═══════════ **ORIGINAL PAPERS** ═══════════

The Stable Carbon and Nitrogen Isotope Compositions of Larvae of Burrowing Shrimps (Crustacea: Decapoda: Gebiidea and Axiidea) from Vostok Bay, Sea of Japan

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Abstract—Larvae of eight burrowing shrimp species from Vostok Bay, Sea of Japan, were analyzed for their carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope composition. In zoeae I of these species, the δ^{13}C values varied in a range characteristic of planktotrophic organisms, with the average values for larvae of gebiids being lower than for larvae of axiids. The highest δ^{15}N values, comparable to those reported for omnivorous zooplankton, were recorded from larvae of *Leonardsaxius amurensis* and *Boasaxius princeps*. The dominance of phytoplankton in the diet of zoeae I of *Nihonotrypaea makarovi* was indicated by the low δ^{15}N values close to the nitrogen isotope ratio of particulate organic matter. According to the nitrogen isotope composition, the larvae of three *Upogebia* species and two *Nihonotrypaea* species held an intermediate position (with δ^{15}N values ranging from 6.2 to 6.4‰). It was found that the diet of the studied burrowing shrimp larvae does not depend on the taxonomic position, and food preferences differ markedly even in zoeae of congener species, which should be taken into account when cultivating decapod larvae under laboratory conditions.

Keywords: zoea I, Gebiidea, Axiidea, stable isotopes, nitrogen, carbon, Sea of Japan

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INTRODUCTION

Decapod crustaceans are typical inhabitants of marine ecosystems, with their free-swimming planktotrophic larvae (zoea) being an important seasonal component of nearshore meroplankton. In food chains, decapod larvae are consumers of smaller planktonic organisms and are also a food item for predatory zooplankton and fish [31]. However, their dietary preferences remain insufficiently studied to date. Previously, decapod larvae were considered to be exclusively predators [44], but, as has recently been found, they are actually omnivorous, and their diet includes bacteria, pico- to micro-sized phytoplankton, zooplankton from nano- to meso-sized groups, detritus, and fecal granules [12, 14, 41, 45, etc.]. By ingesting a wide range of food particles of various sizes and varying degrees of mobility, decapod larvae show selectivity toward certain species of potential prey [14]. It is also known that small larvae (e.g., penaeid shrimp larvae) depend on phytoplankton assimilation to a greater extent, whereas large ones (e.g., homarid lobster larvae) are carnivorous. The trophic level in larvae of many species changes during ontogeny [29]. The availability and quality of food have an effect on the survivability and growth of decapod larvae [12, 49].

Rearing of larval cultures in the laboratory is a method widely used to study the decapod biology. Description of the morphology of larvae obtained from a female belonging to a certain species allows their identification in plankton, which makes a significant contribution to the study of the biodiversity of decapod crustaceans, especially those living secretive lives. Information on decapod larvae diets was also obtained mainly through laboratory-based studies. The optimum diets and maintenance conditions for rearing aquaculture objects, e.g., palaemonid and penaeid shrimp, are tested on a laboratory-reared culture. It has been shown that the number of zoeal stages in some decapod species may vary depending on feeding conditions [16]. In cultivation of decapods of the suborder Pleocyemata, microzooplankton is usually used as feed for larvae: nauplii of *Artemia* sp. [38], or rotifers *Brachionotus* sp., or, sometimes, larvae of rhizocephalan crustaceans [3, 4], or zoeae of other decapods such as crabs *Uca* spp. [34]. The use of these food organisms made it possible to successfully rear larvae of decapod crustaceans of many species before settling or before the first juvenile stages in laboratory conditions. The high mortality of zoea larvae observed in cultivation of some species may be associated with an improper diet.

