Species identity drives ecosystem function in a subsidy-dependent coastal ecosystem

Kyle A. Emery[1] · Jenifer E. Dugan[1] · R. A. Bailey[2] · Robert J. Miller[1]

Abstract

Declines in species diversity carry profound implications for ecosystem functioning. Communities of primary producers and consumers interact on evolutionary as well as ecological time scales, shaping complex relationships between biodiversity and ecosystem functioning. In subsidized ecosystems, resource inputs are independent of consumer actions, offering a simplified view of the relationship between species diversity and function for higher trophic levels. With food webs supported by substantial but variable inputs of detritus from adjacent marine ecosystems, sandy beaches are classic examples of subsidized ecosystems. We investigated effects of consumer species diversity and identity on a key ecological function, consumption of kelp wrack from nearshore giant kelp (*Macrocystis pyrifera*) forests. We assessed effects of species richness on kelp consumption by experimentally manipulating richness of six common species of invertebrate detritivores in laboratory mesocosms and conducting field assays of kelp consumption on beaches. Consumer richness had no effect on kelp consumption in the field and a slight negative effect in laboratory experiments. Kelp consumption was most strongly affected by the species composition of the detritivore community. Species identity and body size of intertidal detritivores drove variation in kelp consumption rates in both experiments and field assays. Our results provide further evidence that species traits, rather than richness per se, influence ecosystem function most, particularly in detrital-based food webs with high functional redundancy across species. On sandy beaches, where biodiversity is threatened by rising sea levels and expanding development, our findings suggest that loss of large-bodied consumer species could disproportionally impact ecosystem function.

Keywords Biodiversity · Generalist consumers · Body size · Detrital subsidies · Sandy beach

Introduction

Biodiversity is declining at local to global scales (Cardinale et al. 2012; Gonzalez et al. 2016) and understanding the ecological implications of these losses is an urgent challenge (Worm et al. 2006; Hooper et al. 2012). Numerous empirical, experimental, and modeling studies have evaluated the extent to which biodiversity affects ecosystem functioning (BEF, reviewed by Naeem 2002; Srivastava et al. 2009; Tilman et al. 2014; Duffy et al. 2017). Many of these studies

✉ Kyle A. Emery
emery@ucsb.edu

1 Marine Science Institute, University of California, Santa Barbara, CA, USA

2 School of Mathematics and Statistics, University of St Andrews, St Andrews KY16 9SS, Fife, UK

have focused on how species richness of plant communities affects primary production (Naeem et al. 1996; Reich et al. 2001; Cardinale et al. 2004, 2007), and nutrient dynamics (Tilman et al. 1996; Hooper and Vitousek 1998; Bracken and Stachowicz 2006; Kahmen et al. 2006). Far fewer BEF studies have examined higher trophic levels, multitrophic systems, or naturally assembled communities (Duffy 2002; Duffy et al. 2007; Lefcheck et al. 2015; Soliveres et al. 2016; van der Plas 2019).

Consumers maintain critical functions in ecosystems, stimulating primary production and facilitating the transfer of energy and nutrients across trophic levels (Duffy 2002; Duffy et al. 2007; Hensel and Silliman 2013; Allgeier et al. 2017). However, evaluations of relationships of biodiversity with ecosystem function across multiple trophic levels are greatly complicated by the reality that consumers are often embedded in a complex food web, vary widely in their relative functional dominance, and interact with a diverse set of primary producers (e.g., Hooper et al. 2005; Thebault and

Loreau 2006; Duffy et al 2007; Creed et al. 2009; Edwards et al. 2010; Filip et al. 2014; Lefcheck and Duffy 2015; Brose and Hillebrand 2016; Daam et al. 2019). Consumer and resource dynamics are not independent in these systems, and the effect of consumers on resources can impact future consumption, production, and ecosystem functioning (Dyer and Letourneau 2003). For example, herbivore and predator diversity may interact to affect basal functions, such as net primary production (Finke and Denno 2005; Ives et al. 2005; Stachowicz et al. 2007; Griffin et al. 2013). These interactions feed back to affect community properties on both ecological and evolutionary timescales, adding complexity (Douglass et al. 2008; Matthews et al. 2011; Gravel et al. 2011; Walsh et al. 2012). As a consequence, experimental studies on consumer diversity, and particularly multitrophic diversity, are logistically difficult and often confined to modeling and experiments using microorganisms (Naeem et al. 2000; Downing and Leibold 2002; Gamfeldt et al. 2005; Brose 2008).

