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Coastal connectivity: structure and function of recipient beach ecosystems respond to variation in kelp subsidies

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Coastal connectivity: structure and function of recipient beach ecosystems respond to variation in kelp subsidies

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Marine Science

by

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December 2021

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ABSTRACT

Coastal connectivity: structure and function of recipient beach ecosystems respond to variation in kelp subsidies

by

Kyle Aaron Emery

Many ecosystems can be described as dynamic, open, and connected systems that are intrinsically linked to the attributes and processes of neighboring ecosystems. Connectivity among these ecosystems is critically important across multiple levels of biological organization. The cross-ecosystem exchange of organic matter is a well-described example of high variability in ecosystem connectivity. Subsidies of material and energy from donor ecosystems can significantly influence the structure and dynamics of recipient communities and food webs. In systems with pulsed resource subsidies variability in subsidy type, amount, and frequency affects consumer populations, species interactions, and food web complexity causing them to differ from systems with consistent *in situ* production. The largest magnitude in observed cross-ecosystem fluxes are from marine to terrestrial systems. An exceptional example of this flux is the substantial subsidy of organic matter exported by highly productive nearshore kelp forests to sandy beaches.

In the marine realm, canopy forming kelps are considered foundation species that structure the surrounding nearshore reef community. Kelp forests provide many ecosystem

functions including food and habitat provisioning, nutrient cycling, increased biodiversity, and subsidies to other habitats. The high turnover of biomass in kelp forests leads to the export of the majority of their net primary production as detritus to adjacent marine ecosystems. A large fraction of that kelp detritus from the donor ecosystem washes ashore on nearby sandy beaches, the recipient ecosystem. Beach ecosystems are characterized by frequent disturbance, low *in situ* primary productivity, and a reliance on marine subsidies. The inputs of wrack to beaches are strongly linked to their community and food web structure and to ecological functioning. Wrack subsidies from kelp forests to beaches are highly variable across space and time. This variation can affect species and populations directly via changes in habitat and food, indirectly through changes in species interactions, and functionally through effects on ecological processes on the beach.

In my first chapter, I examine the role of habitat partitioning in reducing potential negative interspecific interactions across space and time among four co-habiting species of wrack detritivores, talitrid amphipods (*Megalorchestia spp*.), and how this niche partitioning is mediated by tide phase using field studies and mesocosm experiments. In my second chapter, I evaluate the hypothesis that biodiversity promotes ecosystem function by testing the effects of consumer species diversity and identity on kelp wrack processing rates using laboratory experiments and field consumption assays. In my third chapter, I further explore ecosystem functioning on sandy beaches by comparing *in situ* fluxes of CO_2 from intertidal sediment to wrack and detritivore abundance and in relation to laboratory measured respiration rates of detritivore species. In my final chapter, I explore how wrack subsidies structure the sandy beach macroinvertebrate community, enhance species richness and abundance across multiple trophic levels, and stimulate multiple ecological and biogeochemical ecosystem functions. While the important role of linkages between donor and recipient ecosystems is widely known, there is much to learn with respect to how these links function across spatial and temporal scales and across species.

Overall, my findings suggest that the inputs of wrack from kelp forests to beaches is a critical driver of important biotic and abiotic processes that interact to shape the community and promote ecosystem functioning. Four congeners of talitrid species reduce possible negative biotic interactions by partitioning their habitat and surface-active periods and the magnitude of these separations is mediated by tide phase. For the key ecosystem function of kelp wrack processing, consumption rates were not dependent on species richness in the laboratory or field trials. Those rates are body-size dependent and pointed to species identity as a significant factor in this ecosystem function, especially the presence of the two large-bodied species. Expanding on sandy beach ecosystem functioning, I found that wrack abundance across a natural range in variability is a significant driver of sediment CO_2 flux and that wrack consumer respiration rates, determined by laboratory measurements, are a notable component (10.5%) of the net CO_2 flux. The role of wrack in the sandy beach ecosystem is multifaceted, as demonstrated by my field survey of sites across a large natural range of wrack inputs. Wrack abundance structures the detritivore, predator and full wrack-associated macroinvertebrate communities, increases redundancy within the invertebrate food web, enhances shorebird diversity and abundance, and increases ecosystem multifunctionality. My results demonstrate how the dynamic coupling between sandy beach ecosystems and nearshore giant kelp forests is reflected in the role of kelp wrack subsidies in mediating ecosystem diversity, community structure, and ecosystem functioning of beaches.

TABLE OF CONTENTS

Chapter I. Habitat partitioning by mobile intertidal invertebrates of sandy beaches shifts with the tides

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Abstract

Coexistence of similar species can be influenced by the intensity of interspecific interactions, which often depends on availability of limiting resources. Habitat availability varies strongly with tidal phase in many intertidal ecosystems, potentially affecting interspecific interaction strength, particularly for mobile species. Four closely related species of highly mobile intertidal detritivores (talitrid amphipods *Megalorchestia californiana, M. corniculata, M. benedicti, M. minor*) inhabit sandy beaches in southern California, where they consume wave-cast macroalgal wrack originating on coastal reefs. Their coexistence suggests that mechanisms, such as niche separation, are operating to weaken competition among these species. To evaluate this possibility, we explored how tidal phase may mediate temporal and spatial patterns of habitat use among these closely related congeners. We hypothesized that neap tides which reduce intertidal habitat would strengthen temporal separation between species, whereas spatial separation would be greater during spring tides, when more habitat is available. We investigated these questions during spring and neap tide phases using 1) comparisons of intertidal distributions of burrowed amphipods and 2) observations of surface activity of amphipods from pitfall traps and mesocosms. We found significant effects of tide phase and species identity on mean intertidal positions and separation of burrowed amphipods. Intertidal distributions of the four species overlapped during neap tide and were significantly separated during spring tide when more intertidal habitat was available. Surface activity patterns differed among species and were more widely separated in time during neap tide than during spring tide. Consequently, the cumulative activity time of all species on neap tides was twice that observed during spring tides. Our findings suggest that mobile intertidal species, like these

sympatric talitrid amphipods, can avoid interspecific competition by shifting their activity patterns with tide phase and beach condition. As rising sea levels reduce beach habitat, interspecific competition among these important intertidal consumers may increasingly influence their behavior and coexistence.

Introduction

Species coexistence is central to the maintenance and promotion of biodiversity (Chesson 2000). Niche differentiation and consequent reduction in interspecific competition for limiting resources has long been thought to be the most important general mechanism for coexistence (Hutchinson 1961, Tilman and Pacala 1993). The apparent coexistence of ecologically similar species, however, has challenged this idea (Liebold and McPeek 2006, Levine and HilleRisLambers 2009, Mayfield and Levine 2010), and engendered many potential explanations and hypotheses (Wilson 1990a, Palmer 1994, Wright 2002), particularly neutral processes (Hubbell 2011). Nevertheless, specialization of many niche dimensions may not be readily apparent (Futuyma and Moreno 1988); for example, ecologically similar species can avoid competitive exclusion by partitioning their habitat and food resources across time as well as space (Schoener 1974, Sala and Balesteros 1997, Jensen et al. 2017, Cloyed and Eason, 2017, Lea et al. 2020) by developing activity patterns that differ from potential competitors (Gertsch and Riechert, 1976, Albrecht and Gotelli, 2001).

The mechanisms of stabilizing coexistence were summarized by Chesson (2000) and divided into two primary categories based on the role of heterogeneity. Variation-independent mechanisms of stabilizing species coexistence occur in the absence of spatial or temporal heterogeneity and include resource partitioning and frequency-dependent predation (Chesson 2000, Levine and Hart 2020). Variation-dependent mechanisms of stabilizing coexistence include temporal and spatial storage effects, temporal and spatial relative nonlinearity of competition, and fitness-density covariance (Chesson 2000, Levine and Hart 2020). Determining the role of heterogeneity is a scale-dependent question, as heterogeneity, and its importance for coexistence, is expected to decline with habitat area (Snyder and Chesson 2003). The role of spatial scales with respect to species coexistence is complex, but a unifying feature is the role of tradeoffs across environmental conditions and spatial scales (Kneitel and Chase 2004). Coexistence across patches depends on the degree of heterogeneity, dispersal among patches, and species similarity (Mouquet and Loreau 2002), and can occur through habitat (Streams 1987, Stewart et al. 2010) or food selection (Pardo et al. 2015, Oakley-Cogan et al. 2020), or intraspecific aggregation (Ives 1991, Presa Abos et al. 2006). Time is also a segregable niche dimension (Carothers and Jaksic 1984, Castro-Arellano and Lacher 2009). Separation of the timing of resource use (food or habitat), for example, can occur via avoidance or differential activity periods on diurnal or longer scales (Albrecht and Gotelli 2001, Stewart et al. 2002, Adams and Thibault 2006) and successional patterns of colonization (Young et al. 1996, Edwards and Stachowicz 2010).

Such mechanisms of niche separation are profoundly affected by environmental variability, the magnitude of which strongly influences the strength and outcome of competitive interactions (Levins 1979, Li and Chesson 2016). For example, a harsh and fluctuating environment can slow the process of competitive exclusion (Chesson and Huntly 1997, Chesson et al. 2004). In harsh environments, some argue that the intensity and importance of competitive interactions decrease in favor of positive interactions or facilitation (Kawai and Tokeshi 2007, Barrio et al. 2013, Fugere et al. 2012, but see Hart and Marshall 2013). However, such conditions may also make species less tolerant of competitive interactions and promote niche differentiation through environmental fluctuations (Chesson and Huntly 1997). Gutt (2006) suggests that the ability of similar species to coexist, therefore, is dependent on minimizing competitive displacement by maximizing utilization of environmental variability.

Intertidal marine ecosystems provide ideal systems to explore how spatial and temporal heterogeneity affect species coexistence and community dynamics. Studies of competitive interactions in unvegetated soft sediment ecosystems, such as mudflats and sandy beaches, are relatively limited (Peterson 1991) compared to the rocky intertidal, where interactions among sessile or sedentary species can shape zonation and other aspects of community structure (Connell 1961a, Dayton 1971, Paine 1974, Chesson 1985). However, the potentially important role of competitive interactions in soft-sediment marine ecosystems was illuminated by the pioneering work of Peterson (1977, 1982) and Peterson and Andre (1980) on intertidal bivalves in lagoons along with studies of a variety of infaunal taxa (Gallagher et al. 1983, Gallagher et al. 1990, Wilson 1990b, Martinetto et al. 2007, Drolet et al 2013). On the open coast, the intertidal zone of sandy beaches has traditionally been described as a harsh environment where ecological communities are structured primarily by strong physical factors (waves, tides, grain size) rather than biotic interactions (McLachlan, 1990, Defeo et al., 2003). However, this long-standing paradigm has been challenged in recent years (Bruce and Soares 1996, McLachlan 1998a, Dugan et al. 2004) and falls short in addressing the high biodiversity of intertidal communities on sandy beaches that receive large subsidies of marine macrophytes or wrack, such as kelp and seagrass, from nearshore reefs (Dugan et al. 2003, Schooler et al. 2017).

On upper intertidal beaches, numerous similar species of mobile invertebrates depend on wrack subsidies for food and habitat (Colombini et al., 2000, Dugan et al., 2003, Olabarria et al., 2007). One possible mechanism of coexistence for these animals is the spatial or temporal partitioning of intertidal habitat by species. Spatial zonation is common among rocky intertidal organisms, especially sessile biota (Harley and Helmuth, 2003), but is less distinct in the mobile biota of soft-sediment ecosystems (Peterson 1991). On sandy beaches, where mobility of infauna is particularly high, zonation patterns are dynamic, and many species actively migrate on diurnal and tidal scales (Jaramillo and Fuentealba 1993, Jaramillo et al., 1993, Jaramillo et al., 2000, Dugan et al., 2013). These movements can be in response to water levels and the distribution of resources, e.g. wrack deposits, as well as avoidance of potentially negative biotic interactions, such as competition and predation (Colombini et al., 2013). Tides, a zeitgeber of the shore, may benefit sandy beach macrofauna by aiding their orientation and locomotion or providing cues to signal the need to relocate (Scapini 2006, Rossano et al. 2008, Fanini et al. 2016, Scapini et al. 2019). Because they include many components (diurnal, semilunar, lunar and longer) which drive much of the inundation and desiccation patterns on intertidal beaches it is likely they mediate the behavior of sandy beach organisms.

Sandy beaches in southern California can support a species rich and functionally redundant community of upper beach macroinvertebrates (Schooler et al., 2017), providing an ideal system to evaluate how similar species can coexist in a dynamic and harsh ecosystem. We explored niche partitioning among four congeneric species of talitrid amphipods found on southern California beaches in 1) space, via occupation of different levels of the intertidal zone and 2) time, via different periods of activity. We hypothesized that neap tides that reduce the area of preferred intertidal habitat would strengthen temporal niche separation in these species, whereas spatial separation would be more evident during spring tides, when a wider upper intertidal zone is available. We also hypothesized that body size may affect surface activity patterns with the two large-bodied species having an advantage of the two small-bodied species and juveniles.

Methods

Study Sites and Species

Our field surveys (spatial coring and pitfall sampling) were conducted on an unmanaged, unarmored beach with no vehicle access or beach grooming, located east of Goleta Beach County Park in Santa Barbara, California, USA (34˚25’02.1”N, 119˚48’56.7”W) . The mesocosm experiments were conducted at nearby Campus Point beach (34˚24’22.6”N, 119˚50’38.0”W) for access and safety reasons. All species of talitrid amphipods (*Megalorchestia californiana, M. corniculata, M. minor, M. benedicti*) used in the mesocosm study were collected by hand at local beaches (where they are highly abundant) on the morning of each experiment. *M. corniculata* was collected at Isla Vista Beach (34˚24’33.6”N, 119˚52’23.0”W), *M. minor* at R beach (34˚24’58.1”N, 119˚53’12.3”W), and *M. californiana* and *M. benedicti* at Goleta Beach. This guild of congeners is the dominant wrack-associated taxon in the study region in terms of abundance and biomass (Dugan et al. 2003). These highly mobile species are most active on the sand surface at night when they forage on kelp and other wrack. During the day, they occupy freshly dug intertidal burrows in damp sand that are typically aggregated into distinct, often species-specific, beds of characteristically bioturbated sand (Dugan et al. 2013).

Spatial Distribution Surveys

To compare zonation patterns and spatial separation across species, we quantified the distribution and abundance of wrack-associated macroinvertebrates of the upper intertidal zone on two dates with contrasting spring and neap tide phases (August 2nd (spring) and 10th, (neap) 2016). All surveys were conducted during the day when the majority of animals were burrowed in the sand. For each survey, six shore-normal transects were set up to extend from the upper beach boundary (cliff base) to the water table outcrop during low tide. We measured the abundance of macrophyte wrack as cover on each transect using a line intercept method (Dugan et al. 2003). Along each transect we also collected 30 evenly spaced cores (10 cm diameter, 20 cm depth) from the upper beach boundary to the lowest distribution limit of upper beach macroinvertebrates. Each core was placed in a 1.5 mm mesh bag sieve, rinsed in seawater, and the contents were bagged and frozen. Each frozen sample was sorted in the laboratory and invertebrates were identified to species level, counted and weighed. For the purpose of this study, we focused on the spatial distributions of the four congeneric species of talitrid amphipods (*Megalorchestia californiana, M. corniculata, M. minor, M. benedicti*) that coexist on sandy beaches in our study region. Juvenile *Megalorchestia* (length < 8mm) were included as a separate group because they make up a large portion of total talitrid abundance on the beach and prior research has shown that juvenile activity differs from that of adults (Lastra et al. 2010).

Temporal Distribution – Surface Activity

Surface activity patterns of the four *Megalorchestia* species were assessed using observations in controlled mesocosm experiments and through pitfall trapping on the beach during spring and neap tide phases. The observational study used mesocosm containers placed on the upper beach at Campus Point Beach in Santa Barbara, California on contrasting neap and spring tide phases, July 31st and August 7th, 2017 respectively. The mesocosms (n = 4 per species) consisted of 18.9 L buckets filled to a depth of 20 cm with sieved dry sand and wetted using filtered seawater. Eighty individuals of each species were collected the morning of each experiment from the local beaches described above, and single species treatments were set up with 20 individuals per bucket (three replicates per species) with a fresh blade of giant kelp (*Macrocystis pyrifera*) as a food source and habitat element. The sixteen mesocosms were set up in the laboratory and left to acclimate for approximately 6 hours before observations commenced. After the acclimation period, buckets were buried to 20 cm depth on the upper beach (the same depth as the sand in the bucket) to help maintain ambient temperature and lighting conditions. Every hour for 24 hours, the total number of individuals active on the surface were observed for one minute and recorded.

Pitfall traps were used to assess *in situ* surface activity patterns of *Megalorchestia* spp. along the high tide line of Goleta Beach on contrasting neap and spring tide phases (July 16th (neap) and August 8th, 2017 (spring). Traps were placed at the high tide line where most of the fresh kelp wrack is deposited and where these organisms aggregate to feed. After high tide on each sampling date, twelve 470 ml cups with lids were buried flush with the sand surface 0.5 m apart along the high tide line, parallel to the water in randomized order (from 1 – 12). This was replicated in four groups with each group of twelve cups 10 m apart. Seawater mixed with a few drops of dish soap was added to the bottom of each cup to prevent trapped organisms from escaping. One trap in each of the four groups was opened for 30 min every 2 hours for 24 hours. The organisms collected in the traps were transferred to labeled bags and frozen for later processing. The contents from each trap were sorted in the laboratory, identified to species level and counted.

Data Analysis

For the spatial distribution surveys, we calculated the mean position, P, for each species during each tide phase as:

$$P = \sum \frac{n_i * D_i}{\sum n_i}$$

where n_i is the number of individuals at each sampling distance from the bluff D_i. Within-species mean positions were compared between the two tide ranges using Student's t-tests. One-way ANOVA was used to compare mean position by species on the neap tide and on the spring tide. Mean positions of the four species were also compared using a two-way ANOVA with mean positions as the response variable and species and tide as fixed factors. The percent increase in habitat area, H, was calculated as:

$$H = \frac{n - s}{n} * 100\%$$

where n is the mean position of the neap tide high tide strand line and s is the mean position of the spring high tide strand line.

Observational data from the mesocosm experiments were averaged for the four species across the four replicates and were analyzed using circular statistics. We calculated mean time of activity (± standard deviation) for each species on each tide phase based on the number of individuals observed each hour. We also calculated Rayleigh's Z for each species on each tide phase, which serves as a measure of how clumped (high values) or dispersed (low values) observations were around the mean hour over the 24-hour period. Lastly, we determined the total time range of activity by calculating the number of hours from when the first maximum number of individuals of one species was observed to when the last maximum number of individuals of some other species was observed for each tide phase. This time range therefore contained the peaks of activity for all four species and was used to estimate temporal separation among the species on the different tide phases.

Data presented for the pitfall traps include three *Megalorchestia* spp., as *M. corniculata* adults were not caught in pitfall traps. Numerous juvenile *Megalorchestia* were also caught and analyzed as an independent group because their activity may differ from that of adults (Lastra et al. 2010). As with the observational study, we calculated the total time range of activity across the three adult species by determining the number of hours between the first peak of activity for one species and the last peak of activity for the remaining species to estimate temporal separation among the species in the field on the different tide phases. The data from pitfall traps were analyzed using circular statistics to determine the mean time of activity (± standard deviation) for each species based on the mean number of individuals trapped every 2 hours for each tide phase. We also calculated Rayleigh's Z for each species on each tide phase. Circular statistics analyses were done using Oriana v4 (Kovach 2011); all other analyses were conducted with base R (R Core Team 2019) and Tidyverse (Wickham et al. 2019).

Results

Spatial Distribution

Our samples from quantitative field surveys included adult individuals of all four species of *Megalorchestia* as well as unidentified juveniles in both the spring and neap tide phase surveys (Figure 1). From the neap tide to the spring tide survey, the location of the high tide strand line shifted 15 m higher on the beach. The corresponding increase in habitat area, H, was 54.1%. The abundance of macrophyte wrack (cover) did not differ between our neap (3.79 m^2 m^{-1}) and spring (3.31 m^2 m^{-1}) tide surveys (one-way ANOVA, F = 0.42, p =

0.53). The mean positions of *Megalorchestia* in relation to the back-beach limit (bluff base) varied across species and tide phase. Among the four species, *M. californiana* adults were located farthest from the water and closest to the bluff at 29.3 m ± 1.4 m (mean ± standard deviation) on the neap tide and 20.8 m ± 3.5 m on the spring tide. Moving down the beach toward the water, *M. benedicti* were next, with mean positions of 29.9 m ± 1.2 m on the neap tide and 20.9 m ± 4.8 m on the spring tide. *M. minor* were lower on the beach at 31.2 m ± 1.4 m on the neap tide and 26.2 m ± 2.4 m on the spring tide. Mean positions of *M. corniculata* were closest to the water at 32.6 m ± 0.4 m on the neap tide and 26.7 m ± 1.7 m on the spring tide. Juvenile *Megalorchestia* were close to the bluff on average, at 29.2 m ± 3.6 m on the neap tide and 20.5 m ± 5.0 m on the spring tide. The order of mean positions was the same for spring and neap tide ranges with juveniles nearest to the bluff, then *M. californiana*, *M. benedicti*, *M. minor*, and finally *M. corniculata* closest to the water. However, the range of positions for adults of the four species was nearly double on the spring tide (5.9 m) than on the neap tide (3.3 m), and mean positions on the spring tides were differed significantly from mean positions on the neap tide for all four adult species and juveniles (pairwise t tests, p values for all five groups ≤ 0.001). The spread of *Megalorchestia* (i.e. mean position standard deviations) across the beach face was also greater for all species and juveniles on the spring tide with the net increase in SD ranging from 1.0 to 3.6 m. On the neap tide, mean positions of adults of the four talitrid amphipod species and juveniles were spatially compressed, and did not differ significantly ($F = 2.7$, $p = 0.06$, $n = 27$). In contrast, during the spring tide, adults of the four species and juveniles were more widely separated and their mean positions differed significantly ($F = 4.2$, $p = 0.01$, $n = 29$). We found a significant effect of species (two-way ANOVA, $F = 4.8$, $p =$

0.002, n = 56) and tide phase (F = 86.5, p <0.001, n = 56) on mean position, and no significant interaction between species and tide phase (p = 0.5).

Temporal Distribution – Surface Activity

Observations of adults of the four species of *Megalorchestia* in the mesocosms for 24 hours revealed different temporal patterns in surface activity between the neap tide and the spring tide phases. On the neap tide the four species exhibited distinctly different peaks in surface activity, whereas on the spring tide there was large overlap in surface active periods (Figure 2). During the neap tide there was also a greater time range of surface activity (7.5 hours, Appendix S1: Figure S1) compared to the spring tide (4 hours, Appendix S1: Figure S1). The mean hour of surface activity, derived from the number of individuals active each hour, was earlier in the night for the two larger species (*M. californiana* and *M. corniculata*) than for the two smaller species (*M. minor* and *M. benedicti*) on both tide phases (Table 1). Rayleigh's Z values, a measure of clustering, i.e. how concentrated the data is around the mean for each species, varied across tide phases for all species, with only *M. minor* having notably higher values on both tides, indicating relatively narrow windows of peak activity (Table 1).

In the pitfall trap samples we captured adults of three of the four species (no *M. corniculata*), and many juveniles (length < 8mm). As with the mesocosm experiments, the time peaks when individuals were active (caught in pitfall traps) were more distinct on the neap tide compared to the spring tide, where we observed much greater overlap in the surface-active periods of the species (Figure 2). During the neap tide the overall duration of surface activity of the amphipods (adult species and juveniles) was double (14 hours, Appendix S1: Figure S2) that observed for the spring tide (7 hours, Appendix S1: Figure

S2). Similar to results of the mesocosm experiment, the larger species (*M. californiana*) was active earlier in the night compared to the two smaller species (*M. minor* and *M. benedicti*) during both tide phases (Table 1). Large Rayleigh's Z values indicated that *M. californiana* and juvenile *Megalorchestia* had aggregated activity distributions, or relatively tight windows of peak activity, during both tide phases, while the two small-bodied talitrid species were more dispersed across time in their activity (Table 1).

Discussion

The interspecific spatial and temporal niche separation that we found suggests that negative biotic interactions, such as competition, are operating on dynamic open coast sandy beaches. In sheltered habitats, such as mudflats and marshes, soft-sediment infauna spatially partition habitat to reduce competition for space (Woodin 1974, Peterson and Andre 1980, Wilson 1990b). Our results demonstrate that mobile intertidal species inhabiting apparently harsh sandy beach habitats also partition habitat in space and time, and that this partitioning varies with tide phase. The degree of spatial and temporal separation of the four congeneric species of intertidal talitrid amphipods we observed varied strongly with tide phase and the resulting >50% change in habitat availability, with stronger temporal patterns in niche separation on a neap tide when habitat is most limiting, and greater spatial separation on a spring tide when more habitat is available.

