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Burrow morphology of the ghost shrimp *Nihonotrypaea petalura* (Decapoda: Thalassinidea: Callianassidae) from western Kyushu, Japan

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Abstract The callianassid shrimp *Nihonotrypaea petalura* (Stimpson, 1860) is a common member on boulder beaches in Japanese waters. Its burrow morphology was investigated, based on 28 resin casts collected from a steeply sloping beach with dense boulders and 30 from a more gently sloping beach with less dense boulders in Ariake Sound, southern Japan. The structure and dimensions of the burrows from the two beaches were basically the same, and thus a combined mean value could be given to most of their constituent elements. In its entire dimensions, the burrow is greater in lateral extent than depth, with a mean maximum horizontal extension of 145 mm and a mean maximum depth of 119 mm for the shrimp with a mean total length of 31.8 mm. The burrow winds along boulders or cobbles and consists of, from top to bottom, a single surface opening with an ejected mound, a top shaft leading to the uppermost chamber at a mean depth of 48–56 mm, a passage with a regular cross section that is wider than that of the top shaft, and bulbous chambers (mean no. = 4.7) with an irregular cross section associated with branches (mean no. per burrow = 1.2). Bulbous chambers are much larger than the uppermost chamber and are usually connected by passages, with some directly attached to each other. The combined architecture of these features is unique and relatively simple among the burrows of all callianassid species, the majority of which inhabit bare soft sediments. The structure and function of the *N. petalura* burrow are discussed in relation to lifestyle.

Introduction

Decapod thalassinidean shrimps of the family Callianassidae are among the most common macro-invertebrates, occurring mostly from estuarine intertidal to marine subtidal soft sediments. The various shrimp species reside in burrows of varying morphology that are used for shelter, feeding, and reproduction. These burrow architectures have attracted increased attention (see reviews in Dworschak 1983; de Vaugelas 1990; Griffis and Suchanek 1991; Nickell and Atkinson 1995). The target species in almost all studies were from bare soft sediments, reflecting the habitats occupied by the majority of the callianassid shrimps (examples listed in the above reviews plus several papers published thereafter and literature cited therein: Ziebis et al. 1996; Tamaki and Ueno 1998; Bird and Poore 1999; Berkenbusch and Rowden 2000; Dworschak 2000, 2001, 2002).

In Japanese waters, three species of the genus *Nihonotrypaea* are commonly found in intertidal habitats (Manning and Tamaki 1998; Tamaki 2003). Of these species both *N. japonica* and *N. harmandi* are distributed in bare sandflats, whereas *N. petalura* is in boulder beaches (Tamaki et al. 1999). Although the former two species sometimes attain quite high densities of up to 340 and 1,400 m⁻², respectively (Tamaki et al. 1997; Tamaki 2003), the latter species exists more sparsely in sand patches surrounded by boulders, with a density of about 10 m⁻² (Tamaki et al. 1999; K.S. and A.T., unpublished data; Fig. 1). In the Ariake Sound estuarine system, western Kyushu, Japan (the system ranges from Ariake Sound, via Tachibana Bay, to the coastal waters of the East China Sea), it is estimated that *N. petalura* makes up only 6% of the total number of shrimps of the genus *Nihonotrypaea* (Tamaki and Miyabe 2000). The burrow morphologies, together with the associated detailed habitat conditions, have been recorded for the sandflat species only (*N. japonica*: Utashiro et al. 1972; Tamaki and Ueno 1998; *N. harmandi*: Ohshima 1967; Tamaki

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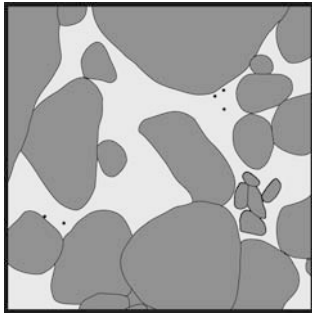


Fig. 1 Example of a 1×1-m surface plot of the substratum inhabited by *Nihonotrypaea petalura*. Dark areas Boulders and cobbles; light areas pebbles and sand; dots surface openings of shrimp burrows

et al. 1992; Tamaki and Ueno 1998). In other parts of the world, there are two similar sets of three congeneric species, (1) *Neotrypaea californiensis*, *N. gigas*, and *N. biffari* on the west coast of North America (MacGinitie and MacGinitie 1968) and (2) *Callianassa candida*, *C. tyrrhena*, and *C. whitei* in the northern Adriatic Sea (Dworschak 1998, 2001, 2002), with the last species in each group being an analogue to *Nihonotrypaea petalura* in terms of their habitat conditions. Although the burrow morphology of *Neotrypaea biffari* was described (as *C. affinis*: MacGinitie and MacGinitie 1968), it was from a specimen constrained in an aquarium. The morphology of burrow casts of *C. whitei* collected in the field was recently described for two incomplete samples (Dworschak 2002). The aim of the present article is to give an account of the detailed structure of the burrow of *Nihonotrypaea petalura* based on a number of resin casts collected in the field, together with the ambient habitat characteristics. In particular, comparison is made between the burrow morphologies from the two typically different habitat types because intraspecific variation in callianassid burrows may exist in response to different environmental conditions (Griffis and Suchanek 1991; Nickell and Atkinson 1995). Furthermore, the burrow structure is compared with those of the two tidal-flat congeners and those of other callianassid species including *Neotrypaea biffari* and *C. whitei*.

Materials and methods

Study sites

From a preliminary survey of the shrimp distribution along the coast of the Ariake Sound estuarine system, it was found that (1) *Nihonotrypaea petalura* was distributed in the waters extending from the outermost one-third of Ariake Sound westward and (2) there were two types of habitat, the steeply sloping beach with more boulders and the gently sloping beach with fewer boulders (Tamaki et al. 1999). In the present study, two typical beaches of such types were selected from the outermost one-third of Ariake Sound, which are hereafter called site Kuchinotsu-Cho (abbreviated as KC, the latter type beach) and site Ariake-Machi (AM, the former type beach) after their town names. Site KC (32°36'N, 130°12'E) is located at the southernmost part of Shimabara Peninsula, which is

just north of the plankton sampling station G-12 in Fig. 1 of Tamaki and Miyabe (2000). Site AM (32°30'N, 130°18'E) is located at the middle part of the northern coast of Amakusa-Kamishima Island, which is just south of the plankton sampling station H-13 in that figure. The two sites are about 13 km apart. The coast of western Kyushu is under a semi-diurnal tidal regime. The maximum tidal range at spring tides around these sites through the year is 4.3 m. At each site one transect was established from the shoreline to around the mean low water spring tide (MLWS) level. The length of the transect was approximately 85 m (KC) or 40 m (AM). The measurement for the elevation profile along each transect was made using a transit theodolite and a pole with a graduated ruler. Consulting the tide table for the reference locality nearest to each site, the elevation above the chart datum (CD) level was determined for the points placed along each transect. Similarly, the positions of the levels of mean low water neap tide (MLWN) and MLWS were determined. The maximum duration of exposure per low tide through the year for each point was estimated by placing a horizontal line for the elevation of that point on a sine curve fitted to the predicted tidal heights over the course of the year.