Not all ecosystems and food webs, however, are characterized by two-way interactions between consumers and producers. Food webs with consumers that depend on allochthonous subsidies, often detritus, as their main resource supply typically have no influence on detrital production or input (Polis et al. 1997; Cebrian and Lartigue 2004; Moore et al. 2004; Leroux and Loreau 2008; Srivastava et al. 2009) although they are strongly affected by subsidy supply (Hoekman et al. 2019). Nevertheless, such subsidized ecosystems can support food webs with a high diversity and abundance of consumers, as reported in streams (Wallace et al. 1997), submarine canyons (Vetter 1995), desert islands (Polis and Hurd 1995), and sandy beaches (Dugan et al. 2003). In these subsidized ecosystems, primary consumers play a vital role, incorporating detrital inputs into the food web and making energy available to higher-level consumers (Heck et al. 2008; Spiller et al. 2010; Hagen et al. 2012). Across terrestrial and aquatic ecosystems, detritus increases the standing stock of all trophic levels by supporting detritivores and providing energy and habitat to predators (Hagen et al. 2012). The separation in space between producers and consumers for subsidized ecosystems means that the effect of consumers can be quantified without ecological or evolutionary feedback or response from the resource donor (Wallace et al. 1997), simplifying the evaluation of BEF relationships.

Sandy beach ecosystems are a widespread coastal interface between marine and terrestrial realms (Luijendijk et al. 2018). Characterized by low in situ primary production, beaches are a classic example of subsidized ecosystems with food webs that rely primarily on marine subsidies (Brown and McLachlan 2006). Where nearshore productivity is high, drift macrophytes (macroalgae and seagrass), or wrack, cast ashore by waves and tides, can sustain rich productive communities of intertidal

detritivores on beaches (Dugan et al 2003; Ince et al. 2007; Schlacher et al. 2017). In turn, these consumer populations support higher trophic levels including predatory arthropods, reptiles, and shorebirds (Tarr and Tarr 1987; Polis and Hurd 1996; Dugan et al. 2003; Spiller et al. 2010). By acting as detritivores and shredders that process macrophyte wrack inputs (Griffiths and Stenton-Dozey 1981; Lastra et al. 2008), facilitating recycling of nutrients in beach sand and nearshore waters (Dugan et al. 2011; Gomez et al. 2018; Lowman et al. 2019), and supporting coastal food webs (Dugan et al. 2003), these abundant invertebrates perform key ecological functions.

To explore BEF relationships in this detritus-based ecosystem, we evaluated the influence of intertidal consumer diversity on a key ecosystem service, wrack processing. We used the consumption rate of the primary subsidy to beaches in our region, drift kelp from highly productive near-shore forests of giant kelp (*Macrocystis pyrifera*) to estimate this ecological function. We hypothesized that consumer species richness would positively influence kelp consumption rates due to facilitation and/or species-specific feeding differences (e.g. scraping vs shredding). To test this prediction we manipulated the richness of six species of common intertidal beach detritivores in laboratory mesocosm experiments. We further evaluated this prediction by comparing field consumption rates of kelp detritus on six beaches spanning a gradient of species richness and abundance of these invertebrates. We assessed the relative role of diversity and species composition on ecosystem function using analyses that separated species richness from species identity.

Methods

Study site and organisms

Sandy beaches of Santa Barbara, California, USA, are characterized by large but variable inputs of stranded giant kelp (*Macrocystis pyrifera*), or wrack (> 500 kg m^{-1} year^{-1}, Dugan et al. 2011) from highly productive nearshore kelp forests. This major subsidy to beaches is consumed by a diverse assemblage of highly mobile intertidal detritivores (Lastra et al. 2008; Michaud et al. 2019). We focused on six intertidal arthropod species that make up $> 90\%$ of abundance of invertebrate detritivores on these beaches: four congeneric species of talitrid amphipods (two large-bodied species, *Megalorchestia corniculata* and *M. californiana,* and two smaller species *M. minor* and *M. benedicti*), a tenebrionid beetle (*Phaleria rotundata*) and an oniscid isopod (*Alloniscus perconvexus*). These taxa are representative of families of important intertidal detritivores on sandy beaches worldwide (Brown and McLachlan 2006).

Richness experiment

To experimentally evaluate effects of intertidal consumer species richness on the consumption of giant kelp (*Macrocystis pyrifera*) wrack, we used a replacement design where consumer abundance in treatments was held constant at 12 individuals, and five levels of species richness (1, 2, 3, 4 and 6 species) were established in which the abundance of a given species decreased correspondingly to maintain the same total abundance (12, 6, 4, 3 and 2 individuals, respectively). Given the size range of the consumer species we tested it was not possible to hold biomass constant in the treatments. We tested all possible species combinations, resulting in 57 unique treatments, each of which was run concurrently in triplicate. Experimental designs to test the effects of diversity on ecosystem function can include maintaining biomass rather than abundance, maintaining the abundance of one species when adding another, and using unique species in each richness level (Allison 1999; Benedetti-Cecchi 2004). We addressed this tradeoff by using a replacement design (Duffy et al. 2003) which allowed us to maintain species evenness within each richness level and evaluate the effect of species identity on function. Our goal was to understand the effect of changing biodiversity on an ecosystem function, not consumption per unit consumer biomass.

