

Feeding Characteristics of Deep-Sea Acorn Worm (Hemichordata, Enteropneusta, Torquaratoridae) from the Bering Sea

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Abstract—Deep-sea hemichordates Torquaratoridae gen. sp. reach high abundance up to 12 spec. m⁻² at the depths of 1830–2130 m on the slope of the Volcanologists Massif in the south-western part of the Bering Sea, dominating in the benthic community at these depths. Their abundance exceeds by two orders the values recorded earlier. In order to clarify this phenomenon, we examined the gut contents of Torquaratoridae gen. sp. The detritus particles and frustules of planktonic diatoms *Thalassiosira*, *Coscinodiscus*, *Actinocyclus*, *Chaetoceros*, *Neodenticula*, and *Grammatophora* were the most common in the gut, as well as the remains of skeletons of benthic invertebrates with little admixture of mineral particles. According to obtained data, Torquaratoridae gen. sp. are mobile deposit feeders with high selectivity to fresh phytodetritus, able to compete with holothurians occupying similar trophic niche. Unusually high abundance of acorn worms is apparently related to high organic matter flux to the seafloor as a result of spring phytoplankton bloom in the surface water layer of the Bering Sea.

Keywords: Enteropneusta, Torquaratoridae, gut contents, Diatomea, deposit feeders, Bering Sea

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In the early 2000s, deep-sea representatives of the hemichordate Enteropneusta were assigned to the new family Torquaratoridae [1–4]. These animals differ significantly both in body structure and lifestyle from other families of Enteropneusta (Ptychoderidae, Spengelidae, and Harrimaniidae), mainly living in shallow waters and having a cylindrical collar region. In deep-sea torquaratorids, the collar region grows laterally, forming wide lateral lips, which are used to collect food from the sediment surface by mucociliary transport [3, 4]. Shallow-water acorn worms usually lead a burrowing way of life, living in U-shaped burrows in the thickness of the sediment. Torquaratoridae are found at wide depth range, from 350 to 4000 m, they are predominantly epibenthic and can even ascend up the water column [1–4]. These are large organisms reaching 28 cm in length [2, 4]. The abundance of torquaratorids at the bottom is usually not high; the previously recorded maximum values are about 10 spec. per 100 m² at the depths of 2712–3954 m [5]. At the same time, the characteristic spiral or “meandering” fecal traces of their vital activity may be a noticeable component of deep-sea bottom land-

scapes [6]. An unexpectedly high number of torquaratorids, up to 12 spec. m⁻², was recently recorded in the Bering Sea on the northern and southern slopes of the Volcanologists Massif at the depths from 1830 to 2290 m [7, 8] (Fig. 1). This indicator was two orders of magnitude higher than the previously observed maximum values. In addition, at this depth, Torquaratoridae gen. sp. dominated in the benthic community, displacing holothurians. The biology of torquaratorids remains poorly understood. The study aims to analyze the feeding peculiarities of Torquaratoridae gen. sp. based on data on the gut contents.

The material was obtained during the 75th (2016) and 82nd (2018) cruises of the R/V *Akademik M.A. Lavrentyev* [7–9] (Table 1).

Specimens of Torquaratoridae gen. sp., which turned out to be a new species (a description will be given in a separate article), were photographed in situ using the Comanche 18 remotely operated underwater vehicle and stored for histological examination in an 8% formalin solution prepared in seawater. The fixative was washed off and the material was dehydrated according to the standard method in alcohols of ascending concentration. Gut contents were studied in two specimens. Fragments prepared for histological examination were embedded in Paraplast blocks and sliced using a Leica RM 2125 microtome to a series of histological slides (10 μm thick). The slides were stained with Caracci’s hematoxylin and eosin alcohol

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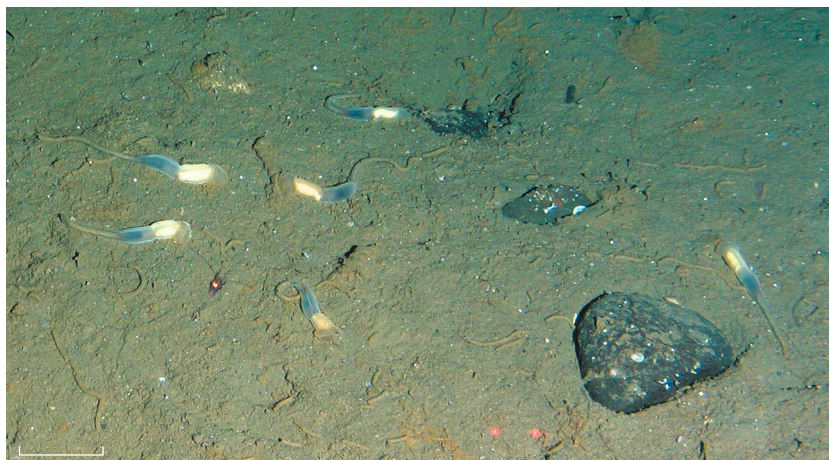


