Hidden burrow associates: macrosymbiotic assemblages of subtidal deep-burrowing invertebrates in the northern part of the Sea of Japan

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Abstract
The activity of deep-burrowing macrofauna strongly influences all biogeochemical processes in sublittoral soft sediments. Despite this key role, these organisms are difficult to sample and, thus, often remain ignored in environmental studies. This study is the first in comprehensively exploring the diversity of the macrosymbiotic communities associated with the dominant subtidal deep-burrowing invertebrates from the southern part of the Russian coast of the Sea of Japan, represented by the species of the genera *Upogebia* Leach, 1814 (Arthropoda: Crustacea: Decapoda) and *Urechis* Seitz, 1907 (Annelida: Polychaeta: Echiura). The associated symbiotic communities mostly consist of obligate, host-specific species, while those species found in burrows of both hosts are probably using them just as refuges. Most symbionts occurred solitary or in heterosexual pairs, likely due to aggressive and strictly territorial behavior. This is certainly a hidden biodiversity, as more than half of the species reported here were not previously known from these “relatively simple and well-studied” boreal marine ecosystems. Our findings also allowed us to describe a new species belonging to the symbiotic genus *Hesperonoe* Chamberlin, 1919 (Annelida: Polychaeta: Polynoidae), based on morphological and molecular evidences, the latter being here presented for this genus for the first time.

Keywords Symbiosis · Communities · *Urechis* · *Upogebia* · NW Pacific · *Hesperonoe*

Introduction
Soft sediment communities are very diverse and play an important ecological role in local biogeochemical cycles (e.g., Rhoads 1974; Meysman et al. 2006). The composition and structure of these communities are greatly influenced by the activity of burrowing macrofauna, which modulates biogeochemical processes such as organic matter processing oxygenation or microbial activity stimulation (Levinton 1995; Aller and Aller 1998; Glud 2008) and are considered as ecosystem engineers in sublittoral sandy or muddy marine bottoms (e.g., Tamaki and Ueno 1998; Dworschak 2000; Sandnes et al. 2000; Felder 2001; Webb and Eyre 2004; Pillay and Branch 2011).

Numerous symbiotic species use burrows of larger marine invertebrates as protected habitats to escape predators, access food, and/or support less environmental stress (Itani 2002; Atkinson and Taylor 2005; Anker et al. 2005, 2015; Goto and Kato 2012; Seike et al. 2012; Itoh and Nishida 2013; Henmi and Itani 2014a, b; Marin 2014; Lavesque et al. 2016; Henmi et al. 2017; Moyo et al. 2017). For example, more than 100 symbiotic species, from protozoans to fishes, are known to inhabit the burrows of large crustaceans (i.e., Gebiidea and Axiidea) along the US Pacific coast (e.g., Campos et al. 2009), while the fauna associated with echiuroids (spoon worms) include more than 50 specific symbiotic species, such as bivalves, polychaetes, brachyuran crabs, alpheid shrimps, copepods, and fishes (Anker et al. 2005). In Russia, the study of the diversity of burrowing crustaceans and their associated fauna has just begun, and numerous symbionts including crustaceans (Marin 2010, 2013, 2015; Marin et al. 2011, 2013; Marin and Turbanov 2016) and a new phoronid species (Temereva and Chichvarkhin 2017) have recently been reported. The parasitic fauna of *Upogebia major*
in Vostok Bay, namely the bopyrid isopods Gyge ovalis (Shiino, 1939) and Progebiiophilus sp. (Crustacea: Isopoda: Bopyridae) and the rhizocephalan Sacculina upogebiae Shiino, 1943 (Crustacea: Rhizocephala: Sacculinidae), also represent new records for the Russian coast of the Sea of Japan. However, a large number of the small inhabitants of these communities still remain unknown likely because they are simply not caught by standard sampling gears. The importance of the associations between the burrowing macrofauna and their symbionts in a given ecosystem is difficult to estimate so that having new data on their diversity and biology will help to take these animals into account in future ecological studies.

Deep-burrowing crustaceans and spoon worms are two of the main groups of soft-bottom engineer species in Peter the Great and Posjeta Bays of the Sea of Japan, which are known to occur in large concentrations, for example, in Vostok Bay (Selin 2013, 2014, 2015, 2017). The shrimp Nihotrypaea japonica (Ortmann, 1891) (Decapoda: Callianassidae) may reach up to 200 inds/m², which represent about one-third of the total local macrozoobenthic biomass (Selin 2015). Virtually all bottoms from 0.2- to 3-m depth in the area are excavated by the several meters long burrows of the ghost shrimp Upogebia major (De Haan, 1841) (Decapoda: Gebiidea: Upogebiidae) (Nickell and Atkinson 1995; Kinoshita 2002), which may reach up to 117 mm in body length (pers. observ.). Nevertheless, the symbiotic assemblages inhabiting these burrows in the region were out of scientific interest.

This article is a part of the project attempting to evaluate the biodiversity of shallow-water infaunal organisms, which revealed the highly diverse symbiotic communities mostly composed of undescribed symbiotic species. Moreover, a careful morphological observation and molecular analysis revealed a new species of the rare symbiotic genus Hesperonoe Chamberlin, 1919 (Polychaeta: Polynoidae), known exclusively from the Northern Pacific (Skogsberg 1928; Hartman 1968; Averincev 1990; Buzhinskaia 2013; Hong et al. 2017; Uschakov and Wu 1965).

