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UNIVERSITY OF SAN DIEGO

San Diego

Algal wrack community composition and succession on a sandy beach in

San Diego, CA

A thesis submitted in partial satisfaction of the
requirements for the degree of

Master of Science in Environmental and Ocean Sciences

by

Marisol Cynthia Palomares

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2020

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University of San Diego

San Diego

2020

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DEDICATION

I dedicate this to my best friend and biggest supporter: my husband Jaemin.

Thanks for moving across the country so I could go to graduate school, and thank you for encouraging me. 사랑해!

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ABSTRACT

Sandy beaches are high-energy impact zones that produce little to no organic material. Much of the organic matter on beaches is washed up on shore in the form of algal wrack, providing a vital source of nutrients, food, and habitat for a variety of organisms on the sandy beach. Over time wrack will decay and decompose, releasing nutrients including nitrogen and phosphorus, which are consumed by benthic microalgae and bacteria. The type of wrack and geomorphology of the beach environments affect decomposition, which in turn supports a variety of different wrack associated macrofaunal communities. Different species of algal wrack will support different species of animals, and can affect the taxonomic composition and number of species present. My research used a combination of manipulative and mensurative experiments to identify wrack associated macrofauna on a San Diego beach. I used the giant kelp species *Macrocystis pyrifera* to compare wrack associated macrofaunal community composition and abundance over a period of 21 days. There were higher abundances of macrofauna within the algal wrack relative to bare sand, and macrofaunal abundance increased over time in the algal wrack. Community composition within the wrack varied over time, with abundance changing by orders of magnitude. These results reinforce other findings demonstrating that algal wrack is an important primary food source and strongly influences macrofaunal communities and higher trophic levels. In the San Diego area algal wrack is an important component of the land-sea interface ecosystem.

Chapter One

Introduction

Sandy beaches are high-energy environments that produce little to no autochthonous organic material (Dugan and Hubbard 2016). Much of the organic matter on beaches arrives in the form of algal wrack, providing an allochthonous source of nutrients, food, and habitat for a variety of sandy beach organisms. Over time, beach-cast wrack decomposes, releasing nutrients that are taken up by benthic microalgae and bacteria (Rossi and Underwood 2002). Algal wrack supports macrofaunal communities rapidly after being washed up on the shore, with both the species of algae that compose the wrack and the beach environment affecting decomposition rate (Gomez et al. 2018). Organisms that feed on wrack and/or feed on primary consumers within the wrack are known as wrack-associated macrofauna (Colombini and Chelazzi 2003, Dugan et al. 2003). The species that compose the wrack support different wrack-associated macrofauna, and can affect taxonomic composition and number of macrofaunal species present (Mellbrand et al. 2011).

Bottom up processes are an important influence on the community structure in marine ecosystems (Polis et al. 1997). In systems with low primary productivity, particularly those with adjacent productive systems, spatial subsidies of organic material are common (Talley et al. 2006). Subsidies are defined as a “resource (prey, detritus, nutrient) from one habitat to a recipient (plant or consumer) from a second habitat, which increases population productivity of the recipient, potentially altering consumer resource dynamics in the recipient

system” (Polis et al. 1997). For a sandy beach ecosystem, much of this input comes from carrion and wrack (Polis and Hurd 1996), with algal wrack the more abundant subsidy, as it more frequently washes up on the shore (Polis and Hurd 1996; Talley et al. unpublished data).

Kelp forests produce a large amount of organic matter, from approximately 300 to 1900 g cm⁻² yr⁻¹ (Foster and Schiel 1985), and they export approximately 43% of the net primary production to neighboring ecosystems (Duarte and Cebrian 1996). Oceanic processes and physical factors such as waves, currents, winds, and coastal topography impact wrack input to beaches (Polis et al. 2004, Gomez et al. 2012). Sandy beaches, conversely, only produce from 0 to 10 gCm⁻²yr⁻¹ of *in situ* organic material (McLachlan & Brown 2006). Thus algal wrack can be an overwhelmingly important source of nutrients to beach communities, with beaches located adjacent to kelp forests or other algal sources receiving the greatest input of algal wrack (Mateo 2010). The life cycle of the dominant species of macroalgae also determines the amount and spatial and temporal variability of input to beaches over time (Barreiro et al. 2011). Seasonality of both the algae and environmental conditions is often the strongest determinant of wrack presence (e.g., Ochieng and Erfteimeijer 1999, Barreiro et al. 2010, Mateo 2010). Within southern California, the mean input of algal wrack to beaches is estimated to be approximately 473 kg of wet weight per linear meter of beach per year (Hayes 1974), and there are an estimated 39,000 – 348,000 drifting rafts of the giant kelp *Macrocystis pyrifera* at any given time in the southern California bight (Hobday 2000).

In temperate areas, sandy beach macrofauna are supported almost entirely by algal wrack (Dugan et al. 2003). Changes of input or availability of wrack can therefore strongly alter the community structure on beaches. Suspension feeders (e.g. hippid crabs and bivalves) and herbivores (including amphipods, isopods, and insects) are the primary consumers of the algal wrack (Dugan et al. 2003). These primary consumers of wrack are a food source for many secondary consumers, including shore birds, seabirds, fishes, and marine mammals. Other taxa also feed on both the wrack and on wrack-associated macrofauna species, including crabs, beetles, and polychaetes (Dugan et al. 2003). Wrack also functions as habitat for a diverse macrofaunal community (Inglis 1989), which in California is mainly composed of arthropods (Dugan et al. 2000).

In the Santa Barbara area of southern California, where these communities have been well-studied, beaches have a higher abundance and diversity of wrack-associated macrofauna within the wrack relative to the bare sand (Dugan et al. 2003). Previous studies in Spain showed that wrack-associated macrofaunal abundance and diversity increased and then decreased over a period of 21 days within the wrack patches (Rodil et al. 2008). The main goal of this project was to increase understanding of wrack-associated macrofaunal communities in San Diego beaches, an urban area that experiences high levels of human influence--from foot traffic to beach grooming to stormwater outfalls. This project used a manipulative experiment to investigate the identity and succession of wrack-associated macrofauna on a San Diego beach. I examined the effects of algal

wrack on macrofaunal community structure (abundance and composition), and how that structure varied over time.