Our treatment mesocosms were plastic tubs (19 cm × 17 cm × 9 cm) filled to ~ 6 cm depth with sieved (1.5 mm) dry sand from Campus Point beach (34.41 N, 119.84 W), mixed with filtered seawater to achieve a moisture level of 10–15% by weight, approximately equivalent to that of the 24-h high tide line where the densest aggregations of these intertidal wrack consumers are typically found. On the morning of each experiment, fresh blades of giant kelp and live consumers were hand-collected. Kelp blades were cut into square pieces of ~ 2 g wet weight and weighed individually. This amount was chosen after preliminary experiments, to ensure that the entire piece was not consumed during the experimental period. We removed a subsample from each piece of kelp, weighed it to the nearest mg, dried it at 60 °C for at least 48 h, and then ashed it in a muffle furnace at 500 °C for four hours to obtain the ash weight. The subsample provided a dry:wet ratio and an inorganic:organic ratio for each piece of kelp that was used to calculate consumption rates (see below). Consumer species were added in their prescribed numbers to the mesocosms and observed for 5–10 min until all had burrowed into the sand, upon which time we added the square of kelp to each mesocosm. The six consumer species we used are largely nocturnal; all experimental units were run for three nights and began and ended in the morning. Trials were run over the course of three weeks during August 2016 and all replicates of a given treatment were run at the same time to ensure no treatment

differences were driven by the differences in animal collections. Changes in the condition of animals collected over the three-week experimental period was unlikely as environmental conditions are most stable during this time of year. We conducted the trials in an environmentally controlled room kept at 20 °C and set to a 14:10 h light:dark cycle, approximating natural conditions at the time of the experiment. Each treatment was misted daily with filtered seawater to maintain moisture levels in the sand and kelp.

At the end of each experiment, the remaining kelp in each mesocosm was removed, gently rinsed, placed into pre-weighed foil packets, and dried at 60 °C for at least 48 h to obtain dry mass. The dried kelp was then ashed in a muffle furnace at 500 °C for 4 hours to obtain the ash weight of the unconsumed kelp plus any attached sand. Extensive rinsing of the unconsumed kelp would have removed not only all attached sand but also a significant portion of the kelp biomass. Therefore, we used the dry:wet and inorganic:organic mass ratios of the initial subsamples to remove the sand mass from the blade mass consumed (B_C) in each replicate as follows:

$$B_C = B_i - B_f,$$

where B_i is initial blade dry mass, taken as the wet mass of kelp measured at the beginning of the assay multiplied by the dry:wet mass ratio of the subsample, and B_f is final blade dry mass, corrected as follows:

$$B_f = B_T - S,$$

where B_T is total dry mass of the remaining blade material and S is sand mass, estimated as the inorganic ash weight of B_T minus the inorganic kelp fraction, calculated as the organic mass of B_T multiplied by the inorganic:organic fraction of the sand-free subsample.

During the experiments, six control mesocosms were run for each trial using an identical setup as described above but with no animals, to account for any kelp biomass loss due to handling or microbial decomposition of the blades. Each trial was corrected using trial-specific controls by subtracting mean control mass loss from each treatment (Silliman and Zieman 2001). The average mass loss from all controls was small, averaging $4.0 \pm 1.5\%$ dry mass (6.0 ± 2.5 mg).

The consumers were collected from each treatment and frozen for 24 h, after which they were rinsed, dried at 60 °C for at least 48 h to obtain dry mass, and then ashed at 500 °C for four hours to obtain ash-free dry weight (AFDW).

Field assays

As a comparative approach to evaluating the effect of species richness on ecosystem function, we conducted feeding assays on six sandy beaches located on a 22-km stretch

of shoreline in Santa Barbara County in October 2016 and April 2017 (map in Electronic Supplementary Material S1). To assess field consumption rates, six freshly collected kelp blades were prepared as for the experiments described above, except entire kelp blades were used. Feeding assays were conducted on a falling tide series such that the next high tide would not wash away the kelp blades. Replicate kelp blades were placed on the sand surface at the high tide line on the six beaches before sunset and collected just after sunrise. The kelp remaining in each kelp blade after the overnight assay was processed as above to determine the consumed dry mass for each replicate.

Prior to each field consumption test, we quantitatively surveyed macrophyte wrack cover and the species richness and abundance of macroinvertebrates in the upper beach zone of the six beaches using methodology adapted from Dugan et al. (2003). Wrack cover was estimated using the line-intercept method (Dugan et al. 2003). Invertebrates were surveyed by collecting 20 evenly spaced cores (10 cm diameter, 20 cm depth) from the upper beach boundary (cliff base or dune toe) to the lowest extent of upper beach invertebrates on six haphazardly placed shore-normal transects. Core samples were aggregated and sieved in 1.5 mm mesh in the field to remove sand and then frozen before sorting in the lab, where animals were identified to species and counted. Counts were converted to number of individuals per meter of shoreline based on the number of cores and their spacing rather than per m^2 to better account for changing beach widths across sites and time (Brown and McLachlan 1990; Schlacher et al. 2008; Dugan et al. 2013). Mean site values were calculated across the six transects for each time point.

