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ORIGINAL PAPERS

Appendicularia in the Bering, Okhotsk, and Chukchi Seas and North Pacific and Their Significance for Feeding of Nekton

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Abstract—The significance of larvaceans (class Appendicularia) for plankton community and feeding of nekton in the Far-Eastern Seas and North Pacific is underestimated, this group of species is poorly represented in scientific literature. The total biomass of larvaceans is below the stocks of dominant groups in the large zooplankton, as copepods, euphausiids, arrowworms, amphipods, and coelenterates, but counted together with their shells (called "houses") they form a comparable stock. In the studied area, the class Appendicularia is represented by four species: widely distributed *Oikopleura vanhoeffeni*, *O. labradoriensis*, and *Fritillaria borealis* and *F.* sp. (perhaps *F. pacifica*) in the southern periphery of this area. Larger and more numerous oikopleurids dominate by both abundance and biomass and are presented in all size fractions of zooplankton, whereas fritillarids are presented mostly in the small fraction. Larvaceans are distributed mainly in the upper epipelagic layer (55–97%), i.e., in the layer of their prey concentration; their density is the highest in the coastal zone with the depth less than 50 m and decreases in deeper areas. They are a significant portion in the diet of many nekton species (41 out of 151 species in the Trophology database of TINRO), including basic commercial fishes, such as pollock, salmons, herring, polar cod, mackerels, sardine and others. Their mucus houses that glow at night, with the animal inside, whose tail vibrates constantly providing movement and nutrition, are attractive for many plankton eaters. Appendicularia have a high occurrence in the food of all size-classes of nekton, although it decreases for larger fish of such mass fish species, as walleye pollock and pink and chum salmons.

Keywords: Okhotsk Sea, Bering Sea, Chukchi Sea, North Pacific, Appendicularia, zooplankton, size fraction, nekton, feeding, oikopleura, fritillaria

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INTRODUCTION

Larvaceans (Appendicularia) are a class of pelagic tunicates widely distributed in the World Ocean, including the North Pacific, Okhotsk Sea, Bering Sea, and Chukchi Sea, where they are represented by common species, as *Oikopleura vanhoeffeni, O. labradoriensis*, *Fritillaria borealis,* and *F.* sp. (Figs. 1–3). The last undefined species is found in the southern Bering Sea and adjacent areas of the North Pacific, it is possibly *F. pacifica*. They dwell mainly in the surface layer, but sometimes are found at depths up to 3 km. In some areas, usually in cold waters, larvaceans are rather numerous, up to 50 ind./m^3. They feed mainly on fine phytoplankton and micro- and nanozooplankton, as well as on fine particles of detritus, and can be food competitors of small pelagic crustaceans. On the other hand, Appendicularia are prey for many fish species [4]. Like other tunicates (salps and pyrosomes), larvaceans are luminous organisms due to the presence of symbiotic luminous bacteria in the body.

O. labradoriensis dominates in the deep-water areas of the Bering Sea, and *O. vanhoeffeni* in the northern coastal and shelf waters of the Bering Sea and Chukchi Sea [14, 17, etc.]. These two visually similar species differ in the shape of the stomach: *O. labradoriensis* have angular lobes of the stomach, while *O. vanhoeffeni* have rounded ones (see Fig. 2). The body length of oikopleurids is up to 2.4 mm, the length of their tail reaches 14 mm. Fritillarids are smaller: their body length is up to 1.4 mm, the tail up to 4 mm (Fig. 3).

To obtain food, larvacea builds a slimy shell (called a "house") with a cone-shaped trapping net of thin mucous threads, that is many times greater in mass and volume than the builder itself (see Fig. 1).

