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Facultative commensalism of free-burrowing, urothoid amphipod with deep burrow-dwelling callianassid shrimp on an intertidal sandflat

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Abstract
Species of the free-burrowing amphipod genus, *Urothoe*, are common macrobenthos on open sandy beaches. On intertidal sandflats, some species are associated with burrows or tubes of large infauna. How this link is formed under sheltered settings was examined. On an intertidal sandflat emersed for 300 m seaward in mid-western Kyushu, Japan, *U. carda* co-occurred with the deep burrow-dwelling callianassid shrimp, *Nihonotrypaea harmandi*. Amphipods resided in the surface 5-cm sediment outside shrimp burrows, as confirmed by sediment coring and burrow casting. In the summertime during 1980 to 1981, the shrimp and amphipod populations were confined to the upper shore at mean densities of 182 and 701 inds m\(^{-2}\), respectively. In winter to spring, when the sediment surface mixing was caused by seasonal wind-induced waves, only the amphipod extended distribution to the lowest shore. By 1983, the shrimp increased mean density by 2.5 times and distribution range to the lowest shore. In the summers of 1984, 2010, and 2015, the amphipod extended distribution to the lowest shore, with small variations in population size. Three marked changes in substrate properties were associated with the shrimp inhabitation: thicker oxidized layer (proxy for oxygenated layer) in the sediment column; looser surface sediment, as evaluated with vane shear strength; and coarser and better-sorted surface sediment with less mud content. At least the former two changes were attributable to shrimp bioturbation, which could provide the amphipod with more permeable and softer substrates, leading to the formation of facultative commensalism.

Introduction
Species of the gammaridean amphipod genus, *Urothoe*, are cosmopolitan members of the benthic macro-infauna on open sandy beaches and shallow subtidal sandy bottoms (Bousfield 1970; Bally 1983; Barnard and Karaman 1991). Their high burrowing ability is an adaptation to shifting sediment, with broad-fusiform body form believed suited to filter-feeding in loosely packed sand
(Bousfield 1970). Among the free-burrowing amphipods, adults of *Urothoe* spp. reside relatively deep in the sediment (Vader 1978; Sudo 1988). *Urothoe* spp. also occur as surf plankton (Fincham 1970; Yu et al. 2002), with males performing nocturnal excursions into the water column probably as a part of mating behavior (Fincham 1970; Sudo 1988; Fernandez-Gonzalez et al. 2014). Some species of *Urothoe* inhabit intertidal sandflats that are more sheltered than open sandy beaches. On sheltered habitats, individuals of some *Urothoe* spp. are associated with deep burrows or tubes of much larger-bodied infauna such as ophiuroids, spatangoid echinoids, and an apodid holothuroid (Vader 1978), an arenicolid polychaete (Lackschewitz and Reise 1998), and a terebellid polychaete (Callaway 2006). Individuals of these *Urothoe* spp. dwell inside (Vader 1978; Lackschewitz and Reise 1998) and/or closely outside (Vader 1978; Lackschewitz and Reise 1998; Callaway 2006) the deeper part of those macrobenthos’ burrows or tubes. Steady oxygen and/or food supply around the large polychaete burrows or tubes were suggested to be attractive to *U. poseidonis* (see Lackschewitz and Reise 1998; Callaway 2006). How and to what degree such *Urothoe* spp. co-occur with their presumed hosts under sheltered settings remain to be elucidated.

In a survey for the density and distribution of macrofauna on an intertidal sandflat in mid-western Kyushu, Japan (Tomioka sandflat; Fig. 1) conducted in the summer of 1979, *Urothoe carda* was the eighth numerically dominant species of a total of 58 species of the benthic community [Tamaki and Kikuchi (1983), with the name, *U. grimaldii*, incorrectly used; total length range: 0.8–5.3 mm (A. Tamaki et al., unpubl data)]. The population of *U. carda* occurred mainly in a zone quasi-parallel to the shoreline densely inhabited by the callianassid decapod shrimp (or ghost shrimp), *Nihonotrypaea harmandi* [see Tamaki and Kikuchi 1983, with the name, *Callianassa japonica*, incorrectly used (see Manning and Tamaki 1998; Yamada et al. 2017)]. Ghost shrimp are known for their bioturbation effects on sediment and consequent influences on benthic community structure and ecosystem functioning (Pillay and Branch 2011). In the present case, the *N. harmandi*...
zone occupied the upper one-third part of the sandflat, with shrimp burrows extending over the whole, 10s-cm thick sediment column (above the mollusc shell layer). The accompanying sediment conditions, such as shifting surface sediment and fully oxidized sediment column, were ascribed to dense burrow stands and bioturbation of the shrimp (Tamaki 1984; Tamaki and Suzukawa 1991; Wardiatno et al. 2003). On an estuarine intertidal sandflat in South Africa, the density of a population of *U. grimaldii* in a bed of the ghost shrimp, *Callichirus kraussi*, changed in accordance with the experimental removal and subsequent recovery of the shrimp population (Wynberg and Branch 1994). Populations of *U. grimaldii* occurred also on South African open sandy beaches with *C. kraussi* absent (Bally 1983). These observations suggest some commensalism of *Urothoe* spp. with ghost shrimp under sheltered settings. Either amphipod residence inside shrimp burrows or its attraction to bioturbated sediment to varying magnitude may be involved in the relationship.