Strong interspecific temporal variation in surface activity of the four amphipod species was observed *in situ* in the presence of congeners, with pitfall sampling, and in mesocosms in the absence of congeners, suggesting that these behavioral patterns were entrained responses to tide phase (Enright 1965, Enright 1972, Hastings 1981, Naylor 1985). Such temporal separation in activity may be a mechanism of avoiding competitive interactions over limiting resources like food and habitat, but may trade off with other potential foraging costs, such as predation and desiccation risk (Williams, 1980, Beyst et al. 2002). During the neap tide phase, when biotic interactions are expected to be more intense due to habitat limitation, a longer overall period of active surface time was observed across the four species than during the spring tide, reflecting interspecific separation of activity peaks. On the spring tide when more habitat was available and spatial separation possible, higher overlap in peak surface activity was observed, suggesting that ideal activity and foraging time might be the same for these similar species absent interspecific interaction. Tidal fluctuation on the sandy beach may therefore provide a means of niche expansion via a reduction in competitor densities (Bolnick et al. 2010, Crego et al. 2018, Petrozzi et al. 2021).

The role of fluctuating conditions, such as tides, in mediating biotic interactions is relatively unexplored, but our study results and others imply that tide phase is an important factor to consider with respect to coexistence, particularly of mobile intertidal species (Berglund 1982, Steibl and Laforsch 2019, Lea et al. 2020). Zonation has been well studied for rocky intertidal shores providing valuable insights on the relative influence of physical factors and biotic interactions in setting patterns (Connell 1972, Menge and Sutherland 1976, Tomanek and Helmuth 2002, Harley and Helmuth 2003). However, the majority of those observational and experimental studies have focused on sessile or sedentary organisms whose zonation is relatively stable over time and mediated by physical stressors including temperature, inundation period, waves, wind, oxygen availability, and desiccation (Connell 1961b, Newell 1976, Lubchenco 1980, Wethey 1984, Underwood and Denley 1984). Although tolerance to physical factors sets up the broader intertidal zones that species can inhabit, within these zones the effects of biotic interactions can be strong including competitive interactions for food and space (Dayton 1971, Paine 1971, Peterson 1982, Yamada and Boulding 1996, Peterson 1991). For the diversity of mobile intertidal species of soft sediment and even of rocky shores, those classic tenets concerning zonation and the relative roles of physical factors and biotic interactions may not apply. The zonation of mobile intertidal species can be tightly coupled to their behavioral adaptations (Gravem and Morgan 2016) with tidal migration of different frequencies a commonly observed response (Dugan et al 2013). On the sandy beach, where all organisms are highly mobile, and interact with water motion, including tidal fluctuations as well as other physical factors by moving (McLachlan 1988b), intertidal zonation patterns are far more dynamic. Understanding how mobile species partition the intertidal zone provides a fresh dimension for evaluating the role of biotic interactions in intertidal habitats.

Activity patterns of intertidal sandy beach invertebrates have been related to species-specific needs, such as burrowing to avoid predation and desiccation during the day or migrating to optimize feeding in the swash, on wrack, or on carrion on the sand surface at night when the temperature and predation risks are lower (Brown and McLachlan 1990, Scapini et al., 1992, Naylor and Rejeki 1996, Cardoso, 2002, Gibson 2003). We would expect wrack availability to significantly influence both community composition and behavior (Dugan et al. 2003, Poore and Gallagher 2013, Fanini et al. 2016, Michaud et al. 2019). However, we found no differences in wrack abundance between the spatial distribution surveys conducted during neap and spring tides in our study. The relatively consistent environmental conditions other than tide during both our surveys strengthens the evidence pointing to the mediating effect of tide phase on species interactions and their mechanisms of avoidance of potentially negative biotic (interspecific and intraspecific) interactions. Biotic rather than environmental factors are likely driving the spatial separations and activity patterns observed for intertidal invertebrates with overlapping niche spaces on sandy beaches.

Different species tailor surface activity periods to time of day, tides, moon phase, predation risk, sea conditions, and more (Colombini et al., 1994, Colombini et al., 1996, Colombini et al. 1998, Fallaci et al., 1996, Colombini et al., 2000, Lastra et al., 2010). At higher trophic levels, shorebirds spatially partition habitat use to reduce antagonistic interactions but also structure their foraging habits around tide level with species-specific foraging times in relation to low tide rather than time of day (Burger et al. 1977, Neuman et al. 2008). On southern California beaches, shorebirds feed using visual cues, tactile probing, and active foraging/gleaning for prey whose abundances fluctuate with the amount of wrack inputs and beach conditions (Dugan et al. 2003, 2008, 2013). Shorebirds opportunistically feed at all intertidal levels ranging from the dry upper beach, through the high tide strandline and into the swash zone (Lafferty 2001, Hubbard and Dugan 2003). While shorebirds feed across the intertidal zone, primarily along or below the high tide strandline where we found the greatest abundance of talitrid amphipods, it is unlikely that talitrid spatial patterning we observed is a mechanism of avoidance of shorebird predation. Rather, the nighttime surface activity observed across species may reduce predation threats from visual predators in addition to the lowering the desiccation risk associated with daytime surface activity.

Mobile species with larger body size likely have a competitive edge over smaller species, allowing them to occupy prime locations and time periods which maximize access to resources and limit risk factors, such as predation, cannibalism by adults on juveniles, and desiccation (Wallace and Temple, 1987, Woodward et al., 2005, Norkko et al. 2013). Interestingly, small juvenile *Megalorchestia* and the species with the smallest adult body size, *M. benedicti*, occupied the widest habitat distribution during both tide phases. While avoidance of negative biotic interactions may drive the observed spatial separation of all of these species during spring tides when more suitable habitat is available, such interactions (i.e. competition, predation, cannibalism (see Duarte et al., 2010)) may be acting on the smaller talitrid amphipod species as well as the juveniles of all species regardless of tide phase. This may push them into less suitable habitats and activity times to avoid competitive exclusion or predation by larger congeners across tide phases.

Our study results suggest that beach habitat loss and intertidal zone compression due to wave events, seasonal changes, El Niño, and sea level rise (Dugan et al., 2013, Vitousek et al., 2017), and coastal armoring (Dugan et al. 2008, Dugan et al. 2017, Myers et al. 2019, Jaramillo et al. 2021) has implications for habitat partitioning to avoid biotic interactions (Gilman et al., 2010). Future reductions of intertidal habitat area due to climate change may increase competitive exclusion, causing a loss of similar species and functional redundancy with consequent effects on biodiversity and ecosystem functioning. Competitive interactions in highly mobile intertidal species can be more challenging to observe than in sedentary or sessile taxa, but niche separation and coexistence of such species may depend on their mobility and ability to respond to changing environmental conditions. Such behavioral plasticity may not only mitigate the effects of changing environmental conditions (Colombini et al. 2013), but also alters the strength of biotic interactions on both temporal and spatial scales. Activity modifications due to circalunar rhythms by the invertebrate community at large may in fact be a mechanism of stabilization for the community and therefore a mechanism of coexistence (i.e. diversity of biological rhythm) (Mougi 2021). Our findings for talitrid amphipods are consistent with a strong role of biotic interactions in structuring the highly mobile intertidal communities of dynamic harsh ecosystems where physical factors have long been assumed to control community structure.

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Tables

Table 1: Mean time of activity (Pacific Daylight Time, UTC -07:00) with standard deviations and values of Rayleigh's Z (high values indicate clumped activity distributions, or relatively tight windows of peak activity observations) for *Megalorchestia californiana* (MCAL), *Megalorchestia corniculata* (MCOR), *Megalorchestia benedicti* (MEBE), and *Megalorchestia minor* (MEMI) and juvenile *Megalorchestia spp.* (J) during the neap and spring tide mesocosm experiments on Campus Point Beach and the neap and spring tide pitfall sampling on Goleta Beach. Values were calculated using the circular statistics program Oriana (v4).

	Neap Tide Mesocosm				**Spring Tide Mesocosm**			
	MCAL	MCOR	MEBE	MEMI	MCAL	MCOR	MEBE	MEMI
Mean	22:35	1:14	7:11	1:33	2:20	2:02	5:56	3:22
SD	1:28	3:01	4:51	3:34	2:56	1:54	3:53	3:18
Rayleigh Z	17.2	9.1	2.2	16.2	8.3	17.2	8.2	32.1

	Neap Tide Pitfall				**Spring Tide Pitfall**			
	MCAL	MEBE	MEMI	J	MCAL	MEBE	MEMI	J
Mean	22:18	10:34	14:37	23:36	0:12	6:58	2:39	0:26
SD	4:00	4:16	6:17	4:43	3:00	5:32	5:49	3:05
Rayleigh Z	31.0	9.1	2.8	56.2	77.2	5.7	4.5	384.2

Figure Captions

Figure 1: Location along the cross-shore beach profile (from bluff = 0 moving towards the ocean) where talitrid amphipods were burrowed during a neap (blue) and spring (gold) tide. The size of each circle corresponds to the number of individuals in the core sample at that location. The black diamonds represent the mean position of the species relative to the bluff. Vertical dashed lines represent the location of the high tide strandline on the neap (blue) and spring (gold) tide.

Figure 2: The mean number of surface active individuals (± SE) of *Megalorchestia californiana* (MCAL), *Megalorchestia corniculata* (MCOR), *Megalorchestia benedicti* (MEBE), and *Megalorchestia minor* (MEMI) observed at each hour in mesocosms during the a) neap and b) spring tides on Campus Point Beach that began at 6:00pm PDT and from pitfall trap samples every two hours (12 samples for the 24-hour period) during the c) neap and d) spring tide phase on Goleta Beach that began at 7:00pm PDT. The grey shading represents nighttime hours from sunset to sunrise.

Figures

Figure 1

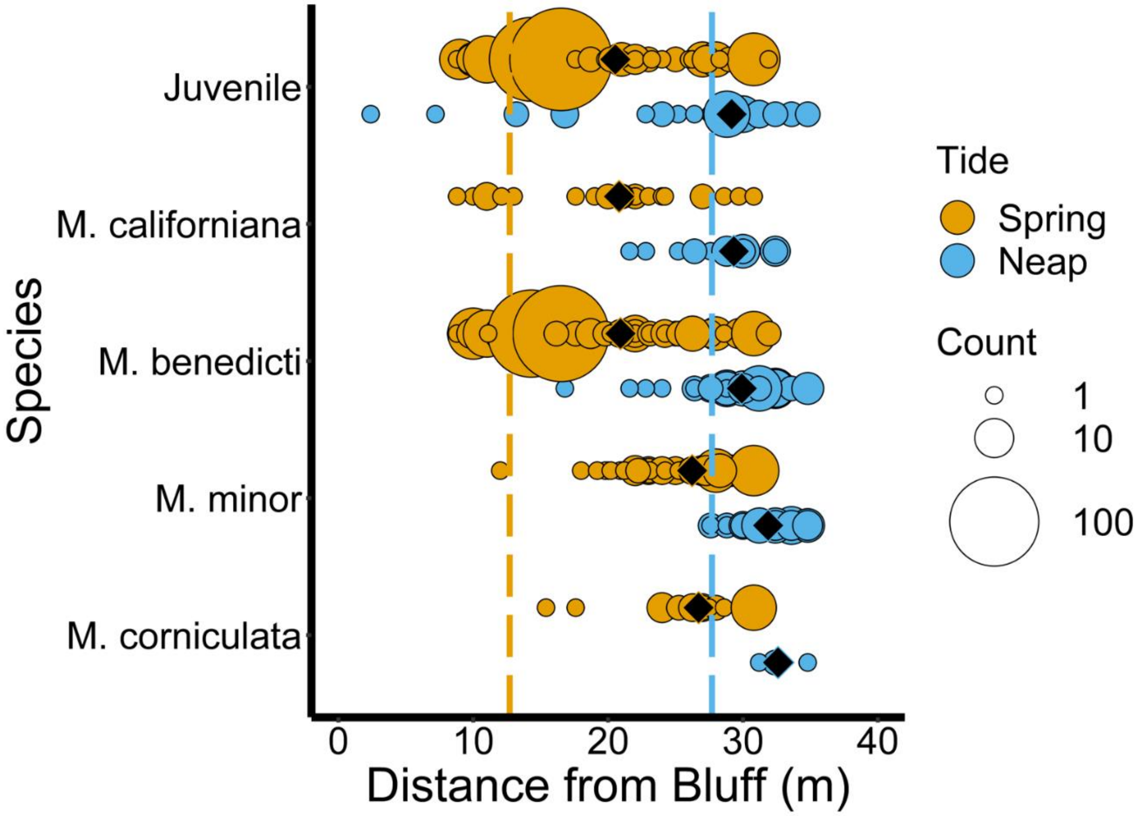
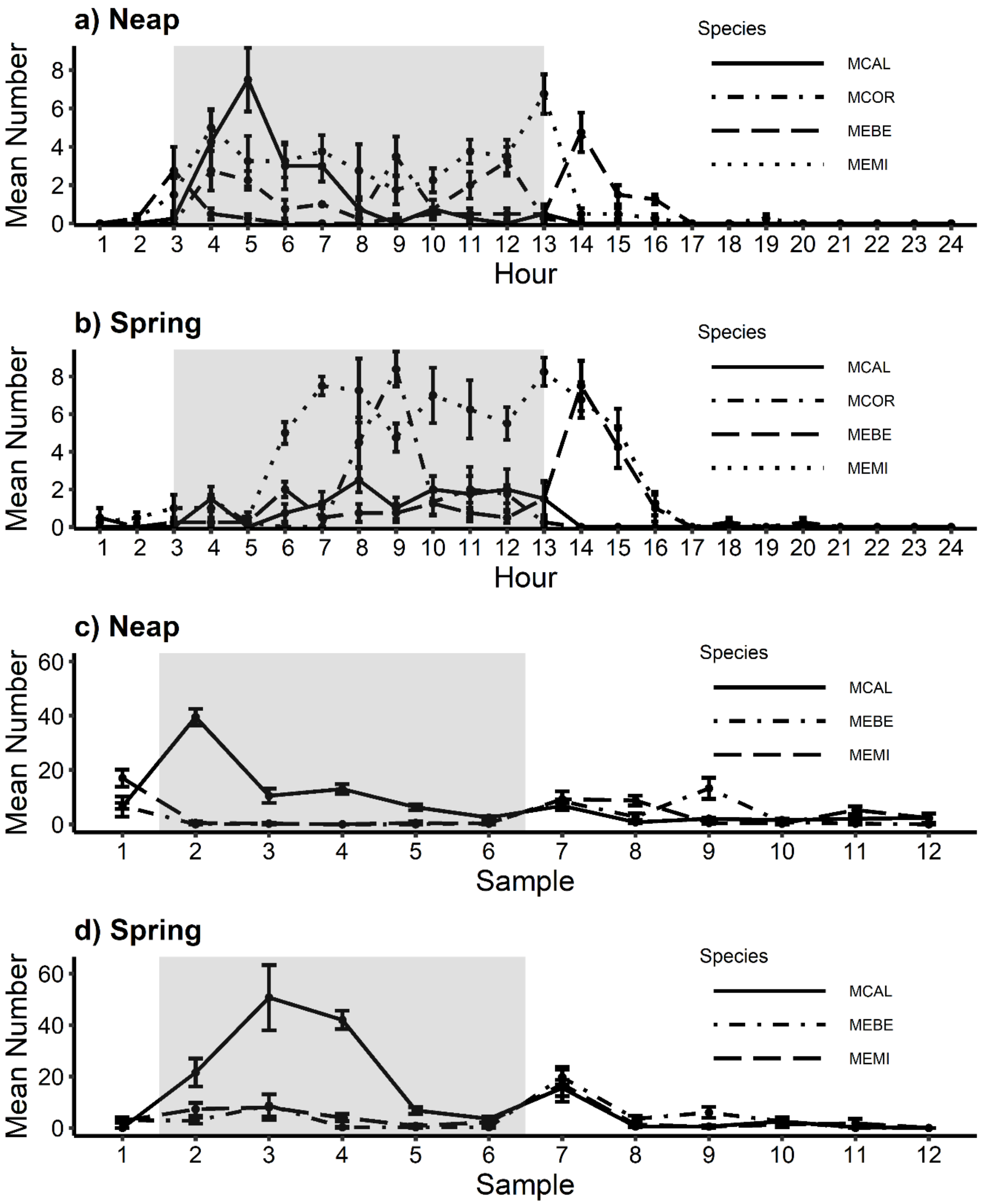


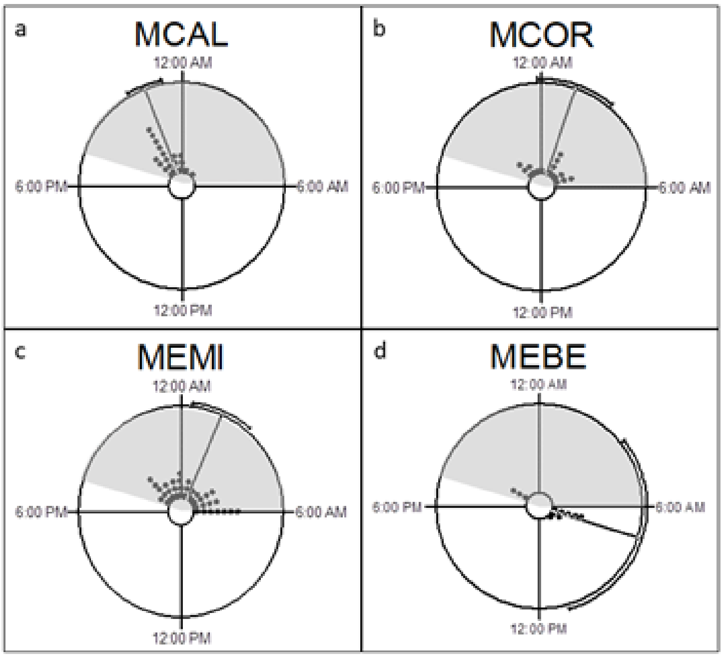
Figure 2


a) Neap
Mean Number
0
2
4
6
8
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
Hour
Species
MCAL
MCOR
MEBE
MEMI
b) Spring
Mean Number
0
2
4
6
8
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
Hour
Species
MCAL
MCOR
MEBE
MEMI
c) Neap
Mean Number
0
20
40
60
1 2 3 4 5 6 7 8 9 10 11 12
Sample
Species
MCAL
MEBE
MEMI
d) Spring
Mean Number
0
20
40
60
1 2 3 4 5 6 7 8 9 10 11 12
Sample
Species
MCAL
MEBE
MEMI

Supplemental Material

Figure S1: Mean time of activity with standard deviation for a) *Megalorchestia californiana* (MCAL) b) *Megalorchestia corniculata* (MCOR) c) *Megalorchestia minor* (MEMI) and d) *Megalorchestia benedicti* (MEBE) observed in mesocosms during the neap (top) and spring (bottom) tide on Campus Point Beach. Each black dot represents one individual observed. Grey shading represents nighttime hours.

Neap



Spring

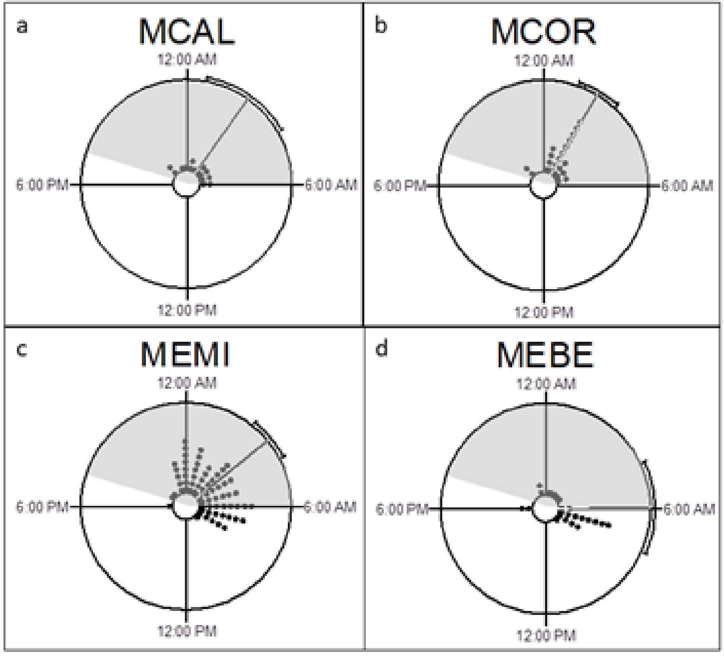
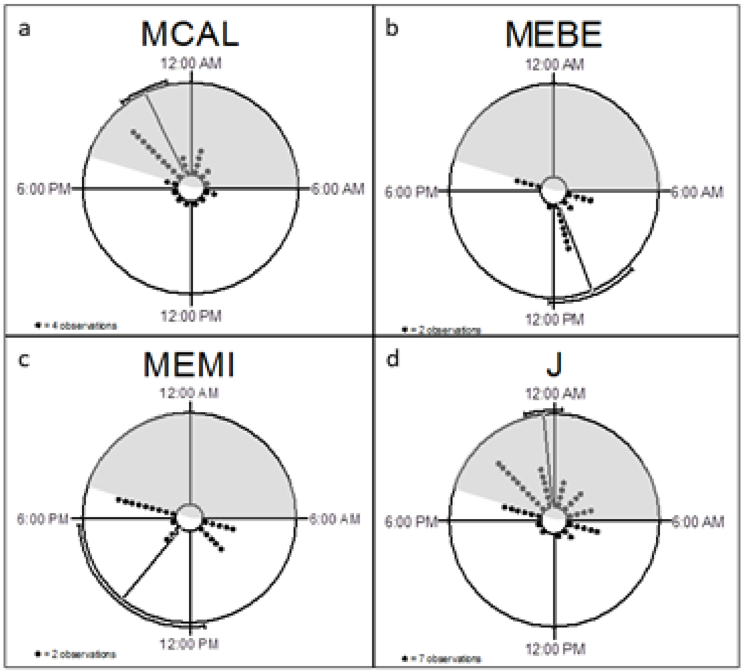
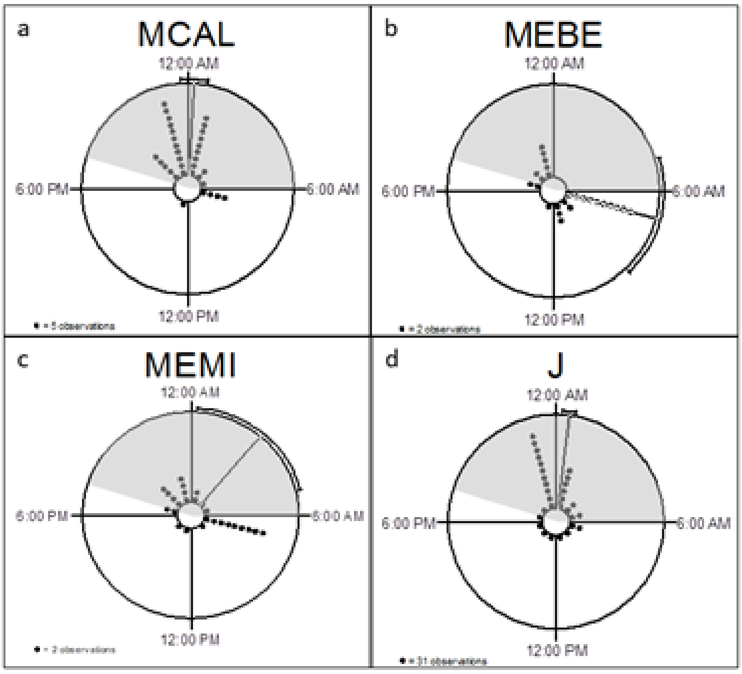


Figure S2: Mean time of activity with standard deviation for a) *Megalorchestia californiana* (MCAL) b) *Megalorchestia benedicti* (MEBE) c) *Megalorchestia minor* (MEMI) and d) juvenile *Megalorchestia spp.* (J) in pitfall trap samples during the neap (top) and spring (bottom) tide on East Goleta Beach. Each black dot represents the number of individuals observed based on the scaling factor provided in each panel. Grey shading represents nighttime hours.

Neap



Spring



Chapter II. Species identity drives ecosystem function in a subsidy-dependent coastal ecosystem

Authors

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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.

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 have focused on how species richness of plant communities affects primary production (Naeem et al. 1996; Reich et al. 2001; Cardinale et al. 2004; Cardinale et al. 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 & 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 nearshore 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} yr^{-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 & 6 species) were established in which the abundance of a given species decreased correspondingly to maintain the same total abundance (12, 6, 4, 3 &

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 x 17 cm x 9 cm) filled to ~6 cm depth with sieved (1.5mm) 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-hour high tide line where the densest aggregations of these intertidal wrack consumers are typically found. Fresh blades of giant kelp and live consumers were collected by hand on each morning the experiments were set up. Kelp blades were cut into square pieces of ~2g 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 hours, 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 minutes 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 3 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 hour 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 hours to obtain dry mass. The dried kelp was then ashed in a muffle furnace at 500˚C for four hours to obtain the ash weight of the unconsumed kelp plus any attached sand. Extensive rinsing of the unconsumed kelp would have removed 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:

$$B_f = B_T - S$$

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 ± 1.5% dry mass (6.0 ± 2.5 mg).

The consumers were collected from each treatment and frozen for 24 hours, after which they were rinsed, dried at 60˚C for at least 48 hours 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 Supplementary Material 1). 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 Supplementary Material 2.

