

## Contribution of macroalgal wrack consumers to dissolved inorganic nitrogen concentrations in intertidal pore waters of sandy beaches

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### ABSTRACT

Sandy beaches are widespread ecosystems that often sustain food webs with allochthonous subsidies of organic matter. We examined the contribution of intertidal talitrid amphipods, a dominant consumer of macroalgal wrack subsidies on sandy beaches in temperate zones, to the remineralization of wrack and resulting nutrient concentrations in intertidal pore water. The abundance of wrack (as cover) is strongly correlated with that of talitrid populations in multi-year data from quantitative surveys (2013–2018). Ammonium ( $\text{NH}_4^+$ ) is the dominant form of dissolved inorganic nitrogen at depths ranging from 0 to 160 cm in intertidal pore water collected in 2013, and pore waters are seldom hypoxic (dissolved oxygen  $< 2 \text{ mg L}^{-1}$ ). We evaluated the effects of intertidal consumers on nutrient regeneration in laboratory mesocosms. Over the course of replicated 5-day incubations, treatments containing talitrid amphipods, *Megalorchestia corniculata*, and giant kelp, *Macrocystis pyrifera*, produced elevated dissolved concentrations of ammonium and nitrate, compared to treatments with only sand, seawater, and kelp. Our measurements suggest talitrid amphipods may elevate ammonium concentrations by  $4\text{--}198 \mu\text{M day}^{-1}$ ; the ammonium produced may be utilized by beach microbes or exported offshore by tidal flushing. Our study highlights the role of intertidal consumers in maintaining important ecosystem functions, such as organic matter processing and nutrient regeneration.

### 1. Introduction

Sandy beaches provide numerous ecological and societal functions and support diverse communities of intertidal animals ranging from invertebrates to mammals and shorebirds (Schlacher et al., 2008; Defeo et al., 2009; Nel et al., 2014). As ecosystems, sandy beaches are characterized by low primary productivity (McLachlan et al., 1993; Ince et al., 2007) and food webs dependent on the delivery of imported organic matter subsidies, such as phytoplankton and drift macrophytes (Polis and Hurd, 1996; Dugan et al., 2003). In temperate latitudes, marine macrophytes or wrack deposited on the beach by waves and tides represents an important subsidy that is consumed, assimilated, remineralized, or buried (Lastra et al., 2008; Gómez et al., 2018; Rodil et al., 2018).

Highly productive nearshore kelp forests are an important source of subsidies to beaches and other ecosystems, such as submarine canyons, along the California coast (Vetter and Dayton, 1999; Liebowitz et al., 2016). Kelp forests export large amounts of drift kelp, much of which is deposited in the intertidal zone of sandy beaches (Hobday, 2000). For beaches located in close proximity to kelp forests, wrack deposition can

exceed  $500 \text{ kg m}^{-1}$  of beach per year (Dugan et al., 2011). This organic material subsidizes intertidal food webs and communities of invertebrate consumers, many of which are prey for shorebirds and fishes. The abundance and diversity of intertidal wrack consumers are correlated with the standing stock of wrack (Dugan et al., 2003; Schooler et al., 2017).

Wrack-associated macrofauna are able to process over half of the wrack material deposited (Lastra et al., 2008) and rapidly remineralize it (Rodil et al., 2018), two functions that are crucial for decomposing wrack when it is deposited frequently and in large quantities (Dugan et al., 2011). There are numerous upper beach and wrack-associated macrofauna, including flies, beetles, and spiders, but talitrid amphipods far exceed other invertebrates in density, biomass and kelp consumption on beaches along the California coast (Dugan et al., 2003; Schooler et al., 2017). While other wrack-associated fauna and higher level consumers, such as small mammals and shorebirds, may contribute to nutrient cycling in sandy beaches, we expected talitrid amphipods to have a large contribution based on their population metrics and kelp consumption rates.

The majority of energy in many food webs flows through detrital

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pathways, and detritivores can be a key part of ecosystem functioning and nutrient cycling (Moore et al., 2004). The role of macroinvertebrate consumers, especially shredders, in making imported organic matter available to other organisms is well-documented for streams (Vanni, 2002) where large amounts of imported detritus are processed (Anderson and Sedell, 1979; Wallace et al., 1982). Shredders (Crowl et al., 2001) and collector-gatherers (Grimm, 1988) increase dissolved nutrient concentrations in streams, and these nutrients can be an important resource to primary producers (Atkinson et al., 2014). In sandy beaches, a number of intertidal macroinvertebrate consumers act as shredders, consuming and fragmenting macrophyte wrack and promoting remineralization of organic matter (Dugan et al., 2003, 2011). Talitrid amphipods (*Megalorchestia* spp.), abundant wrack consumers whose primary excretion product is ammonium ( $\text{NH}_4^+$ ) (Dresel and Moyle, 1950; Spicer and McMahon, 1994), can reach densities exceeding 100,000 individuals  $\text{m}^{-2}$  of beach and consume up to 18 kg of kelp  $\text{m}^{-2}$  of beach month $^{-1}$  (Lastra et al., 2008). They can burrow as deep as 100 cm into the sand (Williams, 1995; Poulin and Latham, 2002), transporting organic matter and fecal matter to subsurface depths while potentially enhancing the flushing of intertidal pore water (Huettel et al., 2014) and stimulating remineralization rates. Intertidal consumers serve as a link between subsidies of imported organic matter, such as wrack, and nutrient recycling.

Abundant intertidal consumers can enhance the availability of imported organic matter to local microbial communities. Microbes play a significant role in transforming permeable sediments into regions of intense biogeochemical activity (Rocha, 2008; Huettel et al., 2014; Woulds et al., 2016). Due to varied organic matter inputs and physical mixing, coastal sediments experience advective flow of pore water and the establishment of diverse microbial communities (Laverman et al., 2012; Boehm et al., 2014; Staley and Sadowsky, 2016). These microbes break down organic matter and produce ammonium in a process termed remineralization. Ammonium is then used by phototrophs or in other nitrogen-transformations (Brzezinski, 1988; Capone et al., 2008; Gustafsson and Norkko, 2016). If beach pore waters remain oxygenated, they support high rates of nitrification, where ammonium is converted to nitrate (Zehr and Ward, 2002; Schutte et al., 2018). Nitrate is then exported into the ocean or can be transported vertically to be used as a terminal electron acceptor by anaerobic microbes in deeper sediments (Froelich et al., 1979).