CHAPTER TWO

2.1 Introduction

Sandy beaches are an important ecosystem (Levin et al. 2001, McLachlan and Defeo 2018) that serves as a boundary between marine and terrestrial habitats, and thus mediates connectivity between these two systems (Defeo et al. 2009). Sandy beaches provide numerous ecosystem services, including protection from erosion, sediment transport, and water filtration (Defeo et al. 2009, McLachlan and Defeo 2018), as well as critical habitat for many species, including clams, whelks, worms, sand hoppers, crabs, sea lice, sand dollars, protozoans, microscopic plants, and bacteria (Brown and McLachlan 1990). In addition to these resident organisms, many other transient species use the beach. For example, coastal mammalian predators (“maritime mammals”; Carlton and Hodder 2003) such as raccoons, foxes, bears, and rodents feed on intertidal organisms (Schlacher et al. 2013). Supralittoral zones also provide nesting grounds for sea turtles and shorebirds (Martin et al. 2006), and many coastal dune animals move across the beach to feed (McLachlan 1991). Beaches also provide support for migrating and resident shore birds by providing important food resources (Dugan et al. 2003).

Sandy beaches are generally a high-energy environment that produces little to no organic material, with minimal in-situ primary production (Inglis 1989). The vast majority of organic material is allochthonous, and this movement of organic material between habitats is a "spatial subsidy", as defined by Polis et al. (1997). Specifically, beach wrack represents a "donor controlled resource", as

the organisms consuming the organic material do not affect the rate that it arrives on the beach (Talley et al. 2006).

Much of the organic matter arrives in the form of algal wrack. In some areas, as much as 2.72 to 77.29 kg per m²yr⁻¹ (dry weight) arrives on sandy beaches (Polis and Hurd 1996). In southern California, wrack input is estimated to be 473 kg wet weight per meter per year (Hayes 1974). This material provides a vital source of nutrients and food for a variety of organisms on the sandy beach, including filter feeders, amphipods, and crabs (Brown and McLachlan 1990). Organisms on sandy beaches are supported by inputs of this organic material from the marine zone, forming a bottom-up food web largely based on algal wrack (Brown and McLachlan 1990).

Wrack also serves as habitat and refuge for supralittoral fauna, mainly arthropods (Olabarria et al. 2007). Wrack is deposited throughout the intertidal zone, creating a mosaic of bare sand and patches of wrack (Rossi and Underwood 2002). Over time, wrack will decay and decompose, releasing nutrients that in turn are used by benthic microalgae and bacteria (Rossi and Underwood 2002). The type of wrack and structure of the beach environment affects decomposition, which in turn affects the wrack-associated macrofaunal communities. Different algal species composing wrack will support different species of animals and can affect taxonomic composition and number of species present (Goecker and Kall 2003). Changes in wrack availability will directly alter the abundances of consumers, with ramifying effects to higher trophic levels (Polis et al. 2004). Wrack-associated macrofauna serve as a primary food source for numerous

vertebrate predators including shorebirds, seabirds, and mammals (Colombini and Chelazzi 2003, Carlton and Hodder 2003). In California this includes the threatened western snowy plover (*Charadrius alexandrinus nivosus*; Dugan et al. 2003).

The mosaic of bare sand and wrack patches can influence the distribution and feeding behavior of wrack-associated macrofauna, and thus the entire food web (Rossi and Underwood 2002). The higher the tidal elevation at which algae is located, the longer it persists on the shore. This higher-tide seaweed is not as influenced by the fluctuations in water levels by waves and tides and will become desiccated more rapidly than lower wrack mats, which are inundated more often (Rodil et al. 2007). This in turn affects how quickly it releases nutrients into the sediments, with consequences for bacterial growth and provision of organic matter to the system (Rodil et al. 2019).

Abundances of macrofauna are significantly higher in wrack than in bare sand (Rodil et al. 2007). Studies done in Chile and Spain show colonization of these algal wrack patches peaked between 3 to 7 days after wrack appeared, within the wrack patches, and then gradually decreased until day 21 (Rodil et al. 2007). Other studies have shown strong associations between macrofauna and fresh wrack, and weak associations between macrofauna and aged wrack (Jaramillo et al. 2006). It is unknown what the colonization rate of wrack by wrack-associated macrofauna is outside of these select few studies. This study aimed to improve our understanding of wrack-macrofaunal associations on San

Diego beaches to better inform decisions surrounding the management of these important ecosystems and recreational areas.

This project used a controlled wrack amendment of a sandy beach to ask the following research questions:

1. How does macrofaunal community structure differ between algal wrack and bare sand?
2. How does macrofaunal community structure within the wrack change through time?

2.2 Methods

Study Site

This study was conducted along a ~170m transect at the southern end of Black's Beach (32°52'42.8"N 117°15'04.7"W), a wave-dominated sandy beach located in the central portion of San Diego, California's 110 kilometers of shoreline (Figure 1). Black's Beach is a 2 kilometer stretch of beach that is a part of the San Diego Scripps Coastal State Marine Conservation Area.

Field Sampling

The experiment ran from August 10-31, 2018, and began at high spring tide, to ensure that algae placed along the wrack line would not be washed away before the planned 21 days had elapsed. Samples of the alga *Macrocystis pyrifera* were collected ~1.5 km offshore of Point Loma, San Diego. That same day, the alga was weighed and separated into 15 individual 5 kg (wet weight) replicates,

and placed at ~10 m intervals along a transect at the high tide mark from the previous night's high tide (~2.15 m MLLW; Figure 1). Three patches were randomly chosen, removed, and taken to the lab on each sampling date (1, 3, 7, 12, and 21 days following deployment). To quantitatively sample organisms within the wrack, a large plastic bag was used to rapidly and completely cover the patch, and then closed around the surface alga before being sealed (referred to as "wrack samples" in the Results section). Macrofauna beneath the wrack was collected with a 30 cm diameter plastic corer penetrating 20 cm deep into the sand (referred to as "sand samples" in the Results). Three cores were taken per wrack mat from near the center of the patch. Three control samples were also taken for each algal patch sampled, by using a 30 cm diameter plastic corer 1m apart from the wrack patch and separated by 1 m, to measure the abundance of macrofauna in bare sand (referred to as "control samples" in the Results). Sand cores were sieved on site through a 1 mm mesh sieve, and organisms were collected and transported to the lab. Field methods were modified from Rodil et al. (2008).

Lab Methods

Algal samples were stored in a -10° C freezer for 24 hours, thawed, then rinsed with water and sieved again through a 1mm mesh sieve. Algae and organisms were separated, and organisms were preserved with 70% ethanol. Organisms were then sorted, counted, and identified to the lowest taxonomic level possible using a dissecting microscope with magnification 10x-25x – this provided family-level identification for most individuals, but all samples were sorted at least to order. Organisms were enumerated by presence of a head in

cases where specimens were not whole. Samples were referenced to the collection at the San Diego Natural History Museum, with the help of several entomologists (see Acknowledgements). A collection of a representative sample of species recovered was retained and catalogued by the author and museum staff at the San Diego Natural History Museum in San Diego, California. Identification was supplemented by using published keys (Morris, Abbott, and Haderlie 1980, Arnett and Thomas 2001, and Marshall 2006).