**Materials and methods**

**Sample collection and treatment**

Samples were mainly collected in the estuary of the Volchanka River in the Vostok Bay, near the scientific station “Vostok” (42° 51′ 14.48° N, 132° 46′ 47.24° E), and in the Troitza Bay (42° 38′ 60.00′′ N, 131° 07′ 27.8′′ E) (see Fig. 1), where the burrowing infauna was dominated by the crustaceans Nihonotrypaea japonica and Upogebia major (Marin and Kornienko 2014; Selin 2015, 2017, 2019), at least in summer from 2009 to date, as well as in the Astafeiva Bay (42° 36′ 52.2′′ N, 131° 12′ 01.1′′ E), where a large population of Urechis unincinctus was studied from 2009 to 2012 (Fig. 1). Hosts and the associated symbiotic community were collected subtidally by scuba diving using a bait suction pump (yabby-pump) (Eleftheriou and McIntyre 2005), which did not allow us to measure the length and volume of the burrows, neither to obtain quantitative estimates of the number of symbionts. To obtain reliable data on a qualitative analysis of the symbiotic communities, at least 50 burrows of each of the host species were examined.

Once preserved, the specimens were photographed under a Leica M165C stereomicroscope linked to a Leica IC80HD digital camera. Scanning electron microscope (SEM, Tescan Vega TS5130MM) micrographs were made after critical point drying and coating with 300 Å of gold, at the Laboratory of Electronic Microscopy of the A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences. All symbionts were measured to the nearest 0.1 mm using a calibrated ocular micrometer under a Leica M165C stereomicroscope.

The similarity of the communities was measured with the Sørensen Index (SI) (Sørensen 1948) as SI = 2C/(S1 + S2), where C is the number of species the two communities have in common, S1 is the total number of species found in community 1, and S2 is the total number of species found in community 2; Jaccard Index (JI) (Jaccard 1908, 1912) was calculated as JI = sc/(sa + sb + sc), where sa and sb are the numbers of species unique to samples a and b, respectively, and sc is the number of species common to the two samples; Sørensen–Dice Index was calculated as SD = 2a/(a + b) + (a + c) (Dice Lee 1945; Sorensen 1948).

**Molecular analysis**

Total genomic DNA was extracted from muscle tissue using the innuPREP DNA Micro Kit (Analytik Jena, Germany) following the manufacturer’s protocol. The gene marker of mitochondrial cytochrome c oxidase subunit I (COI mtDNA) was amplified with the help of primers «m13polylco» (TGTAAAACGACGGCCAGTGAATTTAAGCAT) and «m13polyhc0» (CAGGAAAACGCTATGACTAMACTTWWGGGTAACAAARATCA) (Carr et al. 2011), mitochondrial 16S small subunit rRNA (16S rRNA) with the help of +16SA (CGCCTGTITTATCAA AAACAT) and −16SH (CCGTCCTGACTACGTAGTACG), and nuclear 28S large subunit rRNA (28S rRNA) with the help of +C1 (ACCCGCTGAATTTAAGCAT) and −D2 (TCCGTGTTTCAAGACCGG). All obtained sequences are deposited in GenBank (NCBI) database (https://www.ncbi.nlm.nih.gov/genbank/).
Consensus of complementary sequences was obtained with MEGA 7.0. The best evolutionary substitution model was determined using MEGA 7.0 and jModeltest2.1.141 via the CIPRES Science Gateway V. 3.3 (http://www.phylo.org/). Kimura’s two-parameter (K2P) (Kimura 1980) substitution model was calculated using MEGA 7.0 for pairwise comparisons of sequence divergence between species based on the number of nucleotide substitutions. Phylogenetic analysis was performed for COI using RAxML v.8.0.0 with GTR+I+G evolutionary model for maximum likelihood (ML) analysis. Additional dataset of COI mtDNA sequences of the representatives of the family Polynoidae and related taxa was taken from GenBank (NCBI) database. Unfortunately, no sequences of species of *Hesperonoe* were presented in any of genetic databases to date.

The type material and vouchers are deposited in the collection of Zoological Museum of Moscow State University, Moscow (ZMMU), and the Laboratory of Ecology and Evolution of Marine Invertebrates (LEMMI) of A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, Moscow, Russia.

**Ecological results**

Eleven symbiotic species were found in the burrows of *Upogebia major*, *Upogebia issaeffi* (Balss, 1913), and *Urechis unicinctus* (Table 1; Figs. 1 and 2). The respective symbiotic communities did not differ and, thus, will be considered together in further analyses. All symbiotic species, indicated for each host, belong to approximately the same size class and were found together in the burrows. The large individuals of *Hesperonoe urechis* sp. nov. were found inhabiting the burrows alone with the host spoon worm.

The studied symbiotic communities showed mostly dissimilar species compositions (SI = 0.428; JI = 0.375; SD = 0.428) (Fig. 3). *Sestrostoma balssi*, *Gymnogobius heptacanthus*, and turbellarian *Stylochus/Paraplanocera* sp. were found inside burrows of both *Upogebia* and *Urechis* (Table 1; Fig. 3). The Crustacea (mainly Decapoda) were dominant in diversity and abundance in both symbiotic communities (always comprising more than 60% of all symbiotic specimens), followed by Polychaeta and Turbellaria (in abundance) (Fig. 4; Table 1). The species of Decapoda represent phylogenetically different families, sharing a similar mode of life in the burrows.