Habitat characteristics

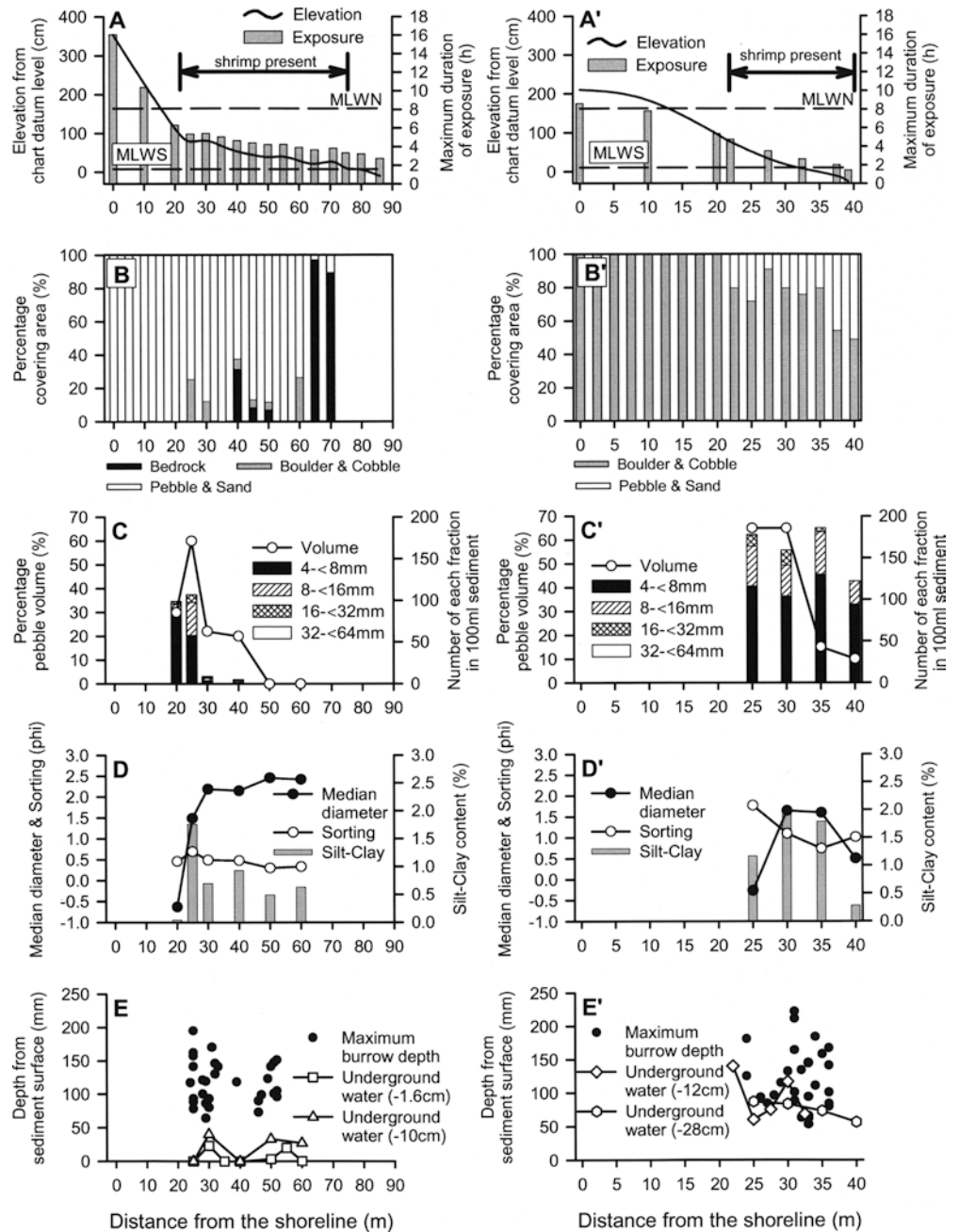
Along each transect, several environmental parameters were measured at stations placed at a minimum distance of 5 m (KC) or 2.5 m (AM) during a sunny daytime low tide. Hereafter, stn x denotes the station x meters distant from the shoreline.

The census for the substratum grain-size compositions was made at the end of March 2002. They were analyzed separately for the three categories, (1) bedrock, boulder (>256 mm), and cobble (256–64 mm); (2) pebble (<64–4 mm); and (3) granule (<4–2 mm), sand (<2–0.063 mm), and mud (silt-clay, <0.063 mm). In the Wentworth particle-grade scales, the cobble-to-granule fraction is collectively called gravel. Our modified grouping would better correspond to the substratum characteristics perceived by *N. petalura*, because the shrimp inhabits those parts of the mixture of the categories 2 and 3 left by category 1. Hereafter, category 3 is simply called sand unless specifically stated, because the contents of the other two fractions were minimal. The areal proportion of the part occupied by bedrock, boulders, and cobbles on the substratum surface was estimated from photographs covering a 1×1-m plot (Fig. 1). Sediment samples containing pebbles and sand were collected to a depth of 20 cm from the surface, which is nearly the maximum burrow depth of the shrimp (see Fig. 2E, E'). Pebble characteristics were represented by both their proportional volume in 100 ml sediment extracted from each sample and the proportional number of grains of the four subdivided fractions in that sub-sample, that is, <64–32, <32–16, <16–8, and <8–4 mm. The granulometric analysis of the sand fraction was made according to Buchanan (1984), with median phi, sorting coefficient [quartile deviation, $QD_{\phi} = (\phi_{75} - \phi_{25})/2$], and silt-clay content determined. The bedrock, boulder, and cobble components of the substrata are seasonally covered with a variety of seaweed growth, especially during March to June (see Fig. 1 in Tamaki et al. 1999). These seaweeds were collected and identified to species. The levels of the underground water table were recorded swiftly at the lowest tide at three points around each station after the surface sediment was removed, with their mean value determined. On the dates of the measurement, the lowest tide levels below the CD level were –10 cm and –1.6 cm (site KC) and –12 cm and –28 cm (site AM). These four tide levels were within the lowest 4.5, 6.0, 4.4, and 1.9% of all semi-diurnal lowest tide levels through the year at each site, respectively.