Statistical Methods

All statistical tests were conducted using the program R[®]. Samples were standardized before statistical analysis to organisms found per square meter. A paired t-test and Wilcoxon rank sum test were used to compare algal wrack abundance to control (bare sand) abundance. Welch's t-test and Wilcoxon rank sum test were used to compare abundance at each time period for all samples. Species diversity was evaluated using Shannon's Diversity index (H).

Differences in macrofaunal community composition between algal wrack, underlying sand, and control samples, and within these sample types across sampling dates, were analyzed using densities (# m⁻²) of each taxon identified to the lowest taxonomic level feasible. All data were $\log(x + 1)$ transformed before analyses to meet the assumptions of normality and homogeneity of variance for the statistical tests used (Clarke 1993; Zar 2009). Multivariate analyses were carried out using Primer-e software (Clarke and Warwick 2001; Clarke and Gorley 2006). Differences in the macrofaunal community between algal wrack, sand, and control plots, and across sample date, were visualized using nonmetric

multidimensional scaling (nMDS) on Bray–Curtis similarity indices of the $\log(x+1)$ transformed faunal data to reduce the dominant contributions of abundant species (Clarke 1993; Clarke and Gorley 2006). Six different random starting points with up to 1,000 steps were used. The stress values from the six runs were examined for stability to determine whether a global solution had been found. Only analyses with stress values of <0.2 were used; stress is a measure of how well the solution (in this case the 2-D nMDS plots) represents the multidimensional distances between the data. Clarke (1993) suggests values <0.1 are good and <0.2 are useful.

Significance testing comparing macrofaunal community composition in algal wrack and underlying sand samples to the control samples, as well as across sample dates, was performed using an analysis of similarity (ANOSIM) procedure on the Bray Curtis similarity matrices. Analyses of dissimilarities of community composition across the locations sampled and sample date were performed using a similarity percentage analysis (SIMPER). The SIMPER results specify which taxa are responsible for the ANOSIM results by comparing the average abundances of each taxon between each sample type (algal wrack, underlying sand, or control) and sample date. The average dissimilarity between the sample types (algal wrack, sand, or control) and sample dates is computed and then broken down into contributions of each taxon. When testing for differences in macrofaunal communities structure (multivariate analyses), the samples of algal wrack were combined with the samples of the sand beneath the wrack. In the univariate analyses, sand and wrack samples were both combined and left

separate to explore the contributions of each fraction to patterns of abundance and diversity through time.

2.3 Results

Broad patterns of colonization and succession

A total of 10,655 organisms from 19 different families and at least 22 different species were collected through this experiment. In the control samples, a total of only 61 individuals from at least 11 different species were collected, and all of these taxa were also found in the algal wrack patches. Eleven unique taxa were found in the algal wrack that did not occur in the control samples. Several aspects of community structure (density of individuals, number of taxa per sample, and abundance of main representative taxa) within the control samples were similar at every time period tested ($p > 0.1$, R statistic < 0 , Table 1).

Colonization of the algal wrack was rapid, with over 90% of taxa colonizing the wrack within 24 hours, and all taxa colonized the wrack by 3 days, (Table 2, Figure 2). There was no notable pattern of colonization in the control samples. Abundance of all organisms was highest in the algal wrack patches compared to the sand underneath the patch and the control samples (Figure 3). When combining wrack samples and the samples of sand beneath, adult Coleoptera and Diptera abundance peaked on day 1, and while Coleoptera and

Diptera larval abundances were highly variable, they were most abundant on day 7 (Figures 4, 5).

Influence of Algal Wrack: Total Abundance

Total macrofaunal abundance within the algal wrack samples was relatively high and highly variable in the first week, before declining and becoming more similar to the sand and control samples at days 12 and 21 (Figure 3). There was a significant difference in macrofaunal abundance through time between the algal wrack and sand samples (Figure 3). Abundance in the sand underlying the wrack was also greater than in the control on days 3 and 7, although quite variable on day 7 (Figure 3).

Diversity

There was a difference in macrofaunal diversity through time between the algal wrack and sand samples (Figure 6). There was high diversity ($H = 1.4$) of wrack-associated macrofauna at day 1 (24 hours after algae had been placed on the shore). Diversity gradually declined until day 12, and then increased again on day 21 (Figure 6). The diversity of the organisms found in the sand beneath algal wrack was highest at day 3, and then decreased until day 12, with a second increase on day 21. In the control samples, diversity was highest for day 3, but fluctuated throughout the 21 days (Figure 5). There was high variability at each time period.

Community structure

Macrofaunal composition in the wrack samples differed between day 1 and all the subsequent days of the experiment driven mostly by the initial

appearance of dipteran, coleopteran and amphipod (*Megalorchestia* spp.) adults, followed by their rapid decline and replacement by dipteran and coleopteran larvae (Figures 4, 5; Table 1). The composition in wrack at day 3 differed from that on day 12 also due to the greater abundance of adult *Megalorchestia* spp. and beetles on the earlier date, and the increased abundance of both dipteran and coleopteran larvae on the later date (Table 1). There were no differences in macrofaunal community composition among dates within the sand samples (S) from under the wrack (ANOSIM $p \geq 0.2$) or the control samples (ANOSIM $p \geq 0.4$).

There was a significant difference in the communities associated with algal wrack and control samples at days 1 and 21 (ANOSIM $p \leq 0.1$, Table 1). At day 1, the difference was due to more adult flies and fewer coleoptera larvae and an adult Tenebrionid beetle, *Phalaris rotundata*, found in the wrack samples than the controls. At day 21, this difference was primarily due to greater abundances of dipteran larvae and fewer *P. rotundata* and coleoptera larvae in the algal wrack than control samples (Table 1). There were no differences in community composition between sand and control samples within any of the sample dates (ANOSIM $p \geq 0.20$).

2.4 Discussion

This study showed that algal wrack presence had strong transient effects on the macrofaunal community abundance, diversity and composition on a sandy beach by seemingly providing food and substrate for adult terrestrial and marine arthropods to colonize and, in the case of dipterans and coleopterans, lay eggs and

use as a nursery for larvae. These results reaffirm that spatial subsidies are critical drivers of sandy beach macrofaunal community structure. Even though the bursts of macrofaunal abundance and diversity, as well as the presence of algal wrack patches themselves, are relatively short-lived, the coming and going of multiple patches across a beach creates a more diverse and dynamic landscape on a broader scale than one with no ephemeral wrack patches (e.g., Fahrig 2004). The presence of algal wrack may be the most important factor in determining macrofaunal population abundance on sandy beaches, since algal wrack is the primary food source and habitat structure for these wrack-associated macrofauna (Dugan et al. 2003).

