

Intensity of herbivory on kelp by fish and sea urchins differs between inshore and offshore reefs

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ABSTRACT: Interactions between water motion, primary productivity, and herbivory are complex. Rates of grazing by fish on tropical coral reefs and by sea urchins on temperate rocky reefs are usually high, but can be low in areas of extreme water motion. Some herbivores can switch between mobile (grazing) and sedentary (drift-feeding) behaviours, and this can be influenced by water motion. We compared the relative consumption of the kelp *Ecklonia radiata* at rocky reefs in western Australia with different wave exposures (inshore versus offshore). No herbivory was recorded offshore, suggesting that wave exposure might inhibit herbivory. We also compared grazing by fish and sea urchins, and grazing versus drift-feeding pathways. Grazing by fish and sea urchins was low, except at one inshore reef where grazing by fish was intense. In contrast, drift-feeding by sea urchins was recorded at all inshore reefs, suggesting that this is a ubiquitous behaviour in the region. We measured productivity of *E. radiata* to determine if spatial patterns in rates of herbivory matched those of productivity. Productivity of *E. radiata* was higher on offshore reefs at one location. The observed difference in consumption between inshore and offshore reefs at both locations suggests that consumption is not limited by productivity, but by exposure. Further, the high productivity offshore combined with low rates of herbivory suggest that offshore reefs might be a source of kelp that subsidises other habitats.

KEY WORDS: Grazing · Drift feeding · Detached algae · Wave exposure · *Ecklonia radiata* · *Heliocidaris erythrogramma* · *Kyphosus sydneyanus*

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INTRODUCTION

Herbivory is a profoundly important ecological process that can limit the distribution and abundance of plants, and that forms a major conduit for energy transfer to higher trophic levels. Grazing—consumption of growing plants—is a ubiquitous determinant of plant abundance and distribution in terrestrial and marine ecosystems (see e.g. reviews by Lubchenco & Gaines 1981, Huntly 1991). In marine ecosystems, grazing by herbivores can suppress plants and thereby modify ecosystems over vast areas, although this phenomenon can be strongly influenced

by larval supply, predator activity, or presence of allochthonous sources of food (e.g. Harrold & Reed 1985, Sala et al. 1998).

One factor that can determine the influence of herbivores is physical stress. In the ocean, a powerful type of physical stress is caused by wave motion. Waves can influence the intensity of grazing through a number of mechanisms, including changing the behaviour of herbivores, affecting mortality of herbivores, influencing settlement and recruitment of both herbivores and algae, or influencing the type and availability of allochthonous food sources. For example, foraging by some species of sea urchins is reduced in conditions of

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high water movement (e.g. Lissner 1980, Kawamata 1998), and sea urchins can be dislodged by even moderate water movement (e.g. Tuya et al. 2007). Spatial variability in the influence of waves occurs due to depth and geomorphologic features that attenuate waves. Due to the ubiquitous influence of water motion, spatial variability in exposure to water motion can lead to spatial variability in the abundances and behaviour of herbivores and, therefore, the intensity of herbivory (e.g. Duggins et al. 2001, Schanz et al. 2002). Along more than ~1000 km of the southwestern coast of Australia, rocky reefs oriented parallel to the coast create an onshore–offshore gradient in wave exposure. This gradient is reflected by differences between exposed (offshore) and sheltered (inshore) reefs in the species composition of macroalgae (Phillips et al. 1997), and the attachment strength and morphology of the small kelp *Ecklonia radiata* (Thomsen et al. 2004, Wernberg & Thomsen 2005). The first aim of the present study was to compare rates of herbivory on offshore and inshore reefs to test whether position along the exposure gradient affects the intensity of herbivory.

In marine ecosystems—at least in contemporary ones—the intensity of grazing by herbivores is typically greatest by fishes on tropical coral reefs, sea urchins on temperate rocky reefs, gastropod molluscs on intertidal rock platforms, and fishes and sea urchins in some seagrass ecosystems (Lawrence 1975, Hawkins & Hartnoll 1983, Steneck 1988, Heck & Valentine 2006). On temperate rocky reefs, intense grazing by dense populations of sea urchins can be the major determinant of the benthos over extensive areas (e.g. Foreman 1977, Andrew & O'Neill 2000). Often, where sea urchins are abundant, rock surfaces are bare or are covered by encrusting algae. In contrast, where sea urchins are sparse or absent, rock surfaces host stands of erect macroalgae. Unlike coral reefs, herbivory by fish in temperate seas is typically a minor influence on the benthos, although there are examples in which herbivory by fish can lead to changes in biomass and composition of primary producers on reefs (e.g. Andrew & Jones 1990, Sala & Boudouresque 1997) and in seagrass meadows (e.g. Tomas et al. 2005b, Prado et al. 2007). Studies that have partitioned grazing by sea urchins and fish are rare (but see Hay 1984, Tomas et al. 2005a); therefore, the second aim of the present study was to measure the relative importance of grazing by fish and sea urchins on temperate rocky reefs in western Australia.

