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Feeding of the pelagic shrimp *Acanthephyra pelagica* (Risso, 1816) (Crustacea: Decapoda: Oplophoridae) in the northern Mid-Atlantic Ridge area in 1984 and 2004

Питание пелагической креветки *Acanthephyra pelagica* (Risso, 1816) (Crustacea: Decapoda: Oplophoridae) в северной части района Срединно-Атлантического хребта в 1984 и 2004 годах

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КЛЮЧЕВЫЕ СЛОВА. Срединно-Атлантический хребет, питание, частота встречаемости, усредненный реконструированный (виртуальный) пищевой комок.

ABSTRACT. Bathypelagic shrimps *Acanthephyra pelagica* (Risso, 1816) were mainly feeding on meso- and bathypelagic fishes of the families Myctophidae and Gonostomiidae in the Mid-Atlantic Ridge (MAR) area in 2004 with *Cyclothone* spp. being a dominant food items. Euphausiids, especially *Meganyctiphanes norvegica*, and decapods of the families Pandalidae, Sergestidae and Benthesicymidae were also part of the diet. These main three groups occupied about 80% of the reconstructed (virtual) food bolus and serve as the principal food of *A. pelagica*. Other prey groups found in the stomachs were sporadic, occasional or transit. This food composition is similar to results obtained in previous studies in 1984. The differences of shrimp diet in 1984 and 2004 were due to the frequency of occurrence and the proportion of euphausiids, shrimps and other malacostracans in the volume of the virtual food bolus. Euphausiids were often found in the diet of *A. pelagica* at depths less than 1000 m in the northern part of MAR area, occupied by Sub-Arctic Intermediate Waters (SAIW). South of the Sub-Polar Front (SPF), in the North Atlantic Central Water, euphausiids were substituted by decapods, and at depths below 1000 m — by decapods, amphipods and mysids.

РЕЗЮМЕ. Батипелагическая креветка *Acanthephyra pelagica* (Risso, 1816) в водах Midle-Atlantic Ridge в 2004 г питалась преимущественно мезо- и батипелагическими рыбами из семейств Myctophidae и Gonostomiidae, среди которых доминировали *Cyclothone* spp. Им сопутствовали эуфаузииды, прежде всего *Meganyctiphanes norvegica*, и креветки из семейств Pandalidae, Sergestidae and Benthesicymidae. Эти три пищевых объекта занимают около 80% объема реконструированного среднего (виртуального) пищевого комка и служат главной пищей *A. pelagica.* Остальные объекты питания, встреченные в желудках, служат спорадической, случайной или транзитной пищей. Такой же суммарный состав пищи наблюдался у креветки и в 1984 г. Отклонения от этого связаны с изменением частоты встречаемости и доли в объеме виртуального пищевого комка эуфаузиид, креветок и других высших ракообразных, служащих спорадической пищей. Эуфаузииды чаще всего встречаются на глубинах менее 1000 м в северной части MAR, занятых SAIW. Они замещаются в пище *A. pelagica* на глубинах более 1000 м креветками, и к югу от SPF, в NACW, креветками, амфиподами и мизидами.

Introduction

Pelagic decapod shrimps play a significant role as food for other shrimps, fish, squids and marine mammals. Thus, they play a significant role as a link between mesoplankton and higher trophic levels, and as agents in transporting organic matter to the deep sea through vertical migrations [Vinogradov, 1968]. The importance of *Acabthephyra pelagica* in the bathypelagic trophic chain is well illustrated by the list of its predators. It was found in the stomachs of several fish species, including the continental slope species *Aphanopus carbo* (Trichiuridae) [Figueira, I957] and *Lepidion eques* (Moridae) [Mauchlin, Gordon, 1980], the offshore species *Dentex macrophtalmus* (Sparidae) and the slope species *Beryx splendens* (Berycidae), *Co-*

riphaenoides rupestris (Macrouridae), *Hoplostethus atlanticus* (Trachichthyidae), *Centrophorus granulosus*, *Merluccius capensis* (Merlucciidae). In addition, this shrimp species is a prey of dolphin *Stenella plagiodon*, squids *Sthenoteuthis pteropus*, *Ommastrephes bartrami,* deep-sea shrimps *Aristeus varidens* and *Aristeopsis edwardsiana* [Burukovsky, 2009].

The data on the diet and food consumption of pelagic decapods are necessary to understand their role in the pelagic ecosystem. *Acanthephyra pelagica* (Risso, 1816) is a bathy-mesopelagic species, common in boreal and subtropical zones of the North Atlantic [Chace, 1947; Crosnier, Forest, 1973; Burukovsky, 1996]. The species was one of the most abundant species along the Mid-Atlantic Ridge (MAR) area during the MAR-ECO expedition in June 2004. There are few data on *A. pelagica* dietary composition: from the northeastern Atlantic [Roe, 1984], from western part of the Mediterranean Sea [Cartes, 1993] and from the slope of the North-western Africa coast [Burukovsky, 2009].

This study analyses material collected in two cruises to the northern Mid-Atlantic Ridge, in 1984 [Burukovsky, 2009] and 2004.

In 1984 sampling was made in the framework of the international research program "Open Ocean" [Burukovsky, 1996]. The aims of this study were species composition, distribution, biology and feeding of the mass species of pelagic shrimps occuring between the Azores islands and the Iberian Peninsula. The western part of this area included the waters of Azorean Zone (AZ) of the MAR. About 30 species of epi-, meso-and bathypelagic shrimps (excluding the species of Sergestidae, precise identification of which at that time was not possible) were found in the studied area. Among all these shrimps *A pelagica* played the most important ecosystem role. Results of this study including general biology of this species and some aspects of its feeding have been published earlier [Burukovsky, 1996, 2009; Burukovsky, Andreeva, 2010)].

The MAR-ECO project aimed to gather information on the mid-ocean ridge macro- and megafaunal assemblages and their distribution patterns in relation to the abiotic environment. Its target area extended from Iceland to the Azores covering waters associated with MAR. Strategies and methods adopted in the international expedition on board RV *G.O. Sars* and MS *Loran* in 2004 were selected in order to maximise data and sample collection in all pelagic and benthic habitats to the maximum depth of 3500 m, spanning organisms within the size range from 1 mm to several meters [Wenneck et al., 2008].

The aim of this work is to describe the food composition of *A. pelagica* collected in the MAR-ECO expedition to the MAR area in 2004 together with the "Open Ocean" expedition of in 1984 focusing at composition of the diet of shrimps, and both spatial (vertical and horizontal) and temporal variation (by comparing data obtained with 20 years interval).

Table 1. Material used to såudy feeding of *Acanthephyra pelagica* in the northern Middle Atlantic Ridge area ("Open ocean", 1984).
Таблица 1. Материал, использованный для изучения питания *Acanthephyra pelagica* северной части района Срединно- Атлантического хребта хребта (экспедиция «Открытый океан, 1984).

