Trophic segregation in a burrow: the stable carbon and nitrogen isotope ratios of the burrowing shrimp *Upogebia major* and its commensal bivalve *Cryptomya busoensis*

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Abstract: Burrows produced by marine invertebrates often harbor other small commensal invertebrates. The mud shrimp *Upogebia* is known to coexist with the myid bivalve *Cryptomya* in a burrow produced by the shrimp. Both species are filter-feeders, and thus interspecific competition or trophic niche segregation may occur in the burrow. Samples for carbon and nitrogen stable isotope analysis were collected from a tidal flat near the tidal inlet of Akkeshi Lake, Hokkaido, northern Japan in April 2013. In addition, stratified benthos sampling was conducted on the tidal flat in August 2018, to clarify the interspecific relationship between *U. major* and *C. busoensis* in the burrow. The stratified benthos sampling showed the vertical distribution of these species, and indicated that both species filter water from the same part of the burrow for feeding. The stable carbon and nitrogen isotope analysis showed that important food sources for both *U. major* and *C. busoensis* are marine phytoplankton and microphytobenthos. In addition, *C. busoensis* is likely to consume terrestrial organic matter whereas *U. major* is unable to utilize it. The partial trophic segregation between the species increases the potential benthic filtering because it allows the *Upogebia* burrow complex to consume a wide variety of organic matter, and it might reduce interspecific competition between the filter-feeding host and its commensal species. These results demonstrate how ecologically similar macrobenthos can coexist in a burrow.

Key words: burrow, commensalism, food source, stable isotope, tidal flat

Introduction

Filter-feeding benthic invertebrates are particularly important in seafloor ecosystems because they reduce the abundance of primary producers and alter the nutrient dynamics in the water column (Officer et al. 1982, Newell 2004, D’Andrea & DeWitt 2009, Seike et al. 2020). The burrows produced by filter-feeding invertebrates also increase the biodiversity in a benthic ecosystem because they often harbor other small commensal invertebrates (Anker et al. 2005, Dworschak et al. 2012). Burrowers (burrow hosts) and the small commensal invertebrates in the burrow (burrow associates) both affect the biogeochemistry of the overlying water (Griffen et al. 2004), as the removal of a large proportion of the suspended organic particles by benthic filtering indirectly regulates the nutrient dynamics in the overlying water. Moreover, high species richness in a burrow might reflect the high level of ecological functions of the burrow because it allows a burrow system to filter a wide variety of organic matter from the seawater. Therefore, determining the ecological functions of both the burrowers and burrow associates is essential to understanding the biogeochemical cycles in marine ecosystems.

*Upogebiidae* are a representative group of ecosystem engineers on tidal flats and shallow-marine seafloors that can feed by filtering suspended organic particles from overlying seawater that circulates through their burrows (Fig. 1C) (Dworschak 1981, 1987, Nickell & Atkinson 1995, Dworschak et al. 2012, Seike et al. 2020). The *Upogebia* shrimp irrigates the burrow with water, which is filtered during suspension feeding. The burrow of *U. major* consists of two sections, an upper U-shaped part and...
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...a lower I-shaped part (Fig. 1C; Kinoshita 2002). The overlying water is pumped through the U-shaped part of the burrow (Dworschak 1981), which is less than \( \sim 50 \) cm deep (Kinoshita 2002). Because *U. major* juveniles (\( \sim 0.5 \) cm in carapace length) also produce U-shaped sections in their burrows (Kinoshita 2002), these shrimps are consistently filter-feeders without relation to their body or burrow size.

The myid bivalve *Cryptomya*, which is also a filter-feeder, lives in the *Upogebia* burrow wall with its siphon extending into the open tube (Itani & Kato 2002, Nara et al. 2008) and the filter-feeding activities of the shrimp and the commensal bivalve, and the particle settlement within the burrow could remove suspended organic particles from the seawater drawn into the shrimp burrow. The filter-feeding activities of these animals and the particle settlement are collectively referred to as the ‘burrow complex’ (Griffen et al. 2004). An aquarium experiment revealed that \( \sim 40\% \) of the total suspended particles in *Upogebia pugettensis* burrows were removed by the commensal bivalve *Cryptomya busoensis* (Griffen et al. 2004).