A variety of biotic and abiotic processes supply and alter dissolved inorganic nitrogen (DIN) concentrations in sandy beach environments. In addition to biological processes, physical forcing regulates DIN concentrations in intertidal beach pore waters. Submarine groundwater discharge and tides flush DIN into nearby subtidal regions and deliver dissolved and particulate organic matter (DOM, POM) (Swarzenski and Izbicki, 2009; Santos et al., 2012; Goodridge and Melack, 2014). Concentrations of DIN in intertidal pore water and the adjacent surf zone are correlated with the quantity of macrophyte wrack present on sandy beaches (Dugan et al., 2011) suggesting that nutrients remineralized from organic matter deposited on sandy beaches are transported to nearshore waters where they may be available to marine primary producers and supplement other offshore sources, such as upwelling.

We hypothesized that consumers and their associated biological processes, such as the shredding, consumption, and subsequent excretion and remineralization of imported macrophyte wrack, have a significant effect on pore water DIN concentrations following wrack deposition on sandy beaches. To evaluate this hypothesis, we investigated the relative importance of a primary intertidal wrack consumer, the talitrid amphipod, *Megalorchestia corniculata*, on the production and composition of DIN in intertidal pore waters on sandy beaches. We examined relationships between supply of organic matter (macroalgal wrack), intertidal consumers, and remineralized nutrients using measurements of kelp wrack cover, talitrid amphipod abundance, and beach pore water DIN concentrations at three beaches in Santa Barbara, California, USA. To investigate the role of these consumers in the

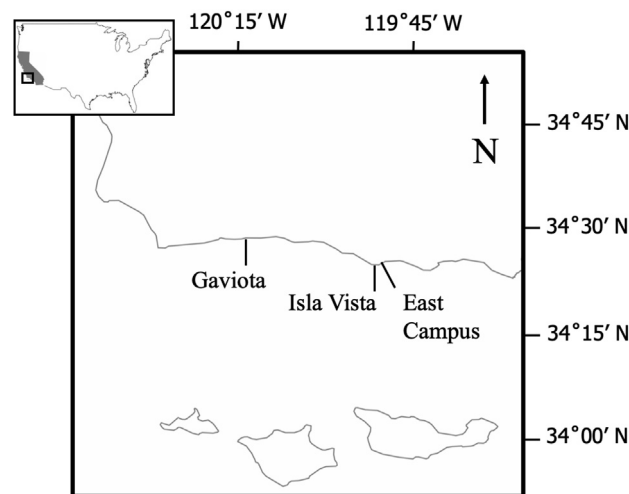


Fig. 1. Beach sites included in the talitrid amphipod abundance, wrack abundance, and pore water nutrient data collection along the coast of Santa Barbara County, California, USA (inset).

remineralization of DIN from kelp wrack, we experimentally estimated the contribution of talitrid amphipod excretion to DIN concentrations using comparison of results from mesocosms containing combinations of sand, seawater, giant kelp blades (*Macrocystis pyrifera*), and adult talitrid amphipods. By combining field and laboratory measurements, we evaluated the nutrient regeneration potential of sandy beach ecosystems inhabited by abundant intertidal wrack consumers that function as shredders of macroalgal detrital subsidies.

## 2. Methods

### 2.1. Study site

Our study focused on the sandy beaches of Isla Vista (Longitude 119.87385 W, Latitude 34.40928 N) and East Campus (Longitude 119.84202 W, Latitude 34.41077 N) beaches in Santa Barbara, California, USA (Fig. 1). The Santa Barbara Coastal Long Term Ecological Research program (SBC LTER) collects long-term datasets of wrack inputs and population metrics (abundance and biomass) of talitrid amphipods (*Megalorchestia* spp.) at these beaches (Dugan, 2018a, 2018b). Intertidal pore water concentrations were also measured at Gaviota State Beach (Longitude 120.22715 W, Latitude 34.47096 N).

All beaches sampled are backed by sea bluffs and experience a microtidal, mixed semidiurnal tidal regime (Dugan et al., 2011). They are all wave-dominated, but East Campus is the only modally reflective beach, so it experiences the lowest wave energy of the beaches sampled (Dugan et al., 2003). Gaviota State Beach is located near a lagoon with a seasonal stream mouth that flows to the ocean following winter rainstorms (Aguilera and Melack, 2018).

### 2.2. Cover of macrophyte wrack and abundance of talitrid amphipod consumers

Surveys of the abundance of talitrid amphipods and macrophyte wrack were conducted every 4 to 8 weeks at East Campus and Isla Vista beaches from 2013 to 2018 during neap low tides. Wrack cover was measured on each sampling date along three shore normal transects that extended from the upper beach boundary to the high swash zone using a line-intercept method (Dugan et al., 2003). Wrack cover represents the total area of wrack ( $\text{m}^2$ ) in a 1-m-wide (shore normal or perpendicular) strip of beach. Measuring wrack cover in this manner allowed for the high variation in beach widths over time (Revell et al., 2011). Samples of talitrid populations were collected along the same

three transects used for the wrack measurements to determine abundance. Talitrid amphipods are active at night and burrow in damp sand during the day. The location of the talitrid-occupied zone changes daily and is tightly coupled to tide levels. Before sampling, the zone of the beach occupied by talitrids was defined by identifying the upper and lower bounds of their burrows on each transect. Core samples were collected in the zone of the beach occupied by talitrid amphipods (Dugan et al., 2003, 2011). Ten evenly spaced cores (10 cm diameter, 20 cm depth) were taken and aggregated into one sample per transect. Each sample was sieved in a 1.5 mm mesh bag and transferred to a labeled Ziploc bag and frozen. In the laboratory, each sample was thawed and sorted for invertebrates which were identified to species, counted, and weighed as blotted wet weight. The abundance from the core samples was scaled to the width of the talitrid zone sampled to obtain total abundance and biomass  $m^{-1}$  of beach for each transect. Mean values for total talitrid species abundance and wrack cover were calculated for each sampling site and date.

### 2.3. Dissolved nutrient concentrations in intertidal pore water

Intertidal pore water was sampled during low tide on January 31, February 28, and April 21, 2013 at East Campus beach, on February 2, March 2, and April 23, 2013 at Isla Vista beach, and on February 1, March 1, and April 17, 2013 at Gaviota State Beach. Shore normal transects of 50 m length from sea cliffs to the surf zone were sampled at varying distances from the cliffs, depending on where sand was available. Depth profile samples were collected at an average of six sites along each transect, depending on beach width. To extract pore water samples, the subaerial water table was located with an auger and sampled using a peristaltic pump and piezometers fitted with a 2.5 cm screen (Woessner, 2007). A minimum of three depths were sampled. Samples were returned to the laboratory on ice, filtered through GF/F filters (0.7  $\mu m$ , Whatman), and frozen until analysis for nutrient concentrations. Ammonium ( $NH_4^+$ ) and nitrate ( $NO_3^-$ ) analyses were performed via the high throughput flow injection analysis method on a Lachat Flow Injection Analyzer (Hach Company) with a limit of detection of 0.5  $\mu M$ .  $NH_4^+$  concentrations were measured by way of a gas diffusion method whereas  $NO_3^-$  concentrations were measured by first reducing to nitrite ( $NO_2^-$ ) and then measured colorimetrically. Dissolved oxygen (DO) was measured in the field using a YSI ProODO meter.