Burrowing shrimp of the infraorders Axiidea and Gebiidea play a substantial role in benthic communities due to their lifestyle. When burrowing, they bioturbate sediment, changing its structure and increasing the rate of degradation of organic substances [13, 17, 28, 47, etc.]. Many of them form aggregations with significant densities, which, e.g., in the callianassids *Nihonotrypaea harmandi* and *N. japonica* off the coast of Japan reached 1440 and 340 ind./m^2, respectively [27]; in Russian waters, a density of about 200 ind./m^2 was reported for *N. japonica* [9]. These are quite large animals with high fecundity. For example, the body length of *Upogebia major* may exceed 10 cm, and the fecundity reaches more than 4000 eggs [10]. In view of the above facts, burrowing shrimp are considered a substantial component of seasonal meroplankton. A total of eight species of burrowing shrimp are known from Vostok Bay (Peter the Great Bay, Sea of Japan): *Upogebia major* (De Haan, 1841), *U. issaeffi* (Balss, 1913), and *U. yokoyai* Makarov, 1938 from the infraorder Gebiidea, and also *Leonardsaxius amurensis* (Kobjakova, 1937), *Boasaxius princeps* (Boas, 1880), *Nihonotrypaea japonica* (Ortmann, 1891), *N. makarovi* Marin, 2013, and *N. petalura* (Stimpson, 1860) [7, 8, 32, 33] from the infraorder Axiidea. These species were reared in laboratory cultures by the generally accepted method, using *Artemia* nauplii as feed. As a result, seven species were grown to the megalopa stage [2, 22−26]; however, only the zoea I stage was described from *N. makarovi* due to the high mortality of its larvae observed already in the early stages [21].

In crustacean larvae, the mandibles, as well as the maxillules, maxillae, and maxillipeds, play the major role in sorting and physical processing of food material [46]. The mandibles are the most important mouthparts used for mechanical processing of food. The morphology of the mandibles in adult crustaceans of various taxonomic groups is known to indicate their diet and the method of nutrition. For example, Burukovsky [1], when considering the mandible structure in relationship with feeding habits of adult shrimp, noted that the molar or incisor processes in predators are reduced, while the grinding surfaces of the mandibles are well developed in detritovores. For decapod crustacean larvae, this relationship has been little studied. However, the blunt grinding mandibles are suggested to be characteristic of herbivorous larvae, the presence of sharp teeth on the mandibles indicates carnivorous zoeae, and intermediate forms of the mandibles are found in omnivorous larvae [12]. Our earlier study showed that the mandible morphology in upogebiid zoeae differs significantly from that in callianassid and axiid larvae [5, 6]. An assumption has been made that the differences in the mandible morphology between *Upogebia* and *Nihonotrypaea* may indicate differences in their diets.

The method of stable carbon and nitrogen isotope analysis is increasingly being used as a tool for analyzing the trophic structure of terrestrial and aquatic ecosystems. The contents of the natural heavy isotopes ^{13}C and ^{15}N in tissues is a natural label that allows assessment of the matter and energy exchange between organisms and entire communities. The carbon isotope ratio is used to identify food sources for animals, while the nitrogen isotope composition makes it possible to determine the position of the animals in trophic chains [11, 30].

The goal of the present study was to determine the trophic positions of larvae of eight burrowing shrimp species from the infraorders Gebiidea and Axiidea in the planktonic community using the isotope analysis method, and, based on these data, to clarify whether the morphological features of the mandibles in gebiid and axiid larvae are related to differences in their diets. The obtained information on the feeding characteristics of larvae of certain species is necessary for describing their trophic position in the ecosystem, as well as for culturing decapod larvae in laboratory conditions.

MATERIALS AND METHODS

Plankton samples were taken in the area of the Vostok Marine Biological Station, Zhirmunsky National Scientific Center of Marine Biology, Far Eastern Branch, Russian Academy of Sciences (Vostok Bay, Sea of Japan) in June and July 2019. Zoeae I of the following burrowing shrimp species were sampled for stable isotope analysis: *Nihonotrypaea japonica*, *N. petalura*, and *N. makarovi* (family Callianassidae); *Boasaxius princeps* and *Leonardsaxius amurensis* (family Axiidae); *Upogebia major*, *U. issaeffi*, and *U. yokoyai* (family Upogebiidae). Larvae were identified to species on the basis of morphological traits using an identification key [2]. The main components of the plankton community were selected from the same samples: mysids, copepods, arrow worms, and also particulate organic matter (POM) represented mainly by phytoplankton. Each sample for isotopic analysis consisted of several whole individuals ($n = 7−25$ ind. depending on the size of larvae); the number of samples (N) for certain species of larvae or a zooplankton component varied from 5 to 14 (Table 1). The samples were dried in a drying chamber at 60°C and then stored in a refrigerator at −18°C.