Collection of burrow casts and laboratory treatments

Burrow casts of *N. petalura* were collected from the high-density zones at the two sites during May to November 2001 (see Fig. 2E, E'). Following Hamano (1990), a polyester-resin liquid mixture

Fig. 2 Environmental parameters along the transect on the boulder beach at site KC (A–E) and at site AM (A'–E'). **A, A'** Elevation profile and maximum duration of exposure per low tide through the year. *MLWN* Mean low water neap tide; *MLWS* mean low water spring tide. **B, B'** Percentage cover of the substratum surface by bedrock; boulders and cobbles; and pebbles and sand, as measured from photographs from a 1×1-m plot (Fig. 1). **C, C'** Percentage volumetric occupancy by pebbles in 100 ml sediment (=pebbles and sand) collected to a depth of 20 cm and the number of grains for the four subdivided fractions of the pebble. **D, D'** Median diameter, sorting (quartile deviation), and silt-clay content of the sand fraction from the sediment sample in C, C'. **E, E'** Maximum depth of each burrow cast of *N. petalura* ($n=28$ at site KC; $n=30$ at site AM) and depth of underground water table at the lowest tide level below the chart datum level on each measurement date (in parentheses)



(volumetric ratio of polyester resin:catalyst 1,000:6–8) was poured into a small plastic collar enclosing one burrow opening on the sediment surface. When burrow openings were alongside of boulders and cobbles, the collar bases were sealed with sand to prevent leakage of the liquid. The burrow casts were retrieved about 24 h later. In the laboratory, after the identification of each component of the burrow, its number was recorded and the length dimensions for the components determined, using a vernier caliper or a graduated ruler to the nearest 0.1 mm or 1 mm. The length of a curve was obtained by fitting a string onto burrow casts. Following Atkinson and Nash (1990), the surface area of each burrow cast was measured twice for its mean value by attaching a layer of aluminum foil of known weight per unit area to the cast. The volume of each burrow cast was estimated by dividing its weight by the density of the polyester-resin liquid (1.12 g ml^{-1}). In the comparison of the dimension of each burrow component between the two sites, a two-tailed Mann–Whitney *U*-test was performed (SPSS 1999).

Estimation of shrimp body size for collected burrow casts

An estimate of the body size for the shrimp inhabiting each burrow cast was obtained from the grand mean value of the mean diameter of each passage (for definition of passage, see Results). This is based on the linear regression equations of several body-size measures on mean passage diameter, which were established from the shrimps (18 males and 17 females) maintained in acrylic aquaria for at least 3 days. The burrows in the aquaria largely ran along their walls. A part of the visible passages was considered as representing a longitudinal section that left half of each columnar passage in the sediment. Two to four such passage diameters were measured with a sliding caliper to the nearest 0.1 mm through the aquarium walls. The shrimps were then removed from the aquaria, fixed in 10% seawater-formalin and the following dimensions measured: (1) total length (along mid-dorsal curvature from tip of rostrum to posterior margin of telson); (2) carapace length (along mid-dorsal curvature from tip of rostrum to posterior margin of

carapace); (3) carapace width (at its widest part from top view) and abdomen width (length at its widest part from top view); and (4) third abdominal somite height plus its pleopod length (combined length from side view).

Body size-frequency distribution of the shrimp populations in the field

To compare the estimated total lengths of the shrimps from the above procedure with the total length-frequency distributions of the natural populations, a total of 1,097 and 754 shrimps were collected from sites KC and AM, respectively, during October 2001 to May 2002.

Results

Habitat characteristics of each site

Site KC

Site KC can be divided into three zones along the transect in terms of the elevation profile (Fig. 2A) and substratum properties (Fig. 2B–D). The uppermost 20-m zone is characterized by the steepest slope with the substratum composed of only pebbles and sand, where no shrimps resided (Fig. 2E). Further seaward, the slope was fairly uniform to the MLWS level at stn 80, with a gradient of 1/54. The substratum of the lowermost 20-m zone is characterized by the prevalence of the slate bedrock (>97% coverage, Fig. 2B), where quite a few shrimp burrows were found from sand patches deposited in small hollows on it. The shrimp were most abundant (mean density of 12.0 m⁻²; K.S. and A.T., unpublished data) in the middle 40-m-wide zone (Fig. 2E), which was below the MLWN level, with the maximum durations of exposure per low tide of 4.0–6.3 h (Fig. 2A). On an areal basis, 62 to nearly 100% surface space unoccupied by the bedrock, boulders, and cobbles was available for shrimp burrow construction (Fig. 2B). Pebbles were present from stn 20 to stn 40 only, making up 20–60% by volume of the sediment, and the numerical proportion of the larger two fractions (16–<32 and 32–<64 mm) was greater at stns 30 and 40 than at stns 20 and 25 (Fig. 2C). The sand fraction shifted from well-sorted to moderately well sorted, very coarse to medium sand (stns 20 and 25) to well-sorted to very well sorted, fine sand (stns 30–60), with consistently low silt-clay contents (0.04–1.8%) (Fig. 2D). The underground water-table levels were generally close to the substratum surface, being 0–2.3 cm below at the lowest tide level of –1.6 cm and 0–4.0 cm below at lowest tide level of –10 cm, respectively, which were well above the shrimp burrow depths (Fig. 2E).

Site AM

The transect fairly uniformly sloped downward from stn 0, via the MLWS level at stn 32.5, to Stn 40, with a gradient of 1/18 (Fig. 2A'). The site can be divided into two zones in terms of the substratum properties

(Fig. 2B'–D'). There was no bedrock at this site. The substratum surface of the upper half zone is covered by boulders and cobbles almost entirely, with pebbles in the rest, where no shrimps resided (Fig. 2B', E'). The shrimp were present in the lower half zone (mean density of 5.7 m⁻²; K.S. and A.T., unpublished data), which was below the MLWN level, with the maximum durations of exposure per low tide of 1.4–5.4 h (Fig. 2A', E'). Boulders and cobbles were still prevalent in this zone, but 9–51% of the area was available for shrimp burrow construction, with the percentage generally increasing seaward (Fig. 2B'). The volumetric proportion of pebbles in the sediment was higher at stns 25 and 30 (65%) than at stns 35 and 40 (10–15%), and the numerical proportion of the smaller two fractions (4–<8 and 8–<16 mm) was fairly high at all stations, accounting for 89–100% (Fig. 2C'). The sand fraction shifted from poorly sorted, very coarse sand (stn 25) to poorly sorted to moderately sorted, medium to coarse sand (stns 30–40), with consistently low silt-clay contents (0.3–2.0%; Fig. 2D'). The underground water-table levels were 6.0–14.0 cm below the substratum surface at the lowest tide level of –12 cm and 5.7–8.7 cm below at the lowest tide level of –28 cm, respectively (Fig. 2E'). These water-table levels were close to the shallowest shrimp-burrow depths.

The seaweed species found on the bedrock, boulders, and cobbles at the two sites are listed in Table 1. Fourteen species at site KC and 11 species at site AM were collected, with 8 species in common. *Codium cylindricum*, *Dilophus okamuriae*, and *Colpomenia sinuosa* at site KC were found only as drifters from offshore. At site AM, *Sargassum fusiforme* was so luxuriant during March to May that the sand patches among boulders

Table 1 Seaweed species collected at sites KC and AM during March to June 2002. Asterisks indicate presence at a site

Species	Site	
	KC	AM
Chlorophyta		
<i>Ulva pertusa</i>		*
<i>Ulvasp.</i>	*	
<i>Codium cylindricum</i>	*	
<i>C. fragile</i>	*	
Phaeophyta		
<i>Dilophus okamuriae</i>	*	
<i>Padina arborescens</i>	*	*
<i>Ishige okamuriae</i>	*	*
<i>I. sinicola</i>	*	*
<i>Colpomenia sinuosa</i>	*	*
<i>Undaria pinnatifida</i>	*	*
<i>Sargassum fusiforme</i>	*	*
<i>S. thunbergii</i>	*	*
Rhodophyta		
<i>Gelidium elegans</i>	*	*
<i>Grateloupia imbricata</i>	*	
<i>G. livida</i>		*
<i>Ahnfeltiopsis flabelliformis</i>		*
<i>Laurencia intermedia</i>	*	*