Five over the eleven symbiotic species were found solitary or in heterosexual pairs. *Pinnixa rathbuni* was found in groups of up to 30 mature and young individuals inside the burrow of spoon worm, while 1, 2, or (rarely) 3 turbellarian specimens were found inhabiting the same burrow of *U. unicinctus* and *Upogebia*.

**Taxonomic account**

Family Polynoidae Kinberg, 1856

Genus *Hesperonoe* Chamberlin, 1919

*Hesperonoe*: Chamberlin 1919: 252; Pettibone 1953: 37; Fauchald 1977: 62; Uschakov 1982: 144; Ruff 1995a: 136; Jirkov 2001: 161.

**Type species**: *Hesperonoe complanata* (Johnson, 1901).

**Diagnosis** (based on Fauchald 1977; Uschakov 1982; Ruff 1995a; Hong et al. 2017). Body flattened with 36–38 segments, having 15 pairs of elytra on segments 2, 4, 5, 7, 9,…, 23, 26, 29 and 32; elytra almost covering dorsum. Bilobed prostomium with cephalic peaks (might be reduced); ceratophores of lateral antennae inserted ventrally. Parapodia biramous. Notochaetae more or less serrated, thick with blunt tip (upper) and longer, slenderer with pointed tip (lower). Neurochaetae all unidentate and serrated, slender with long spinous region tapering to fine tip (upper) and thick with expanded subdistal spinous region and smooth tip (lower).

*Hesperonoe japonensis* Hong, Lee & Sato, 2017

(Figs. 5, 6, and 7)

*Hesperonoe japonensis*. – Hong, Lee and Sato 2017: 2935–2940, Figs. 7–9.

*Hesperonoe hwanghaisensis* (not Uschakov and Wu 1959):

Sato et al. 2001: 983–990, Figs. 4–14; Yamanishi and Sato 2007: 188; Sato 2008: 202; Sato 2012: 223, 1 fig.; Sato et al. 2016: 30–38, Figs. 3–3.

*Hesperonoe* sp.: Sato 2000: 192–195, Figs. 8–6d.

**Material examined.** Adult specimens: 1 spcm (ZMMU Pl-3941) and 1 spcm (LEMMI, dissected), 12 spcms (LEMMI) – Russian Far East, Sea of Japan (East Sea), Peter the Great Bay, Vostok Bay, near scientific station “Vostok,” 42° 51’ 19.0” N, 132° 46’ 30.6” E, in front of the laboratory, 1–1.5-m depth, sandy-gravel bottom overgrown with seagrass, collected with yabby-pump from burrows of the mud shrimps *Upogebia major* and *U. issaeffi*, coll. I. Marin, 30–31 July 2017; 1 spcm (ZMMU Pl-3942), 1 spcms (LEMMI, dissected), 3 spcms (LEMMI) – Posjeta Bay, Troitza Bay, 42° 38’ 60.0” N, 131° 07’ 27.8” E, 1–1.5-m depth, muddy sand, 1–1.5-m depth, sandy-gravel bottom overgrown with seagrass, collected with yabby-pump from burrows of the mud shrimps *Upogebia major* and *U. issaeffi*, coll. I. Marin, 1–3 Aug. 2018.

**Diagnosis** (based on Hong et al. 2017 and present study). Color red in vivo. Bilobed prostomium with sharply tapering cephalic peaks. Median and lateral antennae and all cirri with scattered papillae. A row of conical macrotubercles along posterior edge of elytra in adults (≥ 1.9 mm in body width without parapodia). Microtubercles and papillae over most of elytral surface. Marginal fringe of filiform papillae on posterior and outer-lateral elytral...
Fig. 1 Macrosymbiotic community associated with the spoon worm *Urechis unicinctus* (a); b copepod *Goidelia cf. japonica* Embleton, 1901 (Crustacea: Copepoda: Poecilostomatoida: Cariidiidae); c, d pinnotherid crab *Pinnixa rathbuni* Sakai, 1934 (Crustacea: Decapoda: Pinnotheridae); e polynoid Polychaeta *Hesperonoe urechis* sp. nov. (Polychaeta: Polynoidae); f *Stylochus/Paraplanocera* sp. (Stylochoidea: Polycladida: Platyhelminthes); g brachyuran *Sestrostoma balssi* (Shen, 1932) (Crustacea: Decapoda: Varunidae); h undescribed amphipod *Liljeborgia* sp. (Crustacea: Amphipoda: Liljeborgiidae); i gobiid fish *Gymnogobius heptacanthus* (Hilgendorf, 1879) (Pisces: Gobiidae)
edges. Notochaetae at basal lobes of tentacular cirri. Both thick and thin notochaetae strongly serrated.

**Description.** The largest specimen 20 mm long, 2.7 mm wide without parapodia, 9.8 mm wide with setae, with 40 segments. Body dorsoventrally flattened. Red in vivo (Fig. 5), brownish when preserved.

Prostomium bilobed, about as long as wide, with sharply tapering cephalic peaks (Figs. 6a and 7a). Two pairs of eyes; anterior larger than posterior, near widest region of prostomium, posterior closer together. Ceratophore of median antenna reaching cephalic peaks; style of median antenna long, several times longer than prostomium length (Figs. 6a and 7a). Lateral antennae shorter than prostomium, inserted beneath cephalic peaks (Fig. 6a, c). Median and lateral antennae with scattered papillae (Fig. 7a, b). Palps several times longer than prostomium length, tapering to filiform tips, with minute papillae (Figs. 6a, c and 7a).

