



Wrack resource use by intertidal consumers on sandy beaches

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ABSTRACT

The coexistence of ecologically similar species is often assumed to be facilitated by differential resource and habitat use. For sandy beach ecosystems characterized by low primary productivity, a suite of intertidal consumers relies on subsidies of allochthonous marine macrophytes, or wrack, as both food and habitat. To investigate how intertidal consumers may partition macrophyte wrack resources on sandy beaches, we measured individual consumption rates of four talitrid amphipod species (*Megalorchestia* spp.) on five macrophyte species in laboratory and field trials. Laboratory rates of consumption of macrophytes differed significantly among consumers, but general patterns were similar. Feather boa kelp (*Egregia menziesii*), was consumed at the highest rate by all species, rather than the more abundant giant kelp (*Macrocystis pyrifera*). In the field trials, talitrid amphipods were more abundant under experimental wrack patches containing kelps, and consumption of feather boa kelp was higher than for giant kelp or surf grass (*Phyllospadix torreyi*). Our results demonstrate that a suite of co-occurring talitrid amphipod species rely heavily on kelp wrack and suggest that these abundant intertidal consumers do not partition wrack resources.

1. Introduction

The coexistence of ecologically similar species can lead to functional redundancy that may enhance stability and resilience of ecosystems, communities, and food webs to environmental perturbations (Walker 1992, 1995). Such similar species may use common resources and occupy similar fundamental niches (Walker, 1995), but interspecific competition may limit them to a realized niche (Hutchinson, 1957; Soberon and Peterson, 2005). For example, competition for food resources may lead similar species to partition different types or components of food, reducing negative species interactions and facilitating coexistence (Schoener, 1974, e.g. Marks and Marti, 1984; Stewart et al., 2003; Dammhahn and Kappeler, 2008).

In environments where *in situ* food supply is relatively constant, feeding niche separation may be a common mechanism for coexistence of ecologically similar species (Marks and Marti, 1984; Stewart et al., 2003; Dammhahn and Kappeler, 2008). In subsidized ecosystems, allochthonous inputs of food resources may be highly variable in both quantity and composition (Polis and Hurd, 1996; Orr et al., 2005). This high variability in resource input may prevent potentially competing species from establishing obvious differential resource use or specialization (Wilson and Yoshimura, 1994), resulting in generalist consumers that appear to forage indiscriminately on available resources while

potentially employing a discrete mechanism of differentiation (Behmer and Joern, 2008).

Sandy beaches are a classic example of a subsidized ecosystem (Polis and Hurd, 1996). Beaches are xeric and dynamic habitats with characteristically low *in situ* primary production (Barbour et al., 1985; McLachlan and Brown, 2006; Pickart and Barbour, 2007). As a result, intertidal food webs on beaches are supported primarily by allochthonous subsidies from the coastal ocean (Polis and Hurd, 1996; Colombini and Chelazzi, 2003; Dugan et al., 2003; Orr et al., 2005). In southern California, drift macroalgae and seagrasses from nearshore rocky reefs and seagrass beds provide significant subsidies of organic matter to intertidal consumers on beaches (Dugan et al., 2011). Wrack deposition on an intermediate beach typical of southern California was estimated as 1.7 kg wet weight per meter of shoreline per day for several macrophyte species including *Macrocystis pyrifera* (giant kelp, hereafter *Macrocystis*), *Egregia menziesii* (feather boa kelp, hereafter *Egregia*), and *Phyllospadix torreyi* (surf grass, hereafter *Phyllospadix*) (Dugan et al., 2011). On beaches along the Santa Barbara Channel of California, wrack subsidies provide food and shelter to more than 20 species of mobile intertidal invertebrates (Dugan et al., 2003; Schooler et al., 2017) that can reach high abundances, > 90,000 individuals per meter of shoreline (Lastra et al., 2008). Wrack deposits range in size and species composition from small monospecific patches to meter-wide

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masses with mixed macrophyte composition, presenting a scenario where consumers may choose between these resources for nutritional advantages (Duarte et al., 2010) or to avoid competitors.