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), the Tidyverse package (Wickham et al. 2019), multcomp (Hothorn et al. 2008), lme4 (Bates et al. 2015), and lmerTest (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 mg to 46.9 ± 2.5 mg, Figure 1a). Consumption rates of kelp varied over an order of magnitude and differed significantly among the six species in the single species treatments (Figure 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 six consumer species were driven by the two largest talitrid species (Supplementary Material 3). These two species, *Megalorchestia corniculata* and *M. californiana*, 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 average, 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 (>4x AFDW) in average body size (mean individual AFDW = 12.3 ± 0.3 mg and 2.7 ± 0.1 mg, respectively) (Figure 1a,b). The relationship between consumer biomass and kelp consumption rates was significant for the single species treatments ($n = 18$, $r^2 = 0.5$, $p < 0.001$, df = 1 and 16) and all treatments ($n = 171$, $r^2 = 0.15$, $p < 0.0001$, df = 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 consumption rate and species richness suggested a weak, albeit significant, negative effect of diversity on kelp consumption ($r^2 = 0.02$, $p = 0.05$) (Figure 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 consumption values and found that, on average species mixtures generally underperformed their expected kelp consumption rates by 24.6% (Figure 2b).

The suite of models adapted from Reiss et al. (2011) and Bailey and Reiss (2014) confirmed that species richness alone did not explain observed rates of kelp consumption (Table 1). The model results indicated that species 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 – 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 – 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 3,300 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 180-2,549 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 (Figure 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 (Figure 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 (Figure 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 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 (Figure 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; Dugan et al. 2011), other drift macroalgae and seagrasses, as well as carrion, are consumed by sandy beach invertebrates (Lastra et al. 2010; 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.

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Tables

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. 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 Appendix S1 for more model information.

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		

Figure Captions

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-significant 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*

Fig. 2 (a) Kelp consumption 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

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 Supplemental Material). (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)

Figures
Figure 1

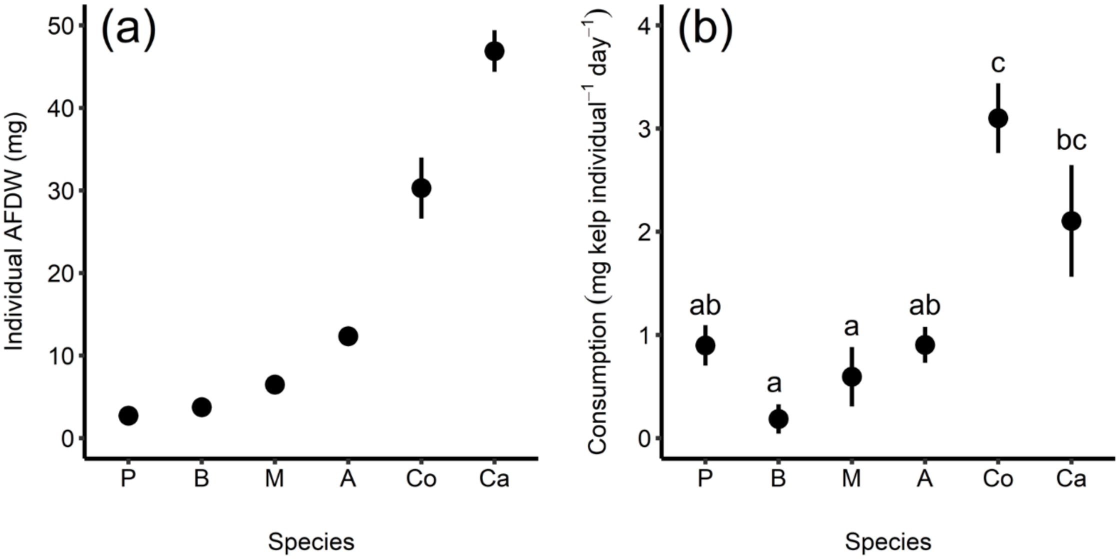


Figure 2

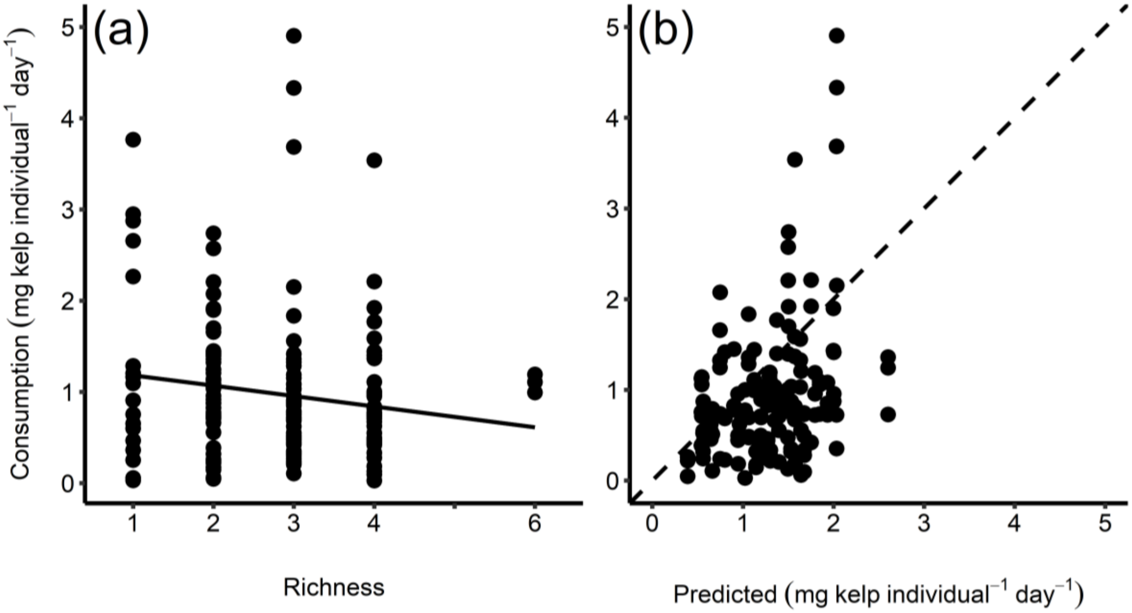
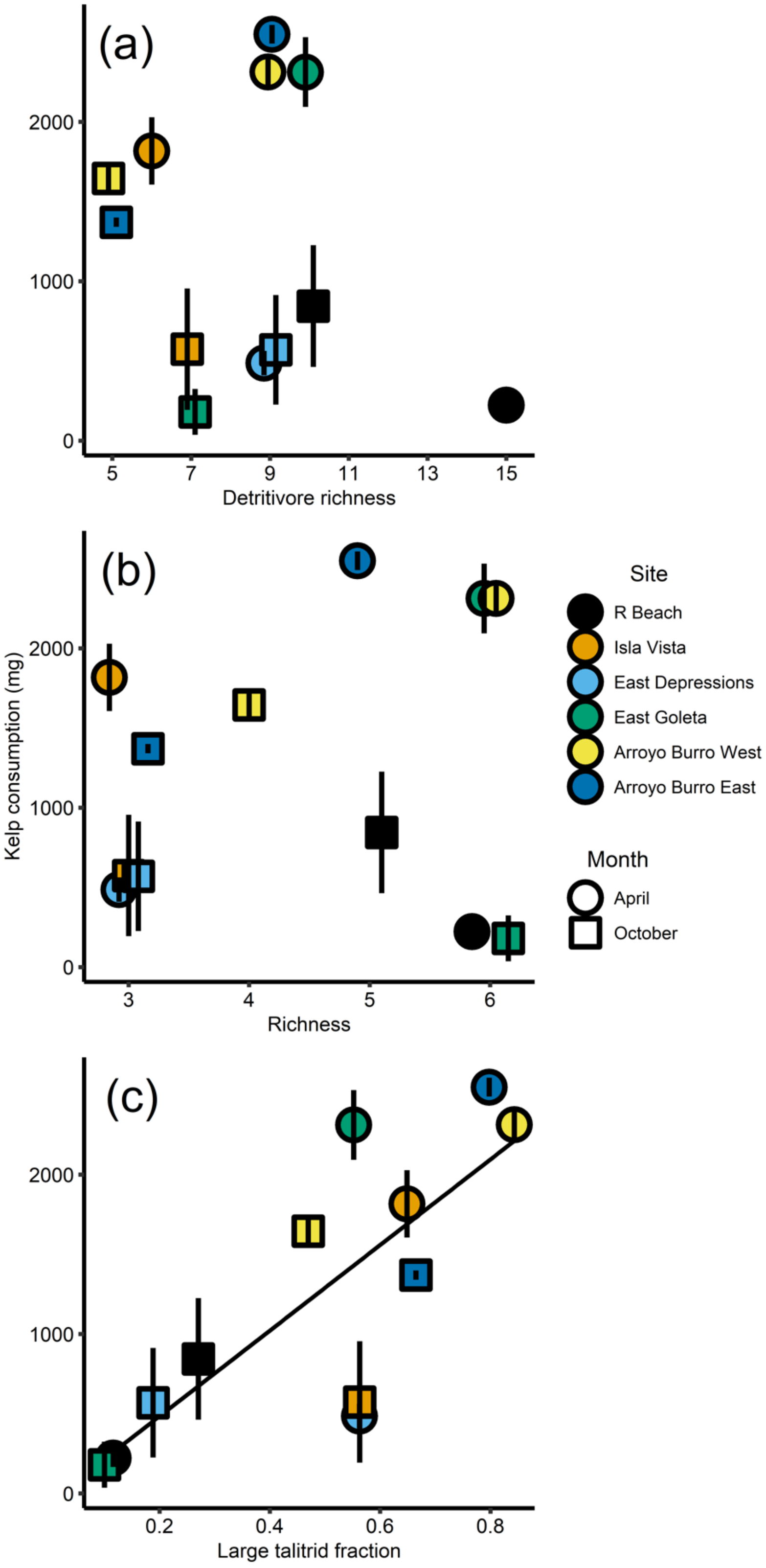

(a)
(b)
Consumption (mg kelp individual^{-1} day^{-1})
0
1
2
3
4
5
1
2
3
4
6
Richness
0
1
2
3
4
5
Predicted (mg kelp individual^{-1} day^{-1})

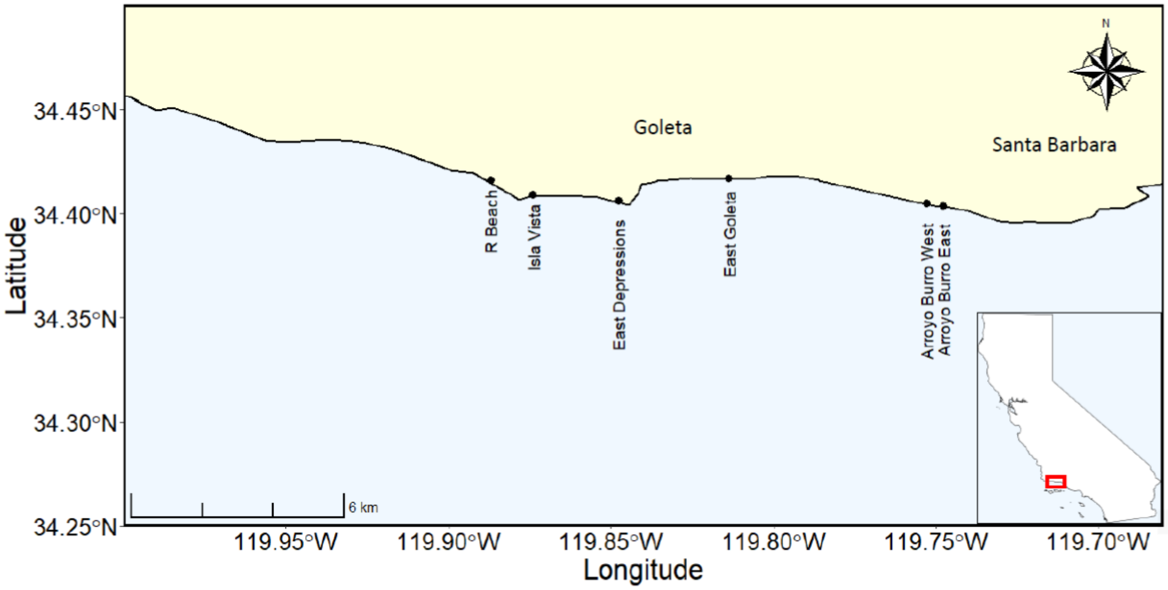
Figure 3



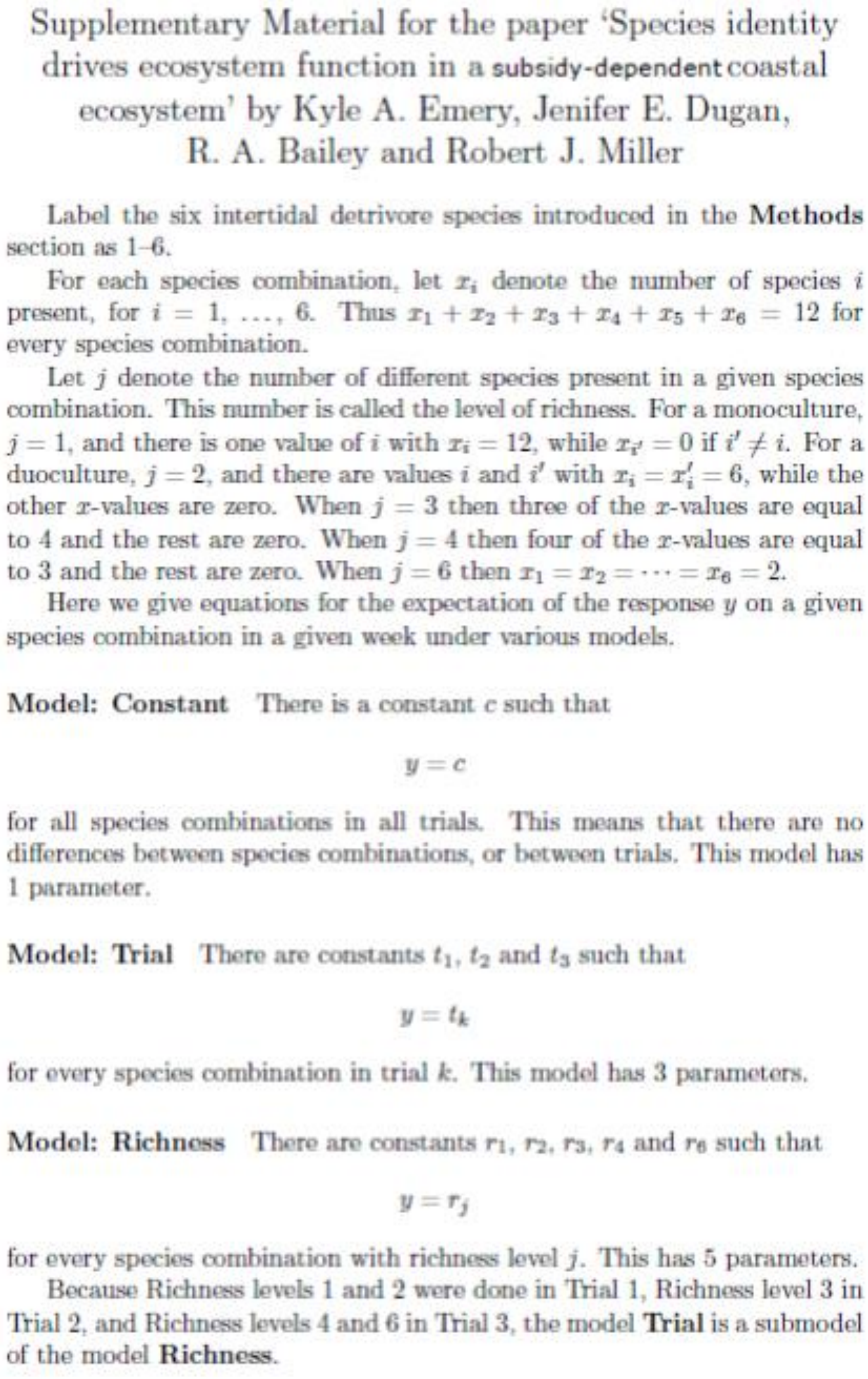
(a)
2000
1000
0
5
7
9
11
13
15
Detritivore richness
(b)
Kelp consumption (mg)
2000
1000
0
3
4
5
6
Richness
Site
R Beach
Isla Vista
East Depressions
East Goleta
Arroyo Burro West
Arroyo Burro East
Month
April
October
(c)
2000
1000
0
0.2
0.4
0.6
0.8
Large talitrid fraction

Supplementary Material

Supplementary Material 1: Site map of the field assay beaches.



Supplementary Material 2:



Supplementary Material for the paper 'Species identity drives ecosystem function in a subsidy-dependent coastal ecosystem' by Kyle A. Emery, Jenifer E. Dugan, R. A. Bailey and Robert J. Miller

Label the six intertidal detrivore species introduced in the **Methods** section as 1–6.

For each species combination, let x_i denote the number of species i present, for $i = 1, \ldots, 6$. Thus $x_1 + x_2 + x_3 + x_4 + x_5 + x_6 = 12$ for every species combination.

Let j denote the number of different species present in a given species combination. This number is called the level of richness. For a monoculture, $j = 1$, and there is one value of i with $x_i = 12$, while $x_{i'} = 0$ if $i' \neq i$. For a duoculture, $j = 2$, and there are values i and i' with $x_i = x_i' = 6$, while the other x-values are zero. When $j = 3$ then three of the x-values are equal to 4 and the rest are zero. When $j = 4$ then four of the x-values are equal to 3 and the rest are zero. When $j = 6$ then $x_1 = x_2 = \cdots = x_6 = 2$.

Here we give equations for the expectation of the response y on a given species combination in a given week under various models.

Model: Constant There is a constant c such that

$$y = c$$

for all species combinations in all trials. This means that there are no differences between species combinations, or between trials. This model has 1 parameter.

Model: Trial There are constants t_1, t_2 and t_3 such that

$$y = t_k$$

for every species combination in trial k. This model has 3 parameters.

Model: Richness There are constants r_1, r_2, r_3, r_4 and r_6 such that

$$y = r_j$$

for every species combination with richness level j. This has 5 parameters.

Because Richness levels 1 and 2 were done in Trial 1, Richness level 3 in Trial 2, and Richness levels 4 and 6 in Trial 3, the model **Trial** is a submodel of the model **Richness**.

Model: Identity There are constants a_1, a_2, a_3, a_4, a_5 and a_6 such that

$$y = a_1x_1 + a_2x_2 + a_3x_3 + a_4x_4 + a_5x_5 + a_6x_6$$

no matter what the level of richness or the trial. This has 6 parameters.

Model: Trial + Identity For every species combination in trial k,

$$y = t_k + a_1x_1 + a_2x_2 + a_3x_3 + a_4x_4 + a_5x_5 + a_6x_6.$$

This has $3 + 6 - 1 = 8$ independent parameters, because we can add 1 to every a_i and subtract 12 from every t_k without changing the result.

Model: Richness + Identity For every species combination with level j of richness,

$$y = r_j + a_1x_1 + a_2x_2 + a_3x_3 + a_4x_4 + a_5x_5 + a_6x_6.$$

This has $5 + 6 - 1 = 10$ independent parameters.

Model: Richness*Identity There are constants a_{ij} for $1 \leq i \leq 6$ and every level j of richness such that, for every species combination which has level j of richness,

$$y = a_{1j}x_1 + a_{2j}x_2 + a_{3j}x_3 + a_{4j}x_4 + a_{5j}x_5 + a_{6j}x_6.$$

Because there is only one species combination involving all six species, and $x_1 = x_2 = x_3 = x_4 = x_5 = x_6 = 2$ for this, we only need one constant for level 6 of Richness.

So there are $6 + 6 + 6 + 6 + 1 = 25$ independent parameters.

Model: Species Combination Each of the 57 species combinations gives a different expectation of y, with no simple explanation of the 57 different parameters.

Figure 1 shows the hierarchy of models that we considered. Each box shows one of the models. The number in each box shows the number of independent parameters for that model.

Following the convention in Figure S2 of Perkins et al. (2015), models in solid boxes are those which are not the sum of smaller models. Sometimes such models are called *irreducible*.

If one model is lower in the diagram than another and is joined to the higher one by a line, or an upwards path of lines, then it is a special case of the higher one. For example, the Constant model is a special case of the Identity model with $a_1 = a_2 = a_3 = a_4 = a_5 = a_6$.

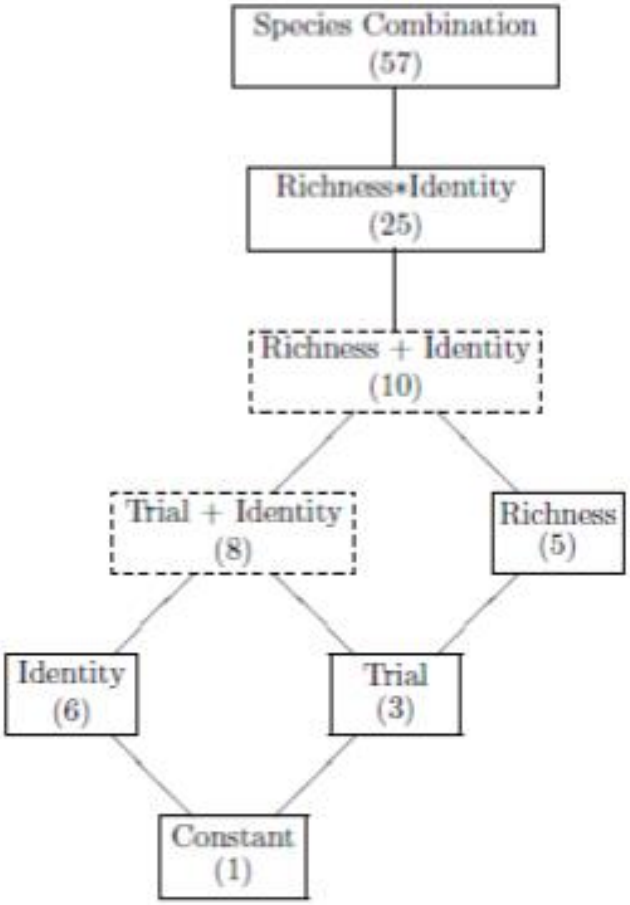


Figure 1: Hierarchy of models considered

This family of models gives the analysis-of-variance (ANOVA) table. This table includes only the irreducible models (but usually omits the Constant model). As explained by Reiss et al. (2011), each row of the ANOVA table corresponds not to a model but to the unique edge in the diagram that goes down from that irreducible model. The number of degrees of freedom shown in that row is the difference between the number of independent parameters for the model at the top of the edge and the number of independent parameters for the model at the bottom of the edge. In other words, it is the degrees of freedom for the extra information in the model at the top of the edge that is not contained in any smaller models.

Once we have the ANOVA table, hypothesis testing starts with the model with the largest number of parameters. At each stage, we consider the F-ratio for all edges leading downwards from the model that we are considering. If the F-ratio for an edge is small, then it is very likely that the simpler model at the bottom of that edge explains the data adequately, so we can move down that edge to that simpler model and carry on. If the F-ratio for an edge is big, then we cannot simplify to the smaller model at the bottom of that edge, so we do not do any further hypothesis tests below that. This procedure is explained by Grafen and Hails (2002).

For example, suppose that we are considering the model Richness∗Identity. The next simpler model is Richness + Identity, and the edge between them corresponds to the row of the ANOVA table labelled Richness∗Identity. That F-ratio is small, so we can simplify the model to Richness + Identity. Now there are two edges down. The edge between Richness + Identity and Richness corresponds to dropping Identity from the model, but the F-ratio for Identity is large so we cannot do that. The edge between Richness + Identity and Trial + Identity corresponds to dropping Richness, and the F-ratio for Richness is rather small so we can simplify the model to Trial + Identity. And so on.

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Supplementary Material 3: Results from the Tukey post-hoc test for the One-way ANOVA of detritivore species consumption rates for all six species in laboratory mesocosms. Comparisons in bold font are significant (*P* < 0.05).