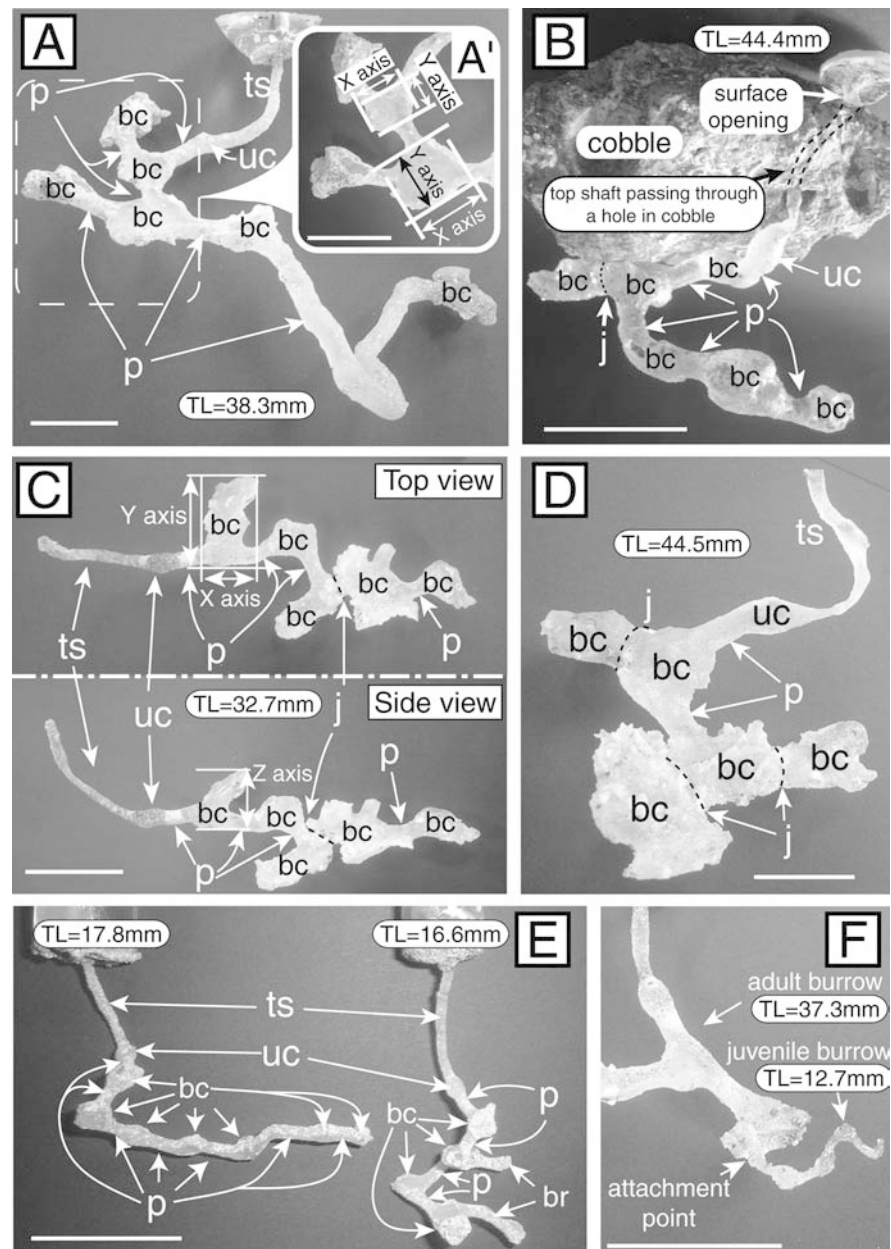
and cobbles in the lower shore were completely concealed by it. The seaweeds may provide the shrimp with plenty of detritus, as fragmented pieces of dead seaweed were buried abundantly in the sediment throughout the year.

Basic burrow structure and definition of dimensions

In total, 30 and 28 complete burrow casts were retrieved from sites KC and AM, respectively. In 16 casts from site KC and 13 casts from site AM, one shrimp was entombed in each (but note Fig. 3F). The other casts had no shrimp inside. All burrow casts had a single surface opening, which was sometimes surrounded by an ejected mound. No funnel-like structure was

observed at the surface opening. This was also the case with shrimp burrows constructed in aquaria; here, the inner walls were lined with mud in places (K.S. and A.T., personal observation). At least a part of the burrow ran alongside boulders and cobbles, which were utilized as either lateral walls or roofs (Fig. 3B). Several burrow components were recognized: (1) top shaft: the shaft leading from the surface opening to the uppermost chamber (defined below), comprising three types, (a) linear (independent of boulders or cobbles), (b) curvilinear, or (c) L-shaped (alongside boulders and cobbles). The top shaft of one burrow cast at site KC went through a hole in a cobble (Fig. 3B); (2) uppermost chamber: the nodule at the base of the top shaft, approximately ellipsoidal in shape. The longer axis was defined in parallel with the main axis of the burrow, the

Fig. 3A–F *N. petalura*. Eight representative burrow casts collected from the two sites. In **F**, a burrow of a juvenile shrimp is attached to a burrow of an adult. The estimated shrimp total length (*TL*) indicated beside each burrow is based on the first equation (1) in the third section of the Results; *bc* bulbous chamber (examples of the definition for its *x*, *y*, and *z* axes are shown in **A'** and **C**); *br* branch; *j* junction between attached bulbous chambers; *p* passage; *ts* top shaft; *uc* uppermost chamber; scale bars = 5 cm



shorter axis and the height being determined orthogonally. For a representative dimension for the latter two combined, their mean value was given (expressed under shorter-axis length). The distal part of the burrow beyond the uppermost chamber ran almost level with it (Fig. 3C) or went deeper, forming tiers (Fig. 3A, D, E). In a few burrows (6/30 at site KC; 1/28 at site AM) the uppermost chamber was absent, the top shaft being directly connected to the uppermost bulbous chamber (defined below); (3) passage: a segment with regular cross sections between chambers, including either a shaft-like or a tunnel-like one (sensu Frey 1973); (4) bulbous chamber: an enlarged chamber with irregular cross sections between passages; 28.0% (site KC) and 14.8% (site AM) of all pairs of the adjacent two chambers were connected directly (Fig. 3C, D). Due to the irregular shape of chambers, the x axis of a chamber was defined in parallel with the main axis of the burrow, the y and z axes being determined orthogonally (Fig. 3C). For a chamber situated at the crossroads or along the winding burrow axis, the x axis was defined

for its longest part (Fig. 3A'); and (5) branch: a segment branching off the main burrow axis or a dead-end passage (Fig. 3E). In two cases at site AM, a smaller burrow cast, which was connected to the main one but apparently different from a branch, was retrieved (Fig. 3F). A part of a juvenile shrimp was entombed there in one case. As a diameter measure for the top shaft, a passage, and a branch, the mean value from the edges and medial point along each component is given to the nearest 0.1 mm (see Table 2 below).