Cirrophores of tentacular cirri large, with digitiform aciculare containing single stout aciculum, with 1–2 notochaetae (Fig. 7b). Tentacular cirri tapering, with relatively large papillae; dorsal pair longer than ventral pair (Fig. 6a, c).

Elytra thin and semitransparent, 15 pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 26, 29, and 32, covering dorsum completely or except mid central dorsum (Fig. 5a, c), with conical macrotubercles along posterior elytral edge (Figs. 6d and 7c, d). Numerous small microtubercles and papillae over most elytral surface (Figs. 6b and 7c, d). Marginal fringe of filiform papillae on posterior and outerlateral elytral edges (Figs. 6b and 7c).

Biramous parapodia with shorter notopodia with tapering tip and larger neuropodia with shorter, rounded postsetal acicular lobes and longer, conical presetal acicular lobes (Fig. 6e). Notopodia with up to 50 notochaetae: 25–26 upper, thick, with marked serrations, tapering to blunt tip (Figs. 6f and 7e) and 23–24 lower, longer, thin, capillary, with marked serration and filiform tips (Figs. 6g and 7e). Neuropodia with up to 50 neurochaetae: 19–20 upper, slender, with long spinous region, tapering to fine tip (Figs. 6h and 7f) and 20–30 lower, thicker, shorter, with expanded subdistal shorter spinous region, and smooth, sharp, slightly hooked tip (Fig. 6j).

Dorsal cirri with long styles extending beyond chaetae, with scattered papillae. Ventral cirri short, tapered, with small papillae. Cirrophores of ventral buccal cirri inserted at base of segment 2; styles long, tapering, similar to ventral tentacular cirri, with scattered papillae (Fig. 6c). Dorsal tubercles present.

**Taxonomic remarks.** The specimens from Peter the Great Bay matched very well the original description based on the type specimens from Japan and that of “Hesperonoe hwanghiaensis” described by Sato et al. (2001, 2016) and Hong et al. (2017). The only intraspecific differences in our specimens are palps varying in length (Figs. 6a, c and 7a). *Hesperonoe hwanghiaensis* differs from *H. japonensis* in having a row of conical macrotubercles in elytra of adults, papillae on the surface of the median and lateral antennae, the thick and thin notochaetae being markedly serrated and notochaetae at cirrophores of tentacular cirri (Hong et al. 2017).

### Table 1. Presence and approximate abundances (number of individuals) of the symbiotic species recorded from each burrowing host.

| Symbiont                        | Upogebia major | Upogebia issaeffi | Urechis unicinctus |
|---------------------------------|----------------|------------------|-------------------|
| **Crustacea**                   |                |                  |                   |
| *Pinnixa rathbuni* Sakai, 1934  |                |                  |                   |
| (Decapoda: Pinnotheridae)       |                |                  |                   |
| *Sestrostoma balssi* (Shen, 1932) Decapoda: Varuniidae) | 1 | 1 | 1 |
| *Betaeus levifrons* Vinogradov, 1950 (Decapoda: Alpheidae) | 1 or 2 \(\tilde{\varphi}\tilde{\varphi}\) | 1 or 2 \(\tilde{\varphi}\tilde{\varphi}\) | – |
| *Liljeborgia* sp. (Amphipoda: Liljeborgiidae) | – | – | 1 |
| *Goidelia cf. japonica* Embleton, 1901 (Copepoda: Poecilostomatoida: Catiniidae) | – | – | >30 |
| Unidentified copepod (possibly *Hemicyclops* sp.) | >30 | >30 | – |
| **Polychaeta**                  |                |                  |                   |
| *Hesperonoe japonensis* Hong, Lee & Sato, 2017 (Polynoidae) | 1 | 1 | – |
| *Hesperonoe urechis* sp. nov. (Polynoidae) | – | – | 1 |
| **Platyhelminthes**             |                |                  |                   |
| *Stylochus/Paraplanoeca* sp. (Stylochoidea: Polycladida) | 1–2 | 1–2 | 2–3 |
| Phoronida                       |                |                  |                   |
| *Phoronis embryolabi* Temereva & Chichvarkhin, 2017 (Phoronidae) | >30 | >30 | – |
| **Pisces**                      |                |                  |                   |
| *Gymnogobius heptacanthus* (Hilgendorf, 1879) (Pisces: Gobiidae) | 1 | 1 | 1 |
Fig. 2 Macrosymbiotic community associated with *Upogebia major* (a) and *U. issaeffi* (b); c Polychaeta *Hesperonoe japonensis* Hong, Lee & Sato, 2017 (Polychaeta: Polynoidae); d, e brachyuran *Sestrostoma balssi*; f alpheid shrimps *Betaeus levifrons* Vinogradov, 1950 (Crustacea: Decapoda: Alpheidae); g gobiid fish *Gymnogobius heptacanthus*; h *Phoronis embryolabi* Temereva & Chichvarkhin, 2017 (Phoronida: Phoronidae); i *Stylochus/Paraplanocera* sp. (Stylochoidea: Polycladida: Platyhelminthes)
GenBank accession numbers. COI mtDNA – MT237710, MT237711; 16S rRNA – MT241162; 28S rRNA – MT241160.