Comparing abundance to previous studies

The number of taxa found in all samples (22) is similar to those found in a comparable study in Santa Barbara County in southern California, which found from 11 to 37 species per beach across 15 different beaches (Dugan et al. 2003). These numbers are also similar to comparable studies from temperate beaches worldwide, which ranged from 13 species per beach (Lastra et al. 2015) to 53 species in algal wrack (Rodil et al. 2008; see Table 3).

The majority of organisms (96%) sampled were adult and larval flies, adult and larval beetles, and *Megalorchestia* species. This too is similar to other studies performed on similar beach types (Table 3). Inglis (1989) found 22 macrofaunal species of which six species (an amphipod, a dipteran, a centipede and three beetles) made up 93% of the community on a beach in New Zealand.

Olabarria et al. (2007) found that two dipteran species and an amphipod made up 77% of the total abundance on a Spanish beach.

The presence of algal wrack strongly influenced community structure compared to bare sand, increasing abundance by two to three orders of magnitude. This reinforces previous studies which found similar results (Dugan et al. 2003, Rodil et al. 2008), and suggests that these results are broadly generalizable across temperate sandy beaches.

Temporal Trends

The change in abundance at each time period was largely forced by the change of beetle and fly larval and adult abundances. There was a trend of abundance monotonically decreasing over time in the algal wrack, largely driven by adult Diptera and Coleoptera species, which peaked at day 1 and then steadily decreased through to the end of the study on day 21. Meanwhile, both beetle and fly larval abundance peaked at day 7. This follows the life histories of these organisms, as adult beetles and flies are among the first to colonize the wrack. They feed and potentially lay eggs on the wrack, which develop into larvae that feed off of the wrack or other wrack-associated macrofauna. Kelp flies can have a life cycle as short as six days from egg to adult (Klosinski 2015). The fly larvae derive nourishment from the decaying wrack matter, and the adults consume bacteria and decomposing wrack (Klosinski 2015). Beetles from the family Staphylinidae were found in algal wrack samples, and are carnivorous, foraging on Diptera larvae. This family has species that can develop from egg to adult in a few days to a few weeks (Frank and Thomas 1999, Echegaray and Cloyd 2013).

Species from the genus *Cafius* in the Staphylinidae family have a life cycle from egg to adult that is approximately 28 to 39 days, and take 6 days to develop from egg to larvae. These species have historically been observed in San Diego County (James et al. 1971). Interestingly, one of the common tenebrionids in this sampling, *Phalaris rotundata*, has been reported to require a month to transform from egg to adult, suggesting much of the energy transferred from kelp to *Phalaris* was transferred rapidly to higher trophic levels (Moore 1976). The population of this species at the neighboring beach to the study site is darker colored than other populations and is endangered (Moore 1974), suggesting that the darker colored *P. rotundata* found in this study is endangered. Other Tenebrionid species can have an incubation period from egg to larvae of 2-6 days (Gomez et al. 1988). Thus the development rates of these species support the pattern of abundance found in the samples. The high variability of diversity at each time period may be due to the small sample size ($n = 3$).

The change in abundance of beetle and fly larval and adult abundances is an example of heterotrophic succession, as the organisms and life stage of these organisms associated with the wrack change through time as the wrack decomposes and desiccates (Colombini and Chelazzi 2003, Olabarria et al. 2007). This change in community composition is typical of 'drift line communities' (Colombini and Chelazzi 2003). The tides wash ashore fresh wrack and older wrack desiccates, creating a mosaic of wrack patches on the beach. Different patches have differing stages of colonization and consumption across the landscape, further enhancing diversity (Rossi and Underwood 2002).

Flies and beetles were abundant in samples collected. Algal flies and herbivorous beetles feed off of the wrack directly, while the carnivorous beetles found likely feed off of the primary consumers of the wrack and their larvae. The succession of wrack-associated macrofaunal communities may be due to ‘niche differences’ among these species that best utilize the resources available to them (Olabarria et al. 2007).

Diversity

While most studies have found talitrid amphipods and isopods to be the primary consumers of wrack (Inglis 1989, Colombini and Chelazzi 2003), this study found beetles and flies to be dominant (Figures 4, 5), consistent with a similar study in Spain (Olabarria et al. 2007). There was historically an abundance of isopods on southern California beaches, including those in San Diego County (Hubbard et al. 2014). These populations have declined over the past 50 years by as much as three orders of magnitude due to habitat loss and habitat alteration from coastal development (Hubbard et al. 2014). Further, isopods are more affected than other taxa by this development because of their low fecundity, limited dispersal, and narrow habitat requirements (Brown 2000). The loss of the upper intertidal zone through human development is associated with declines in diversity and distribution of upper intertidal macroinvertebrates, including isopods and amphipods (Brown 2000). Any robust populations of these isopods occur largely on unarmored beaches with limited vehicle and pedestrian access (Hubbard et al. 2014). While this study took place on a less-trafficked beach backed with cliffs, the location is a popular surfing area and does have some

vehicle access by lifeguards. The urbanization of the San Diegan coastal area may explain some of the lack of isopods found, and supports the theory that this population is in decline, and the need for conservation efforts on sandy beaches. It is also worth noting that samples were taken from a very high intertidal elevation, to capture dynamics at spring high tide, which may have also limited access to isopods, amphipods, and other crustaceans.

Considerations of this study

There were a few artifacts of the experiment and ocean/weather conditions that could have resulted in either over- or under-estimates of abundance and diversity. First, macrofaunal measures made using the individual samples of wrack and the sand beneath may have been either over- or under-estimated because the removal of algal wrack during sampling may have disturbed the macrofauna in the bottom layers of wrack (e.g., caused them to fall off) or at the sand surface just beneath (e.g., caused them to adhere to the algae). Next, wrack stranded on the shore desiccates over time. The algal wrack in this experiment was placed at the wrack line created by an extreme spring high tide, and thus ensured that the wrack would not be wetted again by the tides during the experiment. The algae dried out rapidly within the first two days and remained dried for the duration of the experiment. This represents a suboptimal food source for wrack-associated macrofauna, as these organisms prefer algae that is not as desiccated (Jaramillo et al. 2006). As such, the changes in abundance induced by algal wrack in this study likely represent an underestimate of the effects across an

entire beach, and may also explain the low amphipod and isopod abundances (Lastra et al. 2015).