One way narrowing down the above possibilities regarding the commensalism is to find amphipods embedded in transparent resin casts of ghost shrimp burrows. Another way is to examine temporal changes in the distributions of the amphipod and ghost shrimp. On the Tomioka sandflat, the sediment surface mixing over the whole shore is caused by seasonal wind-induced waves in the wintertime, while the surface outside the *N. harmandi* zone is stable in the summertime (Tamaki 1984, 1987). After 1979, the distribution range of the *N. harmandi* population expanded, having occupied the entire sandflat by 1983 (Tamaki and Suzukawa 1991). This state has continued until 2015 (Tamaki and Takeuchi 2016). Both seasonal change around 1979 and some later years’ summertime distributions in the *U. carda* population would provide clues to clarifying its dependency on *N. harmandi*. In addition, the amphipod spatial distribution pattern might be different between sexes or between adults and juveniles relative to the ghost shrimp distribution. Finally, since *Urothoe* species are adapted to loosely packed sand (Bousfield 1970), the hardness of sediment may affect the distribution of *U. carda* in relation to that of *N. harmandi* on the present sandflat.
Undisturbed state of sediment hardness can be evaluated by vane shear strength *in situ*, where a thin vane blade is inserted into the sediment surface and the sediment maximum resistance to horizontal shearing associated with blade rotation measured (Amos et al. 1988; Sassa and Watabe 2007; Sassa et al. 2011, 2014). The sediment hardness assessed by vane shear strength has been shown to govern the burrowing performances of a crab (Sassa and Watabe 2008), bivalves (Sassa et al. 2011), and amphipods (Sassa et al. 2014) on intertidal sandflats and sandy beaches.

The objective of the present study was to show how the dependency of *U. carda* on *N. harmandi* is formed under a sheltered setting of the Tomioka sandflat and to what degree that commensalism is. First, relative to the ghost shrimp distribution and associated sediment conditions including depth of redox potential discontinuity layer and grain-size composition, the following items were examined for the amphipod population: zonation parallel to the shoreline in the summer of 1980; year-round change in the cross-shore distribution during 1980 to 1981; cross-shore distribution in four summers between 1984 and 2015; and cross-shore distributions of adults of both sexes and juveniles in 2015. Second, vertical distribution of amphipods in the sediment column and presence or absence of amphipods inside resin casts of shrimp burrows were checked. Finally, the cross-shore variation in sediment hardness was examined in relation to shrimp and amphipod distributions.

**Materials and methods**

**Monitoring density and distribution of macrofauna and substrate properties**

The Tomioka sandflat is located on the northwestern corner of Amakusa-Shimoshima Island (130.037°E; 32°521°N) situated west of Ariake Sound (largest estuary in Kyushu) under a semi-diurnal tidal regime (Fig. 1a). The maximum emersed area of the sandflat during low tide in spring-tide periods spans 3.5 km alongshore and 150–550 m cross-shore in Tomioka Bay, with the maximum tidal range of 3.3 m (Fig. 1b). A rectangular area for the census of macrofauna was
established around the northwestern corner of the sandflat, which was 300 m alongshore × 310–325 m cross-shore [to the mean low water level in spring-tide periods (MLWS); Fig. 1c]. Although the census area is sheltered to some extent by the northwest- to north-lying headland and sand spit, yet landward transport of some surface-dwelling macrofauna is caused by northerly wind-induced waves during late autumn to early spring (Tamaki 1987; Tamaki and Takeuchi 2016). In the census area, four parallel, cross-shore transects were placed, which were named Transects A, E, G, and J, with the distance between adjacent transects being 60–120 m. On each transect, the stations for sampling were placed every 10 m from the uppermost one at either the sandflat landward edge or 10 m seaward of it to the lowest one at the MLWS; Stn X-Y designates Y m from the landward edge on Transect X. In the first census conducted in July 1979, four faunal assemblage zones quasi-parallel to the shoreline were delineated (Tamaki and Kikuchi 1983). Each zone was named after its dominant or characteristic species (or genus): from upper to lower shore, the spionid polychaete, *Prionospio aucklandica* (originally as *P. krusadensis*), *Nihonotrypaea harmandi* (originally as *Callianassa japonica*), the bivalve, *Solen strictus*, and the gastropod, *Umbonium moniliferum*. The cross-shore ranges were wider in the *Nihonotrypaea* and *Umbonium* zones than in the other two zones, nearly coincident with those of the habitats of *N. harmandi* and *U. moniliferum*. The whole sediment-column depth spanned 20–30 cm in the *Prionospio* and *Solen* zones, 30–40 cm in the *Nihonotrypaea* zone, and 50–60 cm in the *Umbonium* zone (Tamaki 1984; Takeuchi and Tamaki 2014).