The animal's mouth is turned to the top of the net. There is a grate in front of the house and an exit hole at the back. By constant energetic vibration of the wide flattened tail, the animal induces a water flow through the house. Thrown out with force from the rear opening, the jet of water pushes the house forward reactively. Small, predominantly unicellular algae and animals, as well as small particles of organic matter, are sucked with the flow and concentrated at the top of the trapping net, then enter the mouth. After 4–20 h, the

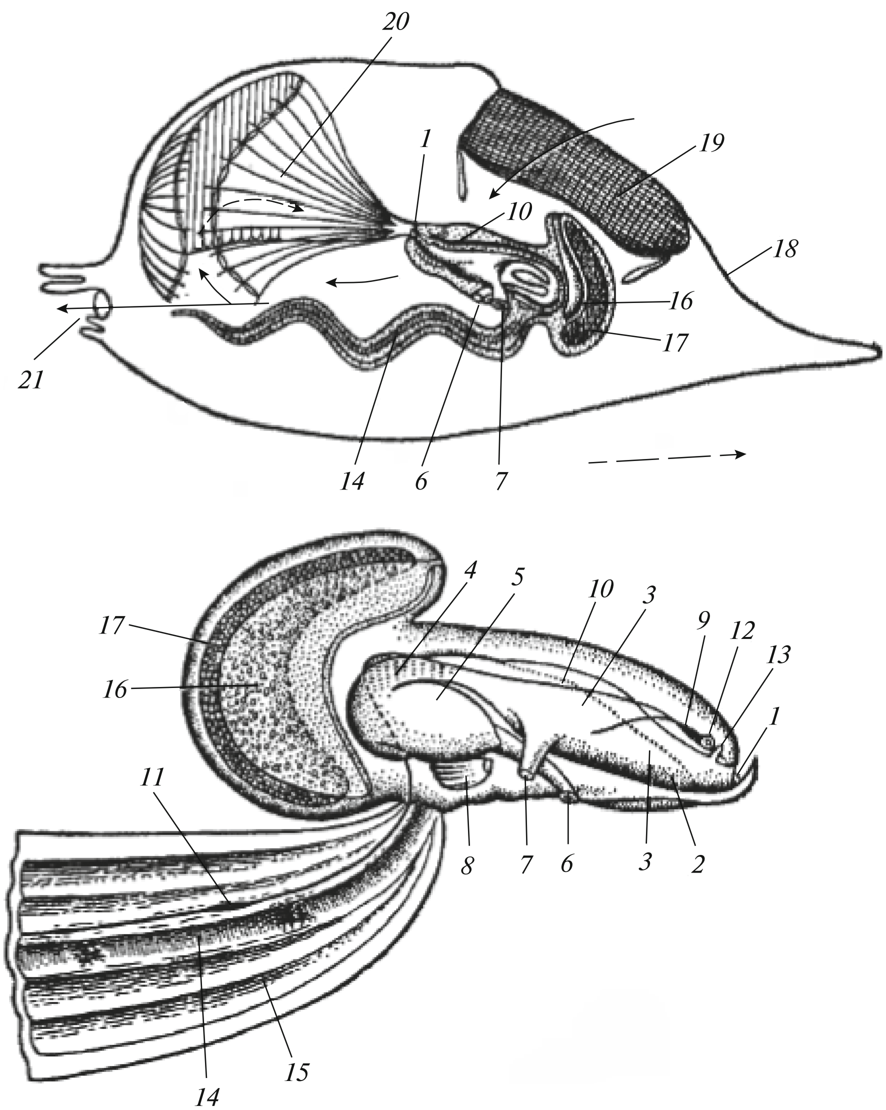

Fig. 1. Appendicularia in a house [4]. *Thin arrows* show the water flows; *dotted arrow* shows direction of the house movement: (*1*) mouth; (*2*) endostyle; (*3*) pharynx; (*4*) esophagus; (*5*) stomach; (*6*) anus; (*7*) branchial opening of stigma; (*8*) heart; (*9*) nerve ganglion; (*10*) nerve spinal trunk; (*11*) its thickening in the caudal section; (*12*) statocyst; (*13*) olfactory fossa; (*14*) notochord; (*15*) tail musculature; (*16*) testis; (*17*) ovary; (*18*) house; (*19*) lattice; (*20*) trapping net; (*21*) opening of the house.

grate becomes clogged, and the flow of water stops. The animal breaks the wall of the house with sharp blows of the tail and swims out; its ectodermal cells begin to produce mucus, from which the animal forms a new house in 1.0–1.5 h [4]. For example, off the coast of Newfoundland, *O. vanhoeffeni* create up to six houses per day [10]. Abandoned houses attract copepods, euphausiids, polychaetes, and other groups of zooplankton that feed on trapped flagellates, coccolithins, silicoflagellates, and diatoms; discarded houses and faecal pellets also make a significant contribution to the vertical transport of material [6, 7].