Data analysis

To compare feeding rates of the six detritivore species, we analyzed consumption rates from the six single species treatments ($n = 18$ total replicates) using one-way ANOVA followed by a Tukey post-hoc test and generation of a compact letter display for the pairwise comparisons. The relationship between kelp consumer rates and consumer biomass was explored with linear regression analysis for the single species replicates ($n = 18$) and for all treatment replicates ($n = 171$). The effect of consumer diversity on kelp consumption rates was evaluated with ANOVA, where kelp consumption was the response variable and richness the explanatory variable. To further explore the relationship between species richness and identity we employed a hierarchical nested ANOVA model adapted from Reiss et al. (2011) and Bailey and Reiss (2014) that separated species richness from species identity and species composition. This set of models tests species richness alone, species identity, the interaction of richness and identity, and species combinations as drivers of observed kelp consumption. The richness

model depends only on the number of species. The species identity model assigns each species its own effect, which is multiplied by the number of individuals of that species present, thereby considering species' abundance, and in polyculture treatments considers these effects to be additive. The richness and identity interaction allows species identity effects to differ at each richness level, and tests for interactions between species due to the changing number of species present at each richness level. Lastly, species combination considers the species identities and their treatment combinations. These related models form a hierarchical structure with increasing complexity (more degrees of freedom). We used ANOVA to compare the goodness of fit for each model with the goodness of fit for the next most complex model in the hierarchy (Grafen and Hails 2002; Reiss et al. 2011). Additional detail on the model structure is in the Electronic Supplementary Material S2.

We evaluated relationships between diversity and abundance of detritivores and kelp consumption rates across the six survey sites using linear mixed effects modeling. We first assessed the relationship between kelp blade consumption ($n = 6$) and our two random factors of site ($n = 6$) and month ($n = 2$). Then, we independently tested the effects of three site-level variables; (1) total richness of upper beach detritivores, (2) richness of the six species used in the laboratory mesocosm experiment and, (3) the proportional abundance of the two largest species relative to total abundance of detritivores. Each of the three linear mixed effects models were then compared to the model with random factors only using ANOVA and provided that the models explained significantly different proportions of the variance, the model with the lowest Akaike Information Criterion (AIC) value was selected. Data display for the field assay consists of site-level values rather than replicates for ease of distinguishing the various sites and timepoints. Analyses were conducted using base R v. 3.5 (R Core Team 2013) and the Tidyverse (Wickham et al. 2019), multcomp (Hothorn et al. 2008), lme4 (Bates et al. 2015), and lmerTest packages (Kuznetsova et al. 2017).

Results

Mesocosm experiment

Adult body size of the wrack detritivores varied over more than an order of magnitude among the six species we tested (mean individual AFDW ± SE, 2.7 ± 0.1 to 46.9 ± 2.5 mg, Fig. 1a). Consumption rates of kelp varied over an order of magnitude and differed significantly among the six species in the single species treatments (Fig. 1b, one-way ANOVA, F value = 12.3, $p < 0.001$, df = 5 and 12). The Tukey post-hoc test indicated that differences in consumption among the
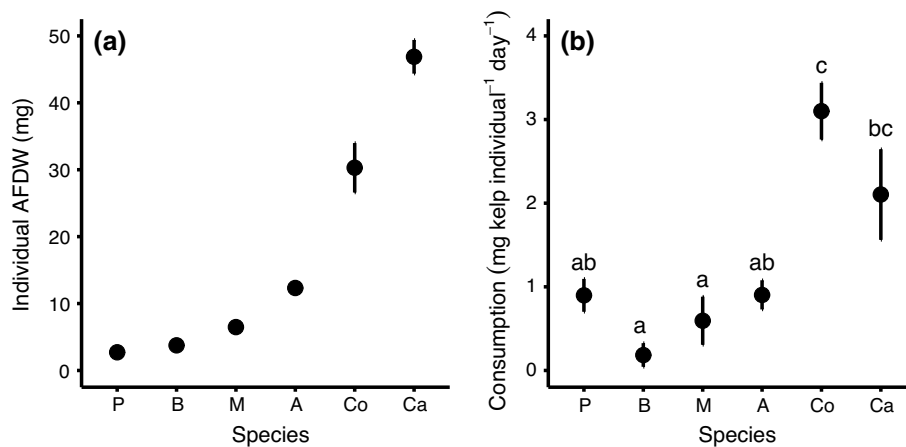
Fig. 1 **a** Mean values ($n=3$) of species-specific individual ash-free dry weights (AFDW, mg). **b** Mean values ($n=3$) of species-specific kelp consumption rates from single species mesocosm treatments. Error bars are standard error and letters identify groups of non-sig-nificant pairings determined by the TukeyHSD post-hoc test. Species codes: P = *Phaleria rotundata*, B = *Megalorchestia benedicti*, M = *Megalorchestia minor*, A = *Alloniscus perconvexus*, Co = *Megalorchestia corniculata*, Ca = *Megalorchestia californiana*