Shrimp total length-frequency distributions from burrow casts and field populations

All linear regression equations of body-size measures (in millimeters) on mean passage diameter (PD, millimeters) obtained from the laboratory aquaria were significant [$n = 35$ (both sexes inclusive) and $P < 0.001$ for each], with high values of coefficients of determination: (1) total length (TL) = $3.76PD + 3.20$, $R^2 = 0.92$; (2) carapace

Table 2 Dimensions (mean \pm SD, range given in parentheses, n number of samples) for each component of the burrow casts of *Nihonotrypaea petalura* at sites KC, AM, and both combined. Note that the numbers of samples for several components are smaller than the total numbers of burrow casts because not all components existed or were measurable in every burrow. Two-tailed Mann-Whitney U -test used to test for significant differences between the two sites (values for the significant items not given in the Combined column). *NS* not significant

Burrow component	Site			
	KC ($n = 30$)	P	AM ($n = 28$)	Combined ($n = 58$)
Top shaft				
Diameter (mm)	4.6 \pm 1.6 (2.0–8.6)	NS	4.9 \pm 1.9 (2.1–9.3)	4.7 \pm 1.7 (2.0–9.3)
Depth (mm)	56 \pm 18 (15–118)	$P < 0.05$	48 \pm 18 (12–100)	
Length (mm)	81 \pm 34 (15–186)	$P < 0.05$	63 \pm 23 (37–138)	
Uppermost chamber				
Longer axis (mm)	16.4 \pm 3.9 (10.7–27.1, $n = 24$)	$P < 0.05$	12.6 \pm 3.7 (5.7–21.0, $n = 27$)	
Shorter axis (mm)	9.7 \pm 2.3 (5.3–13.7, $n = 24$)	NS	8.4 \pm 2.9 (3.6–14.3, $n = 27$)	9.0 \pm 2.7 (3.6–14.3, $n = 51$)
Passage				
Number	3.4 \pm 1.4 (1–6)	NS	4.0 \pm 1.7 (1–7)	3.7 \pm 1.6 (1–7)
Diameter (mm)	7.7 \pm 2.0 (3.0–11.3)	NS	7.6 \pm 2.3 (2.3–11.6)	7.6 \pm 2.2 (2.3–11.6)
Length (mm)	24 \pm 15 (9–68)	NS	32 \pm 41 (6–223)	28 \pm 30 (6–223)
Bulbous chamber				
Number	4.7 \pm 1.5 (2–7)	NS	4.6 \pm 1.5 (1–7)	4.7 \pm 1.5 (1–7)
x axis (mm)	29.7 \pm 12.2 (9.0–59.3)	NS	30.5 \pm 23.0 (5.2–130.4)	30.1 \pm 18.1 (5.2–130.4)
y axis (mm)	24.9 \pm 9.9 (11.0–46.6)	NS	23.1 \pm 9.7 (3.9–47.1)	24.0 \pm 9.8 (3.9–47.1)
z axis (mm)	13.8 \pm 3.9 (6.2–22.7)	NS	13.6 \pm 5.4 (4.2–31.0)	13.7 \pm 4.6 (4.2–31.0)
Mean junction diameter between attached bulbous chambers (mm)	9.8 \pm 3.1 (3.7–15.7, $n = 20$)	NS	10.9 \pm 2.3 (8.7–16.0, $n = 11$)	10.2 \pm 2.9 (3.7–16.0, $n = 31$)
Branch				
Number	1.1 \pm 0.4 (1–2, $n = 8$)	NS	1.3 \pm 0.5 (1–2, $n = 12$)	1.2 \pm 0.4 (1–2, $n = 20$)
Diameter (mm)	7.9 \pm 1.9 (4.9–11.2, $n = 8$)	NS	7.3 \pm 3.1 (2.3–11.3, $n = 12$)	7.5 \pm 2.6 (2.3–11.3, $n = 20$)
Length (mm)	49 \pm 33 (19–124, $n = 8$)	NS	29 \pm 18 (14–75, $n = 12$)	37 \pm 26 (14–124, $n = 20$)

Fig. 4A, B *N. petalura*. Relationships between shrimp size parameters and its burrow passage diameter established from 35 shrimps maintained in the laboratory, with each linear regression line

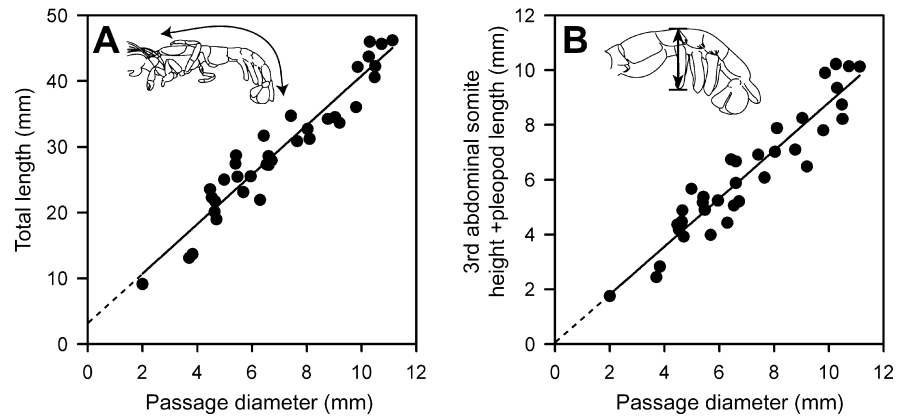
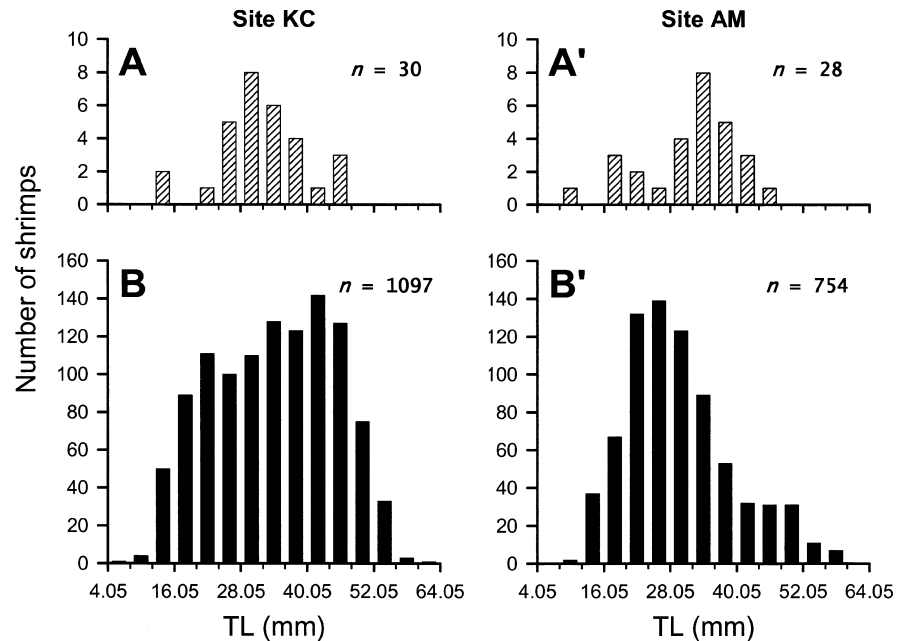


