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Detached kelps from distant sources are a food subsidy for sea urchins

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Abstract Trophic subsidies link habitats and can determine community structure in the subsidised habitats. Knowledge of the spatial extents of trophic interactions is important for understanding food webs, and for making spatial management practices more efficient. We demonstrate trophic linkages between detached (drift) fragments of the kelp *Ecklonia radiata* and the purple sea urchin *Heliocidaris erythrogramma* among discrete rocky reefs separated by kilometres. Sea urchins were abundant at one inshore reef, where the biomass of drift was usually high. There, sea urchins trapped detached kelp at high rates, although local kelp abundance was low. Most detached kelp present on the reef was retained by sea urchins. Detached seagrass, which was abundant on the reef, was not retained by sea urchins in large quantities. Experiments with tethered pieces of kelp showed that sea urchins only consumed detached fragments, and did not consume attached kelps. Comparisons of the morphology of detached fragments of kelp collected from the inshore reef to attached kelps from reefs further offshore showed that a large proportion (30–95%, varying among dates) of the fragments originated at distant reefs (≥ 2 km away). At the inshore reef, the sea urchin *H. erythrogramma* is subsidised by detached kelps, and detached kelp fragments have been transported across

landscapes. Cross-habitat resource subsidies therefore link discrete reef habitats separated by kilometres of non-reef habitat.

Key words Food webs · Trophic linkages · Spatial subsidy · Rocky reefs · Drift algae

Introduction

Organisms that inhabit spatially discrete habitats often participate in trophic interactions that transcend habitat boundaries. Some rely on food resources that originate elsewhere, while some are prey for organisms that forage across multiple habitats. Where organisms rely on food resources that originate elsewhere, populations can be "subsidised" to the extent that they attain densities that local productivity cannot support (Polis et al. 1997). Some of the best examples of this have been documented at ecotones between terrestrial and aquatic habitats, both marine (e.g. Bustamante et al. 1995; Polis and Hurd 1996) and freshwater (e.g. Wallace et al. 1997; Nakano et al. 1999; Nakano and Murakami 2001). However, Stapp and Polis (2003) suggested that such trophic subsidies are present wherever landscapes are heterogeneous.

Cross-habitat resource subsidies have been documented in a variety of habitats (see review by Marczak et al. 2007), but the spatial extents encompassed by the processes that create subsidies are typically poorly resolved. Knowledge of the spatial extents encompassed by these processes is critical for implementing spatial management practices effectively (Lundberg and Moberg 2003; Palumbi 2004). For example, there is evidence that the goals of marine reserves are best achieved with large reserves, and that reserve size and spacing should be determined by the spatial

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extent of key ecological processes (e.g. Gerber et al. 2003). The spatial extents of trophic linkages are also likely to influence how sensitive communities are to perturbations which can profoundly change the structure of communities (Lundberg and Moberg 2003; Valentine and Heck 2005).

The movement of plant detritus across habitat boundaries is one of the most fundamental processes facilitating trophic subsidies (Polis et al. 1997). In marine ecosystems, detached reef algae are an important food source for a wide range of consumers that occupy distant habitats (e.g. Duggins et al. 1989). Once detached from the substrate on which they grow, reef algae are passively transported across habitat boundaries, and can form substantial accumulations at distant locations (e.g. Vetter 1994; Wernberg et al. 2006), where they can support enhanced abundances of consumers. For example, the importance of detached reef algae as a food subsidy to intertidal beach fauna is well documented (see review by Colombini and Chelazzi 2003). Similar patterns have been documented for subtidal habitats, such as sandy bottoms adjacent to reefs (Kim 1992), submarine canyons (Vetter and Dayton 1999; Okey 2003), and seagrass beds (Wernberg et al. 2006).

The availability of detached reef algae can have important ecological consequences. For example, the interaction between the feeding behaviour of sea urchins and the availability of drifting pieces of kelp can have a profound influence on assemblages of organisms that inhabit subtidal rocky reefs. In southern California, the sea urchins *Strongylocentrotus franciscanus* and *S. purpuratus* are typically detritivorous, consuming drifting fragments of macroalgae, but when the abundance of this food source is reduced, they can adopt a behaviour in which individuals graze directly on attached algae, and as a consequence can decimate kelp forests (Harris et al. 1984; Harrold and Reed 1985).

Little is known about the spatial extents encompassed by trophic subsidies such as drifting macroalgae, but in many situations the distances are likely to be large. For example, Kirkman and Kendrick (1997) calculated that 78% of tagged kelp *Ecklonia radiata* had been transported distances >2 km. Similarly, Harrold and Lisin (1989) reported that most giant kelp *Macrocystis pyrifera* floating on the surface washed up on shore within a few kilometres, while some travelled up to tens of kilometres. Resolving the spatial extent of this key trophic process is key to understanding how strongly fauna that consume drift algae rely on trophic linkages that encompass multiple habitats.