six consumer species were driven by the two largest tali-trid species (Electronic Supplementary Material S3). These two species, *Megalorchestia corniculata* and *M. californi-ana*, consumed kelp at the highest mean rates, 3.1 ± 0.3 and 2.1 ± 0.5 mg dry mass individual^{-1} day^{-1}, respectively, in single species treatments while the two smaller species, *M. benedicti* and *M. minor*, consumed much less kelp on aver-age, 0.2 ± 0.1 and 0.6 ± 0.3 mg dry kelp individual^{-1} day^{-1}, respectively. The isopod *Alloniscus perconvexus* and the beetle *Phaleria rotundata* consumed kelp at similar rates, averaging 0.9 ± 0.2 mg individual^{-1} day^{-1} despite their large difference ($> 4 \times$ AFDW) in average body size (mean indi-vidual AFDW = 12.3 ± 0.3 and 2.7 ± 0.1 mg, respectively) (Fig. 1a, b). The relationship between consumer biomass and kelp consumption rates was significant for the single species treatments ($n=18$, $r^2=0.5$, $p<0.001$, d$f=1$ and 16) and all treatments ($n=171$, $r^2=0.15$, $p<0.0001$, d$f=1$ and 169).

We evaluated the effect of biodiversity on an ecological function, in this case kelp consumption rate, using replicated combinations of the six consumer species across five levels of species richness. A linear regression between consump-tion rate and species richness suggested a weak, albeit sig-nificant, negative effect of diversity on kelp consumption ($r^2=0.02$, $p=0.05$) (Fig. 2a). Using species-specific kelp consumption rate values from the single species treatments, we estimated expected consumption values for every mixed species treatment and compared them to the actual consump-tion values and found that, on average, species mixtures gen-erally underperformed their expected kelp consumption rates by 24.6% (Fig. 2b).

The suite of models adapted from Reiss et al. (2011) and Bailey and Reiss (2014) confirmed that species rich-ness alone did not explain observed rates of kelp consump-tion (Table 1). The model results indicated that species

Fig. 2 **a** Kelp consump-tion rates (mg dry kelp individual^{-1} day^{-1}) as a function of species richness in mesocosm experiments. The line represents a linear regression ($r^2=0.02$, $p=0.04$). **b** Observed kelp consumption rates in mesocosm experiments compared to expected kelp consumption rates based on species' performance in single species treatments. Dashed line represents 1:1 line
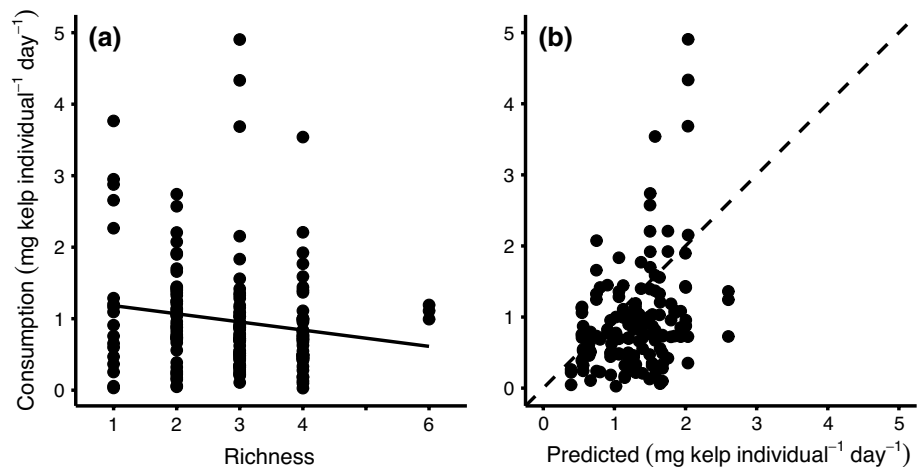
combinations (df = 32, p < 0.00001) and species identity (df = 5, p < 0.00001) were significant drivers of kelp consumption, whereas richness was not. The significance of species combinations is consistent with the finding that species mixtures tended to underperform predicted consumption rates. Additionally, if the monocultures (combined with richness levels) predict the polyculture outcomes, then the model "Richness + Identity" should account for everything apart from random error. Therefore, we compared this model with all treatment outcomes (i.e. "Species Combinations"), and found that, although monoculture consumption rates explain much of the consumption rates in mixed species assemblages, species combinations still noticeably underperformed the expected consumption rates predicted by the monoculture consumption rates (Species combinations | Richness + Identity, df = 47, F = 2.99, p < 0.00001).