Following the above first census’ result, Transect G was selected as a representative transect to monitor the subsequent change in the zonation patterns of *Urothoe carda* and *N. harmandi*. The stations visited on each sampling occasion were selected as a subset from the above-mentioned maximum number of stations. The year-round monitoring was conducted during low tide in spring-tide periods from 18 March 1980 to 9 April 1981, most frequently every month. Eighteen to 22 stations were visited on each sampling occasion. At each station, first, the thickness of redox
potential discontinuity (RPD) layer was measured for a sediment column extracted with a transparent acrylic tube of 100-cm$^2$ circular cross-sectional area $\times$ 35-cm length, in which that layer was identified as the position with clear color changes. Along the boundary circle, the thickness was measured to 1 mm on several points including troughs and crests of small ripples if present (up to 1–1.5 cm in crest height) and the mean value calculated [data given in Tamaki (1984)] – briefly, (1) in the Nihonotrypaea zone, the entire sediment column was brown, suggesting an oxidized condition; (2) seaward of that zone by up to 40 m (mainly in the Solen zone), the surface brown layer was replaced by the gray layer at 10–20-cm depth; and (3) further seaward (in the Umbonium zone), the black-colored layer lay immediately below the brown layer at depths $<10$ cm. In the present study, the brown layer bottom was defined as the RPD layer depth; in cases that it continued beyond 25 cm, the RPD layer thickness was indicated uniformly as 25 cm in the Results. Second, the surface 1-cm deep sediment was collected for granulometric analysis by the standard serial sieving protocol (Buchanan and Kain 1971). Three parameters [median $\varphi$ ($\text{Md}$-$\varphi$), sorting coefficient ($\sigma$: inclusive graphic standard deviation), and mud content (percentage silt-clay fraction in weight)] were obtained. Third, the number of surface openings of N. harmandi burrows was counted for four adjacent 25-$\times$ 25-cm square plots haphazardly marked on the sandflat surface; one individual of N. harmandi dwells solitarily in its Y-shaped burrow with two openings (Tamaki and Ueno 1998). At any station in which all burrow-opening diameters were small (1–2-mm $\varphi$), as compared with a mixture of both small and large (3–6-mm $\varphi$) openings, such a station was recorded as that occupied by only new recruits of the year (Tamaki et al. 1997; Tamaki and Ueno 1998). Finally, at one of the four plots per station, a metal quadrat frame of the same size as above was inserted to a depth of 10 cm and the sediment inside excavated, passed through a 0.5-mm mesh sieve, and fixed with 10% neutralized formalin solution for U. carda specimens. For the specimens collected in 2015, after their sexes were identified based on the number of articulation in flagellum of antenna 2, the mature
and immature categories were determined based on (1) ovigerous or non-ovigerous state (female),
(2) presence or absence of calceoli in antenna 2 (male), and (3) total-length-frequency distributions
(A. Tamaki et al., unpubl data) and the distributions of the four groups on Transect G examined.
On 10–11 August 1980, a census for the whole study area was made along the four transects
(Fig. 1c; at 19–22 stations for each), following the same procedure as above.
After the complete expansion of the *N. harmandi* population over the sandflat in 1983 (Tamaki
and Suzukawa 1991), sampling along Transect G was conducted in each late July–early August of
1984, 1997, 2010, and 2015, basically following the same procedure as above, with some
modifications. In 1997, 2010, and 2015, the sampling stations had to be altered according to the
shortening of the transect length by 20 m due to the reclamation of the uppermost zone of the
sandflat in 1991–1993 [see Tamaki and Takeuchi (2016) for details]. The most landward station was
re-installed at the landward edge of the intact sandflat, which is named Stn G-0 (2010s). This station
is identical to the previous Stn G-20, which is hereafter re-named Stn G-20 (1980s); note that the
most landward station in the 1980s was Stn G-10, not Stn G-0. In cases for no misunderstanding
about years, the parentheses with years are omitted. The position of the MLWS on the transect has
been unchanged, which corresponds to Stn G-310 (1980s) and Stn G-290 (2010s). In 1984 and 1997,
the surface burrow-opening count for *N. harmandi* was made at four adjacent unit (25 × 25-cm²)
plots, while in the 2010s, it was made at eight or nine plots. In 2015, at Stns G-10, 30, and 50, an
acrylic tube with cross-sectional area of 100 cm² was used for collecting macrofauna, in which a
combined sample of six 10-cm deep sediment columns was regarded as equivalent to the usual, one
625-cm² quadrat sample. Granulometric analysis for the surface 1-cm sediment (3 cm only in 2015)
was made by the standard serial sieving protocol for the samples until 1997 and by using a laser
diffraction particle-size analyzer (SALD-3100, Shimazu) for those in the 2010s. To estimate the
individual numbers of adults and newly-recruited juveniles of *N. harmandi* from the burrow-
opening-counts in 2015 from 16 stations (Stns G-0, -10, -30, and every 20-m increment to -290), 10
samples of the whole sediment column were extracted with the coring tube at each of Stns G-30, -90,
-150, -210, and -270, passed through a 0.5-mm mesh sieve, and fixed on 3 August 2016. In the
laboratory, juveniles and adults were separated according to the distinct difference in body size.
Based on a yearly stable tendency for the juvenile distribution pattern over the transect (Tamaki et al.
1997), the juvenile-to-adult number ratio was applied to the 2015 data, in which the two adjacent
stations about each of the above five stations with core samples were assumed to take the same ratio
(the ratio at Stn G-30 was applied also to Stn G-0).
During ±1 h around the lowest-tide time on 1 August 2015, the surface elevation along Transect
G was measured to 1 mm with TRIMBLE R4 GNSS System (Trimble). At each of Stns G-0 to -290
(16 stns), the level of the groundwater table was measured to 1 mm with a ruler 1 min after
shoveling the surface sediment. Then, sediment hardness for the sub-surface depths of 10 mm and 40
mm were measured with a vane blade of 40-mm \( \phi \) and 10-mm depth (FTD2CN-S, Seiken) and of
20-mm \( \phi \) and 40-mm depth (FTD5CN-S, Seiken), respectively, at a point randomly placed between
surface burrow openings of \( N. \) harmandi. To compare the sediment hardness values at 10-mm depth
among the sediments containing a small burrow opening with 1–2-mm \( \phi \), a large one with 4–6-mm
\( \phi \), and outside burrow openings, measurements were made with FTD2CN-S at a location with high
shrimp densities around the lowest-tide time on 1 August 2016 (\( n = 6 \) for each burrow-opening size
and \( n = 13 \) for the latter). In the measurement for the former two, the center of the vane blade was
positioned exactly at each burrow opening. In both 2015 and 2016, the weather was fine and calm.

**Vertical distribution of \( U. \) carda in the sediment column**

To determine the vertical distribution of \( U. \) carda individuals in the substrate inhabited by \( N. \)
harmandi on the Tomioka sandflat during low tide, sediment columns were extracted with a
graduated acrylic tube, and sectioned into multiple layers, passed through a 0.5-mm mesh sieve, and
fixed with 10% neutralized formalin solution. On 15 August 1981, each of the three sediment
columns of a cross-sectional area of 100 cm\(^2\) to a 23-cm depth (brown in color) at Stn G-20 were
sectioned into six layers of 0 (= surface)–1, 1–2, 2–3, 3–5, 5–10, and 10–23 cm and the samples for
each layer combined. On 13 May 2017, each of the six sediment columns of a cross-sectional area of
24 cm\(^2\) to a 15-cm depth (brown in color) at Stn G-30 were sectioned into three layers of 0–5, 5–10,
and 10–15 cm and the samples for each layer combined.