The isotope analysis was carried out at the Laboratory of Stable Isotopes, Far East Geological Institute, Far East Branch, Russian Academy of Sciences, on a FlashEA 1112 organic elemental analyzer coupled via the ConFlo-IV interface with a MAT 253 stable isotope ratio mass spectrometer system (Thermo Finnigan, Germany). Relative contents of heavy isotopes ^{13}C and ^{15}N in the samples were measured as values of the δ notation that describes deviation from the respective isotope principal reference material,

Table 1. The ratios of stable nitrogen (δ^{15}N) and carbon (δ^{13}C) isotopes (mean ± standard error of the mean) in larvae of burrowing shrimp from Vostok Bay, Sea of Japan

Species	Species index	N	δ^{15}N, ‰	δ^{13}C, ‰
Boasaxius princeps	Bp	6	8.0 ± 0.5^{a}	$-19.4 \pm 1.3^{c,\ d}$
Leonardsaxius amurensis	La	9	7.2 ± 0.3^{b}	$-20.6 \pm 0.4^{b,\ c}$
Nihonotrypaea japonica	Nj	8	6.4 ± 0.2^{c}	-19.2 ± 0.5^{d}
Nihonotrypaea makarovi	Nm	5	5.3 ± 0.4^{d}	$-20.6 \pm 0.4^{b,\ c,\ d}$
Nihonotrypaea petalura	Np	5	6.2 ± 0.1^{c}	$-19.3 \pm 0.1^{c,\ d}$
Upogebia issaeffi	Ui	8	6.2 ± 0.2^{c}	-21.0 ± 0.3^{b}
Upogebia major	Um	14	6.3 ± 0.2^{c}	$-21.6 \pm 0.9^{a,\ b}$
Upogebia yokoyai	Uy	10	6.2 ± 0.2^{c}	-22.4 ± 1.5^{a}

Here, N is thenumber of samples taken for analysis; mean values with the same letter indices do not differ significantly ($p > 0.05$, ANOVA Post-hoc HSD test).

expressed in terms of parts per thousand (‰) of the respective standard of isotope composition:

$$\delta X\,(‰) = \left[(R_{sample} - R_{standard})/R_{standard}\right] \times 1000,$$

where X is the stable isotope ^{13}C or ^{15}N, and R is the ratio of isotope contents (^{13}C/^{12}C or ^{15}N/^{14}N). All the δ^{13}C and δ^{15}N values below are presented with respect to the international standards of isotope composition (Pee Dee Belemnite for δ^{13}C and atmospheric nitrogen for δ^{15}N).

The following standards were used for calibration: IAEA CH-6, NBS-22, IAEA N-1, and IAEA N-2 (International Atomic Energy Agency, Vienna). Values of δ^{13}C and δ^{15}N were measured to an accuracy of ±0.10‰. The data of isotope analysis are presented as mean value for several samples (N) of larvae of the same species ± standard error of the mean (SE). The standard error of the mean is shown in figure as whiskers. The significance of differences in the obtained values was tested by the analysis of variance (ANOVA). Statistical processing of the data was carried out using the STATISTICA 8.0 and Microsoft Office Excel packages.

RESULTS

The results of the isotope composition analysis of all the burrowing shrimp larvae samples ($N = 65$) showed a range of carbon isotope ratios of 6.9‰. Variations in δ^{13}C values in larvae were determined by the species of the samples (F = 16.649, $p < 0.0001$). The mean δ^{13}C values for all the studied species ranged from −22.4 to −19.2‰. The highest mean δ^{13}C values were recorded from larvae of the callianassids *Nihonotrypaea japonica* and *N. petalura* (−19.2 and −19.3‰, respectively).