Fig. 1. Torquaratoridae gen. sp. in the natural habitat, on the soft sediments; the southern slope of the Volcanologists Massif, 1933–1953 m. Photo courtesy of the National Scientific Center for Marine Biology of the Far East Branch of the Russian Academy of Sciences; remotely operated underwater vehicle Comanch 18. Scale, 10 cm.

solution. The slides were photographed using a Micmed-6 microscope (LOMO, St. Petersburg, Russia) equipped with an MC-12 digital camera. The slide series is stored in collection under no. 2020-QM-05. The gut contents was studied under a scanning electron microscope (SEM); for this, the material extracted from the intestine was first dehydrated in acetone according to the standard method, dried at the critical point using CO₂ (HCP-2 Critical Point Dryer, Hitachi, 1980) and sprayed with a gold–palladium mixture (EIKO IB-3 Ion Coater, 1980); then it was studied using a JSM-6380LA SEM (JEOL, Japan,

2005) at the *Electron Microscopy in Life Sciences Center for Collective Use*, Moscow State University.

In the post-hepatic intestine section of Torquaratoridae gen. sp., almost the entire volume of the intestine is occupied by a dispersed mixture, consisting of flakes of detritus and the remains of various organisms (Table 2), as followed by the SEM data (Figs. 2a, 2b) and histological analysis (Fig. 2c). Mineral particles are found rarely. No noticeable differences in the composition of the gut contents were observed in the two studied specimens collected at different depths.

Table 1. Stations of collecting Torquaratoridae gen. sp. in the cruises of R/V *Akademik M. A. Lavrentyev*

Cruise no.	Station no.	Sampling date	Coordinates	Depth, m	Figure nos. (present article)
75	LV 75-17	June 27, 2016	55.4609° N 167.2688° E	2289	–
82	LV 82-9	June 18, 2018	55.3451–55.3466° N 167.2750–167.2752° E	1957–1933	1, 2

Table 2. Remains of organisms found in the gut of Torquaratoridae gen. sp.

Group/type of remains	Genera and species	Occurrence on the slides	Figures nos. (present article)
Diatomea	<i>Thalassiosira</i>	Abundant	2a
	<i>Coscinodiscus</i>	Frequently	
	<i>Actinocyclus</i>	Frequently	
	<i>Chaetoceros</i>	Frequently	2b
	<i>Neodenticula seminae</i>	Frequently	
	<i>Grammatophora</i>	Frequently	
Ciliophora (Tintinnina)	<i>Parafavella</i>	Rarely	2c
Demospongiae (spicules)	–	Frequently	
Echinodermata (skeleton fragments)	–	Rarely	
Small scales	?	Frequently	
Faecal pellets		Rarely	
Detritus flakes		Abundant	

