

Islands in the stream: kelp detritus as faunal magnets

D. O. Duggins¹ · M. C. Gómez-Buckley² · R. M. Buckley³ · A. T. Lowe⁴ ·
A. W. E. Galloway^{1,5} · M. N. Dethier^{1,4}

Received: 10 June 2015 / Accepted: 2 November 2015
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Abstract Biomass from nearshore primary producers can be an important subsidy to both pelagic and benthic communities, which are disconnected in space from sources of production. We examine the role of this macrophyte biomass in two habitats (pelagic and nearshore benthic) in terms of both trophic support and spatial refugia. Experimental benthic “islands” of seaweed biomass created nearshore subtidal habitats (at 10–30 m depth) which were colonized by diverse fauna, ranging from abundant harpacticoid copepods, to shrimp and snails, to small fishes. The abundance and species composition of colonizers varied somewhat among kelp species and with the degree of degradation of the kelp. Use of plastic strips as kelp mimics allowed us to decouple primary trophic and refugia effects; plastic attracted some macrofauna but far fewer organisms

in the <1.5 mm size class. Observational data taken from floating pelagic detrital islands showed that these algal rafts similarly attract many small crustaceans and other invertebrates, which then can serve as prey for consumers such as juvenile rockfish. The fauna of the pelagic drift islands was dominated by harpacticoid copepods and gammarid amphipods. Stomach contents of associated juvenile splitnose rockfish were dominated by gammarids and calanoid copepods.

Introduction

Benthic primary producers (primarily seaweeds and eelgrass) are highly productive assemblages in temperate marine systems (Mann 1973; Duarte and Cebrian 1996); kelp forests in particular achieve exceptionally high standing stocks and production (Duggins 1980; Dayton 1985; Reed et al. 2008). While herbivores such as sea urchins can control the development of macrophyte dominated communities, only a small fraction of macrophyte biomass is directly consumed (Mann 1988), leaving the vast majority (e.g., >80 %) to enter nearshore food webs as detritus (e.g., Krumhansl and Scheibling 2012a). This detritus may be in the form of particulate or dissolved organic matter (Newell et al. 1980), or larger sections of intact or semi-intact drift material (Shaffer et al. 1995; Britton-Simmons et al. 2009) that follow three potential pathways. Detritus may be consumed within or adjacent to extant kelp forests by herbivores or detritivores, transported into deeper habitats below the photic zone (Vanderklift and Wernberg 2008; Britton-Simmons et al. 2012), or deposited on shore as beach wrack (reviewed in Hagen et al. 2012).

The export of such detritus from an area of origin into adjacent habitats is likely to be a factor in the structure of

Responsible Editor: F. Bulleri.

Reviewed by K. Krumhansl and an undisclosed expert.

Electronic supplementary material The online version of this article (doi:10.1007/s00227-015-2781-y) contains supplementary material, which is available to authorized users.

✉ D. O. Duggins
dduggins@uw.edu

¹ Friday Harbor Laboratories, University of Washington, Friday Harbor, WA 98250, USA

² Science Department, Steilacoom High School, Steilacoom, WA 98388, USA

³ College of the Environment, Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195, USA

⁴ Biology Department, University of Washington, Seattle, WA, USA

⁵ Oregon Institute of Marine Biology, University of Oregon, Charleston, OR 97420, USA

the ecosystem in recipient areas (Krumhansl and Scheibling 2011; 2012a, b; Filbee-Dexter and Scheibling 2012; Kelly et al. 2012). Typically the resource considered in such spatial subsidies is food, with production in one community being used by consumers in another (Polis et al. 2004). Many examples involve direct consumption of detritus by an herbivore, such as deep water sea urchins eating benthic seaweeds transported from shallow (photic zone) waters (Britton-Simmons et al. 2009). Other examples are less obvious, such as terrestrial mammals (wolves, foxes, weasels, bears) feeding upon the marine fauna associated with beach wrack (e.g., Murie 1959; Fox et al. 2014). In this paper, we present an example of entire habitats being transported across system boundaries. In this case, “islands” of benthic macrophytes (primarily kelp) can be transported many kilometers from their origin and deposited in very different systems (Vanderklift and Wernberg 2010). Islands composed of algal biomass can represent direct food (consumption of algal detritus), indirect food (consumption of associated fauna), or simply physical habitat (i.e., refugia) for associated fauna. Drifting macrophyte rafts also may provide mobile habitat for passively dispersing larvae (Hobday 2000).

In benthic subtidal habitats of the San Juan Archipelago, macrophyte detritus is quite abundant; Britton-Simmons et al. (2012) report that 79 % of randomly selected ROV photos taken from depths reaching 150 m contained recognizable algal or seagrass detritus. This detritus can be rapidly renewed. Drift algae are readily captured by red urchins in this system (Britton-Simmons et al. 2009; Lowe et al. 2015). When all algal pieces captured by urchins in a 25 m² area at ~15 m depth were repeatedly stolen from urchins and weighed, equivalent biomass (~21 g damp weight algae urchin⁻¹ day⁻¹) returned in less than 24 h (A.W.E. Galloway, unpublished data). Less is known about the local dynamics of beach wrack, but beaches along Northeastern Pacific coastlines may accumulate wrack up to 1 m deep and extending over 100 s of square meters (authors, pers. obs.). Wrack input rates and accumulation, while variable and depending strongly on beach and wrack characteristics, have been measured as reaching up to 140 Mg (dry mass km⁻¹) in British Columbia (Orr et al. 2005). Similarly abundant wrack can be found on many of the world’s beaches (reviewed by Colombini and Chelazzi 2003; Orr et al. 2014).