Grazing is only one form of herbivory, another is consumption of plants dislodged from the place they were growing—this behaviour is frequently called 'drift-feeding' when applied to marine herbivores (e.g. Harold & Reed 1985, Day & Branch 2002b). Locations that receive a regular supply of dislodged algae ('drift

algae') can host dense populations of herbivores, even where *in situ* productivity is low (e.g. Bustamante et al. 1995). In the ocean, the availability of drift algae allows a feeding behaviour that enables herbivores to persist in otherwise stressful environments. For example, sea urchins that have an abundant supply of drift kelp can stay within cryptic microhabitats, avoiding a mobile foraging behaviour that might expose them to dislodgement by waves or attacks by predators (e.g. Harold & Reed 1985). In addition, the availability of drift algae can be strongly influenced by waves. For example, the physical 'drag' exerted by waves can dislodge or prune macroalgae (Thomsen & Wernberg 2005). The third aim of the present study was to measure the relative importance of direct grazing and 'drift-feeding', and to assess how this varied between reefs with different levels of wave exposure.

In the present study we compared rates of consumption of the small kelp *Ecklonia radiata* in different treatments designed to separate (1) grazing by fish, (2) grazing by sea urchins, and (3) consumption of dislodged kelp by sea urchins. *E. radiata* is the dominant alga on subtidal rock surfaces in temperate western Australia (Wernberg et al. 2003), and is an important food source for many consumers (Vanderklift et al. 2006, Crawley & Hyndes 2007). We tested whether the 3 types of *E. radiata* consumption differed between inshore (sheltered) and offshore (exposed) reefs on the lower west coast of Australia. We also tested for differences in primary productivity of *E. radiata* between inshore and offshore reefs, in order to assess whether spatial patterns in herbivory might be related to spatial patterns in primary productivity. We tested for the generality of patterns by taking measurements from 6 reefs at each of 2 locations separated by ~200 km.

MATERIALS AND METHODS

Study area. This study focussed on 2 locations on the lower west coast of Australia: Jurien Bay (30° 17.3 S, 115° 02.5 E) and Marmion Lagoon (31° 49.4 S, 115° 44.0 E). We took measurements at 3 reefs at each of 2 positions relative to the shore (inshore and offshore) at both locations (Fig. 1). Maximum depth at the surveyed reefs ranged from 5 to 8 m. The subtidal reefs in these locations are typically dominated by a canopy of large brown algae, usually the small (<2 m) kelp *Ecklonia radiata* or the fucoids *Sargassum* spp., and a diverse assemblage of associated foliose algae (Wernberg et al. 2003). The most abundant large herbivores are sea urchins (Vanderklift & Kendrick 2004) and some fishes (Hutchins 2001, Wernberg et al. 2006). Intensively grazed barrens have not been recorded from reefs on this coast.

The region experiences frequent sea breezes in summer and storms in winter. Storms generate heavy seas and swell, with significant offshore wave heights exceeding 4 m on average 30 times per year (Lemm et al. 1999). The wave energy at the shore is typically reduced by refraction and attenuation of waves by offshore reefs (Masselink & Pattiaratchi 2001). Coastal waters in southwestern Australia typically contain low concentrations of inorganic nutrients (Lourey et al. 2006).

Our measurements focussed on contrasting offshore and inshore reefs in the 2 locations. Offshore reefs were always several km from the shore (range = 2.4 to 6.4 km) and were exposed to oceanic swells, while inshore reefs were typically <1 km from the shore (range = 0.1 to 1.4 km). All measurements were taken during the austral spring–summer (between October 2004 and January 2005).

Data collection. Productivity of *Ecklonia radiata* was measured following a method described by Mann & Kirkman (1981) adapted by Fairhead & Cheshire (2004). We marked individual kelp by punching a hole

into the central lamina, 5 cm from the junction between the stipe and the lamina. We marked 10 individuals in patches of dense kelp at each reef, and collected them 20 to 22 d later. The distance of the hole from the junction between stipe and lamina was then measured in the laboratory (allowing the extension to be calculated by subtraction), and the first 20 cm of the thallus was then cut into 5 cm strips and weighed. The strip with the maximum biomass was then used to calculate biomass accumulation (BA; $g^{-1} ind.^{-1} d^{-1}$) as $BA = xw/5d$, where x is the thallus extension (cm), w is the wet weight (g) of the heaviest strip, and d is the number of days between punching the hole and collecting the kelp. Tagged kelp at one reef (Escape Island, Jurien Bay) could not be retrieved due to consistently poor weather conditions.