**Casting burrows of N. harmandi**

To examine whether or not individuals of *U. carda* dwell inside *N. harmandi* burrows, polyester
resin casts of aggregated burrows were made over a circular area enclosed with a 23.5-cm \(\phi\) bottom-
removed polypropylene container around Stn G-10 on the Tomioka sandflat during low tides from
27 to 28 May 2017, following the burrow casting protocol given in Tamaki and Ueno (1998). In the
laboratory, amphipods embedded in the transparent burrow casts were searched for.

**Results**

**Vertical distribution of Urothoe carda in the sediment column**

In August 1981, all 191 individuals of *Urothoe carda* in the 23-cm deep sediment column on the
Tomioka sandflat were found from the upper 5-cm layer, with 14% in 0–1 cm, 56.5% in 1–2 cm,
23.5% in 2–3 cm, and 6% in 3–5 cm. In May 2017, 112 of a total of 113 individuals present in the
15-cm deep sediment column were found from the upper 5-cm layer, with 1 individual in 5–10 cm.

**Burrow casts of Nihonotrypaea harmandi**

In the 434-cm\(^2\) enclosed area of the Tomioka sandflat in May 2017, the number of casts of Y-
shaped burrows of *Nihonotrypaea harmandi* was 34, including those with either one of the two segments above the node of the *Y* incomplete (Fig. 2). The maximum depth of each burrow ranged from 9.0 to 27.1 cm, with mean (± SD) being 18.2 (± 5.8) cm. The depth of the node of the *Y* ranged from 6.7 to 16.9 cm, with mean (± SD) being 11.6 (± 2.4) cm. The number of casts with only a single shaft retrieved was 19. No individuals of *U. carda* were embedded in the burrow casts, with 341 expected individuals residing in the surface 5-cm layer of the enclosed area, based on their nearby density (113 inds 144 cm$^{-2}$: preceding sub-section).

**Temporal change in the transect distributions of *N. harmandi* and *U. carda* during 1980–1981**

Over the four transects on the Tomioka sandflat on 10–11 August 1980, *N. harmandi* burrows and *U. carda* individuals showed a common zonation pattern quasi-parallel to the shoreline (Fig. 3). The main zone occupied by *N. harmandi* burrows, with RPD depths ≥ 25 cm, shifted from the upper half of Transect J to the upper one-third of Transect A. The overall mean (± SD) *N. harmandi* density from mean density at every station with a non-zero value (including the stations with RPD depths < 25 cm), as estimated from burrow-opening counts, was 182 (± 138) shrimps m$^{-2}$ [$n = 35$ (stns)].

Almost all individuals of *U. carda* occurred in the main *N. harmandi* zone, with mean density over the four transects being 43.8 inds 625 cm$^{-2}$ ($n = 77$). On each transect, two separate density-peaks were present in the upper and mid- to lower part of the *Nihonotrypaea* zone, respectively. On Transects G, E, and A, a substantial part of each transect population of *U. carda* occurred also 10–20 m seaward of the seaward limit of the *N. harmandi* zone (i.e. in the *Solen* zone), with RPD depths of 10–17 cm. Beyond the *Solen* zone [i.e. in the *Umbonium* zone (to the MLWS)], the RPD depths lay closer to the surface, with mean (± SD) for the four transects being 3.4 (± 1.2) cm ($n = 30$).

Along Transect G during March 1980 to April 1981, the seaward limit of the *N. harmandi* adult-inhabited zone expanded by 20 m, from Stn G-130 to Stn G-150, in October, when Stn G-260 was
also established as a separate zone in the lower shore (gray columns in Fig. 4a–m). This colonization was caused by both adult immigration and settlement of new recruits (Tamaki and Ingole 1993; Tamaki 1994). The overall mean density through the year estimated from the mean burrow-opening density at every station with a non-zero value was 181 shrimps m$^{-2}$ ($n = 170$). The mean density of *U. carda* on each sampling occasion ranged from 57.9 (May 1980) to 102.0 (April 1980) inds 625 cm$^{-2}$, with overall mean ($\pm$ SD) through the year being 81.7 ($\pm$ 13.1) inds 625 cm$^{-2}$ ($n = 13$). The population of *U. carda* showed a clear seasonal distribution pattern relative to the *Nihonotrypaea* zone. During July to September, most of the population was confined to the *Nihonotrypaea* zone, and a substantial part was extended beyond that zone to the lowest shore during December to May, with the distributions in June and October transitional. The extended and contracted phases of the *U. carda* population in the *Umbonium* zone (Stns G-180–310) were in parallel with the seasonally changing RPD depths, of which mean ($\pm$ SD) values were 6.8 ($\pm$ 2.4) cm ($n = 21$) during March to May 1980, 5.0 ($\pm$ 2.7) cm ($n = 7$) in June, 2.6 ($\pm$ 1.0) cm ($n = 38$) during July to September, 5.1 ($\pm$ 2.1) cm ($n = 6$; excluding Stn G-260) in October, and 6.2 ($\pm$ 1.5) cm ($n = 18$; excluding Stn G-260) during December 1980 to April 1981. During June to October, there were largely two separate density-peaks of *U. carda* in the upper and mid- to lower *Nihonotrypaea* zone, respectively, and a substantial part of the transect population occurred 10–30 m seaward of the seaward limit of the *N. harmandi* adult-inhabited zone (i.e. in the *Solen* zone), with RPD depths of 8–16 cm. At Stn G-260 in October, both *N. harmandi* density (mean of 240 shrimps m$^{-2}$) and RPD depth (12 cm) were greater than those values at the other lower-shore stations. The *U. carda* density was higher at Stn G-260 than at the two adjacent stations.

