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MARINE BIOLOGY

Distribution, Reproduction, and Feeding of West African Shrimp *Plesionika carinata* Holthuis, 1951 (Decapoda, Pandalidae)

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Abstract—*Plesionika carinata* is endemic in the West African tropical biogeographical realm and is distributed from the western Sahara coast (23°35′ N) to southern Namibia (29° S). A total of 263 individuals with a total carapace length of 31 to 71 mm have been studied. *P. carinata* juveniles are pelagic and occur over depths from 340 to 2000 m or more, mainly over the lower part of the continental slope in summer and over the upper part of the continental slope in autumn. Adults are mainly benthic and occur on the edge of the shelf and the upper part of the continental slope (at depths of 300 to 880 m). Ovigerous females have 750 to 3330 eggs 0.45–0.5 × 0.5–0.65 mm in size on pleopods. *Plesionika carinata* feeds on abundant micronectonic and macroplanktonic crustaceans (euphausiids and pelagic shrimps) at earlier pelagic stages; it is detritophagous/necrophagous and predatory near the bottom when adult.

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Plesionika carinata is an endemic in the West-African tropical biogeographical realm [5]. The waters of western Sahara (23°35′ N) are the northern boundary of its distribution [2, 8, 13] and the waters of Namibia (29° S) are the southern boundary [8–10, 14]. The low level of total knowledge of the species, including its feeding habit, determined the necessity of this research.

MATERIAL AND METHODS

We collected the majority of our materials on the biology of *P. carinata* during a cruise of the R/V *Evrika* in Namibia and Angola. In addition, shrimps were also caught in the waters of Namibia during a cruise of the R/V *Bakhchisarai* and in the southern part of the western Sahara during a cruise of the R/V *Belogorsk* (Table 1). During cruises of the R/V *Professor Stockman* and *Akademik Kurchatov*, also carried out in Namibia, the material was collected using an RTAK-Samyshev pelagic trawl (Table 1). To characterize the bathymetric distribution of *P. carinata* according to bottom trawled materials, we used the collections of several AtlanNIRO research cruises (Table 1).

Over 500 stomachs were dissected to study the food composition in *P. carinata*. Food was found in 263 of them, and 137 stomachs were full.

Prior to studying the stomach contents, shrimps were subjected to biological analysis [4], which included the measurements of the total carapace length, as well as sex determination, determination of the gonad maturation stage in females, and determination of stomach filling points.

The total carapace length was measured from the posterior margin of the eye sockets to the end of the telson with an accuracy of up to a tenth of a millimeter. The sex was determined according to secondary sex characteristics (by the shape of endopodites of pleopods 1, as in all pandalid shrimps), and the gonad maturation stages were determined according to a five-point scale [4]. Stomach filling and food composition of stomachs were studied using the method described in [6]. Depending on the amount of food in the stomach, the ratio of the components in the food bolus was estimated differently. The presence of certain prey was determined in all food-containing stomachs, and these data were used to calculate the frequency of their occurrence (the percentage of stomachs in which a certain prey or component was found in the total number of studied stomachs containing food). In full stomachs, which were estimated at filling point 3 (see below), the volume ratios of the food bolus components were visually determined with an accuracy of up to 10%. We selected full stomachs, since this allowed us to avoid the effect of differently emptied stomachs on the result of assessment of different levels of digestibility of food remains. Prey or other components of the food bolus the share of which was less than 10% were simply listed. According to these data, the reconstructed average or virtual food bolus was then calculated [6].

In addition, we determined the average number of prey in the stomach (the Froerman coefficient, FC [7]). It is calculated as the sum of all frequencies of occurrence of food items (sand or something like sponge