Comparable δ^{13}C values were obtained for zoeae I of *Boasaxius princeps*. Larvae of all the *Upogebia* species showed the lowest mean δ^{13}C values: from −22.4‰ in *Upogebia yokoyai* to −21.0‰ in *U. issaeffi* (Table 1). In the zoea samples of the callianassid *Nihonotrypaea makarovi* and the axiid *Leonardsaxius amurensis*, the carbon isotope ratios were equivalent and had an intermediate value of −20.6‰.

The larval samples of the studied burrowing shrimp species also differed in their nitrogen isotope composition, with the mean δ^{15}N values varying from 5.3 to 8.0‰ (F = 35.952, $p < 0.0001$). The range of variations in nitrogen isotope ratios was 3.9‰. The highest δ^{15}N values were recorded from larvae of the axiids *B. princeps* and *L. amurensis*, 8 and 7.2‰, respectively; the lowest values were from the callianassid *N. makarovi*. Zoeae I of the callianassids *N. japonica* and *N. petalura* showed intermediate δ^{15}N values (6.4 ± 0.2 and 6.2 ± 0.1‰, respectively), and thus differed little in nitrogen isotope composition from larvae of *Upogebia major*, *U. issaeffi*, and *U. yokoyai* (Fig. 1, Table 1).

The carbon isotope composition of the samples of the main plankton community components varied from −22.7 to −20.6‰. The nitrogen isotope composition also varied markedly between the samples, which apparently reflected the position of the objects under study in the trophic hierarchy. For the POM samples that represented a mixture of primary producers, the mean δ^{15}N values amounted to 5.1 ± 0.4‰; for arrow worms, which belong to the predatory component of zooplankton, the values reached 9.2 ± 0.3‰; and for omnivorous zooplankton (small copepods and mysids), intermediate δ^{15}N values were obtained, 7.4 ± 0.1 and 7.6 ± 0.1‰, respectively (Fig. 1).

DISCUSSION

Information about the environmental factors that influence the duration of development and growth of marine invertebrate larvae is important for under-

standing the processes of survival and distribution of larvae and also for identifying the relationships between populations and dynamics of their recruitment. The availability and quality of food is one of the most crucial factors that determines the success of larval development [12, 16, 41, 49]. Most information about the diets of decapod larvae was obtained through laboratory studies, where larvae were fed a diet (often excessive) consisting of certain species of cultured phyto- or zooplankton or a mixture of both. It is obvious that in a natural habitat, where the availability of suitable food organisms varies significantly due to the temporal and spatial patchiness of plankton distribution, decapod larvae use a wider range of food items to meet their energy expenditures: dissolved organic matter, detritus, bacteria, microalgae, protozoa, and zooplankton. This significantly extends the range of opportunities for optimal food selection by different larval forms and stages [12].

Little is known about the diets and food selectivity of burrowing shrimp larvae of the infraorders Gebiidea and Axiidea under natural conditions [14, 42, 45]. As a molecular analysis of gut contents of zoea *Upogebia* spp. from the plankton collected in the English Channel has shown, *Upogebia* larvae are omnivorous and consume a wide range of prey of various sizes and varying degrees of mobility [14]. In experiments of the same study based on the flow cytometry method, the cultured *Upogebia* larvae that were fed various microalgae showed selectivity toward some of them; in addition, they ingested small cells, including nano- and picoplankton.

A study of the functional morphology of the mouthparts and digestive tract contents in larvae of the callianassid *Nihonotrypaea harmandi* confirmed that zoeae of this species can regularly feed on phytoplankton, in particular diatoms [42]. It should be noted that the complete ontogeny of *N. harmandi* was first described from results of laboratory-based experiments where larvae were fed rotifers or *Artemia* nauplii [20, 43]. In later experiments, zoeae that were fed microalga *Chaetoceros gracilis* also successfully reached the megalopa stage [45]. Early zoeal stages of *N. harmandi* occur, as a rule, below the chlorophyll maximum layer. Isotope analysis showed a mean $\delta^{13}C$ value for them of $-18.3‰$ and a $\delta^{15}N$ value of approximately $6.0‰$, which corresponds to a diet consisting of phytoplankton and sinking phytodetritus with heterotrophic protozoans present on it [45].