In some cases, the feeding habit and food sources differ among burrowing hosts and their associates (Kneer et al. 2008), suggesting that they play different roles in consuming organic matter from seafloor ecosystems. However, the food sources of *Upogebia* and *Cryptomya* have not been compared in *in situ* and thus remain unclear, suggesting that the trophic relationships between them (trophic competition or segregation) are also unknown.

The stable isotopes of carbon (\( \delta^{13}C \)) and nitrogen (\( \delta^{15}N \)) provide powerful tools for estimating food sources in a natural community (Post 2002). The food sources of the upogebiid shrimps have been estimated using stable iso-
topes (e.g., Yokoyama et al. 2005b, Kanana et al. 2007, 2008, Antonio & Richoux 2014, Bosley et al. 2017), and were revealed to be mainly marine phytoplankton. In contrast, the stable carbon and nitrogen isotope ratios of Cryptomya have rarely been investigated, except for one study in which Park et al. (2020) found that C. busoensis also consumes marine phytoplankton. The burrow host and associate having the same feeding habits suggests the occurrence of interspecific competition or trophic niche segregation in the burrow, but this possibility has not yet been tested by comparing food sources of the upogebiid shrimp and its commensal bivalve in a tidal flat. We therefore measured the stable carbon and nitrogen isotope ratios to compare the food sources of the burrow producer (U. major) and the burrow associate (C. busoensis). In addition, we measured population density of both species to discuss the trophic competition among them and the effect of their benthic feeding on the overlying water because filtering by a dense population of the upogebiid shrimp can reduce primary producers in a water column (Griffen et al. 2004, Seike et al. 2020). We also investigated the vertical distribution of the two species using a stratified sampling method to clarify where the burrow host and burrow associate filter seawater within the burrow complex. By analyzing the stable isotope ratios and the commensal relationship, we show that the effects of the host animal and burrow associate on benthic filtering in a seafloor ecosystem differ, even within a single burrow complex. Determining the food sources of burrow hosts and their associates might clarify how so many invertebrate species coexist in the limited spaces of burrows.

Materials and Methods

Study site

Field observation and collection of the samples for the stable isotope analysis were conducted on a small tidal flat (~1500 m²) near the tidal inlet of Akkeshi Lake, Hokkaido, northern Japan (Fig. 1; 43°03.05′N, 144°51.44′E). The mud shrimp U. major is the dominant species in this tidal flat while there are some intertidal molluscan species including Mya arenaria oonogai, Macoma contabulata, and Ruditapes philippinarum. The U. major burrow harbors other small commensal invertebrates including the myid bivalve Cryptomya busoensis, the scale worm Hesperone hwanghaiensis, and the gobiid fish Gymnogobius macrognathos (Sato et al. 2016, Henmi et al. 2018). The burrows of U. major are seen throughout the tidal flat surface.

Benthos sampling

The vertical distribution of U. major and C. busoensis was measured by stratified sampling as a part of field courses for undergraduate and graduate students organized by Akkeshi Marine Station, Hokkaido University in August 2018. A plastic pipe, 20 cm in diameter (covering ~0.03 m²) and 55 cm long, was inserted into the substrate of the tidal flat. The sediment within the pipe was excavated with a shovel, and was collected at 5 cm intervals. The collected sediments were then washed through a 1.0 mm mesh sieve. All U. major and C. busoensis individuals remaining on the screen were counted to calculate population density in each layer. Three replicates of the stratified sampling procedure were conducted, and a total of 30 layers (10 layers for each sampling pipe×three replicates) were investigated.