We tested the spatial extent of trophic linkages created by the movement of detached kelp *E. radiata* between discrete rocky reefs, and its consumption by the purple sea urchin *Heliocidaris erythrogramma*, in south-western Australia. Subtidal reefs in this region are commonly dominated by

E. radiata (Fowler-Walker and Connell 2002; Wernberg et al. 2003b). *E. radiata* is a small kelp (typically <2 m long) that is mainly found in temperate Australasia and South Africa. In terms of gross morphology and canopy structure it is very similar to many common species of kelps of the northern hemisphere (e.g. *Eisenia arborea* and *Laminaria digitata*). The purple sea urchin *H. erythrogramma* is typically present in low densities (<1 m^{-2}), but in some reefs it attains high densities (>5 m^{-2}: Vanderklift and Kendrick 2004). In some other parts of Australia, grazing by *H. erythrogramma* exerts a strong influence on benthic community structure (Wright and Steinberg 2001; Johnson et al. 2004; Valentine and Johnson 2005). However, in south-western Australia, it consumes mainly detached fragments of large brown macroalgae, such as *E. radiata*, and it exerts only a minor influence on the benthos, even where it is abundant (Vanderklift and Kendrick 2005). This is an unusual pattern for high-density populations of sea urchins (Lawrence 1975; but see Day and Branch 2002a).

We first tested whether *H. erythrogramma* disproportionately retains *E. radiata* in comparison to other detached macrophytes and whether it consumes drifting fragments of *E. radiata* more than kelps attached to the reef. We then used linear discriminant analysis of spatial patterns in kelp morphology to identify the origin of detached kelps present at a reef with high densities of *H. erythrogramma*—we focussed on kelp morphology because previous studies have shown strong spatial patterns in morphological characteristics (Wernberg et al. 2003a), and we hypothesised that these patterns would allow us to predict the origins of detached kelp fragments. Based on this analysis, we estimated the spatial extent over which the movement of detached kelps link discrete reef habitats.

Methods

Study area and survey design

The study was done on subtidal rocky reefs off the coast of Fremantle, Western Australia (31°51′S, 115°42′W). In this area, chains of islands and high-relief reefs have formed from aeolianite limestone ridges that run parallel to the shore (Searle and Semeniuk 1985), and form discrete patches of hard substrate interspersed with unvegetated sand or seagrass. Between the ridges the seafloor is comprised of unvegetated soft sediments and low-relief rock (<20 m depth). Nearshore circulation in the area is predominantly wind-driven, and increases in wind speed can rapidly generate directional currents at the seafloor (Searle and Semeniuk 1985; Pattiaratchi et al. 1997).

We surveyed five discrete reefs, which ranged in depth from 6 to 12 m. Reefs were specifically chosen to represent

the range of possible sources of detached kelp—two reefs (Casuarina Shoal and Seaward Reef: 3.2 km apart) were on an offshore ridge, two reefs (Straggler Rocks and The Roarers: 4.1 km apart) were on a ridge further inshore, and the fifth reef (Mewstone) was furthest inshore (6.4–8.7 km from the offshore reefs) and hosts high densities of sea urchins (Vanderklift and Kendrick 2004). We surveyed the abundances of sea urchins, and the biomasses of detached macroalgae and seagrass, at each of these reefs on four dates in each of two seasons (the austral summer and winter). We collected detached and attached individuals of *Ecklonia radiata* for morphological measurements on three dates in each season.

Sea urchin counts

Abundances of the purple sea urchin *Heliocidaris erythrogramma* were surveyed by recording densities in 5 m^2 belt transects. A 5-m piece of lead-core rope was placed haphazardly on the reef and individuals within 50 cm of each side of the rope were counted. Five replicate transects were completed per reef on each date.

Spatial and temporal patterns in sea urchin densities were analysed with a mixed model analysis of variance, with the factors Reef (fixed effect with five levels), Season (fixed effect with two levels), and Date (random effect nested in Season, with four levels per season). In the case of a significant difference among means, the nature of differences was resolved using SNK tests.

Biomass of detached macrophytes

Detached macroalgae and seagrass (drift) were collected by hand from ten replicate 1 m^2 quadrats at each reef on each date. All drift that was retained by *H. erythrogramma* (i.e. was captured and held by podia) was collected and stored separately. In the laboratory, drift was sorted to species and dried for 48 h at 60 °C before measurement of dry weight (grams).

Spatial and temporal patterns in total drift biomass, and the biomass of drift kelp *E. radiata*, were analysed with a mixed model analysis of variance, using the same model as that used for sea urchin abundance. For each of the four main taxa of detached macrophytes (the brown algae *E. radiata* and *Scytothalia doryocarpa*, and the seagrasses *Amphibolis* spp. and *Posidonia coriacea*), paired *t* tests were used to assess whether fragments were present mainly as "loose" (i.e. fragments drifting on the sea floor) or "retained" (i.e. fragments captured by sea urchins). For these analyses, all quadrats with *H. erythrogramma* were pooled across dates, and separate analyses were performed for the three reefs where *H. erythrogramma* were recorded regularly.