Field consumption assay

Background levels of macrophyte wrack cover on the six study beaches varied greatly ranging from 1.3 to 4.7 m^2 m^{-1} (mean 3.0 m^2 m^{-1}) in October and 0.1–2.3 m^2 m^{-1} (mean 0.8 m^2 m^{-1}) in April. However, cover of the primary food resource, giant kelp, was less variable over time ranging from 0.2 to 1.1 m^2 m^{-1} (mean 0.56 m^2 m^{-1}) in October and 0.08–1.9 m^2 m^{-1} (mean 0.56 m^2 m^{-1}) in April. Species richness of intertidal detritivores varied from 5 to 15 species in surveys of the six beaches in October 2016 and April 2017. Total abundance of detritivores ranged from 3300 to 29,000 individuals m^{-1} of shoreline among the study sites, and the six species we evaluated in our BEF experiments made up 92–100% of the total abundance. The fraction of total abundance of the kelp detritivore community composed of the two large-bodied talitrid amphipods, *Megalorchestia corniculata* and *M. californiana*, ranged from 10 to 84% among sites and dates.

Mean values of overnight consumption of kelp in field feeding assays varied greatly across the six study beaches, ranging from 180 to 2549 mg dry kelp day^{-1}. Site and month were not significant drivers of the observed variability in kelp consumption rates (p = 0.11). There was no relationship between total consumer richness and overnight kelp consumption (Fig. 3a, p = 0.08) across the six beaches; this result also held when richness was limited to the six species of detritivores used in the mesocosm experiment (Fig. 3b, p = 0.68). Neither of these models explained more of the observed variance than the site and month model (p = 0.14 and p = 0.78, respectively). Species identity, however, was a strong predictor of the observed consumption of kelp in our field assays: the relative abundance of the two species of large-bodied talitrid amphipods explained a significant portion of the variation in kelp consumption among beaches (Fig. 3c, t = 5.7, p < 0.0001, trendline displayed represents simple linear regression (also significnant) for display purposes). This model was also a significant improvement over the site and month model (Chi-square = 20.8, p < 0.0001).

Discussion

Our results from laboratory experiments and field assays suggest that species richness of intertidal detritivores does not strongly influence the rate of processing of marine detrital subsidies, a key ecological function on sandy beaches. Rates of kelp wrack consumption in both mesocosm experiments and the field assays were better predicted by species identity than by diversity. In mesocosm experiments, kelp consumption rates in mixed-species treatments were nearly 25% below predicted values based on the single species treatments. In the field, processing of kelp wrack by intertidal consumers was strongly influenced by the relative abundance of the two largest species of talitrid amphipods, rather than the species richness of the intertidal detritivore

Table 1 Results of ANOVA for nested model set derived from Reiss et al. (2011) and Bailey and Reiss (2014) on laboratory mesocosm results for response variables of trial, richness, identity and species combination

| Comparison	Degrees of freedom	Sum of squares	Mean square	F	p
Trial (3) | Constant (1)	2	350.2	175.1	4.13	0.02
Richness (5) | Trial (3)	2	143.4	71.68	1.69	0.2
Identity (6) | Constant (1)	5	4246.7	849.34	20.04	< 0.00001
Richness*identity (25) | Richness + Identity (10)	15	1652.9	110.19	2.6	0.002
Species combination (57) | Richness*Identity (25)	32	4309.8	134.68	3.18	< 0.00001
Residuals	114	4830.9	42.38		

Trial refers to the week the treatment was conducted, richness is the number of species, identity is the species-specific effect, and species combination refers to the specific assemblage composition of each treatment. Each row in the table corresponds to a difference between two models. The number in parentheses is the number of model parameters, the "|" means "given", and degrees of freedom is the difference between the numbers of parameters in the two models. See Electronic Supplementary Material S1 for more model information

Fig. 3 a Overnight kelp consumption for field assays compared to ▶ total observed richness of upper beach detritivores for six beaches in October 2016 (squares) and April 2017 (circles) (site colors: R Beach—black, Isla Vista—orange, East Depressions—light blue, East Goleta—green, Arroyo Burro West—yellow, Arroyo Burro East—blue. A site map is available in the Electronic Supplementary Material S1). **b** Overnight kelp consumption for field assays compared to observed richness of the six common species used in the mesocosm experiment. **c** Overnight kelp consumption for field assays compared to the fraction of the abundance of the six consumer species occupied by the two large talitrid amphipod species (*Megalorchestia corniculata* and *Megalorchestia californiana*) (Linear mixed effects model, $t = 5.7$, $p = 0.000079$). The simple linear regression between site means (also significant) is shown for display purposes ($r^2 = 0.59$, $p = 0.0022$). Error bars are standard error of consumption rates ($n = 6$)

community. Our finding that species identity is relevant to how ecosystem functioning may change if one species were substituted for another points to the role of consumer body size, but also indicates that results of BEF studies are context dependent based on the community metrics varied. While our focus was on the effect of changing community richness with evenness maintained, data indicate that community biomass is also an important variable in the magnitude of this ecosystem function.

