Benthic Filtering Reduces the Abundance of Primary Producers in the Bottom Water of an Open Sandy Beach System (Kashimanada Coast, Japan)

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Abstract The effect of benthic filtering by the upogebiid shrimp Austinogebia narutensis on the abundance of primary producers in the water column was investigated on a wave-dominated nearshore zone in central Japan facing the Pacific Ocean. Chlorophyll a concentration in the bottom layer of the water column decreased significantly with increasing population density of A. narutensis, suggesting that shrimp feeding reduces the abundance of phototrophic microorganisms in the bottom layer. Because the upogebiid shrimp commonly occur in the nearshore zone of sandy beaches, similar effects of their benthic filtering as reported in this study can be expected in areas where the shrimp is as densely present.

1. Introduction

Benthic burrowing animals inhabiting marine sediments drastically alter the physicochemical conditions of seafloor sediments and overlying waters (Kristensen, 1984; Ziebis et al., 1996; Lohrer et al., 2004, 2013, 2015; Huettel et al., 2014; Seike et al., 2018). One example is filtration by dense populations of suspension-feeding benthic organisms, which can potentially reduce the abundance of primary producers (phytoplankton and suspended benthic microalgae) in overlying waters. The removal of a large proportion of the suspended organic particles by benthic filtering indirectly regulates the nutrient dynamics in such ecosystems (Asmus & Asmus, 1991; D’Andrea & DeWitt, 2009; Newell, 2004; Officer et al., 1982). Proving the nature of benthic filtering is thus important for a better understanding of marine ecosystems. However, the effect of benthic filtering on ecosystems has only been investigated in semienclosed (sheltered) settings, such as tidal flats, inner bays, and estuaries; to the best of our knowledge, no study of offshore sandy or muddy bottoms on open coasts has been conducted.

The sandy beach system, a wave-deposited accumulation of sediment lying between the modal wave base and the upper swash limit (sensu Short, 1999), is the commonest environment type in coastal settings facing the open ocean and comprises ~30% of the ice-free coastlines worldwide (McLachlan & Brown, 2006; Short, 1999). Sandy beach ecosystems are locally and globally threatened by human activities, including coastal engineering to protect infrastructure and sea level rise (Defeo et al., 2009; Dugan et al., 2010). Interactions between benthic organisms and the seafloor environment are less well understood for sandy beach ecosystems. In particular, organism-environment interactions in the nearshore zone (water depths of <30 m and 2–3 km offshore from the coastline, sensu Short, 1999) remain poorly understood. For these reasons this study aimed to investigate the effect of benthic filtering by the suspension-feeding shrimp Austinogebia narutensis (Decapoda: Upogebiidae) on the abundance of primary producers in the water column along the Kashimanada coast, central Japan, facing the northwestern Pacific Ocean (Figure 1).
Previous studies have demonstrated that upogebiid shrimp affect the abundance of primary producers and the nutrient dynamics of the water column. The shrimp move seawater through their burrows and feed by filtering suspended organic particles from the water before discharging the filtered water to the sea floor (Figure S2g in the supporting information) (Dworschak, 1981, 1987; Dworschak et al., 2012; Nickell & Atkinson, 1995). On tidal flats, the shrimp are potentially capable to filter the entire overlying water column each day, thereby removing large proportions of the available phytoplankton, which affects the nutrient dynamics of the ecosystem (D'Andrea & DeWitt, 2009; Dworschak, 1981; Griffen et al., 2004). Although many previous studies have proved the environmental effects of upogebiid shrimp in semienclosed...
ecosystems, no studies have been conducted on the effect of these shrimp in sandy beach environments facing the open ocean.