The route ashore for much of this detritus involves floating aggregates dominated by macrophytes with gas-filled structures (e.g., *Nereocystis*, *Macrocystis*, *Fucus*, *Zostera*) that keep the material on the sea surface until it washes ashore or sinks into deep water. These aggregates, which we refer to as drift habitats (DH), are common though seasonal in many nearshore marine systems, and are observed as much as 96 km offshore in the Northeastern

Pacific (R. Buckley, unpublished data). Macrophyte islands are thought to provide important transitional habitats for numerous fish species throughout the world (Shaffer et al. 1995; Buckley 1997; Nordstrom and Booth 2007; Yamasaki et al. 2014; Goldstein et al. 2014; Gutow et al. 2015) because they can provide both aggregations of invertebrate prey (Muscart et al. 2015) and refuge from larger predatory fishes (Kingsford and Choat 1985; Gorelova and Fedoryako 1986; Wright 1989). Less is known about fauna associated with macrophyte aggregations lacking floats, which sink to the benthos and can drift into very deep water, but the occurrence of such aggregations in our study area is very common (Britton-Simmons et al. 2012) and such deposits support exceptional secondary productivity in temperate subtidal habitats (Vetter 1994; Okey 2003).

In this paper, we consider the importance of accumulations of kelp detritus across multiple habitats including nearshore benthic and pelagic environments. Using experimental and observational techniques, we investigated faunal associations with benthic aggregations of kelp detritus as well as floating drift habitats (DH) comprised primarily of kelp. Our goal was to determine whether such detrital aggregates can act as critical food sources and habitat to communities in marine environments. Our study of benthic aggregations used an experimental approach to compare the relative habitat and energetic value of macrophyte detritus in the photic zone where it is produced (shallow water) to detritus in deeper regions where this material represents a habitat or energy subsidy. For drift habitats, we sampled inside and outside floating aggregates and examined the gut contents of associated rockfish.

Study site and methods

Benthic habitats

Bags of kelp fronds and kelp mimics were deployed to the benthos in Summer 2011 and 2012 in the subtidal zone at Pt. Caution, San Juan Island, Washington (Lat: 48.575, Long: 123.008) using SCUBA. We conducted three experiments, each involving attaching mesh bags (“islands,” similar to litter bags used, for example, by Krumhansl and Scheibling 2012b) to the benthos and collecting them after a period of aging and colonization by other organisms. Macrophytes dominate the rocky substrate to 18 m depth in this system (Britton-Simmons et al. 2009); we therefore conducted experiments at ~10 m below MLLW (“shallow”: in kelp zone) where natural communities experience input of kelp detritus that may be rather fresh, and ~30 m (“deep”: outside of kelp zone) where kelp detritus is common but presumably aged or degraded relative to shallow-water habitats.

Islands were designed to replicate natural accumulations of drift macrophytes in terms of density and interstitial space. Bags were cylinders approximately 60 cm tall and 35 cm diameter, made of nylon mesh with openings large enough (2 cm) to exclude only large macrofauna. The amount of algae per island was standardized by surface area (ca. 1.9 m²), rather than biomass, to provide similar habitats among treatments.

First, in June 2011 we contrasted colonization of three substrate types: either one of the most common local kelp species, *Nereocystis luetkeana* or *Agarum fimbriatum*, or 6-mil black plastic. We included this non-organic plastic treatment to decouple direct food web mechanisms from associations based strictly on habitat creation (e.g., following Duggins and Eckman 1994). To further control for material differences, all kelp and plastic were cut into strips with equivalent widths before being added to bags. Bags ($N = 3$ per treatment) were attached to a lead line laid at 30.5 m depth and collected after 4 weeks. Second, in August 2011 we contrasted bags of *Nereocystis* all placed at 30 m depth but collected after 1, 2, or 3 weeks ($N = 3$ bags per time interval). Third, in June 2012 we repeated the three-substrate experiment at 10–12 m depth at the lower edge of a natural kelp bed using bags containing *Nereocystis*, *Agarum*, or plastic. The third experiment ran for 4 weeks and was sampled only at the end.

In addition, during experiments 1 and 3, we quantified epibenthic zooplankton in and adjacent to benthic islands each week of the experiment. We used a “Stream Machine” water gun to suck 1.1 l of water out of the middle of each treatment bag, plus an “ambient” sample collected just above the substrate approximately 1 m away from the plastic-strip treatment bag. These “slurp” samples were concentrated in situ in custom-modified vials made from 50-ml Falcon tubes. The cone of the tube was cut off and replaced with 20- μ m Nitex mesh, allowing us to concentrate the sample under water into a container that could be sealed and transported back to the laboratory. Upon return, samples were transferred to vials and preserved in 1.7 % paraformaldehyde.