Wrack resource inputs vary widely in availability across time and space (Dugan et al., 2003; Orr et al., 2005; Revell et al., 2011), and competition for these resources among intertidal consumers may be most intense when wrack inputs are low. Wrack is colonized by a variety of beetle, fly, and crustacean species, but talitrid amphipods, *Megalorchestia* spp, are major wrack consumers that function as intertidal shredders of this abundant subsidy, and were estimated to consume an average of 55% of the *Macrocystis* wrack input to a beach of the Santa Barbara Channel during summer (Lastra et al., 2008). Multiple species of these abundant talitrids can co-occur under the same wrack patches and along the same stretches of beach, suggesting that they rely on similar resources. Given the availability of different macrophyte wrack species on beaches, we hypothesized that these talitrids may utilize these macrophyte species differently, facilitating their coexistence. To evaluate this hypothesis, we quantified the consumption rates of four intertidal detritivore species, talitrid amphipods in the genus *Megalorchestia*, on different macrophyte wrack species when provided a single food source. To assess wrack preferences of these species under natural conditions, we manipulated macrophyte composition of experimental wrack deposits in the field and quantified talitrid amphipod responses in species composition, abundance, and wrack consumption rates.

2. Methods

2.1. Study system

Santa Barbara beaches receive variable amounts of macrophyte wrack from local kelp forests and rocky intertidal ecosystems (Dugan et al., 2011) and harbor diverse invertebrate communities that use wrack as habitat and food (Dugan et al., 2003; Schooler et al., 2017). *Macrocystis pyrifera* (giant kelp) forms dense forests in the Santa Barbara Channel and typically dominates wrack biomass on sandy beaches (Dugan et al., 2003). *Egrecia menziesii* (feather boa kelp, Lessoniaceae) is also a common component of wrack on local beaches, although typically lower in abundance than *Macrocystis* (Lastra et al., 2008; Dugan et al., 2011). The marine angiosperm *Phyllospadix torreyi* (surf grass, Cymodoceaceae) is also abundant, with inputs reaching over 50% of wrack biomass on some Santa Barbara beaches (Dugan et al. 2003, 2011; Lastra et al., 2008). Other macroalgae are also common but far less abundant; two of the more common species are *Ulva intestinalis* (Ulveaceae, hereafter *Ulva*), a green alga, and *Porphyra* spp. (Bangiaceae, hereafter *Porphyra*), a red alga (Dugan et al., 2011).

Intertidal driftline communities of sandy beaches in southern California, and Santa Barbara in particular, are dominated by four co-occurring species of talitrid amphipods (*Megalorchestia californiana*, *M. corniculata*, *M. minor*, and *M. benedicti*) that consume macrophyte wrack along with a suite of insects, including kelp flies and beetles.

2.2. Single species consumption

To determine if the consumption rates of macrophyte species differed among the four *Megalorchestia* species, we quantified the feeding rates of adults of each talitrid amphipod species on fresh *Macrocystis*, *Egrecia*, *Ulva*, *Porphyra*, and *Phyllospadix* wrack in laboratory trials. Adult talitrid amphipods larger than 8 mm were collected in July and August of 2017 from East Goleta Beach (N 34.417283, W -119.817984), Isla Vista Beach (N 34.409210, W -119.873757), and R Beach (N 34.315591, W -119.886240) on the mornings of each consumption trial, approximately five hours prior to commencing the consumption trials. Adults of each species were only collected at the large end of their size range. Dry sand was collected and sieved through a 1.5 mm mesh bag to remove any animals or debris and then mixed

with filtered seawater to obtain a consistency comparable to that of sand at the driftline where these species are commonly found. Each macrophyte species was collected from the intertidal zone on Isla Vista Beach (*Egrecia*, *Ulva*, *Porphyra*, and *Phyllospadix*) or from the reef offshore Isla Vista (*Macrocystis*) (N 34.405272, W -119.870187) and maintained in flow-through seawater tanks at ambient seawater temperatures for up to 24 h prior to use in feeding trials.

Experimental mesocosms consisted of individual 16 cm x 14.5 cm x 8 cm clear plastic containers with lids perforated to allow air flow to which approximately 100 cm³ of damp sand was added. Twelve adult individuals of a single species were haphazardly selected, added to each container, and allowed to burrow prior to the addition of a food resource. Three replicates of each food treatment and three replicates of controls without consumers were used in each trial. Approximately 1 g wet weight of a single macrophyte species was added to the sand surface in each feeding treatment and the control containers. A subsample consisting of one core (4 cm²) from the macrophyte portion of each container was retained for ash-free dry mass measurement (see below).

