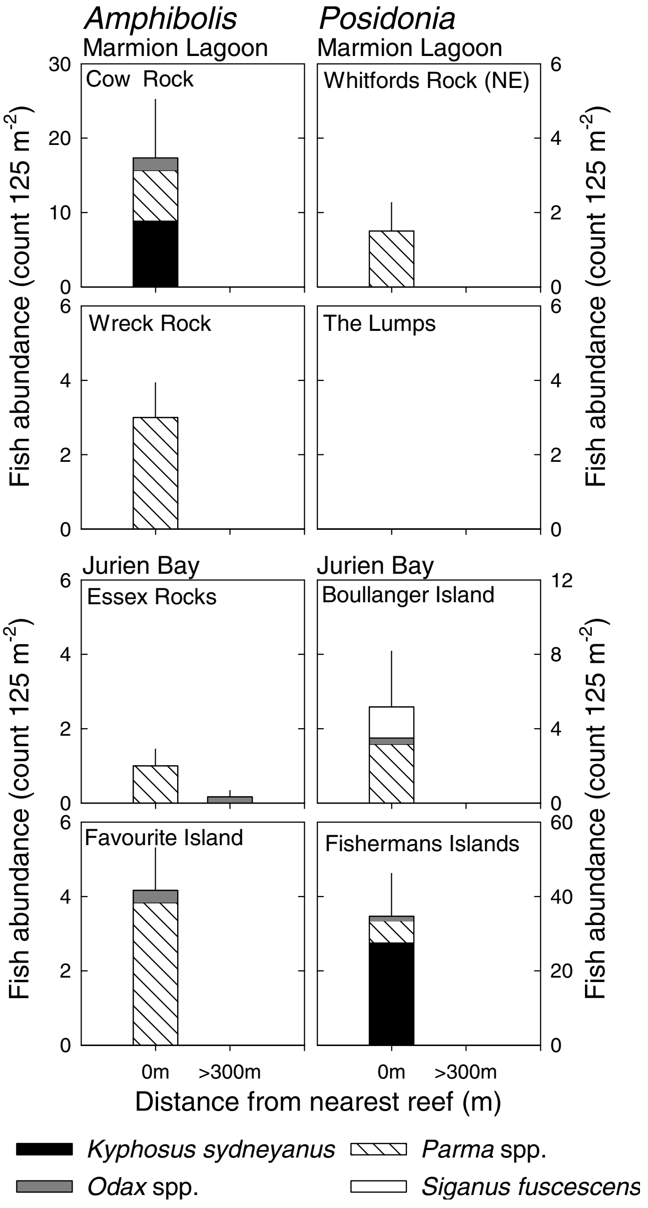

Fig. 2 Mean abundance of herbivorous fish (± SE, $n = 6$) in seagrass meadows adjacent to reefs in Marmion Lagoon and Jurien Bay

Table 4 Results of ANOVA testing the effect of location (fixed factor), seagrass type (fixed factor), reef within location and seagrass type (nested random factor) and distance (fixed factor) on the abundance of herbivorous fish

Source of variation	*df*	MS	*F*	*P*
Location	1	0.3443	0.67	0.459
Seagrass	1	0.0322	0.06	0.814
Reef(L × S)	4	0.5126	8.43	**0.000**
Distance	1	8.2578	15.20	**0.018**
L × S	1	1.9899	3.88	0.120
L × D	1	0.2759	0.51	0.515
S × D	1	0.0139	0.03	0.881
Reef (L × S) × D	4	0.5433	8.93	**0.000**
L × S × D	1	2.1670	3.99	0.116
Residual	80	0.0608		

Data were transformed (Log $x+1$) and subsequently passed tests of equal variances (Cochrans C-test, $P>0.05$) and normality (visual inspection of residuals). $P<0.05$ highlighted in bold

algae, but there were differences between individual reefs within each location. These differences are likely to be caused by environmental variations among reefs. For example, in south-western Australia algal assemblages have been shown to vary between reefs with different geology (Harman et al. 2003; Kendrick et al. 2004), wave exposure (Phillips et al. 1997; Goldberg and Kendrick 2004) and vertical relief (Harman et al. 2003; Kendrick et al. 2004). Differences in wave exposure and geology might also cause differences in the abundance of detached algae by influencing algal detachment rates (Thomsen and Wernberg 2005).

Ecklonia radiata was a dominant component of the attached and detached reef algae at both locations. Interestingly, the proportion of *E. radiata* was more than twice as great in the detached relative to the attached assemblage, probably reflecting that the large, tough kelps are more easily dislodged (Thomsen and Wernberg 2005), disintegrate slower and perhaps are less readily eaten than the smaller, more delicate foliose red and green algae that may be more palatable than brown algae (Montgomery and Gerkin 1980).