Finally, during August 2018, there was unusually high surface water temperature in San Diego, with the highest ocean temperature recorded since record keeping began (Robbins 2018). Because of this, all kelp offshore above the thermocline began to senesce. This may have expedited decomposition on the beach. Decomposing wrack releases nutrients into the sand, and microbiota increase with increasing ageing time (Lastra et al. 2015). Because microbes become more abundant on decomposed wrack, this adds nutritional value for consumers (Lastra et al. 2015). The rapid decomposition and increased nutritional value of kelp placed out on the shore may have influenced the community composition, and explain the abundance of beetles and flies found. Increasing global temperatures will accelerate wrack decomposition and beach metabolism (Lastra et al. 2018), and results of this study may be an indicator of future changes experienced by sandy beach ecosystems.

Conclusions

Algal wrack is a critical driver of the sandy beach ecosystem, and this study reinforces and geographically expands previous work. Algal wrack is a principal influence on the sandy beach community as it is the primary food source and provides habitat for a variety of organisms (Dugan et al. 2003). The study demonstrates that algal wrack supports an abundant community of macrofauna and other organisms, forming a significant bottom-up factor that affects the

wrack-associated community, including species diversity and abundance, on a sandy beach in San Diego.

Wrack-associated organisms are disproportionately vulnerable to beach impacts, such as erosion and sea level rise (Schooler et al. 2017). Sandy beaches are encountering ‘coastal squeeze’, in which they are being pressured from expanding coastal development and rising sea levels (Defeo et al. 2009). Another anthropogenic impact on sandy beaches is beach grooming, the practice of clearing away wrack and debris with heavy machinery. Many studies have shown the detrimental impacts of this practice to this ecosystem (Dugan et al. 2003, Rodil et al. 2008, Defeo et al. 2009). The City of San Diego performs regular beach grooming on city beaches, and the results of this study supports minimizing this practice. Management practices should take into account the importance of algae along the coast and plans should be modified accordingly to preserve the abundance and diversity of species along sandy shores, and to maintain its function in connecting marine and terrestrial food webs.

CHAPTER THREE

Discussion

Algal wrack occurrence along the beach affects macrofaunal abundance, diversity, and composition. Algae are a critical driver of the sandy beach ecosystem in that they provide food and substrate for arthropods, dipterans, and coleopterans (Dugan et al. 2003). These organisms are primary consumers for shore birds, mammals, and other resident and transient organisms along the beach (Rodil et al. 2008). The abundance of organisms found during this study are similar to those done in comparable studies in California.

There were greater number of organisms by two to three orders of magnitude in algal wrack patches compared to the bare sand. Algal wrack was immediately colonized by day 1, largely by adult flies. By day 3, both adult flies and beetles were extremely abundant (over 500 individual beetles and 2000 individual flies per wrack patch at day 3). By day 7, the wrack community was dominated by larvae from these same taxa, and by day 21, macrofaunal abundance and composition within the wrack resembled those from the control samples, suggesting that flies had completed their life cycle and that the wrack may have been too desiccated for further consumption by other wrack-associated macrofauna. Wrack-associated macrofauna prefer fresher and wetter algae and so as time passes, these organisms are more likely to feed on algal wrack more recently washed to the shore (Olabarria et al. 2007).

Significance

Wrack-associated organisms are disproportionately vulnerable to beach impacts, such as sea level rise and erosion (Schooler et al. 2017), and shorter-term activities, such as beach grooming and vehicle use. Beach grooming, the practice of clearing away wrack on beaches, occurs in populated areas to remove wrack and trash, making the beach more attractive for recreational activities. Over 160 km of southern California's beaches are regularly groomed (Dugan et al. 2003). Beach grooming removes a vital source of nutrients and habitat for many organisms from the sandy beach ecosystem. Not only does beach grooming remove unwanted debris and algal wrack, it disturbs resident organisms and roughens sand, allowing greater surface area to be eroded by wind (Defeo et al. 2000). Since wrack patches are critical to so many organisms, there are deleterious effects of grooming, including the reduction of species richness, abundance, and biomass (Dugan et al. 2003, Fanini et al. 2005). These impacts cascade up the food web and impact higher trophic levels by reducing amount of prey available (Dugan and Hubbard 2009). Beach grooming also directly impacts many shorebirds, by destroying nests and indirectly depleting their food supply. In California, threatened snowy plovers are directly negatively impacted by grooming causing loss of eggs (Page et al. 1995). Grooming destroys other beach nesting organisms such as turtles and fishes, and can kill the young of these species (Martin et al. 2006).

Repeated grooming alters the distribution of native plants, sediment transport, and local topography (Nordstrom et al. 2007). In California, Dugan et

al. (2010) showed that grooming directly and indirectly negatively impacts the coastal dune and strand habitats. Native plants have lower seed banks, survival, and reproduction on groomed beaches compared to ungroomed. Coastal strand ecosystems have become unvegetated barren habitats due to grooming (Dugan et al. 2010). Regular grooming also discourages hummock and dune formation by removing driftwood and cobbles and could affect the processes of sediment accumulation and loss (Nordstrom et al. 2007, Dugan et al. 2010).

One management practice to conserve beach biodiversity is to implement grooming only in designated areas, while leaving part of a beach or nearby beaches ungroomed. Marine protected areas in California should also extend to cover all of a sandy beach, instead of the common mean high tide (Dugan and Hubbard 2016). Restricting beach grooming in marine protected areas will protect biodiversity in these areas further.

Sandy beach ecosystems are continuously pressured by human activities, including climate change consequences such as sea level rise. The ecosystem services and functions provided by this coastal area are incredibly important. Beach grooming is an overlooked component in conservation efforts, and with the quantification of wrack-associated macrofauna I hope to increase understanding and awareness about the importance of algal wrack on sandy beaches.

Tables

Table 1. Results of ANOSIM and SIMPER analysis showing comparisons of macrofaunal community composition within algal wrack samples (W) over time, within control samples (C) over time, and between algal wrack and control samples within sample date (number corresponds to days algae was left on the beach). N=3 replicate samples taken from each treatment on each sample date. ANOSIM Global R=0.14, P=0.026. Only pairwise comparisons with $p \leq 0.10$ are shown. All pairwise comparisons within sand (S) and control (C) samples among dates were $p \geq 0.20$ and comparisons between sand (S) and control (C) samples within sample dates were $p \geq 0.20$. Shown are the taxa contributing to 50% of variability in macrofaunal community composition between groups (SIMPER).