Burrow density measurements

Field counts of burrow-producing invertebrates, such as upogebiid shrimps, can be used to determine population densities because the abundance of burrow openings reflects the population density (Butler & Bird 2007, D’Andrea & DeWitt 2009). Prior to the stratified benthos sampling, we measured the burrow density to estimate the population density of U. major using the same sampling pipe. Because U. major burrows show a Y- or U-shape morphology with 2 openings on the seafloor surface (Kinoshita 2002), the number of burrows divided by 2 equals population density of the shrimp. The burrow density was determined by counting the number of burrow openings within a plastic pipe 20 cm in diameter (covering ~0.03 m²). The smallest burrow opening measured in this study was ~5 mm. Three replicate measurements were made for the burrow counts. Also, the number of C. busoensis per single U. major burrow was calculated as the measured total number of the bivalve divided by the measured population density of U. major.

Stable isotope analysis

Stable isotope samples of Upogebia major and C. busoensis were collected from the same tidal flat in April 2013. The collected U. major (carapace length: 5.6–24.4 mm) were stored immediately after collection at −20°C while C. busoensis (shell length: 6.4–13.9 mm)
were placed in clean seawater for 12 h to evacuate gut contents before storage at −20°C. The muscle tissues of *U. major* and all tissues of *C. busoensis* were used for the stable isotope analysis. Because the *C. busoensis* individuals had a small amount of muscle tissue, we analyzed whole soft tissue of the bivalve. Previous studies showed that there are no clear differences in carbon and nitrogen isotope values between muscle and whole soft tissues of bivalves (Yokoyama & Ishihi 2006).

We examined the marine phytoplankton, microphytobenthos, and terrestrial organic matter, as potential food sources. Marine phytoplankton was collected from surface water sample at an offshore station located 3 km south of Akkeshi Marine Station, Hokkaido University. Microphytobenthos was collected at the tidal flat (Fig. 1). Terrestrial organic matter was collected from riverine water at a freshwater channel located 5 km from the mouth of Bekenbushi River (Fig. 1; 43°06.45′N, 144°53.51′E). In addition to the potential food sources described above, other environmental materials, such as the burrow wall of *U. major* and estuarine particulate organic matter (estuarine POM) were collected from the tidal flat to support the isotope analysis. Water samples for estuarine POM was collected at a flood tide. All samples for the stable isotope analysis were collected in April 2013 except for terrestrial organic matter, which was collected in August 2014.

Marine phytoplankton, terrestrial organic matter, and estuarine POM were filtered from the water samples and retained on 47 mm Whatman GF–F glass filters filtered from the water samples. Microphytobenthos on the tidal flat surface was extracted by a modified method reported by Kuwae et al. (2008): approximately 1 mm depth tidal flat sediment samples were retrieved using a spatula, and spread on a tray to a depth of ∼5 mm, a 65-µm mesh nylon screen was laid over the sediment, and precombusted glass wool was placed over the screen; the tray was kept moist by applications of sprayed filtered seawater and in the dark, overnight at ambient temperatures (−10°C); then the glass wool containing microphytobenthos was removed.

All isotope samples were stored at −20°C prior to acidification in 1 N HCl to remove inorganic carbon and dried at 60°C. Lipids were not removed from the samples because lipid removal raises not only the δ13C fractionation by 0.4–1.5‰ but also the δ15N fractionation by 0–0.8‰, resulting in large fractionation values outside of the range of currently accepted δ13C and δ15N trophic enrichment (Yokoyama and Ishihi 2006). The isotopic samples were analyzed using a Delta V Advantage isotope ratio mass spectrometer (Thermo Fisher Scientific, Massachusetts, USA) coupled to an elemental analyzer (Flash 2000, Thermo Fisher Scientific) installed at the Atmosphere and Ocean Research Institute, The University of Tokyo, Japan or using an IsoPrime mass spectrometer (Elementar, Langenselbold, Germany) coupled to a vario MICRO cube combustion device (Elementar), which was also installed at the Atmosphere and Ocean Research Institute. Stable isotope ratios are expressed in the δ notation as the deviation from a standard, in parts per thousand (%), according to the following equation:

\[ \delta ^{13}C, \delta ^{15}N(\%) = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 10^3 , \]

where R is 13C/12C or 15N/14N. Vienna PeeDee Belemnite (VPDB) and atmospheric nitrogen (N2) were used as the isotope standards for carbon and nitrogen, respectively. The analytical precision of the mass spectrometry systems, based on the standard deviation of internal reference replicates, was <0.2‰ for both δ13C and δ15N.