The biology and ecology of larvaceans in the North Pacific, Bering and Chukchi Seas are described in many publications [6–9, 11–16, 18–20, and others]. Appendicularia in the Okhotsk Sea are only briefly mentioned in tabular materials on composition of plankton or fish food. In this study, the larvaceans in all these regions are considered in more detail as an essential part of their planktonic communities and the food supply of nekton. Therefore, the main attention is paid to quantitative indices of spatial and vertical distribution of biomass and abundance, the stocks of Appendicularia species by the regions, seasonal and

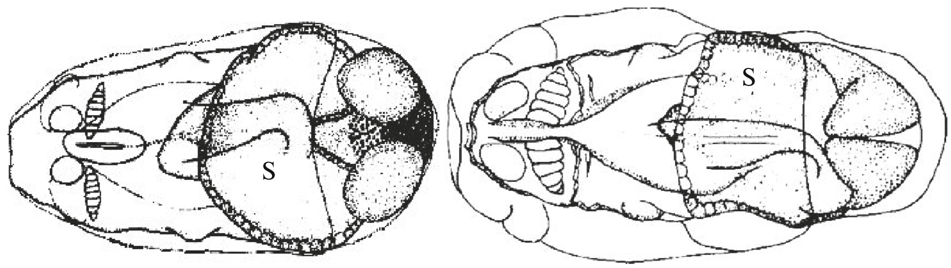

Fig. 2. The shapes of the stomach (*S*): rounded for *O. vanhoeffeni* and angular for *O. labradoriensis* (view from above) [8].

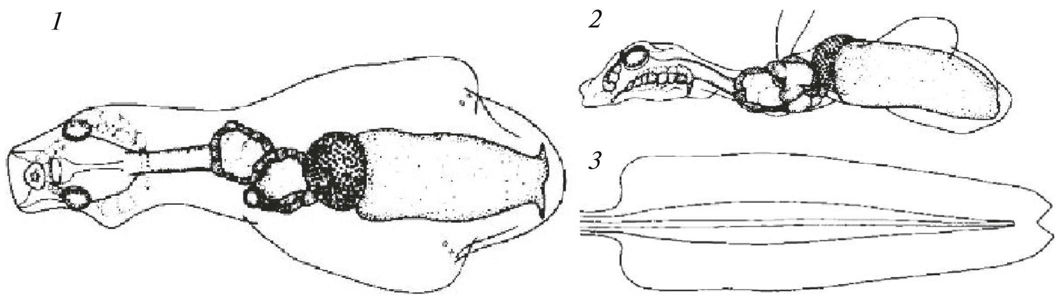

Fig. 3. *Fritillaria borealis*: (*1*) top view, (*2*) side view, (*3*) tail [8].

long-term dynamics, and their role in the diet of mass nekton species.

MATERIALS AND METHODS

The study is based on materials on biomass and abundance of Appendicularia and their content in food of nekton collected in the local databases "Zooplankton" and "Trophology" supported in TINRO. In total, the data of 21.134 plankton and 11.557 trophological stations are analyzed.

All plankton and trophological samples were collected and processed according to the methodology developed in TINRO [2]. A Juday BSD net (mouth 0.1 m^2, mesh size 0.15 mm) was used for plankton sampling by total tows from the 200–0 m layer, or bottom–0 at shallows. Zooplankton samples were divided into three fractions by filtering through two sieves with the mesh of 0.5 and 1.2 mm: small, 0.6–1.2 mm; medium-sized, 1.2–3.2 mm; and large, 3.2–3.5 mm. All larvaceans were calculated in each sample and their number was re-calculated into biomass using the following standard wet weights for small- and medium-sized Fritillaria specimens: 0.014 and 0.053 mg, respectively, and for small-, medium-sized, and large Oikopleura specimens: 0.042, 0.450, and 3.200 mg, respectively. Samples for nekton feeding in the epipelagic layer were taken from catches of midwater trawl and processed fresh in shipboard laboratories. The data were averaged by biostatistical areas ([5], with additions from [1]), and spatial distribution of biological indices was considered for central points of these areas (integral stations) that allowed us to avoid small-scale "noise" and to reveal general features on a quasi-stationary level (Fig. 4).