Station number	Date and time	Coordinates	Horizon of the haul, m	Number of specimens
79/35	13.08.1984 19.10–20.10	46°00′N 18°01′W	540–730	23
85/38	14.08.1984 21.35–22.35	43°16.5″N 18°01′W	510–693	42
108/46	20.08.1984 00.45–02.15	42°28.3′N 19°04.2′W	1050	64
115/49	21.08.1984 22.05–23.15	45°59.9′N 19°50.4′W	500	25
166/72	09.09.1984 20.35–22.05	40°58.7′N 22°57.0′W	770–840	17
176/76	12.09.1984 00.50–02.20	46°07.8′N 23°17.9′W	1100–1200	114
186/81	14.09.1984 04.05–06.05	41°39.0′N 24°00.0′W	1260	70
200/88	17.09.1984 20.50–22.20	45°22.0′N 25°.59.9′W	850–1075	70
221/95	22.09.1984 21.30–23.00	42°39.5′N 28°45.1′W	850-–1200	67
229/99	24.09.1984 22.55–00.25	45°54.8′N 29°00.0′W	910–1000	114
Total				606

Materials and methods

The first survey was conducted on board RV *Professor Siedlecki* in the area to the north and to the east of the Azores Islands (bounded by coordinates 46–37° N and 29–14°W) between 1 August and 29 September 1984. Shrimps were fished using a pelagic "krill trawl" 15/41x4 with mouth opening 150–175 m^2 and mesh size (diagonally) 12 mm in the cod end. There 103 pelagic trawling were carried out and *A. pelagica* was found in 22 of them. In total 766 stomachs of shrimps were examined. Food remains were found in 606 stomachs, 181 stomachs were full (Table 1).

In the second survey in 2004 material was collected on board RV *G.O. Sars* along MAR from 60°16′07″N to 41°11′19″N, and 36°43′24″W to 23°15′42″W between 09 June and 01 July 2004 (Fig. 1). Three different double-warp mid-water trawls were used for the collection of pelagic decapods [Wenneck et al., 2008]. The large mid-water fish trawl "Egersundtrawl"(vertical opening 90–180 m, and cod-end mesh size 22 mm, streched), the Aakratrawl (vertical opening 20–35 m, and cod-end mesh size 22 mm, stretched) and the Macrozooplankton trawl ,"krill trawl", (6 × 6 m mouth opening and 6 mm meshes, stretched, from the mouth to the cod-end). The Aakratrawl and the Macrozooplankton trawl were equipped with multi-samplers, opening and closing by a pre-programmed timer, to provide samples from three and five discrete depths respectively.

Decapods were preserved in 4% borax-buffered formaldehyde. The fixed specimens were later transferred to 70% ethanol, for permanent deposition at the Zoological Museum of Bergen University. Stomachs

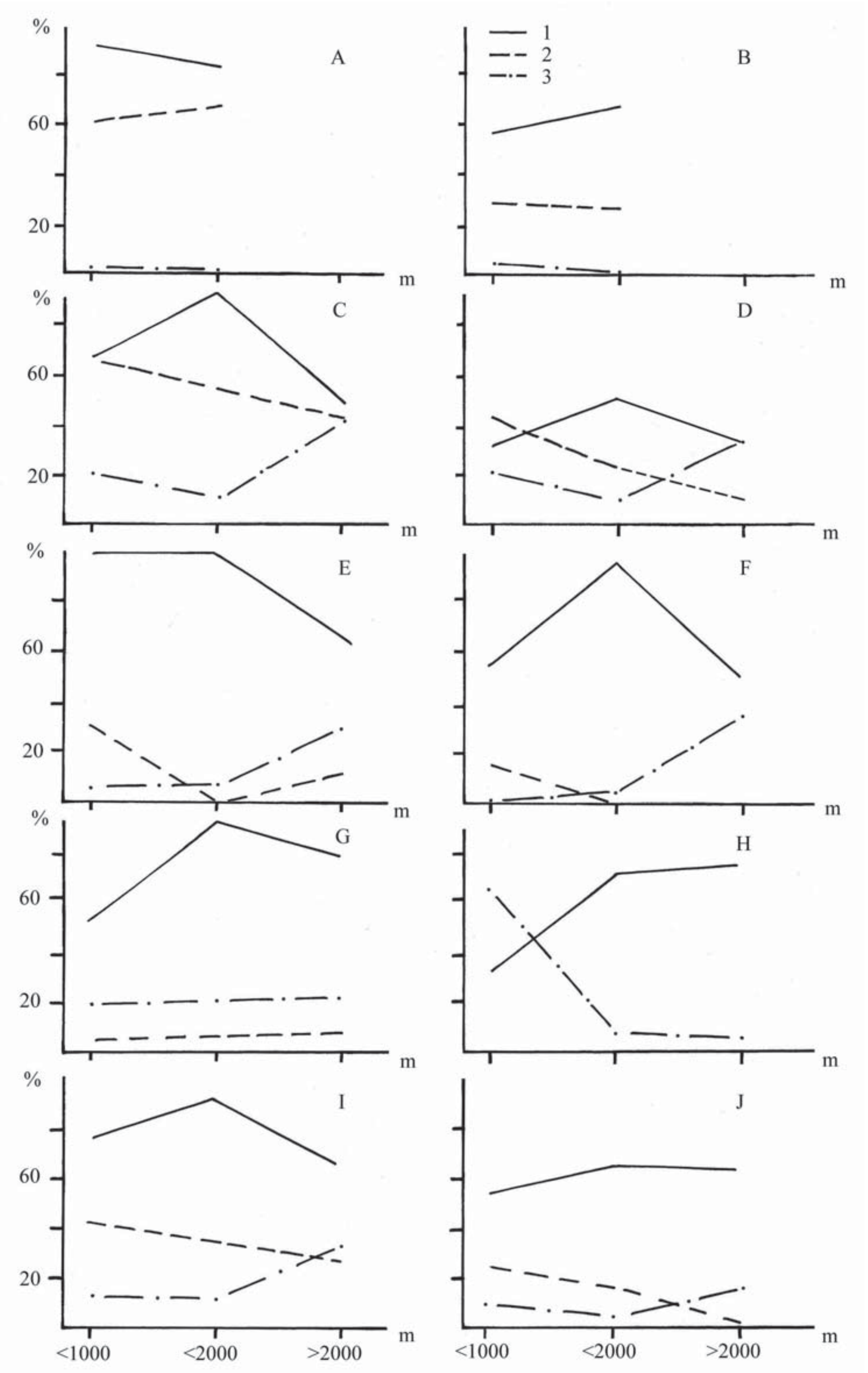

Fig. 1. Bathymetric variability of food composition of shrimp *Acanthephyra pelagica* in the Midle-Atlantic Ridge area. A, C, E, G, I — frequency of occurrence; B, D, F, H, J — share in the volume of virtual food bolus. A, B — Reykjanes Ridge; C, D — Charles Gibbs Fracture Zones; E, F — Faraday Seamounts Zone; G, H —Azores Zone; I, J — summary for Midle-Atlantic Ridge.

1 — fish (Osteichtyes); 2 — Euphausiacea; 3 — Decapoda shrimps.

Рис. 1. Батиметрическая изменчивость состава пищи у креветки *Acanthephyra pelagica* на Срединно-Атлантическом хребте. A, C, E, G, I — частота встречаемости; B, D, F, H, J — доля в объеме виртуального пищевого комка. A, B — хребет Рейкьянес; C, D — зона разлома Чарльза Гиббса; E, F — зона подводной горы Фарадей; G, H — зона Азорских о-вов; I, J — суммарный для Срединно-Атлантического хребта.

1 — рыбы; 2 — Euphasiacea; 3 — креветки Decapoda.

composition of *Acanthephyra pelagica* was studied in 440 specimens (Table 2). Food remains was found in 374 stomachs, 160 stomachs were full.

The size of the studied shrimps (carapace length — CL) ranged from 10 to 25 mm, but CL of 77.5% individuals was within 16–21 mm. This suggests that the ontogenetic variability of feeding of this shrimp species had no effect on the results. When examining stomachs content we used the method developed by Burukovsky [2009]. The extracted stomach was placed in a Petri dish. The degree of stomach fullness was determined following a 4-rank system: 0 — stomach is empty; 1 — food bolus is less than half of the stomach; 2 — food bolus fills about half (from one to two thirds) of the volume of the stomach; 3 — stomach is full. Stomach contents were investigated in a drop of water under a stereomicroscope.