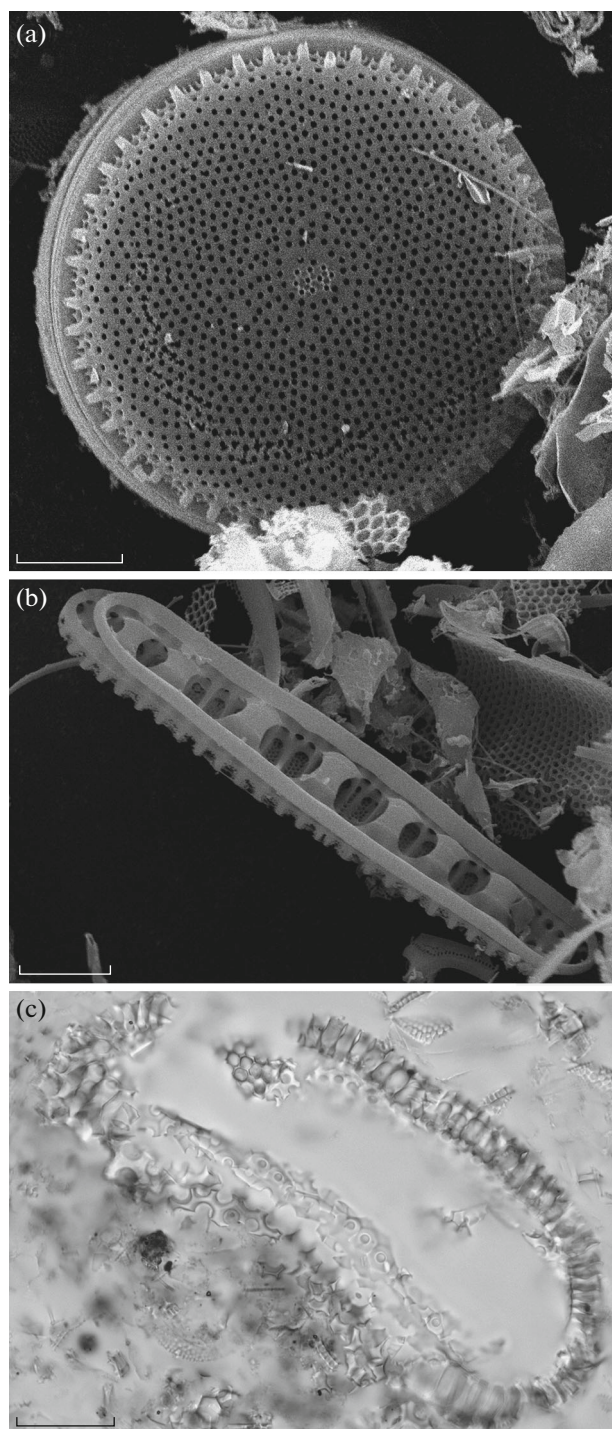


Fig. 2. The remains of organisms most often found in the intestines of *Torquaratoridae* gen. sp. (a) Frustule of the diatom *Thalassiosira* sp. (SEM). (b) Frustule of the diatom *Neodenticula seminae* (SEM). (c) Fragment of the skeleton of the planktonic ciliate *Parafavella* sp. (photo from a histological slide). Scale: (a, b) 5, (c) 30 μ m.

Most often, the diatom frustules are found in the gut contents. The variety of Diatomea is very great; both centric and pennate forms are observed (Figs. 2a, 2b). Among centric diatoms, representatives of the genera

Thalassiosira (Fig. 2a), *Coscinodiscus*, and *Actinocyclus* (class Coscinodiscophyceae) dominate. The frustules of these diatoms are found in the intestines of *Torquaratoridae* gen. sp. both as intact and as cell fragments. Pennate diatoms are represented by the genera *Neodenticula* (Fig. 2b) and *Grammatophora*. In addition to diatoms of the listed genera, forms similar to *Thalassiothrix longissima* and *Rhizosolenia* sp. are found; they dominate by abundance in the surface sediment layer of the Bering Sea along with *Thalassiosira trifulta* [10].

In addition, the finely perforated fragments of the shells of the planktonic ciliates *Parafavella* sp. are found in the gut (Fig. 2c), as well as single spicules of Demospongiae (microsclerae and fragments of macrosclerae, both smooth and spiny), elements of the calcareous skeleton of ophiuroids and holothurians. Some fecal pellets of other animals are also found.

Therefore, the detritus particles and frustules of planktonic diatoms are dominant components of the gut contents of *Torquaratoridae* gen. sp., accompanied by little admixture of mineral particles. Similar main food items were found earlier in the guts of various species of deep-sea holothurians and other detritivores in the Bering Sea [11]. *Torquaratoridae* gen. sp., analyzed in the present study, probably occupy a trophic niche close to epibenthic holothurians [12].

According to the gut contents, torquaratorids belong to detritivores with a high specialization in phytodetritus, the most high-calorie food for deep-sea detritivores, as observed also for sea cucumbers. In addition, torquaratorids may ascend into the water column as the sea cucumbers do, using the intestine contents as ballast, which is “dumped” before moving to new feeding sites in the flow of near-bottom current [5].