Species Comparison			**95% Confidence Interval**	
All Detritivores	**Difference in Means**	**Significance**	**Lower Bounds**	**Upper Bounds**
M. Benedicti - M. minor	-0.41	0.93	-1.89	1.07
M. corniculata - M. minor	2.51	***0.00***	1.03	3.98
M. californiana - M. minor	1.51	***0.04***	0.03	2.99
A. perconvexus - M. minor	0.31	0.98	-1.17	1.79
P. rotundata - M. minor	0.30	0.98	-1.17	1.78
M. corniculata - M. benedicti	2.91	***0.00***	1.44	4.39
M. californiana - M. benedicti	1.92	***0.01***	0.44	3.39
A. perconvexus - M. benedicti	0.72	0.59	-0.76	2.20
P. rotundata - M. benedicti	0.71	0.60	-0.76	2.19
M. californiana - M. corniculata	-1.00	0.28	-2.47	0.48
A. perconvexus - M. corniculata	-2.20	***0.00***	-3.67	-0.72
P. rotundata - M. corniculata	-2.20	***0.00***	-3.68	-0.72
A. perconvexus - M. californiana	-1.20	0.14	-2.68	0.28
P. rotundata - M. californiana	-1.21	0.14	-2.68	0.27
P. rotundata - A. perconvexus	-0.01	1.00	-1.48	1.47

Chapter III. Sandy beach ecosystem CO_2 flux is driven by cross-ecosystem subsidies and consumer populations

Authors

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Abstract

Ecotones and the sharp environmental gradients they represent are often zones of high biodiversity and ecosystem functioning. Many of these crucial interface ecosystems are at risk for disproportionate impacts of climate change. Under increasing pressures from land and sea, shorelines exemplify this concern. Sandy beaches are shoreline ecosystems, where cross-ecosystem subsidies of marine wrack support diverse, productive food webs. We measured CO_2 flux from the beach to the atmosphere, a proxy for a key ecosystem function, and wrack decomposition, on 14 beaches of California's Channel Islands that varied greatly in wrack standing stock. At each site, we surveyed intertidal wrack and associated macroinvertebrates and measured sediment CO_2 flux at the high tide line where peak CO_2 flux is found on the study beaches. Wrack abundance (cover) varied by three orders of magnitude across sites (0.03 to 12 m^2 m^{-1}). Richness, biomass, and abundance of wrack-associated macroinvertebrates were positively correlated with wrack abundance and varied one (1 to 23 species), two (10 to 2248 g m^{-1}), and three (339 to 112,747 individuals m^{-1}) orders of magnitude, respectively. CO_2 flux was highly variable among sites, ranging from 0.05 to 1.2 g CO_2 m^{-2} $hour^{-1}$, and was strongly correlated with wrack abundance. Estimated rates of beach-scale respiration for macroinvertebrate wrack consumers, based on abundance and laboratory measured respiration rates, ranged from 8 to 449 mg CO_2 $hour^{-1}$ m^{-1}. The estimated fraction of beach CO_2 flux from wrack consumers varied from 0.6 to 28% among sites, averaging 10.5%. Our results demonstrate tight coupling of subsidies, intertidal consumers and ecosystem function on beaches, an ecosystem that is critically imperiled by rising sea levels and coastal development.

Introduction

Global environmental change, manifested through increasing temperatures, urbanization and development, sea level rise, and decreased biodiversity is negatively impacting ecosystems (Scavia et al. 2002, Parmesan and Yohe 2003, Pecl et al. 2017). To predict how an ecosystem may respond to change, it is imperative to understand how it functions under current conditions (Jochum et al. 2021). No terrestrial or aquatic system is immune from the effects of anthropogenic change and researchers are actively exploring how ecosystems respond (Kennedy 1995, Danovaro et al. 2001). Comparing aspects of biodiversity and ecosystem function in response to natural spatial variation can be a strong tool for predicting the effects of anthropogenic driven changes on ecosystems (Barnes et al. 2018). Variance in ecosystem functions or metrics across space can be substituted for variation over time and can be used to project the trajectories of an ecosystem function as conditions change (Blois et al. 2013, Lester et al. 2014, Frauendorf et al. 2020, Horrocks et al. 2020, Qiu and Cardinale 2020). For example, the temperature variation associated with montane elevation gradients has been used as a proxy for measuring the impacts of warming on important ecosystem functions, such as leaf litter decomposition (Faber et al. 2018) and stream nutrient uptake (Marti et al. 2009) and variation in invasive species distributions can be used to assess their impact on native species and communities (Thomaz et al. 2012).

Ecosystems in which areas of high biodiversity and ecosystem functioning are spatially concentrated may be more vulnerable to change and losses of these hotspots may have far greater proportional impacts to the ecosystem. One such example, especially prevalent at terrestrial-aquatic interfaces, are hotspots of enhanced biogeochemical activity relative to the rest of the system (McClain et al. 2003) creating locations of disproportionately high process rates compared to the rest of the ecosystem (McClain et al. 2003). Examples of hotspots include nutrient cycling hotspots driven by the patchy distribution of fish in streams (McIntyre et al. 2008), nutrient transformation hotspots by mussel aggregations (Atkinson and Vaughn 2015), plant diversity hotspots due to large ungulate carcasses (Bump et al. 2009), hotspots of leaf litter decomposition and denitrification in vernal pools (Capps et al. 2014), and increased biodiversity and sulfide production via chemosynthesis on whale fall carcasses (Baco and Smith 2003, Treude et al. 2009). These hotspots may be driven by consumers responding to the subsidy, further enhancing nutrient remineralization (McIntyre et al. 2008). While hotspots in an ecosystem generally describe functions or processes, they can also represent community-based hotspots, such as source populations of pelagic larvae (Leslie et al. 2005), changes in plant species composition (Collins and Xia 2015), areas of disproportionately high biodiversity (De Monte et al. 2013, Elsey-Quirk et al. 2019), regions of high metacommunity connectivity (Melia et al. 2016) and locations of functionally rare species (Grenie et al. 2018). Recently, the theory of ecosystem hotspots has evolved to “ecosystem control points” to better encompass the fact that these locations affect the dynamics of the entire ecosystem and that they are spatially and temporally dynamic (Bernhardt et al. 2017). These areas, whether related to function, biodiversity, or abundance are important to characterize as they may be more vulnerable to change and result in disproportionately greater losses.

Intertidal ecosystems may be particularly vulnerable to change because of the compounding effects of marine and terrestrial influences (Helmuth et al. 2006, Helmuth et al. 2011). Some intertidal ecosystems are uniquely vulnerable because of their inherent dependence on resources from other ecosystems (Schlacher et al. 2008, Krumhansl et al.

2014). Ecosystems with low primary productivity can be supported by cross-ecosystem subsidies of organic matter (Polis et al. 1997) which may increase the flux of re-mineralized compounds at the system level (Lennon 2004). Cross-ecosystem exchange of organic matter is ubiquitous, links coastal systems, and structures the food web (Liebowitz et al. 2016, Gounand et al. 2018, Emery et al. Chapter 4). Changes to the donor or recipient ecosystem can therefore negatively impact diversity and functioning in the recipient ecosystem (Krumhansl and Schiebling 2012, Schooler et al. 2017). Sandy beaches are a prime example because of their low *in situ* primary productivity and high dependence on marine macrophyte wrack, utilized by various organisms for food and habitat (Dugan et al. 2003, Lastra et al. 2008, Michaud et al. 2019). On sandy beaches, the high tide strandline is the primary deposition zone and a hot spot of ecosystem functions (i.e. biogeochemical processes) and the primary habitat and foraging zone of upper beach macroinvertebrates, shorebirds and small mammals (Colombini and Chelazzi 2003, Dugan et al. 2011, Dugan and Hubbard 2013, Schlacher et al. 2017, Page et al. 2021, Hyndes et al. In Preparation). This zone is particularly vulnerable to management practices (armoring, grooming) and climate change impacts (Schooler et al. 2019, Vousdoukas et al. 2020, Barnard et al. 2021, Jaramillo et al. 2021). For example, projections for California predict the loss of this upper beach zone for many beaches by 2050 and full beach erosion for much of the coastline by 2100 (Vitousek et al. 2017, Myers et al. 2019, Barnard et al. 2021).

The remineralization of wrack to its inorganic components is carried out through several pathways including shredding and consumption by detritivores and microbial decomposition/activity. Macroalgal wrack acts as a hot spot with higher levels of beach to atmosphere CO_2 fluxes than bare sand, which is attributed primarily to microbial activity

(Gomez et al. 2018). The type of macroalgal wrack also has an impact on both CO_2 flux and nutrient remineralization (Rodil et al. 2019). In addition, global warming is likely to enhance to CO_2 and nutrient release from wrack on beaches (Lastra et al. 2018, Lastra et al. 2020). The flux of CO_2 from wrack in field observations is highest along the high tide strandline, where it does not dry but rather is re-wetted by tides and waves (Liu et al. 2019). CO_2 flux also varies with wrack composition and patch size with greater values in mixed species wrack deposits and in thicker wrack deposits (Coupland et al. 2007). With respect to fauna, macroinvertebrates process wrack through consumption (Lastra et al. 2008, Emery et al. 2021), which enhances nutrient remineralization compared to wrack decomposition in the absence of consumers (Lowman et al. 2019). CO_2 flux on sparsely populated beaches is low and predominantly associated with microbial activity (Spilmont et al. 2005). Still, experimental wrack patches permitting or excluding macrofauna estimated their contribution to be ~20% of the total CO_2 flux (Gomez et al. 2018).

In this study, we hypothesized that beach-scale sediment CO_2 flux on sandy beaches would increase along a natural gradient in wrack cover. We also expected macroinvertebrate detritivores to significantly contribute to CO_2 production when abundant. To test these hypotheses, we measured CO_2 flux and surveyed wrack cover and macroinvertebrate communities on sandy beaches on four of California's Channel Islands. Channel Islands beaches are highly remote and generally have little to no direct impact from humans compared to mainland California beaches. We measured respiration rates for common and abundant wrack-associated macroinvertebrates in the laboratory and used these values to estimate their contribution to the total beach-scale CO_2 flux.

Methods

Study Sites and Survey Schedule

We surveyed 14 sandy beaches on four of the California Channel Islands (Figure 1). Surveys were conducted in September 2016, 2017, and 2018 for Santa Rosa Island (33.98 N, -120.10 W), October 2016 and August 2017 and 2018 for Santa Cruz Island (34.01 N, -119.77 W), November 2017 and October 2018 for San Miguel Island (34.04 N, -120.37 W) and October 2018 for Catalina (33.39 N, -118.43 W). Summer and fall are representative periods of maximum beach width, wrack cover, and macroinvertebrate populations prior to winter storm-driven erosion.

Field and Laboratory Measurements

At each study site we measured marine wrack cover, macroinvertebrate richness, abundance, and biomass on three shore-normal transects (five transects for Santa Rosa Island surveys) from the back-beach limit (cliff base, dunes, etc.) to the upper swash limit within two hours of low tide. Wrack cover was measured using a line intercept method and averaged for each site visit (Dugan et al. 2003). Upper beach macroinvertebrates were sampled by taking two sets of 10 aggregated sediment cores per transect (not sampled during 2018 San Miguel Island survey due to unexplode ordinance risk). The first set of ten cores were evenly spaced from the back-beach limit to the top of the talitrid amphipod burrow zone. The second set of cores were evenly spaced from the top to the bottom of the talitrid amphipod zone. Talitrid amphipods are generally the most abundant upper beach organism and burrow the lowest on the beach face of the wrack-associated species. Each set of 10 cores was aggregated and sieved through a 1.5mm mesh bag in the surf zone, transferred to one-gallon Ziplock bags and frozen. In the laboratory samples were sorted and organisms identified mostly to species level, counted, and weighed to the nearest mg wet weight and averaged for each site visit.

We took five sediment CO_2 flux measurements at each site on the 24-hour high tide line using an EGM-5 Portable CO_2 Gas Analyzer with an SRC-2 Soil Respiration Chamber and collars (PP Systems, Amesbury, MA, USA). Measurements were taken along the high tide strandline because this zone of the beach is the most biologically active (fresh wrack deposition, highest macroinvertebrate abundance) and we found that above this zone the sand is dry and has little to no flux and below this zone the sand is saturated and also has little to no CO_2 flux (Supplementary Figure 1). For each measurement, the chamber was flushed air by holding it upright for 25 seconds, placed on the collar and equilibrated for 10 seconds, and then run for 180 seconds to produce an integrated linear respiration rate (g CO_2 m^{-2} $hour^{-1}$). We calculated the mean respiration rate for each site visit. These rates reflect net ecosystem metabolism measurements and in all cases were net fluxes out of the beach, there was no net uptake of CO_2.

Based on the abundance of wrack consumer species in the sediment core samples, we chose the most common and abundant species to make laboratory measurements of species-specific respiration rates to explore differences across species and the potential contribution of these species to the net respiration rates measured on the study beaches. Six adult-sized individuals were run for each species. Two isopod species (*Alloniscus perconvexus* and *Tylos punctatus*), a beetle (*Phaleria rotundata*), and four talitrid amphipods (*Megalorchestia californiana*, *M. corniculata*, *M. benedicti*, and *M. minor*) were collected on beaches in Santa Barbara County, California, USA and analyzed within 24 hours of collection.

Respiration rates of each species were estimated using stop-flow respirometry. Eight respirometry chambers, consisting of 50 cc plastic syringes, were connected to the system for each testing period. The system was set up with push-mode plumbing where airflow stemmed from a compressed air canister, which contained a mixture of gas equivalent to normal atmospheric air, and was passed through mass flow controllers (Sierra Series 830 Mass Flow Controller; Sierra Instruments, Monterey, CA, USA) that maintained airflow at a constant rate of 60 mL min^{-1}. Two scrubber columns, consisting of two layers of Drierite separated by a layer of Ascarite (II), were placed upstream from the respirometry chambers. The airflow was distributed to the chambers by way of a multiplexor, which split the airflow between each chamber (RM8 multiplexor, Sable Systems, Inc., Las Vegas, NV, U.S.A.), as well as directing another channel of air to the reference cell of a CO_2 analyzer ((LI-7000, LI-COR, Lincoln, NE, U.S.A.). Airflow through each of the eight respirometry chambers was switched automatically by programming the multiplexor to a period of 8 minutes per chamber, except for a control chamber that was opened for 90 seconds. While each chamber received airflow, CO_2 levels (ppm) were recorded with the LI-COR analyzer once per second. The respirometry system was flushed with atmospheric air for 10 minutes before and after each recording.

The analyzer was calibrated daily before the experiment began and displayed consistent baseline levels (> six weeks) and was calibrated weekly during the experiment to check for any drift in the measurements. Nitrogen gas was used as a reference gas along with 100 ppm CO_2 span gas to calibrate the analyzer to the proper measuring scale and to regularly test the instrument’s accuracy. The total volume of CO_2 gas (ppm) in each chamber was recorded using Expedata v.1.1.18 (SSI). The respirometry chambers were cleaned after every test with a solution of isopropyl alcohol before being rinsed and dried. The temperature of the room was recorded during all testing periods using a thermistor probe placed directly outside the respirometry chambers. All respirometry trials were performed at room temperature (mean 20.62°C; 19.15 - 21.92°C range) under natural light conditions. Following these measurements, individuals were frozen and later measured for dry weight (drying oven, 48 hours at 60ºC) and ash-free dry weight (loss on ignition, 4 hours at 500ºC) to the nearest mg.

Out of the eight respirometry chambers, six were dedicated to measure the respiration rates of individual organisms, and two were left empty every measurement period. The first (control-1) served as a control to ensure measured CO_2 volumes were not changed by outside factors at any point during the recording, and thus was measured with the same eight minutes of open flow as the six test chambers containing. The other empty respirometry chamber (control-2) provided a baseline CO_2 level for the recording, quantifying any background levels of CO_2 that might inflate the final respiratory rate values of individuals in the other chambers. The CO_2 levels of the control-2 chamber were recorded for 90 seconds before and after each of the other chambers. Within each respirometry trial, the amount of CO_2 gas (ppm) produced by each individual and the background control chamber was recorded once every 68 minutes, with the six chambers holding animals and control-1 open to gas flow for eight minutes, and the baseline chamber (control-2) open for 90 seconds at regular intervals between the other chambers.

Data Analysis

We used ordinary least squares (OLS) linear regression to explore the relationship between mean macrophyte wrack cover ($m^2\ m^{-1}$) and beach CO_2 flux (g $CO_2\ m^2\ hour^{-1}$).

Next, we established a relationship between macrophyte wrack cover and total site macroinvertebrate species richness. We then compared total species richness to both log-transformed mean abundance of upper beach macroinvertebrates (individuals m^{-1}) and to beach CO_2 flux. Next, we tested for relationships between CO_2 flux and log-transformed mean upper beach macroinvertebrate abundance and biomass (g m^{-1}). Lastly, we utilized linear mixed effects models fit by maximum likelihood to compare a model of CO_2 flux with air temperature, upper beach width, wrack cover, species richness, and abundance as fixed factors and site nested within year as random factors to a null intercept model with the same random factors (Zurr 2009). Analyses were conducted with R (R Core Team 2020) and the Tidyverse (Wickham et al. 2019), and nlme (Pinheiro et al. 2021) packages.

The stop-flow respirometry setup meant that the raw output of CO_2 (ppm) as measured by the LI-COR analyzer represented the total volume (i.e. build-up) of CO_2 gas in each chamber after a 68-minute period. The raw measures of CO_2 (ppm) produced by each individual were converted to CO_2 (mL) using the transformation and macro utility tools in Expedata v.1.1.18 (SSI). The rate of CO_2 produced per minute (VCO_2; mL CO_2 min^{-1}), a proxy for respiration rate, was then calculated by taking the area (the volume of CO_2) under each CO_2 curve measured for each eight minute window of time in which the CO_2 output of each individual was measured. The volumes of CO_2 gas recorded in the animal chambers and control-1 were then standardized by averaging the 90 second control (control-2) chamber values to obtain a common baseline for each 68-minute testing interval. This baseline was applied to each of the integrated VCO_2 curves using the macro utility tool in Expedata v.1.1.18 (SSI). The first two hours of respiration rate measurements were discarded to allow for animal acclimation to the measurement system. Rate measurements, calculated from the baseline-corrected VCO_2 (mL CO 2 min^{-1}) values from the third hour, were averaged for the 6 replicates per species to produce mean species respiration rates. We aggregated talitrid amphipod respiration rates across species to develop a genus-level respiration rate. We used OLS linear regression to develop a model of respiration rate (mg CO_2 $hour^{-1}$ $individual^{-1}$) against log-transformed ash-free dry weight (mg).

Next, we scaled our laboratory-based species respiration rate measurements to whole-beach rates based on the biomass of the seven detritivore species. For each species, beach scale estimates of biomass (dry mg m^{-1}) were multiplied by the respective respiration rates (mg CO_2 $hour^{-1}$ dry mg^{-1}) to obtain estimates of total detritivore respiration (mg CO_2 $hour^{-1}$ m^{-1}). To place these values into an ecosystem-level context, we estimated the proportion of our beach scale measurements of CO_2 flux that can be attributed to these seven highly abundant detritivore species. As most of the beach CO_2 flux occurs in talitrid amphipod zone along the high tide strandline and above and below this zone CO_2 flux rapidly declines (Supplementary Figure 1), we scaled our CO_2 measurements to the size of this active zone by multiplying the flux rate by the width of this zone for each beach. Then, we estimated the proportion of this flux that could be attributed to the consumer species by dividing the beach-scale CO_2 flux rate by the estimated consumer CO_2 flux rate.

Results

Marine macrophyte wrack abundance (cover) varied across three orders of magnitude across all beaches and surveys (0.03 to 12.0 m^2 m^{-1}, Table 1). Similarly, the abundance and biomass of upper beach macroinvertebrates varied across three (339 to 112,747 individuals m^{-1}) and two (10.4 to 2247.7 g m^{-1}) orders of magnitude, respectively. Total species richness of upper beach macroinvertebrates varied from 1 and 23 species among sites. Measurement of CO_2 flux made along the high tide strandline were also highly variable across our surveys and ranged from 0.05 to 1.2 g CO_2 m^{-2} $hour^{-1}$ (Table 1). We found a strong linear relationship between our *in situ* measures of beach CO_2 flux and wrack abundance (Figure 2, $R^2 = 0.60$, $p < 0.0001$). Wrack abundance and the species richness of upper beach macroinvertebrates were tightly coupled across island beaches (Figure 3, $R^2 = 0.48$, $p < 0.0001$). There was also a strong positive relationship between species richness and log-transformed abundance for upper beach macroinvertebrates (Figure 4A, $R^2 = 0.40$, $p < 0.0001$). With respect to CO_2 flux, we found a significant relationship between species richness of upper beach macroinvertebrates and CO_2 flux (Figure 4B, $R^2 = 0.32$, $p < 0.001$). Relationships between CO_2 flux and both log-transformed abundance and biomass of upper beach macroinvertebrates were weaker ($R^2 = 0.13$, $p = 0.04$, $R^2 = 0.12$, $p = 0.05$, respectively). Results of a linear mixed effects model considering air temperature, upper beach width, wrack cover, and species richness and abundance of macroinvertebrates as fixed factors and site nested within year as random factors explained significantly more variation in CO2 flux than the null model of only random factors (ANOVA, Likelihood Ratio = 37.34, $p < 0.0001$) and identified marine wrack cover as the primary driver of CO_2 fluxes (LME, t-value = 4.53, $p = 0.0001$).

Laboratory measured respiration rates for seven upper beach macroinvertebrate detritivore species (n = 6 adults per species) varied more than an order of magnitude among species, yielding values of 0.17 ± 0.01 (standard error) mg CO_2 $hour^{-1}$ for *Megalorchestia corniculata*, 0.15 ± 0.02 mg CO_2 $hour^{-1}$ for *M. californiana*, 0.05 ± 0.01 mg CO_2 $hour^{-1}$ for *M. minor*, 0.04 ± 0.01 mg CO_2 $hour^{-1}$ for *Alloniscus perconvexus*, 0.03 ± 0.01 mg CO_2 $hour^{-1}$ for *Tylos punctatus*, 0.02 ± 0.001 mg CO_2 $hour^{-1}$ for *M. benedicti*, and 0.01 ± 0.001 mg CO_2

$hour^{-1}$ for *Phaleria rotundata* (Figure 5A, Supplementary Figure 2). Talitrid amphipods, *Megalorchestia* spp., are typically the most abundant upper beach macroinvertebrate across southern California, and two or more species coexist on many beaches. We found that respiration rates are a strong function of body size at the genus level (Figure 5B, $R^2 = 0.91$, $p < 0.0001$). *Megalorchestia spp.* CO_2 flux (mg CO_2 $hour^{-1}$) can be calculated as:

$$y = -0.076 + 0.142x$$

where y is CO_2 flux and x is log-transformed individual ash-free dry weight (mg).

We used the laboratory measured respiration rates and field measurements of population biomass for these seven species of detritivores at each site, to estimate their cumulative contribution to CO_2 flux rates for each site (Figure 6). Mean beach-scale respiration rates for the community of detritivore species ranged from 7.7 to 449.4 mg CO_2 $hour^{-1}$ m^{-1} shoreline. It was dominated by the isopods *Tylos punctatus* and *Alloniscus perconvexus* and the beach hopper *Megalorchestia minor* on island beaches to the south and east (Catalina Island and Santa Cruz Island). On the remaining beaches to the west (Santa Rosa Island and San Miguel Island) consumer respiration was dominated by beach hoppers, predominantly *Megalorchestia californiana*, *Megalorchestia corniculata*, and juveniles. With these consumer respiration rates, we estimated the fraction of beach ecosystem-scale CO_2 flux that could be attributed to the abundant wrack-associated macroinvertebrates and found high site variability, ranging from 0.6% to 27.9% with an overall mean of 10.5% (Figure 7).

Discussion

The standing stock of marine wrack was highly variable across our study beaches and was a strong predictor of sediment CO_2 flux. Wrack abundance was also a strong driver of species richness for upper beach macroinvertebrates, many of which are detritivores that feed on wrack. Species abundance and sediment CO_2 flux increased with species richness of these intertidal macroinvertebrates, indicating potential functional linkages between wrack cover, macroinvertebrate community dynamics, and sediment CO_2 flux. Wrack detritivores functionally operate as the shredders of the beach and can enhance the availability of wrack to meiofauna and microbes, promoting greater total decomposition and respiration of organic matter (Wallace and Webster 1996, Graca 2001, Carlisle and Clements 2005). Increased detritivore abundances, as opposed to predators, can enhance ecosystem CO_2 flux and said flux directly originates from the consumed detrital organic matter (Atwood et al. 2014, Ouyang et al. 2021). Such a relationship would be a direct indicator of an important ecosystem function on sandy beaches, wrack processing, which is primarily driven by the consumptive processes of organisms from microbes (Koop et al. 1982, Rodil et al. 2015) to macroinvertebrate detritivores (Lastra et al. 2008, Michaud et al. 2019, Emery et al. 2021).

Consumer respiration rates scaled to the beach-level indicated that the dominant contributor to ecosystem-scale CO_2 varied among island sites. However, as with wrack consumption rates (Emery et al. 2021), individuals of the two largest talitrid species have much higher respiration rates. Assuming equal abundances, the functional role of these species relative to the other common detritivores cannot be understated and highlights the importance of considering species identity and functional roles in conservation planning (Henderson et al. 2019, Schenone and Thrush 2020, Hines and Eisenhauer 2021). The relationships between macrophyte wrack cover, macroinvertebrates, and CO_2 flux indicate the important role of wrack as a basal resource for the beach food web and the strong response by macroinvertebrates and associated ecosystem functions (Emery et al. Chapter

4). Our results indicated that upper beach macroinvertebrate wrack consumers likely contribute 10.5% of the ecosystem-level CO_2 flux. By considering the ecological community at large, we can make more informed and constrained ecosystem-scale flux estimates and prepare to identify and assess the effects of global climate change (Barnes et al. 2018, Jochum et al. 2021).