Consumption of *Ecklonia radiata* was measured following a method described by Vanderklift & Wernberg (2008). Uneroded laterals that were free of epiphytes were collected, placed between 2 sheets of acrylic glass (the top sheet clear and the bottom sheet white), and photographed. Laterals were secured by a clothes peg and assigned to one of 4 treatments: (1) caged, enclosed in a cage of plastic mesh (Nylex Gutter Guard: mesh size 3×3 mm) to exclude all large herbivores; (2) drift, clothes peg attached to a ~50 cm length of monofilament fishing line; (3) understorey, clothes peg attached to a length of chain placed on the reef surface; and (4) canopy, clothes peg attached to a float tied to a ~50 cm length of black nylon cord. The drift treatment was intended to mimic the action of detached kelp and estimate consumption by sedentary herbivores (sea urchins); the understorey treatment was intended to mimic kelp at the level of the understorey and estimate consumption by all large mobile herbivores; and the canopy treatment was intended to mimic kelp at the level of the canopy and estimate consumption by herbivorous fish only. After 2 to 3 d, the laterals were collected and rephotographed. Photographs of each piece before and after deployment were analysed using image analysis software (ImageJ, rsb.info.nih.gov/ij/) to calculate surface area, and the consumption ($\% loss d^{-1}$) of each lateral was then calculated. The error in area measurements between photographs was up to $\pm 9\%$ (verified from repeat photographs of laterals

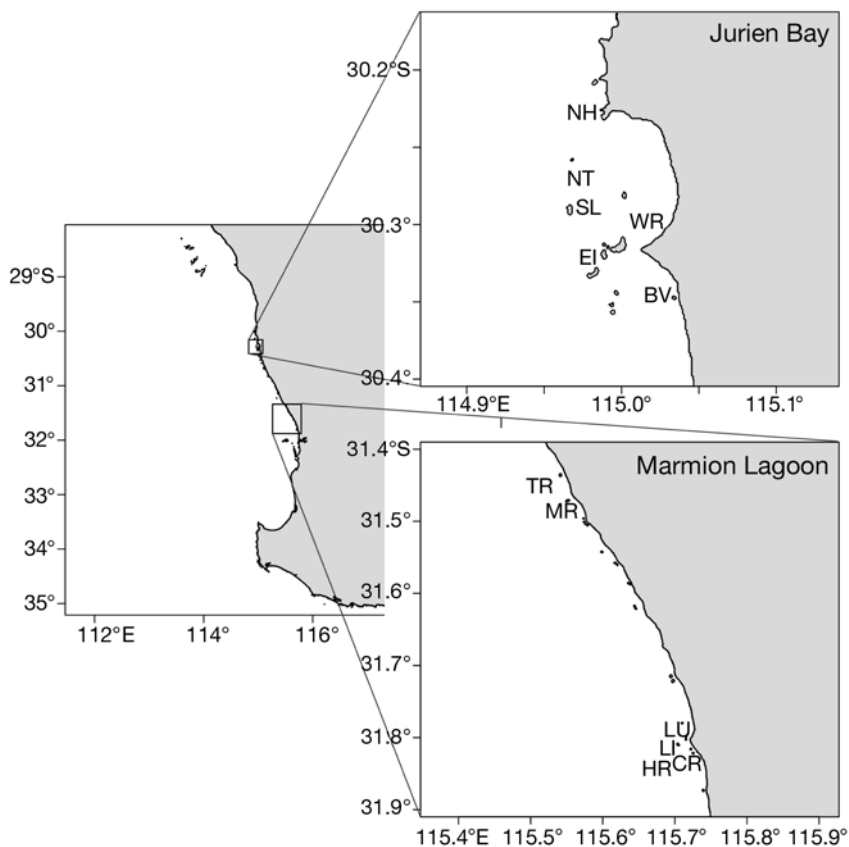


Fig. 1. Surveyed reefs in Jurien Bay and Marmion Lagoon, western Australia. Offshore reefs: NT = North Tail, SL = Seaward Ledge, EI = Escape Island, TR = Two Rocks, HR = Horseshoe Reef, LI = Little Island. Inshore reefs: BV = Booka Valley, NH = North Head, WR = Wire Reef, CR = Cow Rocks, MR = Map Reef, LU = Lumps

with no grazing or erosion), so any change in area <10% was considered to be 0%. A previous study in which drift and understorey mimics were placed in plots cleared of all herbivorous invertebrates revealed little or no loss due to erosion (Vanderklift & Wernberg 2008).