Habitat and ecology. The specimens of *H. japonensis* were collected from burrows of *Upogebia major* and *U. issaeffi*, which were particularly abundant between the rootstocks of *Zostera marina* Linnaeus, 1753; *Z. asiatica* Miki, 1932 (Zosteraceae); and *Phyllospadix japonicus* Makino, 1897 (Cymodoceaceae) overgrowing the sandy-gravel bottoms of the studied area. In Japanese waters, the species was associated with the same species of *Upogebia*, as well as with *Austinogebia narutensis* (Sakai, 1986) (Crustacea: Decapoda: Upogebiidae) (Sato et al. 2001, 2016; Hong et al. 2017; present paper). Only one mature adult was collected from each burrow, suggesting a territorial behavior. The worm shared the same burrow with turbellarian *Stylochus/Paraplanocera* sp., the alpheid shrimp *Betaeus levifrons* and the brachyuran crab *Sestrostoma balssi* (Marin 2010; Marin et al. 2011; Table 1; Fig. 2).

**Geographic distribution.** Type locality: Akkeshi Bay, Hokkaido Island, Japan. Present in the western part of the Northern Pacific, from Peter the Great Bay of the Sea of Japan (East Sea) to the southern island of Japan (Kyushu).

**Hesperonoe urechis** sp. nov.

http://zoobank.org/790BA302-0A5E-4746-9795-CCBAF4EDE189

(Figs. 8, 9, and 10)

Material examined. Holotype, 1 adult spcm (ZMMU Pl-3943) – Russian Far East, Sea of Japan (East Sea), Posjeta Bay, Troitza Bay, 42° 38′ 60.0″ N, 131° 07′ 27.8″ E, 1–1.5-m depth, muddy sand, inside a burrow of the spoon worm *U. unicinctus*, yabby-pump, coll. Marin, I., Antokhina T., 24 Aug. 2009; 1 spcm (LEMMI) – Peter the Great Bay, Astafieva Bay, 42° 36′ 52.2″ N, 131° 12′ 01.1″ E, 1–1.5-m depth, clear sand bottom, inside a burrow of the spoon worm *U. unicinctus*, yabby-pump, coll. Marin, I., Antokhina T., 25 Aug. 2009.

Diagnosis. Prostomium bilobed, with pro stomal peaks reduced to small processes. All antennae and cirri without papillae. Tentaculophores without chaetae. Elytra smooth, without or with median microtubercles, without marginal papillae. Distinct dorsal tubercles present. Upper thick notochaetae with minute serration. Yellow-brown in vivo, with a metallic sheen.

Description. Holotype fragmented in two parts, anterior with 28 segments and posterior with 8 segments; 71 mm in total length and 7 mm wide without parapodia, 15 mm wide with setae. Body dorsoventrally flattened. Dorsum yellow brown in vivo, with a metallic sheen, orange when preserved (Fig. 8).

Prostomium bilobed, slightly wider than longer, with cephalic peaks reduced to small processes on frontal prostomial margin, with two palps and three antennae (Figs. 8b and 9a). Two pairs of dorsal black eyes, ovate in shape, equal in size, anterior pair near middle of widest prostomial region, posterior pair on rear prostomial margin. Style of median antenna slender, 1.5 times longer than lateral ones, same length as prostomium, inserted anteriorly in median notch, with distinct ceratophore (Figs. 8b and 9a). Lateral antennae inserted ventrally, with short tapered styles, shorter than median antennae and prostomium length, with distinct ceratophores (Figs. 8b and 9a). All antennae not papillated, without subdistal inflation. Palps stout, 2.5 times longer than prostomium length, not papillated (Fig. 9a).

First segment non-visible dorsally, with two pairs of tentacular cirri without papillae, dorsal pair slightly longer than...
Fig. 5 *Hesperone japonensis* Hong, Lee & Sato, 2017: a–c dorsal view, *in vivo*; d, e polychaete specimens attached to host’s abdomen. White arrows highlight the position of the worms.
Fig. 6  *Hesperonoe japonensis* Hong, Lee & Sato, 2017:  

- **a** dorsal view of the anterior end;  
- **b** elytron from the middle part of body;  
- **c** ventral view of the anterior end;  
- **d** enlargement of the posterior edge of the elytron at the position indicated by arrow;  
- **e** posterior view of a right parapodium of the 9th segment;  
- **f** upper notochaeta;  
- **g** distal part of the lower notochaeta;  
- **h** distal part of the upper neurochaeta;  
- **i** middle neurochaeta;  
- **j** lower neurochaeta.  

Scale bars: (a, b, c, e) 1 mm; (d, f, g, h, i, j) 200 µm
Fig. 7 *Hesperonoe japonensis* Hong, Lee & Sato, 2017: a dorsal view of the anterior end; b cirrophore of tentacular cirri with notochaeta; c posterior edge of elytron with filiform papillae and microtubercles; d posterior edge of elytron with filiform papillae, microtubercles, and conical macrotubercles; e upper (left) and lower notochaetae (right); f upper neurochaetae (left). (ctc) Cirrophore of tentacular cirri. (nc) Notochaetae. (ac) Aciculum. (la) Lateral antenna. Scale bars: a, 0.5 mm; b, c, d, 100 µm; e, f, 200 µm
Elytra 15 pairs almost completely covering dorsum except for last few segments in vivo (Fig. 8a, c). Anterior fragment of holotype with 13 pairs of elytra on segments of: 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 26; posterior fragment without elytra, only with cirrigerous segments. Elytra oval, smooth, sometimes with central microtubercles, margin without papillae (Figs. 9b, c and 10a, b).

Biramous parapodia with reduced rounded notopodia and larger neuropodia (Figs. 9i, j and 10b). Neuropodia with shorter, rounded postsetal acicular lobes and longer, conical presetal acicular lobes with digitiform supra-acicular extension (Fig. 9j). Tips of acicula penetrate neuropodial postsetal acicular lobes (Fig. 9i).