We used the Bayesian stable isotope mixing model in the Stable Isotope Analysis R (SIAR) package (Parnell et al. 2010) to estimate the proportional contributions of *U. major* and *C. busoensis* food sources based on their δ13C and δ15N signatures. The SIAR model determines the probability distributions of the sources that contribute to the observed mixed signal, while accounting for the uncertainty in the signatures of the sources and for isotopic fractionation. The Bayesian mixing models can yield robust estimates of diet and quantify trophic competition arising in overlapping niches (Parnell et al. 2010); therefore, they have been widely used in recent marine ecological studies (e.g., Higgs et al. 2016, Bosley et al. 2017, Kanaya et al. 2018). We defined three sources (marine phytoplankton, microphytobenthos, and terrestrial organic matter) as the end-members for the isotopic mixing model because they constitute the main organic matter sources in the tidal flat. Widely accepted values for the trophic enrichment factors (0.4 ± 1.3‰ for δ13C and 3.4 ± 1.0‰ for δ15N per trophic step: Post 2002) were used. In addition, taxon-specific trophic enrichment factors were also used. The trophic enrichment factors for muscle tissue of the ghost shrimp *Nikonotrypaea harmandi* (2.0‰ for carbon and 3.9‰ for nitrogen: Yokoyama et al. 2005a) was used for *U. major*. The trophic enrichment factors for whole soft tissue of *Ruditapes philippinarum* juveniles (0.6‰ for carbon and 3.4‰ for nitrogen: Yokoyama et al. 2005a) was used for *C. busoensis*.

**Results**

**Benthos sampling**

Stratified sampling showed the vertical distribution ranges and abundances of *U. major* and *C. busoensis*. The mud shrimp *U. major* occurred at depths of >10 cm, and its density per layer ranged from 11 to 21 individuals m−2. The total number of the shrimp (the sum of all layers) was 85 individuals m−2. The myid bivalve *C. busoensis* occurred at depths of 0–50 cm from the seafloor surface. The density of the bivalve per layer ranged from 11 to 944 individuals m−2. The total number of the bivalve (the sum of all layers) was 3629 individuals m−2.
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Burrow density

Average *U. major* burrow opening density was 361 burrow openings m$^{-2}$, indicating the shrimp density was 180 individuals m$^{-2}$. Calculated number of the bivalve per single *U. major* burrow was 20 individuals.

Stable isotope

The carbon and nitrogen isotope values differed between the species (Fig. 3 and Table ES1). The average δ$^{13}$C and δ$^{15}$N ratios in *U. major* ($-16.1 \pm 1.9\%$ and $11.8 \pm 0.2\%$, respectively) were greater than in *C. busoensis* ($-18.5 \pm 0.6\%$ and $2.0 \pm 1.0\%$, respectively). Average ratios of δ$^{13}$C and δ$^{15}$N in marine phytoplankton ($-19.2 \pm 0.2\%$ and $6.9 \pm 0.4\%$, respectively), and tidal flat sediment ($-22.9 \pm 0.2\%$ and $4.9 \pm 0.3\%$, respectively) were progressively less than in *U. major* and *C. busoensis*. The average δ$^{13}$C and δ$^{15}$N ratios in microphytobenthos were respectively $-11.8 \pm 0.2\%$ and $7.0 \pm 0.2\%$, respectively, which was greater than in *U. major* and *C. busoensis* although the δ$^{15}$N ratio in the former was less than in the benthic organisms. Terrestrial organic matter showed the lowest values for both δ$^{13}$C and δ$^{15}$N values (Fig. 3). The burrow-wall signatures were closest to those of the tidal flat sediments, with extensive overlap, as expected, as the wall material is mostly composed of tidal flat sediments (Supplementary Table S1). In addition, estuarine POM showed almost the same values with marine phytoplankton (Supplementary Table S1).