Abundances of herbivorous invertebrates (focussing mainly on the sea urchin *Heliocidaris erythrogramma*, although other large sedentary invertebrates were also included) were counted in five 5 × 1 m transects per reef. Abundances of herbivorous fishes were counted by SCUBA divers in three 25 × 5 m transects per reef.

Statistical analyses. All data were intended to be analysed using mixed model ANOVA. However, the absence of measurements of *Ecklonia radiata* productivity for Escape Island meant that the full ANOVA model could not be applied. Instead, data for Jurien Bay and Marmion Lagoon were analysed separately. In both cases, data were analysed using nested ANOVA, with the factors Exposure (fixed, 2 levels: offshore and inshore) and Reef (random and nested in Exposure, with 3 levels in each case except for offshore reefs at Jurien Bay, for which there were 2 levels). Because not all tagged kelp were relocated at each reef, data were reduced to an equal number of individuals (n = 5) by exclusion of randomly selected individuals. Untransformed data were used after Cochran's tests confirmed that variances were approximately equal.

Data for daily rates of consumption of tethered kelp laterals contained many zeros, and so parametric statistics were unsuitable. Instead, these data were analysed using permutational multivariate ANOVA (PERMANOVA; Anderson 2001). This method is based on distances, and the statistical significance of factors is tested by permutation. Because some of the replicate tethers were missing, the original data were not balanced, so data were reduced to n = 5 by exclusion of randomly selected tethers. A mixed effects analysis was used, with the factors Treatment (4 levels, fixed), Exposure (2 levels, fixed), Location (2 levels, random), and Reef (random and nested in the Exposure × Location interaction, with 3 reefs in each combination). Euclidean distances were calculated from untransformed data, and the permutation tests used 4999 permutations of residuals under a reduced model.

Patterns in densities of invertebrates and fish were analysed by mixed effects ANOVA with the factors Exposure (2 levels, fixed), Location (2 levels, random), and Reef (random and nested in the Exposure × Location interaction, with 3 reefs in each combination). Prior to analyses, data were transformed to conform to assumptions of heteroscedasticity and normality.

RESULTS

Ecklonia radiata productivity

Primary productivity (measured as biomass accumulation) of individual *Ecklonia radiata* was 0.12 to 4.12 g wet weight (WW) ind.⁻¹ d⁻¹, with means of 1.1 ± 0.8 g WW ind.⁻¹ d⁻¹ at Marmion Lagoon and 1.5 ± 1.0 g WW ind.⁻¹ d⁻¹ at Jurien Bay. At Jurien Bay, primary productivity of individual *E. radiata* was 0.8 g WW ind.⁻¹ d⁻¹ higher on offshore reefs than inshore reefs (95% CI = 0.13–1.52; ANOVA: MS = 4.14, *F* = 144.6, *p* = 0.001) (Fig. 2). There were no differences between inshore and offshore reefs at Marmion Lagoon (MS = 0.41, *F* = 0.48, *p* = 0.53). There was no significant variation among reefs within an exposure level at either location (*p* > 0.3).

Ecklonia radiata consumption

Differences in the daily rate of consumption varied inconsistently among treatments from inshore and offshore reefs (significant Treatment × Exposure interaction), and from different reefs within each position (significant Treatment × Reef interaction) (Table 1). Measurable consumption of *Ecklonia radiata* laterals occurred at all 6 inshore reefs, but no measurable consumption occurred at any of the 6 offshore reefs: visual inspection of the laterals from offshore reefs confirmed that consumption did not occur (Fig. 3). Of the 4 treatments, only one (drift) was consumed at all 6 inshore reefs (Fig. 3), and one (caged) never showed any evi-

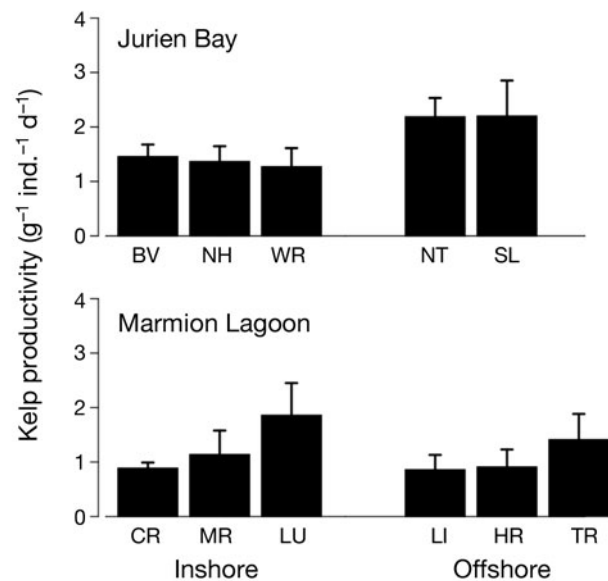


Fig. 2. *Ecklonia radiata*. Productivity of tagged *E. radiata* (g⁻¹ wet weight d⁻¹; n = 5, ±SE) at inshore and offshore reefs in Jurien Bay and Marmion Lagoon. Abbreviations as in Fig. 1