### 2.4. Experimental mesocosms

Two identical experimental trials to measure talitrid amphipod excretion were conducted in May 2018. Dry sand was collected from Isla Vista beach and sieved using 1.5 mm mesh. The sand was not rinsed so that existing microbial communities would remain intact and mesocosm conditions would approximate *in situ* conditions on the beach. Kelp blades were collected from the Isla Vista Reef kelp forest and submerged in a flow-through seawater tank until needed. Twelve high-density polyethylene (HDPE) buckets were assembled containing 8.5 cm of dry sand (surface area = 715  $cm^2$ ) mixed with 1.25 L of unfiltered seawater. Six of the twelve buckets received a single fresh kelp blade (approximately 50 g wet weight) that was replaced every two days; this time frame was chosen to mimic the continuous supply of fresh kelp wrack deposited on the beach. Kelp blades, once deposited on the shore, can be almost entirely consumed overnight (87% wet weight) (Lastra et al., 2008). Three of the buckets that contained kelp also received 40 adult talitrid amphipods (*Megalorchestia corniculata*), collected the morning of the trial at Isla Vista beach. *M. corniculata* is the dominant species on the beaches sampled. Talitrid amphipods were the only consumers present in our mesocosms. Three of the remaining six buckets which did not receive kelp were spiked with Rhodamine to measure pore water flushing rates. The three remaining buckets without kelp were the controls and contained only sand and seawater.

The four treatments were repeated during both trial runs to create six total replicates of each treatment. All buckets were fitted with a screened top to prevent the organisms from escaping and a valve at the bottom to allow for pore water extraction. The buckets were exposed to natural light cycles at a temperature of 22 °C. Water was sampled from the bottom valve three times in the first 24 h, and once every 12 h thereafter. At each time, 100 mL of pore water was extracted using a 60 mL syringe connected to the valve, and 100 mL of fresh seawater was poured onto the surface of the sand. Water samples were filtered through GF/F filters prior to analysis for dissolved nutrients. Water samples were analyzed for  $NH_4^+$  immediately using the ortho-phthalaldehyde (OPA) method (Holmes et al., 1999; Taylor et al., 2007) and measured on a Turner Trilogy fluorometer. Additional samples were frozen until analysis for  $NO_3^-$  concentrations with the high throughput flow injection analysis method using a Lachat Flow Injection Analyzer. The limits of detection for the  $NH_4^+$  and  $NO_3^-$  methods are 0.05  $\mu M$  and 0.5  $\mu M$ , respectively.

### 2.5. Data analysis

Data analysis and visualization were performed in Microsoft Excel (2015) (v. 15.24) and R Statistical Software (v. 3.4.3) using the *ggplot2*, *tidyr*, *nlme*, and *multcomp* packages (Wickham, 2016, 2018; Hothorn et al., 2017; Pinheiro et al., 2018). For all statistical analyses, an alpha ( $\alpha$ ) value of 0.05 was used unless otherwise noted. For the mesocosm experiment, a linear mixed effects model for each trial was created for each nutrient measured, using treatment as a fixed effect and bucket replicate as a random effect (Zuur, 2009). This approach was preferred over performing a repeated measures ANOVA so that post hoc tests could be run using the *glht* function of the *multcomp* package (Hothorn et al., 2017).

## 3. Results

### 3.1. Wrack cover and talitrid abundance

Mean values of the cover of marine macrophyte wrack ranged from 0.01 to 28.3  $m^2 m^{-1}$ . Total abundance of talitrid species ranged from 0 to 320,000 individuals  $m^{-1}$  of shoreline. Log transformed wrack cover and the abundance of talitrid amphipods were significantly correlated (Fig. 2), and marine wrack cover explained a significant proportion of the variance in talitrid abundance. Talitrid abundances increased with wrack cover until reaching a threshold of  $\sim 10 m^2 m^{-1}$  of wrack cover (Fig. 2). This asymptote in talitrid abundance, in addition to high variability in abundance at low wrack cover, likely contributed to the relatively low  $R^2$  value reported ( $R^2 = 0.37$ ).

### 3.2. Nutrient concentrations in beach pore waters

*In situ* pore water nutrient concentrations were measured at three beaches in 2013 to provide context for the nutrient concentrations recorded in the laboratory mesocosms. At East Campus beach, mean concentrations of  $NH_4^+$  were an order of magnitude greater than mean concentrations of  $NO_3^-$ , except in surface seawater collected on one date, 28 February 2013 (Tables 1 and 2). Samples were collected from shallower depths at East Campus beach than at the other two beaches because the volume of sand over the underlying bedrock platform was 50% less than at Isla Vista and Gaviota beaches. At Isla Vista beach, mean concentrations of  $NH_4^+$  were also an order of magnitude higher than mean concentrations of  $NO_3^-$ , except on one date, 23 April 2013, when  $NO_3^-$  concentrations were  $> 100 \mu M$  between 60 and 140 cm deep. At Gaviota beach, mean  $NH_4^+$  concentrations were greater above 100 cm, whereas  $NO_3^-$  concentrations were greater below 100 cm. Overall,  $NH_4^+$  was the dominant inorganic nitrogen species found in intertidal pore waters sampled on sandy beaches during the spring of 2013, and concentrations were typically greatest between depths of 20

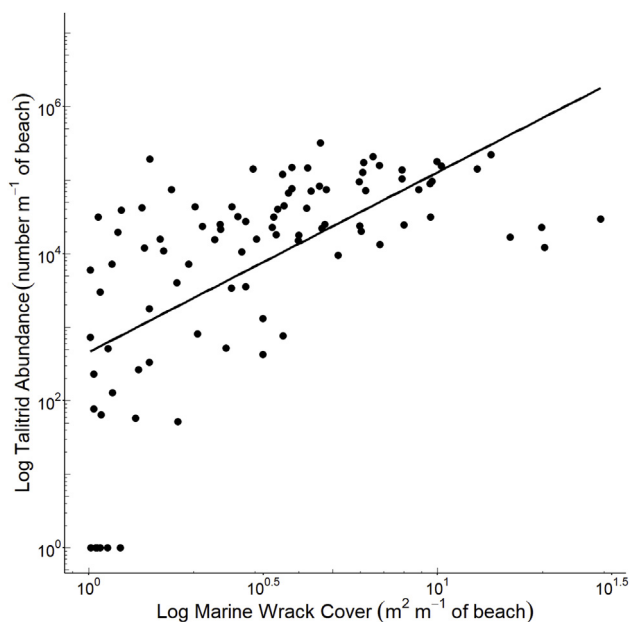


Fig. 2. Relationship between log-transformed values of mean abundance of talitrid amphipods and marine wrack cover for each sampling date at Isla Vista and East Campus beaches from 2013 to 2018 ( $R^2 = 0.37$ ,  $p < 0.0001$ ,  $n = 94$ ). Data were log-transformed to better compare datasets and reduce skewness.

and 100 cm.  $\text{NO}_3^-$  concentrations were greater between 60 and 140 cm than at other depths.