Pairwise Tests

Groups	Taxa Responsible	Contribution %
W-1, W-3	Diptera larvae	22
	Diptera	11
	<i>Megalorchestia</i> spp.	10
	<i>Cercyon fimbriatus</i>	9
W-1, W-7	Diptera larvae	19
	Diptera	10
	Coleoptera larvae	9
	Diptera sp.	9
	<i>Megalorchestia</i> spp.	8
W-1, W-12	Diptera larvae	28
	Coleoptera larvae	11
	Diptera sp.	7
	<i>Megalorchestia</i> spp.	7
W-1, W-21	Diptera larvae	28
	Corophiidae	8
	Coleoptera larvae	7
	<i>Megalorchestia</i> spp.	6
	<i>Cercyon fimbriatus</i>	6
W-3, W-12	Diptera larvae	21
	Coleoptera larvae	13
	<i>Megalorchestia</i> spp.	9
	Staphylindae sp.	7
	Tenebrionid	6
W-1, C-1	Coleoptera larvae	24
	<i>Phaleria rotundata</i>	20
	Diptera	9
W-21, C-21	Diptera larvae	29
	<i>Phaleria rotundata</i>	18
	Coleoptera larvae	15

Table 2. Time in days of first and last appearance of taxa in the algal wrack and control samples.

Taxa	First Appearance		Last Appearance	
	Wrack/Sand	Control	Wrack/Sand	Control
<i>Phalaria rotundata</i>	1	1	21	21
Staphylinids	1	1	21	1
Histerid	1	1	21	1
Hydrophilid	1	None	3	None
<i>Cercyon fimbriatus</i>	1	None	3	None
Curculionidae	1	7	21	7
<i>Emphyastes fucicola</i>	1	7	3	7
<i>Labarrus pseudoliuidus</i>	1	None	1	None
Anthicidae	3	none	21	none
<i>Sapintus</i> sp.	7	None	7	None
Elateridae	1	None	7	None
Hymenoptera	1	None	21	None
Formicidae	1	None	3	None
Diptera	1	1	21	3
Diptera larvae	1	7	21	12
Crustacean	1	3	12	3
Isopod	1	7	12	12
Corophiidae	1	None	21	None
<i>Megalorchestia</i> spp.	1	1	21	7
Dermaptera	3	None	7	None
<i>Euborellia annulipes</i>	3	None	3	None
Hemiptera	3	None	21	None
Saldidae	3	None	3	None

Table 3. Wrack-associated macrofauna dominant species and densities found from selected studies.

Study	Location	Total Number of Wrack associated macrofauna Species Found per beach	Species	Abundance (in linear meters)	Collection Location on Beach (Tidal Height)
This study	Southern California	22 unique taxa	Wrack-associated macrofauna	3000 individuals per meter in algal wrack	2.15m MLLW, spring high tide
Dugan et al. 2003	Southern California		Wrack-associated macrofauna	85 to 17,230 individuals m ⁻¹	Spring low tide
Lavoie 1985	Central California	53			High spring tide
Lastra et al. 2015	Spain	13	Talitrid Amphipods	29,001 individuals m ⁻¹	Spring tide, 3.5 – 4m
Ruiz-Delgado et al. 2015	Spain	36			High spring tide and current driftline
Olabarria et al. 2007	Spain	53			Low tide
Jaramillo et al. 2006	Chile		Talitrid Amphipods	17 to 16,000 individuals m ⁻¹	Spring low tide
Rodil et al. 2008	Chile	29			Highest mark of drift line
Griffiths and Stenton-Dozey 1981	South Africa	27			High spring tide
Inglis 1989	New Zealand	22			

Figures

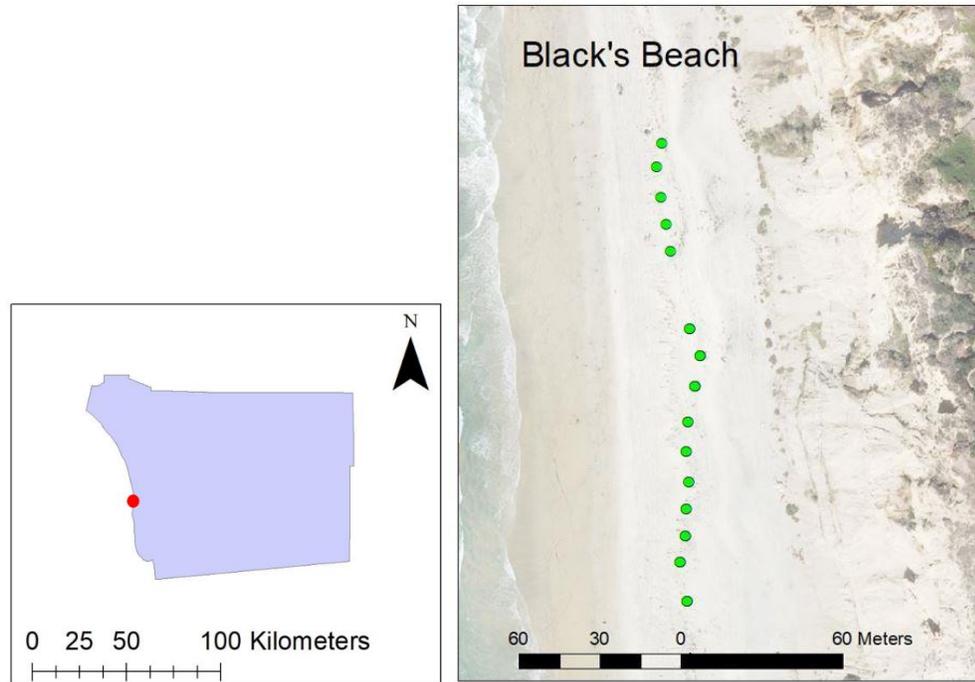


Figure 1. Map of San Diego county highlighting where study took place (red dot), and map showing locations of algal wrack (green circles) placed on Black's Beach ($32^{\circ}52'42.8''\text{N}$ $117^{\circ}15'04.7''\text{W}$).

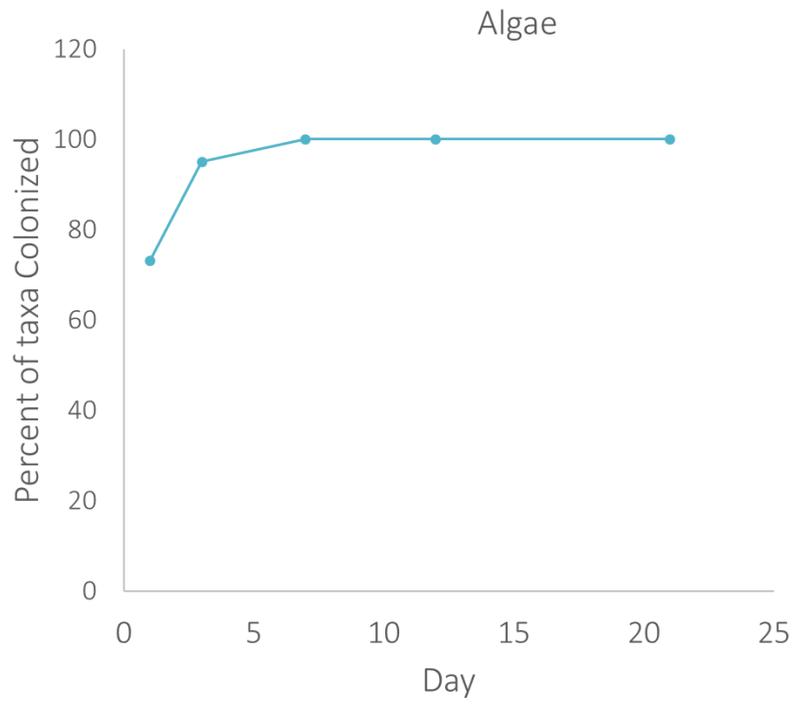


Figure 2. Percent of taxa which colonized the algal wrack patches over time.