Table 1. Results of permutational multivariate ANOVA on daily rates of consumption of *Ecklonia radiata*, testing for differences between treatments, locations, exposure, and among reefs. Values in **bold** are significant at $\alpha = 0.05$; p-value is derived by a permutation test

Source of variation	df	MS	F	p
Treatment	3	213.20	14.25	0.067
Exposure	1	670.00	24.63	0.424
Location	1	27.20	0.30	0.560
Reef (Exposure \times Location)	8	89.76	3.64	0.001
Treatment \times Exposure	3	213.20	14.25	0.031
Treatment \times Location	3	14.96	0.15	0.925
Treatment \times Reef (Exposure \times Location)	24	97.24	3.94	<0.001
Exposure \times Location	1	27.20	0.30	0.567
Treatment \times Exposure \times Location	3	14.96	0.15	0.931
Residual	192	24.69		

dence of consumption. At inshore reefs, consumption of drift kelp was significantly higher than consumption of caged and understory kelp (Monte Carlo pairwise comparison: $p \leq 0.01$) but not of canopy kelp ($p = 0.09$). Grazing marks and field observations of consumption indicated that consumption of drift kelp was exclusively by sea urchins (10 of 30 inshore drift kelp showed evidence of consumption by sea urchins). Only one species, the purple sea urchin *Heliocidaris erythrogramma*, was observed to consume the drift pieces (M. A. Vanderklift pers. obs.), although other species of sea urchin were present.

Consumption by herbivorous fish was predominantly recorded on canopy-level kelp at a single inshore reef, where this consumption was higher than all other treatments (Monte Carlo pairwise tests: all $p < 0.05$). Field observations and the size of the bite marks indicated that consumption was probably due to silver drummer *Kyphosus sydneyanus*, a large (maximum length ~ 70 cm) kyphosid. Consumption of understory kelp was uncommon, recorded on only 4 of 60 tethers; observations of grazing marks indicated that grazing was probably due to fish (2 tethers) and sea urchins (2 tethers).

Abundance of herbivores

The purple sea urchin *Heliocidaris erythrogramma* was the most abundant sea urchin recorded in our surveys, comprising 78% of all sea urchins. Densities of *H. erythrogramma* did not vary significantly between inshore and offshore reefs (Table 2, Fig. 4), but showed significant spatial variation at the largest scale (significant Location effect), being more abundant at Jurien Bay than Marmion Lagoon (Table 2).

Four taxa of herbivorous fishes were recorded in our surveys: *Kyphosus sydneyanus*, *K. cornelii*, *Odax cyanomelas*, and *Parma* spp. When combined, their densi-

ties did not vary consistently between inshore and offshore reefs (Table 3, Fig. 5), and the only statistically significant source of spatial variation was among reefs within locations (Table 3). Silver drummer *K. sydneyanus* comprised 23% of the total herbivorous fish count, and reflected the same patterns, with no consistent variation between inshore and offshore reefs, and statistically significant among-reef variability (Table 3, Fig. 5). The reef that hosted the highest densities of *K. sydneyanus* (Cow Rocks in Marmion Lagoon) was the same reef where substantial consumption of the canopy tethers was recorded.

DISCUSSION

Rates of herbivory on *Ecklonia radiata* were overall much greater at inshore (more sheltered) reefs, than at offshore (more exposed) reefs; some consumption occurred at all inshore reefs, but no consumption occurred at any offshore reefs. However, there were no overall