To collect experimental bags without losing any of the associated macrofauna and meiofauna, divers brought larger bags made of plankton net material (190 μ m Nitex mesh) to the bottom, rapidly slipped them around the mesh bags, and immediately closed the bag. In the laboratory, these double bags were emptied into tubs and washed down with filtered seawater, and the contents filtered on coarse (1.5 mm) and fine (20 μ m) screens to collect macrofauna and meiofauna, respectively. Material from the mesh bags was visually inspected to ensure all fauna were effectively removed from the experimental substrates. All remaining kelp and plastic pieces were gathered, blotted, and weighed. Invertebrates and fishes from all samples were preserved

in 5 % formalin and later sorted and identified to at least ordinal or family level. All macrofauna per treatment were counted rather than being subsampled. Meiofauna were subsampled following the methods of Van Guelpen et al. (1982). All of the animals in the concentrated epibenthic samples were counted to determine the relative abundances of taxa.

We analyzed multivariate faunal community data using SIMPER and PERMANOVA (Anderson et al. 2008) in PRIMERv6 (Clarke and Gorley 2006). Factors used in multivariate analyses included substrate (macrophyte species) and depth. We used non-metric multidimensional scaling (NMDS; Anderson et al. 2008) to visualize multivariate community patterns. Macrofaunal abundances were square-root-transformed to downweight common taxa; we used a 4th root transform for meiofaunal abundances because these were very heavily dominated by one taxon. Resemblance matrices were usually Bray–Curtis except for one zero-rich dataset for which we used a modified Gower resemblance (Anderson et al. 2008).

Drift habitats

DHs were first sampled between June and November 1997. These datasets were part of an unpublished thesis (Gómez-Buckley 2000), as were the fish data below. Qualitative assessments of DH communities were performed by collecting an entire DH ($N = 5$; surface areas ranged from 0.5 to 20 m², and larger DHs were not sampled) with a large net that retained algae and organisms larger than 300 μ m. Diver observations from under the DH found that fishes were closely associated with the algal habitat and at the least disturbance went further into the algal mass, not out into open water (Buckley 1997). Samples were transported back to the laboratory in 190-l plastic trash bins where fish were relaxed in MS22 and preserved in buffered formalin for stomach analysis (described in detail in Shaffer et al. 1995; Gómez-Buckley 2000). Zooplankton (subsamples) were also preserved in formalin. Algae were sorted by species after being rinsed in filtered seawater; rinse water was collected and filtered (300 μ m) for assessment of epibenthic species possibly missed in the filtered sample. For qualitative comparison with DH zooplankton, plankton tows ($N = 6$) were conducted in open water at least 10 m away from any DHs or kelp bed.

Because the 1997 DH sampling was qualitative (data are presented as percentage of total sample inside versus outside DHs), in August and February of 2013 and August 2014 we used a different method to quantitatively assess zooplankton abundance inside and outside DHs ($N = 9$ of each). Quantitative plankton tows are impossible inside DHs so instead we filtered a known volume of water pumped from 0.5 m below the surface in the center of the

DH. Water was passed through a standard 200- μm plankton net and into a large (190-l) plastic trash can until it was full. A similar method was used for samples well outside (100 m) the DH. All zooplankters from each sample were counted rather than being subsampled. Organisms ranging from large amphipods to tiny cladocerans passed through the pump without apparent damage.

Results

Benthic habitats

Three-substrate experiments

At both depths (ca. 10 and 30 m), after 4 weeks only rotting remnants of *Nereocystis* blade material remained in most bags, but *Agarum* tissue was still abundant (Fig. 1), and the plastic appeared unchanged (not illustrated). Thus, the availability of habitat for use by animal colonists varied with kelp species and with time.

Macrofauna (>1.5 mm) that colonized bags in the deep water (2011) and shallow-water (2012) experiments after 4 weeks were mostly crustaceans, gastropods, and polychaetes (listed in Online Resource 1). We found 37 taxa deep and 35 shallow among the three substrate types (*Agarum*, *Nereocystis*, and plastic). A 2-way PERMANOVA comparing across depths (but note that depths were not independent of years) showed significant differences in macrofaunal communities among both substrates and depths, with a marginally significant interaction term (Table 1). Deep and shallow communities were generally distinct (Online Resource 2), except that deep *Agarum* had similar macrofauna to shallow *Agarum*.

In shallow water, substrate significantly affected macrofaunal communities (PERMANOVA, Table 1). At this depth, *Agarum* had different macrofauna from plastic (far more shrimp, amphipods, and hermit crabs), but neither was significantly different from *Nereocystis*. Examining the taxa driving the depth differences, shallow communities were dominated by shrimp and the small gastropods *Lacuna* sp. and *Alvania* sp. (Fig. 2). *Agarum* overall was distinct from both *Nereocystis* and plastic, whose communities overlapped (NMDS plots in Online Resource 2). Shallow *Nereocystis* macrofauna were extremely variable, as was the amount of kelp tissue left in the bags after 4 weeks (error bar, Fig. 1). However, even though only a small fraction of *Nereocystis* remained after 4 weeks, for some taxa the associated fauna was still more abundant than in the plastic treatment (Fig. 2).