Dissolved oxygen concentrations appeared fairly consistent across all sites and dates sampled (Table 3). In most cases, except for Isla Vista beach on 2 March 2013, dissolved oxygen concentrations in beach pore waters remained above the  $2 \text{ mg L}^{-1}$  threshold, below which conditions are typically classified as hypoxic. At East Campus beach, dissolved oxygen concentrations in intertidal pore water hovered around  $2.5 \text{ mg L}^{-1}$  on all three dates; concentrations of oxygen increased with depth on 28 February 2013 but decreased on all other dates. Dissolved oxygen concentrations in pore waters at Isla Vista beach fluctuated around  $2.4 \text{ mg L}^{-1}$  on 2 February 2013, around  $1.6 \text{ mg L}^{-1}$  on 2 March 2013, and around  $3.0 \text{ mg L}^{-1}$  on 23 April 2013 with no clear pattern with depth. At Gaviota beach, pore water displayed the clearest dissolved oxygen pattern on both sampling days, with concentrations increasing with depth to the highest pore water dissolved oxygen concentrations we recorded ( $5.8 \text{ mg L}^{-1}$ ).

The pore water data in Tables 1–3 presents values partitioned by sediment depth in 20 cm increments, providing greater spatial resolution than previously reported. These data were published in an aggregated format, not by depth, in the supplementary materials provided

Table 1

Mean ammonium ( $\text{NH}_4^+$ ) concentrations ( $\mu\text{M}$ ), with standard deviations, in pore water samples collected in 2013 at three beaches along the Santa Barbara coastline. Empty cells indicate either no water was sampled at that depth or bedrock was reached prior to that depth. Values that were found to be below the limit of detection are reported at  $0.5 \mu\text{M}$ , which is the limit of detection of the analytical method.

Depth (cm)	East Campus			Isla Vista			Gaviota		
	1/31/13	2/28/13	4/21/13	2/2/13	3/2/13	4/23/13	2/1/13	3/1/13	4/17/13
Surf zone	–	0.5	90.5	0.5	0.5	0.9	0.5	0.5	0.7
0–19	–	–	$158.2 \pm 148.1$	73.0	–	–	12.7	–	$11.3 \pm 8.4$
20–39	$171.3 \pm 279.2$	$200.5 \pm 228.6$	121.0	$244.2 \pm 261.6$	$78.2 \pm 69.8$	3.3	–	$32.7 \pm 1.2$	$17.5 \pm 4.7$
40–59	$195.8 \pm 317.7$	$178.7 \pm 0.1$	–	$120.7 \pm 48.5$	$112.3 \pm 51.8$	–	$14.9 \pm 9.5$	$15.3 \pm 26.0$	12.6
60–79	$184.8 \pm 238.3$	204.8	–	$369.7 \pm 336.3$	–	$7.3 \pm 2.1$	$11.3 \pm 15.3$	$12.0 \pm 10.0$	15.5
80–99	–	–	–	$133.1 \pm 128.4$	$276.9 \pm 382.5$	$26.4 \pm 34.5$	$7.6 \pm 6.5$	0.5	$15.6 \pm 20.6$
100–119	–	–	–	42.3	10.3	–	$3.9 \pm 6.0$	0.5	$1.3 \pm 0.7$
120–139	–	–	–	$2.9 \pm 2.5$	$13.8 \pm 9.0$	$31 \pm 36.9$	$0.3 \pm 0.3$	–	–
140–160	–	–	–	–	$18.9 \pm 18.4$	$73.3 \pm 10.8$	–	–	–

by Goodridge and Melack (2014). Consistent with our findings, they found mean values of ammonium concentrations were one or more orders of magnitude greater than mean values of nitrate concentrations, except at Isla Vista beach on 23 April 2013 and Gaviota beach on all dates, and mean dissolved oxygen concentrations were seldom hypoxic ( $< 2 \text{ mg L}^{-1}$ ) (Goodridge and Melack, 2014).

### 3.3. Experimental mesocosms

In our experimental mesocosms, the concentrations of dissolved  $\text{NH}_4^+$  ranged from 79 to  $572 \mu\text{M}$ , and mean concentrations of  $\text{NH}_4^+$  in the outflow for both trials ( $n = 6$  for each treatment) for the sand, sand + kelp, and sand + kelp + talitrid treatments were  $219 \mu\text{M}$ ,  $223 \mu\text{M}$ , and  $412 \mu\text{M}$ , respectively (Fig. 3). In the first trial, the mean concentrations of  $\text{NH}_4^+$  differed significantly among treatments (linear mixed effects model (LMEM),  $F(2) = 28.22$ ,  $p = 0.0009$ ,  $n = 98$ ). The treatment containing talitrids was significantly different than the treatment containing only sand (Tukey's post hoc,  $p < 0.0001$ ) and the treatment containing sand and kelp (Tukey's post hoc,  $p < 0.0001$ ). In the second trial, the median concentrations of dissolved  $\text{NH}_4^+$  in the outflow also differed significantly among treatments (LMEM,  $F(2) = 80.38$ ,  $p < 0.001$ ,  $n = 106$ ). Although this trial's  $\text{NH}_4^+$  data were found to be non-normally distributed and therefore were rank transformed, we also ran a model in which the data were not rank-transformed, and we found the same result to be true (LMEM,  $F(2) = 240.59$ ,  $p < 0.0001$ ,  $n = 106$ ). The treatment containing talitrids was again significantly different than both the treatment containing only sand (Tukey's post hoc,  $p < 0.0001$ ) and the treatment containing sand and kelp (Tukey's post hoc,  $p < 0.0001$ ).

Concentrations of dissolved  $\text{NO}_3^-$  in mesocosm outflow ranged from 167 to  $688 \mu\text{M}$  among all three treatments, and mean values of concentrations of dissolved  $\text{NO}_3^-$  in both trials for the sand, sand + kelp, and sand + kelp + talitrid treatments were  $307 \mu\text{M}$ ,  $329 \mu\text{M}$ , and  $441 \mu\text{M}$ , respectively. In the first trial, the mean values of concentrations of dissolved  $\text{NO}_3^-$  differed significantly among treatments (LMEM,  $F(2) = 19.11$ ,  $p = 0.0025$ ,  $n = 107$ ). The treatment containing talitrids was significantly different than the treatment containing only sand (Tukey's post hoc,  $p < 0.0001$ ) and the treatment containing sand and kelp (Tukey's post hoc,  $p < 0.0001$ ). In the second trial, the mean concentrations of dissolved  $\text{NO}_3^-$  differed significantly among treatments (LMEM,  $F(2) = 10.43$ ,  $p = 0.0111$ ,  $n = 106$ ). The treatment containing talitrids was significantly different than the treatment containing only sand (Tukey's post hoc,  $p = 0.0004$ ) and the treatment containing sand and kelp (Tukey's post hoc,  $p = 0.0001$ ).