It is known that upogebiid shrimp inhabit both tidal flats and nearshore zone environments of sandy beaches facing open oceans. For example, Sakai (2006) and Sato et al. (2016) reported that A. narutensis occurs on nearshore bottoms at water depths of 5–30 m on the Pacific Ocean coasts from the Japanese archipelago to Taiwan island, covering a large proportion of the temperate zone in the northwestern Pacific. In addition, several upogebiid shrimp species have been reported from offshore bottoms of sandy beaches facing the northeastern Pacific Ocean, from Alaska to Panama (Wicksten, 1989; Williams, 1986) and the Atlantic Ocean (Sakai, 2006). However, as described above, no studies focusing on the effect of upogebiid shrimp on the water environment have been conducted in an open coastal environment.

This study tested the hypothesis that the upogebiid shrimp A. narutensis reduces the abundance of primary producers in the water column on an open sandy coast. We investigated this hypothesis using multiple complementary approaches, that is, by measuring in situ shrimp density and chlorophyll a concentrations, burrow dimensions from resin casts, and stable carbon and nitrogen isotope ratios. We furthermore tested an alternative hypothesis, by a spatial correlation study to salinity with chlorophyll a.

### 2. Material and Methods

#### 2.1. Study Sites

Fieldwork was carried out on the nearshore zone sandy bottoms along the Kashimanada coast, central Japan, facing the northwestern Pacific Ocean (Figure 1a). We established six perpendicular lines (Figure 1a), starting at ~9- m depth, ending at ~20- m depth, with three stations at each line, at 9, 14, and 19 m (Figure 1b). The sampling stations on each transect line were numbered in order from the shoreward (shallow) to the seaward (deep) directions. For example, “St. 3-1,” “St. 3-2,” and “St. 3-3” denote the position where the water depth was ~9, 14, and 19 m on Transect Line 3, respectively (Figure 1b). The environmental setting of each station and a detailed description of the data acquisition process are presented in the supporting information.

#### 2.2. Burrow Morphology

The morphology of the upogebiid shrimp burrow provides information on the subsurface feeding ecology of the shrimp (Nickell & Atkinson, 1995). Therefore, to investigate the feeding ecology of A. narutensis inhabiting the nearshore zone in this study, we made casts of burrows at St. 5-3 during scuba diving fieldwork in November 2010 and July 2011. The low population density of the shrimp at this station enabled us to obtain near-complete burrow cast without any crosscutting with each other. Burrow parameters (shaft diameter, entire burrow depth, and width) were subsequently measured in the laboratory.

Fossil counterparts of marine invertebrate burrows are known from geological records worldwide. These fossils are classified as ichnogenus and ichnospecies, based on their overall morphology and details of the structure of the burrow wall. To compare the A. narutensis burrows with those from geological records, it was therefore essential to have information on the wall structure. In this study, the wall structure of the A. narutensis burrows was observed from sediment core samples using a plastic pipe of 60-mm diameter and 130-cm length.

#### 2.3. Burrow Density Measurement and Benthos Sampling

Because the abundance of burrow openings reflects the population density (Butler & Bird, 2007; D’Andrea & DeWitt, 2009), the number of burrow openings observed on the seafloor reflects the shrimp population density at the time a survey is conducted. The burrow density was determined by counting the number of burrow openings within a quadrate (30 × 30 cm², 10 replicates, Figure S5 in the supporting information) during scuba diving fieldwork in July 2013.

Quantitative benthos sampling was conducted at all sampling stations in July 2013. Seafloor sediment in the quadrate (30 × 30 cm², ~10 cm in depth, five replicates) were suctioned and sieved (1-mm mesh) using an airlift suction sampler.
2.4. Stable Carbon and Nitrogen Isotope Analysis

*Austinogebia narutensis* shrimp were collected for the stable isotope analysis with dredge sampling at Line 5 in the summers of 2011–2013. Also, supplementary shrimp samples were collected at Lines 1–3. Potential food sources of the shrimp, such as the surface water particulate organic matter (sPOM), bottom water POM (bPOM), and seafloor sediments, were also collected at Line 5 (St. 5-3) close to our research base, Hazaki Oceanographical Research Station where various environmental parameters are monitored every day. Seawater samples (~3 L) for isotope analysis were collected in Van Dorn bottles in July 2011. The Bayesian stable isotope mixing model in the Stable Isotope Analysis in R (SIAR) package (Parnell et al., 2010) was used to partition the proportional contributions of the potential food sources to the *A. narutensis* shrimp based on their $\delta^{13}$C and $\delta^{15}$N signatures. We show the mean and the 95% confidence interval of the estimate of the proportional contribution of each source. The origins of the POM samples were assessed by investigating their stable carbon isotope signature and C/N ratios. Detailed descriptions of the isotope data acquisition and subsequent processing are presented in the supporting information.