Overall, deep communities were dominated by gammarid amphipods and majid crabs (Fig. 2). When the deep water (2011) experiment is examined by itself, the substrate

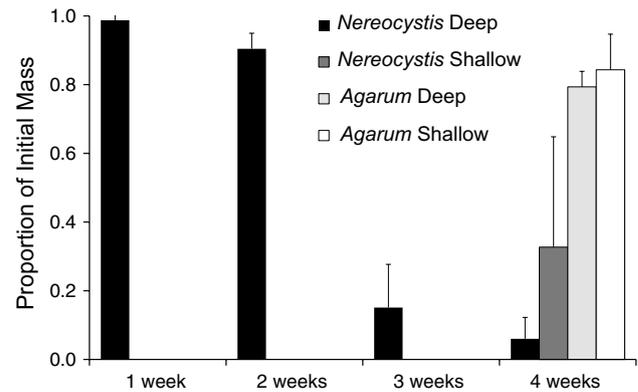


Fig. 1 Proportion of blade mass of *Nereocystis* remaining in the bags after 1–3 weeks (deep water colonization through time) and of *Nereocystis* and *Agarum* after 4 weeks (substrate comparison experiments deep and shallow). Bars are mean and one SD

types had clearly different macrofauna (NMDS in Online Resource 2, one-way PERMANOVA, Table 1), although *Nereocystis* and plastic were not different in a pairwise test. The biggest drivers of these differences were juvenile and adult shrimp, which were abundant in *Agarum* and plastic, but absent among the *Nereocystis* remnants (SIMPER, Fig. 2). The herbivorous snails *Lacuna* sp. and *Margarites* sp. were abundant in *Agarum*, uncommon in *Nereocystis*, and absent in plastic. Amphipods were most abundant in *Agarum*, fewer in *Nereocystis*, and least abundant in plastic. Fishes (mostly small cottids and stichaeids, Online Resource 1) were absent from the *Nereocystis* but similar (although uncommon) in the *Agarum* and the plastic. Echinoderms and chitons were rare in all samples. Thus, clearly the structure provided by the plastic and/or the mesh bag itself was important to at least some of the macrofauna.

Across both depths, SIMPER analyses showed that substrate differences are driven by *Agarum* having higher abundances of most taxa (Fig. 2), as well as higher taxa richness (Fig. 3). *Nereocystis* overall had the next most abundant macrofauna except for shrimp, which were consistently abundant in the plastic (Fig. 2). The patterns of amount of kelp tissue remaining (Fig. 1) and richness and abundance of macrofauna suggested an overall effect of the amount of “blade” remaining in each bag after 4 weeks. Analyses on the scale of replicate bags show that regardless of substrate type, more blade mass correlated with greater taxon richness (Fig. 4a; r^2 value for all points is 0.48). A similar relationship was found with overall macrofaunal abundance (not shown: $r^2 = 0.59$).

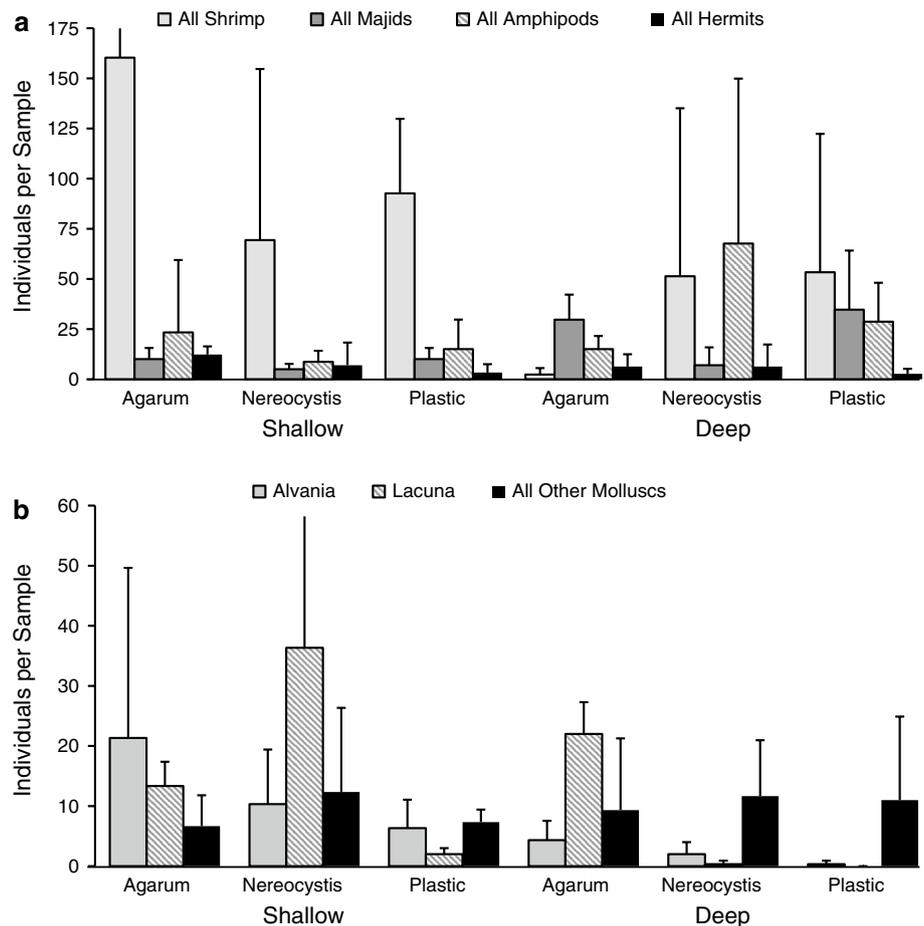
The meiofaunal (>20 μm) samples in both the deep- and shallow-water experiments were heavily dominated by harpacticoid copepods (83–99 % of the total individuals). Meiofaunal taxon richness at the level identified (ordinal and family; Online Resource 1) was low, although species