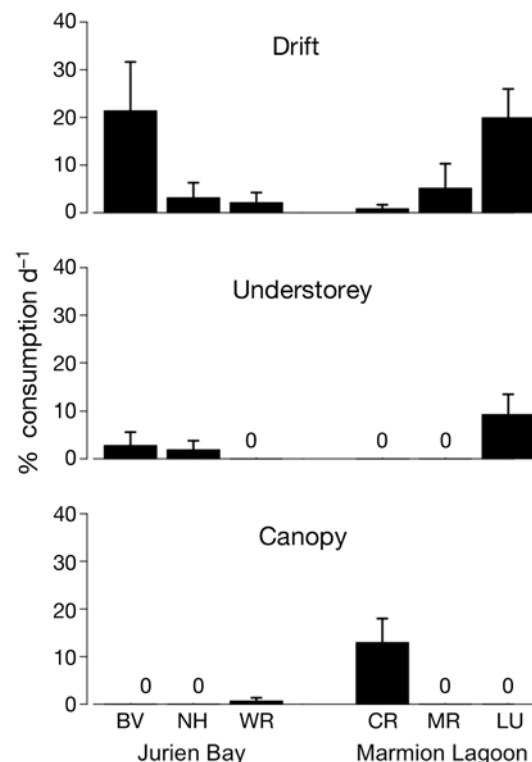


Fig. 3. *Ecklonia radiata*. Consumption of tethered pieces of kelp (\pm SE, $n = 5$) at inshore reefs in Jurien Bay and Marmion Lagoon. Results for offshore reefs and for the caged treatment are not shown because no consumption was recorded. Abbreviations as in Fig. 1

Table 2. Results of mixed effects analyses of variance on $\ln(x+1)$ -transformed counts of the purple sea urchin *Heliocidaris erythrogramma*, testing for differences in location, exposure, and among reefs. Values in **bold** are significant at $\alpha = 0.05$

Source of variation	df	MS	F	p
Exposure	1	0.55	17.63	0.149
Location	1	8.17	12.85	0.007
Location \times Exposure	1	0.03	0.05	0.830
Reef (Location \times Exposure)	8	0.64	1.72	0.118
Residual	48	0.37		

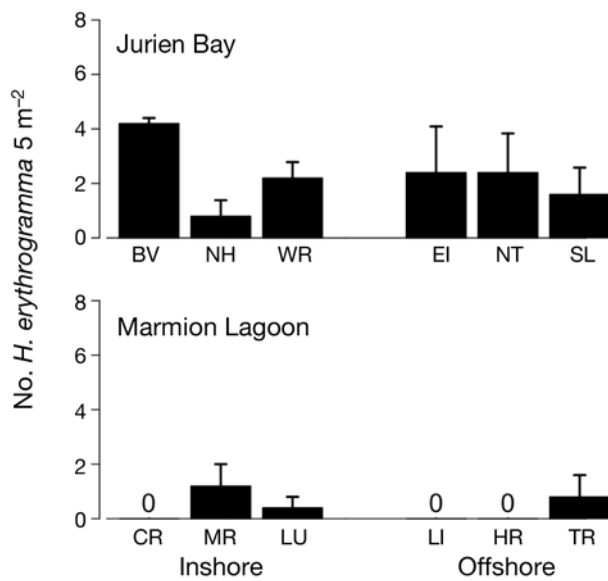


Fig. 4. *Heliocidaris erythrogramma*. Densities of the purple sea urchin *H. erythrogramma* (\pm SE, $n = 5$) at inshore and offshore reefs in Jurien Bay and Marmion Lagoon. Abbreviations as in Fig. 1

Table 3. Results of mixed effects ANOVA on $\ln(x+1)$ -transformed counts of herbivorous fish, testing for differences in location, exposure, and among reefs. Values in **bold** are significant at $\alpha = 0.05$

Source of variation	df	MS	F	p
All herbivorous fish				
Exposure	1	0.23	8.8	0.207
Location	1	1.47	1.43	0.266
Location \times Exposure	1	0.03	0.03	0.878
Reef (Location \times Exposure)	8	1.03	2.65	0.030
Residual	24	0.39		
<i>Kyphosus sydneyanus</i>				
Exposure	1	0.23	1.94	0.396
Location	1	3.88	2.67	0.141
Location \times Exposure	1	0.12	0.08	0.783
Reef (Location \times Exposure)	8	1.45	4.60	0.002
Residual	24	0.32		

differences in the densities of the main herbivores (sea urchins and fishes), and consumption was not strongly related to herbivore density. (There was a statistically significant correlation between density of *Kyphosus sydneyanus* and consumption of 'canopy' tethers, but this was due to high values of each at a single site.) Herbivory almost always occurred in the form of consumption of drifting kelp. Productivity of kelp was higher on offshore reefs at Jurien Bay, but not at Marmion Lagoon.

Low rates of grazing by fish and sea urchins

Results from the present study show that direct grazing on kelp by herbivorous fish and sea urchins is relatively minor on the lower west coast of Australia. Unequivocal evidence of direct grazing on kelp by fish (i.e. consumption of tethers available only to swimming organisms) was substantial at only one reef (Cow Rocks: 13% consumption d^{-1}). This reef was also characterised by relatively high abundance of the herbivorous fish *Kyphosus sydneyanus* and low biomass of kelp (see Wernberg et al. 2006, authors' unpubl. data). High abundances of *K. sydneyanus* at this reef have also been recorded during previous surveys (Wernberg et al. 2006), suggesting high temporal consistency. This result suggests that grazing on kelp by herbivorous fish might be locally important at some reefs in southwestern Australia. Although grazing by fish is typically low on temperate reefs in the region, localised areas of intense grazing by fish do occur elsewhere (e.g. Andrew & Jones 1990, Sala & Boudouresque 1997).