Experimental mesocosms were maintained at 20 °C in a temperature-controlled room for 72 h. Fluorescent lights on timers were used to simulate ambient light conditions (12-h light/12-h dark). All containers were misted with fresh seawater daily to prevent desiccation. At the conclusion of each trial, all remaining macrophyte pieces were removed from the containers, rinsed in seawater, and placed in individual pre-weighed aluminum foil weighing boats. All animals were removed from containers using a 1 mm sieve and rinsed in fresh water. Trials were rerun if all 12 animals did not survive the entire trial. To obtain dry and ash-free dry mass values, all macrophyte cores and remaining macrophyte fragments were dried at 60 °C for at least 72 h and then ashed at 400 °C in a muffle furnace for 4 h. To eliminate consideration of sand adhered to the macrophyte fragments, we used ash free dry weights of the initial macrophyte core samples to obtain organic to inorganic matter ratios for each replicate. We also measured dry weight and ash free dry weight of the remaining consumed macrophyte blades. The mass loss during ashing of the remaining experimental macrophyte fragments equated to the fraction of organic matter remaining after consumption. We then used the organic to inorganic mass ratios of the cores to estimate the total remaining blade mass and the fraction lost to consumption according to the equation:

$$\text{Total consumption} = \text{Blade dry wt} - (\text{consumed inorganic matter} + \text{consumed organic matter}).$$

The average mass loss of the controls was subtracted from the total mass loss of experimental samples to account for mass loss associated with handling and microbial decomposition.

All statistical analyses were performed in R 3.3.3 (R Core Team, 2017). We performed one-way ANOVA analyses for each individual consumer species with macrophyte species as a fixed factor and consumption rate as the response variable. Tukey multiple comparisons with a 95% family-wise confidence level were used to compare means.

2.3. Wrack colonization experiment

To evaluate how wrack species composition may influence the macroinvertebrate assemblages that colonize newly deposited patches of wrack in natural conditions, we manipulated the macrophyte species composition of experimental wrack patches on a local beach (East Goleta Beach) that supports populations of all four *Megalorchestia* species (Dugan et al. unpublished data). Four macrophyte treatments were used: *Macrocystis*, *Egrecia*, *Phyllospadix*, and a mixture of equal parts of the three species. In July of 2017, macrophytes were collected at locations listed above and used to create experimental wrack patches. Three replicate patches of each treatment were made and three groups of patches were set up, each containing one replicate of each treatment, along the 24 h high tide line on a falling neap tide series. Each patch was placed two meters away from adjacent patches and the replicate groups of patches were 10 m apart. All wrack patch treatments were the

same initial size at approximately 0.6 m in diameter and 0.15 m in height to ensure similar patch volume and visual cues to beach invertebrates. Treatments were deployed in the field for a period of 72 h.

To quantify consumption of major species of wrack macrophytes during the field experiment, a feeding assay was performed after 24 h. Fresh blades of each major macrophyte species (*Macrocystis*, *Egrecia* and *Phyllospadix*) were secured to ensure they remained adjacent to their corresponding experimental wrack patch. Cores of each blade sample were taken at the time of deployment for use in calculating consumption as in Section 2.2. For use as handling and microbial decomposition controls, additional blades of each macrophyte were placed on damp sand and left in a cool seawater room in the laboratory overnight. Initial wet weights were obtained for each blade sample, and remaining blade dry weights (following 24 h consumption in the field) were obtained after 72 h in a 60 °C drying oven. Ash free dry mass was measured for all samples after ashing at 400 °C in a muffle furnace for 4 h. Total consumption estimates were obtained using organic to inorganic ratio calculations as in Section 2.2. A one-way ANOVA analysis was performed using arcsine transformed values of the fraction of blade consumed as the response variable and wrack species as a fixed factor.

Macrofauna colonizing the experimental wrack deposits during the field experiment were quantified by core sampling using 10 cm diameter cores collected to a depth of 20 cm. An initial core sample was collected adjacent to each treatment patch to evaluate ambient community composition in bare sand. One core sample of each wrack patch replicate and a paired control core sample of bare sand 1 m away were collected in daylight hours on each day of the experiment. All core samples were sieved in seawater in 1.5 mm mesh to remove sand and retain animals, transferred to labeled plastic bags, and frozen. Frozen core samples were rinsed in DI water and sorted to quantify all animals and macrophyte fragments. Talitrid amphipod individuals were sorted by species, sexed, and body length measured to the nearest mm using a digital caliper.