Fig. 5A, B *N. petalura*. TL-frequency distributions from the two sites. **A, A'** Estimated distributions for the inhabitants of the cast burrows (striped bars), based on the first equation (1) in the third section of the Results. **B, B'** Actual distributions for the shrimps collected from the field during October 2001 to May 2002 (solid bars)



length = $0.79PD + 0.94$, $R^2 = 0.89$; (3) carapace width = $0.62PD + 0.47$, $R^2 = 0.82$; (4) abdomen width = $0.63PD + 0.02$, $R^2 = 0.85$; and (5) abdomen height plus pleopod length = $0.88PD + 0.06$, $R^2 = 0.89$. The graphs for (1) and (5) are shown in Fig. 4. Of the five equations, equation 5 was closest to the $y = x$ line. This best fit was also confirmed from the shrimp position in their burrow passages in the aquaria (K.S. and A.T., personal observation). The range and mean (\pm SD) PD of the burrow casts from site KC were 3.0–11.3 mm and 7.7 ± 2.1 mm ($n = 30$); these values from site AM were 2.3–11.6 mm and 7.6 ± 2.3 mm ($n = 28$). There was no significant difference in the PD values between the two sites ($P = 0.71$). Thus it can reasonably be assumed that the inhabitants of the burrow casts at the two sites were derived from populations of the same TL (equation 1). The estimated TL-frequency distributions, with a class interval of 4 mm, for the inhabitants of the cast burrows from sites KC and AM were made by putting the grand

(i.e. from all passages) mean PD value for each burrow cast into equation 1 (Fig. 5A, A'). The estimated TL for the burrow-cast inhabitants ranged from 14.4 to 45.9 mm at site KC, with mean (\pm SD) being 32.0 ± 7.7 mm, and from 11.9 to 46.8 mm at site AM, with mean (\pm SD) being 31.7 ± 8.7 mm. This makes it meaningful to compare further the number and dimensions of the other burrow components between the two sites. From an earlier study, the maturation size for both sexes was estimated at 24.9 mm TL (K. Kubo and A. Tamaki, unpublished data). The TL in the natural populations (both sexes inclusive) ranged from 7.6 to 62.5 mm at site KC, with mean (\pm SD) being 34.0 ± 11.0 mm, and from 8.9 to 59.8 mm at site AM, with mean (\pm SD) being 29.6 ± 9.7 mm (Fig. 5B, B'). Thus the casts of burrows inhabited by the very large or very small shrimps were not obtained, except for the two associated casts of the burrows of juvenile shrimp (Fig. 3F).

Comparison of burrow components and their dimensions between two sites

The number and dimensions of each burrow component (top shaft, uppermost chamber, passage, bulbous chamber, and branch) at the two sites are compiled in Table 2. Except for the depth and length of the top shaft and the longer-axis length of the uppermost chamber, no significant differences in the parameter values were detected between the two sites. Thus a combined, representative value for each component is given in the rightmost column in the table. The top-shaft diameters were narrower than the passage diameters in all but one burrow that had an identical value. The dimensions for the entire-burrow parameters (horizontal extensions, maximum depth, total burrow length, surface area, volume) and the percentage volumetric occupancy by each component listed in Table 2 at the two sites are compiled in Table 3. The horizontal extension (y axis) in the table means the extension that is perpendicular to the axis of the maximum horizontal extension (x axis). The volumes of the individual components were estimated by the approximation of their shapes to either columns [for top shaft, passages, branches, with each (grand) mean diameter as bottom diameter and (total) length as height] or spheroids (for uppermost chamber and bulbous chambers, with the x axis length in the latter regarded as the long axis and the mean of the y and z axis lengths as the short axis). Between the two sites, there were no significant differences in all but one parameter, namely, percentage occupancy by the passages

($P=0.05$). Thus a combined, representative value for each item is given in the rightmost column of Table 3. It is noted that the bulbous chambers accounted for about 75% of the entire burrow volume.

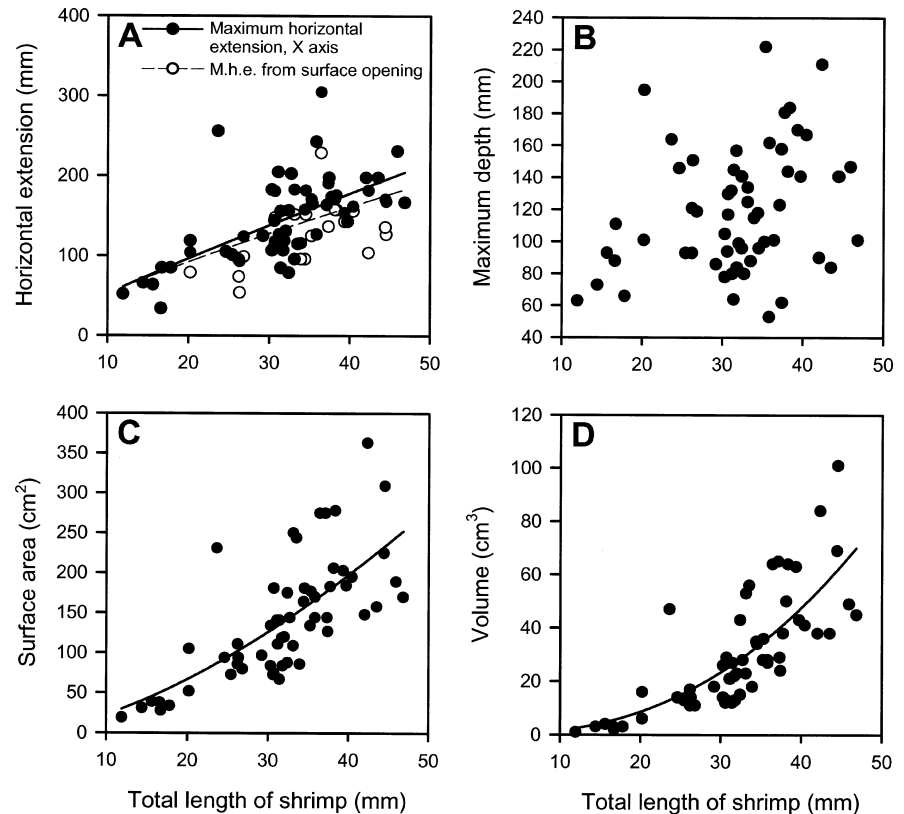
Relationships between entire-burrow dimensions and shrimp size

The regression equations of each entire-burrow dimension listed in Table 3 other than maximum depth on shrimp size [TL in millimeters, $n=58$] were established based on either the linear function ($y=a+bx$) or several nonlinear ones: (1) polynomial quadratic ($y=a+bx+cx^2$), (2) polynomial cubic ($y=a+bx+cx^2+dx^3$), (3) exponential ($y=ae^{bx}$), and (4) power ($y=ax^b$). The selection of the best fitted of these functions was made in light of the highest value of coefficients of determination (SPSS 1999): (1) maximum horizontal extension (x axis, millimeters) = $4.332\text{TL}^{1.005}$ ($R^2=0.55$, $P<0.001$); (2) horizontal extension (y axis, millimeters) = $1.343\text{TL}^{1.126}$ ($R^2=0.49$, $P<0.001$); (3) maximum horizontal extension from burrow opening (millimeters) = $5.353\text{TL}^{0.918}$ ($R^2=0.46$, $P<0.001$); (4) total burrow length (millimeters) = $31.476\text{TL}^{0.652}$ ($R^2=0.34$, $P<0.001$); (5) surface area (square centimeters) = $0.264\text{TL}^{1.789}$ ($R^2=0.72$, $P<0.001$); and (6) volume (cubic centimeters) = $0.001\text{TL}^{2.868}$ ($R^2=0.81$, $P<0.001$). The graphs for (1) and (3), (5), and (6) are shown in Fig. 6A, C, and D, respectively. Only a slight relationship between maximum depth (millimeters) and