Table 1 PERMANOVA results from all benthic experiments

Analysis	Factor	df	MS	Pseudo-F	P (Monte Carlo)	Global R
Macrofauna both depths (2-way)	Depth	1	5879.6	6.385	0.001	0.667
	Substrate	2	3731.1	4.052	0.002	0.634
	Depth × Subst	2	1609.5	1.748	0.058	
Deep macrofauna	Substrate	2	3388.6	3.150	0.014	0.695
Shallow macrofauna	Substrate	2	1993.1	2.515	0.032	0.564
Meiofauna both depths (2-way)	Depth	1	4819.6	14.088	0.002	0.728
	Substrate	2	1215.2	3.552	0.015	0.337
	Depth x Subst	2	249.9	0.731	0.573	
Deep meiofauna	Substrate	2	841.6	3.351	0.027	0.564
Shallow meiofauna	Substrate	2	666.4	1.539	0.23	0.119
<i>Nereocystis</i> macrofauna	Week	2	1629.4	1.602	0.164	0.177
<i>Nereocystis</i> meiofauna	Week	2	728.62	1.874	0.139	0.136
Epibenthic samples	Depth	1	2938	4.162	0.018	0.146
	Week	2	2878	4.077	0.001	0.100
	Substrate	2	2477	3.510	0.004	0.085

All factors in all tests were fixed. Meiofauna (including epibenthic samples) results are for 4th root transforms, macrofauna for square root. *Nereocystis* macrofaunal analyses were run using a modified Gower resemblance because the data were very zero rich

Fig. 2 Mean and one SD counts of macrofaunal individuals per taxon per sample after 4 weeks; **a** Crustacea, **b** Molluscs. Tops of two bars are omitted for clarity; shrimp in shallow *Agarum* is at 281; *Lacuna* in shallow *Nereocystis* is at 70



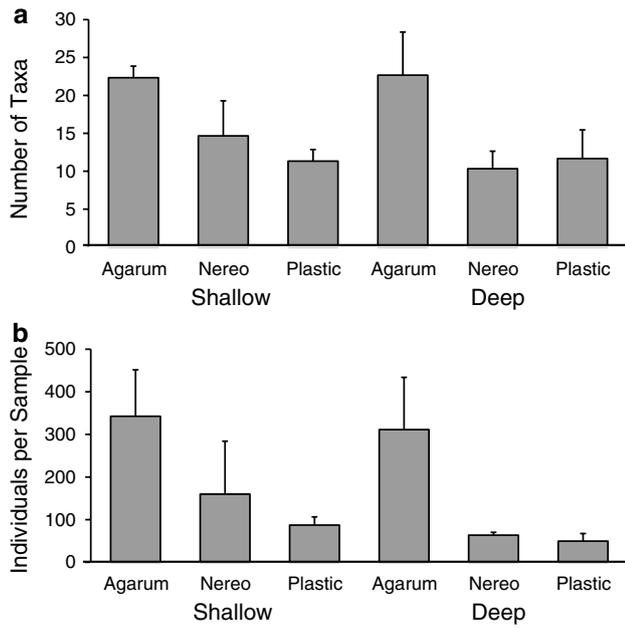


Fig. 3 Taxa richness (a) and overall abundance (b) of macrofauna in the substrate comparison after 4 weeks. Bars are mean of 3 replicates and one SD

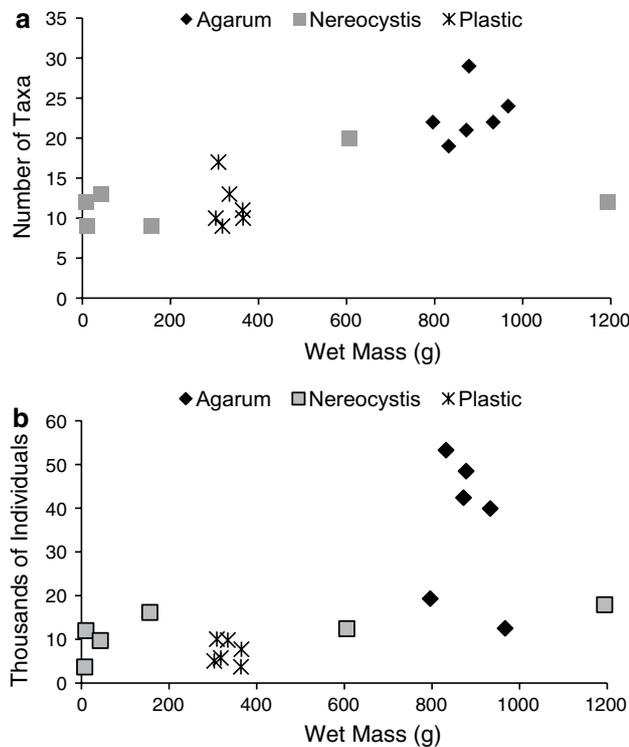


Fig. 4 Regression of “blade” mass with a macrofaunal taxa richness and b meiofaunal densities after 4 weeks in both deep and shallow experiments