Table 1. Volume of materials used in study

Area (geographical latitude)	Vessel	Sampling period	Number of catches	Depth range (m)
For biological analysis and food composition (bottom catches)				
08°25′ S	R/V *Evrika*	December 8, 1982	1	400
11°44′ S	R/V *Evrika*	December 1982	1	425
17°32′–23°59′ S	R/V *Evrika*	January 23–February 5, 1983	1	310–425
19°16′–20°43′ S	R/V *Bakhchisarai*	January 18–January 25, 1986	2	420–426
21°03′ N	R/V *Belogorsk*	November 11, 1980	1	770–780
For biological analysis and food composition (pelagic catches)				
19°56′–19°53′ S	R/V *Professor Stockman*	April 18–June 16, 1985	33	over 415–550, from 50 to 200
17°30′–20°51′ S	R/V *Akademik Kurchatov*	January 23–January 31, 1986	19	over 690–2330 from 100 to 750
For description of bathymetric distribution according to bottom trawling data				
23°56′–21°00′ N	Fishing freezer trawler (FFT) *Belogorsk*	October 19–November 12, 1980	62	29–1230
11°56′–10°45′ N	FFT *Belogorsk*	March 3–March 9, 1981	36	13–735
08°59′–04°10′ N	FFT *Belogorsk*	January 16–February 20, 1981	117	13–805
20°32′–16°06′ N	Medium fishing freezer trawler (MFFT) *Strelnya*	November 20–December 9, 1987	75	18–342
20°32′–16°06′ N	MFFT *Strelnya*	January 23–February 11, 1988	54	26–805
20°32′–16°06′ N	Freezer seiner trawler *Atlantida*	August 9–September 21, 1988	91	100–857
02°32′ N–11°47′ S	Atlantic fishing freezer trawler *Fiolent*	January 15–May 20, 1976	168	22–1160
17°00′–34°00′ S	Large fishing freezer trawler *Gizhiga*	December 5, 1975–January 16, 1976	147	100–1260
17°22′–28°20′ S	Super fishing freezer trawler *Vol’nyi veter*	January 13–February 13, 1986	98	124–490

spicules are not included here), which is divided by 100. For this, all stomachs with food are used, irrespective of the level of their filling.

The prey were calculated and measured using the ruler of the eyepiece micrometer of a binocular loupe with the maximum allowable accuracy, depending on lens magnification. Since shrimps significantly grind their them, it is by no means always possible to fully measure prey. For this purpose, we usually used those parts of the body (primarily, skeletal elements) that can be measured (e.g., scale, crystalline lens, otoliths, or vertebrae in fish, chaetas in chaetognathans and annelid worms, statoliths in mysids, etc.).

RESULTS

Bathymetric distribution. *P. carinata* occurs both in benthic and pelagic gears; therefore, we describe the bathymetric distribution of the species separately with respect to different fishing methods.

The total range of vertical distribution of *P. carinata* in benthic trawl catches varies from 300 to 880 m (Fig. 1), although the real limits of the bathymetric distribution of this species on the bottom are smaller. For instance, in the waters of Mauritania, it occurred only twice at depths of less than 500 m and five times at a depth of over 700 m; the catch was two to three individuals per hour during trawling in both cases. At depths of 600 to 700 m, this species occurred only three times in amounts less than ten specimens per catch. In all the other trawls, the number of shrimps varied from 10 to 375 specimens. In the waters of Mauritania, the central eastern Atlantic, and Angola, the frequency of occurrence of *P. carinata* in this depth range was 100% and it was among the dominant species of the taxocene of shrimps on the upper part of the continental slope [1, 3, 11]. According to the results of

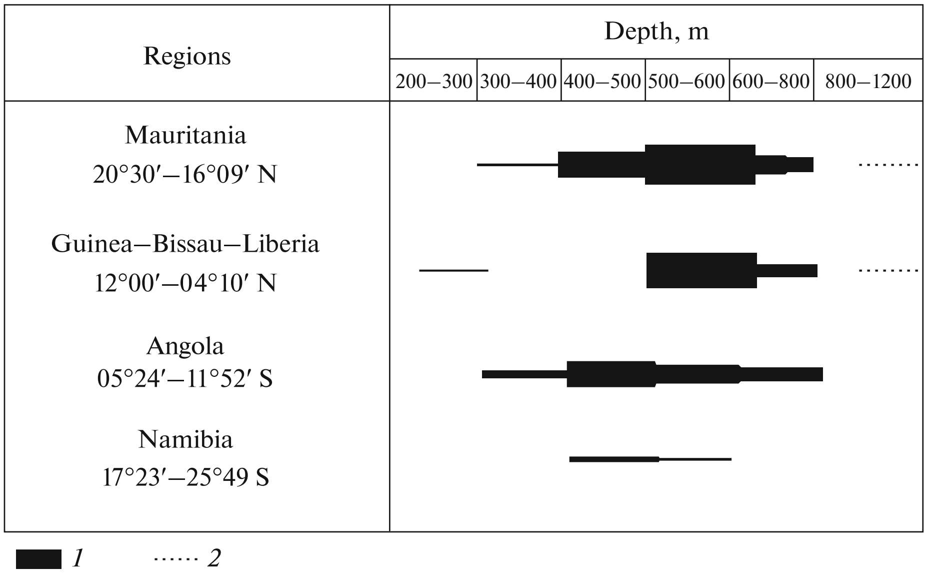

Fig. 1. Bathymetric distribution of *Plesionika carinata* according to results of benthic trawling (frequency of occurrence): (*1*) frequency of occurrence 100%, (*2*) trawling not performed in this region at these depths.

bottom catches, the vertical distribution range of *P. carinata* sharply narrows in the waters of Namibia, at the southern borders of the range. It occurred here only at depths of 395 to 420 m, and the frequency of its occurrence did not exceed 20% [8–10].