Notopodia with up to 40 notochaetae: 15–22 upper, thick, with faint serrations, smooth, aciculiform, with rounded tips (Figs. 9d and 10d) and 17–23 lower, lower, thin, with marked serration and filiform tips (Figs. 9e and 10e). Neuropodia with 70+ neurochaetae of about equal width, noticeable serrated (Fig. 10b), upper, slender, with long spinous region tapering to fine tip (Figs. 9f and 10f), lower ones shorter than upper, with short expanded subdistal spinous region and smooth, sharp tip (Figs. 9g and 10g), with transitional neurochaetae between upper and lower (Fig. 9g). Lower and upper neurochaetae of about equal width and length.

Dorsal cirri with large cylindrical cirrophores and smooth long styles extending beyond chaetae, without distal inflation. Dorsal tubercles well developed (Figs. 8b and 9i). Ventral cirri short, tapered, not extending to lower edge of neuropodia (Fig. 9i, j).

**Taxonomic remarks.** *Hesperonoe urechis* sp. nov. can be distinguished from all other species of the genus by its relatively long body (up to 7 cm in mature specimens). It resembles *H. adventor* (Skogsberg in Fisher and MacGinitie 1928), but differs in: (1) the absence of papillae on all antennae, palps and cirri (heavily ciliated in *H. adventor*); (2) microtubercules, if present, located in the median area of elytra (on the edge of ones as in *H. adventor*); (3) thick upper notochaetae with faint serrations (distinct pectination in *H. adventor*); and (4) rounded prostomium with reduced cephalic peaks (tapering lateral peaks in *H. adventor*, according to Hartman (1968)). The original description indicated the presence of two mammilliform anterior processes, which may almost be absent (Skogsberg 1928).

The new species is also resembling *Hesperonoe andriashevi* Averincev, 1990, but differs in having (1) small processes on prostomium (lacking in *H. andriashevi*); (2) up to 45 notochaetae and 70 neurochaetae (5–7 and ~15 in *H. andriashevi*); (3) two types of neurochaetae (only one in *H. andriashevi*); and (4) median elytral microtubercules (absent in *H. andriashevi*). The elytra of *H. andriashevi* were reported as non-completely covering dorsum. However, its description was based on one elytron (Averincev 1990). *Hesperonoe andriashevi* differs from all other species of *Hesperonoe* in having 13 pairs of elytra and neurochaetae that cannot be clearly subdivided into two types so that its position within *Hesperonoe* was cast in doubt by Hong et al. (2017), but not by Averincev (1990). Upper and lower neurochaetae of *H. urechis* sp. nov. are different, but there are some transitional chaetae between them. A similar distribution of neurochaetae occurs in other species of *Hesperonoe,* such as *Hesperonoe corensis* Hong, Lee & Sato, 2017. The fact is that it may be difficult to clearly subdivide neurochaetae into two types, thus supporting the necessity to modify the generic diagnosis of the genus as suggested by Averincev (1990).

**Genetic differences.** Uncorrected pairwise distances (*p*-distances) between *H. japonensis* and *Hesperonoe urechis* sp. nov. is 0.152 ± 0.008 substitution per 100 nucleotides (about 15%) that clearly support their interspecific differences.

**GenBank accession numbers.** COI mtDNA – MT237712, MT237713; 16S rRNA – MT241163; 28S rRNA – MT241161.

**Habitat and ecology.** The specimens of the new species were collected from intertidal muddy sand flats. They are commensals of the shallow-water spoon worm *Urechis unicinctus,* which lives in large U-shaped burrows in muddy and sandy sediments in inter- and subtidal zones in the Sea of Japan and the Yellow Sea (Abe et al. 2014; personal observation). The symbiotic fauna of *U. unicinctus* in Peter the Great Bay includes turbellarian *Stylochus/Paraplanocera* sp., the pinnotherid crab *Pinnixa rathbuni,* an amphipod *Liljeborgia* sp., the copepod *Goidelia* cf. *japonica* Embleton, 1901, and gobid fish *Gymnogobius heptacanthus* (Hilgendorf, 1879) (Marin 2016; Table 1; Fig. 1).

**Etymology.** The species is named after the generic name of its host – *Urechis unicinctus.*

**Geographic distribution.** *Hesperonoe urechis* sp. nov. were found in the southern part of Peter the Great and Posjeta Bays of the Sea of Japan (Russian Federation) (Fig. 11). Although the distribution of the new species is probably related with that of *Urechis unicinctus* (see Abe et al. 2014), it has never been collected from burrows in the northern part of Peter the Great Bay (Vostok Bay and adjacent areas), which have been intensive sampled with the same method. Similarly, no records are known from the southern region of the distribution.

**Discussion**

The symbiotic communities associated with the dominant burrowing invertebrates, such as the spoon worm *Urechis caupo* Fisher & MacGinitie, 1928 (Annelida: Echiura: Urechidae), and the ghost shrimps *Neotrypaea californiensis*
(Dana, 1854) (Crustacea: Decapoda: Callianassidae) and Upogebia pugettensis (Dana, 1852) (Crustacea: Decapoda: Upogebiidae), or tube builders, such as the parchment worm Chaetopterus aff. variopedatus (Renier, 1804) (Annelida: Polychaeta: Chaetopteridae), inhabiting the mud flats along the US coast, are mostly studied in the Northern Pacific (Ricketts et al. 1985; Manning and Felder 1991). The burrows of the species of Urechis, like those of almost all other echiuroids, often host numerous symbionts, such as shrimps, crabs, bivalves, and even fishes (e.g., Fisher and MacGinitie...
Fig. 9  *Hesperonoe urechis* sp. nov.  