2.5. Measurement of Chlorophyll $a$ Concentrations and Salinity

We evaluated the abundance of primary producers in the water column by measuring the concentration of chlorophyll $a$. Seawater samples (140 ml) for chlorophyll $a$ analysis were collected on 3–15 July 2013 using Van Dorn bottles at three levels in the water column at each sampling station (Figure S5 in the supporting information): 1 m below the water surface (upper), 1 m above the sea floor (bottom), and at midwater depth in the water column (middle). The midwater depth is varying with water depth; that is, the data of the middle layer cannot be directly compared between the different sampling depths. The water samples were filtered using 47-mm Whatman GF/F glass fiber filters, which were stored at $-20$ °C until analysis. Following extraction of the filtered material with N, N-dimethylformamide, the chlorophyll $a$ concentrations were determined using a Turner Design 10-AU fluorometer at the Atmosphere and Ocean Research Institute of The University of Tokyo. We measured the salinity of all the water layers with a conductivity-temperature sensor (A7CT-USB, JFE Advantech) during the fieldwork.

3. Results

3.1. Burrow Morphology

A total of 13 near-complete *A. narutensis* burrow casts was obtained (Figures 2c and S6 and Table S3 in the supporting information). Ten burrows showed a Y- or U-shape morphology with two openings, whereas the remainder (three burrow casts) showed a gently inclined morphology (J-shape) with a single opening, resulting in a mean number of 1.77 openings per burrow.

Resin peels made from the vertically sectioned sediment cores showed the wall structure of the *A. narutensis* burrows. In contrast to the surrounding fine-grained sandy sediments (0.11–0.14 mm in median diameter, Table S1 in the supporting information), the walls are composed of muddy sediments (Figure 2d). The outer walls have a knobby surface, whereas the inner walls are smoothed by the activities of the shrimps (Figure 2e).

3.2. Spatial Variation in Burrow Density and Other Benthic Invertebrates

The burrow density (number of burrow openings per square meter) ranged from 0.0 to 752.2 (Figure 2a and Table S2 in the supporting information). The burrow density significantly differed among the sampling sites (Kruskal-Wallis test; $p < 0.01$). They occurred densely near the center of the coastal study area (Transect Lines 2–4), whereas there were almost no burrows near the southern end of the study area (Transect Lines 5–6). The burrow density showed no significant correlation with water depth (Pearson correlation, $r = 0.30$, $p > 0.05$).

Few benthic species other than *A. narutensis* were found at the study sites (Table S5 in the supporting information).

3.3. Stable Carbon and Nitrogen Isotope Analysis

The relative contributions of sPOM, bPOM, and the seafloor sediment to the food source of the *A. narutensis* were 2.4% (0.1–8.5%), 91.5% (74.4–99.0%), and 6.1% (0.2–22.2%), respectively (Figure 2f). The C/N ratios for the sPOM and bPOM samples showed that they were composed of marine primary producers (Figure S7a in the supporting information). The carbon isotope compositions of both POM samples also showed that they
originated from marine primary producers, but their compositions varied among the water depths: sPOM was composed of marine phytoplankton and bPOM of a mixture of marine phytoplankton and suspended benthic microalgae (Figure S7b in the supporting information).