The low level of direct consumption of understory tethers by sea urchins (only 2 of 60 tethers showed characteristic sea urchin bite marks) suggests that grazing by sea urchins is generally low across the region. The low rates of grazing contradict suggestions of general patterns of intercontinental differences (e.g. higher rates of grazing in Australasia than the north Pacific; Steinberg et al. 1995), and contrast with the higher rates of grazing recorded in New Zealand (5 to 7% d^{-1} ; Steinberg et al. 1995) and in New South Wales (~25% d^{-1} ; Steinberg & van Altena 1992). This contrast supports the conclusion that regional differences in the intensity of grazing exist in temperate Australasia (Connell 2007). Demonstrating the basis for these broad differences remains a challenge for ecologists. It is possible that the distribution range of a single species, the sea urchin *Centrostephanus rodgersii*, could explain the differences. *C. rodgersii* is a key grazer in eastern Australia, where its grazing activities result in large areas devoid of erect algae (e.g. Fletcher 1987, Andrew & O'Neill 2000), but it is absent from the west coast, and the congener *C. tenuispinus* does not

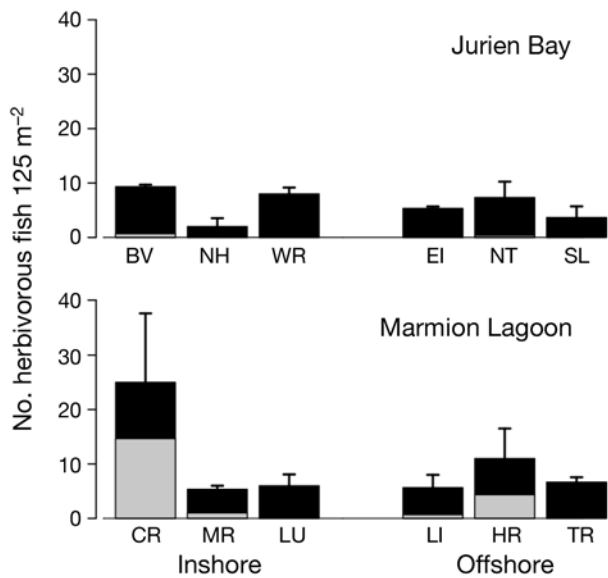


Fig. 5. Densities of herbivorous fish (\pm SE, $n = 3$) at inshore and offshore reefs in Jurien Bay and Marmion Lagoon. Light grey shading: abundance of *Kyphosus sydneyanus*; black: abundance of all other herbivorous fishes. Abbreviations as in Fig. 1

appear to have the same impact. *Heliocidaris erythrogramma* is another species with the capacity to cause barrens in some areas of eastern Australia (Wright & Steinberg 2001, Valentine & Johnson 2005), yet although it is present on the west coast, it is not associated with barrens. Connell & Irving (2008) speculated that this pattern could relate to feeding behaviour, in which *H. erythrogramma* will adopt a drift-feeding behaviour until their density exceeds that which can be sustained by the drift available. The results of the present study are consistent with this idea.

In general, the densities of sea urchins recorded in the present study were low ($< 1 \text{ m}^{-2}$), and low rates of grazing might simply reflect these low densities. However, a study at a nearby location also found low rates of grazing, although densities of sea urchins were markedly higher (5.8 m^{-2} ; Vanderklift & Wernberg 2008). There is increasing evidence that, although grazing by sea urchins undoubtedly modifies ecosystems at some places, density of sea urchins alone does not lead to high rates of grazing, as many species assume a drift-feeding behaviour (Castilla & Moreno 1982, Harrold & Reed 1985, Day & Branch 2002a, Shears et al. 2008).

Most herbivory was drift-feeding by sea urchins

In the present study, most of the consumption measured was on drifting fragments of kelp, and this consumption was typically by sea urchins: 10 of 30 drift

tethers inshore showed evidence of consumption by urchins. This form of consumption was recorded at each of the inshore reefs at both locations, indicating that it is generally important along the coast. Consumption of drifting fragments of algae is a common behaviour among sea urchins (e.g. Castilla & Moreno 1982, Harrold & Reed 1985), and this behaviour might be especially advantageous in situations in which a mobile foraging behaviour might be hazardous—for example, where wave motion can dislodge sea urchins or where the risk of being eaten by predators is high.