Consumption of detached kelp

Consumption of detached kelp by *H. erythrogramma* was assessed by tethering experiments. We measured the relative consumption of detached (drifting) versus attached kelp by including treatments to mimic both. To mimic detached kelp, we fastened a clothes peg to a piece of kelp, and then tied one end of a length of nylon fishing line to the clothes peg and the other end to a metal stake hammered into the reef. This allowed the kelp to drift over the reef. To mimic attached kelp, we fastened the clothes peg directly to a metal stake.

We separated consumption by *H. erythrogramma* from other sources of tissue loss (degradation and consumption by other organisms) by placing sets of each type of tether in plots in which *H. erythrogramma* had been removed (–U plots, $n = 2$), and plots in which *H. erythrogramma* were left at naturally occurring densities (+U plots, $n = 2$). We used 16 m^2 plots that had been set up previously (see Vanderklift and Kendrick 2005 for details). Prior to our tethering experiments, mean densities of *H. erythrogramma* in +U plots were 12.5 ind m^{-2} (± 2.8 SE, $n = 8$), and mean densities in –U plots were 0.6 ind m^{-2} (± 0.3 SE, $n = 8$). The –U plots were maintained free of *H. erythrogramma* for the duration of the experiment.

Prior to deploying the tethers, photographs were taken of the kelp pieces. Tethers were deployed for three days, and then the pieces were collected and rephotographed. Consumption was calculated as the percentage change (loss) in area as measured with image analysis software (Sigma-Scan). Ten replicate pieces of kelp were included in each treatment. The experiment was done twice, once in December 2003 and once in March 2004.

Determining the origins of detached kelps

The detached kelps we collected were rarely intact and it was not possible to rely on the extensive suite of morphological characters used in previous studies of attached kelps (Wernberg et al. 2003a; Fowler-Walker et al. 2006). However, we found that the majority of drifting kelp pieces had at least one intact lateral (bladelet extending horizontally from the main axis of the primary lamina), and that four morphological characters could be recognised in most drifting laterals: width (cm), thickness (mm), rugosity (number of corrugations cm^{-1}) and spinosity (number of surface spines mm^{-2}). Our morphological measurements therefore concentrated on laterals, and on these four characters. Laterals of *E. radiata* ($n = 25$, haphazardly selected from the central third of separate kelp thalli, all growing attached to rock) were collected from each of the five reefs at three dates in each season. On the same dates, drifting pieces of *E. radiata* were collected from Mewstone (except for winter,

when drift was not collected on one date), and the same morphological measurements were done on one intact lateral from each piece.

To test whether patterns in morphology of kelp laterals varied among reef lines (which would allow us to predict the origin of drifting kelps), and whether any differences changed with season, we assessed spatial and temporal patterns in morphological variables by MANOVA, following the same model used in the univariate ANOVA outlined above. Homogeneity of variances for each variable was first tested using Cochran's test, and normality was assessed using normal probability plots. Data were ln(x+1)-transformed where necessary.

The predicted origin of each piece of drifting kelp was derived using linear discriminant analysis, using the MASS package in the statistical software R (http://www.r-project.org/). The laterals collected from attached kelps were used as a "training" dataset to build a predictive model based on a three-group classification (Mewstone, The Roarers–Straggler Rocks, Seaward Reef–Casuarina Shoal). This model was then used to predict the group membership of the detached kelps (i.e. the reef line where the kelps originated), with prior probabilities of classification even across groups. We tested the efficiency of the model at correctly classifying kelps by leave-one-out cross-validation, in which each individual kelp used in the "training" dataset (i.e. with a known origin) was classified after developing the linear discriminant model without that individual. Because a proportion of correct classifications can be expected by chance, even when there are no real differences among groups, the classification success was compared to the null expectation, using a bootstrapping procedure where data were randomly re-allocated 1,000 times, with the leave-one-out classification success calculated for each random re-allocation.