According to our data, in the larvae samples of the three studied *Upogebia* species from Vostok Bay the nitrogen isotope ratios were similar, being lower than those for omnivorous zooplankton, but higher than for POM. Consequently, like *Upogebia* larvae in the plankton from the English Channel, they can consume a variety of foods including phytoplankton of various sizes and protozoans.
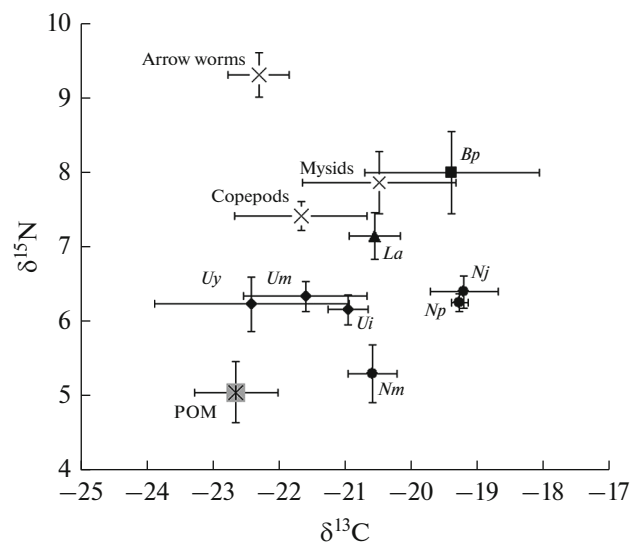
Fig. 1. The ratios of stable carbon and nitrogen isotopes (mean ± standard error of the mean) in zoeae I of eight burrowing shrimp species of the infraorders Gebiidea and Axiidea and the main components of the plankton community in Vostok Bay, Sea of Japan. For species indexes, see Table 1; POM, particulate organic matter.

Among the callianassid larvae samples that we studied, the nitrogen isotope ratio in larvae of *Nihonotrypaea japonica* and *N. petalura* was higher by $0.1—0.2‰$ than the values obtained for *N. harmandi* [45]. In zoeae I of *Nihonotrypaea makarovi*, this ratio was, vice versa, lower by $0.7‰$ and close to the $\delta^{15}N$ value that we obtained for POM ($5.1 ± 0.4‰$), which indicates the dominance of the plant component in the diet of *N. makarovi* larvae. As in *N. harmandi* larvae [42], the remains of pennate diatoms and traces of abrasion of the masticatory surface of the molar process were found on the mandibles of zoeae I of *N. makarovi* [5], which also suggests that larvae of this species are herbivorous.

The larvae of the axiids *Boasaxius princeps* and *Leonardsaxius amurensis* that showed the highest $\delta^{15}N$ values among the studied species of the plankton community occupied a trophic position corresponding to organisms of omnivorous zooplankton (copepods and mysids) (Fig. 1). Both species, as well as *B. princeps,* whose development includes eight zoeal stages (larvae reached the megalopa stage within 38 days after hatching), were successfully reared in the laboratory [24, 26]. This was probably facilitated by a diet close to natural, with recently hatched nauplii of *Artemia* sp. used as feed. As the results of the isotope analysis showed, the natural diet of the studied *Upogebia* larvae, as well as those of the callianassids *N. japonica* and *N. petalura* (with $\delta^{15}N$ values within a range of $6.2—6.4‰$), differs markedly from the diet of larvae of *B. princeps* and *L. amurensis*. However, *Artemia* nauplii were also successfully used as feed for culturing

larvae of these species [18, 19, 22, 23, 25, 35]. In this case, the success was probably facilitated by the excessive concentration of food in the culture or by the presence of microorganisms, along with zooplankton, in the larval culture, which partially satisfied the needs of larvae for food at the initial stages of zoea development. The challenges in the cultivation of *N. makarovi* larvae arose, among other things, due to the fact that such a diet turned out to be unacceptable for them: according to the results of the isotope analysis, larvae of this species prefer plant food.