**Temporal change in the transect distributions of *N. harmandi* and *U. carda* during 1984–2015**

Along Transect G on the Tomioka sandflat in 1984, 1997, 2010, and 2015, all stations were
occupied by *N. harmandi*, with mean (±SD) shrimp densities over the stations (inds m$^{-2}$), as estimated from burrow-opening counts, declining from 461 (± 104) in 1984 [$n = 16$ (stns); Stn G-10 (uppermost station: *Prionospio* zone) excluded], via 214 (± 63) in 1997 ($n = 15$; Stn G-0 excluded), to 69 (± 38) in 2010 ($n = 18$) and 104 (± 38) in 2015 ($n = 16$) (Fig. 5a–d). The marked reduction in shrimp densities from 1984 to 1997 was caused by heavy predation by the stingray, *Dasyatis akajei*, which continued from 1995 onward (up to the present) (Takeuchi and Tamaki 2014; Tamaki and Takeuchi 2016). Stingrays excavate deep pits during foraging for shrimps, which had the maximum impact on the shrimp population in the mid-shore due to the thinnest sediment columns there (20s cm; Takeuchi and Tamaki 2014). Also in 2010, the spatially different stingray impact was reflected in the higher shrimp densities in the upper and lower shores and the lowest ones in the mid-shore. In 2015, the densities in the mid-shore were not lower than in the upper and lower shores. This was most probably due to the higher new recruits’ densities in the mid- to lower shore, as indicated in the distribution of estimated densities of juveniles and adults over the transect (Fig. 5e).

In 1984, 1997, and 2015, the RPD depths were > 25 cm at all stations except for Stn G-10 (data not shown in Fig. 5). In 2010, although most RPD depths were > 25 cm, the values of 8–20 cm emerged in the mid-shore (Fig. 5c). In 1984, *Urothoe carda* occurred over the whole transect, with 26–147 (range) and 74.2 [mean; $n = 17$ (stns)] inds 625 cm$^{-2}$ (Fig. 5a; hereafter 625 cm$^{-2}$ is omitted for density values). In 1997, the densities over the whole transect were lower than in 1984, with up to 65 inds and the mean of 9.3 inds ($n = 16$), and 75% of the whole members occurred from the upper 50-m part of the transect (Fig. 5b). In 2010, the same tendency as in the ghost shrimp distribution was observed, with the highest *U. carda* densities of 51 and 105 inds being at Stns G-30 and G-220, respectively, and the mean density over the whole transect being 34.6 inds ($n = 18$) (Fig. 5c). Also in 2015, the lower densities in the mid-shore was sandwiched by the highest densities in the upper and lower shores.
(107–108 and 125 inds at Stns G-30–G-50 and G-270, respectively), with the mean density over the whole transect being 64.4 inds (n = 16) (Fig. 5d). The spatial variation in the density of *U. carda* resembled that of *N. harmandi* adults (Fig. 5e). Furthermore for *U. carda*, in the upper-half shore, the mature and immature individuals of both sexes were distributed separately in its lower and upper parts, while in the lower-half shore, the distribution centers of mature and immature individuals of both sexes were at the two lowest stations, decreasing toward each lowest density at Stn G-130, though the tendency in the mature male was less clear due to its low densities (Fig. 5f).

**Temporal change in sediment grain-size composition and snapshot underground properties**

The distributions of *Md*$_{\phi}$, *σ*_I, and mud content of the surface sediment along Transect G on the Tomioka sandflat in July–August of 1980–2015 are shown in Fig. 6a–c, respectively. In all years, the particle was finer landward, as is general for tidal flats. In 1980 and 1984, from lowest to uppermost shores, the sediment type shifted from well-sorted to moderately-sorted, fine to coarser very fine sand. The mud content in 1980 exhibited a dip in the lower part of the *Nihonotrypaea* zone (Stns G-20–G-130). In 1997, as compared with the 1980s, especially in the transect mid- to lowest part, (1) median particle diameter became slightly larger within the fine sand category, (2) sorting became largely better within the moderately well-sorted category, and (3) mud content became less. This trend continued afterward, especially with a marked increase in median grain size and decrease in mud content. In 2010 and 2015, from lowest to uppermost shore, basically, the values of *Md*$_{\phi}$ shifted from medium to coarser-fine sand categories, and the values of *σ*_I shifted from very well- to moderately-sorted categories. The greater spatial variations in the *Md*$_{\phi}$ and *σ*_I in 2015 than in 2010 might be due to the deeper sediment samples in the former with greater heterogeneities (3 vs. 1 cm). The locally high mud contents at Stns G-150 and -190 in 2010 corresponded to the lowest densities of *N. harmandi* there (Fig. 5c).
The sandflat surface elevation inclined gently along Transect G in 2015, with a gradient of ca. 1/250 over 290 m. The groundwater tables were close to the sandflat surface [range = −2.5 (below surface) to 2.5 (above surface: overflow) cm; mean (± SD) = 0.6 (± 1.4) cm; n = 16 (stns)]. The distribution of sediment hardness over the transect is shown in Fig. 7. The vane shear strengths at 4-cm depth were higher in the upper and lower shores and lowest in the mid-shore, coincident with the spatial variation in the densities of both *U. carda* individuals (Fig. 5d, f) and *N. harmandi* adults (Fig. 5e), while those strengths at 1-cm depth varied in a small range around a much lower value.