A one-way ANOVA analysis was performed with macrophyte treatment as a fixed factor and total talitrid abundance as the response variable. Tukey multiple comparisons with a 95% family-wise confidence level were used to compare means. A paired *t*-test was performed between the control and treatment cores to compare consumer use of wrack against bare sand.

3. Results

3.1. Single species consumption

Consumption rates of the five macrophyte species differed significantly for each consumer species (One-way ANOVA, $p < 0.05$, Table 1). Tukey post-hoc analyses determined that consumption of *Egrecia* was higher than all other wrack types, and all consumers consumed significantly more *Egrecia* than *Phyllospadix* ($p < 0.05$). *Egrecia* consumption was higher than *Macrocystis* for all consumer species, and this difference was significant for three of the four talitrid species, *M. californiana* ($p < 0.01$), *M. benedicti* ($p < 0.01$), and *M. minor* ($p = 0.02$), but not for *M. corniculata* ($p = 0.10$). The consumption rates of *Ulva*, *Porphyra*, or *Phyllospadix* did not differ significantly for all four talitrid species ($p > 0.05$). *M. californiana* and *M. corniculata* are

Table 1

Results of one-way ANOVA analyses for consumption experiments on the four consumer species analyzed separately, with macrophyte species as a fixed factor and consumption as the response variable.

	DF	SS	MS	F-value	P-value
<i>M. californiana</i>	4	52,460	13,115	24.400	< 0.01
<i>M. corniculata</i>	4	34,823	8706	7.712	< 0.01
<i>M. minor</i>	4	10,615	2653	4.597	0.023
<i>M. benedicti</i>	4	20,853	5213	6.605	< 0.01

larger than *M. minor* and *M. benedicti* adults, suggesting that their overall consumption (Fig. 1) is higher due to differences in biomass.

3.2. Wrack colonization experiment

The average abundance of wrack consumers differed significantly among wrack type treatments after three days (One-way ANOVA, $F = 4.472$, $df = 3$, $p < 0.01$). Tukey post-hoc analyses determined that the average abundance of talitrid amphipods under *Egrecia* was higher (87.0 ± 15.0 individuals) than under all other wrack types (Fig. 2) but only differed significantly from *Phyllospadix* (11.0 ± 4.7 individuals; $p = 0.02$). The average abundance of talitrid amphipods was similar under *Macrocystis* (52.0 ± 7.8 individuals) and the mixed wrack treatments (52.6 ± 21.7 individuals; $p > 0.05$). Significantly fewer individuals were present in control cores in bare sand than in cores taken underneath wrack patches for *Egrecia* and *Macrocystis* treatments (*t*-test, $df = 2$, $p < 0.02$; Fig. 2). Overall *M. californiana* and *M. benedicti* were the most abundant species under experimental wrack patches while *M. minor* and *M. corniculata* were far less abundant. The colonization of the two most abundant species, *M. californiana* and *M. benedicti* are displayed in Fig. 3. The abundance of *M. benedicti* peaked after 72 hours corresponding to a decline in abundance of *M. californiana* under patches containing kelp (*Egrecia*, *Macrocystis*, and the mixed wrack patches; Fig. 3).

3.3. Wrack colonization experiment: feeding assay

The fraction of blade consumed differed significantly among the three wrack species in field trials (One-way ANOVA, $F = 8.156$, $df = 2$, $p < 0.01$, Fig. 4). Average consumption of *Egrecia* blades (0.68 ± 0.1 , Fig. 4) was higher than that of *Macrocystis* blades, but those differences were not significant (0.48 ± 0.1 , Tukey post-hoc, $p > 0.05$). However, the consumption of *Egrecia* was significantly higher than *Phyllospadix* consumption (0.21 ± 0.1 , Tukey post-hoc, $p < 0.01$).