Ecosystem function may be strongly influenced by the number of species present if different processes require functionally distinct species (Perkins et al. 2015) or if the actions of one or more species facilitate others (Tonin et al. 2018). Given that feeding habits, intertidal habitat, and other functional traits of the invertebrate consumers in this experiment were similar and individual biomass varied greatly, our finding that species richness was not a strong driver of ecosystem function on beaches is perhaps not surprising. Our results are consistent with those from detritivore communities in a variety of terrestrial and aquatic ecosystems including grasslands, floodplains, streams and salt marshes (Cragg and Bardgett 2001; Reiss et al. 2010; Treplin et al. 2013; O'Connor et al. 2016; Little and Altermatt 2018). Instead, species identity was a better predictor of ecosystem functioning than richness in our sandy beach ecosystem. A strong role of species identity in function has been reported in a variety of systems (Handa et al. 2014; Gagic et al. 2015), including leaf litter breakdown by freshwater detritivores (Jonsson and Malmqvist 2000; Stoker et al. 2017; Santonja et al. 2018), grazing of marine algal biomass (Duffy et al. 2001; O'Connor and Crowe 2005; Godbold et al. 2009), urban food litter consumption by arthropods (Youngsteadt et al. 2014), and nutrient regeneration by marine bioturbators (Ieno et al. 2006).

Patterns of resource dynamics in subsidized ecosystems and the species traits of consumers that rely on these resources may underlie these findings. In ecosystems with stable and diverse primary producer communities, the resulting resource heterogeneity and stability is conducive
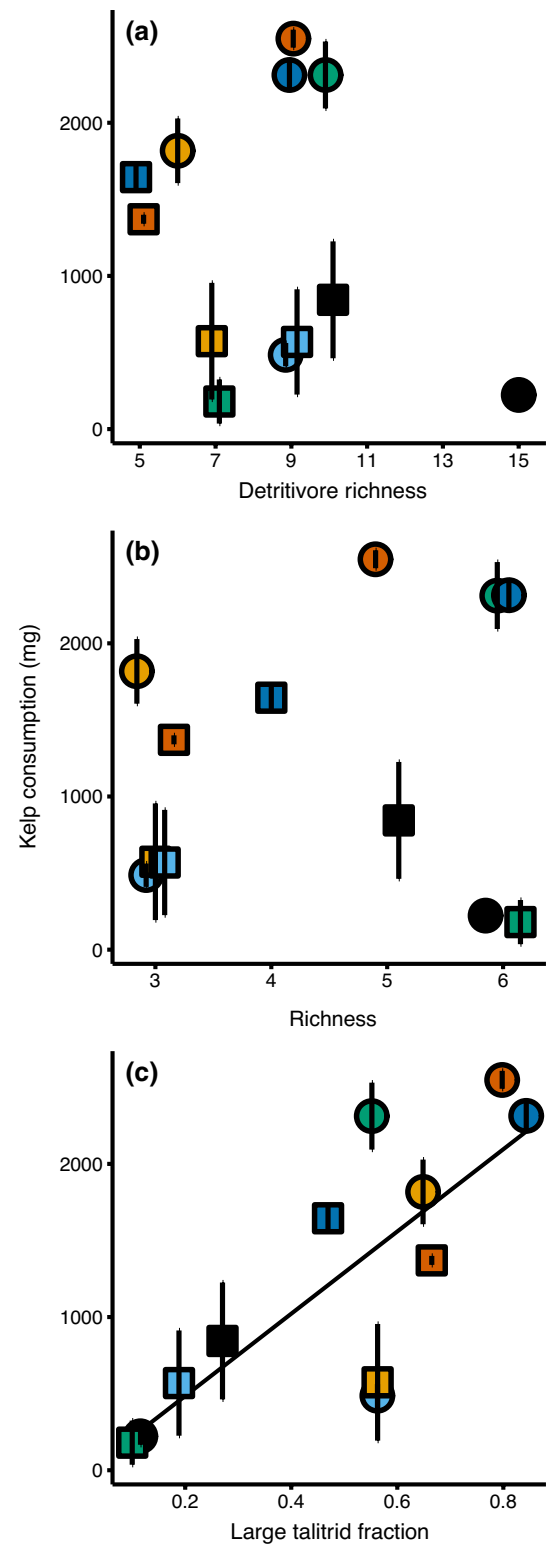
to specialization by consumers (Reboud and Bell 1997; Kassen 2002). Niche partitioning by these specialists results in complementarity as different species use different resources (Finke and Snyder 2008) and increasing diversity leads to greater overall resource exploitation and ecosystem

functioning (Thebault and Loreau 2003; Ives et al. 2005; Finke and Snyder 2008; Filip et al. 2014). In contrast, when the type or availability of resources is more stochastic, as in many subsidized food webs, generalist consumers tend to have an advantage (Reboud and Bell 1997; Ma and Levin 2006; Narwani and Mazumder 2010). The highly dynamic supply of kelp wrack and other marine subsidies on sandy beaches may thus promote a relatively high abundance of generalist consumer species (Hutchinson 1961; Mihuc and Minshall 1995; Verberk et al. 2010), weakening BEF relationships due to greater functional redundancies across the community (Ives et al. 2005; Novotny et al. 2010; Filip et al. 2014).