- **a** Dorsal view of the anterior end with round prostomium with small processes;  
- **b** elytron with small group of microtubercles in the center;  
- **c** microtubercles;  
- **d** upper notochaeta;  
- **e** lower notochaeta;  
- **f** upper neurochaeta;  
- **g** middle neurochaeta;  
- **h** lower neurochaeta;  
- **i** posterior view of a left parapodium of the 14th segment;  
- **j** posterior view of a right parapodium of the 13th segment.  

Scale bars:  
- (a, b, d, e) 2 mm;  
- (c) 1 mm;  
- (f, g, h, i, j) 200 μm.
In turn, the burrows of *U. pugettensis* are inhabited by 15 commensal species, seven of them obligate (Haig and Abbott 1980; Ricketts et al. 1985; Hornig et al. 1989; Fisher and MacGinitie 1928; MacGinitie 1934; Fisher 1946; Hart 1964; MacGinitie and MacGinitie 1968; Butler 1980; Morris et al. 1980; Ricketts et al. 1985; Zmarzly 1992; Jensen 1995; Ruff 1995b; Martin and Britayev 1998, 2018). At the same time, the symbiotic assemblages associated with burrows of large invertebrate burrowers are less completely studied along Asian coasts of the NW Pacific, despite the numerous reports of symbiotic brachyurans and caridean shrimps (Davie 1992; Itani 2002; Itani et al. 2002a, b, 2005; Yamauchi and Konishi 2005; Marin 2008, 2010, 2016; Anker and Marin 2009; Marin et al. 2011; Marin and Kornienko 2014; Henmi and Itani 2014a, b; Henmi et al. 2017), copepods (Miyake 1982; Ho 1928; Anker et al. 2005; Itani et al. 2005; Goto et al. 2017). In

![Fig. 10 Hesperonoe urechis sp. nov.:](image)

- a: elytron of middle part of body
- b: microtubercules on a center of an elytron
- c: posterior view of a left parapodium of the 14th segment
- d: upper thick notochaeta with minute serration
- e: lower thin notochaeta
- f: upper neurochaeta
- g: lower neurochaeta

(Unt) upper notochaeta; (Lnt) lower thin notochaeta; (Unr) upper neurochaeta; (Lnr) lower neurochaeta. Scale bars: (a, b) 2 mm; (c) 1 mm; (d) 200 µm
Fig. 11 Distribution of Hesperonoe japonensis and Hesperonoe urechis sp. nov. in the Sea of Japan and around Japan Islands (upper) and total distribution of known representatives of the genus Hesperonoe in the Northern Pacific (lower)
and Kim 1991; Itoh and Nishida 1998, 2013; Kim 2000; Ijichi et al. 2017), bivalves (e.g., Shoji 1938; Qi et al. 1989; Kato and Itani 1995, 2000; Itani et al. 2002a, b; Kil and Park 2009; Goto et al. 2017), polychaetes (Hong et al. 2017), and fishes (Henmi and Itani 2014a; Henmi et al. 2014). Accordingly, Anker et al. (2005) for echiuroids. The species composition of the symbiotic communities from the NE Pacific is very similar to that from the NW Pacific coasts, at least for echiuroids (Anker et al. 2005). However, a detailed analysis has never been carried out.

Burrows of large invertebrates are very attractive for symbionts as they are stable and long-lasting habitats, which are long-time maintained in good conditions (MacGinitie and MacGinitie 1968). Most specialized symbionts use these burrows as a shelter from predators, but are trophically unrelated with their hosts, except those species that steal food from the spoon worm filtering net (Itoh and Nishida 2013; Henmi and Itani 2014b; Henmi et al. 2017; Burukovsky and Marin 2018).

The symbiotic communities associated with deep-burrowing invertebrates in the Russian waters of the Sea of Japan are also very rich and diverse and still include many undescribed species, as very probably the turbellarian Stylochus/Paraplanocera sp. and the amphipod Lifseborgia sp. (Marin, 2020), while our findings of representatives of Stylochus/Paraplanocera undetermined species, as very probably the turbellarian Phoronis embryolabi, is firstly recorded from the Russian coasts of the Sea of Japan as a symbiont of Urechis unicinctus, as it was previously recorded from only burrows of Upogebia spp. only (Marin et al. 2011). However, the species was previously recorded from burrows of both hosts in Japan (Itani 2002, 2004; Itani et al. 2002a, 2005). Other symbiotic crustaceans were previously recorded from the area (see Marin 2010, 2016; Marin et al. 2011; Marin and Kornienko 2014; Marin and Smelnikov 2016). The horsehoe worm Phoronis embryolabi was described as living commensally inside burrows of the callianassid shrimp Nihonomtrypaea japonica (see Temereva and Chichvarkin 2017), but it is also very abundant in our samples in the sediments around the burrows of Upogebia spp., so we may suggest a symbiotic association with this host too. Moreover, the relative Phoronis species are known as symbionts of burrowing shrimps of the genus Upogebia (Thompson 1972; Santagata 2004).