In comparing the values of sediment hardness among the points at small and large burrow openings of *N. harmandi*, and at outside-burrow-opening points in 2016, the value for sediments on another intertidal sandflat [Okoshiki sandflat in Ariake Sound (cf. Yamada and Kobayashi 2007); Fig. 1a] during low tide in 2010 were used additionally (n = 5; S. Sassa and S. Yang, unpubl data) (Fig. 8). That sandflat is dominated by large sand waves and shares essentially the same sediment granulometric characteristics (median diameters: 0.18–0.28 mm) and the groundwater table up to the surface (in troughs of the sand waves) with those of the Tomioka sandflat. Although a large number of *N. harmandi* and *N. japonica* existed in 1998 (Wardiatno et al. 2003), no surface burrow openings of both species were found at the time of measurement in 2010 (points with “no burrow openings”). The lowered abundance of *N. japonica* population in recent years are common to several intertidal sandflats in Ariake Sound (Takeuchi et al. 2013). The difference in the median values of vane shear strength among the four points was tested for significance by Kruskal-Wallis test, followed by Steel-Dwass multiple comparison test, using “R”-based software “EZR” (Kanda 2013). There was a significant difference among the four points (Kruskal-Wallis $X^2 = 25.7, df = 3, P < 0.001$), and the mean-value order from high to low was: large burrow opening, small burrow opening, no burrow openings, and outside-burrow openings. Except for the pair between small and no burrow openings, all other pairs were significantly different ($P < 0.01$ or 0.05).
Discussion

The stable association of *Urothoe carda* with *Nihonotrypaea harmandi* on the Tomioka sandflat was evident from (1) their common upper-shore distribution on the four transects in the summer of 1980 (Fig. 3) and on one of these transects (Transect G) in the summertime of 1980 (Fig. 4e–i) and (2) their whole-shore distributions on Transect G in the summers of 1984, 2010, and 2015, when the entire sandflat had been occupied by *N. harmandi* (Fig. 5a, c, d). Through these years, the mean density of *U. carda* (no. inds 625 cm$^{-2}$) over Transect G varied in a small range from 35 to 82. The mean density value was 9 in 1997, when most individuals were in the upper part of the transect despite the whole-shore distribution of *N. harmandi* (Fig. 5b). It is thus inferred that the base of the *U. carda* population lay primarily in the upper *N. harmandi* zone and that, in its higher-abundance phase, excess individuals of the *U. carda* population made a range extension into the mid- to lower *N. harmandi* zone. Frequent shuffling their dwelling sites on the present sandflat during nocturnal submergence periods is suggested (A. Tamaki et al., unpubl data). In 2010 and 2015, the *U. carda* densities peaked in the upper and lower shores separately, with the lowest densities in the mid-shore (Fig. 5c, d). This was in parallel with the spatial variation in the *N. harmandi* density, especially that of adults, not of juveniles (Fig. 5e, f). In the upper-half shore in 2015, the center of the distributions of mature individuals (adults) of both sexes of *U. carda* was at 90 m from the uppermost shoreline, while that of immature individuals (juveniles) was within 50 m from there (Fig. 5f). Such a bimodal distribution within the upper shore was observed on most sampling occasions during 1980 to 1981 (Figs. 3 and 4), which might have also been due to the segregation of adults and juveniles. The peak position of juveniles situated landward of that of adults was recorded for a number of macrobenthic species on the present sandflat, which was suggested to be caused by hydrodynamic sorting by body size (Tamaki 1987; Tamaki and Suzukawa 1997; Tamaki and Takeuchi 2016). The salinity of the
groundwater along Transect G measured during low tide in June, 1998 indicated the values of
9.0–17.4 in the upper 50-m zone and 31.2–32.0 in the seaward zone, suggesting the penetration of
ground freshwater from the land into the former zone (Wardiatno et al. 2003). The low salinity in the
upper sandflat may be sub-optimum for *U. carda* adults but optimum for some species including
*Prionospio aucklandica* and the anthurid isopod, *Cyathura muromiensis* (see Tamaki and Kikuchi
1983). On some intertidal sandflats, a peculiar benthic assemblage occurred in each uppermost area
with ground freshwater discharge (Zipperle and Reise 2005; Dale and Miller 2008).

Despite its long-term stability, the association between *U. carda* and *N. harmandi* on the
Tomioka sandflat was not always obligate. This was evident from the observations on the extended
distribution of *U. carda* beyond the *N. harmandi*-inhabited zone by 10–30 m seaward along the four
transects and Transect G in the summer of 1980 (Figs. 3 and 4d–g) and by all remaining length of
Transect G during winter to spring in 1980 and 1981 (Fig. 4a–c, k–m). Thus, *U. carda* can be
regarded as a facultative commensal of *N. harmandi*. As no individuals of *U. carda* were found
inside the resin casts of *N. harmandi* burrows (Fig. 2), they are assumed to exist in the interstitial
space between these burrows. Such a micro-scale distribution pattern is similar to that of *U.
poseidonis* associated with, but not inside, the tubes of the terebellid polychaete, *Lanice conchilega*,
on an intertidal sandflat (Callaway 2006). The dwelling depth in the sediment column was 0–5 cm
for *U. carda* and down to 10–15 cm for *U. poseidonis* (see Lackschewitz and Reise 1998; Callaway
2006). A similar association between free-burrowing amphipod and ghost shrimp may exist for *U.
grimaldii* and *Callichirus kraussi* on South African estuarine intertidal sandflats (cf. Wynberg and
Branch 1994). Facultative commensalism of smaller macrobenthos with *N. harmandi* on the present
sandflat was reported for the cirolanid isopod, *Eurydice nipponica*, which primarily occurs on
exposed sandy beaches along the coastline of Kyushu (Tamaki and Suzukawa 1991, 1997). Some
bioturbation effects of *N. harmandi* would become beneficial to both *U. carda* and *E. nipponica*
under the present sheltered setting. Compared with *U. carda*, *E. nipponica* was confined to the *Nihonotrypaea* zone year-round in 1980–1981, and not only distribution range but also population size increased from 1984 onward (Tamaki and Suzukawa 1991, 1997; A. Tamaki, unpubl data).

Though either facultative or obligate one is unknown, callianassids-associated commensalism in highly mobile smaller macrobenthos on sandy bottoms was reported for ostracods (Riddle 1988), amphipods (Posey 1986; Riddle 1988), bivalves (Aller and Dodge 1974; Tudhope and Scoffin 1984), and polychaetes (Riddle 1988; Wynberg and Branch 1994).