We used the SIAR model of isotope signatures to infer the main food sources of *U. major* and *C. busoensis* (Figs. 4 and 5). The SIAR models based on the both trophic enrichment factors showed similar patterns. Results based on the widely accepted values for the trophic enrichment factor were as follows: For *U. major*, the median percentage contributions and 95% confidence intervals for marine phytoplankton, microphytobenthos, and terrestrial organic matter were 48.0% and 12.1%–74.8%, 45.8% and 22.0%–71.0%, 5.2% and 0.3%–22.8%, respectively (Fig. 4). For *C. busoensis* the equivalent values were 47.2% and 16.0%–82.3%, 32.6% and 11.0%–50.8%, 20.0% and 4.8%–34.4%, respectively (Fig. 4). Results based on the taxon-specific values for the trophic enrichment factor were as follows: For *U. major* the inferred the median percentage contributions and 95% confidence intervals for marine phytoplankton, microphytobenthos, and terrestrial organic matter were 59.1% and 19.2%–91.2%, 32.8% and 5.9%–59.8%, 6.6% and 0.3%–29.2%, respectively (Fig. 5). For *C. busoensis* the equivalent values were 62.2% and 19.0%–94.6%, 22.8% and 2.7%–47.8%, 14.9% and 1.5%–
34.4%, respectively (Fig. 5).

Discussion

The higher estimated shrimp density from the burrow opening counts (180.4 shrimp individuals m$^{-2}$) than from the stratified benthos sampling (84.9 shrimp individuals m$^{-2}$) was expected because the *U. major* burrows can be >2 m deep from the tidal flat surface (Kinoshita 2002) that would be deeper than the maximum depth of the stratified sampling (50 cm). Because almost all burrows of *U. major* have 2 burrow openings (Kinoshita 2002), our burrow aperture counts thus are likely to yield relatively accurate estimates of the density of deep-burrowing shrimps, such as *U. major* and perhaps other upogebiid shrimps. However, some upogebiid shrimps are known to produce their burrows with more or less than 2 burrow openings (Dworschak et al. 2012), suggesting pre-investigation on numbers of burrow openings for each shrimp species is essential if we are to utilize burrow opening counts for population density estimation.

As for *U. major*, the measured population density of *C. busoensis* is likely to be underestimated with stratified samples. Although the highest densities of *C. busoensis* occurred at depths of 40–45 cm where horizontal tubes of the U-shaped part of the *U. major* burrow are dominant (Fig. 1C), their vertical distribution continued to depths of >45 cm (Fig. 2). The sampling depth was probably insufficient to include the total bivalve individuals, especially those inhabiting deeper layers (>45 cm). Peterson (1977) reported that *Cryptomya californiensis*, which inhabits burrows produced by the callianassid shrimp *Neotrypaea californiensis*, occurs >50 cm below the seafloor surface. The vertical shaft of the *U. major* burrow can extend to depths of >2 m (Kinoshita 2002). To improve the assessment of *C. busoensis* density, deeper (>2 m) stratified sampling with a longer core is needed.

As described in the introduction, the burrow of *U. major* consists of two sections, an upper U-shaped part and a lower I-shaped part (Fig. 1C; Kinoshita 2002). The depth of the U-shaped part of the *U. major* burrow is less than ~50 cm (Kinoshita 2002). The stratified benthos sampling showed the maximum density of *C. busoensis* was at a depth of 40–45 cm, indicating that the majority of the bivalve population attaches to near the bottom of the U-shaped part in the burrow. The upogebiid shrimp irrigates and filters the water within the U-shaped part (Dworschak 1981). Hence, both species must feed on suspended organic matters arriving from the U-shaped part of the burrow.

The sympatric and dense occurrence of both filter-feeding species in a single burrow implies potential competition between *U. major* and *C. busoensis* for food. However, the SIAR model based on stable isotope signatures showed that food sources of the two species partially differ. Although we used the SIAR model based on the two different trophic enrichment factors, the tendency of the food source contributions was almost same for both species. The important contributions to the food sources of *U. major* and *C. busoensis* are marine phytoplankton and microphytobenthos (Figs. 4 and 5). On the other hand, terrestrial organic matters are unlikely to be utilized by *U. major* whereas it is consumed by *C. busoensis*.