The species of Hesperonoe are among the most noticeable symbionts of various burrowing invertebrates. Despite the current lack of knowledge on their diversity and ecology, it is possible to conclude that relatively large-sized species, such as H. adventor and H. urechis sp. nov., tend to be associated with spoon worms, while the relatively small-sized species, namely H. complanata, H. coreensis, and H. japonica, tend to live associated with different ghost shrimps (Thalassinidea) (MacGinitie and MacGinitie 1968; Morris et al. 1980; Ricketts et al. 1985; Ruff 1995a; Martin and Britayev 1998, 2018; Sato et al. 2001, 2016; Hong et al. 2017) (see Fig. 11). Usually one single specimen of H. urechis sp. nov. occurs in each burrow, from where other conspecific individuals are actively expelled, likely due to food rather than to space limitations. The scale worm feeds mainly on detritus trapped in the host mucus net (Fisher and MacGinitie 1928; Ricketts et al. 1985), and its particular feeding mode is now being studied using stable isotopes (Marin, unpublished data). This agile worm is rarely, if ever, found outside the innkeepers’ burrows, and often dwells in the immediate proximity of the host. The juveniles associated with burrowing shrimps are commonly attached to the ventral or lateral surface of the thorax or abdomen of the host. As soon as they become adults, they detach themselves from the host carapace to move freely on the inner surface of the host burrow (MacGinitie 1935; MacGinitie and MacGinitie 1968; Sato et al. 2001). Almost all species of Hesperonoe, especially the small-sized H. japonica, H. coreensis, and H. complanata, have a uniform bright red coloring (Sato et al. 2001), probably as a result of being rich in blood pigments like other symbionts living in relatively oxygen-poor conditions (Martin and Britayev 1998, 2018).

As part of this investigation, we were able to obtain molecular genetic data of the species of the polychaete genus Hesperonoe Chamberlin, 1919 (Polychaeta: Polynoidae) for the first time. Several gene markers were amplified, sequenced, and compared. The obtained molecular genetic data (Fig. 12) confirms the relationships between two described species, although they greatly differ in their appearance and size. The divergence for more than 15% by COI mtDNA (e.g., Carr et al. 2011) clearly supports the interspecific differences between the species within the genus Hesperonoe. The genus Hesperonoe is well isolated on the general phylogenetic reconstruction (tree) of the Polynoidae family (Fig. 12) and is associated with a clade including such genera as Harmothoe Kinberg, 1856; Enipo Malmgren, 1865; Gattyana McIntosh, 1897; Eunoe Malmgren, 1865; and Grubeopolynoe Pettibone, 1969. However, the taxonomy of these genera is rather complicated, and many of them could be polyphyletic. Nevertheless, the phylogenetic relationships of the genus Hesperonoe lie beyond the aims of our research. The autapomorphy of the clade Hesperonoe–Grubeopolynoe is the presence of the setae (notosetae) of two types, short blunt and slender tapering.

Finally, we conclude that, in the relatively simple boreal ecosystem, the existence of hidden biodiversity is confirmed by the finding of at least three undescribed species, which correspond to a 30% of the total observed symbiotic species. If we take into account the recent records and redescription of
two species of symbiotic decapods (Marin 2010; Marin et al. 2011) and the recently described phorid species (Temereva and Chichvarkhin 2017), the number of new species discovered in these communities will increase up to 60%. The symbiotic assemblages associated with burrowing shrimps (Gebiidea) and spoon worms (Echiura) are quite different at the species level, but coincident at higher taxa level, which may support a common origin for these associations. There are also clear differences in species composition of the symbiotic assemblages of boreal and tropical ecosystems. Related host species of Upogebia are inhabited by the same species of symbionts with low host specificity in boreal ecosystems (Table 1), whereas the tubes of related host species of Chaetopterus spp. are inhabited by different, although some closely related, associates, showing higher specificity of symbionts in relation to the host in tropical ecosystems (Britayev et al. 2017).

The presence of such diverse symbiotic communities seems not only to be associated with the ability to escape in burrows from predators but also to receive/stain food from their host without leaving holes. Accordingly, we suggest that the symbiotic assemblage may be more abundant and diverse when associated to Urechis unicinctus, as the host feeding can also be a food resource for the symbionts (Fisher and MacGinitie 1928; Anker et al. 2005; Burukovsky and Marin 2018). In turn, the species of Upogebia only pump water through their burrow to filter food particles with their appendages (Dworschak 1981, 1983, 1987; Kinoshita 2002). In fact, the only possibility to obtain food that the symbionts of Upogebia has is either to creep over the host’s body (crabs and polychaetes) or attach on its carapace (the bivalves Neaeromya rugifera (Carpenter, 1864) or the species of the genus Peregrinamor Shōji, 1938 (Mollusca: Bivalvia: Lasaeidae) (Kato and Itani 2000)) to be able to steal the food that gets stuck in the bristles of appendages and body of Upogebia (Fig. 5d, e).

It is also known that symbiotic assemblage is influenced by physical factors and habitat requirements. Species richness and community composition associated with the spoon worm Ochetostoma erythrogrammon Leuckart & Rüppell, 1828 (Annelida: Echiura: Thalassematidae) in the Ryukyu Archipelago, Japan, are greatly influenced by the granulometric characteristics of the sediment, separating them for shrimp- (Alpheus barbatus Coutière, 1897) and scale worm–dominant (Lepidonotus sp.) sites (Goto and Kato 2012).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable. The study is compliant with CBD and Nagoya protocols.

Data availability All data generated or analyzed during this study are included in this published article; analyzed genetic sequences are available in GenBank (NCBI) database.

Author contribution IM conceived and designed research. IM and AT conducted sampling in the Sea of Japan, identified animals, and analyzed data. Both authors read and approved the manuscript.

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