For *U. poseidonis* individuals associated with their presumed polychaete hosts, the sub-surface permeable sediment around those burrows or tubes was suggested to form an attractive interstitial space with elevated dissolved oxygen concentration and/or increased food supply (Lackschewitz and Reise 1998; Callaway 2006). Increased permeability in the sediment may also enable the amphipod to filter-feed more efficiently there (cf. Bousfield 1970). The thickness of the surface oxidized layer in yellow or brown color above the RPD depth, with the reduced layer beneath it in gray to black colors, nearly coincides with the thickness of the surface oxygenated layer on sheltered intertidal sandflats and dissipative sandy beaches (Fenchel and Riedl 1970; McLachlan 1978; McLachlan and Turner 1994). Thus, although pore-water dissolved oxygen concentration of the sediment was not measured in the present study, the surface oxidized sediment layer thickness (SOSLT) could be used as a proxy for the surface oxygenated sediment layer thickness. Consistently through 1980 to 2015, the whole sediment column in the zone densely inhabited by *N. harmandi* adults was oxidized, where the population of *U. carda* mainly occurred (Figs. 3–5). The oxidized substrate also affects the bacterial community on the present sandflat (Wada et al. 2016). The surface sediment’s greater median size, better sorting, and lower content of silt-clay that took place through these years (Fig. 6a–c) could also make the sediment more permeable. These granulometric parameter changes might have been caused by the bioturbation of *N. harmandi*, horizontally expelling finer fractions of the...
surface sediment away and burying its very coarser fraction deep into the sediment column (Tamaki 1994; Wardiatno et al. 2003), of which mechanism remains to be examined. The range of those sediment grain-size parameter values through all years appears acceptable by *U. carda*. In the zone seaward of the *N. harmandi*-inhabited upper shore during 1980 to 1981, the SOSLT and the intermediate to high densities of *U. carda* occurred coincidently: (1) the extended distributions of both oxidized sediment column and *U. carda* by 10–30 m seaward (into the *Solen* zone) in the summertime, (2) the smallest SOSLT and the absence or quite low densities of *U. carda* beyond the *Solen* zone in the summertime, with dense spionid polychaete tube mats in the *Solen* to upper *Umbonium* zone (Tamaki and Kikuchi 1983; Tamaki 1984, 1985), and (3) the larger SOSLT and the intermediate or high densities of *U. carda* in the *Solen* to *Umbonium* zones through the winter and early spring. The threshold SOSLT allowing the existence of *U. carda* appeared to be 5 cm (Figs. 3 and 4), which was equal to the maximum depth of *U. carda* individuals in the sediment column.

Regarding a possible mechanism causing the above event (1), it is noteworthy that the hydraulic activity of the ghost shrimp, *Neotrypaea californiensis*, induced lateral transport of oxygenated water into the surrounding sediment as well as into their burrows in laboratory aquaria (Volkenborn et al. 2012). Woodin et al. (2010) proposed that those large bioturbators residing in burrows with permeable walls, including arenicolid polychaetes, be called infaunal hydraulic ecosystem engineers. The seasonal change in the SOSLT in the above events (2) and (3) was in accordance with that of the sediment silt-clay content at Stn G-160 (1980s), ranging from 0.7% in winter to 1.7% in summer, and with the greater degree of the sediment surface mixing by northerly wind-induced waves during the late autumn to early spring (Tamaki 1984, 1987). Such a seasonal change is generally found for sheltered intertidal sandflats, with the deposition of oxygen-consuming organic matter during the warmer and calmer season and the wind-wave disturbance during the colder and stormier season (Fenchel and Riedl 1970; McLachlan 1978).
The lateral and vertical sediment displacement by the *N. harmandi* population in high densities on the Tomioka sandflat may soften its inter-burrow substrate for *U. carda* individuals to efficiently move through and re-burrow into. The sediment hardness of intertidal sandflats depends on suction (i.e. negative pore water pressure relative to atmospheric pressure) and their packing states, the latter changing considerably with suction dynamics under tide-induced groundwater table fluctuations (Sassa and Watabe 2007). On sandy beaches, the sediment hardness due to suction development and suction-dynamics-induced sediment compaction acted as a limiting factor for the survival and distributions of amphipods (*Talorchestia brito* and *Haustorioides japonicus*) by preventing their burrowing behavior (Sassa et al. 2014). On the Tomioka sandflat, the groundwater table was nearly the same as the surface elevation during low tides, indicating that suction is absent throughout tidal cycles and that the hardness of the sediment depends solely on its packing state. The shape of the outline of vane shear strengths at 4-cm depth over Transect G (Fig. 7) was very similar to that for adult *N. harmandi* density (Fig. 5e) [and for *U. carda* density (Fig. 5f)]. This would have reflected a work for rotating the vane blade to destroy burrows encountered at that depth (Fig. 2), which was confirmed by the highest shear strength value at 1-cm depth exactly beneath the large burrow openings and the second highest value exactly beneath the small burrow openings recorded in 2016 (Fig. 8). The 1-cm depth shear strengths in 2015 comparable to those outside and lower than at burrows in 2016 would represent the packing state of the sediment outside *N. harmandi* burrows. Such outside-burrow-opening shear strength on the Tomioka sandflat was significantly lower than the shear strength with no burrows on the Okoshiki sandflat (Fig. 8), despite the same sediment-Mdϕ ranges between the two sandflats and no suctions during low tides in trough parts of sand waves on the latter sandflat (Yamada and Kobayashi 2007; Sassa and Watabe 2009). This suggests that the bioturbating activity of *N. harmandi* individuals altered the sediment packing state through the displacement and rearrangement of sand particles among their highly dense burrows, which resulted
in the looser and more permeable sediments than those solely subjected to physical displacement.