Table 3 Entire-burrow dimensions (mean \pm SD, range given in parentheses, n number of samples) for the burrow casts of *N. petalura* at sites KC, AM, and both combined. Two-tailed Mann–Whitney U -test used to test for significant differences between the two sites (values for the significant item not given in the Combined column). *NS* not significant

Entire-burrow dimensions	Site			
	KC ($n=30$)	P	AM ($n=28$)	Combined ($n=58$)
Maximum horizontal extension, x axis (mm)	140 \pm 51 (64–305)	NS	151 \pm 55 (34–256)	145 \pm 53 (34–305)
Horizontal extension, y axis (mm)	67 \pm 27 (30–125)	NS	75 \pm 38 (23–153)	71 \pm 33 (23–153)
Maximum horizontal extension from burrow opening (mm)	125 \pm 44 (54–231)	NS	143 \pm 54 (34–256)	134 \pm 50 (34–256)
Maximum depth (mm)	118 \pm 32 (64–195)	NS	121 \pm 46 (53–222)	119 \pm 39 (53–222)
Total burrow length (mm)	319 \pm 79 (159–472)	NS	297 \pm 111 (107–566)	308 \pm 96 (107–566)
Surface area (cm ²)	144 \pm 71 (31–309)	NS	140 \pm 81 (19–363)	142 \pm 76 (19–363)
Volume				
Total (cm ³)	31 \pm 23 (3–101)	NS	29 \pm 20 (1–84)	30 \pm 22 (1–101)
Occupancy (%)				
Top shaft	4.7 \pm 3.1 (1.0–12.0)	NS	5.8 \pm 4.8 (0.8–18.9)	5.2 \pm 4.0 (0.8–18.9)
Uppermost chamber	2.7 \pm 2.7 (0.0–12.7)	NS	2.3 \pm 1.8 (0.0–8.9)	2.5 \pm 2.3 (0.0–12.7)
Passages	11.8 \pm 6.3 (0.9–22.9)	$P=0.05$	16.0 \pm 7.7 (4.6–34.5)	
Bulbous chambers	78.3 \pm 10.1 (48.1–95.3)	NS	72.0 \pm 15.3 (30.3–94.5)	75.3 \pm 13.2 (30.3–95.3)
Branches	2.5 \pm 7.1 (0.0–34.4)	NS	3.9 \pm 6.3 (0.0–25.2)	3.2 \pm 6.7 (0.0–34.4)

Fig. 6A–D *N. petalura*. Relationships between entire-burrow dimensions and total length of shrimp (all $n = 58$), with curves for the nonlinear regression equations given in the last section of the Results. In **B**, no regression curve is given because excluding the six smallest shrimps, no significant correlation between the two parameters was detected. In **A**, 38 open circles overlap with solid circles. M.h.e. Maximum horizontal extension



shrimp size was detected ($r=0.31$, $P<0.05$; Fig. 6B). However, this relationship was not significant when the six smallest shrimps were excluded ($r=0.11$, $n=52$, $P=0.42$). Over the two sites, the deepest maximum depth was 222 mm (Fig. 2E, E'). The shallowest maximum depths at site KC were below the underground water tables, while those at site AM were at a similar depth.

Discussion

To date, few callianassid shrimp species have been found to occupy a boulder shore habitat. For one of the two species that are “analogous” to *Nihonotrypaea petalura* (see the Introduction), MacGinitie and MacGinitie (1968:289, Fig. 134) showed a simple U-shaped burrow of *Neotrypaea biffari* constructed in a homogeneous sediment of the aquarium, approximately 23×8 cm (horizontal extension \times depth) in size. The shape is apparently different from that of *Nihonotrypaea petalura*. No burrow casts of *Neotrypaea biffari* under natural conditions have been made. The above authors described the filter-feeding behavior of the shrimp. This is consistent with a widely recognized mode of filter/suspension feeding by the occupants of simple U- or Y-shaped burrows in callianassid and upogebiid shrimps (Griffis and Suchanek 1991; Nickell and Atkinson 1995). MacGinitie and MacGinitie (1968) also mentioned that *N. biffari* always lived in pairs in the field. There were no

such burrow casts containing two adult shrimps of *Nihonotrypaea petalura*. For the other “analogous” species, Dworschak (2002:67, Fig. 2c, d) described two incomplete burrow casts of *Callianassa whitei* obtained from the field, lacking in the lowest portions. The gross appearance of the burrow of *C. whitei* resembles that of *N. petalura* in that both run winding along boulders and cobbles, with alternating chambers and passages and with bulbous chambers and branches in places. However, there are differences between *C. whitei* and *N. petalura*: (1) existence of surface mounds around burrow openings (absent vs present); (2) number of surface openings (at least two vs one); (3) diameter of the top shaft compared with that of passages (similar vs narrower); and (4) allometric entire-burrow dimensions as expected from the passage diameter as a shrimp-size estimate (greater in *C. whitei*). In fact, as to (4), all actual values for the two *C. whitei* burrows were beyond the regression curves and the maximum depth found in the present study (Fig. 6). Dworschak (2002) deduced *C. whitei* as a suspension feeder due to its burrow characteristics with no mounds, no seagrass inside, and mainly a simple ‘Y’ configuration (Griffis and Suchanek 1991; Nickell and Atkinson 1995). To our knowledge, the burrow morphologies of these three species are relatively simple when compared with those of other callianassid shrimp.

It has been pointed out that intraspecific variations in callianassid burrow structures exist in response to different environmental conditions (Griffis and Chavez

1988; Griffis and Suchanek 1991; Dworschak and Ott 1993; Nickell and Atkinson 1995; Berkenbusch and Rowden 2000; Miller and Curran 2001). In the present study, despite several distinct differences in habitat and population characteristics between the two sites, including beach slope, substratum properties, underground water-table level, and shrimp density (Fig. 2), the burrow structures of *N. petalura* and their dimensions from the two sites were basically the same except for four minor differences, namely, depth and length of the top shaft, longer-axis length of the uppermost chamber, and percentage volumetric occupancy by the passages (Tables 2 and 3; Figs. 3 and 6). Thus in the subsequent argument we regard the combined mean value of each burrow component as the representative one (the rightmost column in Tables 2 and 3) for the shrimp with a mean TL of 31.8 mm (from equation 1 in the third section of the Results).