Survival rates of the talitrid amphipods in the experimental treatments were high, averaging 98% after five days. Both trials experienced an initial period during which the talitrid amphipods acclimated to the mesocosms before beginning to feed at regular intervals. This observation was supported by the lower  $\text{NH}_4^+$  values recorded during the

**Table 2**

Mean nitrate ( $\text{NO}_3^-$ ) concentrations ( $\mu\text{M}$ ), with standard deviations, in pore water samples collected in 2013 at three beaches along the Santa Barbara coastline. Empty cells indicate either no water was sampled at that depth or bedrock was reached prior to that depth. Values that were found to be below the limit of detection are reported at  $0.5 \mu\text{M}$ , which is the limit of detection of the analytical method.

Depth (cm)	East Campus			Isla Vista			Gaviota		
	1/31/13	2/28/13	4/21/13	2/2/13	3/2/13	4/23/13	2/1/13	3/1/13	4/17/13
Surf zone	–	4.7	1.5	7.9	1.1	1.1	4.5	0.9	20.4
0–19	–	–	$1.7 \pm 1.1$	0.5	–	–	0.5	–	$1.0 \pm 0.2$
20–39	$1.6 \pm 0.9$	$1.8 \pm 1.8$	0.6	0.5	0.5	12.1	–	0.5	$1.2 \pm 0.5$
40–59	$1.5 \pm 2.0$	$23.5 \pm 33.3$	–	0.5	0.5	–	0.5	$4.1 \pm 7.4$	0.5
60–79	$21.0 \pm 50.2$	67.0	–	0.5	–	$259.5 \pm 366.1$	$4.2 \pm 5.2$	$14.7 \pm 24.6$	0.5
80–99	–	–	–	$1.0 \pm 0.8$	$3.8 \pm 5.7$	$90.2 \pm 117.5$	$0.8 \pm 0.6$	35.4	$17.4 \pm 13$
100–119	–	–	–	4.5	0.5	–	$95.4 \pm 93.3$	227.6	$41.2 \pm 66.8$
120–139	–	–	–	$5.2 \pm 5.6$	0.5	$175 \pm 246.5$	$61.6 \pm 62.1$	–	–
140–160	–	–	–	–	$2.3 \pm 2.5$	$1.1 \pm 0.8$	–	–	–

first few time points before concentrations increased to levels that remained relatively constant for the duration of the trial. The concentrations of dissolved  $\text{NO}_3^-$  had a slightly different pattern with stable values towards the beginning of each trial and increasing during the final day of the trial. Initial  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations, at  $t = 0$  h, were several orders of magnitude greater than ambient seawater concentrations. This may have been due to nutrients desorbing from the unwashed sand placed in the mesocosms. Overall, concentrations of dissolved  $\text{NH}_4^+$  and of  $\text{NO}_3^-$  were greater in the mesocosms containing talitrid amphipods. However,  $\text{NO}_3^-$  concentrations varied more than  $\text{NH}_4^+$  across times and trials.

The mesocosm trials also included a Rhodamine WT treatment (data not included) to approximate relative pore water flushing rates. Initially, the buckets received seawater containing 200 ppb Rhodamine. Instead of an incremental decrease in concentration, we recorded an immediate decrease in Rhodamine (65 ppb) at the first sampling time-point, and then a minor (1–2 ppb) decrease in concentration each day thereafter. Rhodamine WT consists of two isomers, and the meta isomer may sorb to soil and minerals (Vasudevan et al., 2001). Therefore, the immediate decrease in concentration may have been due to the meta isomers' sorption whereas the remaining decrease was due to anticipated dilution by added seawater.

#### 4. Discussion

The positive relationship we found between the density of talitrid amphipods and the abundance of wrack on East Campus and Isla Vista beaches is consistent with findings from earlier studies which suggest intertidal species richness, abundance, and biomass are strongly correlated with wrack abundance (Dugan et al., 2003, 2015; Nielsen et al., 2017). In late summer when beaches consistently have upper intertidal zones and are able to retain more wrack (Revell et al., 2011), talitrid abundances typically reach their maximum values, as do wrack and

nutrient concentrations in pore waters (Dugan et al., 2011; Revell et al., 2011). Although wrack deposition may increase in the winter, talitrid populations typically decline seasonally due to wave action and beach erosion from storms or episodic ENSO events (Revell et al., 2011).