In conclusion, for some species of *Urothoe* on sheltered intertidal sandflats, the bioturbation or tube/burrow of some large macrobenthos would provide amphipods with more permeable and softer sediments, generating elevated dissolved oxygen concentration and increased pore space to possibly facilitate amphipods’ efficient burrowing and filter-feeding. Facultative commensalism of highly mobile species with those sedentary large macrofauna would form one stable functional component of the benthic community among other components on sheltered sandflats, including the one due to amensalism exerted from ghost shrimps on filter-feeding molluscs (e.g. Tamaki and Takeuchi 2016).

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Compliance with ethical standards

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Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.
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**Fig. 1** a Study region and location of the Tomioka (intertidal) sandflat along the shoreline in mid-western Kyushu, Japan. Water-depth isopleths every 10 m were made by contouring (Surfer® 8: Golden Software, Inc.) for the point data provided by Hydrographic and Oceanographic Department, Japan Coast Guard. All tidal flats are indicated in black. The Okoshiki sandflat is situated in the middle part of Ariake Sound. b Enlarged map of the Tomioka sandflat. The intertidal sandy part and rocky or boulder part are indicated in light gray and white, respectively. c Four cross-shore transects (Transects A, E, G, and J) on the monitoring area of the Tomioka sandflat. The sandy part is indicated in light gray. The 10-m wide white-colored zone at the landward edge stands for the hard substrate in 1979–1991, from which the 20-m wide seaward zone down to the broken line was reclaimed during 1991 to 1993. MLWS: mean low water level in spring-tide periods.
Fig. 2 Polyester resin casts of burrows of *Nihonotrypaea harmandi* made around the uppermost Tomioka sandflat during 27–28 May 2017
Fig. 3 Distribution of *Urothoe carda* densities, mean (± SD) surface burrow-opening densities of *Nihonotrypaea harmandi*, and redox potential discontinuity (RPD) depths below the sediment surface along the four cross-shore transects on the Tomioka sandflat (Fig. 1c) on 10–11 August 1980. The numbers of 25- × 25-cm quadrat frame per station were one for *U. carda* and four for *N. harmandi*. Each RPD depth was determined as the thickness of the brown-colored layer (blank part in the panel) above the gray- or black-colored layers (black part), with the values ≥ 25 cm indicated uniformly as 25 cm. The four macrofaunal assemblage zones along Transect G are indicated on the left [designated by genera of representative species (Tanaki 1985)]. MLWS: mean low water level in spring-tide periods. The RPD values on Transect G based on data in Tanaki (1984)
Fig. 4  a–m Spatial variations in *Urothoe carda* densities, mean (± SD) surface burrow-opening densities of *Nihonotrypaea harmsandi*, and redox potential discontinuity (RPD) depths below the sediment surface along Transect G on the Tomioka sandflat (Fig. 1c) during March 1980 to April 1981. The numbers of 25-× 25-cm quadrat frame per station were one for *U. carda* and four for *N. harmsandi*. The stations with both large (3–6-mm φ) and small (1–2-mm φ) burrow openings and those with only small burrow openings are indicated by gray and blank columns, respectively. Each RPD depth was determined as in Fig. 3, based on data in Tamaki (1984).
Fig. 5 a–d Spatial variations in *Urothoe carda* densities, mean (± SD) surface burrow-opening densities of *Niphonotrypaea harmandi*, and redox potential discontinuity (RPD) depths below the sediment surface along Transect G on the Tomioka sandflat (Fig. 1c) in late July to mid-August in 1984, 1997, 2010, and 2015. Note that the uppermost-shore station in 1997 to 2015 (Stn G-0) was the previous Stn G-20 (1980s). The numbers of 25-× 25-cm quadrat frame per station were one for *U. carda* and four (in 1984) and eight or nine (in 2010 or 2015) for *N. harmandi*. The stations with both large (3–6-mm φ) and small (1–2-mm φ) burrow openings and those with only small burrow openings are indicated by gray and blank columns, respectively. Each RPD depth was determined as in Fig. 3. In 1984, 1997, and 2015, the RPD depths at all stations except for the uppermost-shore station were ≥ 25 cm (not shown in a, b, d). e Mean (± SD) surface burrow-opening densities of adults and juveniles of *N. harmandi* along Transect G on 1 August 2015, as estimated from the total burrow-opening counts in d and the actual proportion of adults and juveniles in the coring tube samples collected on 3 August 2016. f Densities of the four groups (mature and immature individuals of each sex) of *U. carda* along Transect G on 1 August 2015. The total number of individuals at each station (d) was divided into these groups based on A. Tamaki et al. (unpubl data).
Fig. 6 a–c Spatial variations in median φ, sorting coefficient (σ; inclusive graphic standard deviation), and mud (= silt-clay) content of the surface 1-cm sediment along Transect G on the Tomioka sandflat in the summers of 1980, 1984, 1997, 2010, and the surface 3-cm sediment in 2015 (sample at Stn G-0 was lost). In 1980, the Nihonotrypaea harmandi-inhabited zone was from Stns G-20 to G-130, and from 1984 afterward, the whole transect was occupied by this species. The values in 1980 and 1984 based on data in Tamaki (1984) and Tamaki and Suzukiwa (1991)
**Fig. 7** Distributions of the vane shear strengths at 4 cm and 1 cm below the sediment surface outside *Nihonotryaceae harmaicen* burrow openings along Transect G on the Tomioka sandflat during low tide on 1 August 2015.
Fig. 8 Mean (± SD) vane shear strengths at 1 cm below the sediment surface at small *Nihonotrypaea harandi*-burrow-opening points (1–2-mm φ), large burrow-opening points (4–6-mm φ), outside-burrow-opening points on the Tomioka sandflat during low tide on 1 August 2016 and on trough parts of sand waves with no burrow openings on the Okoshiki sandflat (Fig. 1a) during low tide on 14 June 2010 (from S. Sassa and S. Yang, unpubl. data). Each pair with significant difference by Steel-Dwass multiple comparison test is indicated by * (0.01 < P < 0.05) and ** (0.001 < P < 0.01)