The remains of preys were identified to the taxonomic level of class or order. The number of prey items were counted, and their body parts were measured (mainly skeletal elements such as fish scales and vertebrae, crystalline lens, otoliths of fishes; chaetae of chaetognaths and statoliths of mysids, etc.) using a calibrated ocular micrometer.

The term “food item” was used for edible parts of the stomach contents (detritus, remains of plants and animals) of a given taxon. The term “components of food bolus” or “food components” included food items plus any inedible items (grains of sand, spicules of sponges, etc.) that were found in stomachs sometimes in large numbers.

Regardless of stomach fullness, the presence of any prey was recorded and then used to estimate its frequency of occurrence (as percentage of stomachs with given prey or food component of all stomachs with food). In full stomachs, components of food bolus were estimated by volume with 10% precision. These data were used to re-construct the virtual food bolus. Prey items or components with less than 10% of the volume were not used for calculation.

The frequency of occurrence of food items, their numbers in stomach, prey size and other food components may be regarded as reduction food indicators during digestion. The reconstructed averaged (or virtual) food bolus is regarded as the integral indicator of feeding [Burukovsky, 2009]. The other indicators are as following:

– Mean number of prey items in the stomach (Froerman’s index: K_f — see in [Burukovsky, 2009]) or sum of all frequencies of occurrence of all food items divided by 100, with sand and others non-edible inclusions not included.

– Frequency of prevalence. This is frequency of occurrence of stomachs where a given component of food bolus is present in more than 60% of the volume, i.e. prevailed. This parameter is calculated for full stomachs only.

Both parameters are integrated into a more general approach that enables a transition from descriptive characteristics of feeding of a given species to identification of the type of feeding or foraging in a predatory shrimp species. In this study the term “predator” is used to describe animals feeding on live prey irrespective of their sizes and taxonomic position.

These particular and integral indicators of feeding must be used together because they complement each other: the first are discrete and the second are continual parameters of feeding. If used separately, they give a biased view on feeding of a given species. As an example let us look at the role of foraminiferans in feeding of some studied shrimps. Their frequency of occurrence reaches up to 60–70%, and foraminifers in this case are the most frequently occurring food items. But their proportion by volume in the virtual food bolus does not exceed 0.1– 0.2%. The joint analysis of these two parameters enables to estimate the real consumption of foraminifers by a given shrimp species. This integral approach is even clearer in analysis of ontogenetic variability in frequency of occurrence and volume ratio of food components. For example, if a decrease in frequency of occurrence of a given prey with increase in predator size is observed together with an increase of proportion by volume in the food bolus, it would mean that upon growth this shrimp feeds on this prey less frequently but in larger quantities.

Results

Food composition (Table 3)

The form of prey fragments found in the full stomachs of *A. pelagica* suggests that this species is a typical predator. These were usually relatively large fragments. There were not only fragments of crustaceans, but also some soft tissues. Fish in the stomachs were found as fragments of soft tissues and bones.

Consumed fishes belonged to the families Gonostomiidae, Melamphaidae and Myctophidae. The diameters of the eye lens of the fish were 0.1–0.8 mm, mainly 0.4–0.6 mm. Otoliths were as large as 0.3–0.9 mm, and the diameter of fish scales ranged between 0.9 and 2.2 mm.

The stomachs usually contained remains of a single fish specimen. Two individuals were found only once. Two of the fish species were identified by scales, otoliths and jaws form. The first one was *Diogenichthys atlanticus* with the length of 14–16 mm (= approximately 16% of the length of the shrimp body). The second fish was *Sternoptyx diaphana* of length about 29 mm or about 30% from the body length of its predator. In addition, *Poromitra* sp. (?) remains were found twice.

Fragments of the fish *Cyclothone* sp. were the most frequently found prey item and observed in the stomachs of shrimps from different regions of MAR. During the 2004 MAR-ECO expedition, four species of *Cyclothone* were identified in the trawls (Sutton et al., 2008): *C. microdon*, *C. braueri*, *C. pseudopallida* and *C. pallida*. The first two species dominanted of the meso- and bathypelagic fish communities. Their numbers at depths less than 1000 m in some areas of MAR

Table 2. Material on feeding of *Acanthephyra pelagica* in North Middle Atlantic Ridge (MAR-ECO, 2004).
Таблица 2. Исследованный материала по питанию *Acanthephyra pelagica* северной части Средне-Атлантического хребтка Срединно-Атлантического хребта (экспедиция Mar-ECO, 2004).

Station number	Date	Coordinates	Bottom depth, m	Depth of the haul, m	Number of specimens
Reykjanes Ridge Zone					
2-326-1001	09.06.2004	59°52.06′N 25°49.53′W	2264	2070–1500	3
2-326-1002	09.06.2004	59°53.99′N 24°44.78′W	2314	750–370	28
2-327-1005	09.06.2004	59°57.08′N 25°45.94′W	2219	1803–1555	2
4-329-1013	11.06.2004	60°18.02′N 28°25.45′W	1664	1301–744	11
4-329-1014	11.06.2004	60°16.07′N 28°24.88′W	1353	729–472	20
6-331-1021	12.06.2004	57°09.05′N 31°07.60′W	2309	1493–2124	8
7-332-1025	13.06.2004	57°05.11′N 31°21.62′W	2418	1530–1180	17
8-333-1027	13.06.2004	56°19.18′N 34°16.52′W	1552	1330–1243	21
8-334-1033	14.06.2004	59°52.06′N 24°59.53′W	1344	0–300	33
Total for area					143
Charlie Gibbs Fracture Zone					
12-338-1043	16.06.2004	53°04.83′N 34°35.82′W	1514	1181–680	6
12-339-1046	16.06.2004	52°57.56′N 34°38.25′W	2112	1750–815	14
12-339-1048	16.06.2004	52°51.63′N 34°40.09′W	3229	293–0	3
14-340-1049	17.06.2004	53°06.01′N 36°43.45′W	3153	2534–2304	2
14-340-1050	17.06.2004	53°05.52′N 36°43.24′W	3130	2284–1496	4
14-340-1051	17.06.2004	53°04.01′N 36°42.57′W	3172	1478–665	29
14-340-1053	17.06.2004	53°01.67′N 36°41.87′W	3103	175–25	12
14-341-1054	18.06.2004	53°05.36′N 36°43.16′W	3109	2792–1060	5
16-343-1058	19.06.2004	51°26.87′N 33°26.98′W	3794	3008–2239	2
18-345-1067	20.06.2004	52°25.15′N 34°17.39′W	3231	2316–1444	8
18-345-1069	20.06.2004	52°28.06′N 31°44.36′W	3926	716–177	18
18-346-1072	20.06.2004	52°32.94′N 31°53.49′W	3935	1774–805	5
Total for area					108
Faraday Seamounts Zone					
22-349-1082	23.06.2004	50°36.35′N 27°29.06′W	3705	2731–2309	6
22-349-1083	23.06.2004	50°34.93′N 27°29.49′W	3520	2301–1774	5
22-350-1088	23.06.2004	50°21.16′N 27°30.92′W	3650	1800–850	18

Table 2 (contituing)
Таблица 2 (продолжение)