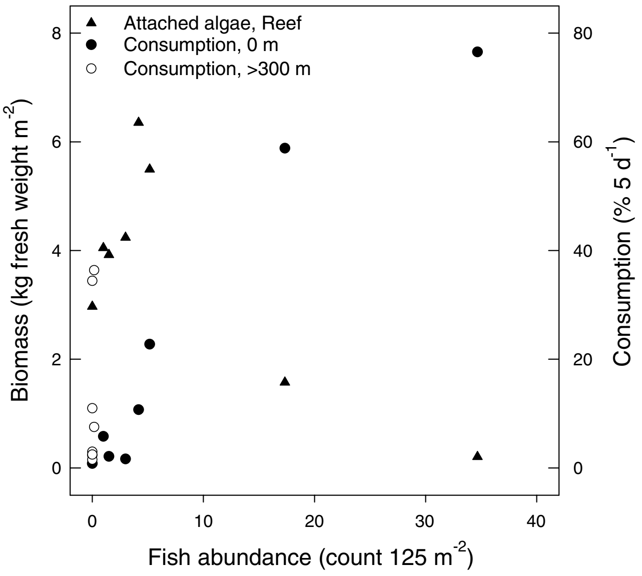

Fig. 3 Relationship between the densities of herbivorous fish in seagrass meadows immediately adjacent to reefs and the biomass of attached macroalgae growing on the reefs, and the mean consumption of tethered pieces of kelp in seagrass immediately adjacent to the reefs (0 m) and > 300 m away from the reefs

Our results are temporally restricted because they reflect patterns during a short period of the late austral summer. Importantly, however, weather conditions during this time of year are generally benign, and are dominated by south-westerly sea breeze conditions (Searle and Semeniuk 1985). Dislodgment of reef algae occurs mainly during storms (e.g. Seymour et al. 1989) so the supply of detached reef algae to the seagrass beds is probably positively correlated with storm frequency and intensity. Our estimates of abundance of detached reef algae within the seagrass beds are, therefore, likely to be conservative estimates, and patterns during other times of the year, for example when winter storms dominate the weather, might be different.

The type of seagrass canopy did not have any effect on the patterns of distribution of detached reef algae within the seagrass beds. It has previously been shown that shoot size and density may have relatively little influence on the amount of macroalgae accumulated within strap-like seagrasses (Bell et al. 1995) such as *Posidonia*. It appears from our results that even the stark difference in seagrass shoot morphology between *Posidonia* and *Amphibolis* does not have any influence on the ability of the seagrass canopy to retain drifting algae. One simple explanation could be that in relatively dense meadows, where the bulk of water flow is directed to the roof of the canopy (Granata et al. 2001), detached algae do not percolate into the canopy but simply tumble across it.

Spatial extent of export

There was no simple negative relationship between the biomass of detached reef algae and distance from reef and we therefore reject the hypothesis that the biomass of detached reef algae decreases away from reefs. Although there was considerable variability among reefs in the pattern of distribution of detached reef algae with increasing distance from reefs, some trends were present. First, there was no correlation between the biomass of attached algae on reefs and detached reef algae at any distance. Second, at most reefs, the greatest accumulations of detached reef algae occurred immediately adjacent to the reef (0 m). Third, at many reefs there were considerable accumulations at the farthest distance (> 300 m). These patterns indicate that the amount of detached reef algae available to consumers in the seagrass meadow cannot be predicted even immediately adjacent to reefs and thus that the accumulation of detached reef algae is influenced by factors other than simply what is on the reefs and the distance away from

Table 5 Results of ANOVA testing the effect of location (fixed factor), seagrass type (fixed factor), reef within location and seagrass type (nested random factor) and distance (fixed factor) on the consumption (% 5 day^{-1}) of kelp tethers

Source of variation	*df*	MS	*F*	*P*
Location	1	91.2625	22.15	**0.009**
Seagrass	1	1.1612	0.28	0.624
Reef(L × S)	4	4.1207	7.72	**0.000**
Distance	3	6.3706	1.60	0.241
L × S	1	6.1488	1.49	0.289
L × D	3	3.0508	0.77	0.535
S × D	3	0.1393	0.03	0.991
Reef(L × S) x D	12	3.9829	7.46	**0.000**
L × S × D	3	12.9734	3.26	0.060
Residual	224	0.5338		

Data were transformed (Log $x+1$) and subsequently passed tests of equal variances (Cochrans C-test, $P>0.05$) and normality (visual inspection of residuals). $P<0.05$ highlighted in bold

this source. Consequently, the linkages between reef and seagrass habitats appear complex and may take place over considerable distances. For example, reef geomorphology and seabed topography may affect local water circulation patterns (Granata et al. 2001) and, thus, redistribution of detached algae around individual reefs and within seagrass beds; accumulations at the foot of the reef appear to be associated with holes and crevices trapping the algae (personal observation). Algae in these accumulations are probably transient, carried away by the flow created when waves and currents hit the reef, to accumulate further away where the water also tend to be deeper and thus calmer.