4. Discussion

Our results suggest that a suite of co-occurring talitrid amphipod species all utilize macrophyte wrack, particularly kelps, and do not appear to partition these resources among species. All intertidal consumer species we tested readily consumed the less abundant kelp, *Egrecia*, at rates exceeding the other macrophytes, including the numerically dominant kelp, *Macrocystis*. Given the relatively low abundance of *Egrecia* on beaches compared to *Macrocystis* (Lastra et al., 2008; Dugan et al., 2011), consumers may be competing for access to *Egrecia* when it washes onto the shore if it is a preferred food or habitat resource. In the experimental wrack manipulation in field conditions, abundance of talitrid consumers was higher under *Egrecia* patches than under *Macrocystis*, suggesting that consumers may also preferentially inhabit wrack patches containing *Egrecia*.

Our results on relative rates of consumption from field feeding assays were consistent with our laboratory results. The consumption of *Egrecia* blades after 24 h in the field was higher than that of *Macrocystis*, although this difference was not statistically significant. An earlier field feeding assay in which 87% of *Macrocystis* and only 52% of *Egrecia* blades were consumed at a beach dominated by *M. corniculata* included the tough stipe/rachis of *Egrecia* in their estimates (Lastra et al., 2008) limiting direct comparisons with our results. In addition, *M. corniculata* was the only species that did not consume significantly more *Egrecia* than *Macrocystis* in our laboratory feeding trials, and this species only occurred in very low abundance in our field experiment. *Phyllospadix*, like other seagrasses, has been assumed to be primarily a shelter resource for beach invertebrates (Lastra et al., 2008; Poore and Gallagher, 2013), but the two smaller talitrid amphipod species consumed surf grass at rates comparable to their consumption of *Macrocystis*, demonstrating its importance as food to these species.

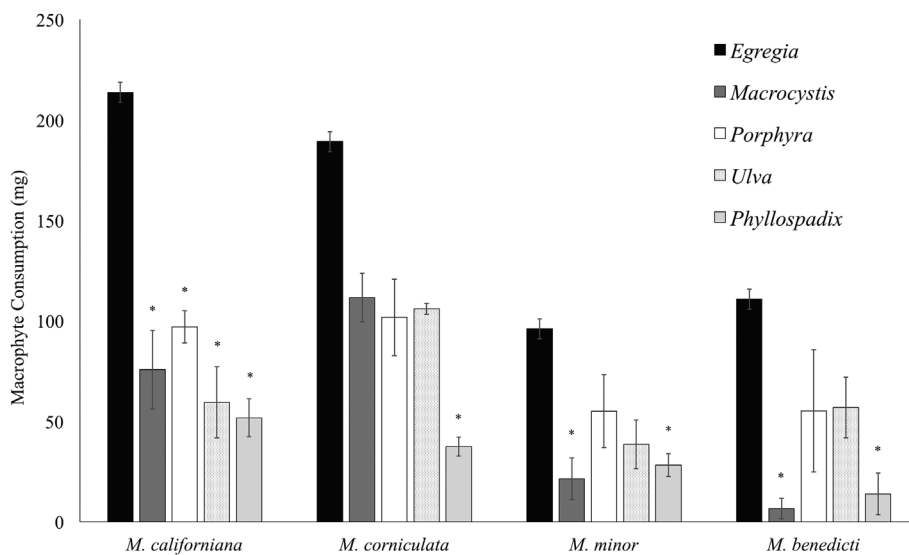


Fig. 1. Mean values of total dry mass of macrophytes consumed by four talitrid amphipod species (12 individuals per replicate) after 72 h. Consumption values are corrected for mass loss in controls. Error bars represent standard error (n = 3). Asterisks indicate the mass consumed is significantly different from *Egredia* (Tukey post-hoc, p < 0.05).