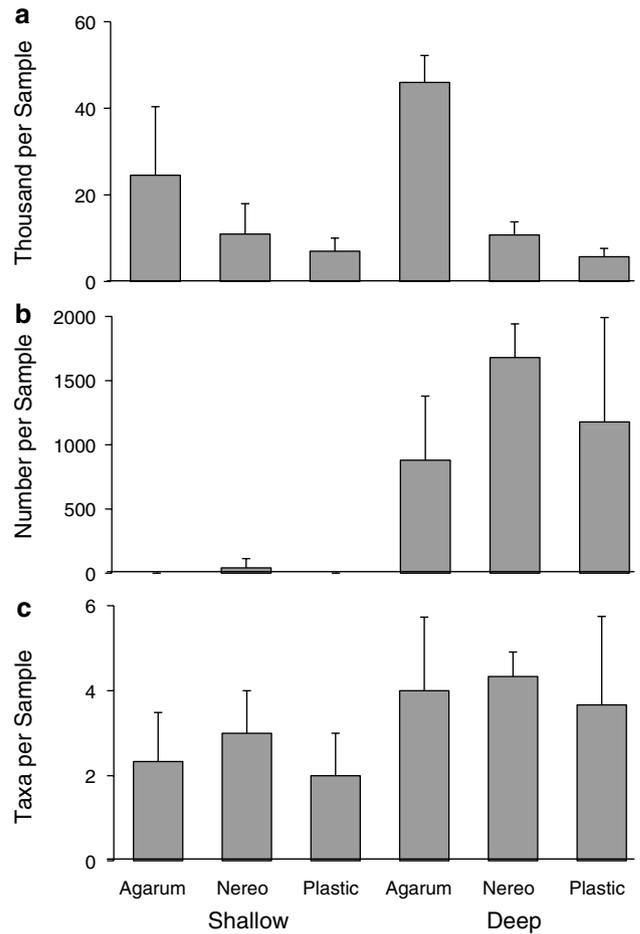


Fig. 5 Abundances of the two dominant meiofaunal taxa a harpacticoids, b amphipods, and c overall taxon richness in all treatments. Bars are means of three replicate bags and one SD

richness (not documented) could have been high. As with macrofauna, more blade mass correlated with greater meiofaunal abundance (Fig. 4b, $r^2 = 0.40$). Meiofaunal communities (Online Resource 2) were significantly affected by both depth and substrate (PERMANOVA, Table 1), with no interaction. SIMPER analyses showed that 52 % of shallow versus deep differences were driven by abundances of harpacticoids and amphipods (with 4th-root-transformed data), both of which were more abundant in deep water (Fig. 5). Foraminifera (not illustrated) were also more abundant in the deep experiments. In deep water, we found a few additional taxa, but these were all rare, usually only 1–2 individuals out of the 300+ animals counted per sample. Differences among substrates (regardless of depth) were driven largely by abundances of harpacticoids in *Agarum* and amphipods in *Nereocystis*. In the shallow experiment

alone, substrate had no significant effect on meiofaunal communities (Table 1), but it did in the deep water experiment (Table 1), although there were no significant pairwise comparisons among substrates (few possible permutations). Amphipods (Fig. 5), forams, and ostracods tended to be most abundant in *Nereocystis*.

Nereocystis colonization through time

Overall, the organisms colonizing bags of *Nereocystis* blades did not change dramatically through time (over 3 weeks); in neither meio- nor macrofauna was there a significant effect of week (PERMANOVAs, Table 1). The macrofauna in this experiment were similar to those seen in the *Nereocystis* bags in the substrate comparison; majid crabs, amphipods, *Lacuna* sp., and in some cases shrimp were abundant (Online Resource 1); all other taxa were present only as occasional individuals. All macrofauna were very patchy, however (see variances in Online Resource 3), contributing to the lack of significant trends (Table 1). Total macrofaunal richness remained at 10–15 taxa per sample across all 3 weeks, and mean abundances were consistent at 60–65 individuals per sample; thus, there were no trends through time in these summary parameters.

As in the substrate comparison, most meiofauna found in the *Nereocystis* bags were harpacticoids, plus some amphipods, calanoid copepods, and polychaete larvae (Online Resource 4); all other taxa were rare. Meiofaunal communities did not vary among weeks (Table 1), but overall abundance did drop sharply in the third week (from 12 to 17,000 individuals in weeks 1 and 2 to only about 7000 in week 3). This decline correlated with the abrupt reduction in remaining blade biomass at that time (illustrated in Fig. 1) and resulted in a clear positive relationship between *Nereocystis* blade mass and the total abundance of meiofauna ($r^2 = 0.51$; not illustrated).

Epibenthic fauna

As with the meiofauna in the bags collected at 4 weeks, the dominant taxa in the “slurp” samples from inside the bags each week were harpacticoids, and to a much lesser extent forams (found almost exclusively shallow); other taxa (various larvae and other small crustaceans) were in very low abundances in all samples. “Ambient” samples, taken at ~1 m distance from the bags, were quite depauperate (2 deep samples had no biota). Online Resource 2b shows the community similarities among all the slurp samples and illustrates this differentiation of the ambient samples. Subsequent analyses omitted ambient and used all replicates, not averages.

A 3-way PERMANOVA of epibenthic communities by depth, substrate, and week was significant for all 3 factors,

with no significant interactions (Table 1). The main driver of depth differences was the large (but very patchy: Online Resource 4) number of forams in shallow water, especially in *Nereocystis*. Because shallow and deep experiments were done in different years, this could be a year difference rather than a real depth difference. Pairwise comparisons among substrates show that communities in *Agarum* and *Nereocystis* are similar, and both are different from plastic. SIMPER analyses suggest that *Nereocystis* had more forams than either *Agarum* or plastic (Online Resource 4), and *Agarum* had more harpacticoids than plastic. Patterns across weeks are driven by harpacticoids generally increasing in abundance with time.