Meanwhile, shrimps occurred in pelagic catches in this region. In summer 1985, they occurred over all depths from 340 m; however, they were most frequently found far from the shore in the zone influenced by the Benguela current over depths of more than 2000 m (Fig. 2a) and at depths of 100 to 500 m, mainly at 200 m (Fig. 2b); as a result, they got under its current, the boundary of which is at depths of 100 to 110 m [7]. In late autumn (May) 1986, shrimps stayed closer to the shore, over the upper part of the continental slope over depths of 600 to 800 m (Fig. 2a). This means that shrimps move from deeper lying horizons to a depth of 50 m during this period (Fig. 2b).

Brief Biological Characteristics. The biological characteristics were based on materials taken from Namibia (17°30′–23°59′ S). This is the southern periphery of the *P. carinata* range; however, the material was collected using both benthic and pelagic gears. The size of shrimps from bottom catches collected during summer in the southern hemisphere (December to February) (total length) was 31 to 71 mm (31 to 65, mode 52 mm, in males and 30 to 71, mode 57 mm, in females). Almost 73% of females had gonads at mature stage II. Only 7% of females were at the maturation stage (mature stage III–V), and none of these females had eggs on pleopods. Consequently, these shrimps mainly had the feeding period.

In pelagic gear-based catches, the size of shrimps varied from 17 to 68 mm. Secondary sex characters were not found in male individuals with a length of less than 31 mm; therefore, most shrimps were referred to as immature individuals. During dissection, the female gonads were actually at mature stage I. Only nine of the 59 studied individuals had gonads at matu-

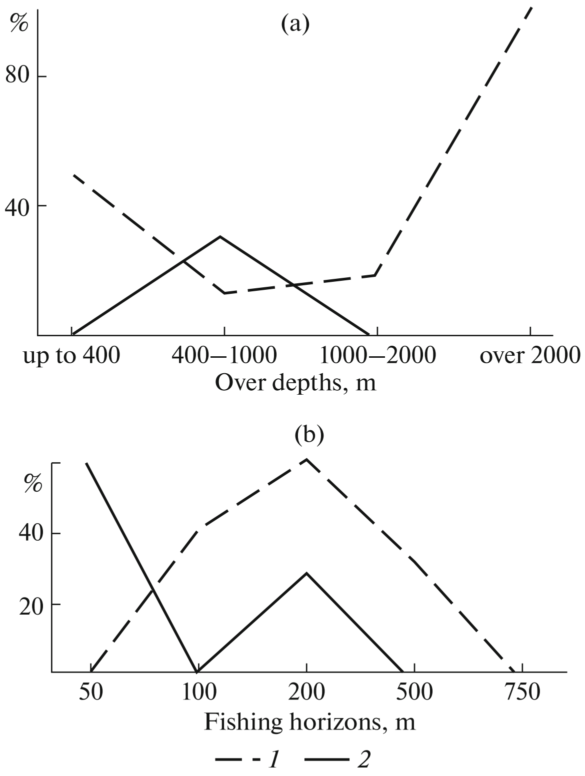

Fig. 2. Bathymetric distribution of *Plesionika carinata* in pelagic zone. (a) Horizontal distribution (the higher the depth, the farther from shore), (b) vertical distribution horizons (frequency of occurrence). (*1*) Summer; (*2*) autumn.

rity stage II and only four of them (with a carapace size of 59 to 68 mm) had eggs on pleopods that had just been laid. They were caught over the continental slope (over depths of 800 and 1500 m at a distance of approximately 600 to 800 m from the bottom in both cases). Ovigerous females had 750 to 3330 eggs with diameters of 0.45–0.5 × 0.5–0.65 mm on pleopods.