Results

Density of sea urchins

Densities of *Heliocidaris erythrogramma* varied significantly among reefs, but a significant Reef × Date interaction meant that this result could not be interpreted simply (Table 1). However, SNK tests indicated that densities at Mewstone (the reef furthest inshore) were almost always significantly higher than densities at all other reefs; the only exception to this occurred in June 2004, when densities recorded at The Roarers were equivalent (Fig. 1a). Few *H. erythrogramma* were ever recorded at Casuarina Shoal or Seaward Reef, the two reefs furthest offshore (Fig. 1a). There were no significant broad temporal patterns in density of *H. erythrogramma* (no significant effect of Season or

Table 1 Results of mixed model analysis of variance testing for differences in densities of the sea urchin *Heliocidaris erythrogramma*

Transformation	Log(x+1)			
Source of variation	df	MS	F	P
Reef	4	65.97	65.34	**<0.001**
Season	1	0.93	1.36	0.287
Date (Season)	6	0.68	1.50	0.183
Reef × Season	4	1.30	1.29	0.301
Reef × Date (Season)	24	1.01	2.22	**0.002**
Residual	160	0.45		

Bold type indicates statistical significance at $P < 0.05$

Date). The overall mean density of *H. erythrogramma* at Mewstone during this study was 28.9 transect^{-1} (±3.1 SE, $n = 40$), or 5.8 m^{-2}.

Biomass of detached macrophytes

The biomasses of all detached macrophytes combined (total drift), and of drift kelp *Ecklonia radiata*, varied significantly among reefs, and among dates, but significant Reef × Date interactions meant that these patterns could not be interpreted simply (Table 2). However, SNK tests indicated that biomasses of total drift were usually highest at Mewstone (5 of 8 dates), while differences among the other reefs were more irregular (Fig. 1b). Patterns were similar for drift *E. radiata*, with the most common pattern yielded by SNK tests that biomasses at Mewstone were significantly higher than all other reefs (3 of 8 dates). Although the highest biomasses occurred during winter months (Fig. 1c), not all dates surveyed during winter yielded high biomasses of drift, and seasonal patterns were not significant.

The biomass of drift was dominated by four taxa: the seagrasses *Amphibolis* spp (35%) and *Posidonia coriacea* (35%), the kelp *E. radiata* (11%) and the fucoid *Scytothalia doryocarpa* (7%). Together these taxa comprised 88% of the biomass of loose drift pooled over all reefs and dates. The same four taxa also dominated drift retained by *H. erythrogramma*, but with different rankings: *S. doryocarpa* (41%), *E. radiata* (26%), *Amphibolis* spp (13%), *P. coriacea* (6%).

The hypothesis that each of these macrophyte taxa was present mainly as drift retained by *H. erythrogramma* was tested separately for Mewstone, Straggler Rocks and The Roarers (Casuarina Shoal and Seaward Reef were not tested because few sea urchins were recorded at these reefs). At Mewstone, the biomass of *E. radiata* retained by *H. erythrogramma* was not significantly higher than the biomass of loose *E. radiata* ($t = 0.03$, $P = 0.48$); however, this result was heavily influenced by one extreme value
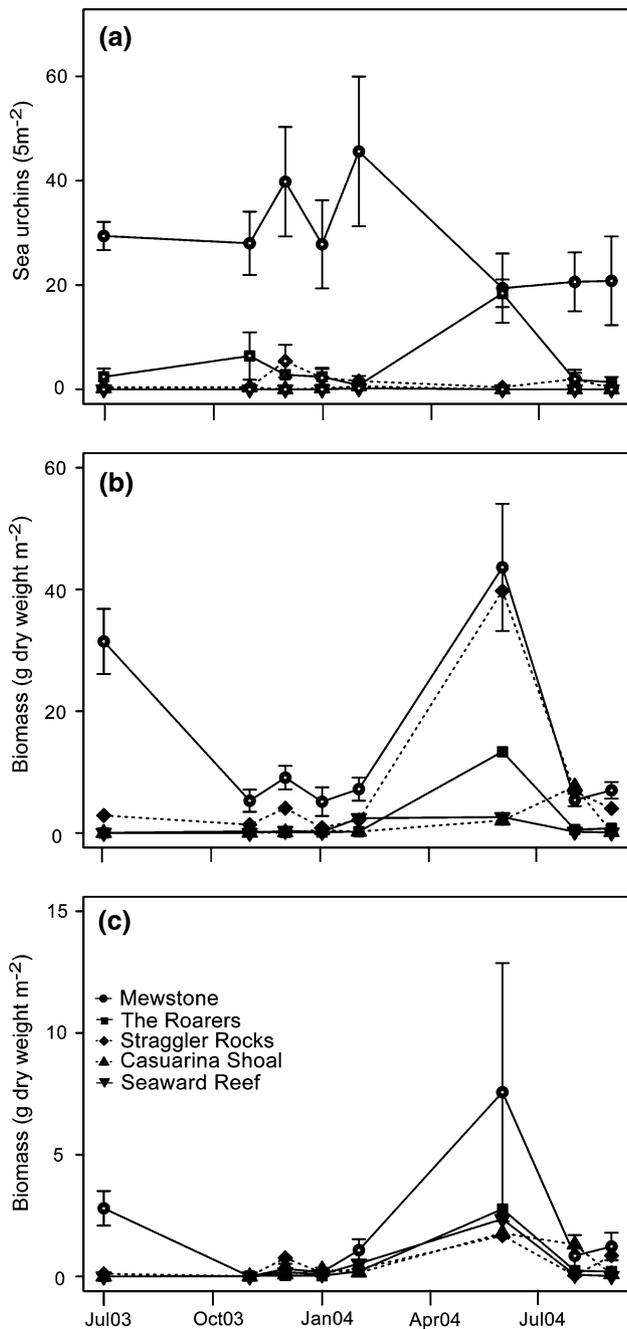
Fig. 1 a Densities of the purple sea urchin *Heliocidaris erythrogramma* and biomasses of **b** total drift, and **c** drift kelp *Ecklonia radiata*, at each of the five reefs surveyed (±SE, *n* = 4 for densities of sea urchins, *n* = 10 for biomass of drift)