22-350-1089	23.06.2004	50°18.45′N 27°31.84′W	3634	780–0	30
24-351-1090	24.06.2004	49°35.42′N 28°8.81′W	3077	2768–2314	4
26-354-1103	25.06.2004	48°00.18′N 27°31.84′W	3537	1800–2600	9
Total for area					72
Azora Zone					
28-356-1109	27.06.2004	42°54.04′N 27°44.59′W	2890	2202–2295	1
28-356-1110	27.06.2004	42°52.07′N 27°43.75′W	2822	2308–1474	15
28-357-1115	27.06.2004	41°41.06′N 27°52.87′W	2657	1770–829	6
28-357-1116	27.06.2004	42°49.14′N 27°56.98′W	2300	800–0	2
30-358-1118	28.06.2004	42°54.74′N 29°18.38′W	2828	2283–1480	6
30-358-1120	28.06.2004	42°48.85′N 27°16.43′W	2443	598–175	2
30-358-1121	28.06.2004	42°57.02′N 23°15.42′W	1949	186–36	4
31-360-1199	28.06.2004	42°47.02′N 30°05.42′W		1434–1434	13
32-362-1129	29.06.2004	42°29.52′N 30°08.68′W	2411	2008–1495	3
32-362-1130	29.06.2004	42°28.07′N 30°08.64′W	2289	1523–652	11
32-362-1131	29.06.2004	42°26.52′N 30°08.62′W	2364	675–188	2
34-363-1134	30.06.2004	41°44.77′N 30°00.01′W	2154	1887–1490	5
34-363-1135	30.06.2004	41°43.27′N 29°59.93′W	2177	1494–674	9
34-363-1136	30.06.2004	41°44.88′N 29°59.92′W	2317	684–205	2
34-363-1137	30.06.2004	41°41.06′N 29°59.96′W	2317	203–0	3
34-364-1139	30.06.2004	41°31.02′N 29°54.51′W	2230	1800–800	8
36-365-1141	30.06.2004	41°29.92′N 28°27.18′W	2654	2042–1920	4
36-365-1143	30.06.2004	41°29.64′N 28°20.76′W	2602	1493–825	15
36-365-1145	30.06.2004	41°29.18′N 28°23.52′W	2698	180–0	2
36-366-1148	01.07.2004	41°11.19′N 28°14.26′W	2399	800–0	4
Total for area					117
Total					440

was about 20% of the total number of pelagic fish at the depths below 750 m. *C. microdon* in the northern part of the MAR was 88% of the total number of pelagic fish. The average weight of *C. microdon* ranged from 1.1 to 2.4 g [Sutton et al., 2008]. Most likely, this species was one of the main preys of *A. pelagica*.

Decapod species found in the stomachs belonged the families of Sergestidae, Benthesicymidae (*Gennadas* sp.), Oplophoridae (*Acanthephyra* sp., *Oplophorus spinosus*) and Pandalidae (*Stylopandalus richar-*

Table 3. Food composition in *Acanthephyra pelagica* in the northern Middle Atlantic Ridge area (1984 and 2004).
Табл. 3. Состав пищи у креветки *Acanthephyra pelagica* северной части Срединно-Атлантического хребта (1984 и 2004).

Prey	Food composition					
	Frequency of occurency, %		Virtual food bolus, %		Frequency of prevalence, %	
	1984	2004	1984	2004	1984	2004
Fish (Osteichtyes)	80.0	83.9	49,8	61.2	50,9	58.7
Euphausiacea	32.3	42.5	22,1	15.8	18,2	14.4
Chaetognatha	18.1	16.3	0,6	1.1	0,6	0.6
Copepoda	13.6	6.1	3,6	0.3	3,6	–
Decapoda shrimps	8,2	13.4	10,8	10.1	12,1	8.7
Cnidaria (Siphonophora-?)	8.2	0.8	3,8	–	4,2	–
Cephalopoda (squids-?)	3.8	2.7	0,9	+	–	–
Mysida	3.0	1.1	3,8	1.1	3,0	–
Mollusca Heteropoda	3.0	0.5	0,6	0.6	1,2	0.6
Mollusca Pteropoda	2.1	–	0,7	–	–	–
Amphipoda	1.6	4.5	1,4	4.5	1,2	–
Foraminiphera	0.5	0.5	–	–	–	–
Thaliacea (salps)	0.5	–	0,8	–	–	–
Ostracoda	0.2	–	–	–	–	–
Isopoda (Bopiridae)	0.2	0.3	–	–	–	–
Eggs (unidentified)	0.2	0.8	–	–	–	–
Anomura	–	0.3	–	0.4	–	0.6
Radiolaria	–	1.3	–	+	–	–
Tintinnida	–	1.1	–	–	–	–
Diatomea	–	0.3	–	–	–	–
Not identified remains	5.8	14.3	1,1	4.0	–	1.9
Not identified crustaceans	0.2	3.6	–	0.8	–	0.6
Number of stomachs	606	374	181	160		
Froerman's index	1.82	1.93			95.3	85.5

di). In a food bolus the fragments of one individual only were met.

The euphasiids *Thysanopoda* sp., *Nematoscelis* sp. and *Meganyctiphanes norvegica* were found in the stomachs of "Open Ocean" samples. In the MAR-ECO samples we had found only *M. norvegica*. Mysids found in shrimp feeding belonged to the Eucopiidae family (*Eucopia* sp.). Among the amphipods the representatives of Hyperiida including the Phronimidae were observed. These crustaceans were found by single specimens in shrimps stomachs but sometimes there were several pairs of chewing appendages of euphausiids mandibles (up to 7, i.e. remnants of four individuals). It is possible that *A. pelagica* may behave as a "grazing" predator [Burukovsky, 2009] when feeding of small crustaceans. But it is also possible that chewing appendages of mandibles that are resistant to digestion might have accumulated in the stomach. The copepods dominating in the stomachs of *A. pelagica* were *Oncaea venusta* and *Pleuromamma* sp. The length of the copepods was about 1 mm. Their number varied from 1 to 20 individuals (only once). In one specimen, remains of large predatory copepods (~1.5–2 mm — *Pareuchaeta* sp.?) were found.

The remains of squids found in the stomachs were identified as Enoploteuthidae. Whole or parts of squid beaks (0.5 mm rostrum length) and eyes lens (0.45–0.75 mm diameter) were often found in the shrimp stomachs. This suggests that cephalopods are the items of *A. pelagica*'s diet and do not interfere with the food spectrum of shrimps when they are caught in the trawl ("net" feeding). Among other pelagic molluscs Heteropoda (*Carinaria* sp.) should be noted. They are characterized by the distinctive radular teeth with lengths from 0.2 to 0.7 mm.

Chaetognatha which lack skeletal structures are probably rapidly digested and are usually identified by their maxillary bristles. Their length varies from 0.25 to 1.7 mm (1.0–1.3 mm mainly), corresponding to 20 to 70 mm total body length of the whole chaetognath (according to our measurements of chaetognaths from the plankton catches).

Cnidaria were usually represented by cnidocysts but on two occasions, eudoxid Siphonophora were found.

Along with relatively large prey in stomachs very small food items were revealed. They included radiolaria, foraminifera, tintinnids and even some diatoms. They were usually found sporadically but on one occasion 10 radiolaria (0.25–0.5 mm in diameter) and about 30 tintinnids (approximately the same size) were detected in one single stomach. We suggest that these organisms were eaten by the prey of *A. pelagica*. The male Bopiridae (ectoparasitic Isopoda) and the copepods *O. venusta*, which are ectoparasites, probably got into the shrimps stomachs with their temporary hosts (e.g. fish). Because these two groups of food objects were only the indirect prey of *A. pelagica*, we referred to them as transit food [Nigmatullin, Toporova, 1982].