Description of Food Remains. The most noticeable component of the contents of *P. carinata* stomachs is detritus. It is a loose gray or olive–brown mass, sometimes with a clear greenish color, which is easily dispersed in a water drop but sometimes has a slightly gellike texture. Under the microscope, this mass appears to consist of very small shapeless particles, among which empty cnidae and diatom skeletal debris can be found. The basic mass maintains its poor granularity even at ×900 magnification. It often includes accumulations of tabletlike greenish irregularly shaped bodies of possibly bacterial origin. This basic mass embodies a large amount of finely fractured material that is, however, slightly coarser than the above-mentioned material. It includes small foraminifers (globigerines), tintinoidea shells, cnidae, radiolarians, fragments of sponge spicules (an intact spicule was never found), sand particles, chewable appendages of euphausiid mandibles, crustacean chaetae, shapeless chitinlike fragments and fragments of skeletal plates from echinoderms, and frayed fish scales. The fact that our material was collected on the edge of the shelf, mainly in arid zones with the dominance of biogenic sedimentogenesis (see [3, 6]), suggests that shrimp fed on autochtonous detritus, which can reach even larger depths in areas with high productivity of the pasture trophic chain [12, 16].

The other components of the food bolus can be divided into two groups, depending on the state of their remains. These are primarily euphausiids, among which we were able to identify only *Thysanopoda* sp. They occurred both as sometimes rather numerous (up to ten specimens) chewing surfaces of detritus-enclosed mandibles with a diameter of 0.5 mm and as intact clean individuals with a length of 13–20 mm. In the latter case, detritus was always absent in shrimp stomachs. All transitions from crustaceans that were simply torn to pieces or were semidigested to clearly semidamaged crustaceans enclosed in detritus at different depths were observed between these states. In the first case, one specimen of freshly caught euphausiids and the remains of two to three semidigested individuals could be seen. In the second case, it was particularly interesting to find an absolutely intact, but squashed and seemingly chewed phausiid. The shrimp seemed to have eaten an individual that had recently died.

The shrimps eaten by *P. carinata* included representatives of four families: Sergestidae (fragments of carapaces without soft tissues), Oplophoridae (fragments of juvenile *Oplophorus novaezealandiae* de Man, 1931), and Pasiphaeidae (*Pasiphaea semispinosa* Holthuis, 1951) individuals, which were freshly eaten and always present in an amount of one specimen per stomach (the length was 30–40 mm), and Pandalidae (leaflike scales from the surface of the carapace typical of the genus *Plesionika* or body fragments that sometimes occupy the entire stomach volume; this can hardly indicate cannibalism; it is more likely that they had been trawl feeding). All shrimps except the unknown Plesionika are obligate pelagic.

Fish remains were found in the stomachs as an accumulation of scale fragments together with detritus or as bones, e.g., the head bone, but without pronounced soft tissues in one case. Judging by the teeth, these were the remains of predatory fish (a small species or, more likely, juveniles). It was possibly eaten dead.

The remains of squids (the family Enoploteuthidae) were presented as fragments of tentacles with a length of 14 and 20 mm. They were probably captured being already in the trawl and, therefore, could not be referred to food components [14].

Copepods (*Pleuromamma* sp.) that were eaten alive were found in the stomachs of *P. carinata* caught with a pelagic trawl.

All other food components occurred as small fragments or separate skeletal remains (e.g., typical chelae of crustaceans from the order Tanaidacea).

Food Spectrum. With respect to the frequency of occurrence, the food of *P. carinata* (Table 2) is completely and equally dominated by euphausiids and detritus, which are found in almost every stomach (73 and 68.1%, respectively). Foraminifers occur three times less frequently. Since these are planktonic globigerines, it can be assumed that they are a constituent part of detritus, where they entered after the death of the shell host. Shrimps, fish, copepods, and chaetognathans occur six to seven times less frequently or even more rarely. The other numerous items represented a constituent part of detritus (see above) or should be considered as random food items.

The virtual food bolus is generally formed by three food items: euphausiids (occupying almost half of the bolus), detritus (which is slightly less than one-third of its volume), and shrimps (13% of the volume of the food bolus). Collectively, they make up almost 90% (87.9) of its volume. Fish occupy 2.9% of the volume. The remaining approximate 7% is occupied by nine food items (see Table 2), which rarely occurred; however, they occupied no less than 10% in certain food boluses.

These three main food items also dominate most frequently in full stomachs, reaching 60% of their volume or more.