(weighing 53.0 g, more than five times the next highest value), and when this value was removed from the analysis, the biomass of *E. radiata* retained by the sea urchins was significantly higher than the biomass of loose *E. radiata* (*t* = 3.30, *P* < 0.001; Fig. 2). The average biomass of *S. doryocarpa* retained by *H. erythrogramma* was higher than loose biomass, but this difference was narrowly nonsignificant (*t* = 1.44, *P* = 0.07; Fig. 2). The biomasses of loose

seagrasses *Amphibolis* spp. and *P. coriacea* were, on average, higher than the biomasses of urchin-retained seagrasses (Fig. 2).

Consumption of detached kelp

Consumption of tethered kelp laterals varied significantly between treatments on both tethering occasions (MS = 3061.1, $F_{(3,34)}$ = 11.5, *P* < 0.001 for December 2003; MS = 8978.0, $F_{(3,36)}$ = 18.6, *P* < 0.001 for March 2004; Fig. 3). On both occasions, SNK tests indicated that drifting kelp pieces in plots with *H. erythrogramma* were consumed significantly more than any other treatment (*P* < 0.001); no other pairwise comparisons were significant (Fig. 3).

Origin of detached kelps

There was evidence of heteroscedasticity for the four variables we used to measure the morphology of *E. radiata*, so all data were ln(*x*+1)-transformed, which tended to equalise variances. Overall, the morphology of *E. radiata* varied significantly among reefs on each date (significant Reef × Date interaction: Pillai's trace = 0.642, $F_{(80, 2880)}$ = 6.89, *P* < 0.001). The same pattern was reflected by each of the morphological variables individually, with all yielding the same significant interaction (in each case *F* > 2.8, *P* < 0.001). Because this indicated that the differences in morphology among reefs were not consistent among dates, predictions of the origins of detached kelps were calculated separately for each date. Kelps from Seaward Reef–Casuarina Shoal were morphologically distinct from kelps from Mewstone on each occasion (Fig. 4). Kelps from The Roarers–Straggler Rocks were morphologically intermediate between those from Mewstone and Seaward Reef–Casuarina Shoal (Fig. 4).

The predicted origin of most of the detached kelps collected at Mewstone was from reefs further offshore for four of five dates (Table 3). Only in January 2004 were most detached kelps (70%) predicted to have originated at Mewstone itself (Table 3, see also locations of drift kelps in Fig. 4). At other dates, the proportion of kelps originating at Mewstone was predicted to be 5–40%. Between 20 and 59% drift kelps were predicted to have originated at the reef line encompassing The Roarers–Straggler Rocks (~2 km away), and 10–38% were predicted to have originated at the reef line encompassing Seaward Reef–Casuarina Shoal (~6–8 km away).

The classification model was robust, with leave-one-out cross-validation correctly classifying 68–92% kelps collected from Mewstone, 52–72% of kelps collected from The Roarers–Straggler Rocks, and 86–94% of kelps from Seaward Reef–Casuarina Shoal (Table 3). All were significantly different (*P* < 0.001) from the null expectation of no

Table 2 Results of mixed model analysis of variance testing for differences in biomasses of total drift and drift kelp *Ecklonia radiata*

Transformation		Total drift			*Ecklonia radiata*		
		Log(*x*+1)			Log(*x*+1)		
Source of variation	df	MS	F	P	MS	F	P
Reef	4	47.6	17.83	**<0.001**	1.67	4.96	**0.004**
Season	1	37.3	3.15	0.126	7.97	2.30	0.179
Date (Season)	6	11.8	27.9	**<0.001**	3.46	16.41	**<0.001**
Reef × Season	4	2.9	1.10	0.378	0.83	2.45	0.073
Reef × Date (Season)	24	2.7	6.30	**<0.001**	0.34	1.60	**0.037**
Residual	360	0.4			0.21		