Remains of other food items (see Table 2) were of less importance compared to the components described above. In any case the obtained data are sufficient to characterize *A. pelagica* as a predator.

Other components in the diet are considered as unidentified remains. These remains can be divided into two groups. The first group includes remains of unidentified crustaceans, represented by bristles, very small fragments of chitinized structures and other fragments which lack distinguishing characters. We assume that these are the remains of the larval forms with soft covers, easily destroyed in the stomach. They were very rarely found (0.2–3.6%) but in some stomachs these remains were revealed in great numbers and occupied more than half of the total volume.

The second group of unidentified remains included compact black boluses which were found in the back of the cardial part of the empty stomachs and the friable light grey or brownish-red detritus mass. This mass was detected in the stomachs with stomach fullness 2 (according to the 4-rank system) or in full stomachs where part of the food showed indication of digestion. We consider the first group of remains as unassimilated part from earlier feeding acts, while the second group probably includes tissues of partially digested prey

The general characteristics of food composition of *A. pelagica* are given in Table 2. For comparison, results from both 2004 and 1984 are presented. Based on the frequency of occurrence, all prey items found in the *A. pelagica* stomachs can be divided into the following main groups (Table 2). The main food category is fish, which was found in almost every stomach (frequency of occurrence 80.0–83.9%). The second group includes euphausiids (frequency of occurrence 32.3–42.5%), chaetognaths, copepods and decapods (and also Cnidaria in 1984) with frequency of occurrence 5–18% can be attributed to a minor group. Other prey can probably be regarded as accidental food items (Table 2).

Based on the reconstructed (virtual) food bolus, fish is dominating making up half of the total volume (49.8–61.2%). Euphausiids constitute 22.1–15.8% and shrimps 10.8–10.1% of the total volume. These three groups of prey occupy 86.1–90.7% of the total virtual food bolus volume. All other prey which takes some part of the virtual food bolus can be considered as sporadic and not regularly found prey which, consequently, can play an important role in *A. pelagica* feeding.

The total frequency of dominance is 95.3-85.5%, which means that in almost every full stomach there is an item which occupies more than 60% of its volume. It also applies to the sporadic prey. This phenomenon is characteristic of attacking and "grazing" predators [Burukovsky, 2009].

According to our description of the diet, *A. pelagica* can be attributed to the group of attacking predators although the Froerman's index of this species is close to 2 (1.82–1.93), which usually characterize "grazing" predators [Burukovsky, 2009].

Except from the copepods all prey of *A. pelagica* are macroplanktonic or micronektonic animals which feed on zooplankton. Pelagic shrimps can be attributed to attacking predators. Consequently *A. pelagica* is a macroplanktonic and micronektonic predator hunting on small mesopelagic fish, and may thus control their abundance.

Variability of food composition between years

The feeding of *A. pelagica* above Azorean Zone (AZ) of the MAR in the North Atlantic Subtropical Convergence was first investigated in August–September 1984. This corresponded to the southern part of the area general where the material for this study was collected and it allowed comparison of the composition of *A. pelagica* diet approximately in the same area with a time inter of 20 years.

In August–September 1984 spawning of *A. pelagica* took place. In September the shrimp population was recruited by juveniles [Burukovsky, Andreeva, 2010]. Thus the size range of studied specimens was much broader in September 1984 than in June 2004 when the material was collected. During this period in the study area only two oviparous individuals were met. The most advanced in maturation females were in the pre-spawning condition. Different maturity stage composition of population in these years may explain why only 18.9% of shrimps had full stomachs in 1984, while in 2004 the proportion of shrimps with full stomachs was twice as high (36.4%). This difference connected with pre-spawning shrimps feeds more actively than shrimps in spawning state (after egg laying on pleopods).

Despite such differences between the 1984 and 2004 samples with regard to geography, bathymetry and biological season, the differences in their food composition were small. Indeed the frequency of occurrence of the most common prey (fish, euphausiids and chaetognathans) was similar (Table 3).

The frequency of occurrence of prey decapods was more variable but made up almost the same part of the volume in the virtual food bolus in 1984 and 2004 (10.8 and 10.1% respectively). The greatest differences in *A. pelagica* food composition between 1984 and 2004 were related to the less frequent prey. Higher frequency of cnidarian and copepod in the shrimps diet in 1984, in comparison to the data of 2004, may be explained by greater number of juvenile *A. pelagica* in the sample. It is known that cnidarians and copepods play a particularly important role in the juvenile shrimps feeding [Burukovsky, 2009].

It can be concluded that fish, euphausiids and shrimps are obligate dominant food components of adult *A. pelagica* in the MAR area. These preys are found in almost every stomach; they dominate among the others prey and account for more than 80% of the virtual food bolus.

Bathymetric distribution and variability of food composition (Table 3)

A. pelagica occurs at the depth range from 200 to 3500 m, mainly at the 700–1800 m ([Burukovsky, Andreeva, 2010], materials of MAR-ECO, 2004). The species can be attributed to the interzonal group [Beklemishev et al., 1982] inhabiting in the bathypelagial but migrating to the mesopelagial.

The range of vertical distribution and the pattern of diurnal migrations of this species varies from the north to the south. It is associated with the characteristic vertical structure of the Nord-Atlantic Central Water (NACW). Fasham and Foxton [1979] considered this area is a biotope of *A. pelagica* in the North Atlantic. It would be more correct to call this water mass "residence" (Latin *station* = English residence) of the species. The minimum depth of its vertical distribution during the night (200–300 m) has been observed at 18° and 53°N. The deepest upper limit of the vertical range both in the night and the day hours was observed at 40° N. Apparently in other areas the bathymetric distribution of A, pelagic follows a similar pattern [Foxton, 1972; Fasham, Foxton, 1979; Burukovsky, Andreeva, 2010].

In the daytime the upper limit of *A. pelagica* distribution deepens to the 800–900 m. However the depth of the center of species abundance in the daytime and at night changes very little [Domanski, 1985].

In the area of the North Atlantic Subtropical Convergence, where our materials were collected in 1984 (between 43–46° N in the west and 37–46° N in the east), *A. pelagica* was found at 460 m (at night), but occurred mainly deeper than 700 m. At the depth deeper than 1000 m the frequency of occurrence of *A. pelagica* in the hauls was 100% [Burukovsky, 1996, Burukovsky, Andreeva, 2010].

The daily diurnal vertical movement of *A. pelagica* is superimposed on its ontogenetic migrations. Larval hatching occurs at the depths more than 1000 m and then larvae and juveniles rise up to the depth of 700–800 m in the course of growth, where males and females are presented by specimens of similar size. Then females grow to greater size compared to males which in turn descent to the depth greater than 1000 m. Specimens of different size and age separately undergo vertical ontogenetic migrations [Burukovsky, Andreeva, 2010].

This complex mechanism of the vertical movements considerably complicates the study of vertical variability in the food composition of *A. pelagica* because it is not known exactly at what depth a particular prey items found in the stomachs were caught.

The complexity appears to be even greater in the case of collection methods in the MAR-ECO program. There sampling was made along an oblique trajectory from 3000 m to the surface, while nets were opened and closed with a signal from the ship. The duration of each tow was 10–40 min per depth stratum [Wenneck et al., 2008]. The difference of depths between the beginning and the end of trawling varied between 250–900 m, usually 500–600 m

As a result each catch consisted of shrimps caught at the different depths. The height of stratum had considerably varied. Some catches covered, for example, the lower layers of the epipelagial and mezopelagial or meso- and bathypelagial zones. It did not allow us to analyze separately the food composition of shrimps from the different depth zones.