Unfortunately, little material was available for studying the ontogenetic variability in the food composition, since almost a half of all the collected shrimps have a size of 50 to 59 mm and there were too few smallest and largest individuals. Therefore, all the

Table 2. Food composition in shrimp *P. carinata*

Food items	Frequency of occurrence, %	Value in virtual food bolus, %	Frequency of dominance in food bolus, %
Euphausiids	73.0	45.8	47.4
Detritus	68.1	29.1	21.2
Foraminifers	19.2	–	–
Shrimps	12.2	13.0	11.2
Fish	10.6	2.9	2.2
Fish scale	9.9	0.4	–
Copepoda	7.2	0.8	0.7
Chaetognathans	7.2	0.3	–
Echinoderms	4.6	–	–
Tintinoidea	3.4	–	–
Cnidarian	2.7	–	–
Isopoda	1.9	1.4	–
Squid	1.1	1.3	–
Drip fat	1.1	0.2	–
Tandaidacea	0.4	–	–
Polychaete	0.4	0.1	–
Amphipoda	0.4	–	–
Radiolaria	0.4	–	–
Unidentified remains	5.3	2.8	0.7
Sand particles	14.1	0.7	–
Sponge spicules	10.3	–	–
Total stomachs	263	138	138
Froerman coefficient	2.31	Frequency of dominance 84.9	

shrimps had to be roughly divided into three size groups. As a result, only the following trend in ontogenetic changes in the composition of food components is observed.

Constantly high, the frequency of euphausiid occurrence (Fig. 3) exhibits only a low trend towards its increase in larger shrimps. The share of euphausiids in the virtual bolus decreases by 10% in large shrimps. Twofold changes in the share of eaten shrimps in the virtual food bolus are also observed. The frequency of occurrence and share of detritus also decrease in the food boluses, but this decrease is low.

At the same time, the share of fish is increased in the diet of *P. carinata*. Changes in the frequency of occurrence of other food items are more or less chaotic. One can only note that the frequency of occurrence of sand particles and foraminifers has the same variations as that of detritus, which is quite natural if we assume that shrimp captured them by chance together with detritus.

DISCUSSION

It can be stated that *P. carinata* is a heterotrophic animal that is bathypelagic at the early stages of ontogenesis. It can be classified as a benthopelagic species. This species can also leave bottom layers for spawning. In the waters of Namibia, *P. carinata* penetrated further south (probably together with the Angolan current) in the summer when the material was collected. Spawning presumably falls in summer, when shrimp can be found over all (often large) depths from 340 to more than 2000 m. By contrast, it stays over the upper part of the continental slope in autumn. The short observation period did not provide sufficient material for more precise characteristics of its ontogenesis; however, these short-term observations make it possible to explain some features of the food composition in *P. carinata*.

The trophic character of *P. carinata* is controversial. It combines the features of detritophage, necrophage, and, partly, attacking predator. Judging by the single stomach, which is more than 60% filled with copepods, *P. carinata* can also act as a grazing predator [6]. Both the Froerman coefficient, which is 2.31, and the dominance coefficient, which approaches 100% (i.e., almost every full stomach has one food item occupying no less than 60% of the volume of the food bolus), reflect this variety of *P. carinata* to a certain extent [6]. Presumably, this is because the shrimp attacks living prey when in the water column and prefers dead bodies and detritus when at the bottom.

This results in a paradoxical pattern: the combination of a rather long list of food items that were found in the food boluses with the absolute dominance of only three of them: detritus, euphausiids, and shrimps. If we also take into account that detritus is a benthic food item, while euphausiids and shrimps found in the stomachs are microplankton or micronecton dwellers, the paradoxicality of the trophic character of *P. carinata* is even more apparent. This emphasizes the ecological portrait of a sharply heterotrophic animal that exhibits the same activity in hunting for macroplanktonic crustaceans in the water column and for juvenile micronectonic crustaceans and feeds on detritus and dead bodies of the same pelagic prey at the bottom.

At the current level of knowledge (we have collections that were sampled only in summer), it can be stated that *P. carinata* is an opportunist predator that combines detritophagy and necrophagy with the hunting strategy of an attacking predator throughout its life. At the early stages of ontogenesis, *P. carinata* is significantly more closely related to the pelagic zone, where it feeds on abundant macroplanktonic and microplanktonic crustaceans; in most cases, it then becomes detritophagous and necrophagous due to transition to benthic life.

This is confirmed by the fact that we found *P. carinata* in the feeding of *Merluccius polli* (Merlucciidae) and *Hoplostethus petrosus* (Trachichthyidae), which are bottom-dwelling.