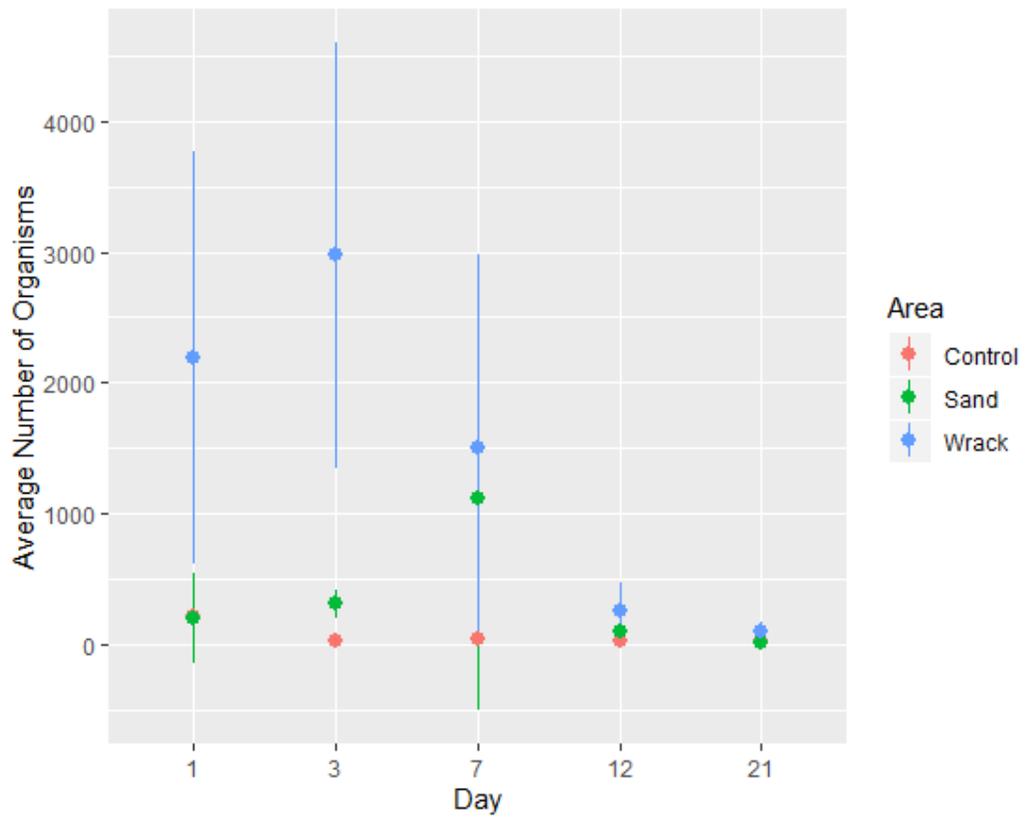


Figure 3. Average number of organisms found over time. Wrack refers to organisms found in the algal wrack patch, sand refers to organisms found beneath each algal wrack patch and control are organisms found in bare sand. Organisms are standardized to # m² and the error bars represent one standard error.

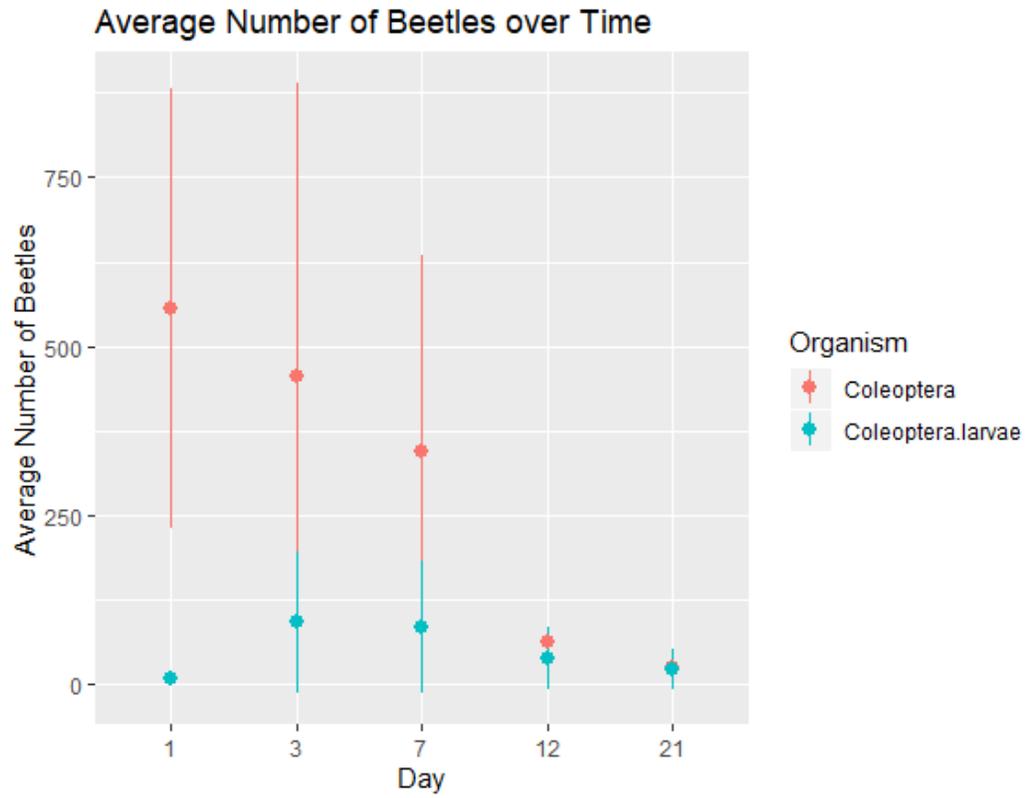


Figure 4. Average number of beetles over time in and beneath an algal wrack patch. Each error bar is 1 standard error. Organism count is standardized to # m².