The rationale for the occurrence of the partial trophic segregation between *U. major* and *C. busoensis* can be explained as follows: Mechanism of filter-feeding for the species provides clues to this phenomenon. The *Upogebia* shrimps gather suspended particulate organic matters from seawater within a burrow using long setae attached to their appendage (Dworschak et al. 2012). On the other hand, bivalves including *Cryptomya* spp. filter the suspended particles inside their body using gills (Jorgensen 1990). This indicates that size of filtered particulate matters may differ substantially depending on the filtering mechanism, i.e., external or internal filtering by the invertebrates. The commensal bivalve *C. busoensis* is, therefore, able to consume finely fragmented terrestrial organic matters. Some bivalves are known to have a cellulase and can directly assimilate terrestrial organic matters such as land plant detritus (Brock & Kennedy 1992, Kanaya et al. 2008). The low δ13C and δ15N ratios of *C. busoensis* also imply direct assimilation of terrestrial organic matters (plant detritus) using cellulase.

The trophic dynamics occurring in the upogebiid burrow complex (the upogebiid shrimp, its burrow, and burrow associates, such as *Cryptomya* bivalves) can potentially affect the nutrient dynamics of entire ecosystems (Dworschak 1981, Griffen et al. 2004, D’Andrea & DeWitt 2009). The combination of food sources of the burrow host (*U. major*) and the burrow associate (*C. busoensis*) are likely to differ and alter their impacts on ecosystems. Although symbiotic relationships of *C. busoensis* have only been reported in *U. major* burrows to date, other species of *Cryptomya* are known to live symbiotically with hosts from various taxonomic groups with a range of feeding habits, including upogebiid shrimp, callianassid shrimp, and echiuran and annelid worms (Itani & Kato 2002, Nara et al. 2008). For example, *C. truncata* occurs in the burrows of both filter-feeding shrimps of the genus *Upogebia* and the deposit-feeding shrimp *Nihonotrypaea japonica* in the tidal flats of Japan (Itani & Kato 2002, Nara et al. 2008). On the Pacific coast of North America, *C. californica* also occurs in the burrows of the filter-feeding shrimp *U. pugettensis* (Griffen et al. 2004), the deposit-feeding shrimp *N. californiensis* (Peterson 1977), and the filter-feeding echiuran worm *Urechis caupo* (Julian et al. 2001).

The results of the present study show that the food sources of the burrow host (*U. major*) and the burrow associate (*C. busoensis*) partially differ. The *U. major* burrow complex can actively consume terrestrial organic matter only if the burrow contains *C. busoensis*, although some of the suspended sediment containing terrestrial organic matter might be passively trapped in the burrow. Therefore,
the faunal composition within a burrow affects the nature of the filtering performed by the burrow complex, not only regarding the efficiency of the benthic filtering but also the type of organic matter filtered by the benthos. High species richness in a burrow increases its potential benthic filtering because it allows the burrow complex to consume a wide variety of organic matter. Therefore, a diversity of burrow associates is important for the functions of a burrow complex in the biogeochemical cycles of seafloor ecosystems.

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Supplementary materials

Supplementary Table S1. Carbon and nitrogen stable isotope values for each sample.

References

Anker A, Murina GV, Lira C, Caripe JV, Palmer AR, Jeng MS (2005) Macrofauna associated with echinuran burrows: a review with new observations of the innkeeper worm, Ochetostoma erythrogrammon. Leuckart and Ruppell, in Venezuela. Zool Stud 44: 157–190.

Antonio ES, Richoux NB (2014) Trophodynamics of three decapod crustaceans in a temperate estuary using stable isotope and fatty acid analyses. Mar Ecol Prog Ser 504: 193–205.

Bosley KM, Copeman LA, Dumbauld BR, Bosley KL (2017) Identification of burrowing shrimp food sources along an estuarine gradient using fatty acid analysis and stable isotope ratios. Estuar Coast 40: 1113–1130.