Exact definition of the species was difficult in mass processing of plankton and trophological samples, so the quantitative indices were determined in general for oikopleurids (two species) and fritillarids (two species).

The index of stomach fullness (‰) was calculated as ratio of the food weight in stomach to the fish or squid body weight; the same index was calculated particularly for oikopleurids as ratio of the weight of oikopleurids in stomach to the body weight.

RESULTS AND DISCUSSION

Appendicularia in Plankton

The distribution of plankton stations with the number of Appendicularia less than 1 ind./m^2 is shown at Fig. 5 and spatial distribution of their abundance in the epipelagic layer by species and size fractions at Fig. 6. These maps concern the entire period of research, so we display the maximum ranges, but the distribution differs in certain years and seasons.

There are some problems with counting Appendicularia because of the destruction of the slimy houses by a plankton net and in the process of the sample fixation with formalin. The animal bodies remain only in the samples, often without tails, which usually have a

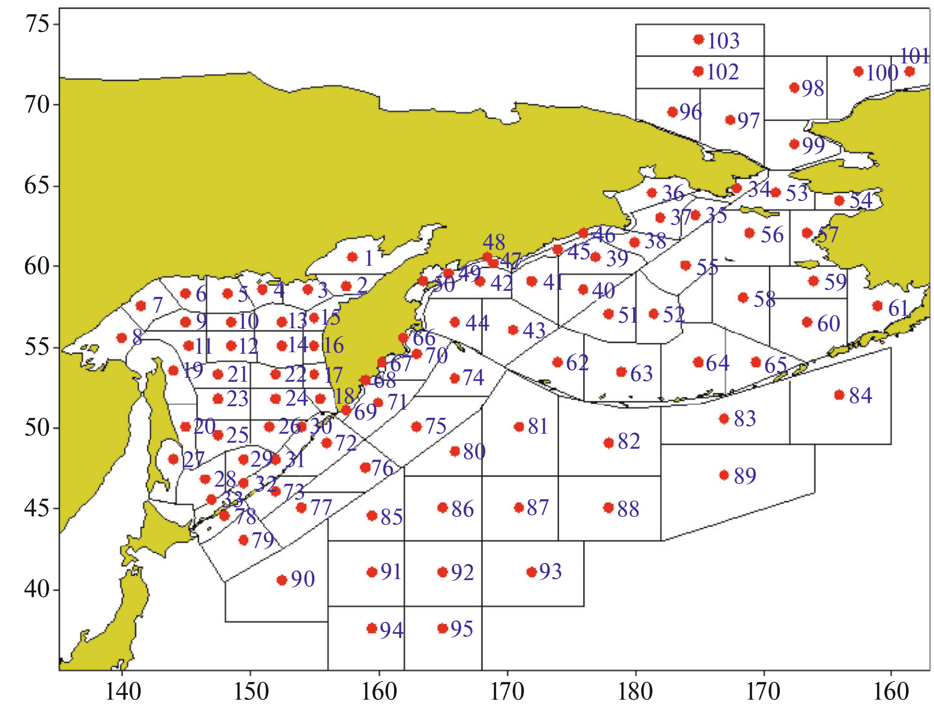

Fig. 4. Boundaries and numbers of biostatistical areas.