The peculiar or common features of the *N. petalura* burrow can be shown by comparison with those of the two congeneric species inhabiting tidal flats, *N. japonica* and *N. harmandi* (see Tamaki and Ueno 1998 for the structure and mean dimensions of the burrows of these latter two species; the estimated mean TL was 61.7 mm in *N. japonica* and 31.1 mm in *N. harmandi*). First, boulders and pebbles are indispensable for the persistence of the *N. petalura* burrow. In homogeneous sediments from the sand fraction at sites KC and AM or from tidal-flat sediments inhabited by *N. japonica* or *N. harmandi* in the laboratory aquaria, *N. petalura* could successfully construct burrows, but their tunnel-like passage parts and bulbous chambers easily collapsed in as little as 1 day (K.S. and A.T., personal observation). Second, the burrow of *N. petalura* is wider than it is deep; the allometric increase in the horizontal dimensions of the burrow with growth of the shrimp was not accompanied by an increase in depth (Fig. 6). The ratio of maximum depth to maximum horizontal extension in the burrow of *N. petalura* ($0.8 = 119 \text{ mm}/145 \text{ mm}$) is much smaller than in that of *N. japonica* ($4.0 = 392 \text{ mm}/98 \text{ mm}$) or that of *N. harmandi* ($4.1 = 364 \text{ mm}/88 \text{ mm}$). Third, the possession of a single surface opening is common to both *N. petalura* and *N. japonica* in contrast to the symmetrical Y-shaped burrow of *N. harmandi*. Fourth, surface mounds are present in all species. Fifth, any funnel-like structure at the surface opening, which can act as a physical trap for material on the sediment surface (Nickell and Atkinson 1995; Ziebis et al. 1996; Dworschak 2001; Kimura et al. 2002), is absent in the burrow of *N. petalura* in contrast to its presence in the burrows of tidal-flat species. Sixth, the presence of both the top shaft, with a narrower diameter as compared with the passages below, and the subsequent smaller uppermost chamber, as compared with the chambers below, is observed in all species. Seventh, the chambers between passages are more voluminous than in the burrows of tidal-flat species in which they simply serve as the place for turnaround. For example, the ratio of mean bulbous chamber diameter $[(x + y + z)/3]$: Table 2] to passage diameter is 3.0 in the burrow of

N. petalura, in contrast to 2.0 in that of *N. japonica* or 2.1 in that of *N. harmandi*. The enlarged chamber of the *N. petalura* burrow was not an artifact caused by polyester-resin liquid diffusing into the coarser sediment, because the shrimp within the finer sediment from tidal flats in the laboratory aquaria made bulbous chambers of equivalent size (K.S. and A.T., personal observation). Finally, a juvenile's burrow attached to an adult's burrow (Fig. 3F) was also recorded in *N. harmandi* (Tamaki et al. 1992). Most probably, settling larvae had entered the surface openings of the adult burrows to later branch off independently, as reported for *Neotrypaea californiensis* (Swinbanks 1981).

It is widely recognized that in callianassid shrimp burrows the uppermost shaft with a narrower diameter is effective in generating an intensified water flow for feeding, irrigation, and removal of fine waste/occluding material by virtue of the Venturi effect (Nickell and Atkinson 1995; Ziebis et al. 1996; Tamaki and Ueno 1998; Bird and Poore 1999; Berkenbusch and Rowden 2000; Dworschak 2001). Observations of the behavior of *Nihonotrypaea petalura* in the laboratory aquaria indicated both the blow-out of sediment clods from the uppermost chamber and the introduction of the overlying water by the pleopod beating of the shrimp positioned just below the uppermost chamber, with its head directed downward and upward, respectively (K.S. and A.T., personal observation). The latter behavior appeared to be not for filter/suspension feeding but simply for burrow irrigation and/or subduction of food material from the sediment surface. Both the regular cross section of the passage and the close shrimp-to-burrow fit (Fig. 4B) is also considered suggestive of filter/suspension feeding, but these attributes could be for adequate ventilation (Nickell and Atkinson 1995; Bird and Poore 1999). In fact, we have seen only deposit-feeding behavior, gleaning for sediment inside the burrow. Another feeding behavior was observed earlier in the laboratory aquaria (H. Ueno, K. Kubo, and A. Tamaki, unpublished data). The shrimp emerged partly from the surface opening on the sediment surface to directly seize fragments of seaweed (Table 1) and food pellets used for penaeid shrimp aquaculture, which were then stored in bulbous chambers or tamped into passage walls and later retrieved. The shrimp, in its burrow, quickly responded to the "odor" emanating from food pellets. These behaviors were never observed in *N. japonica* and *N. harmandi*. During daytime low tide in the field, such direct seizing behavior for *Sargassum fusiforme* has been observed only once at site AM (K.S. and A.T., personal observation). Thus *N. petalura* might be regarded as a facultative drift catcher (and the subsequent seagrass/algae harvester). Facultative drift catching is not uncommon in deposit-feeding callianassid shrimps inhabiting tidal flats in temperate regions (e.g. Griffis and Chavez 1988; Dworschak 1987, 2001). In *N. petalura*, considering the narrower top shaft and the absence of seaweed fragments in the burrow casts, this mode of feeding would not be as usual as in some (sub)tropical

species (type 3 species in Fig. 1 of Griffis and Suchanek 1991). However, drift catching might appear mainly at night as in *Callianassa longiventris* (Dworschak and Ott 1993).

That the shallowest depths of the *N. petalura* burrows reached the deepest underground water-table levels (Fig. 2E') seems reasonable since the shrimp must endure desiccation stress during exposure (Griffis and Chavez 1988). One possibility for much shallower burrows of *N. petalura* compared to *N. japonica* or *N. harmandi* (Tamaki and Ueno 1998) is the lower tolerance of the former species for hypoxic conditions that easily occur in the deeper part of callianassid burrows (Forster and Graf 1995). The maximum duration of exposure per low tide experienced by *N. petalura* (5.4–6.3 h; Fig. 2) is nearly equal to that experienced by *N. harmandi* (6.0 h) and shorter than that of *N. japonica* (8.7 h; see Wardiatno et al. 2003 for data on the latter two species). High tolerance of *N. japonica* to hypoxic conditions was demonstrated both in the laboratory (Mukai and Koike 1984) and in the field (Wardiatno et al. 2003). The bulbous chambers in the *N. petalura* burrow, which was estimated to occupy 75% of its total volume (Table 3), would contribute to increased oxygen concentrations in the deeper part of the burrow (Ziebis et al. 1996). Another possibility for the shallow burrow depth of *N. petalura* is that the shrimp would not need to retreat very deep to escape from large predators disturbing the substratum surface owing to the hindrance effect of boulders and cobbles. Such surface predation pressure could be a selective force that has caused deep-burrow construction by ghost shrimps inhabiting bare tidal flats. For example, the population of *N. harmandi* on a nearby sandflat has considerably declined recently due to the increased predation by the stingray *Dasyatis akajei* (Flach and Tamaki 2001). The deep spiral burrow made by the laomediid shrimp *Axianassa australis* is postulated to function as an anti-predator structure (Felder 2001).

In conclusion, the burrow morphology of *N. petalura*, especially the combination of the constituent elements, is unique when compared with those of the two “analogous” species, *Neotrypaea biffari* and *Callianassa whitei*, as well as those of other callianassid species.

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