Therefore, we could only roughly classify all studied shrimps caught at the depths less or about 1000 m, between 1000 and 2000 m, and deeper than 2000 m. According to the vertical distribution pattern of *A. pelagica* this zone can be considered as the night foraging part of habitat, a core area of species abundance in the water column and an area of reproduction within the species' range.

Since fish, euphausiids and shrimps were dominant prey items in *A. pelagica*, we examined vertical variability of their frequency of occurrence and fraction in the volume of the virtual food bolus. The vertical variations in other food items were small.

The entire study area was divided into 4 subareas depending on bottom topography and oceanographic conditions (see Table 1) [Søiland et al., 2008]: Reykjanes Ridge (RR), Charles Gibbs Fracture Zone (CGFZ), Faraday Seamounts Zone (FSZ), and Azorean Zone (AZ). The variability in the dominant food items were analyzed separately for each depth layer in each area, and for the entire sampling area (Iceland-Azores) (Fig. 1). The figures demonstrate general trends in the bathymetric patterns of the frequency of occurrence and proportions of the main food items in the virtual food bolus of *A. pelagica*.

These trends are the follows (Fig. 1 A–H).

1. The most common food items of adult shrimps (55–104 mm: [Burukovsky, Andeeva, 2010]) in all areas and at all depths is fish. Fish dominates in the virtual food boluses but the largest proportions of fish (by volume) were found between 1000 and 2000 m.

2. Euphausiids were the most frequently found prey item in *A. pelagica* stomachs at depths less than 1000 m. At this depth euphausiids play the greatest role in the virtual food bolus composition. The contribution of euphausiids to the diet of *A. pelagica* shows decrease from north to south.

3. The changes in the frequency of occurrence and the role in the virtual food bolus of shrimps were following those of euphausiids. The share of decapod shrimps was increasing with depth thus substituting the share of euphausiids.

All these general trends are well expressed in the summary Figures 1 I, J.

Habitat distribution and geographical variability of food composition

As it was mentioned earlier, the entire area of study, the MAR to the north of Azores was divided to four subareas depending on bottom topography and oceanographical conditions (from north to south): Reykjanes Ridge (RR), Charles Gibbs Fracture Zone (CGFZ),

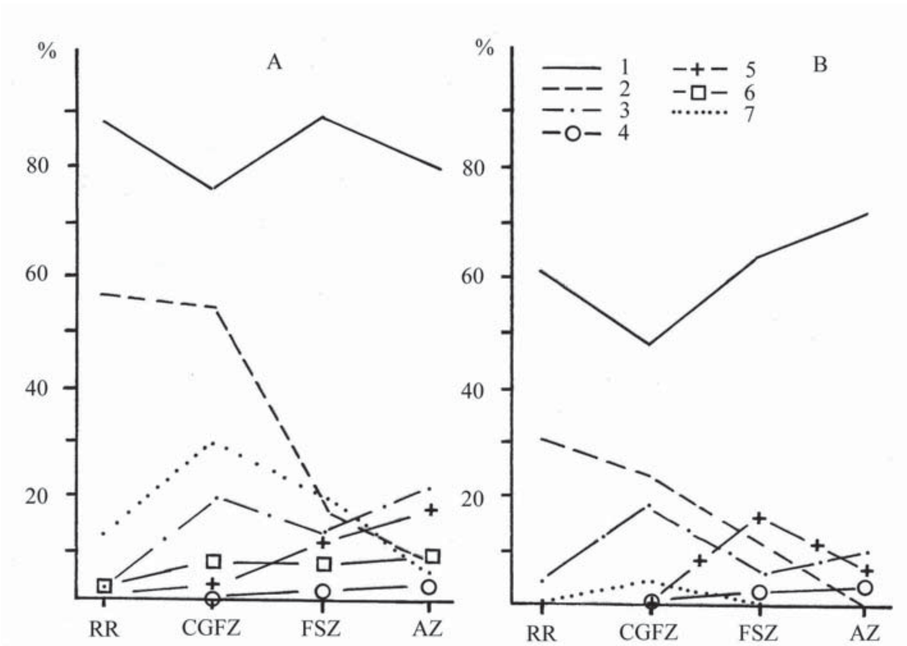

Fig. 2. Geographical variability of food composition of shrimp *Acanthephyra pelagica* in the Midle-Atlantic Ridge subareas (see text). A — frequency of occurrence; B — share in the volume of virtual food bolus.

1 — fish (Osteichtyes); 2 — Euphausiacea; 3 — Decapoda shrimps; 4 — Mysidacea; 5 — Amphipoda; 6 — Cephalopoda; 7 — Chaetognatha.

Рис. 2. Географическая изменчивость состава пищи у креветки *Acanthephyra pelagica* в подрайонах Срединно-Атлантического хребта (см. текст). A — частота встречаемости; B — доля в объеме виртуального пищевого комка.

1 — рыбы (Osteichtyes); 2 — Euphausiacea; 3 — креветки Decapoda; 4 — Mysidacea; 5 — Amphipoda; 6 — Cephalopoda; 7 — Chaetognatha.

Faraday Seamounts Zone (FSZ), Azora Zone (AZ). In the RR and CGFZ areas the upper 500 m of the water column are occupied by the Modified North-Atlantic Water (MNAW), which is substituted deeper by the Sub-Polar Intermediate Water (SAIW), a more cold and less saline water mater forming the Subpolar Front [Søiland et al., 2008].

To the south in FSZ and AZ zones (right up to the Azores islands), the surface water is warmer and salty because of the presence North-Atlantic Central Water (NACW). NACW dominates in the southern part of the investigated area from the surface to the depths exceeding 1000 m. *A. pelagica* is associated with these waters. To the north at the depths exceeding 1000 m cold Labrador Sea Water (LSW) and Mediterranean Water (MW) are circulated. Since the species' residence is generally limited from the top by the 500 m isobaths *A. pelagica* should occur in the LSW in the northern part of the studied area, and in the NACW in the southern part.

Fish dominated the diet of *A. pelagica* in each zone, both according to the frequency of occurrence and contribution to the virtual food bolus. However, in the north (RR zone), fish made up about 60% of the virtual food bolus volume, decreasing to 47.3%, in the GGFZ zone and increasing again to 71.3% in the south (AZ zone) (Fig. 2 B).

In contrast, the frequency of occurrence of euphausiids and their contribution to the virtual food bolus volume decreased sharply southward and was almost negligible in the AZ. In the RR and CGFZ euphausiids were found in every second stomach, and in the AZ they occurred almost three times rarely. South of the CGFZ euphausiids were substituted by shrimps and other malacostracans (Amphipoda, Mysidacea) and also Chaetognatha. Consequently, the diversity of food items in the diet of *A. pelagica* increases southward.