3.4. Spatial Variation in Chlorophyll $a$ Concentrations and Salinity

The chlorophyll $a$ concentration in the water column ranged from 0.38 to 7.78 $\mu$gL$^{-1}$. In the upper layer, the concentration was high near the southern and northern ends of the study area, which were relatively close to

Figure 2. Spatial variations in the abundance of the upogebiid shrimp *Austinogebia narutensis*, and the subsurface ecology of the shrimp based on its burrow morphology and a stable isotope analysis. (a) Spatial (latitudinal) variation in the abundance of *A. narutensis* burrow openings. (b) Oblique view of the seafloor at station St. 2-3. Note the dense occurrence of *A. narutensis* burrow openings. (c) Cast of *A. narutensis* burrow (Cast No. 12). (d) A resin peel sample made from a vertically sectioned sediment core, showing a section of an *A. narutensis* burrow. The burrow wall consists of muddy sediment with a knobby exterior surface. (e) Sketch of (d). (f) Contributions of food sources including surface water POM (sPOM), bottom water POM (bPOM), and seafloor sediment to the diet of *A. narutensis*, based on the SIAR model using stable isotope composition (Parnell et al., 2010). (g) Schematic diagrams showing the benthic-filtering of the *A. narutensis* shrimp based on its burrow morphology and the stable isotope compositions. The shrimp irrigates its burrow with water and filters the water in a suspension-feeding process: The overlying water is pumped through the burrows and suspended organic particles (marine phytoplankton and suspended benthic microalgae) are removed from the water column by the filtering of the shrimp.
river mouths (Figure 3a). The middle layer showed no clear latitudinal (alongshore) variation (Figure 3b). In the bottom layer, the concentration of chlorophyll \( a \) was high near the southern end, but the northern end showed relatively low values (Figure 3c). The salinity in the water column ranged from 30.70 to 33.47. Relatively low salinity waters were distributed in the upper layer near the southern end of the study area (Figure 3d). In contrast, the middle and bottom layers contained relatively high salinity water and showed no clear spatial variation in salinity (Figures 3e and 3f).

The chlorophyll \( a \) concentration in the upper layer was correlated negatively with salinity (Pearson correlation, \( p < 0.01 \), Figure 4d). In contrast, the chlorophyll \( a \) concentrations in the middle and bottom layers did not correlate significantly with salinity (Pearson correlation, \( p > 0.05 \), Figures 4e and 4f).

The chlorophyll \( a \) concentration in the upper and middle layers showed no significant correlation with burrow density (Pearson correlation, \( p > 0.05 \), Figures 4a and 4b). In contrast, the chlorophyll \( a \) concentration in the bottom layer was negatively correlated with burrow density (Pearson correlation, \( p < 0.01 \), Figure 4c).
4. Discussion

The dominant burrow morphology of the *A. narutensis* burrows in the nearshore bottom of the Kashimanada coast was Y or U shaped with two openings, whereas few burrows showed J-shape with single opening. Based on criteria relevant to the feeding ecology of burrowers (Nickell & Atkinson, 1995), a Y- or U-shaped and J-shaped morphology suggest suspension (filter) feeding and deposit feeding, respectively. On the other hand, the stable isotope analysis in the present study showed that *A. narutensis* on the Kashimanada coast feeds mainly on bPOM and feeds rarely on seafloor sediment (Figure 2f), because the δ¹³C value for *A.*
naratensis muscle tissues differs from that of the seafloor sediment (Figure S8 in the supporting information). This result indicates that A. narutensis is a filter feeder and primary consumer in the sandy beach ecosystem. Therefore, the trophic position of A. narutensis is the same as that of other upogebiid shrimps inhabiting tidal flats (e.g., Kanaya et al., 2007). Austinogebia narutensis inhabiting a tidal flat in Japan has also been reported to form similar Y- or U-shaped burrows with two openings (Kinoshita & Itani, 2005), suggesting that there is commonality in the burrow morphology of A. narutensis among environmental settings.