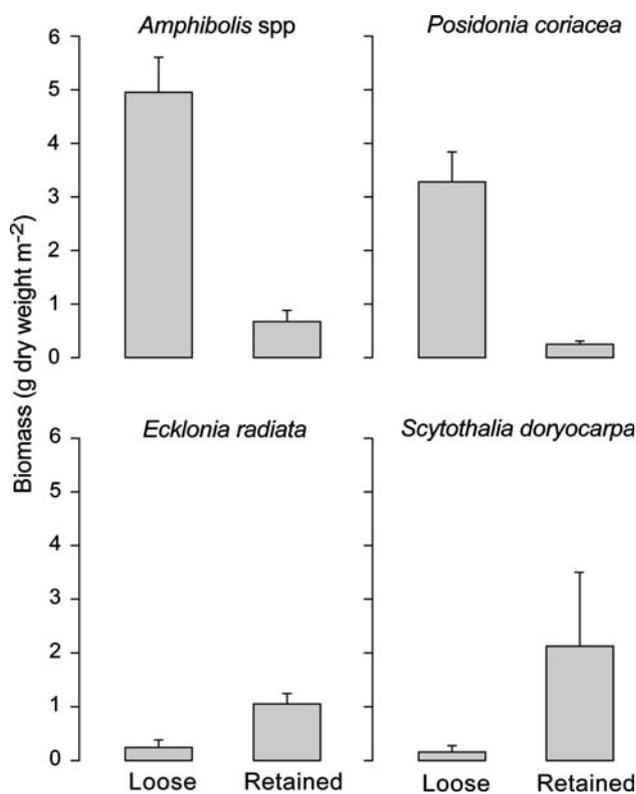Bold type indicates statistical significance at *P* < 0.05

Fig. 2 Biomass (±SE, *n* = 67) of detached macrophytes that were "loose" (i.e. laying loose on the reef surface) or "retained" (i.e. captured by the sea urchin *Heliocidaris erythrogramma*) at Mewstone. The data for *E. radiata* exclude one extremely high value

differences among groups, which predicts 33.3% success (Table 3). The somewhat lower success rates for kelps from The Roarers–Straggler Rocks (52–72%) are probably due to their intermediate morphological characteristics. Importantly, misclassifications of kelps from Mewstone were typically due to classification as part of The Roarers–Straggler Rocks reef line (error rate 22.4%), and rarely as part of the Seaward Reef–Casuarina Shoal reef line (error rate 1.6%). Conversely, misclassifications of kelps from Seaward Reef–Casuarina Shoal were rarely due to classification as Mewstone (error rate 0.8%). This indicates that detached

kelps classified as originating from Seaward Reef–Casuarina Shoal were very unlikely to originate from Mewstone. The prediction that 30–95% of detached kelps originated at reefs ≥2 km offshore, and the prediction that 10–38% of detached kelps originated at the most distant reef line (6–8 km further offshore) is therefore very robust.

There was no difference in the frequencies of detached kelps originating from different reefs in terms of presence as loose or urchin-retained drift (χ^2 tests with Bonferroni-corrected α all nonsignificant); we infer from this that the urchins showed no preference for kelps with any particular morphological features, and therefore will retain and consume detached kelps from any location.

Discussion

Sea urchins are subsidised by kelps from distant reefs

Our results demonstrate a cross-habitat resource subsidy between sea urchins and their main food source that encompasses spatial extents of kilometres. Abundances of the purple sea urchin *Heliocidaris erythrogramma*, and biomasses of detached macrophytes, were typically higher at Mewstone. There, sea urchins trapped and ate detached kelp *Ecklonia radiata*. Much of the detached kelp originated from offshore reefs.