Brook V, Kennedy VS (1992) Quantitative analysis of crystalline style carbohydrates in five suspension-and deposit-feeding bivalves. J Exp Mar Biol Ecol 159: 51–58.

Butler S, Bird FL (2007) Estimating density of intertidal ghost shrimps using counts of burrow openings. Is the method reliable? Hydrobiologia 589: 303–314.

D’Andrea AF, DeWitt TH (2009) Geochemical ecosystem engineering by the mud shrimp Upogebia pugetensis (Crustacea: Thalassinidea) in Yaquina Bay, Oregon: density-dependent effects on organic matter remineralization and nutrient cycling. Limnol Oceanogr 54: 1911–1932.

Dworschak PC (1981) The pumping rates of the burrowing shrimp Upogebia pusilla (Petagna) (Decapoda: Thalassinidea). J Exp Mar Biol Ecol 52: 25–35.

Dworschak PC (1987) Feeding behaviour of Upogebia pusilla and Callianassa tyrrhena (Crustacea, Decapoda, Thalassinidea). Inves Pesq 51: 421–429.

Dworschak PC (2015) Methods collecting Axiidea and Gebiidea (Decapoda): a review. Ann Naturhist Mus Wien B 117: 5–21.

Dworschak PC, Felder DL, Tudge CC (2012) Infraorders Axiidea de Saint Laurent, 1979 and Gebiidea de Saint Laurent, 1979 (formerly known collectively as Thalassinidea). In: Treatise on Zoology-Anatomy, Taxonomy, Biology (eds Schram FR, von Vaupel Klein JC). Brill, Leiden, pp. 109–219.

Griffen, BD, DeWitt TH, Langdon C (2004) Particle removal rates by the mud shrimp Upogebia pugetensis, its burrow, and a commensal clam: effects on estuarine phytoplankton abundance. Mar Ecol Prog Ser 269: 223–236.

Henni Y, Inui R, Goto R, Itani G (2018) First record of Gymnogobius macrognathos on Akkeshi mud flat, Hokkaido, Japan and utilization of Upogebia major burrows. Jpn J Ichthyol 65: 199–203.

Higgs ND, Newton J, Attrill MJ (2016) Caribbean spiny lobster fishery is underpinned by trophic subsidies from chemosynthetic primary production. Curr Biol 26: 3393–3398.

Itani G, Kato M (2002) Cryptomya (Venatomya) truncata (Bivalvia: Myidae): association with thalassinidean shrimp burrows and morphometric variation in Japanese waters. Venus 61: 193–202.

Jørgensen CB (1996) Bivalve filter feeding revisited. Mar Ecol Prog Ser 142: 287–302.

Julian D, Chang M, Judd J, Arp A (2001) Influence of environmental factors on burrow irrigation and oxygen consumption in the muddy invertebrate Urechis caupo. Mar Biol 139: 163–173.

Kanaya G, Niiyama T, Tanimura A, Kimura T, Toyohara H, Tosuji H, Sato M (2018) Spatial and interspecific variation in the food sources of sympatric estuarine nereid polychaetes: stable isotopic and enzymatic approaches. Mar Biol 165: 101.

Kanaya G, Takagi S, Kitsuki E (2008) Spatial dietary variations in Laternula marilina (Bivalvia) and Hediste spp. (Polychaeta) along environmental gradients in two brackish lagoons. Mar Ecol Prog Ser 359: 133–144.

Kanaya G, Takagi S, Nobata E, Kituchi E (2007) Spatial dietary shift of macrozoobenthos in a brackish lagoon revealed by carbon and nitrogen stable isotope ratios. Mar Ecol Prog Ser 345: 117–127.

Kinoshita K (2002) Burrow structure of the mud shrimp Upogebia major (Decapoda: Thalassinidea: Upogebiidae). J Crust Biol 22: 474–480.

Kneer D, Asmus H, Vonk JA (2008) Seagrass as the main food source of Neaxius acanthus (Thalassinidea: Strahlaxiidae), its burrow associates, and of Corallianassa coutierei (Thalassini-