The range of mean CO_2 flux rates observed in our study on bare sand (n = 34 observations) (0.05 to 1.18 CO_2 flux (g CO_2 m^{-2} h^{-1}) were comparable to sparse examples of *in situ* sediment CO_2 flux rates from sandy beaches (Table 2). For wrack strewn beaches in southwestern Australia, values of 0.16 g CO_2 m^{-2} h^{-1} on bare sand and 1.05 g CO_2 m^{-2} h^{-1} directly through wrack were similar to our flux measurements (Coupland et al. 2007). Experimental studies that measured the sediment CO_2 flux rate directly through wrack patches placed on the beach ranged from 0.03 to 0.71 g CO_2 m^{-2} h^{-1} (Table 2) (Gomez et al. 2018, Lastra et al. 2019, Rodil et al. 2019). Extensive *in situ* ecosystem metabolism studies exist for other soft-sediment intertidal, including seagrass meadows, salt marshes, and mangrove forests, both during submersion and emersion, and often in the context of blue carbon budgeting (Leopold et al. 2015, Berger et al. 2020, Xiao et al. 2020). CO_2 flux rates from salt marsh (Morris and Whiting 1986, Magenheimer et al. 1996, Ford et al. 2012, Martin et al. 2018), tidal flat (Sasaki et al. 2012, Migne et al. 2016) and mangrove (Kristensen et al. 2008, Bulmer et al. 2015, Leopold et al. 2015) sediments measured during emersion were of the same or within one order of magnitude of the rates measured in this study. Sediment CO_2 flux rates in our highly subsidized ecosystem were higher than most sandy beach measurements but comparable to systems with generally high levels of detritus, like salt marshes and mangroves. The magnitude of sandy beach sediment CO_2 fluxes is comparable to other soft sediment coastal ecosystems (Table 2) and directly related to detrital inputs (This study, Lastra et al. 2020).

We found that respiration by the most common and abundant species on our study beaches, wrack detritivores, likely comprises ~10% of the sediment CO_2 flux. A macrofaunal exclusion experiment on sandy beaches in Portugal estimated a 20% contribution to CO_2 flux (Gomez et al. 2018). Burrowing invertebrates are important contributors to CO_2 fluxes across intertidal ecosystems due to bioturbation enhancement of organic matter remineralization (Alkemade et al. 1992). The presence of fiddler crab (*Uca* spp.) burrows plus respiration from occupied burrows greatly increase the CO_2 flux from intertidal mangrove sediments (Kristensen et al. 2008). Similarly, in salt marshes, crabs increased the flux of CO_2 from intertidal sediments (Guimond et al. 2020, Xiao et al. 2021). Evidence from other ecosystems echoes the important role of macroinvertebrates with respect to greenhouse gas fluxes. Litter decomposers from forest ecosystems increased soil CO_2 flux by 18% (Collison et al. 2013) and ant mounds contributed 7% of total marsh wetland CO_2 flux (Wu et al. 2013). In urban wetlands, each doubling of invertebrate densities increased methane and carbon dioxide fluxes by 42% and 15%, respectively (Mehring et al. 2017). Benthic macrofauna increase methane fluxes by 8-fold and account for 9.5% of total Baltic Sea methane emissions (Bonaglia et al. 2017). In sandy coastal sediments, the presence of a burrowing polychaeta resulted in a 50% increase in CO_2 release (Tang and Kristensen 2007). In Antarctica, the dominant soil invertebrate responsible for 2 – 7% of soil CO_2 flux is rapidly declining in abundance due to climate warming and the implications of losing this dominant species with respect to ecosystem functioning in such a low-diversity system may be significant (Barrett et al. 2008, Henderson et al. 2020). As with other ecosystems, most of the sediment CO_2 flux from sandy beaches is likely emanating from microbial respiration of wrack, although meiofanua may also significantly contribute (Jedrzejczak 2002, Colombini and Chelazzi 2003, Gomez et al. 2018). Still, it is important to highlight that the detritivore consumer guild is an important contributor to the total overall flux and likely facilitate microbial respiration (Gomez et al. 2018).

Ecosystem functioning on sandy beaches is tightly coupled to marine subsidies and the incorporation of subsidies into the food web (Emery et al. Chapter 4). Because of the dynamic nature of this ecosystem, we expect large fluctuations in functioning with spatial and temporal variation in habitat, wrack inputs, and invertebrate populations. This is especially true of the upper beach zone, the area from the high tide strand line to the upper beach limit (i.e. cliff or dune base), where deposition and retention of wrack subsidies predominantly occurs. Here, wrack subsidies strongly influence community structure increasing biodiversity, abundance, and biomass of macroinvertebrates and drive many ecological processes including prey for shorebirds and other vertebrates, secondary productivity, and nutrient regeneration in this relatively narrow strip of intertidal habitat (Dugan et al. 2003, Dugan et al. 2011, Emery et al. Chapter 4, Page et al. 2021, Cornish et al. In Preparation). This wrack subsidy supported upper beach zone effectively functions as a biogeochemical hotspot at the land-marine ecotone (Coupland et al. 2007). Other hotspots of CO_2 production compared to the surrounding habitat include ant mounds on the forest floor (Risch et al. 2005, Jílková and Frouz 2014) termite mounds compared to the surrounding savanna soils (Risch et al. 2012), and dung pats when occupied by beetles (Penttila et al. 2013).

Like many ecotones with high relative levels function, this zone of the sandy beach ecosystem is the critically imperiled in the face of the combination of rising sea levels and anthropogenic development including coastal squeeze (Myers et al. 2019, Vousdoukas et al. 2020, Barnard et al. 2021, Jaramillo et al. 2021). The upper beach zone in Southern California is expected to largely disappear by the end of the century (Vitousek et al. 2017) and may have already reached a tipping point on bluff backed and armored beaches (Barnard et al 2021). The functional capacity of this zone is often reduced by widespread management practices that include grooming (wrack removal) and armoring (Dugan et al. 2017, Schooler et al. 2019, Jaramillo et al 2021). Food web dynamics may also be altered by warming temperatures, increased nutrient loading, and shifting resource availability (Wernberg et al. 2013, Boada et al. 2017, Smale 2020, Lowman et al. 2021). Ecological hotspots which provide disproportionate ecosystem functions need to be identified and targeted for conservation and restoration (Gilby et al. 2019). Gleaning insight from natural ecosystem variability to project for future conditions will allow managers to best plan for and adapt to a changing environment.

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Tables

Table 1: Mean values of CO_2 flux and marine wrack cover for the surveys conducted at each study site. SCI = Santa Cruz Island, SRI = Santa Rosa Island, SMI = San Miguel Island, CAT = Catalina.

Year	**Island**	**Site**	**CO_2 Flux (g CO_2 m^{-2} $hour^{-1}$)**	**Marine wrack cover (m^2 m^{-1})**
2016	SCI	Christy's	0.078	0.277
2016	SCI	Coches	0.078	0.493
2016	SCI	Forney's	0.15	0.313
2016	SRI	AB Rocks	0.2	1.420
2016	SRI	Bechers	0.34	1.654
2016	SRI	China Camp	0.226	2.160
2016	SRI	Ford Pt	0.128	0.200
2016	SRI	Sandy Pt	0.384	4.180
2016	SRI	Soledad	0.408	11.988
2016	SRI	Water Canyon	0.056	0.434
2017	SCI	Christy's	0.128	0.253
2017	SCI	Coches	0.076	0.597
2017	SCI	Forney's	0.128	0.947
2017	SMI	Cuyler's	0.066	0.107
2017	SRI	AB Rocks	0.126	2.026
2017	SRI	Bechers	0.216	4.180
2017	SRI	China Camp	0.226	0.690
2017	SRI	Ford Pt	0.168	0.158
2017	SRI	Sandy Pt	0.378	4.842
2017	SRI	Soledad	1.184	9.588
2017	SRI	Water Canyon	0.05	0.032
2018	CAT	Ben Weston	0.14	2.433
2018	CAT	Emerald Bay	0.1	0.430
2018	CAT	Little Harbor	0.21	1.643
2018	SCI	Christy's	0.222	0.990
2018	SCI	Coches	0.12	0.317
2018	SCI	Forney's	0.258	0.550
2018	SMI	Cuyler's	0.098	0.067
2018	SRI	Bechers	0.464	3.212
2018	SRI	China Camp	0.088	2.030
2018	SRI	Ford Pt	0.178	0.346
2018	SRI	Sandy Pt	0.46	4.642
2018	SRI	Soledad	0.672	6.388
2018	SRI	Water Canyon	0.086	0.344

Table 2: The range of mean values of CO_2 flux on sandy beaches from the literature. Flux rate measurements are denoted as from sand, wrack, and/or experimental manipulations.

Location	Description	Substrate	Mean CO_2 flux ($g\ CO_2\ m^{-2}\ h^{-1}$)	Reference
Channel Islands, California, USA	14 beaches, Aug - Nov, 2016 - 2018. Wrack dominated by *Macrocystis pyrierfa* and *Phyllospadix torreyi*	Sand	0.230	This Study
Port Foster, Deception Island	*In situ* measurements through bare sand on 12 beaches in Feb 2016 and Feb and Mar 2017 wrack dominated by *Palmaria decipiens* and a Feb 2016 experiment with flux measured through *Palmaria decipiens* and adjacent bare sand	Sand (*In Situ*)	0.053	Lastra et al. 2020
		Wrack (Experiment)	0.271	
		Sand (Experiment)	0.022	
Galicia, Spain	Experiment on Ladeira beach, Jun and Jul 2014 with flux measurements from placed *Saccorhiza polyschides* and adjacent bare sand	Sand	0.007	Lastra et al. 2019
		Fresh Wrack	0.033	
		Aged Wrack	0.119	
Galicia, Spain	Experiment on two beaches in Mar 2015 with flux measurements from placed *Saccorhiza polyschides, Cystoseira baccata, Sargassum muticum, Undaria Pinnatifida* and adjacent bare sand	Sand	0.016	Rodil et al. 2019
		Wrack	0.610	
Galicia, Spain	Experiment on Ladeira beach in Jun 2011 with flux measurements from placed *Laminaria spp.* patches and adjacent bare sand	Sand	0.051	Gomez et al. 2018
		Wrack	0.707	
Southwest Australia	16 beaches in Nov 2006. Wrack dominated by *Posidonia australis* and *Sargassum* spp.	Sand	0.160	Coupland et al. 2007
		Wrack	1.050	

Wimereux, France	One beach, Apr 2000 - May 2003 occasionally high concentrations of microalgae *Euglena spp.* and *Phaeocystis spp.*	Sand	0.002	Spilmont et al. 2005
Wimereux, France	One beach in October 2000	Sand	0.002	Migne et al. 2002

Figure Captions

Figure 1: Locations of the study beaches and wrack abundance on the California Channel Islands, California, USA. Color-scale indicates the mean cover of macrophyte wrack for each site.

Figure 2: The relationship between mean CO_2 flux (g CO_2 m^{-2} $hour^{-1}$) and mean macrophyte wrack cover ($r^2 = 0.60$, $p < 0.00001$). Data point shape indicates the study island and data point color indicates the study beach. Data points are mean values per site visit (n = 1 to 3) from 2016 to 2018.

Figure 3: The relationship between upper beach wrack-associated species richness and marine macrophyte wrack cover ($r^2 = 0.48$, $p < 0.00001$). Data point shape indicates the study island and data point color indicates the study beach. Data points are mean values for all site visits (n = 1 to 3) from 2016 to 2018.

Figure 4: The relationship between upper beach wrack-associated species richness a) log-transformed mean upper beach wrack-associated species abundance ($r^2 = 0.40$, $p < 0.0001$) and b) mean CO_2 flux(g CO_2 m^{-2} $hour^{-1}$) ($r^2 = 0.32$, $p < 0.001$). Data point shape indicates the study island and data point color indicates the study beach. Data points are mean values per site visit (n = 1 to 3) from 2016 to 2018.

Figure 5: a) Mean (n = 6) species specific respiration rates (mg CO_2 $hour^{-1}$) for adults of seven common and abundant wrack-consuming macroinvertebrates and b) genus-level relationship for *Megalorchestia* spp. between respiration rate and individual log-transformed ash-free dry weight ($r^2 = 0.91$, $p < 0.00001$).

Figure 6: Beach-scale respiration rates (mg CO_2 $hour^{-1}$ m^{-1}) of the seven species of wrack-consuming macroinvertebrates derived from their lab-measured respiration rates and field measurements of dry biomass. Data points are mean values for all site visits (n = 1 to 3) from 2016 to 2018 and sites are ordered within each island by decreasing wrack cover.

Figure 7: Estimates of the proportion of beach-scale CO_2 flux that can be attributed to the seven species of wrack-consuming macroinvertebrates at our study sites.

Figures

Figure 1

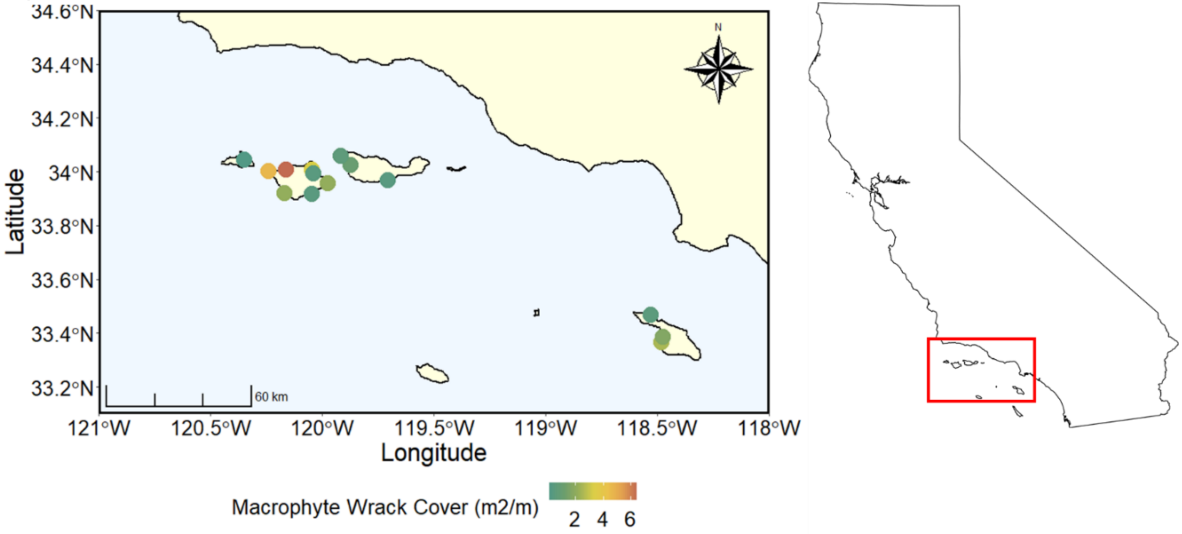


Figure 2

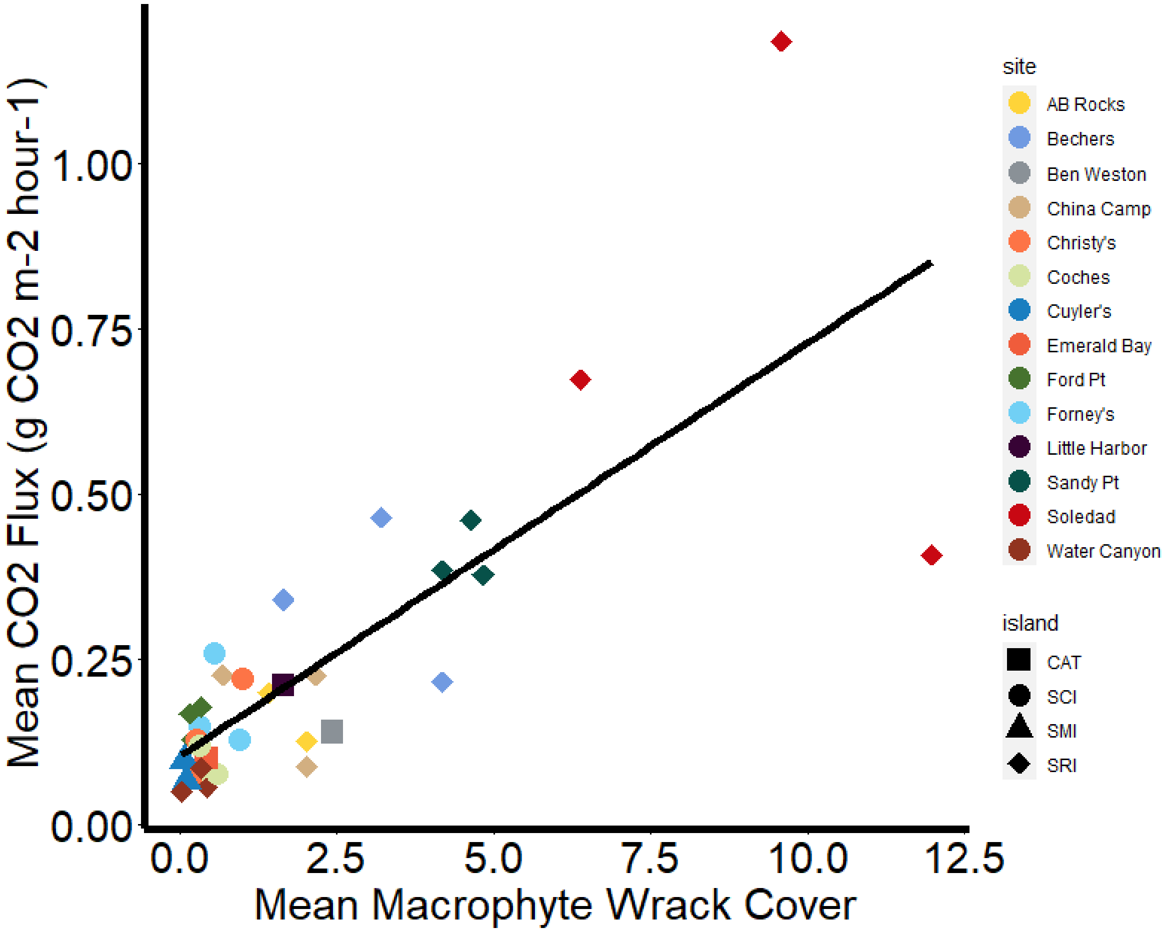
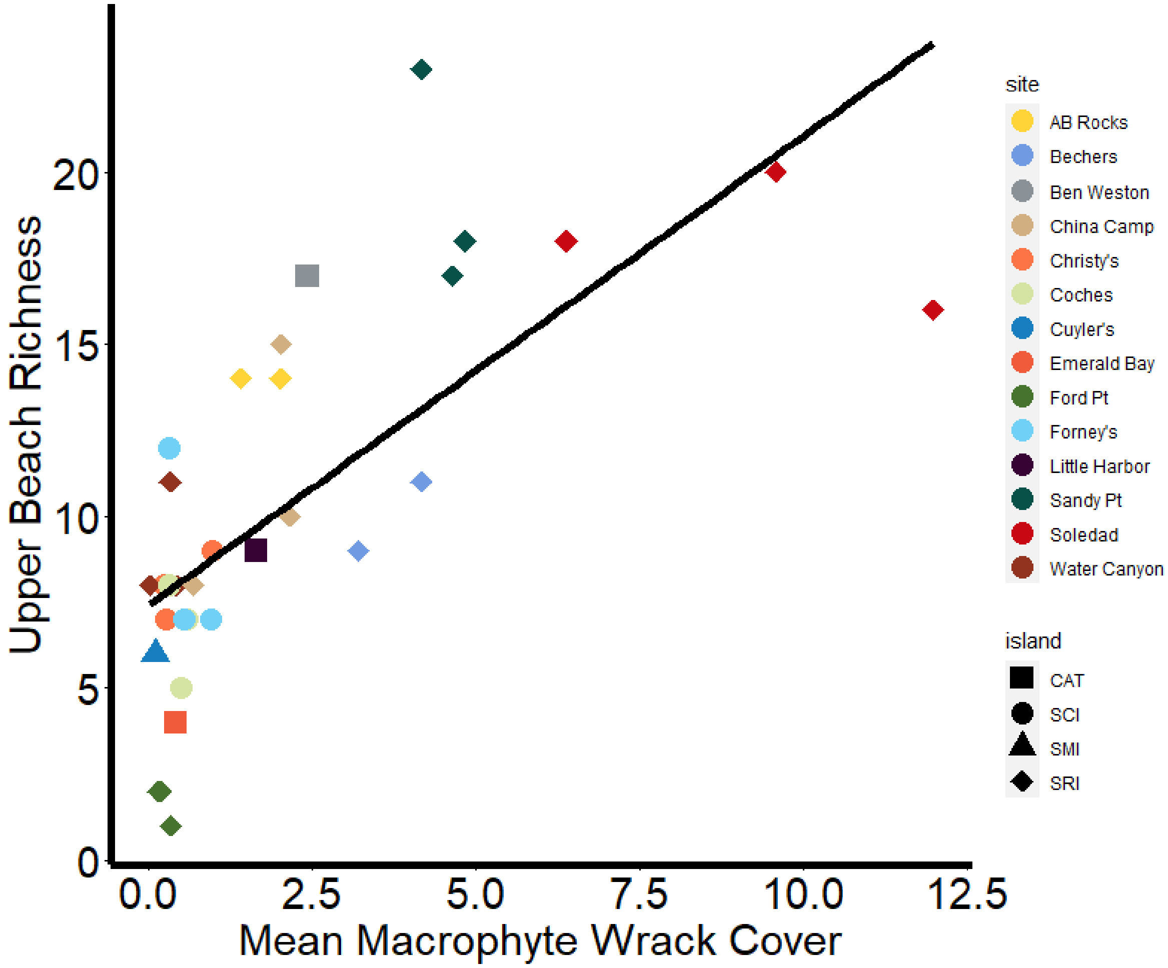

Mean CO2 Flux (g CO2 m-2 hour-1)
1.00
0.75
0.50
0.25
0.00
0.0
2.5
5.0
7.5
10.0
12.5
Mean Macrophyte Wrack Cover
site
AB Rocks
Bechers
Ben Weston
China Camp
Christy's
Coches
Cuyler's
Emerald Bay
Ford Pt
Forney's
Little Harbor
Sandy Pt
Soledad
Water Canyon
island
CAT
SCI
SMI
SRI

Figure 3



Upper Beach Richness
0
5
10
15
20
0.0
2.5
5.0
7.5
10.0
12.5
Mean Macrophyte Wrack Cover
site
AB Rocks
Bechers
Ben Weston
China Camp
Christy's
Coches
Cuyler's
Emerald Bay
Ford Pt
Forney's
Little Harbor
Sandy Pt
Soledad
Water Canyon
island
CAT
SCI
SMI
SRI

Figure 4

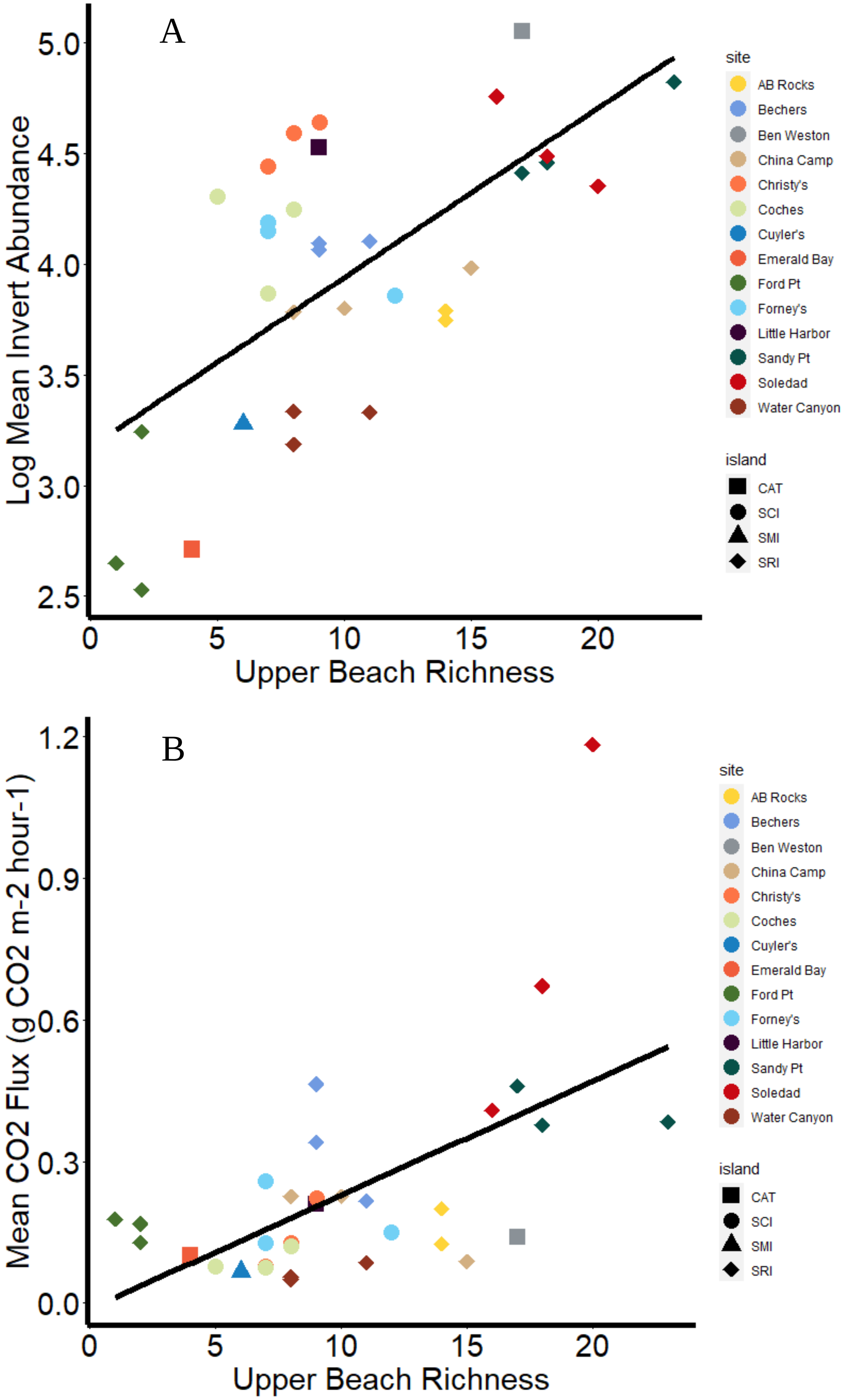

A
Log Mean Invert Abundance
5.0
4.5
4.0
3.5
3.0
2.5
0
5
10
15
20
Upper Beach Richness
site
AB Rocks
Bechers
Ben Weston
China Camp
Christy's
Coches
Cuyler's
Emerald Bay
Ford Pt
Forney's
Little Harbor
Sandy Pt
Soledad
Water Canyon
island
CAT
SCI
SMI
SRI
B
Mean CO2 Flux (g CO2 m-2 hour-1)
1.2
0.9
0.6
0.3
0.0
0
5
10
15
20
Upper Beach Richness
site
AB Rocks
Bechers
Ben Weston
China Camp
Christy's
Coches
Cuyler's
Emerald Bay
Ford Pt
Forney's
Little Harbor
Sandy Pt
Soledad
Water Canyon
island
CAT
SCI
SMI
SRI