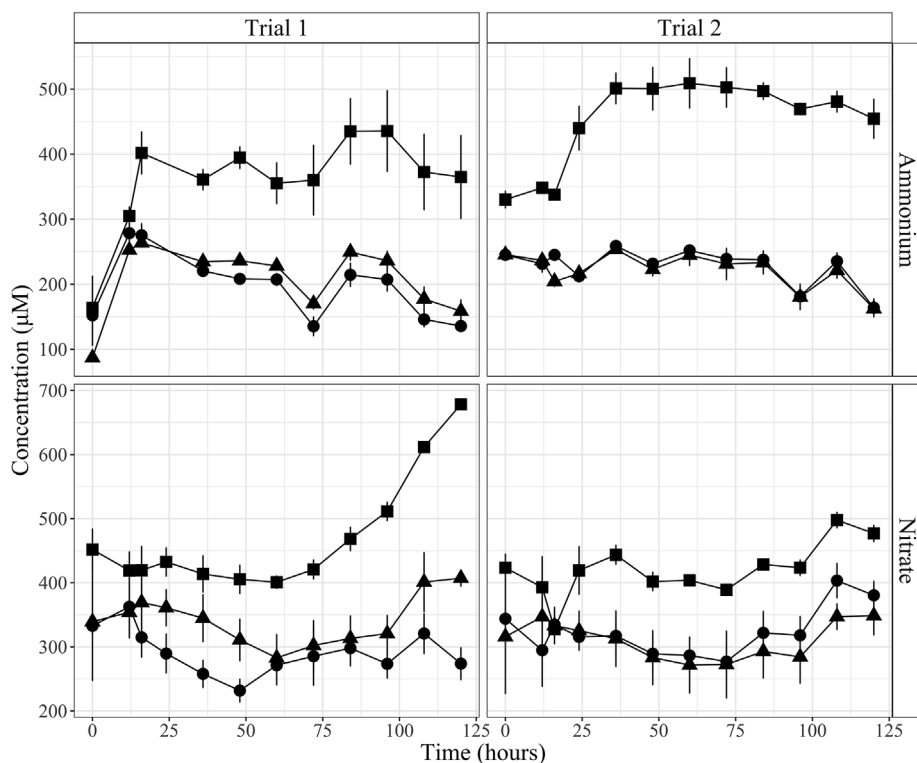
In addition to the strong links between wrack and talitrid abundances, wrack abundance and concentrations of dissolved nutrients in beach pore water can be highly correlated. Dugan et al. (2011) demonstrated a significant positive relationship between wrack abundance as cover and dissolved inorganic nitrogen (DIN) concentrations in intertidal pore water, as well as in the surf zone, on Santa Barbara beaches in late summer. A recent study involving a variety of wrack types, including *Saccorhiza polyschides* and *Undaria pinnatifida*, also supported the connection between wrack biomass and *in situ* dissolved nutrient concentrations (Rodil et al., 2018). The growing evidence supporting wrack-consumer and wrack-nutrient relationships, supports the role of intertidal macrofauna in organic matter decomposition and, consequently, nutrient cycling in beach ecosystems (Gómez et al., 2018). Talitrid amphipods are the dominant burrowing invertebrate found along the high tide line of beaches in the study region (Dugan et al., 2003) and are the primary consumer of kelp wrack (Lastra et al., 2008). Other upper beach invertebrates that consume kelp, such as the tenebrionid beetle, *Phaleria rotundata*, and the isopod *Alloniscus perconvexus*, are also common on local beaches but at much lower densities. In saturated sand closer to the low tide line, the ophiurid polychaete *Thoracophelia mucronata* may be abundant (Dugan et al., 2015) and may contribute to kelp detritus consumption and oxygenation of pore waters. These other intertidal consumers and bioturbators may also influence pore water chemistry and remineralization of organic matter on beaches, but this has yet to be examined.

Ammonium concentrations in beach pore waters were usually greater than nitrate concentrations (Tables 1 and 2). Other studies support the observation that  $\text{NH}_4^+$  is the dominant form of inorganic nitrogen in beach pore waters (Santos et al., 2009; Goodridge and

**Table 3**

Mean dissolved oxygen concentrations ( $\text{mg L}^{-1}$ ), with standard deviations, in pore water samples collected in 2013 at three beaches along the Santa Barbara coastline. Empty cells indicate either no water was sampled at that depth or bedrock was reached prior to that depth.

Depth (cm)	East Campus			Isla Vista			Gaviota		
	1/31/13	2/28/13	4/21/13	2/2/13	3/2/13	4/23/13	2/1/13	3/1/13	4/17/13
Surf zone	8.2	8.6	7.7	7.9	8.2	8.2	8.0	8.3	–
0–19	–	–	$2.5 \pm 0.4$	2.9	–	–	1.8	–	–
20–39	$2.5 \pm 0.4$	1.9	2.0	$2.9 \pm 0.6$	$1.4 \pm 0.7$	4.6	–	2.5	–
40–59	$2.2 \pm 0.4$	$2.7 \pm 0.9$	–	2.1	$1.5 \pm 0.2$	–	$2.6 \pm 0.2$	$2.5 \pm 0.5$	–
60–79	$2.1 \pm 0.5$	3.6	–	$2.4 \pm 0.6$	–	$2.9 \pm 0.5$	$2.5 \pm 0.2$	$3.4 \pm 2.1$	–
80–99	–	–	–	$2.2 \pm 0.2$	$1.6 \pm 0.3$	$2.7 \pm 0.9$	$2.1 \pm 0.2$	5.1	–
100–119	–	–	–	2.4	1.8	–	$3.5 \pm 2.0$	5.8	–
120–139	–	–	–	$2.0 \pm 0.4$	$1.7 \pm 0.1$	$2.8 \pm 0.2$	$4.6 \pm 4.0$	–	–
140–160	–	–	–	–	1.8	$3.0 \pm 0.4$	–	–	–



**Fig. 3.** Ammonium ( $\text{NH}_4^+$ ) and nitrate ( $\text{NO}_3^-$ ) concentrations measured in outflow pore waters collected from mesocosm trials performed in May 2018. Three treatments (sand [●], sand + kelp [▲], sand + kelp + talitrids [■]) ( $n = 3$ ) were run for two trials each, and mean values with standard error bars are presented.

Melack, 2014) and marine sediments (Gustafsson and Norkko, 2016). With one exception,  $\text{NH}_4^+$  concentrations in beach pore waters at all three sites were several orders of magnitude greater than concentrations of adjacent surf zone seawater suggesting the accumulation of DIN in intertidal aquifers. The exception occurred on 21 April 2013, when sand levels are typically at a minimum (Barnard et al., 2012), and tidal flushing of pore water DIN is expected to be high. Concentrations of  $\text{NO}_3^-$  in pore water were occasionally several orders of magnitude greater than seawater values, but pore water concentrations were more often reported at or below the limit of analytical detection, except on 17 April 2013 when seawater contained high concentrations of  $\text{NO}_3^-$ . However, the relative concentrations of dissolved nitrogen species may vary seasonally in the study area as high concentrations of  $\text{NO}_3^-$  in samples of pore water at the daily high tide line can be found in late summer (Dugan et al., 2011) when sand levels are highest (Barnard et al., 2012). Concentrations of both inorganic nitrogen species in surf zone seawater were consistent with values reported by the SBC LTER, which typically range from 0 to  $1.5 \mu\text{M}$  for  $\text{NH}_4^+$  and 0 to  $6 \mu\text{M}$  for  $\text{NO}_3^-$  (Brzezinski et al., 2013).

The observed variation in DIN species and concentrations in beach pore waters with depth of sampling may be related to the distribution of talitrid amphipods, which can burrow to depths of 100 cm (Williams, 1995; Poulin and Latham, 2002). Elevated concentrations of  $\text{NH}_4^+$  ( $> 100 \mu\text{M}$ ) occurred at depths from 0 to 100 cm, and elevated  $\text{NO}_3^-$  concentrations were found in deeper horizons, from 60 to 140 cm deep. Increased  $\text{NH}_4^+$  concentrations in beach pore waters shallower than 100 cm where talitrid amphipods were most abundant, namely East Campus and Isla Vista beaches, may be associated with these abundant detritivores, since  $\text{NH}_4^+$  is their primary excretion product (Dresel and Moyle, 1950). High  $\text{NH}_4^+$  concentrations in shallower pore waters may also be due to aerobic microbial remineralization of organic matter, which may be possible given dissolved oxygen concentrations above  $2 \text{ mg L}^{-1}$  at these depths (Table 3).