Drift habitats

While a total of 17 species of algae and seagrass were observed to comprise DHs (Gómez-Buckley 2000), the overwhelming majority of the biomass was represented by *Nereocystis*, with *Fucus* spp. and *Zostera* spp. also abundant. All other species had negligible biomasses. Relative contribution of the three major components varied among DHs, and there were no clear seasonal patterns (Gómez-Buckley 2000).

Eight species of fishes were observed associated with DHs, but only splitnose rockfish (*Sebastes diploproa*) were abundant in the DH samples. A total of 177 *Sebastes* were collected from 5 DHs, while the total of all other species was 29 individuals. Only one *Sebastes* was found in samples taken outside DHs, although net avoidance could have accounted for that difference.

Results of both qualitative (1997) and quantitative (2013 and 2014) zooplankton sampling inside and outside of DHs showed similar patterns. Qualitative samples are reported as proportions of the total organisms counted, grouped by major taxa (Fig. 6a). DH samples were dominated by harpacticoid copepods and gammarid amphipods, while nearby plankton tows were heavily dominated by calanoid copepods (seen also in fucoid-dominated DH by Shaffer et al. 1995). In the quantitative samples (with water volumes standardized), the relative abundances of different zooplankton taxa varied among sampling months (Online Resource 5), but when each sampling date is treated as one replicate pair, there were consistent patterns inside versus outside DHs (Fig. 6b, Online Resource 5). As in the qualitative samples, inside DHs there were significantly more gammarid amphipods and harpacticoid copepods than in the open-water plankton. Open-water samples had significantly more calanoid copepods, while nauplii (primarily of copepods and barnacles) were not different between habitats (Fig. 6b).

There was substantial concordance between *Sebastes* gut contents and the taxa of zooplankton found predominantly

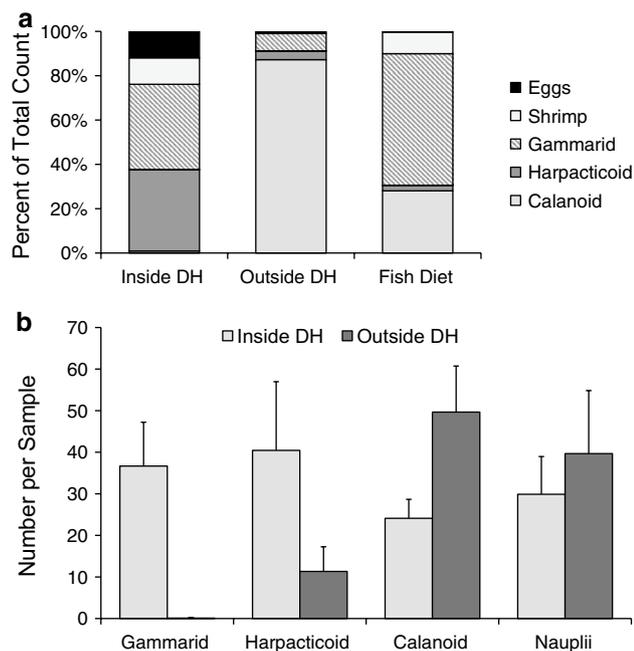


Fig. 6 **a** Relative abundances of major taxa in three types of qualitative samples taken from the floating drift habitats, outside the DH, and from fish gut contents. For each, we report the proportion of the total organisms counted in each of 5 categories. Sample sizes were 5 DH samples, 6 plankton samples outside DH, and 137 splitnose rockfish gut contents. **b** Densities of planktonic crustaceans inside and outside drift habitats. Differences between habitat types were tested with paired *t* tests (*bars* = means and one SE among 9 samples): amphipods $p = 0.004$; calanoids $p = 0.042$; harpacticoids $p = 0.026$; nauplii $p = 0.135$

in DHs. The stomach contents (of 137 individuals; some did not preserve well) were dominated by gammarid amphipods (38–78 % of total items per fish) followed by calanoid copepods (18–40 %; Fig. 6a). This suggests that the fish may have been avoiding the smaller harpacticoid copepods, which were very abundant in DH samples (Fig. 6b) but were the fourth most abundant component of the *Sebastes* stomach contents. The gut contents thus suggest that rockfish are using DHs for feeding as well as possible refugia from predation.

Discussion

Accumulations of macrophyte biomass are ubiquitous in deep water, surface water, and beaches in temperate habitats globally (Vetter 1994; Vetter and Dayton 1999; Dugan et al. 2003; Vanderklift and Wernberg 2008; Britton-Simmons et al. 2012; Krumhansl and Scheibling 2012a, b). Our results show that these detrital “islands,” both benthic and pelagic, serve as attractors for small invertebrates and for higher-order consumers including small fishes and that

both food and structural living space are important. Small crustaceans were extremely abundant, especially harpacticoid copepods and amphipods. Shaffer et al. (1995) found that floating detrital islands composed largely of *Fucus* have similar associated crustaceans. In drift island habitats, fish stomach contents illustrated an important trophic connection between splitnose rockfish and kelp-associated crustaceans. While we did not examine seasonal differences in either plankton or *Sebastes* gut contents, Shaffer et al. (1995) found a seasonal shift in the diet of juvenile *Sebastes* that suggested that younger individuals consume mostly planktonic copepods, but older fish (in the fall) switch to the larger amphipod prey found in drift habitats. The presence of cottid and stichaeid fishes in the benthic islands suggests a parallel food web dependent on macrophyte detritus in those habitats.