Figure 5

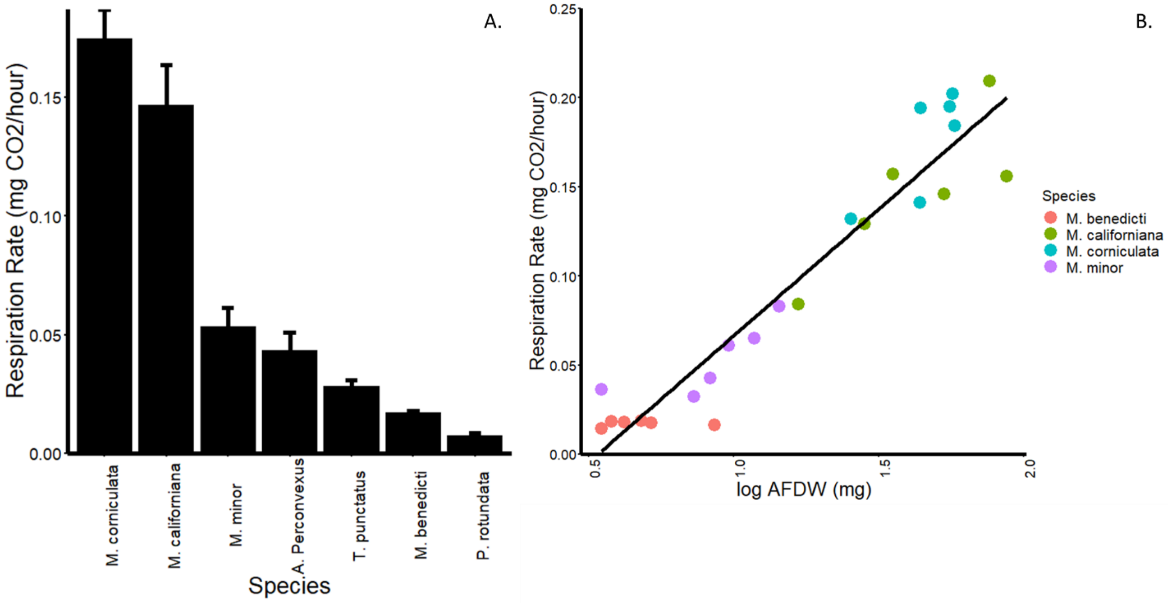

A.
Respiration Rate (mg CO2/hour)
0.00
0.05
0.10
0.15
M. corniculata
M. californiana
M. minor
A. Perconvexus
T. punctatus
M. benedicti
P. rotundata
Species
B.
Respiration Rate (mg CO2/hour)
0.00
0.05
0.10
0.15
0.20
0.25
0.5
1.0
1.5
2.0
log AFDW (mg)
Species
M. benedicti
M. californiana
M. corniculata
M. minor

Figure 6

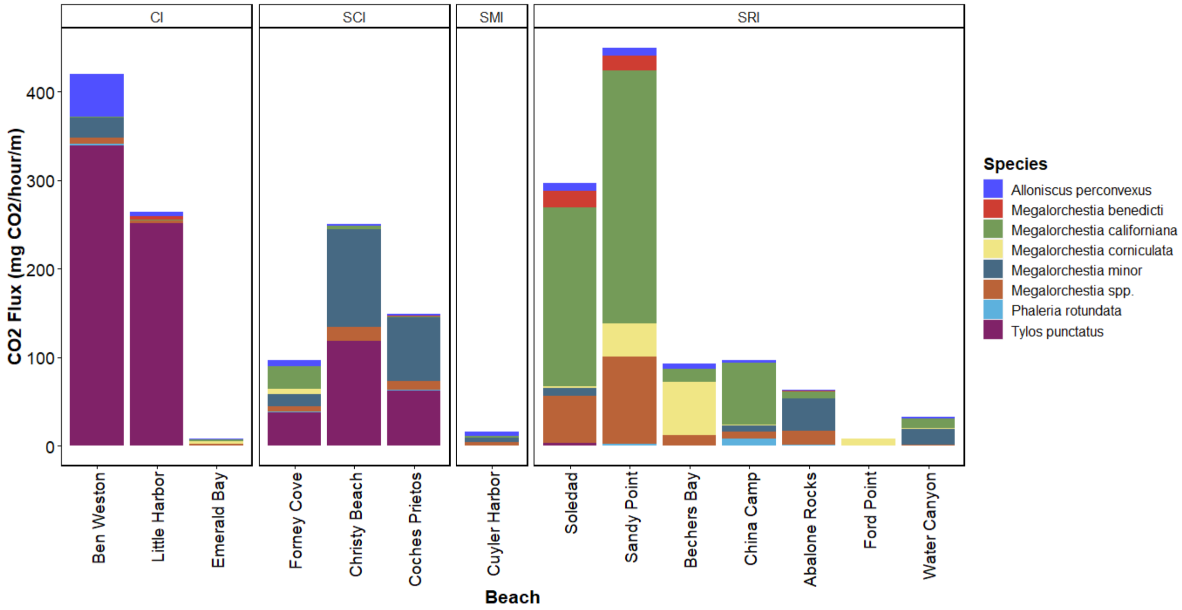
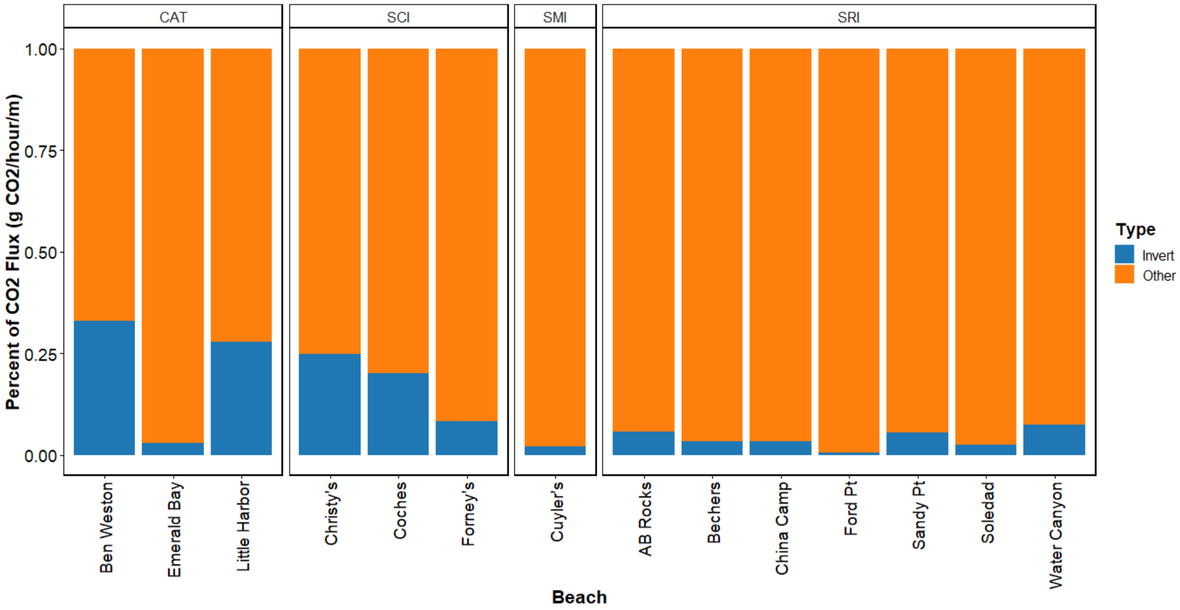
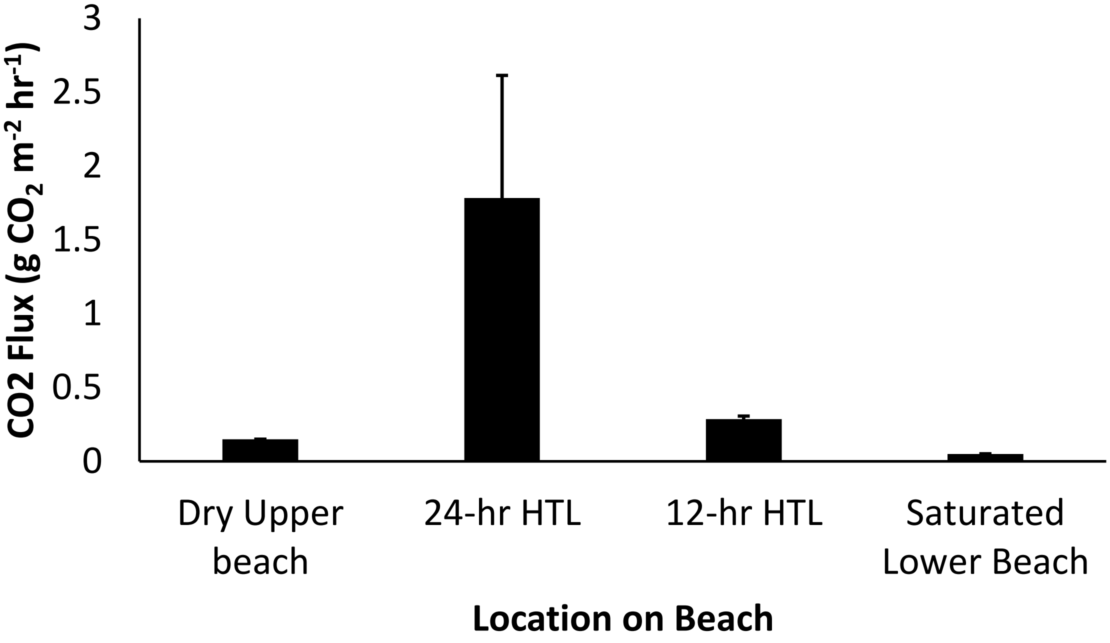

CI
SCI
SMI
SRI
CO2 Flux (mg CO2/hour/m)
0
100
200
300
400
Ben Weston
Little Harbor
Emerald Bay
Forney Cove
Christy Beach
Coches Prietos
Cuyler Harbor
Soledad
Sandy Point
Bechers Bay
China Camp
Abalone Rocks
Ford Point
Water Canyon
Beach
Species
Alloniscus perconvexus
Megalorchestia benedicti
Megalorchestia californiana
Megalorchestia corniculata
Megalorchestia minor
Megalorchestia spp.
Phaleria rotundata
Tylos punctatus

Figure 7

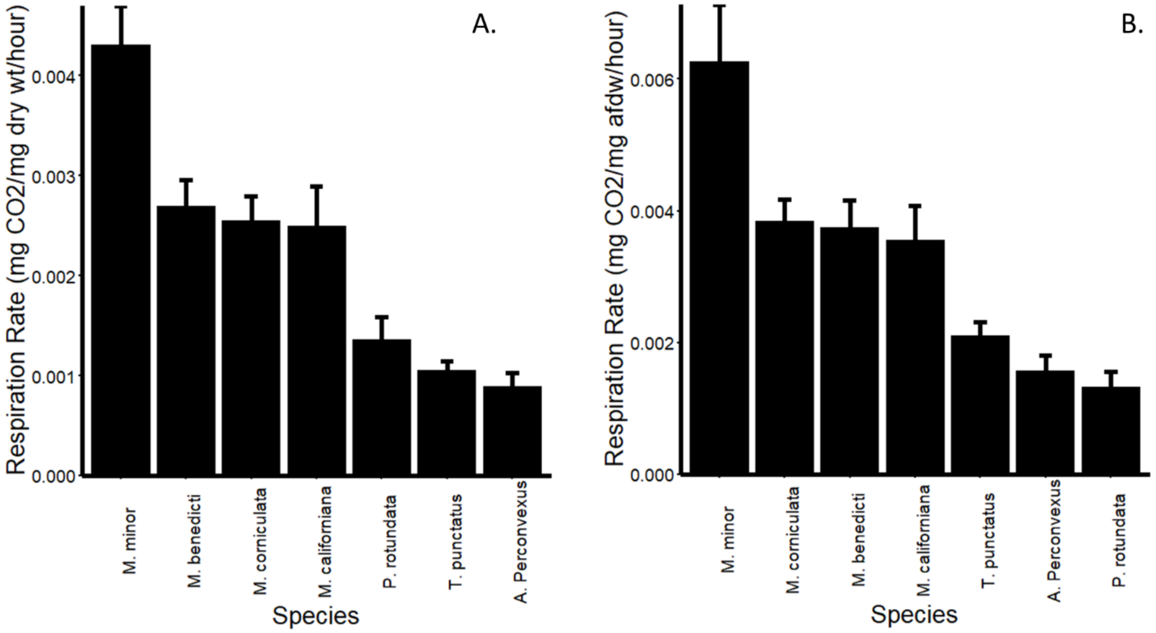

CAT
SCI
SMI
SRI
1.00
0.75
0.50
0.25
0.00
Percent of CO2 Flux (g CO2/hour/m)
Ben Weston
Emerald Bay
Little Harbor
Christy's
Coches
Forney's
Cuyler's
AB Rocks
Bechers
China Camp
Ford Pt
Sandy Pt
Soledad
Water Canyon
Beach
Type
Invert
Other

Supplementary Figures

Supplementary Figure 1: Mean ± SE CO_2 flux (g CO_2 m^{-2} $hour^{-1}$) at different locations across the beach face including the dry upper beach, the 24-hour high tide line, the 12-hour high tide line and the saturated lower beach.



Supplementary Figure 2: Mean ± SE (n = 6) species specific respiration rates (mg CO_2 hour^{-1}) per A) unit dry weight and B) unit ash-free dry weight for adults of seven common and abundant wrack-consuming macroinvertebrates.



Chapter IV. Community structure and ecosystem multifunctionality of sandy beaches respond to variation in marine wrack subsidies

Authors

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Abstract

Connectivity that facilitates the flow of organic matter across ecosystem boundaries can profoundly influence community assembly and ecosystem functioning. Variation in the magnitude and timing of cross-ecosystem subsidies from donor to recipient ecosystems can strongly affect the structure of recipient populations, communities, and food webs as well as ecosystem functioning. To explore the responses of recipient community structure and functioning to subsidy magnitude, we exploited a strong natural range (2 orders of magnitude) in subsidies of marine wrack from nearshore rocky reef donor ecosystems to recipient sandy beach ecosystems along 100 km of coastline. For wrack subsidy dependent intertidal macroinvertebrates, species richness varied from 4 to 15 species and abundances from 1,057 to 53,720 individuals m^{-1} among beaches. The dominant detritivore guild, talitrid amphipods (*Megalorchestia spp.*), comprised 10.7 to 99.5 % (average 74%) of total wrack invertebrate biomass. The amount of wrack a beach received significantly increased diversity and biomass of detritivorous macroinvertebrates. Predatory invertebrate biomass increased with increasing prey availability (detritivore biomass). Higher on the food web, species richness and abundance of vertebrate predators, represented by shorebirds, were significantly correlated with marine wrack abundance and the richness and abundance of wrack-associated macroinvertebrates. Redundancy of the intertidal wrack-based food web increased significantly with wrack subsidy amounts. At the wrack food web scale, subsidy amounts along with indicators of wrack supply – beach directional orientation and the long-term mean kelp canopy biomass offshore of each site – predicted the full community structure. Ecosystem multifunctionality provided a synthetic view of the effects of variation in subsidies on several key ecological functions (pore water nutrients, sediment CO_2 flux,

invertebrate richness, secondary production, flying insect abundance, shorebird richness), all of which were enhanced across the large range in wrack subsidies. Sandy beach ecosystems that received more wrack subsidies were more biodiverse, supported greater abundance and biomass across multiple trophic levels and higher redundancy in their food webs, as well as exhibiting higher levels of ecosystem functioning. Our results for beaches receiving a wide range of wrack subsidies provide valuable new insights on potential ecological effects of projected beach and/or kelp forest loss on structure and function of these vulnerable recipient ecosystems. Our findings suggest that as climatic forcing, manifested by ocean warming and sea level rise, alters the supply of subsidies and the ability of sandy beaches to receive and retain wrack, resident macroinvertebrate communities, higher level consumers like shorebirds, food webs and numerous ecosystem functions of beach ecosystems will be profoundly altered. Our results also suggest that maintaining cross-ecosystem connectivity is critical for preserving biodiverse, high functioning, and resilient ecosystems in a changing climate.

Introduction

Community composition and ecosystem functioning can be profoundly impacted by climate and anthropogenic driven changes (Cramer et al. 2001, Dixo et al. 2009, Hawkins et al. 2009, Doney et al. 2012), highlighting the critical need to understand ecosystem dynamics across space and time (Malhi et al. 2020). Population and ecosystem spatial dynamics are tied to altered connectivity within and across ecosystems (Munday et al. 2009, Carr et al. 2017), which controls critical cross-ecosystem flows of resources or subsidies that support processes, consumers, and entire food webs (Sheaves 2009, Hyndes et al. 2014, Rodil et al. 2015, Zuercher and Galloway 2019). Within a given ecosystem type, disruptions to connectivity can cause a variety of negative consequences to reproduction and larval supply, genetic diversity, habitat fragmentation and therefore isolation of species, behavior, and more (Munday et al. 2009, Magris et al. 2014, Carr et al. 2017).

Gauging how changes in connectivity may affect an ecosystem requires a strong quantitative understanding of the responses of structure and function. Ecosystem function measurements indicate the status and/or rate of processes within and across ecosystems, providing valuable information on how ecosystems change over time (Schwartz et al. 2000) or allowing comparisons across spatial scales, from plots to sites, regions, and ecosystems (Keuskamp et al. 2013, Pasari et al. 2013, Lohrer et al. 2015). Measures of ecosystem functions can provide a baseline for evaluating the effects of disturbance on local to regional scales and on relatively short timescales (i.e., storms) to long-term change (i.e., climate variations and change). For example, common forest disturbances, like wind, fire, and bark beetles, generally result in negative effects on ecosystem functions (Thom and Seidl 2016). Similarly, analyses of long-term data sets indicate ecosystem function is shifting with climate change across ecosystems (Pettorelli et al. 2012, Grimm et al. 2013, Nagelkerken and Connell 2015). Experimental studies which simulate projected future conditions have also documented negative effects on ecosystem functions (O'Meara et al. 2017, Edwards et al. 2020).

Much of what we know about relationships between biodiversity and function is based on experimental studies that are most often conducted using microorganisms (Naeem et al. 2000, Gamfeldt et al. 2005, Bestion et al. 2020) and manipulated plant communities (Tilman et al. 1996, Pfisterer and Schmid 2002, Zavaleta et al. 2010, Weisser et al. 2017). Biodiversity may enhance some ecosystem functions while depressing others (Wardle et al. 1997, Troumbis et al. 2000, Balvanera et al. 2006, Cardinale et al. 2006, Soliveres et al. 2016), whereas ecosystem multifunctionality allows for quantification of the net effect of some ecosystem attribute (i.e. biodiversity) on multiple functions (Byrnes et al. 2013, Lefcheck et al. 2015). Ecosystem multifunctionality can be calculated using several methodologies (Byrnes et al. 2013) and although this tool is not without limitations (Bradford et al. 2014a, Bradford et al. 2014b, Gamfeldt and Roger 2017), it can provide a more thorough and integrative index of ecosystem functioning (Byrnes et al. 2014, Manning et al. 2018, Giling et al. 2018). Ecosystem multifunctionality studies in more complex, multitrophic systems are lacking (Soliveres et al. 2016, Barnes et al. 2018, Schuldt et al. 2018, Eisenhauer et al. 2019), especially in natural communities rather than experimental or manipulated settings (Sagarin and Pauchard 2009, van der Plas 2019). Ecosystem multifunctionality generally increases with increasing biodiversity because a larger species pool typically contains more functional types (Hector and Bagchi 2007, Gamfeldt et al. 2008, Dooley et al. 2015, Soliveres et al. 2016, Meyer et al. 2017, Hautier et al. 2018, Schuldt et al. 2018). However, neutral or negative responses to increasing biodiversity can be related to factors like competitive interactions or redundancy (Gamfeldt and Roger 2017, Pennekamp et al. 2018 Bagousse-Pinguet et al. 2019, van der Plas 2019). Issues in ecosystem function research related to species richness, such as the sampling effect (Huston 1997), can be avoided by analyzing multifunctionality as a response to variation in more basal metrics, such as percent cover or counts of the primary food or habitat resource (Soliveres et al. 2014, Angelini et al. 2015, Ramus et al. 2017, Zirbel et al. 2019, Thomsen et al. 2019, Schenone and Thrush 2020). While multifunctionality studies of primary producer communities are common (Zavaleta et al. 2010, Maestre et al. 2012), little is known for subsidized ecosystems that rely on allochthonous inputs of organic matter rather than *in situ* primary production.

Cross-ecosystem subsidies of organic matter are fairly ubiquitous across terrestrial and aquatic ecosystems (Polis and Hurd 1996, Nakano and Murakami 2001). Ecosystems with limited *in situ* primary production that rely on allochthonous subsidies from other ecosystems can support complex, multitrophic food webs and communities (Dugan et al. 2003, Richardson et al. 2010, Schneider et al. 2011, Recalde et al. 2015). Organic matter subsidies that support multiple trophic levels range over 8 orders of magnitude in annual biomass inputs and span a great variety of ecosystems, subsidy types, and mechanisms of transport (Gounand et al. 2018). These allochthonous subsidies include terrestrial organic matter inputs to lakes (Cole et al. 2006), leaf litter into and adult insects out of freshwater streams (Richardson et al. 2010), carcass and algal inputs to deep marine canyons (Smith et al. 2015, Ramirez-Llodra et al. 2016), and macrophyte subsidies to sandy beaches (Dugan et al. 2003, Ince et al. 2007, Mellbrand et al. 2011) which stimulate primary and/or secondary productivity in recipient ecosystems (Anderson and Polis 1999, Ince et al. 2007, Heck et al. 2008, Spiller et al. 2010). In subsidized ecosystems consumer diversity (Dugan et al. 2003, Anderson and Wait 2008, Szkokan-Emilson 2008), abundance (Rose and Polis 1998, Barrett et al. 2005, Jaramillo et al. 2006) and biomass (Polis and Hurd 1996, Lastra et al. 2008, Earl and Semlitsch 2012) can scale with the amount of the subsidy. Effects of subsidies on food webs have been shown to propagate across trophic levels and become integral factors in ecosystem functioning (Zhang et al. 2003, Marcarelli et al. 2011).

Characterized by low in situ primary production, sandy beaches are widely distributed intertidal ecosystems that are heavily subsidized by marine macrophyte (wrack) inputs in many temperate regions (Colombini and Chelazzi 2003, Hyndes et al. In Preparation). Sandy beaches can be highly connected to adjacent, productive ecosystems, such as kelp forests and seagrass beds, that export large amounts of their primary production as drift macrophytes or wrack (Lastra et al 2008, Liebowitz et al. 2016). Many studies concluded that intertidal macroinvertebrate communities of sandy beaches were primarily structured by physical processes and factors, such as grain size and wave dynamics (Defeo et al. 1992, McLachlan et al. 1993, Defeo and McLachlan 2011). However, growing evidence suggests that wrack inputs to beaches can strongly affect community structure by increasing the abundance and biomass of consumer groups, such as detritivores and predators, including shorebirds, as well as invertebrate diversity (Dugan et al. 2003, Goncalves and Marques 2011, Schlacher et al. 2017). These inputs of wrack have been linked to numerous ecosystem functions including kelp processing and nutrient cycling (Lastra et al. 2008, Dugan et al 2011, Gomez et al. 2018, Lowman et al. 2019, Emery et al. 2021). The larger-scale and biogeographical patterns of community composition on sandy beaches have been widely examined (Lastra et al. 2006, Defeo and McLachlan 2013, Rodil et al. 2012). However, to clarify the role of subsidies in these intertidal communities, local scale studies, especially with respect to inputs of subsidies, are needed (e.g. Schooler et al. 2017). In this study, we took advantage of a strong natural range in wrack inputs from kelp forests to explore how these inputs structure the macroinvertebrate communities of sandy beaches and stimulate their functioning. We investigated the degree to which variation in inputs of subsidies from reefs to sandy beaches affected responses across multiple trophic levels in the recipient community. We predicted that local scale variation in wrack inputs can strongly affect diversity and biomass patterns on sandy beaches and that ecosystem multifunctionality, based on a diverse suite of metrics, would vary with the magnitude of wrack subsidies.