Changes in  $\text{NH}_4^+$  concentrations in beach pore waters are not always due to excretion or remineralization processes; they may also be indicative of changing redox environments. Schutte et al. (2018) found that oxidation of  $\text{NH}_4^+$  into  $\text{NO}_3^-$  can occur at rates of  $0.84 \mu\text{mol m}^{-2}$

$\text{h}^{-1}$ , and therefore a steady supply of  $\text{NH}_4^+$  from either excretion or remineralization sources could result in increased  $\text{NO}_3^-$  concentrations. Higher observed  $\text{NO}_3^-$  concentrations may be evidence of nitrification. The decline of  $\text{NO}_3^-$  concentrations below 140 cm on one date (23 April 2013), may indicate another transition zone where pore waters become anoxic; although the dissolved oxygen data suggest concentrations low enough to be considered hypoxic in a few cases, there may also be anoxic microsites that could induce anoxia at small scales (Lehto et al., 2014). In these conditions,  $\text{NO}_3^-$  could serve as an alternative terminal electron acceptor, and  $\text{NH}_4^+$  would become the dominant form of DIN (Froelich et al., 1979). The drop in  $\text{NO}_3^-$  concentrations should then be accompanied with an increase in  $\text{NH}_4^+$  concentrations, as observed on 23 April 2013. Due to most sampling occurring in winter and spring, beach sands were not sufficiently deep at all sites on all dates sampled to contain a zone that was demonstrably anoxic. However, in late summer or early fall (August–October), beach sands are typically widest and have the largest quantity of sand, so their depth may allow them to develop anoxic layers where  $\text{NH}_4^+$  may accumulate (Dugan et al., 2011; Goodridge and Melack, 2014).

Our study is the first to quantify excretion rates of talitrid amphipods, relative to other remineralization processes, using both field and laboratory measurements. Our results indicate that talitrid amphipods were capable of contributing to high  $\text{NH}_4^+$  and  $\text{NO}_3^-$  in beach pore waters (Fig. 3). Our mesocosm approach allowed us to approximate the combined effects on DIN concentrations of excretion and irrigation due to talitrid kelp consumption and burrowing. In both trials, treatments with talitrid amphipods produced higher concentrations of  $\text{NH}_4^+$  ( $189 \pm 78 \mu\text{M}$ ) and  $\text{NO}_3^-$  ( $112 \pm 63 \mu\text{M}$ ) than the treatment with sand and kelp blades alone. If we assume the differences in  $\text{NH}_4^+$  concentrations between the talitrid and non-talitrid treatments with kelp was due to  $\text{NH}_4^+$  as a talitrid excretion product, we can use those concentrations to calculate individual talitrid excretion contributions. With 1.25 L of seawater, 40 talitrid amphipods per mesocosm, and an incubation that lasted 5 days, the DIN contribution per talitrid amphipod ranges from 0.69 to  $1.67 \mu\text{moles day}^{-1}$ . This can also be expressed as 0.40 to  $0.97 \mu\text{g-N individual}^{-1} \text{ h}^{-1}$ . Excretion rates for two marine amphipod species, *Ampelisca* spp. and *Scina cornigera*, were

reported as 0.02 and 0.25  $\mu\text{g-N individual}^{-1} \text{ h}^{-1}$ , respectively, while the excretion rate for two freshwater amphipod species, *Pontoporeia hoyi* and *Hyalella azteca*, were reported as 0.02  $\mu\text{g-N individual}^{-1} \text{ h}^{-1}$  (Vanni et al., 2017). This comparison suggests that our estimated excretion rate for *Megalorchestia corniculata* is up to 2 times greater than for other aquatic amphipod species that primarily consume algal detritus. A lack of bioturbation may also have caused water to pool at the bottom of the control treatments. Talitrid amphipods perform an important function as they burrow, homogenizing pore water nutrient concentrations, and the concentrations measured in the control treatments may reflect an overestimation due to pooling of  $\text{NH}_4^+$ -concentrated water at the intake valve in the bottom of the mesocosms. If the  $\text{NH}_4^+$  concentrations of the no-talitrid treatments were overestimated, the relative contribution of talitrid excretion to overall pore water  $\text{NH}_4^+$  concentrations may be even greater than calculated.

Individual organismal excretion rates may also be scaled up to compare to the *in situ* nutrient concentrations (Tables 1 and 2). Our field measurements of talitrid densities ranged from 0 to 320,000 individuals  $\text{m}^{-1}$  of shoreline (Fig. 2). Based on the area sampled with the cores, these values translate to 0 to 31,000 talitrid amphipods  $\text{m}^{-2}$  of beach. Using a mean beach sand porosity of 0.34 reported by Goodridge and Melack (2014), the talitrid amphipod abundance measured, and the range of excretion values calculated above, we estimated that talitrid amphipods could increase pore water  $\text{NH}_4^+$  concentrations by 4.1–9.9  $\mu\text{M day}^{-1}$ , 36.6–88.5  $\mu\text{M day}^{-1}$ , and 81.9–198.1  $\mu\text{M day}^{-1}$  at the 25th, 50th, and 75th percentile talitrid abundances, respectively. Scaling this to  $\text{m}^{-1}$  of shoreline, our results represent an increase in  $\text{NH}_4^+$  concentrations ranging from 2.2  $\text{mmol NH}_4^+ \text{ m}^{-1} \text{ day}^{-1}$  (25th percentile of talitrids  $\text{m}^{-1}$  and low range excretion rate) to 122.6  $\text{mmol NH}_4^+ \text{ m}^{-1} \text{ day}^{-1}$  (75th percentile of talitrids  $\text{m}^{-1}$  and high range excretion rate). Since talitrid abundances are based on only the top 20 cm of sand, our excretion values may be underestimates. Nonetheless, these calculations suggest that talitrid amphipods, when supplied with sufficient kelp wrack, may regenerate *in situ*  $\text{NH}_4^+$  concentrations in a matter of hours to days.

Microbial processes were also taken into consideration when accounting for variations in DIN concentrations in the mesocosms. The processes responsible for  $\text{NH}_4^+$  regeneration were monitored by comparing the treatments containing talitrid amphipods, which would include excretion and microbial processes, to the treatments containing only sand and kelp, where only microbial remineralization could take place. The difference in  $\text{NH}_4^+$  concentrations between sand only and sand and kelp treatments was negligible (Fig. 3), while the treatment with talitrid amphipods produced much greater  $\text{NH}_4^+$  concentrations throughout both trials. This would suggest that simply adding organic matter, in the form of wrack, did not stimulate microbial degradation in the same way it stimulated wrack consumer metabolism.