The highest numbers of A. narutensis in the study area exceeded 400 individuals per square meter (Figure 2a and Table S2 in the supporting information). This is comparable to the density of populations of upogebiid shrimp previously reported from intertidal settings (D’Andrea & DeWitt, 2009; Griffen et al., 2004; Kinoshita, 2002; Kinoshita et al., 2003). As sandy beaches comprise one third of the ice-free coastlines worldwide (McLachlan & Brown, 2006; Short, 1999), it is likely that there are enormous numbers of upogebiid shrimp inhabiting coastal regions. Nonetheless, upogebiid populations in the nearshore zone have not previously been quantified. These previously overlooked upogebiid populations should be evaluated to enable greater understanding of coastal ecosystems.

The population density (number of burrow openings) showed alongshore variation (Figure 2a and Table S2 in the supporting information). The density was highest at the central region of the coastal study area (Line 2) and decreased to the north and south margins. Such a unimodal distribution pattern has been well documented for intertidal sandy beach species (Defeo & McLachlan, 2005). Gradients in physical factors, including freshwater discharges from rivers, are considered to be a cause of the alongshore patterns.

Sandy beaches tend to be located between outlets of large rivers, as was the case in the present study. The Kashimanada coast is located between the Nakagawa (north end) and Tonegawa (south end) rivers. Freshwater is generally harmful for marine species and prevents the colonization and growth of sandy beach animals (Defeo & McLachlan, 2005). However, the effect of freshwater discharge on A. narutensis is likely to be much less than that on intertidal species because its habitat is at water depths >10 m in open coastal areas, where freshwater influences are unlikely because the bottom layer is composed of relatively high salinity water (Figure 3f). Nevertheless, freshwater discharges could indirectly affect the distribution of A. narutensis through associated factors that affect the distribution patterns of intertidal species.

Freshwater discharge has another effect on coastal marine ecosystem. The nutrient supply from rivers is widely considered to affect the abundance of primary producers in coastal waters (Harrison et al., 2008). In fact, the nutrient supply from the Tonegawa and Nakagawa rivers affects the abundance of the primary producers (chlorophyll a concentration) in the area (Adachi & Nakayama, 2009). The results of the present study show that the chlorophyll a concentration in the upper water decreased with increasing salinity (Figure 4d), suggesting that nutrient input from the rivers caused for elevated upper layer chlorophyll a concentrations near the river mouths (Figure 3d).

In contrast, the bottom and middle layers contained no low-salinity water and showed no significant correlation between salinity and chlorophyll a concentration, suggesting that the freshwater discharge had a limited effect on the bottom and middle layers. In other words, the freshwater discharges did not produce alongshore variation of chlorophyll a concentration in the middle and bottom layers. The population density of A. narutensis showing the unimodal distribution pattern along the coastline are, therefore, unlikely to be controlled by the abundance of primary producers (chlorophyll a).

Because bPOM was composed of a mixture of marine phytoplankton and benthic microalgae, the high chlorophyll a concentration in the bottom waters was attributed to the stirring up of the seafloor sediments containing benthic microalgae. The two factors that increased the abundance of primary producers (i.e., the nutrients supplied by freshwater and suspended benthic microalgae) were not present in the middle layer, which explains the low chlorophyll a concentrations in that layer.

In contrast to salinity, the burrow density showed a significant negative correlation with chlorophyll a concentration in the bottom layer (Figure 4c). Few benthic species other than A. narutensis suggests that this shrimp is the major primary consumer at a water depth of >10 m in the sandy bottom environment in the study area. These supports the hypothesis that suspension feeding by A. narutensis reduces the abundance of primary producers in the overlying water.
The dense population of *A. narutensis* along the Kashimanada coast also supports the benthic filtering hypothesis. The effect of water filtering by the upogebiid shrimp on the water column environment has been reported in tidal-flat and semiclosed ecosystems (D’Andrea & DeWitt, 2009; Dworschak, 1981; Griffen et al., 2004). In those studies, the population densities of upogebiid shrimp were <200 individuals per square meter. On the Kashimanada coast, the maximum population density of *A. narutensis* is >400 individuals per square meter (Table S2 in the supporting information), which greatly exceeds that in the semiclosed ecosystems reported in previous studies, suggesting that *A. narutensis* assemblages on the Kashimanada coast can reduce and control the abundance of primary producers in this environment. We also used a simple calculation to assess the impact of *A. narutensis* filter feeding on the abundance of primary producers in the bottom water, based on the filtering efficiency reported by Griffen et al. (2004). Assuming a closed system of 1-m$^3$ volume, the calculation suggested that the abundance of primary producers in the bottom layer could be reduced to a level consistent with the observed chlorophyll $a$ concentration after 1–3 hr of filtering by the shrimp. Therefore, benthic filtering by *A. narutensis* can potentially reduce the abundance of primary producers in the bottom water.