The steep slope of the Volcanologists Massif extends from a depth of approximately 350 m down to 4200 m at its base in the Commander Basin. Throughout the slope, benthic communities replace one another, with rather narrow vertical layers occupied by different dominant species [7]. As a rule, these layers extend for 100–300 m each; in the depth range of 400–2300 m, the change of dominant species is accompanied by a change in the ratio of soft and hard sediments, sometimes represented by pebbles powdered with fine sediments [7]. Starting from a depth of about 1400 m and down the slope, sea cucumbers *Synallactes chuni* appear and dominate at soft sediments, torquaratorids begin to play here a noticeable role. At the depth range of 1830–2130 m and down to 2290 m, torquaratorids dominate; *Synallactes chuni* still occur here, but its abundance is low. Below 2290 m, the holothurians, namely, *Paelopatides solea*, is a dominant group again. At the depths of 1830–2290 m, torquaratorides are both abundant on soft sediments and occur on silts with a high content of solid fractions (gravel and rock debris) and on hard substrates [7]. It

is still difficult to conclude on certain features of the biology of poorly studied torquaratorids ensuring their dominance, although in a narrow depth range, but competing for food with holothurians, which prevail almost everywhere on soft sediments at great depths in the ocean [13].

The Bering Sea belongs to the highly productive regions of the world ocean [14]. The spring phytoplankton bloom in the western part of the Bering Sea begins in April and is accompanied by the development of a large number of diatoms with the dominant genus *Thalassiosira* [15]. After the spring peak of the phytoplankton development, an intense flux of organic matter is formed from the surface water layer down to the bottom. The increased content of phytodetritus at the bottom after the spring bloom persists for several months [12] and provides food for numerous populations of detritus feeders, including Enteropneusta.

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COMPLIANCE WITH ETHICAL STANDARDS

All authors have read the final version of the manuscript. All applicable international, national and institutional guidelines for the use of animals have been followed.

CONFLICT OF INTEREST

The authors have no financial or any other conflicts of interest.

REFERENCES

- Holland, N.D., Clague, D.A., Gordon, D.P., et al., *Nature*, 2005, vol. 434, pp. 374–376.
- Holland, N.D., Jones, W.J., Jacob, E., et al., *Zoosystema*, 2009, vol. 31, no. 2, pp. 333–346.
- Holland, N.D., Kuhnz, L.A., and Osborn, K.J., *J. Morphol.*, 2012, vol. 273, no. 7, pp. 661–671.
- Jabr, N., Archambault, P., and Cameron, C.B., *Can. J. Zool.*, 2018, vol. 96, pp. 1221–1229.
- Osborn, K.J., Kuhnz, L.A., Priede, I.G., Urata, M., Gebruk, A.V., and Holland, N.D., *Proc. Roy. Soc. Ser. B*, 2012, vol. 279, no. 1733, pp. 646–1654.
- Jones, D.O.B., Alt, C.H.S., Priede, I.G., Reid, W.D.K., Wigham, B.D., Billett, D.S.M., Gebruk, A.V., Rogacheva, A., and Gooday, A.J., *Deep Sea Res. II*, 2013, vol. 98.
- Rybakova, E., Galkin, S., Gebruk, A., Sanamyan, N., and Martynov, A., *PeerJ*, 2020, vol. 8, e8628.
- Galkin, S.V., Mordukhovich, V.V., Krylova, E.M., Denisov, V.A., Malyutin, A.N., Mikhailik, P.E., Polonik, N.S., Sanamyan, N.P., Shilov, V.A., Ivin, V.V., and Adrianov, A.V., *Okeanologiya*, 2019, vol. 59, no. 4, pp. 687–690.
- Galkin, S.V. and Ivin, V.V., *Okeanologiya*, 2019, vol. 59, no. 1, pp. 153–154.
- Katsuki, K. and Takahashi, K., *Deep-Sea Res. II*, 2005, vol. 52, pp. 2110–2130.
- Sokolova, M.N., *Pitanie i troficheskaya struktura glubokovodnogo makrobentosa* (Nutrition and Trophic Structure of Deep-Sea Macrobenthos), Moscow: Nauka, 1986.
- Witbaard, R., Duineveld, G.C.A., Kok, A., van der Weele, J., and Berghuis, E.M., *Prog. Oceanogr.*, 2001, vol. 50, pp. 423–441.
- Billett, D.S.M., *Oceanogr. Mar. Biol. Annu. Rev.*, 1991, vol. 29, pp. 259–317.
- Sorokin, Yu.I., in *Kompleksnyye issledovaniya ekosistemy Beringova morya: Sb. nauch. trudov* (Integrated Study of the Bering Sea Ecosystem: Collection of Works), Sapozhnikov, V.V., Ed., Moscow: VNIRO, 1995, pp. 264–276.
- Mordasova, N.V., *Okeanologiya*, 1994, vol. 34, no. 4, pp. 557–563.

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