Colonization of benthic islands was rapid in some experiments and proportional to the amount of kelp detritus present (Fig. 4). In our benthic experiments, the colonization of different substrates resulted in different faunas. Both *Agarum* and *Nereocystis* accumulated more fauna than plastic (even with very reduced biomass of *Nereocystis* after several weeks), confirming that biological aspects (e.g., primary production, grazing, or biochemical cues) as well as structure are likely to be important. Both kelp treatments started off with similar biomass of fresh material, but especially in deep water, *Nereocystis* degraded and disappeared much more rapidly than *Agarum*, consistent with laboratory observations (Dethier et al. 2014). The rapid degradation of *Nereocystis* correlated with big drops through time in both herbivores and meiofauna, although an enriched faunal “signal” (relative to the plastic) was still observed in *Nereocystis* treatments where the majority of kelp biomass was gone.

Fresh *Agarum* contains high concentrations of defensive polyphenolic compounds (Steinberg 1985), but we saw no clear evidence of negative effects of these chemicals on colonists of the benthic islands. Dethier et al. (2014) showed that the value of *Agarum* as a detrital food item may increase as it degrades, perhaps due to a decrease in phenolics although this was not measured in our study. *Agarum* islands generally had more individuals of both macro- and meio-invertebrates than did *Nereocystis*, and had higher macrofaunal richness. At least some of this effect relates to the very slow degradation rate of *Agarum* and thus the large amount of biomass remaining on the sampling date (4 weeks); it remains a good structural habitat long after *Nereocystis* blades have rotted away. The positive effect of long-lasting structure may help outweigh potential negative chemical effects.

Degradation rates and changes to nutritional quality during algal breakdown differ between algal species, as seen in subtidal experiments similar to ours but deployed

over a longer time interval (Krumhansl and Scheibling 2012b). They studied degradation and colonization of the green alga *Codium fragile* and the laminarian *Saccharina latissima* over 16 weeks; both species became better food (reduced chemical defenses and reduced C/N ratio, respectively) over time. Their highest abundance of colonized fauna was seen in *Saccharina* and was found at roughly the same timescale as ours (4–8 weeks).

Our approach, which used both real and plastic kelp detritus mimics, allowed us to separate the trophic and structural components that may act to attract epifauna to subtidal drift algal islands (Duggins and Eckman 1994; see also Goldstein et al. 2014). The higher abundances and diversity of faunal species in the plastic treatment than the adjacent epibenthic samples point to a role of structure alone, although part of the structural role may have been to provide surface area for biofilms; biofilms present on both degrading kelp and aging plastic may well serve as attractants to invertebrate colonists, but investigating them was beyond the scope of this study. The plastic islands had few organisms in the epibenthic samples but nonetheless more than ambient samples, which were very depauperate. Macrofauna among the plastic “blades” included many amphipods and shrimp, quite a few majid crabs, and some mollusks; the refuge effect of the plastic (or the mesh bag itself) appeared particularly important for crustaceans, although this treatment still had low numbers relative to the kelp. The most abundant mollusks were tiny *Alvania* in shallow-water bags; these eat “diatoms or microalgal films” (McLean and Gosliner 1996) which likely were starting to accumulate on the plastic after 4 weeks and deserve further investigation. The mollusks on deeper plastic samples were mostly *Amphissa* sp., which are thought to be scavengers; they could have either been using the plastic islands as refuge habitat, or consuming some of the other invertebrates there.

Natural drift habitats both provide complex structure and are capable of supporting multiple trophic levels (citations in Introduction). Their ecological roles may have as much to do with this structure as with their contribution of primary production (Wright 1989; Rothäusler et al. 2009). Drift habitats dominated by kelp species such as *Nereocystis* can be large and three dimensional; pneumatocysts float at the surface, but dense curtains of blades sink 6–8 m below these floats. The associated fauna is dominated by epibenthic and planktonic crustaceans which serve as food for juvenile fishes; as in our data, other authors (Buckley 1997; Nordstrom and Booth 2007) have noted that juvenile rockfish and other fishes are attracted to these habitats, probably by both the abundant prey items and the refuge from their predators provided by the blades.

Floating macrophyte (or plastic) islands also can serve as a dispersal mechanism (Hinojosa et al. 2010; Wichmann

et al. 2012; Goldstein et al. 2014) for species otherwise incapable of long-distance transport (including kelp itself, e.g., Hernández-Carmona et al. 2006), although we did not examine this phenomenon in our study. Overall, faunas associated with both benthic and planktonic macrophyte islands appear to be diverse (e.g., Wichmann et al. 2012) and copious compared to adjacent areas. The transported algal mass and entire mobile “habitat” may be an important factor to recipient-system occupants as nursery areas or food sources, particularly in low-productivity habitats such as aphotic deep waters.

Acknowledgments We thank L. Dennee-Lee, A. Gjurasic, A. Gómez-Buckley, and J. Schulte for helping to sort zooplankton samples; K. Page for work on some of the floating habitats; numerous dive assistants from FHL; and the Friday Harbor Laboratories and School of Aquatic and Fishery Sciences for use of space and facilities. W. Raymond and R. Whippo assisted with subtidal experiments. This work was supported by the National Science Foundation (NSF; Biological Oceanography Division of Ocean Sciences grant 0925718) and an RET supplement. We appreciate the constructive comments of K. Krumhansl and one additional reviewer.

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