Discussion

A. pelagica occurs in the Atlantic, Pacific and Indian Oceans. The distribution range of this shrimp consists of two unequal by sizes parts, in the north and in the south. The northern part of area is limited only by the physical boundaries of the northern Atlantic. In the west *A. pelagica* occurs from the Davis Strait to Bermuda Islands [Chace, 1940, 1947], i.e. from about 60° N to 30° N. Within longitudes 20– 25° W this species is found between 60° and 18° N [Foxton, 1972], and further to the east the northern record of the species is from the Rockall area (54°30' N: [Hargreavs, 1984]). In the East Atlantic the northernmost finding of *A. pelagica* is in the Biscay Bay (47°24' N: [Abbes, Casanova, 1973]). Besides of this the species inhabits in the Mediterranean Sea [Zariquiey Alvarez, 1968; d'Udekem d'Acoz, 1999]. Further south Lagarder [1971] referred to some records of *A. pelagica* by earlier authors but the species was not found in the Morocco waters [Burukovsky, 1980]. However *A. pelagica* is relatively common in the West Sahara (24–21° N: [Burukovsky, 1982], Mauritania [Burukovsky, Romensky, 1995], Senegal [Crosnier, Forest, 1973], Guin-

Table 4. Food composition in *Acanthephyra pelagica* from other depth horizons of the northern Middle Atlantic Ridge area.
Таблица 4. Состав пищи у креветки *Acanthephyra pelagica* в районе северной части Срединно-Атлантического хребта.

Prey	Frequency of occurrence, %			Virtual food lump, %		
	<1000 m	1000–2000 m	2000 m and deeper	<1000 m	1000–2000 m	2000 m and deeper
Fish (Osteichtyes)	86.8	54.1	70.9	54.7	65.5	63.4
Euphausiacea	66.2	24.1	20.9	25.6	17.3	2.7
Chaetognatha	11.0	9.0	19.8	–	2.8	–
Decapoda shrimps	9.6	6.0	27.9	10.5	7.2	14.8
Copepoda	7.3	0.7	9.3	–	–	–
Cephalopoda (squids-?)	2.9	0.7	3.5	–	0.2	–
Cnidaria (Siphonophora-?)	–	0.7	1.2	–	–	–
Foraminifera	0.7	–	1.2	–	–	–
Radiolaria	1.5	0.7	–	–	0.2	–
Mollusca Heteropoda	0.7	–	1.2	–	–	–
Amphipoda	5.9	1.5	4.6	6.5	2.0	5.2
Tintinnida	1.5	0.7	3.5	–	–	–
Eggs (unidentified)	2.2	–	–	–	–	–
Mysidacea	0.7	0.7	2.3	–	1.5	0.7
Diatomea	–	–	1.2	–	–	–
Decapoda Anomura	–	–	1.2	–	–	1.6
Isopoda	–	–	1.2	–	–	–
Not identified	12.5	5.2	23.3	2.7	3.3	6.6
Not identified crustaceans	1.5	3.8	4.6	–	–	2.5
N stomachs examined	136	133	86	55	61	44

ea-Bissau and Sierra Leone waters where the species reaches the southern border of distribution (about 10° N) in the North Hemisphere [Burukovsky, 1989]. Juvenile shrimp were caught here in February–March 1981; the area was characterized by abnormally strong input of the Canary Current cold water [Burukovsky, 1989].

In the North Pacific *A. pelagica* has not yet been recorded, although the species composition of pelagic shrimps in this area is rather well studied [Hanamura, 1979; Krygier, Pearcy, 1981; Kikuchi, Omori, 1985; Hendrickx et al., 1996].

In the South Hemisphere the species is known in all three oceans. In the South-East Atlantic *A. pelagica* inhabits in the area between 16° and 34°S [Burukovsky, Romensky, 1982, 1985]. In the open parts of ocean (8°24′–01°10′W) the southernmost is at 48°02′ S and in the west part — in the Scotia Sea (50°S) [Burukovsky, Romensky, 1982].

A. pelagica occurs throughout the western part of the Indo-West Pacific. In the western Indian Ocean the species is found from 8° S (our unpublished data) and to the north-west from Madagascar (13°22′S: [Crosnier, 1987]) (i.e. from the tropics) to the South Africa [Barnard, 1950]. The northern most finding of this species in the Indo-West Pacific (8°) is in the Banda Sea [Bate, 1888] S. In the Pacific *A. pelagica* is widely distributed from Chile to New Zealand (74°36′ – 162°W [Barkhatov, 1983; Wasmer, 1986]) as well as to the south of Australia [Iwasaki, Nemoto, 1987]. In this area the species occurs from subtropics (33° S) to sub-Antarctic (66°S) [Wasmer, 1986; Iwasaki, Nemoto, 1987].

A. pelagica occurs at the depths of 200–2000 m, mainly at the 700–1800 m (see references above). However according to the depth stratified sampling in 2004 (MAR-ECO), *A. pelagica* can reach depths of 3500 m. Thus, *A. pelagica* can be considered as an interzonal species inhabiting in the bathypelagial but migrating to the mezopelagial.

In the southern part of the northern MAR area *A. pelagica* were caught in 1984 with the general frequency of 35.7% but at depths exceeding 1000 m it was recorded in each haul. The species accounted for 11.8% of the total pelagic decapods by number and 15.7% — by biomass.

The comparison of *A. pelagica* food composition along the MAR in 1984 and 2004 revealed a very high degree of similarity despite the 20-year interval between the studies. In both cases, the dominant food of shrimp was fish which was found in almost every stomach and occupied a half or more of the food bolus volume. Among fish, representatives of meso- and bathypelagic Gonostomiidae, mainly *Cyclothone* spp., dominated. In 2004 *Cyclothone microdon* was dominant (almost 90% of the total number of other meso- and bathypelagic fish [Sutton et al., 2008]. The second and third most important groups of prey were euphausiids and shrimps respectively. These three groups of prey occupy at least 80% of the virtual food bolus volume and, therefore, represent the main food of *A. pelagica*. Other prey (mysids, amphipods) which was dominating in the diet of a few individuals only (more than 60% of the stomachs volume), were referred to as accidental food, and is not considered as regular available food for *A. pelagica*. In most cases one single prey dominated in full stomachs. This indicates that *A. pelagica* is a makroplanktonic and micronektonic attacking predator.

Our results from the MAR area are in agreement with previous studies on *A. pelagica* from other areas. The diet of *A. pelagica* has previously been studied using material from North-West Africa (Morocco – Mauritania [Burukovsky, Gaevskaya, 1983; Burukovsky, 2009]), North-east Atlantic [Roe, 1984] and from the western Mediterranean [Cartes, 1993]. All these studies showed a dominance of fish in the diet, followed by large crustaceans (decapods and euphausiids). When describing the food composition of *A. pelagica* in the western Mediterranean, Cartes [1993] presented results similar to our data on food composition and frequency of occurrence of the main prey of *A. pelagica*. Among the identified fish *Cyclothone* sp. dominated. Roe [1984] identified *Cyclothone braueri* as the dominating prey of *A. pelagica* in the north east Atlantic

The relative share of euphausiids and decapods varied between different areas. In the West African waters [Burukovsky, 2009], the frequency of occurrence of euphausiids was lower (4.6%), and the proportion of decapod shrimps was higher (39.7% of the virtual food bolus volume) than in the MAR area (our study). Similarly, Cartes [1993] found lower occurrence of euphausiids in the diet of *A. pelagica* compared to the North-East Atlantic [Roe, 1984].

We conclude that major components of the diet of *A. pelagica* have been persisting in the eastern part of its North Atlantic range for more than 25 years. However within this area some variability in the food composition is observed. These variations may be due to the following factors.

1.The food composition changes according to sex. There is no information in the literature on differences in diet between males and females. We compared the composition of the food bolus in one-size males and females but actual differences were not found.

2. The ontogenetic variability in food composition. This has been investigated earlier by Burukovsky [2009] The frequency of occurrence, composition of virtual food bolus, the frequency of the dominance, number of dominants were found to change with increasing of body length, without any significant trend.