The underperformance of observed relative to predicted rates of kelp consumption in our laboratory mesocosm experiments (Fig. 2b) suggests that negative interspecific competitive interactions may have increased with species richness (Bond and Chase 2002; Bastian et al. 2008; Gessner et al. 2010). Competition for shared resources can be high in communities comprised of generalist consumers (Thebault and Loreau 2003; Ives et al. 2005). Species may respond to interspecific competition by shifting their diet (Finke and Snyder 2008) or their behavior across time and space (Mihuc and Minshall 1995; Mihuc 1997). Although giant kelp is the primary form of macroalgal detritus on southern California beaches (Dugan et al. 2003, 2011), other drift macroalgae and seagrasses, as well as carrion, are consumed by sandy beach invertebrates (Lastra et al. 2008; Bessa et al. 2014; Michaud et al. 2019). The intertidal consumer species we investigated all readily consumed blades of giant kelp; however, in nature they may adjust their behavior or diet to avoid interspecific competition. Such niche partitioning would represent a form of complementarity (Loreau and Hector 2001; Thebault and Loreau 2003; Poisot et al. 2013; Tonin et al. 2018) that would not be observed in a study considering a single resource type. Although not tested here, this type of complementarity could result in greater total detritus consumption when multiple detritivore species and types of wrack detritus are present.

The ecological function of kelp wrack consumption was largely driven by the relative abundance of the largest detritivore species in our field study. Body size is a key species trait (Brose et al. 2006; Norkko et al. 2013) and large-bodied species often make disproportionately high contributions to ecosystem function (Seguin et al. 2014; Brose et al. 2016; Tonin et al. 2018). Indeed, species traits or functional attributes are better predictors of ecological functions in multitrophic systems (Lefcheck and Duffy 2015). Species that contribute significantly more to an ecosystem function tend to be the dominant species in a community while rare species that are generally low in abundance contribute much less (Smith and Knapp 2003; Dangles and Malmqvist 2004; Klemmer et al. 2012; Wohlgemuth et al. 2016). When

function is driven by species identity and a dominant species is present, ecosystem functioning is expected to be negatively correlated with diversity (Creed et al. 2009). The highest functioning species must also be the dominant species for process rates to be high at the ecosystem scale (Creed et al. 2009; Treplin et al. 2013). Our finding that an important ecological function was maximized when the two highest functioning species were the dominant species adds to the growing evidence supporting the role of species identity and dominance in the provisioning of key ecosystem functions, especially in soft-sediment ecosystems (Henderson et al. 2019, Schenone and Thrush 2020).

Threats to biodiversity from a changing climate are well recognized (Thomas et al. 2004), but our understanding of impacts on key species traits, like body size, is lacking. Warming temperatures associated with climate change can lead to decreases in animal body size due to higher metabolic rates and faster development, particularly in ectotherms (Gardner et al. 2011; Sheridan and Bickford 2011; Ohlberger 2013). For example, a significant negative relationship between sea temperature and body size has been reported for populations of sandy beach invertebrates, including a talitrid amphipod, across a wide latitudinal gradient (Jaramillo et al. 2017). Large-bodied species may also be particularly vulnerable to extinction as the climate warms (Cardillo 2006; Brose et al. 2016). Consequently, as these key species disappear, ecosystem functioning may decline more than predicted by diversity losses alone.

Globally, sandy beach ecosystems are threatened by sea level rise, urbanization, erosion, and coastal armoring (Schlacher et al. 2007; Defeo et al. 2009; Dugan et al. 2017; Schooler et al. 2017; Vitousek et al. 2017). In combination or alone, impacts from these threats commonly result in the degradation or loss of the upper beach zone required by intertidal wrack consumers (Dugan et al. 2008; Myers et al. 2019). On beaches worldwide, especially along highly developed shores, coastal management regimes that remove wrack (grooming or raking) and armor the shore to protect coastal development and infrastructure (Defeo et al. 2009) increase disturbance and reduce beach biodiversity (Dugan et al. 2003; Jaramillo et al. 2012; Schooler et al. 2019). On urbanized beaches in southern California, where intertidal diversity is lower than beaches in less developed areas, the two large-bodied talitrid species that we found to be the most effective kelp consumers are often sparse or absent (Schooler et al. 2019), suggesting that impacts to these key species from coastal management and climate change are already significantly degrading sandy beach ecosystem function on developed coasts.

Biodiversity is often used as a primary metric to set goals, establish baselines, and measure success of conservation efforts (Schwartz et al. 2000; Srivastava and Vellend 2005). Our results, however, reinforce the need to also consider the

roles of individual species and species traits in ecosystem functioning (Cadotte et al. 2011; Henderson et al. 2019). In many ecosystems, including the subsidized sandy beach communities studied here, ecosystem function and services may depend mainly on dominant and high-functioning species (Winfree et al. 2015). Identifying these key species and traits is necessary to predict the impacts of species loss on ecosystems and their vital functions, and to prioritize them for conservation and management.

Availability of data and material The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

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