Methods

Beach Sampling

We quantitatively surveyed wrack cover, invertebrate and shorebird communities, and a suite of ecosystem functions at 24 sandy beaches across ~100 km of coastline in Santa Barbara and Ventura counties, California, USA (Figure 1). Study sites were selected to represent a range of expected kelp subsidy inputs based on tracer trajectories from a Regional Ocean Modeling System solution for the Santa Barbara Channel parameterized to kelp forest locations (Romero et al. 2013, Ohlmann et al. In Preparation). Site selection was based on two factors, 1) all study sites had a lack of direct manipulation (i.e. no grooming, nourishment, etc.) and 2) an upper beach zone with at least 2.0 m of dry upper beach above the 24-hour high tide line during our survey period. All beaches were surveyed within two hours of low tide (0.762 m or less) during October and early November 2017, prior to the seasonal onset of larger swells and storms. At each site, measurements and samples were collected on three shore normal transects that extended from the upper beach limit (cliff base or dune toe) to the top of the swash zone. The abundance and composition of wrack including buried material was measured on each transect using a line-intercept method (Dugan et al. 2003) to quantify the cover of wrack and provide an estimate standing stock for a 1m wide shore-normal band of intertidal habitat. The distance from the upper beach limit to the upper swash zone was used to calculate the percent cover of wrack on each transect.

The diversity, abundance, and biomass of the wrack-associated upper beach macroinvertebrate community was surveyed using a series of 10 cm diameter, 20 cm deep cores along each transect. Transects were split into two zones – the dry upper beach zone and the talitrid amphipod burrow zone. The upper zone extended from the upper beach limit to the top of the talitrid amphipod burrow zone. The talitrid amphipod burrow zone extended from the upper limit of burrows to the lower limit of burrows on each transect. Talitrid amphipods occupy the lowest intertidal zone of the wrack-associated upper beach macroinvertebrates. Within each zone, ten evenly spaced cores were taken and aggregated into a fine mesh bag with apertures of 1.5 mm. Each aggregated sample was rinsed free of sand in the surf and emptied into labeled one-gallon zip-lock bags, chilled, transported to the laboratory and frozen. In the laboratory, these samples were defrosted and rinsed into sorting trays with DI water and sorted to separate invertebrates from retained wrack and sediment. Invertebrates were identified to species level, counted, and weighed to the nearest mg (blotted wet weight). The sex of all talitrid amphipods (except for juveniles < 5mm) and body length were measured for use in estimation of secondary productivity. Secondary production of talitrid populations was estimated using a length to ash free dry weight (AFDW) relationship and the equation of Edgar (1990). As the dominant detritivore on the study beaches, the secondary production of talitrid amphipods represents production available to higher level consumers.

Flying insects (Diptera and Coleoptera) are an important component of the wrack associated community and food web. Larvae of intertidal fly and beetle species develop in and feed on wrack and both larvae and adults are consumed by predatory invertebrates and birds. However, these intertidal insects are generally under-surveyed by sediment cores. The abundance of flying insects was estimated separately from the sediment cores on each transect using sticky traps that yielded a catch per unit effort value. On each transect, two rolls of ribbon fly paper (Revenge) were unrolled and placed (pinned at each end into the sand with stake flags) on top of two different patches of fresh kelp wrack located near the 24-hour high tide line. The sticky traps were deployed for 15 minutes then collected into labeled one-gallon zip-lock bags and frozen. In the laboratory all flying insects (i.e. *Fucellia* spp., *Coelopa* spp., Cafius spp., Staphylinidae spp.) were categorized and counted on each sticky trap. Abundances from the two traps on each transect were summed and mean abundances were calculated using the values from the three transects for each site.

To estimate the function of nutrient cycling and retention, samples of intertidal pore water for nutrient analyses were collected by digging pits at the high tide line on each transect and allowing pore water to fill the pits before using a 60 ml BD syringe to sample surface pore water. Pore water samples were filtered through glass fiber GF/F filters into two 20 ml glass scintillation vials and then frozen. Nutrient analyses of defrosted samples for ammonia and nitrate + nitrite concentrations using simultaneous flow injection analysis (precision ± 5% for all analytes) were conducted in the Marine Science Institute Analytical Laboratory at the University of California, Santa Barbara.

To estimate the function of intertidal community respiration, the flux of CO_2 from the damp sand at the 24-hour high tide line was measured using the PP Systems EGM-5 coupled to an SRC-2 soil respiration chamber (accurate to <1% over calibrated CO_2 range). The chamber was placed on a collar inserted two centimeters into the sand surface at the 24-hour high tide line at a location adjacent to the transect and on bare sand, not directly over surface deposits of macrophyte wrack. The flux measurements were made over three minutes and we report the linear flux rate ($g\ CO_2\ m^{-2}\ h^{-1}$). This measurement of community level net respiration includes microbial decomposition and invertebrate respiration. Any primary production offset was likely small to non-existent because measurements were not made over wrack or vegetation and sampling sites were located above the zone where interstitial or surf zone diatoms would be present.

Shorebirds were used to represent the highest trophic levels in intertidal food webs of beaches. Surveys of shorebirds were conducted at each study site on the date of the initial beach survey and during two additional replicate shorebird surveys between October 2017 and February 2018. Shorebirds were identified to species level and counted along a 1 km stretch of beach centered on the location where wrack and invertebrate surveys were conducted. We anticipated completing the shorebird surveys by December 2017, but access to our sites was severely restricted due to the December 2017 Thomas Fire and the January 2018 Montecito debris flow. Despite the delay due to these disasters, all shorebird surveys were completed during their main overwintering period in the Santa Barbara Channel region

(Hubbard and Dugan 2003), so no major change in community composition or abundance of these birds was expected.

Data Analysis

Total marine wrack percent cover was calculated by taking the total length of marine wrack deposits measured on each cross shore transect and dividing that value by the width of the beach from the upper beach limit to the water table outcrop. We used Spearman's Rank Order correlation to determine if there was a spatial gradient in wrack subsidies (as cover) with coastline distance from the northernmost study beach. Species richness of wrack-associated macroinvertebrates is reported as total site species richness. Invertebrate abundance and biomass were scaled based on core spacing to represent the number or biomass of each species m^{-1} of shoreline (Brown and McLachlan 1990, Dugan et al. 2003). All invertebrates were characterized into one of two functional groups – detritivores or predators. The detritivores are dominated by talitrid amphipods (*Megalorchestia* spp.), a cosmopolitan species that consumes wrack on beaches worldwide (Lastra et al. 2008, Michaud et al. 2019). Other species in this group include isopods (*Alloniscus perconvexus* and *Tylos punctatus*) and beetles (for example, *Phaleria rotundata*), which are also common and widely distributed wrack consumer guilds. Common predatory invertebrates include several beetle families (*Caribidae, Histeridae, Staphylinidae*) and spiders (*Salticidae*). Abundance and biomass were summed by functional group for each transect at every site. Diversity of order 1 for each functional group was calculated for each transect at every site,

$$1D = \exp{(H)}$$

where H is the Shannon entropy index (Jost 2006). Diversity of order 1 is a frequency weighted value derived from the abundance of each species and does not favor rare or common species (Jost 2006).

The role of marine wrack subsidies in structuring sandy beach invertebrate communities was analyzed using PiecewiseSEM (Lefcheck 2016). We used marine wrack percent cover along with diversity of order 1 and biomass of both functional groups with hypothesized unidirectional pathways in linear mixed effects models (Pinhiero et al. 2019) with site as the random factor (Table 1A). PiecewiseSEM does not evaluate reciprocal relationships, so each hypothesized pathway is unidirectional, and it is important to note that variables can be both predictors and responses (Lefcheck 2016). Predictor variable data were standardized to a mean of 0 and standard deviation of 1 (Miller et al. 2018).

We also calculated species dominance (D) within the detritivore and predator functional groups for each site. This index, ranging from 0 to 1, with higher values representing increased dominance, was calculated from the Simpson diversity index (S),

$$D = 1 - S$$

using the R package vegan (Oksanen et al. 2019). We used one-way ANOVA to compare dominance among detritivores to log-transformed detritivore biomass at each site and dominance among predators to log-transformed predator biomass at each site to determine if diversity (i.e. evenness) or dominance increase with biomass for both consumer guilds.

We explored the relationship between food web redundancy (i.e. number of species of detritivores and predators) and subsidies for wrack-associated macroinvertebrates using ordinary least squares (OLS) linear regression. To evaluate potential drivers of the composition of the wrack-associated macroinvertebrate community we used distance-based redundancy analysis, which searches for linear relationships between dissimilarity indices and environmental variables (Legendre and Anderson 1999). We considered percent cover of wrack, dry beach width, slope at high tide strand line, beach segment length (sandy shoreline distance between two boundaries measured in Google Earth), beach segment orientation as compass degrees of the shore-normal line (0°/360° = North measured in Google Earth, and the 30 year mean Landsat-derived estimates of kelp canopy biomass (wet kg) offshore of each study beach (Bell et al. 2021). The dissimilarity index used was determined with rank correlation coefficients between the indices and predictor gradient separation using the *rankindex* function and the distance-based redundancy analysis was run with the *capscale* function, both from the *vegan* R package (Oksanen et al. 2007). We then ran ANOVA on the ordination results to determine overall model significance and an ANOVA by model terms to test for significant variables.

Higher trophic levels, including birds, small mammals and reptiles can respond to wrack subsidies on beaches via increased availability of invertebrate prey (both detritivores and predators). We used our surveys of shorebird species richness and abundance to evaluate their response to variation in prey diversity and abundance across our 24 study beaches. We used OLS linear regression analyses to compare shorebird species richness and abundance to wrack cover, invertebrate species richness, and invertebrate abundance because shorebird data was collected at different spatial (1 km) and temporal (3 months) scales from the wrack and invertebrate data used in the PiecewiseSEM.

To evaluate ecosystem functioning, we selected six ecosystem functions we consider to be responses to wrack subsidies: pore water nutrients, sediment CO_2 flux, invertebrate richness, talitrid secondary production, flying insect abundance, and shorebird richness. We compared wrack cover to a synthetic measure of function, ecosystem multifunctionality, where multiple ecosystem functions are standardized and combined into a unitless metric using the R package multifunc (Byrnes et al. 2014). The average value of standardized ecosystem functions was compared to marine wrack cover for each of the 24 sites. Ecosystem functions were scaled to values between 0 and 1 based on the maximum observation for each of the functions we considered. The mean of those values was used as each site's average ecosystem function value and compared to percent wrack cover at each site using OLS linear regression.

Results

We observed high variation for most of the measured ecosystem response variables across the 24 study beaches. The standing stock of marine wrack, reported here as percent cover, ranged over an order of magnitude, from 0.9% to 11.6% (Supplementary Table 1). Wrack cover was spatially variable among sites and was not a function of distance along the coastline (Spearman's rho = -0.28, p = 0.19). Invertebrate communities responded strongly to the abundance of wrack subsidies (estimated by cover). The total species richness of upper beach macroinvertebrates ranged from 4 to 15 species and was significantly correlated with wrack abundance (Figure 2A, $r^2 = 0.58$, $p < 0.001$). Mean values of invertebrate abundance, which ranged from 1,057 to 53,720 individuals m^{-1} beach, were similarly related to wrack abundance (Figure 2B, $r^2 = 0.22$, $p = 0.01$). Mean values of secondary production of the dominant invertebrate and primary food source for higher trophic level consumers (predatory beetles, shorebirds, etc.), talitrid amphipods ranged 0.07 to 5.84 g m^{-1} beach day^{-1} (ash-free dry weight) and was correlated with wrack ($r^2 = 0.21$, $p = 0.01$). Flying insect abundance as mean catch per unit effort ranged from less than 1 individual to 594 individuals and was also correlated with wrack ($r^2 = 0.13$, $p = 0.05$).

Two important sandy beach biogeochemical parameters, pore water nutrient concentrations and the sediment CO_2 flux rate, that can be indicators of community function, varied widely across the 24 study beaches. Mean values of nutrient concentrations (total dissolved inorganic nitrogen or DIN) in intertidal pore water varied three orders of magnitude across our 24 study beaches, ranging from 4.8 to 2,331.1 μM DIN. Mean CO_2 flux from sediment at the high tide strand line varied an order of magnitude among beaches with values ranging from 0.09 to 0.35 g CO_2 m^{-2} h^{-1}.

We explored the relationship between wrack subsidies and the invertebrate community response by analyzing several potential unidirectional pathways with PiecewiseSEM (Figure 3A). Results from our PiecewiseSEM indicated that wrack cover was a strong predictor of the biomass of invertebrate detritivores (Table 1B, standardized regression coefficient (SRC) = 0.26, $p = 0.04$) and of predatory invertebrates (Table 1B, SRC = 0.47, $p < 0.0001$). Wrack cover also strongly drives detritivore diversity (Table 1B, SRC = 0.51, $p = 0.0001$). Detritivore biomass, in turn, was a good indicator of predator biomass (Table 1B, SRC = 0.36, $p = 0.0004$). Lastly, predator diversity was strongly predicted by predator biomass (Table 1B, SRC = 0.48, $p = 0.0002$), however this was not the case for detritivores. All pathways identified as significant by the model were positive (Figure 3B). Marginal (variance explained by fixed effects) and conditional (variance explained by fixed and random effects) R^2 values for each response variable are provided in Table 1A.

The diversity of macroinvertebrate predators was predicted by predator biomass in the PiecewiseSEM. As predator diversity increased with predator biomass, we found that species dominance (range 0.18 to 1.0) decreased with increasing predator biomass (ANOVA: $r^2 = 0.37$, $p = 0.003$). Detritivore diversity did not increase as detritivore biomass increased in our PiecewiseSEM. As such, we found that detritivore species dominance (range 0.24 to 0.88) increased, albeit marginally, with increasing detritivore biomass (ANOVA: $r^2 = 0.12$, $p = 0.09$).

Species redundancy of the intertidal macroinvertebrate food web increased with the amount of wrack subsidies for detritivores ($r^2 = 0.25$, $p = 0.007$). That relationship with wrack subsidies was stronger for predatory macroinvertebrates ($r^2 = 0.61$, $p < 0.0001$). The distance-based redundancy analysis of the full wrack-associated macroinvertebrate community using Gower's dissimilarity was significant ($F = 2.1$, $p = 0.003$). Within this model we found, again, that wrack cover was a significant driver of community assembly ($F = 2.8$, $p = 0.009$) as was beach orientation ($F = 4.2$, $p = 0.01$) and the long-term mean of offshore kelp canopy (i.e. availability) ($F = 3.0$, $p = 0.03$).

Higher trophic level predators represented by shorebirds responded strongly to the spatial variation in wrack subsidies and invertebrate prey communities on the scale of our study. Total species richness of shorebirds varied from 2 to 14 species and mean values of the abundance of shorebird ranged from 1 to 172 individuals km^{-1} beach across the 24 beaches. We observed a significant relationship between the species richness (Figure 4A, $r^2 = 0.36$, $p = 0.001$) and abundance (Figure 4B, $r^2 = 0.30$, $p <0.01$) of shorebirds and the percent cover of marine wrack. We found strong positive correlations between shorebird richness and the species richness of wrack-associated macroinvertebrates (Figure 4C, $r^2 =$

0.46, $p < 0.001$) and the abundance of shorebirds and the abundance of wrack associated macroinvertebrates (Figure 4D, $r^2 = 0.51$, $p < 0.001$). Similarly, the species richness of shorebirds ($r^2 = 0.50$, $p < 0.0001$) and abundance ($r^2 = 0.47$, $p = 0.0001$) was significantly related to the secondary productivity of the dominant wrack consumer, talitrid amphipods.

Our results on the effect of marine wrack subsidies on six ecosystem functions that covered key aspects of ecological and biogeochemical parameters on sandy beach ecosystems (pore water nutrients, sediment CO_2 flux, invertebrate richness, talitrid amphipod secondary production, flying insect abundance, shorebird richness) provided additional insights on the role of subsidies in this natural ecosystem. The average value of the six standardized ecosystem functions ranged from 0.19 to 0.91. The relationship between the subsidy amount as percent cover of marine wrack and the average value of standardized ecosystem functions was significantly positive (Figure 5, $r^2 = 0.43$, $p < 0.001$).

Discussion

Connectivity between coastal subsidized ecosystems can be highly coupled to biodiversity and ecosystem functioning (Dias et al. 2016, Liebowicz et al. 2016, Zuercher and Galloway 2019). In our study, the magnitude of wrack subsidies a sandy beach receives strongly affected both the structure and functioning of intertidal macroinvertebrate communities. Responses to wrack subsidies included the species richness, abundance, and biomass of invertebrate detritivores and predators, the richness and abundance of vertebrate predators, represented by wintering shorebirds, and ecosystem multifunctionality. Our demonstration of these strong effects of subsidies on a local scale within the same biogeographical region and littoral cell (Patsch and Griggs 2006), where physical factors such as grain size and wave climate are relatively similar, strongly confirms the role that allochthonous subsidies can play in structuring sandy beach and other ecosystems. Our results add to the growing body of experimental and observational studies that reinforce the importance of allochthonous inputs in structuring communities across a range of subsidized ecosystems including caves (Schneider et al. 2011), streams (Wallace et al. 2015), and lake shorelines (Jonsson and Wardle 2009). To better evaluate the relative importance of biological as well as physical factors in structuring intertidal invertebrate communities of sandy beaches future analyses of these ecosystems must incorporate measurements of subsidies, including wrack, carrion and phytoplankton, into study designs (Hyndes et al. In Preparation).

Wrack subsidies influenced all trophic levels of the intertidal food web of beaches. For macroinvertebrate detritivores, the standing stock of the wrack subsidy (as cover) was a strong predictor of biomass (Figure 3B), which was expected as consumer abundance tends to track resource abundance (Hawes et al. 2003). Greater wrack inputs increase the biomass of detritivore consumers, which in turn makes this subsidy available to higher trophic levels including both invertebrates and vertebrates. For macroinvertebrate predators, the standing crop of wrack subsidies represents two key resources: 1) the direct provisioning of habitat and 2) the indirect provisioning of food supply through enhanced availability of their detritivore prey. This indirect link is illustrated by the finding that detritivore biomass strongly predicts predator biomass (Figure 3B), confirming that population dynamics of intertidal macroinvertebrate predators on beaches are strongly affected by the availability of their prey. Our model also found that macroinvertebrate predator biomass was a strong predictor of predator diversity, yet this relationship was not detected for detritivores, indicating that these two consumer guilds are structured differently as guild biomass increases. This was also evident in our analysis of species dominance where we found that within the predatory macroinvertebrate guild, species dominance decreased with increasing biomass. Among macroinvertebrate detritivores, species dominance marginally increased with increasing biomass. The different community trajectories indicate that as the predatory invertebrate guilds grow, evenness remains the same or increases whereas for detritivores evenness tends to decline. When macroinvertebrate detritivore biomass is high, most of that biomass can be attributed to talitrid amphipods, the dominant kelp wrack consumers (Lastra et al. 2008, Michaud et al. 2019, Emery et al. 2021), yet for intertidal predators there does not appear to be a dominant species.

Our analysis of redundancy patterns for wrack-associated invertebrates revealed the critical role of subsidies in the structure and potential resilience of sandy beach food webs. Species redundancy (total species richness) of detritivores increased with increasing levels of marine wrack subsidies. More species may be present because a larger volume of inputs may be more diverse in resource type or form than a small volume of subsidies, presenting more opportunities for consumers (Allen et al. 2012). Interestingly, the increase in redundancy of predatory invertebrate species with wrack inputs was greater than observed for detritivores. This may result from less intraguild competition (including predation) or greater resource diversity (i.e. prey complementarity) for predators when wrack is abundant (Griffen and Byers 2006, Roubinet et al. 2018). Ecosystems can support more species when the ecosystem is more productive or when more resources are available (Wright 1983, Srivastava and Lawton 1998, Mittelbach et al. 2001, Cardinale et al. 2009). The increase in species richness with subsidy supply is indicative of increasing functional redundancy within the ecosystem. Functional redundancy can serve as a buffer in the event of species loss (Walker 1992) or disturbance, but only when ecosystem process rates have reached a plateau (Jonsson and Malmqvist 2000).

Food web complexity/redundancy is correlated with wrack subsidies and factors associated with wrack input and retention. Beach orientation has implications for subsidy inputs with respect to the direction of the beach; whether it is facing or sheltered from incoming waves and currents. The long-term mean value for offshore kelp canopy biomass is an indicator of subsidy supply as most kelp plants delivered to beaches originate within ~5 km of the kelp forest (Ohlmann et al. In Preparation). Multiple lines of evidence within consumer trophic guilds and across the entire wrack-associated invertebrate community indicate the strong link between the beach food web and subsidy dynamics. Thus, such trophic redundancy when subsidies are high is likely enhancing the resilience of the beach ecosystem food web and reducing the risk of extinction cascades (Sanders et al. 2018, Eisaguirre et al. 2020). Sandy beaches may, in fact, be a rare example of a coastal marine ecosystem type with fairly high functional redundancy (Micheli and Halpern 2005, Emery et al. 2021).

Our results for shorebirds and wrack subsidies from reefs highlight the multitrophic effects of cross-ecosystem subsidies on sandy beaches and have implications for potential effects of these subsidies in recipient ecosystems. Wrack subsidies provide food and habitat for intertidal invertebrates (Ince et al. 2007) that are also important for the wintering success of migratory shorebirds and the breeding success of resident shorebird species, including the western snowy plover (*Charadrius nivosus nivosus*), a federally listed threatened species (Neumann et al. 2008, Brindock and Colwell 2011). The species richness and abundance of shorebirds responded significantly to the standing crop of wrack subsidies (as cover), and to the richness and abundance of intertidal macroinvertebrate prey supported by those subsidies (Figure 4). As common predators of wrack associated macroinvertebrates, the species richness and abundance of shorebirds on sandy beaches has been linked to the abundance of prey resources and wrack abundance in previous studies (Dugan et al. 2003, Schlacher et al. 2016, 2017). The richness and abundance of shorebirds responded similarly to secondary productivity of talitrid amphipods in our study, demonstrating how wrack subsidies are integrated into and propagate throughout the food web of the recipient ecosystem. Similar responses to marine subsidies have been observed for shorebirds, reptiles, and small mammals that either respond directly to subsidy levels or utilize subsidy-associated resources, such as invertebrate prey (Carlton and Hodder 2003, Dugan et al. 2003, Barrett et al. 2005, Schlacher et al. 2013, 2017, Page et al. 2021), suggesting a general pattern of multitrophic community enhancement that strongly scales with subsidy magnitudes.

As a more synoptic measure of the role of wrack subsidies in the functioning of the sandy beach ecosystems, we demonstrated that aggregated ecosystem functioning increases with the amount of subsidy a recipient ecosystem receives (Figure 5). CO_2 flux served as a measure of wrack utilization and processing by microbes and invertebrates, representing an estimate of net community respiration (Gomez et al. 2018, Rodil et al. 2019, Lastra et al. 2020). Nutrient concentrations in intertidal pore water are another measure of wrack processing and nutrient recycling facilitated by microbe and invertebrate activity on beaches (Dugan et al 2011, Rodil et al. 2019, Lowman et al. 2019). Wrack-associated invertebrate diversity is at risk (Dugan et al 2013, Schooler et al. 2017, Barnard et al 2021) and, although not always the case, biodiversity is known to enhance ecosystem functioning (Tilman et al. 2014). We used secondary production of the dominant beach invertebrate guild, talitrid amphipods, as a representative measure of invertebrate secondary production (Cardoso and Veloso 1996, Petracco et al. 2012). Flying insect abundance was incorporated because they can be an important component of the beach food web that are under sampled with sediment cores (Inglis 1989, Hodge et al. 2017). Lastly, we looked at species richness of wintering migratory shorebirds, important higher trophic level consumers in the beach food web (Hubbard and Dugan 2003, Schlacher et al. 2017). Our overall ecosystem function measure that factored in biogeochemical, biodiversity, and food web-based metrics, demonstrated ecosystem functioning increased with allochthonous subsidies of macrophyte wrack. Our results for open coast sandy beaches concur with those from multifunctionality studies of the effects of macroalgal cover on biogeochemical and community-based metrics in intertidal mud and sand flats (Ramus et al. 2017, Thomsen et al. 2019).