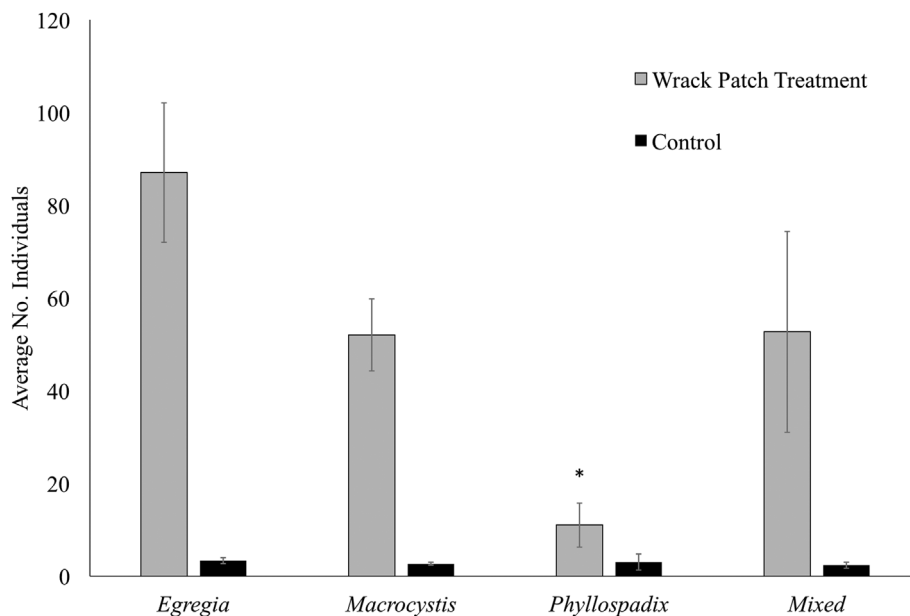


Fig. 2. Mean values of abundance of talitrid amphipods by macrophyte wrack patch treatment and in controls of bare sand after 72 h. Error bars signify standard error (n = 3). Asterisks indicate the talitrid abundance is significantly different from *Egredia* patches (Tukey post-hoc, p < 0.05).

The finding of higher consumption rates for a macrophyte wrack species that is less abundant could be a result of greater palatability, nutritional content, or structural differences among macrophyte species (Littler and Littler, 1980; Cronin and Hay, 1996; Pennings et al. 1998, 2000; Cruz-Rivera and Hay, 2003; Barile et al., 2004; Parker et al., 2008; Duarte et al., 2010). *Egredia* has slightly higher caloric value by weight than *Macrocystis* (3.07 versus 2.85 kcal/g dry weight), but lower caloric content than *Ulva* spp., *Porphyra* spp. and *Phyllospadix* spp. (4.00, 4.31 and 3.79 kcal/g dry weight, respectively) (Paine and Vadas, 1969). Conversely, kelp (*Macrocystis* and *Egredia*) had the highest C:N ratio (average of 18.4) of the species we examined, indicative of lower protein content compared to *Ulva* (average of 8.5), *Porphyra* (average of 9.0) and *Phyllospadix* (average of 14.6) (Tallis, 2009). Further research is warranted to elucidate factors that could explain the preference for *Egredia* over the other species.

Marine macrophyte inputs support detrital food webs in the study region and globally (Griffiths et al., 1983; Polis and Hurd, 1996; Colombini and Chelazzi, 2003; Dugan et al., 2003; Jaramillo et al., 2006; McLachlan and Brown, 2006; Lastra et al., 2008; Rodil et al.,

2008). The high biomass of macrophytes deposited on beaches in the study region supports a particularly diverse and abundant array of invertebrate and vertebrate consumers (Dugan et al. 2003, 2011; Schooler et al., 2017). In turn, the processing of macrophyte wrack by intertidal consumers is an important ecosystem function that can influence the remineralization of wrack-derived nutrients (Dugan et al., 2011; Lowman et al., 2019). Evaluating the consumption of different wrack resources by intertidal consumers provides critical insights into their ecological role as shredders and the subsequent processing of drift marine macrophytes on sandy beaches. Quantifying relationships between detrital consumers and wrack subsidies on sandy beaches is crucial for understanding ecosystem functioning and its potential responses to environmental change.

Detritus can increase system stability and persistence by influencing food web composition and dynamics with strong resulting effects on trophic structure and biodiversity (Moore et al., 2004). Functional redundancy of species within the same trophic level can also foster resilience of ecosystem functioning in the face of extinctions (Naem, 1998). In highly dynamic beach ecosystems with high detrital input in