Nevertheless in all studied life history stages, fish dominated in the *A. pelagica* diet. Malacostracans, primarily euphausiids and shrimps, sometimes mysids or amphipods showed relatively substantial contribution to the diet as well. Food composition of specimens from the continental slope includes anomurans. The malacostracan groups can be mutually substituted probably depending on their availability for *A. pelagica*.

It is difficult to say anything about the role of chaetognathans which are relatively common items in the stomachs of *A. pelagica* but are seldom found as entire individuals. Chaetognathans usually found in the stomachs as circumoral bristles. Most probably Chaetognatha with siphonophores and Mollusca Heteropoda (*Carinaria* sp.) are the third rank items in the *A. pelagica* diet.

Copepods most probably play an important role in the food bolus of juvenile shrimps with body length less than 25 mm. Euphausiids begin to dominate in the food bolus volume in medium-sized individuals (55–70 mm). This shrimps' size group is represented by the largest juvenile individuals, immature females and small males which dominated in the catches from the lowest depths. Probably at this size *Meganyctiphanes norvegica* become more available for this group of shrimps compared to the other prey and to some extent fish is displaced from the shrimp feeding. But in spite of this, fish occupied about 40% of the stomach volume of shrimps from this size group [Burukovsky, 2009].

It can be concluded that the feeding "specialization" of *A. pelagica* at all ontogenetic stages (except the earliest ones) is consumption of macroplanktonic and micronektonic fish from the Myctophidae and Gonostomiidae.

3. Vertical variability in food composition. The vertical variability in food composition of *A. pelagica* was not studied earlier. Burukovsky [2009] could only conclude that among euphausiids *M. norvegica* prevailed in the *A. pelagica* food in 1984 at the most shallow depths where shrimps were found (about 500 m). The analysis of the peculiarities of food composition changes of *A. pelagica* in relation to the depth of capture on the basis of the MAR-ECO-2004 materials has limitation despite of using a closing macroplanktonic trawl. We could state however that in all studied subareas of MAR at all depths fishes were strongly dominating in shrimp feeding with regards to the frequency of occurrence and the fraction in the volume of the virtual food bolus.

The frequency of occurrence of euphausiids and their role in shrimps feeding decreases with depth, but in contrast, the role of pelagic decapods is increasing. The decline in euphausiids with depth in the diet of *A. pelagica* is understandable, because their numerical abundance decreased logarithmically with depth [Letessier et al., 2011]. Only in the AZ zone the frequency of occurrence of shrimps in the diet is low at all depths and their share in the virtual food bolus is significant only at depths less than 1000 m and decreases sharply with increasing depth. However, the material for the study of the vertical variability of feeding in this zone was limited. Besides of this, differences in food composition in relation to depth tend to increase from north to south, being thus a consequence of geographical variability of the *A. pelagica* feeding pattern.

4. Geographic variation of food composition. The study of the geographic variation of *A. pelagica* food composition has been previously carried out by Burukovsky [2009]. He noted that on the continental slope of North-West Africa *A. pelagica* hunt in the water column as well as at near bottom and can even capture a prey from the bottom. As a result there are purely benthic items in the shrimp stomachs such as remains of gastropods and bivalves, polychaetes, Anomura, benthic foraminifera. Such components of food bolus as particles of sand, some fragments of carbonate structures and even detritus (it filled completely the stomach of one individual) appear in shrimps stomachs. But it has little influence on the role of the major food items in shrimps feeding. All these components of food bolus are occasional or accidental food items.

In the North-West Africa the taxonomic composition of food items is different compared to the MAR area. The bathypelagic shrimp *Stylopandalus richardi* was, for example, substituted by the nectobenthic shrimp *Plesionika carinata*. Among mysids and lophogastrids *Gnathophausia* sp. is frequently recorded in the continental slope area instead of the Eucopiidae in the MAR area. Among the euphausiids *M. norvegica* is completely absent there.

However geographical variation in the food composition of *A. pelagica* is observed within the MAR area according the MAR-ECO 2004 as well. The food composition of *A. pelagica* in the southern half of the study area (FSZ and AZ) differs from the northern half of the area first of all in a sharp decrease in the contribution of euphausiids (primarily due to the falling out of the dominant *M. norvegica*). Euphausiids are replaced by decapods and other malacostracans (mysids and amphipods).

These differences can be explained by the differences in oceanographical condition along the MAR. The northern area is separated from the southern part by the Subpolar Front (SPF) which acts as a boundary between SAIW and NACW. This probably is the reason for such drastic change in the food composition of *A. pelagica* in the MAR area. Similar pattern of geographical differences in pelagic species distribution has been shown for several pelagic taxa [Gaard et al 2008; Hosia, 2008; Sutton et al., 2008].

M. norvegica is a boreal–arctic species and is widespread in the North Atlantic and penetrates into the Arctic seas. Lomakina [1978] reported that in the central part of the North Atlantic this species was distributed to 53°N. According to Karpinsky [1991] and Letessier [2011] *M. norvegica* was recorded in the MAR area at 49°N. Probably SPF restricts the species penetration to the south or leads to the species displacement to the north. This conditions the availability of *M. norvegica* as a prey for *A. pelagica.*

In 1984 the material was collected in the FSZ and AZ regions located to the south 53°N. In this part of the MAR area euphausiids were practically absent in the species diet in 2004, while in 1984 they were found in the stomachs with the frequency of 32.3% and occupied 22.1% of the volume of virtual food bolus.

This suggests that the role of *M. norvegica* in different parts of the MAR area varies despite of the general similarity in food composition of *A. pelagica* in 1984 and in 2004. This is due to the fact that *M. norvegica* was found in the trawl catches in 1984 in the MAR area as far south as to 41°39′N. In 1984 *M. norvegica* dominated among euphausiid with the frequency of occurrence in trawl catches as high as 43.7%; the mean abundance (CPUE per hour of trawling) was equal 34.7 specimens, CPUE biomass reached to 160 kg, and the mean biomass value was 6240 g [Burukovsky, Denisenko, 2014]. In the same area in 2004 *Euphausia krohni* and *Thysanoessa longicaudata* were most abundant species [Letessier et al., 2011].

In 1984 the material was collected in August and September that corresponds to the middle of the hydrological summer season when SPF usually holds the extreme northern position [Dubravin, 2001]. In 2004 the material was collected in June which is normally yet the late hydrological spring when SPF only begins to displace to the north [Dubravin, 2001].

If we assume that *M. norvegica*, a dominant euphausiid in the North Atlantic [Lomakina, 1978; Karpinsky, 1991] is an indicator of SAIW waters, their virtual disappearance from the *A. pelagica* diet in 2004 suggests that in the hydrological spring in 2004 SPF occupied more northern position than in the hydrological summer in 1984.

Conclusions

A. pelagica is distributed in three oceans as an inhabitant of the meso-and bathypelagial. Even in a relatively small area of the MAR, the species uses several water massess as habitats, i.e. LSW, NAIW, and mainly NACW. In all studied areas *A. pelagica* demonstrated a remarkable similarity of food composition.

Meso- and bathypelagic fish and malacostracans (euphausiids, shrimps, amphipods and mysids) were dominated in shrimp stomachs in all stations. These preys occupy about 80% of the virtual food bolus while proportions of different groups of crustaceans and the species composition may vary from one station to another.

Judging from the nearly constant Froerman's index (about 2: [Burukovsky, 2009]) and the frequency of the dominance (more than 80%), the diet and the trophic position of the species in the pelagic community shows a high degree of consistency, both in time and space. *A. pelagica* is a mainly attacking predator feeding on macroplankton and micronekton.

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