The features of the parametric distribution of *P. carinata*, which is limited to depths from 300 to 880 m, i.e., by the edge of the shelf and the upper part of the continental slope over the boundary between the meso- and bathypelagic zone, where they are adjacent to the continental slope, served as the basis for the following analogy.

Previously, we described an interesting ecological system consisting of several shrimp species [3]. It was found in the upper part of the continental slope in areas with well-developed terrigenous sedimentogenesis. In West African waters, it includes an obligate detritophage (*Nematocarcinus africanus* Crosnier et Forest 1973), whose bathymetric distribution range coincides quite exactly with that of *P. carinata*, as well as large benthic shrimps acting as attacking predators from the family Aristeidae (*Aristeus varidens* Holthuis, 1952 and *Aristeopsis edwardsiana* (Johnson, 1867)), which reach considerably larger depths in their bathymetric distribution than their prey, generally represented by *N. africanus*. With respect to features, this community belongs to consortiums, where detritophage *N. africanus* performs the function of an edifying species, while aristeid shrimps acting as attacking predators play the role of consortium species [3].

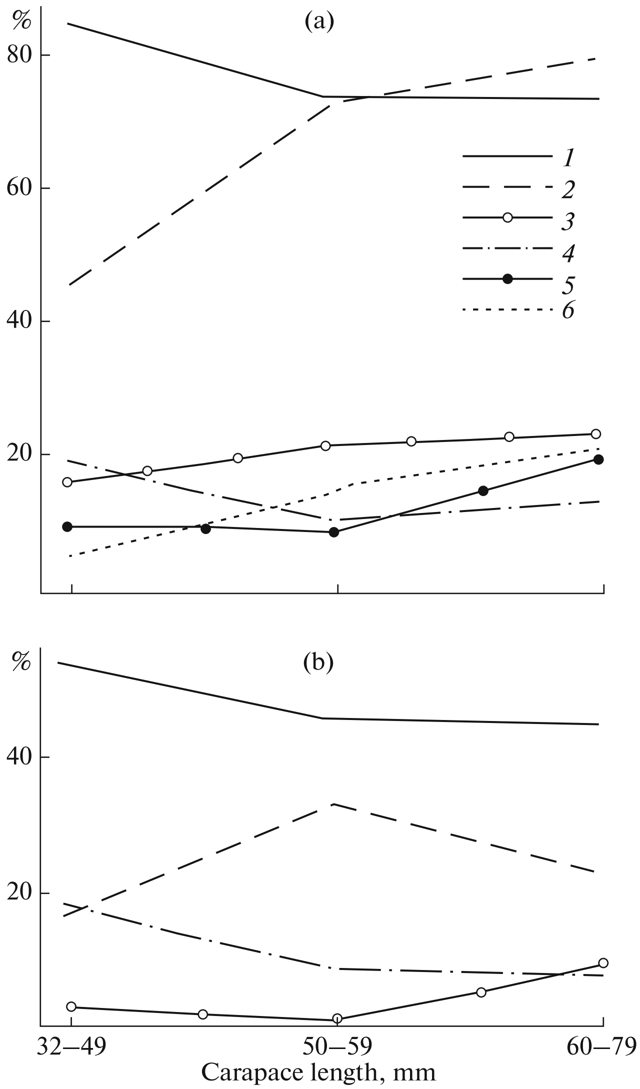

Fig. 3. Ontogenetic variability in food composition in *Plesionika carinata*. (a) Frequency of occurrence in stomachs, (b) share in volume of virtual food bolus. (*1*) Euphausiids, (*2*) detritus, (*3*) fish, (*4*) shrimp, (*5*) foraminifers, (*6*) sand particles.

The lower boundary of the bathymetric distribution of *N. africanus* is determined by the fact that the depths of 400 to 700 m are a peculiar boundary zone in which the share of organic matter sharply decreases in the water column, the content of organic nitrogen reaches the minimum, and the carbon/nitrogen ratio is maximum, which indicates a decrease in the share of proteinaceous substances compared to nonassimilable hydrocarbons. This results in a peculiar gradient stable enough to be an ecological factor. We proposed the term "trophogradient" or "trophocline" [3]. It is this gradient that inhibits deeper penetration of the detritophage *N. africanus* and, possibly, *P. carinata*. The disappearance of *N. africanus* leads to the disappearance of the consortium itself, as a result of which the former consorts begin to feed on pelagic animals that make large vertical migrations; i.e., they move from the detrital to the pasture food chain.

What is realized in the consortium consisting of several shrimp species is performed by a single species in the case under consideration, namely, by *P. carinata*, in its ontogenesis.

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