The carbon isotope composition analysis of all 65 samples of burrowing shrimp larvae showed that the carbon isotope ratios in them remained within the limits characteristic of nearshore planktonic organisms, but, nevertheless, had quite a great range of variations. The lowest $\delta^{13}C$ values were in larvae of *U. major*, *U. issaeffi*, and *U. yokoyai*. The carbon isotope ratios in larvae of all the studied axiids were higher than in *Upogebia* larvae and varied within a range from $-20.6‰$ for *N. makarovi* and *L. amurensis* to $-19.2‰$ for *N. japonica*. The marked differences in carbon isotope ratios may indicate different food sources for the animals [36]. For example, decapod larvae can consume various phytoplankton species or dead microalgae cells at different degrees of degradation [45]. We did not preliminarily degrease the larval samples; therefore, the recorded variations in the $\delta^{13}C$ values can probably indicate, to some extent, the differences in the lipid content of tissues between the studied organisms [37]. However, as is known from literature, the lipid content of decapod larvae is low: e.g., in zoea larvae of the spider crab *Maja brachydactyla*, lipids account for $1.72 \pm 0.25\%$ of the dry weight [40]; in larvae of the rock lobster *Jasus edwardsii*, lipids make up 7.9 to 12.5%, depending on the ontogeny stage [39].

The structure of food webs in an aquatic habitat is closely related to the body size of their constituent organisms. Body size largely determines the trophic level of consumers and their prey [48]. The size of decapod larvae also often determines their trophic position in planktonic food webs: small larvae usually feed on phytoplankton, while large ones feed on zooplankton [30]. According to the previously obtained data, zoeae I of the burrowing shrimp that we studied can be arranged into the following size series: *L. amurensis* >*N. makarovi* > *B. princeps* > *U. major* > *N. japonica* > *N. petalura* > *U. issaeffi* > *U. yokoyai* [2, 21−26]. This generally reflects their positions in the food web, with the exception of *N. makarovi* larvae, whose diet is dominated by the plant component despite their rather large size.

The assumption that differences in the mandible morphology of larvae of *Upogebia* and *Nihonotrypaea* indicate differences in their diets has not been confirmed, since, according to the results of the isotope analysis, larvae of three *Upogebia* and two *Nihonotry-paea* species formed a group with very similar $\delta^{15}N$ values. Nevertheless, in axiid and callianassid larvae, which have a common pattern of mandible structure, these values differed markedly. The congener species *N. makarovi* and *N. japonica* do not differ in the morphology of zoea I mandibles [5]; however, their $\delta^{15}N$ values were 5.3 ± 0.4 and $6.4 \pm 0.2‰$, respectively. Consequently, the mandible structure in larvae of the burrowing shrimp species under study does not reflect the characteristics of their diet. Previously, it was suggested [15] that decapod larvae have taxon-specific sets of traits in the mandible structure that can be used to clarify the phylogeny of their species. Our studies have confirmed that dietary features do not conceal the phylogenetically significant morphological characteristics of mandibles in decapod larvae.

Thus, according to the data we obtained, the carbon isotope composition of zoeae of the decapod species under study varied in a range characteristic of planktotrophic organisms; however, the $\delta^{13}C$ values in the studied axiid species were higher than in *Upogebia*. The highest $\delta^{15}N$ values, comparable to the data reported for omnivorous zooplankton, were obtained for larvae of *L. amurensis* and *B. princeps*. The low $\delta^{15}N$ values recorded from zoeae of *N. makarovi* were close to the nitrogen isotope ratio in POM and indicated the dominance of phytoplankton in the diet. Larvae of three *Upogebia* and two *Nihonotrypaea* species held an intermediate position (with $\delta^{15}N$ values from 6.2 to 6.4‰). It can be concluded from the above facts that the diets of the burrowing shrimp larvae we studied do not depend on the taxonomic position of the species. The structure of the larval mouthparts, in particular, the mandibles, does not always reflect their food preferences, since diet may differ markedly even in zoeae of congener decapods, which should be taken into account when cultivating them in laboratory conditions.

COMPLIANCE WITH ETHICAL STANDARDS

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

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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