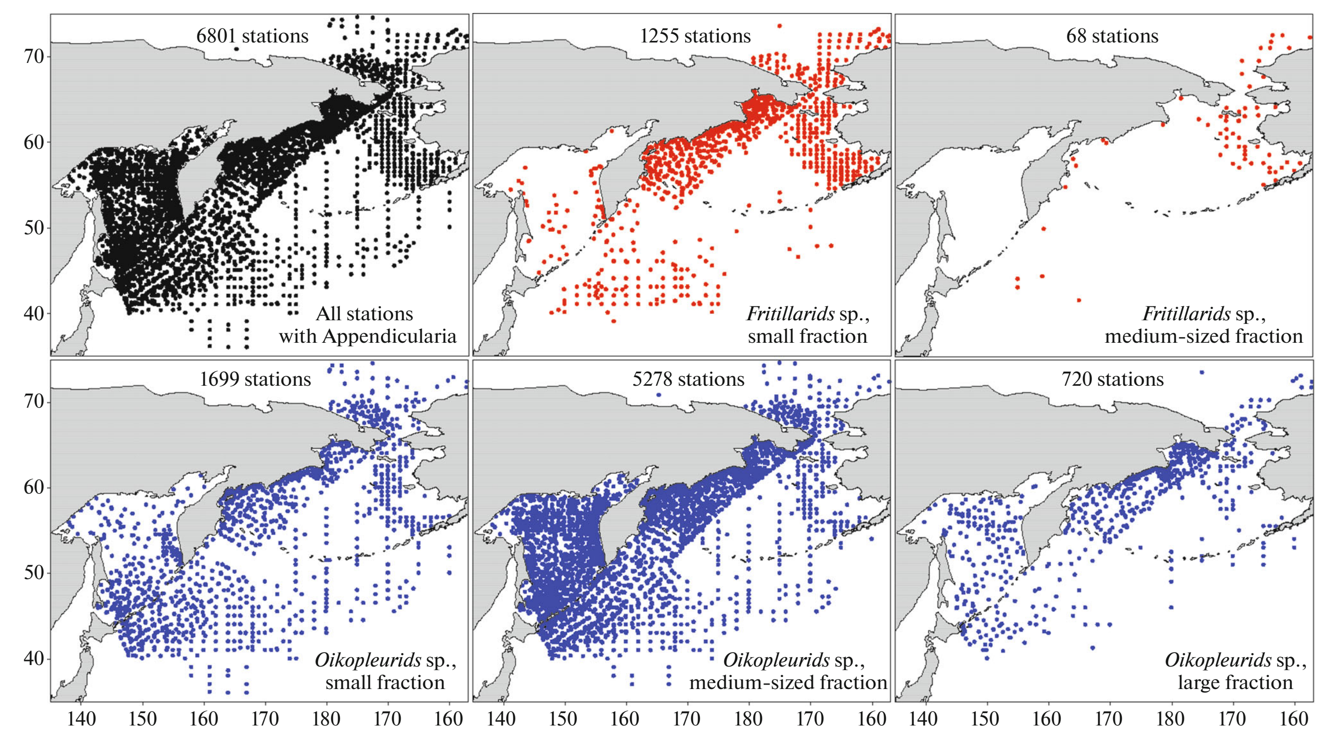

Fig. 5. Plankton stations with findings of Appendicularia (1984–2021).