Local kelp abundance at Mewstone is low (Vanderklift and Kendrick 2005), but *H. erythrogramma* in this region consumes mainly large brown algae (Vanderklift et al. 2006). Our tethering experiments show that it relies heavily on detached fragments. *H. erythrogramma* is largely sedentary—it tends to remain in depressions and crevices in the rock, and rarely moves about, so the evidence indicates a "sit-and-wait" feeding strategy. Our survey of the distribution of drift showed that retention of brown macroalgae (*Ecklonia radiata* and *Scytothalia doryocarpa*) is high in proportion to local availability, while retention of seagrass is low. Comparisons of the morphologies of detached fragments of kelp to attached kelps indicate that a substantial
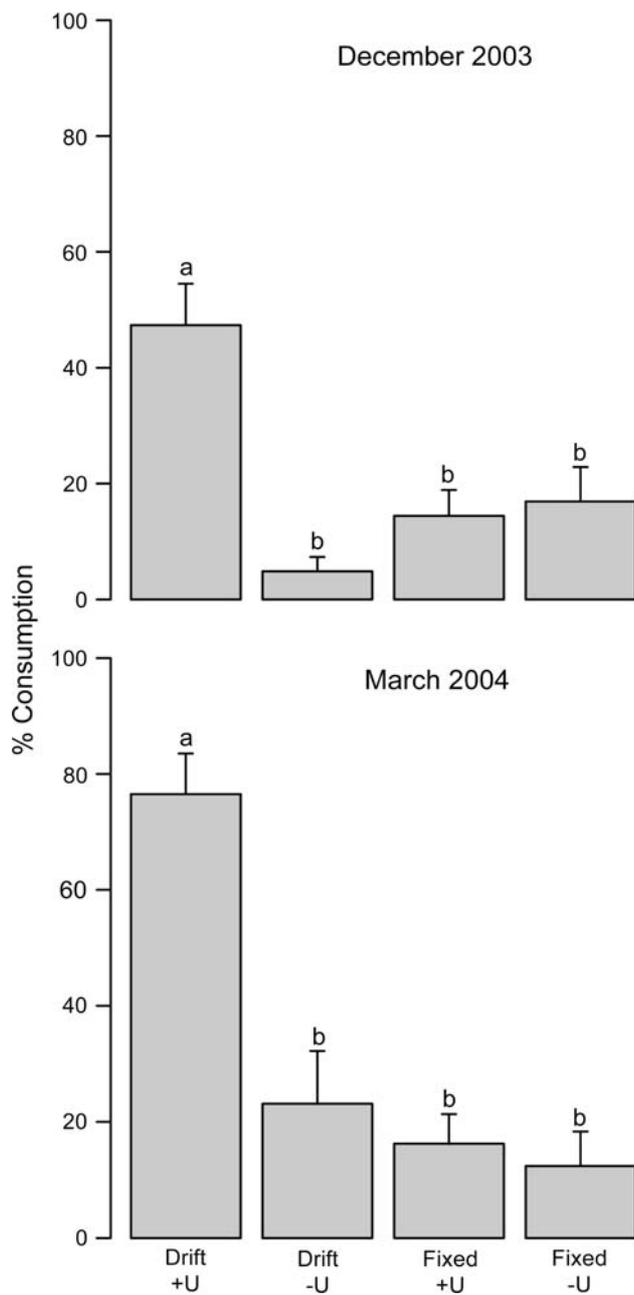
Fig. 3 Consumption (% consumed over three days, ±SE, *n* = 10) of tethered pieces of drifting and fixed *Ecklonia radiata* in plots with (+U) and without (−U) the sea urchin *Heliocidaris erythrogramma*. Groups sharing the same superscript letter (*a*, *b*) are not significantly different (determined by SNK tests)

Fig. 4 Linear discriminants of attached kelps of known origins, and projections of drift kelps collected from Mewstone, but with unknown origins, onto the linear discriminants

proportion of these fragments (30–95%) originated from offshore reefs, and had thus been transported ≥ 2 km, with 10–30% transported ≥ 6 km. When the biomass of drift kelp at Mewstone was highest (June 2004: mean = 7.57 g m^{-2}), 95% of the individual kelps were predicted to have originated offshore. This suggests that subsidies of drift kelp might occur in pulses, probably due to storm events that increase swell, which likely increases rates of
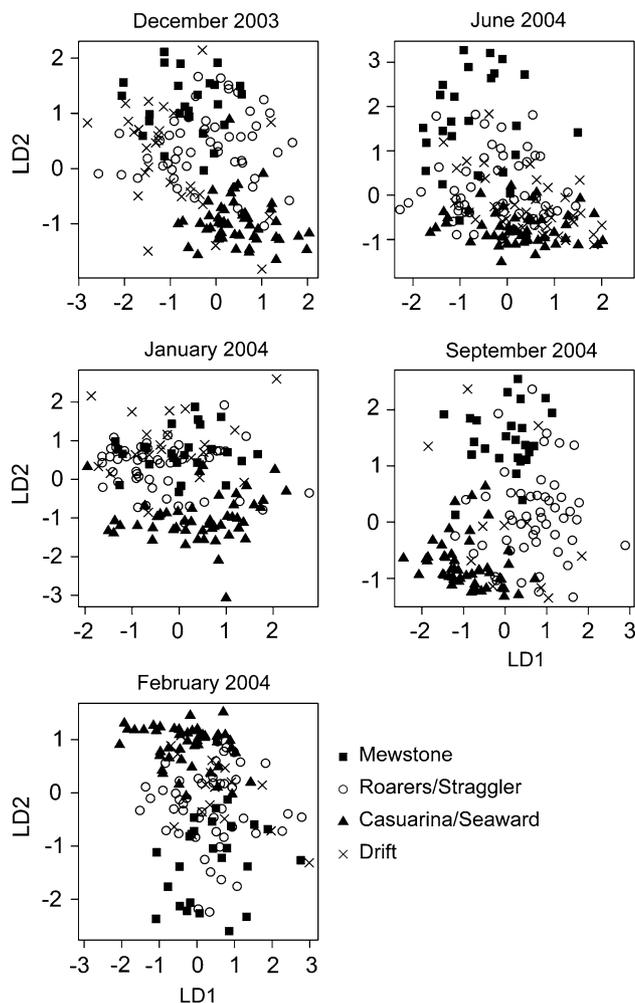
kelp dislodgement and facilitates more rapid transport through higher current velocities at the seafloor.