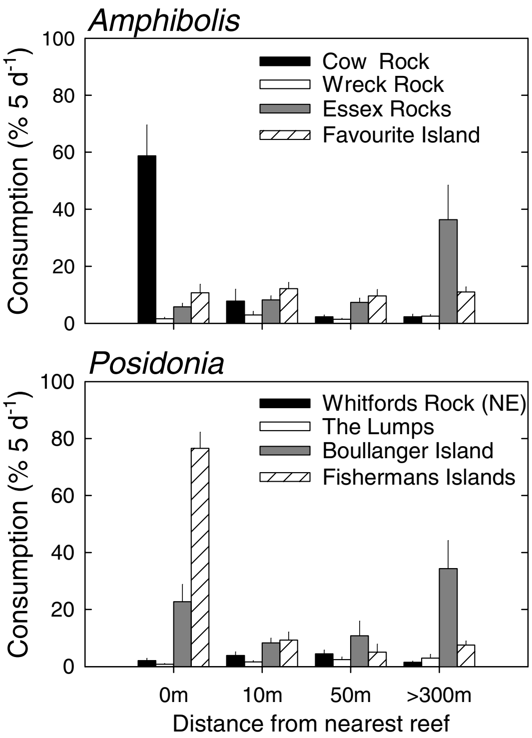

Fig. 4 Mean consumption (± SE, $n=8$) of tethered pieces of kelp (*Ecklonia radiata*) at different distances away from reefs and into adjacent seagrass meadows

Abundance of herbivorous fish and consumption of drift algae

More herbivorous fish were found near reefs than far from reefs, a similar result to that reported by Howard (1989). Immediately adjacent to reefs (0 m), there was a strong positive correlation between the densities of herbivorous fish and the rates of consumption—at the two reefs where herbivorous fish were abundant, consumption exceeded 50%. The most abundant fish species recorded at these two reefs was *K. sydneyanus*, which feeds predominantly on brown algae (Rimmer and Wiebe 1987; Moran and Clements 2002). These patterns, and our observations of fish bites, suggest that much of the consumption we recorded on the tethered kelps was due to herbivorous fish.

We recorded few herbivorous fish far from the reef, yet consumption at some places exceeded 30% in 5 days. Our observations of the grazing marks indicate that this was also due to consumption by fish, but we are unsure of the identity of the species involved. Consumption by *K. sydneyanus* is unlikely, as this is a reef-associated species with fidelity to high-relief limestone reefs

Table 6 Summary of results of pair-wise comparisons (SNK-tests) of % consumption at all reefs where there was a significant effect of distance

Comparison	Number of reefs
0 > 10 m	2 (25%)
0 > 50 m	3 (38%)
0 > > 300 m	2 (25%)
> 300 > 0 m	1 (13%)
> 300 > 10 m	2 (25%)
> 300 > 50 m	2 (25%)

Listed are the number of reefs where the comparisons were significant ($P<0.05$) and the percentages of total number of reefs

(Howard 1989; Harman et al. 2003). Several species of odacids are commonly found within *Posidonia* and *Amphibolis* beds (Hyndes et al. 2003). Most are relatively small, well camouflaged and have a cryptic behaviour, hiding within the canopy. These fishes could have been overlooked in the visual transects, and might account for the grazing of the kelp tethers.

Small invertebrates such as amphipods are unlikely to have consumed significant amounts of kelp on the tethers because these animals usually require the kelp to be broken down into smaller fragments (Robertson and Lucas 1983; Norderhaug et al. 2003). Total consumption of detached macroalgae in the seagrass beds is therefore likely to be considerably higher than our estimates when including invertebrate consumption of more heavily degraded macroalgae over longer time periods.

Another pattern worth noting was the negative relationship between the density of herbivorous fish immediately adjacent to the reefs (0 m) and the biomass of attached macroalgae on the reefs. The pattern of association alone does not give us insights as to the nature of the relationship, but the high rates of grazing on our tethered pieces of kelp at some places support the idea that herbivorous fish, when in high densities, might exert an influence on the biomass of attached macroalgae. We cannot, of course, discount the possibility that some feature of the reefs influence both the macroalgae and the fish. If fish grazing does, however, influence the attached algal assemblage, it can also have indirect effects on the strength of reef–seagrass linkages over large spatial extents by modifying the availability of algae to be exported.

Detached macroalgae form a trophic link between reefs and seagrasses

Ecosystem function may depend more on the diversity of habitats and their interactions than on the diversity of individual species (Giller et al. 2004; Hawkins 2004), and consequently, Hawkins (2004) emphasised the need to measure the magnitude and spatial extent of cross-habitat linkages. We found the distribution of detached reef algae within seagrass beds adjacent to reefs to be spatially variable, with some areas containing large accumulations, and other areas containing relatively little. Detached reef algae in seagrass beds at a single time is therefore a patchy resource. However, at landscape scales, and over longer time periods, the supply of detached macroalgae is likely to be relatively predictable. We suggest that detached reef algae form a significant trophic link to seagrass beds in south-western Australia and that this trophic link extends to distances of at least hundreds of metres away from individual reefs.

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