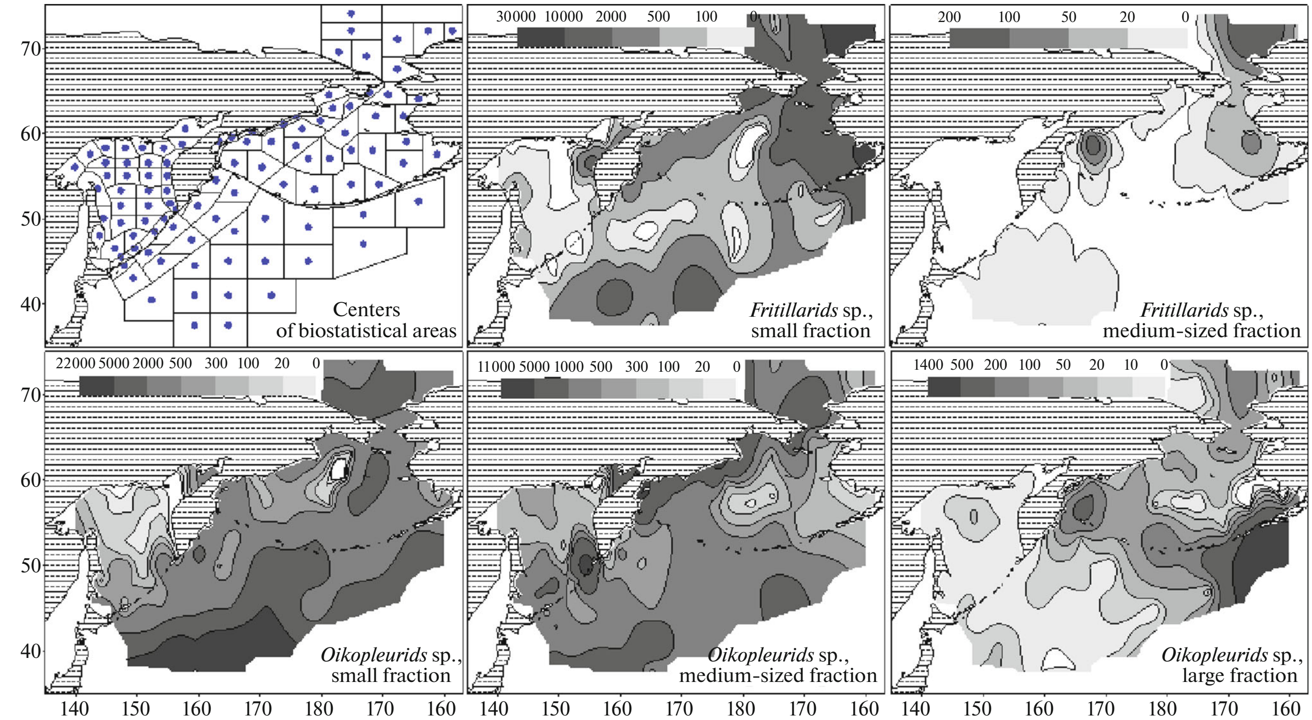

Fig. 6. The distribution of Appendicularia in the epipelagic layer, ind./m^2.

small or medium size, whereas the larvaceans with their houses are much larger. Apparently, these large houses attract many fish as prey. Indeed, the houses themselves, even those left by animals, have a certain value as food, since they contain small organisms stuck in the trapping net. Therefore, the role of Appendicularia in the plankton community and in feeding of nekton is significantly and systematically underestimated. The larvaceans without houses are considered as the most significant subdominant group of the large fraction of zooplankton (Table 1), but together with their houses, they may well be among the dominant ones, as they are rather numerous due to their efficient filtering system. In the Bering Sea, larvaceans are more abundant than all other mesozooplankton groups, except small copepods [17], although they are the sixth group of the large fraction by biomass (stock), after Copepoda, Euphausiacea, Amphipoda, Chaetognatha, and Coelenterata. There is no doubt that their biomass together with the houses (up to six per day) is much higher and may be higher than the biomass of these leading groups.

Oikopleurids occur in all three size fractions. Their number naturally decreases with age because of natural mortality, grazing, and spawning, as the eggs come out through a gap in the back of the body, after which the spawned individuals perish in the day [15]. Therefore, the large adults are found in samples only for a

Table 1. The mean stock of nondominant groups in large zooplankton including Appendicularia, 10^3 t

Region	Mysidacea	Decapoda	Cumacea	Ostracoda	Pteropoda	Polychaeta	Species, size fractions				All Appendicularia
							Oikopleurids, small fraction	Oikopleurids, medium fraction	Oikopleurids, large fraction	Fritillaris, small- and medium-sized fractions	
Bering Sea	188	400	256	33	995	233	89	693	446	74	1651
Okhotsk Sea	515	42	3	40	630	12	9	458	29	3	594
North Pacific	104	157	398	353	1188	1106	1000	2024	1868	63	4711
Chukchi Sea	312	104	2	6	375	4	104	410	205	100	939
Entire studied area	1118	703	658	432	3188	1355	1202	3585	2548	240	7895

Table 2. The mean biomass and abundance of Appendicularia in the epipelagic layer