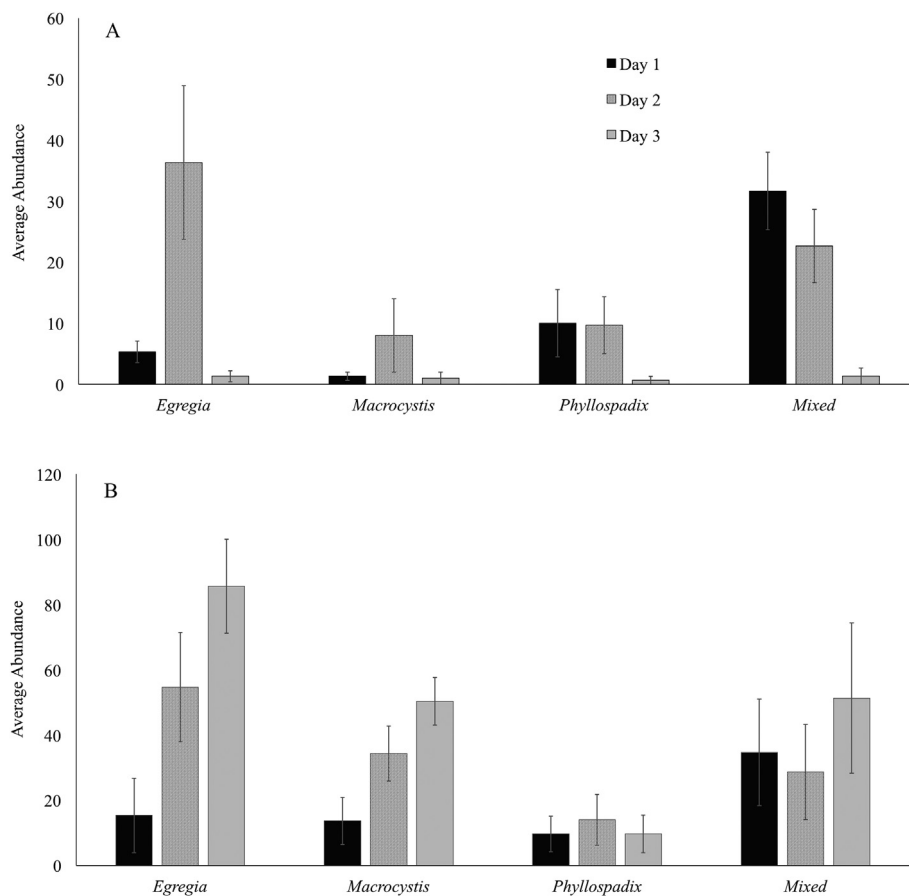


Fig. 3. Values of mean abundance of (A) *M. californiana* and (B) *M. benedicti* under *Egregia*, *Macrocystis*, *Phyllospadix*, and mixed treatment patches over three days. Y-axis values differ between species and correspond to average abundance between replicates. Error bars represent standard error (n = 3).

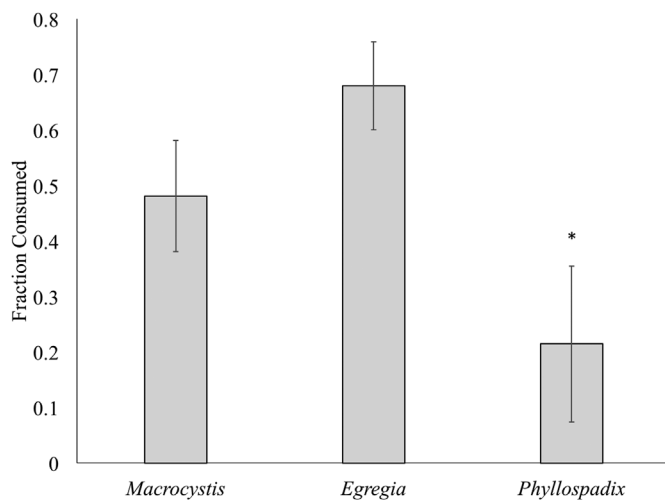


Fig. 4. Fraction of total blade consumed after 24 h in the field corrected for control mass loss. Error bars represent standard error (n = 6). Asterisks indicate the fraction consumed is significantly different from *Egregia* (Tukey post-hoc, p < 0.05).

the form of macrophyte wrack, consumption and shredding of wrack by multiple species of intertidal detritivores (talitrid amphipods) may stabilize the processing and decomposition rate of these important subsidies across variation in species metapopulations, as well as intertidal food webs. The apparent coexistence of this suite of abundant intertidal consumers on sandy beaches, despite their similar use of the same wrack resources, suggests that competition for food is not a strong

driver in this subsidy-dependent ecosystem.

Contributions

KMM, KAE, DMH, JED, and RJM designed the experiment. KMM and KAE performed the experiment and analyzed the collected data. KMM led the writing of the manuscript with contributions from all co-authors.

Declarations of interest

None.

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