Although to date the significance of benthic filtering has primarily been considered only for semiclosed water settings, such as tidal flats and embayments, the results of the present study clearly demonstrate that the effect of benthic filtering on the abundance of primary producers not only occurs in the water column of open sandy coasts and also has a significant impact on the environment.

In contrast to the bottom layer, the chlorophyll $a$ concentration of the middle and upper layers showed no significance correlation with burrow density (Figures 4c and 4b). Therefore, the effect of benthic filtering along this open sandy coast was limited to waters overlying the sediment. The effective area of benthic filtering in the sandy coast differed from that of coastal embayments and tidal flats, where filtering of the entire water column through burrows can occur due to limited water depth (water volume) in the settings.

Upogebiid shrimps including *A. narutensis* not only consume most of the suspended primary producers in bottom waters but also are the major prey of large marine carnivores including benthic sharks, eels, and water birds (Komai et al., 1999; Navedo & Masero, 2007; Kaifu et al., 2013; Arai, 2014). For example, the stomach contents of star-spotted dogfish *Mustelus manazo* collected from the Kashimanada coast were reported to be mainly composed of a species of upogebiid shrimp, probably *A. narutensis* (Arai, 2014). This indicates that the shrimp plays an important role in trophic pathways in seafloor ecosystems in the nearshore zones of open sandy coasts.

Upogebiid shrimp have been reported from several sandy bottom sites of the nearshore zone worldwide. For example, *A. narutensis* occurs in nearshore zone bottom environments of certain open sandy coasts in eastern Asia (Sakai, 2006), and other upogebiid shrimp have been reported from offshore subtidal bottom environments on coastlines of the Pacific Ocean (Wicksten, 1989; Williams, 1986) and the Atlantic Ocean (Sakai, 2006). These reports and the present study indicate that upogebiid shrimp commonly inhabit subtidal bottoms of sandy beaches throughout the world, except in high-latitude polar seas (Dworschak et al., 2012) and that they make a major contribution to benthic filtering. Investigating the spatial distribution of these shrimp and their effect on benthic filtering is essential to understanding the dynamics of primary producers and trophic pathways in open sandy coasts. Because little is known of the interactions between benthic animals and the seafloor environment along sandy beaches facing open ocean environments, more studies similar to that described here need to be conducted.

From post-Mesozoic nearshore zone deposits, trace fossils comparable burrows of upogebiid shrimp have been recognized: The entire burrow morphology of *A. narutensis* is comparable to the Y-shaped trace fossil *Parmaichnus stironensis*, which occurs in Pleistocene marine deposits (Pervesler & Uchman, 2009). Because the Y-shaped burrow morphology is known to act as a filter-feeding device (Nickell & Atkinson, 1995), the trace fossil producer probably also was a suspension feeder, like *A. narutensis*. The knobby burrow wall of *A. narutensis* seen on vertically sectioned sediment cores (Figures 2d) is also comparable to the trace fossil *Ophiomorpha* which has occurred since the Mesozoic (Frey et al., 1978; Leaman et al., 2015). The presence of a structure similar to the *A. narutensis* burrow in the geological suggests that similar shrimp species have been around for long time, are distributed globally, and probably globally play an important role in filtering the water column.
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