Herbivory restricted to inshore reefs

Differences between inshore and offshore reefs (our proxy for exposure to waves) existed for primary productivity of *Ecklonia radiata* (but only at one location), and were strong for consumption of tethered pieces of kelp (no consumption was recorded offshore), but were not detected for abundances of any of the groups of herbivores we studied.

Based on a mean density of adult sporophytes of *Ecklonia radiata* of 11 to 30 m^{-2} (Wernberg et al. 2005), our estimates of productivity equate to $1\text{--}123 \text{ g WW m}^{-2} \text{ d}^{-1}$. These estimates are comparable to Kirkman's (1984) estimates of daily productivity (17 to $120 \text{ g WW m}^{-2} \text{ d}^{-1}$). Rates of productivity are lower in cooler winter months, but nevertheless yearly rates of productivity are substantial ($20.7 \text{ kg WW m}^{-2}$; Kirkman 1984). As little of the biomass produced is grazed directly at most reefs, this creates a substantial potential supply of drift; indeed, large volumes of drift kelp are conspicuous on some beaches in the area (e.g. Ince et al. 2007).

The higher productivity at offshore reefs at Jurien Bay might reflect greater water movement or clearer water, both of which can enhance growth (Hurd 2000). The findings with respect to productivity are consistent with patterns of $\delta^{13}\text{C}$; offshore kelp at Jurien Bay, but not Marmion Lagoon, has lower $\delta^{13}\text{C}$ values than those of inshore reefs (Babcock et al. 2006). Low $\delta^{13}\text{C}$ is consistent with discrimination against ^{13}C , and may occur when the diffusive boundary layer, which frequently limits carbon diffusion to aquatic plants and algae (Hemminga & Mateo 1996), is reduced. Algal productivity is known to increase with increasing water velocity (see Hurd 2000), partly through the breakdown of this diffusive boundary layer. The pattern of higher productivity at offshore reefs is therefore consistent with low $\delta^{13}\text{C}$ values if offshore wave energy is sufficient to break down diffusive boundary layers. The absence of difference in productivity and $\delta^{13}\text{C}$ among reefs at Marmion Lagoon may reflect less variation in current velocities at the site, though we do not have data to test this. The patterns in $\delta^{13}\text{C}$ suggest that the spatial patterns in productivity we observed

might be temporally consistent. If this is the case, it further implies that offshore reefs at Jurien Bay yield a higher productivity per unit area than inshore reefs. As no herbivory was recorded offshore, a greater proportion of offshore kelp productivity is potentially available for export to adjacent habitats, further suggesting a spatial differential in the significance of offshore and inshore reefs as a source of drift kelp for herbivores in recipient habitats.

The observed difference in consumption between inshore and offshore reefs at both locations suggests that consumption is not limited by productivity, but by exposure. Wave exposure can affect rates of herbivory by influencing the abundance or behaviour of herbivores (Duggins et al. 2001). The lack of differences in abundances of herbivorous fish and sea urchins is inconsistent with an influence of waves on abundance. Results from the present study are more consistent with water movement reducing foraging of herbivores offshore. This is consistent with studies that have shown differences in rates of herbivory at varying magnitudes of water motion (e.g. Kawamata 1998, Schanz et al. 2002).

The absence of consumption of drift kelp at offshore reefs does not seem consistent with expectations, as reduced foraging might be expected to increase the amount of time sea urchins spend in a sedentary 'sit-and-wait' behaviour. In fact, *Heliocidaris erythrogramma* in the study region typically occupies crevices or small hollows in the reef, from which they move rarely or not at all (M. A. Vanderklift pers. obs.); individuals from both exposed and sheltered reefs are likely adopting this behaviour. However, this requires urchins to be able to encounter drifting material, and the lack of consumption at offshore reefs might reflect more rapid movement of drift, or perhaps some other mechanical inhibition of the urchin's ability locate and capture drift material.

Understanding the nature of the interactions between wave exposure, primary productivity, and rates of herbivory is important, especially in the context of long-term changes in the processes that generate storms in southwestern Australia, which are occurring due to atmospheric warming in the southern hemisphere (Frederiksen & Frederiksen 2007). Storms are a major source of mortality for kelp, and a major agent for making kelp available as drift. Continued reductions in the frequency and/or severity of storms might therefore benefit grazers by reducing spatial and temporal exposure to storm waves. However, such reductions might also change the supply of drift kelp by decreasing rates of dislodgement and transport, an outcome that would disadvantage herbivores that rely on drift kelp. Given the importance of trophic linkages between inshore and offshore reefs (Vanderklift & Wernberg 2008), our uncertainty about how sensitive these linkages are to perturbations, and the need to

account for these linkages (e.g. Valentine & Heck 2005), an increased understanding of these interactions is vital.

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