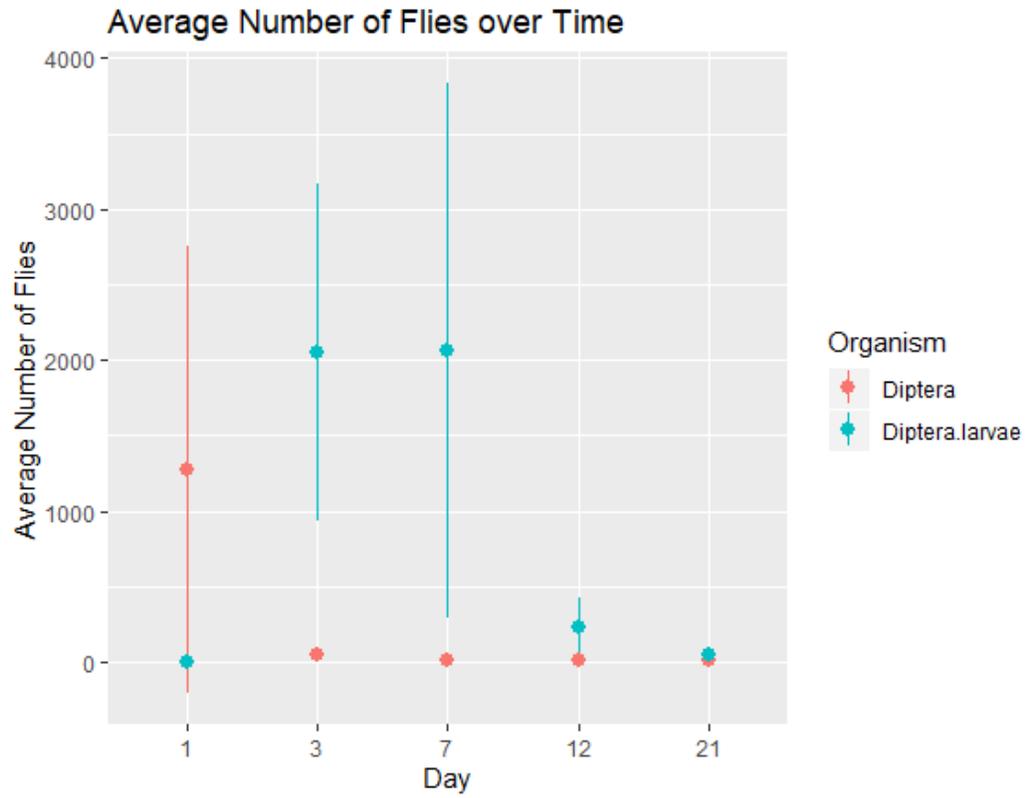


Figure 5. Average number of flies over time in and beneath an algal wrack patch. Each error bar is 1 standard error. Organism count is standardized to # m².

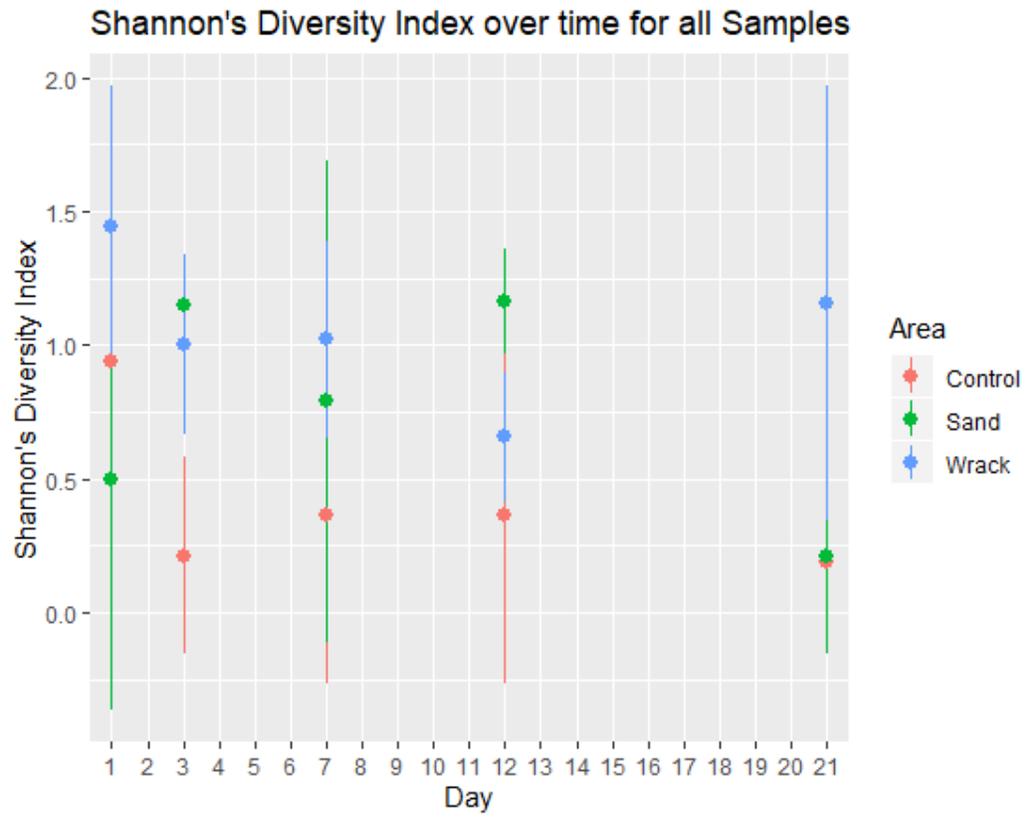


Figure 6. Shannon's diversity index (H) over time for organisms found within algal wrack, beneath algal wrack, and in controls. Each error bar is 1 standard error.

Appendix

Community Structure within algal wrack compared to sand beneath algal wrack

In comparing the community structure of organisms found within the algal wrack to those found beneath it, there was a significant difference at Day 1, 3, 12, and 21 (Table 2) (ANOSIM $R < 0.1$). At day 1, 19.5% of this difference was due to the presence of hymenoptera in the sand samples, and 12.13% of the difference was due to Diptera present in the wrack samples. At day 3, 15.08% of the difference was due to *Meglorchestia* species mainly in the sand samples and 12.93% was due to Isopod species found in the sand samples. At day 12, 22.75% of the difference was from diptera larvae found in the wrack and 20.43% of the difference was from the tenebrionid species *Phaleria rotundata* found in the sand. At day 21 28.03% of the difference was from diptera larvae in the wrack samples and 17.05% of the difference was from the weevil species *Emphyastes fucicola* found in the sand samples.

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