In south-western South Africa, consumption of detached kelps by intertidal limpets allowed limpet populations to reach high densities and exert a strong top-down influence on local production of algae (Bustamante et al. 1995). In contrast, experiments with *H. erythrogramma* at Mewstone have shown that it does not exert an influence on the biomass or species composition of macroalgae growing on the reef, but through its drift-trapping behaviour it exerts a large influence on the retention of detached macroalgae on the reef (Vanderklift and Kendrick 2005). Potentially, the availability of large quantities of drift maintains densities of sea urchins that are among the highest in southern and temperate western Australia (Fowler-Walker and Connell 2002; Vanderklift and Kendrick 2004), while at the same time allowing coexistence with erect macroalgae (Vanderklift and Kendrick 2005). In addition, *H. erythrogramma*

Table 3 Predicted origin of detached kelps collected at Mewstone, classified by linear discriminant analysis based on four morphological characters, and success rates for the classification of kelps of known origin by leave-one-out cross-validation

	n	Proportion of detached kelp pieces predicted to have originated from			Leave-one-out cross-validation success rate				
		Mewstone	The Roarers/ Straggler Rocks	Seaward Reef/ Casuarina Shoal	Overall	P	Mewstone	The Roarers/ Straggler Rocks	Seaward Reef/ Casuarina Shoal
Summer									
December 2003	30	0.40	0.30	0.30	0.80	<0.001	0.80	0.66	0.94
January 2004	20	0.70	0.20	0.10	0.70	<0.001	0.68	0.52	0.90
February 2004	17	0.12	0.59	0.29	0.70	<0.001	0.68	0.54	0.86
Winter									
June 2004	42	0.05	0.57	0.38	0.75	<0.001	0.72	0.66	0.86
September 2004	11	0.27	0.45	0.27	0.82	<0.001	0.92	0.72	0.88

P values were derived from a bootstrap procedure using 1,000 permutations of the data

disproportionately retains certain types of detached macroalgae, such as *E. radiata* and *S. doryocarpa*. So, while *H. erythrogramma* does not exert the strong influence on benthic community structure that it does elsewhere by grazing (Wright and Steinberg 2001; Johnson et al. 2004; Valentine and Johnson 2005), it might exert a positive influence on some species by increasing the availability of detritus, in the same way that the sea urchin *Parechinus angulosus* benefits juvenile abalone *Haliotis midae* in South Africa (Day and Branch 2002a; Day and Branch 2002b).

Spatial extents encompassed by trophic subsidies

The influence of trophic subsidies can be an important influence on community structure. Where local productivity is low, such subsidies allow consumers to attain densities that are otherwise impossible (e.g. Polis and Hurd 1996; Stapp and Polis 2003). Where local productivity is not limiting, subsidies can influence ecological interactions that in turn determine the relative abundances of different species (Menge et al. 1997; Menge et al. 2003). In this study, we have identified that the spatial extent of an ecologically important trophic subsidy encompasses landscape scales, and have identified linkages that encompass up to 8 km. This spatial extent compares to the distances travelled by floating *Macrocystis pyrifera* (Harrold and Lisin 1989), yet *E. radiata* does not have pneumatocysts and is negatively buoyant. Kirkman and Kendrick (1997) reported tracking detached *E. radiata* over several kilometres at another location in Western Australia, and Wernberg et al. (2006) found detached kelps to be present in seagrass beds up to 1,100 m from the nearest reef—these studies show that movement of even the negatively buoyant *E. radiata*, presumably due to wave-driven currents at the sea floor, can be significant. Detached kelps and other macroalgae are an important food source for organisms that inhabit subtidal reefs, intertidal rock platforms, beaches and seagrass beds along hundreds

of kilometres of coastline in Western Australia (Lenanton et al. 1982; Scheibling 1994; Wernberg et al. 2006), and the spatial extents of those trophic linkages are also likely to encompass kilometres.

Allochthonous subsidy by kelps to organisms in other habitats is likely to be a widespread phenomenon, as kelps are a ubiquitous element of shallow temperate coasts (Dayton 1985; Schiel and Foster 1986; Steneck et al. 2002), and most kelp production ends up as detritus, much of which is exported (Cebrian 1999). Kelp detritus is known to be generally important for beach fauna, allowing fauna to exist where local production is low (see review by Colombini and Chelazzi 2003). There is also evidence that kelp subsidies are important to organisms in other habitats. For example, many abalone and sea urchins feed extensively on drifting macrophyte fragments. The availability of such subsidies can also have wide-ranging indirect effects that can profoundly change community structure (Harrold and Reed 1985; Bustamante et al. 1995). Perturbations that influence kelp abundance could therefore affect kelp-dependant organisms over a wide area.

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