There is a critical need to understand ecosystem functioning within naturally assembled communities (van der Plas 2019). Variation in subsidies to sandy beaches underlies the differences we observed in community structure and ecosystem multifunctionality along a strong natural yet local scale range in these subsidies. While studies of multifunctionality including soil microorganisms (Wagg et al. 2014, Delgado-Baquerizo et al. 2016) terrestrial detritivores (Manning et al. 2017, Piccini et al. 2018) and aquatic macroinvertebrates (Duffy et al. 2003, Perkins et al 2015) focus on the role of animal richness, we show a strong response of functions (including biodiversity) to the availability of the basal resource, in this case macrophyte wrack (see Angelini et al. 2015, Thomsen et al. 2017). Across ecosystem types and trophic levels, biodiversity is considered a key for maintaining ecosystem multifunctionality (Lefcheck et al. 2015), however we demonstrate that the subsidy itself underpins biodiversity, and without the subsidy the ecological functions would be limited and/or missing from this ecosystem. The response metrics explored in this study strongly indicate that subsidy dynamics and associated ecosystem functions are tightly coupled and fluctuate greatly across space, even on a 100 km scale. Highly dynamic resources have strong impacts on biodiversity and ecosystem multifunctionality when present (Angelini et al. 2015). Similarly, a diverse resource supply can support more species through food and habitat provisioning (Hansen and Coleman 1998, Siemann et al. 1998, Haddad et al. 2001, Haddad et al. 2009).

Cross-ecosystem organic matter, passively transported to the sandy beach, is actively processed and transported to other ecosystems by consumers. Consumptive and decomposition processes by wrack-associated intertidal species results in regeneration of nutrients from wrack subsidies directly on the beach (Gomez et al. 2018, Lowman et al. 2019, Rodil et al. 2019). While these recycled nutrients can be returned to nearshore coastal ecosystems (Dugan et al. 2011, Goodridge and Melack 2014), a potentially much larger scale export of nutrients may be associated with mobile consumers (Anderson and Polis 1999, Williams et al. 2018). Higher trophic level consumers, like the shorebirds here, but also small mammals, utilize highly subsidized beaches and likely transfer a significant portion of allochthonous organic matter away from the beach and source ecosystems (Payne and Moore 2006, Mellbrand et al. 2011, Hyndes et al. 2013, Page et al. 2021). Mobile consumers can transport subsidy-derived energy and nutrients out of recipient ecosystems and deposit it elsewhere through excretion, death, and other mechanisms (Wheeler et al. 2014, Bampoh et al. 2019, Collins et al. 2020). This movement of resources can facilitate production and growth in the new system, terrestrial or aquatic, further connecting seemingly disparate ecosystems (Bauer and Hoye 2014) and highlighting the importance of an increased understanding of the role of subsidies and cross-ecosystem connectivity (Baruch et al. 2021).

Source ecosystems are intrinsically linked to the inputs of subsidies on sandy beaches (wrack, Liebowicz et al. 2016), and in other connected recipient ecosystems (carrion, phytoplankton, etc. Richardson et al. 2010, Schlacher et al. 2013, Zuercher and Galloway 2019). This means that conservation and restoration of a recipient ecosystem can be dependent on the state of the adjacent donor ecosystem (Gillis et al. 2017, Buckner et al. 2018, Wasson et al. 2021). Cross-ecosystem subsidies are critical for biodiversity and the provisioning of ecosystem services and functions, but subsidies can be hindered through reduced ecosystem connectivity including factors that impact donor ecosystems (Sheaves 2009, Olds et al. 2012, Mitchell et al. 2013, Thompson et al. 2017). Many factors affect connectivity between ecosystems and in the case of our study, changes to either the subsidy (species, biomass, etc.) or the connectivity between donor and recipient ecosystems could have dramatic effects on the recipient communities and food webs and the associated ecosystem functions. Giant kelp forests, the source ecosystem for sandy beaches in our study, face myriad challenges including warming ocean temperatures (Filbee-Dexter et al. 2016, Smale 2019), over-grazing by sea urchins (Ling et al. 2015, Boada et al. 2017, Rogers-Bennett and Catton 2019), decreasing nutritional quality (Lowman et al. 2021), and other local scale drivers of change (Krumhansl et al. 2016) which can lead to reductions in kelp biomass and subsequent export of this vital subsidy to beaches (see Revell et al. 2011). Kelps are foundation species on rocky reefs (Arkema et al. 2009, Castorani et al. 2018, Miller et al. 2018) as are marsh grasses in a salt marsh (Gedan and Bertness 2010) and trees in a forest (Ellison et al. 2005) through their ability to structure associated communities while also provisioning food and habitat. Given the functional importance of subsidies to the beach ecosystem, marine wrack subsidies, like kelp, are as much a foundation species in the recipient ecosystem as they are in the donor ecosystem. On sandy beaches, which are generally devoid of primary producers, marine wrack subsidies can function as foundation species by structuring the associated invertebrate community, providing food and habitat, and by stimulating numerous ecosystem functions.

While subsidy declines due to changes in kelp forests is of growing concern, changing dynamics within the recipient ecosystem may also disrupt this connectivity. Sandy beaches are heavily managed through grooming (raking) of wrack and coastal armoring, all of which lead to declines in the retention of subsidy itself and in the diversity and abundance of subsidy dependent biota (Dugan et al. 2003; Dugan et al 2008, Jaramillo et al 2020, Heerhartz et al. 2014, Schlacher et al. 2007, Schooler et al. 2017, Schooler et al. 2019). Larger scale impacts to the beach are also expected with sea level rise and climate dynamics (i.e. El Niño) (Barnard et al. 2015, Barnard et al. 2017, Vitousek et al. 2017, Myers et al. 2019, Barnard et al 2021). Loss of upper beach habitat and/or subsidy removal can effectively eliminate the connection to nearshore primary producers and prevent the incorporation and propagation of that subsidy of energy through the beach food web. Our results suggest that if wrack subsidies decline the multitrophic community and important biogeochemical processes of beach ecosystems would be significantly depressed. The space for time approach utilized in our study highlights the potential major negative impacts to ecosystem functioning that may be expected as climate forcing effects on sea level and kelp forests, in addition to coastal development, intensify.

Maintaining this connection requires resilient kelp forests on the supply side (Boada et al. 2017) and beaches with sufficient habitat scope to receive and process the subsidy (e.g. Myers et al. 2019). Stressors to both ecosystems from warming, sea level rise, and direct anthropogenic impacts that can eliminate the subsidy or leave the recipient ecosystem uncapable of retaining and processing the subsidy will cause impacts across spatial scales (Vitousek et al. 2017, Myers et al. 2019, Rogers-Bennett and Catton 2019, Smale 2019). Escalating pressures on coastal ecosystems already drive shifts in species distributions, declines in biodiversity, and reductions to ecosystem functioning (Harley et al. 2006). Maintaining cross-ecosystem connectivity in the face of these challenges is critical for coastal conservation efforts, including biodiversity, special status species, marine protected areas, and ecosystem functioning. Ecosystem connectivity should be a research and conservation priority as climate change impacts continue to impact sensitive coastal ecosystems, potentially altering the supply of key resource subsidies to recipient ecosystems.

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Tables

Table 1: Linear mixed effects models used in PiecewiseSEM with site as the random factor. Also provided are R^2_m (marginal R^2) and R^2_c (conditional R^2) for the response variables.

A.

Model	**R^2_m**	**R^2_c**
Detritivore biomass ~ Wrack % cover	0.06	0.53
Detritivore diversity ~ Detritivore biomass + Wrack % cover	0.24	0.49
Predator biomass ~ Detritivore biomass + Wrack % cover	0.43	0.45
Predator diversity ~ Detritivore diversity + Predator biomass + Wrack % cover	0.34	0.42

B.

Response	**Predictor**	**Standardized Regression Coefficient**	**p value**
Detritivore biomass	Wrack % cover	0.26	0.04
Detritivore diversity	Wrack % cover	0.51	< 0.001
Predator biomass	Detritivore biomass	0.36	< 0.001
Predator biomass	Wrack % cover	0.47	< 0.0001
Predator diversity	Predator biomass	0.48	< 0.001

Figure Captions

Figure 1: The 24 sandy beach sites sampled in Santa Barbara and Ventura Counties, California.

Figure 2: The relationship between marine wrack percent cover and A) total invertebrate species richness and B) mean invertebrate abundance (individuals m^{-1} beach) at our 24 study beaches.

Figure 3: A) Hypothesized pathways between variables. Variables are both predictors and responses. Each pathway was used in linear mixed effects models using PiecewiseSEM. B) Significant pathways (p-value (grey)) are displayed with arrows scaled to the size of the standardized regression coefficients (black). Conditional R^2 values are given for each response variable (blue). Note that all significant pathways were positive.

Figure 4: The relationship between marine wrack percent cover and A) Shorebird species richness and B) mean shorebird abundance (individuals km^{-1} beach). In addition, positive relationships were found between C) shorebird species richness and invertebrate species richness and D) shorebird abundance (individuals km^{-1} beach) and mean invertebrate abundance (individuals m^{-1} beach) at our 24 study beaches.

Figure 5: The relationship between marine wrack percent cover and the average value of six standardized ecosystem functions for our 24 study beaches. The ecosystem functions included here are pore water nutrient concentrations, CO_2 flux, invertebrate species richness, talitrid amphipod secondary production, flying insect abundance and shorebird species richness.

Figures

Figure 1

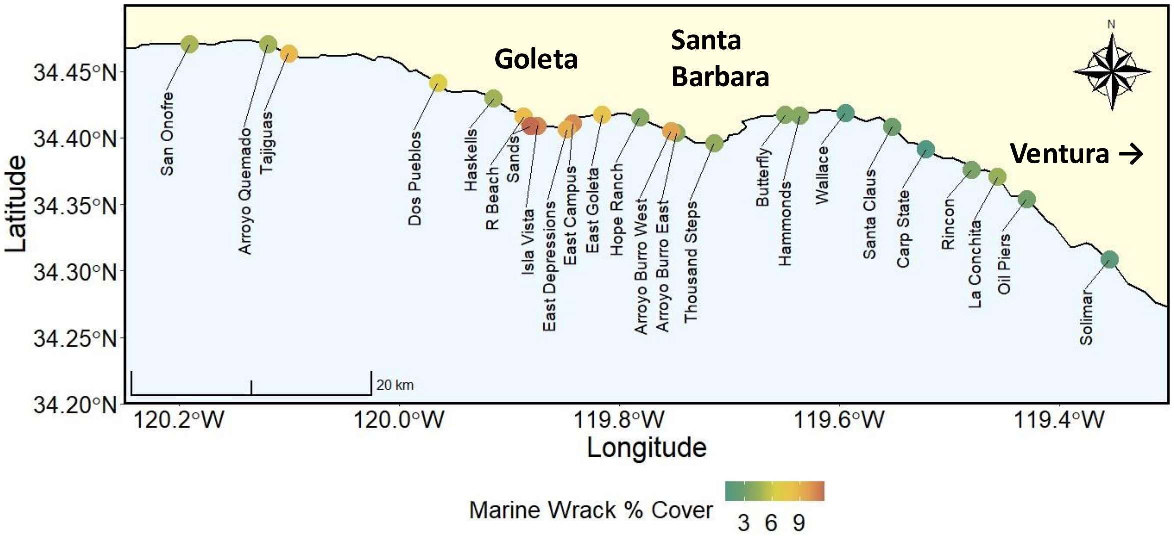


Figure 2

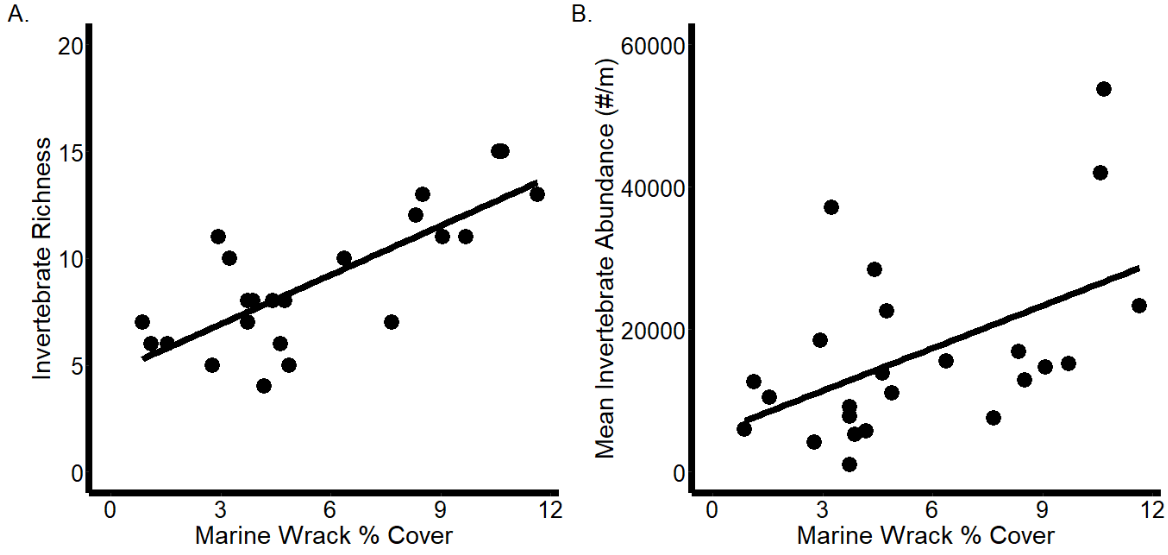

A.
20
15
10
5
0
Invertebrate Richness
0
3
6
9
12
Marine Wrack % Cover
B.
60000
40000
20000
0
Mean Invertebrate Abundance (#/m)
0
3
6
9
12
Marine Wrack % Cover

Figure 3

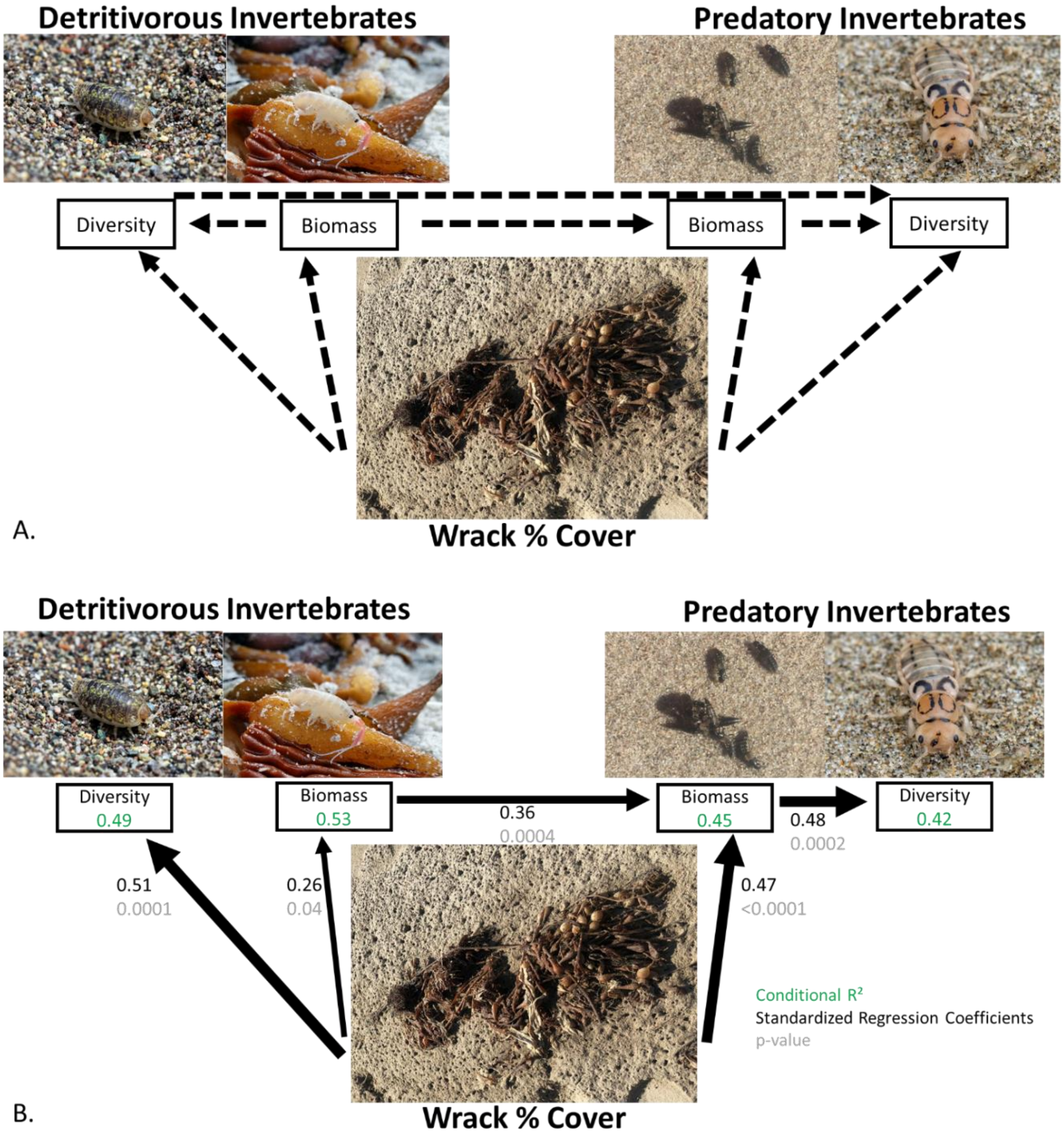
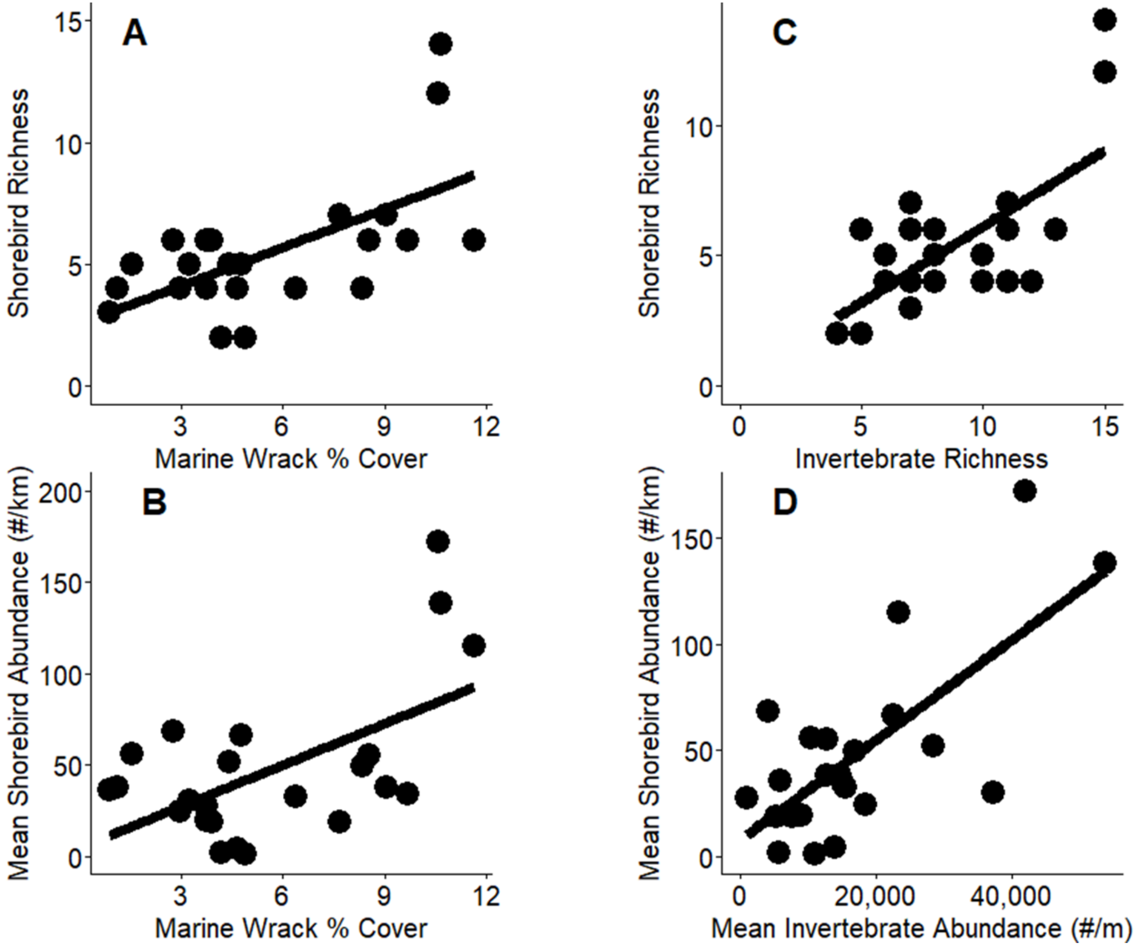
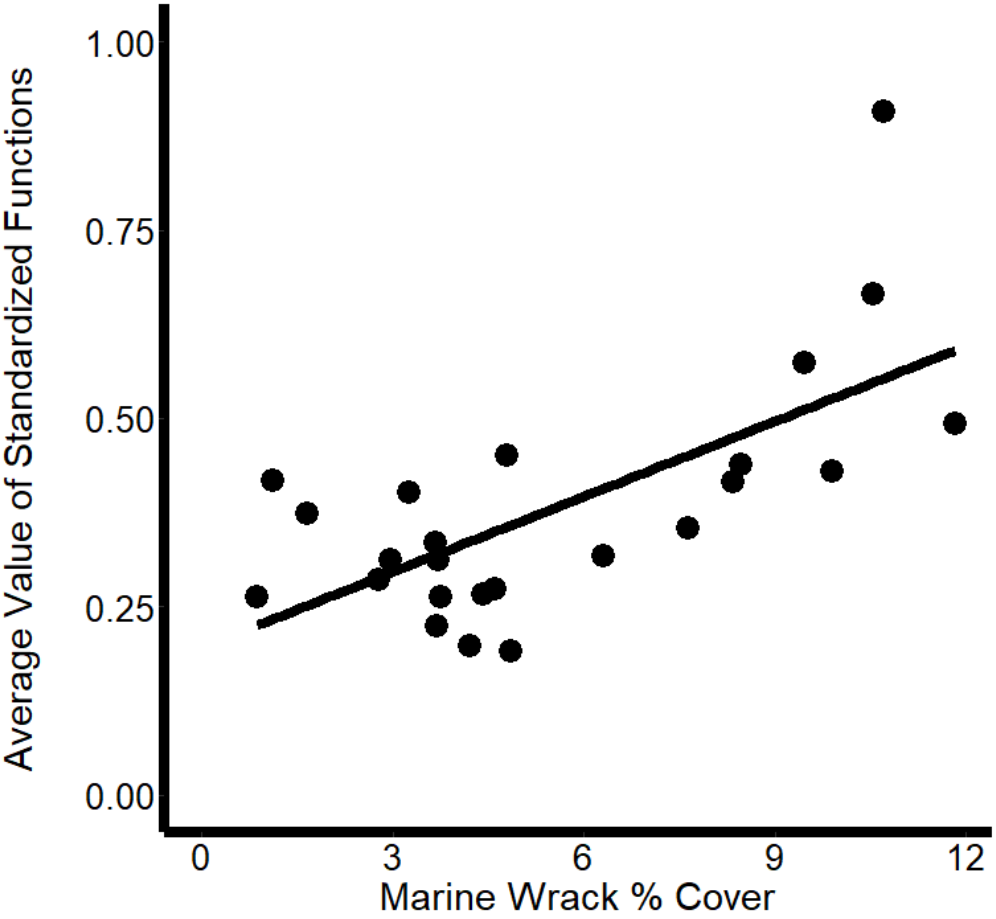

Detritivorous Invertebrates
Predatory Invertebrates
Diversity
Biomass
Biomass
Diversity
Wrack % Cover
A.
Detritivorous Invertebrates
Predatory Invertebrates
Diversity
0.49
Biomass
0.53
0.36
0.0004
Biomass
0.45
0.48
0.0002
Diversity
0.42
0.51
0.0001
0.26
0.04
0.47
<0.0001
Conditional R²
Standardized Regression Coefficients
p-value
Wrack % Cover
B.

Figure 4



A
Shorebird Richness
0
5
10
15
3
6
9
12
Marine Wrack % Cover
C
Shorebird Richness
0
5
10
0
5
10
15
Invertebrate Richness
B
Mean Shorebird Abundance (#/km)
0
50
100
150
200
3
6
9
12
Marine Wrack % Cover
D
Mean Shorebird Abundance (#/km)
0
50
100
150
0
20,000
40,000
Mean Invertebrate Abundance (#/m)

Figure 5


1.00
0.75
0.50
0.25
0.00
Average Value of Standardized Functions
0
3
6
9
12
Marine Wrack % Cover

Supplementary Material

Supplementary Table 1: Mean wrack cover at each of the 24 study beaches as total wrack cover (m^2 m^{-1}) and percent wrack cover.

Site	Wrack Cover (m^2 m^{-1})	Wrack Cover (%)
Thousand Steps	0.9	4.2
Arroyo Burro East	1.3	3.9
Arroyo Burro West	2.1	9.7
Arroyo Quemado	1.0	4.7
Butterfly	1.0	3.7
Carpinteria State	0.4	0.9
Dos Pueblos	1.7	6.4
East Campus	5.0	10.6
East Depressions	3.2	9.1
East Goleta	2.8	7.7
Hammond's	1.0	3.7
Haskell's	0.9	4.6
Hope Ranch	1.2	3.7
Isla Vista	3.2	10.7
La Conchita	2.1	4.4
Oil Piers	1.8	2.9
R Beach	3.8	8.3
Rincon	1.6	3.2
San Onofre	0.9	4.9
Sands	5.0	11.6
Santa Claus	1.3	2.8
Solimar	0.8	1.5
Tajiguas	2.1	8.5
Wallace	0.4	1.1