Our results showing the control treatments maintained  $\text{NH}_4^+$  pore water concentrations that were several orders of magnitude greater than typical seawater concentrations (Brzezinski et al., 2013), suggested, as have others (Charbonnier et al., 2016), that microbes play a significant role in recycling bioavailable nitrogen in sandy beach environments. Beach microbial communities vary significantly, particularly in relation to distance from the shoreline (Staley and Sadowsky, 2016). The high tide line where kelp is deposited and talitrids burrow may select for microbes adapted to drier conditions and organic matter input in the form of wrack. Microbes in this region rely on shredders, such as talitrid amphipods, to deliver organic matter from macroalgal wrack to depth since they are unable to immediately access the fresh wrack when it is deposited on the sand. Another consideration for microbial communities present in this zone of beach are the macroalgae-colonizing microbes imported by the kelp wrack itself. These epiphytic populations vary based on available substrate, which depends on the algal species, the age of the tissue, and the season (Laycock, 1974; Lachnit et al., 2011). Microbial biofilms may contribute to the initial decomposition of kelp wrack after it has washed onshore since some

have the ability to break down antibacterial polyphenol compounds excreted by macroalgae (Bengtsson et al., 2011; Sosik and Simenstad, 2013; Dethier et al., 2014). Thus, both within-sediment and epiphytic macroalgal microbes may contribute to the DIN concentrations measured in beach pore waters.

Nitrifying microbes may have increased dissolved  $\text{NO}_3^-$  concentrations in our mesocosms. If beach pore waters are provided with a constant supply of  $\text{NH}_4^+$  in an aerobic environment, then  $\text{NO}_3^-$  concentrations can overtake  $\text{NH}_4^+$  concentrations (Dugan et al., 2011; Schutte et al., 2018). Nitrification rates were likely elevated in the mesocosms containing talitrid amphipods, because their excretion delivered large quantities of available  $\text{NH}_4^+$ . There was an evident correlation between the talitrid treatments and higher  $\text{NO}_3^-$  concentrations (Fig. 3). If  $\text{NH}_4^+$  excreted by talitrid amphipods was consumed by nitrifiers, this could lead to an underestimate of the relative contribution of talitrid excretion to  $\text{NH}_4^+$  concentrations. Despite this potential underestimation, the results of our mesocosm trials suggested pore water DIN concentrations are greater in the presence of talitrid amphipods than in the presence of sediment microbial communities alone.

To estimate the flux of DIN from beach pore waters into the nearby coastal ocean, Goodridge and Melack (2014) suggested it is necessary to determine mean pore water residence time, the amount of allochthonous organic matter a beach receives and how rapidly the DIN concentration signal is amplified by consumer and microbial remineralization. Using  $\text{Rn}^{222}$  isotopic dilution techniques, they found the residence time of beach pore waters to be positively correlated with tidal amplitudes, resulting in a mean residence time range of 4.4–6.4 days. The study also modeled potential scenarios of the temporal evolution of DIN concentrations (Goodridge and Melack, 2014, Fig. 3) and found that with increasing residence time, dissolved organic carbon (DOC) to total dissolved nitrogen (TDN) ratios decreased while DIN concentrations increased. In their model, DIN increased in the first few days of pore water residence and attained equilibrium for the remainder of the model scenario (Goodridge and Melack, 2014). This closely mirrors the DIN curves of our mesocosm treatments containing talitrid amphipods (Fig. 3), except ours reached higher  $\text{NH}_4^+$  concentrations in the first 24 h before leveling off for the remainder of the trial. Goodridge and Melack (2014) commented that *Macrocystis pyrifera* wrack and other organic matter deposition events potentially contribute to increasing DIN concentrations in beach pore water, and they suggest that organic matter loading has a greater influence on pore water DIN concentrations than pore water residence time at local Santa Barbara beaches. Based on this reasoning, the presence of giant kelp and talitrid amphipods, in addition to existing microbes, was likely related to the rapid increase in  $\text{NH}_4^+$  concentrations observed in our mesocosms.

Detrital subsidies account for a significant component of the energy flowing through many ecosystems and their associated food webs (Polis and Strong, 1996; Srivastava et al., 2009), and may be utilized within the ecosystem from which it originated or transferred to another system. Detritus is critically important to ecosystems where it forms the base of the food web, such as leaf litter in streams or macrophyte wrack on sandy beaches. Although detritus has been shown to have propagating effects up the food web, it is most important for the consumers of this organic matter (Wallace et al., 1997; Dugan et al., 2003). The high wrack breakdown rates by talitrid amphipods (Lastra et al., 2008) are comparable to leaf litter breakdown by shredders (Hieber and Gessner, 2002). The significant relationship between wrack inputs and talitrid amphipod abundance (Fig. 2) is mirrored in stream ecosystems, where Graca (2001) found a correlation between leaf litter deposition and shredder densities. Invertebrate shredders and other consumers in stream ecosystems have been shown to contribute significantly to nutrient dynamics in stream ecosystems, specifically as they pertain to nitrogen species (Vanni, 2002; Dodds et al., 2000; Atkinson et al., 2014). In comparison, we demonstrate that an intertidal shredder species accounts for a significant increase in the flux of nutrients from

the particulate pool into the dissolved pool within a sandy beach ecosystem (Fig. 3). When making cross-ecosystem comparisons, it is important to consider the degree to which detrital subsidies might act as nutrient sources. Certain species may act as keystone nutrient recyclers when a given system is oligotrophic. For example, *Astyanax aeneus* is a fish species that relies on nutrient-rich terrestrial subsidies in an otherwise low-nutrient stream environment (Small et al., 2011). The intertidal environment we describe presents a similar scenario, with talitrid amphipods heavily reliant on, and correlated with, macroalgal wrack deposition on sandy beaches and high rates of DIN remineralization.

As beaches become developed and increasingly armored, the deposition and retention of wrack subsidies may decline, affecting the biodiversity and abundance of intertidal macroinvertebrates (Dugan et al., 2008, 2013). By reducing the widths of upper beach habitat zones, coastal armoring reduces wrack deposition and retention as well as wrack consumer abundance and diversity (Dugan and Hubbard, 2006; Dugan et al., 2008; Sobocinski et al., 2010). Projections of sea-level rise indicate that Santa Barbara County beaches will lose an average of 70% of the upper beach zones, primary talitrid amphipod habitat, by 2070 (Myers et al., 2017; Vitousek et al., 2017). This scenario is likely to lead to diminished organic matter supplies (i.e. wrack) and fewer consumers recycling nutrients into the nearshore system for uptake by local primary producers, such as surfgrass and kelps. In addition to these factors, warming temperatures are likely to increase the release of DIN from decomposed wrack (Lastra et al., 2018), which could further disrupt the availability of DIN for nearby primary producers and microbial communities. In the face of these environmental changes, a greater understanding of the contribution of detrital consumers, such as talitrid amphipods, to overall ecosystem function is needed.

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