Group of species	Size fraction	Bering Sea	Okhotsk Sea	North Pacific	Chukchi Sea	Bering Sea	Okhotsk Sea	North Pacific	Chukchi Sea
		Abundance, ind./m^3				Abundance, ind./m^2			
Oikopleurids sp.	Small fraction	8.6	1.0	21.6	49.3	1109	167	4244	2614
	Medium-sized fraction	7.5	4.9	4.1	19.9	971	807	813	1056
	Large fraction	0.50	0.03	0.50	1.5	62	6	104	79
Fritillarids sp.	Small fraction	22.0	0.9	4.2	149.0	2847	150	831	7904
	Medium fraction	0.10	0.01	0.01	1.26	13.0	1.5	1.1	67.0
		Biomass, mg/m^3				Biomass, mg/m^2			
Oikopleurids sp.	Small fraction	0.36	0.04	0.91	2.07	47	7	178	110
	Medium-sized fraction	3.38	2.18	1.86	8.96	437	363	366	475
	Large fraction	1.53	0.11	1.70	4.77	198	18	333	253
Fritillarids sp.	Small fraction	0.31	0.01	0.06	2.09	40	2	12	111
	Medium-sized fraction	0.005	0	0	0.067	0.7	0.1	0.1	3.5

short period of time, and their average abundance is low (Table 2). The lowest abundance and biomass of oikopleurids is observed in the Okhotsk Sea. Mass spawning of *O. vanhoeffeni* (and possibly *O. labradoriensis*) in the Bering Sea is extended in time and continues in the spring–summer [18]. Approximately at the same time, the spawning occurs in the North Atlantic [9]; conditionally, this timing can be considered for the Okhotsk Sea, too. In the warmer waters of the North Pacific, the spawning obviously occurs earlier. Appendicularia develop without metamorphosis, i.e., all larval stages pass in the egg and the already formed animal is hatched.

Fritillarids are found in the small- and medium size fractions only, mostly in the small one. They are more abundant in the Chukchi Sea (Table 2).

The seasonal dynamics of quantitative indices cannot be considered for larvaceans in all researched regions, since they are very different in their environments. Beyond the Chukchi Sea where the surveys were conducted in 2 summer months only, the Okhotsk Sea is distinguished by more severe conditions, including the ice cover; it is followed by the Bering Sea and North Pacific. Within each of these regions, the northern and southern parts are also climatically heterogeneous that is usually neglected in the data averaging. The months of year have different coverage by plankton stations that depends on timing of surveys focused on certain commercial species of nekton, as pacific salmon in the Okhotsk and Bering Seas in summer–autumn and walleye pollock in the Okhotsk Sea in spring (this is the reason that winter plankton samples are absent in the Bering Sea and scarce in the Okhotsk Sea). This is the reason some seasons do not provide much data on Appendicularia, despite the very large total amount of the data collected over more than 30 years. Some fluctuations on the graphs of seasonal dynamics (Fig. 7) are not representative enough, and their "trust level" should be controlled referring to Table 3. Usually Appendicularia are found in one sample among 10–100 samples, so their quantitative indices cannot be determined using a small number of zooplankton samples. In our collections, the minimum abundance of oikopleurids is observed in the Bering Sea from November to May, and fritillarids are absent in the Okhotsk Sea from December to June and in the North Pacific in May, August, and November.

N. Shiga [16] identified five stages of development for *O. vanhoeffeni*, according to the external characteristics of their gonads:

(1) no gonad (tail 0.33–2.75 mm);

(2) small and thin gonad in the form of testicle (0.69–3.76 mm);

(3) ovary is already larger than testicle, but width of gonad is noticeably less than the body width (0.94–12.60 mm);

(4) width of gonad is approximately equal to the body width (11.8–14.5 mm);

(5) adults: width of the developed gonad is greater than the body width (12.6–13.3 mm).

Thus, oikopleurids in the small- and medium-sized fractions are at the first–third stages of development and those in the large fraction, on the third–fifth stages. All spawning oikopleurids are on the fifth stage of development.

The medium-sized oikopleurids prevail by number in the Bering and Okhotsk Seas, but the small ones prevail in the North Pacific. The large oikopleurids are not numerous everywhere (Fig. 7). The medium-sized fraction predominance is caused either by the smaller individuals pushing through the mesh or by their rapid growth; the latter seems more likely. In the Bering Sea,

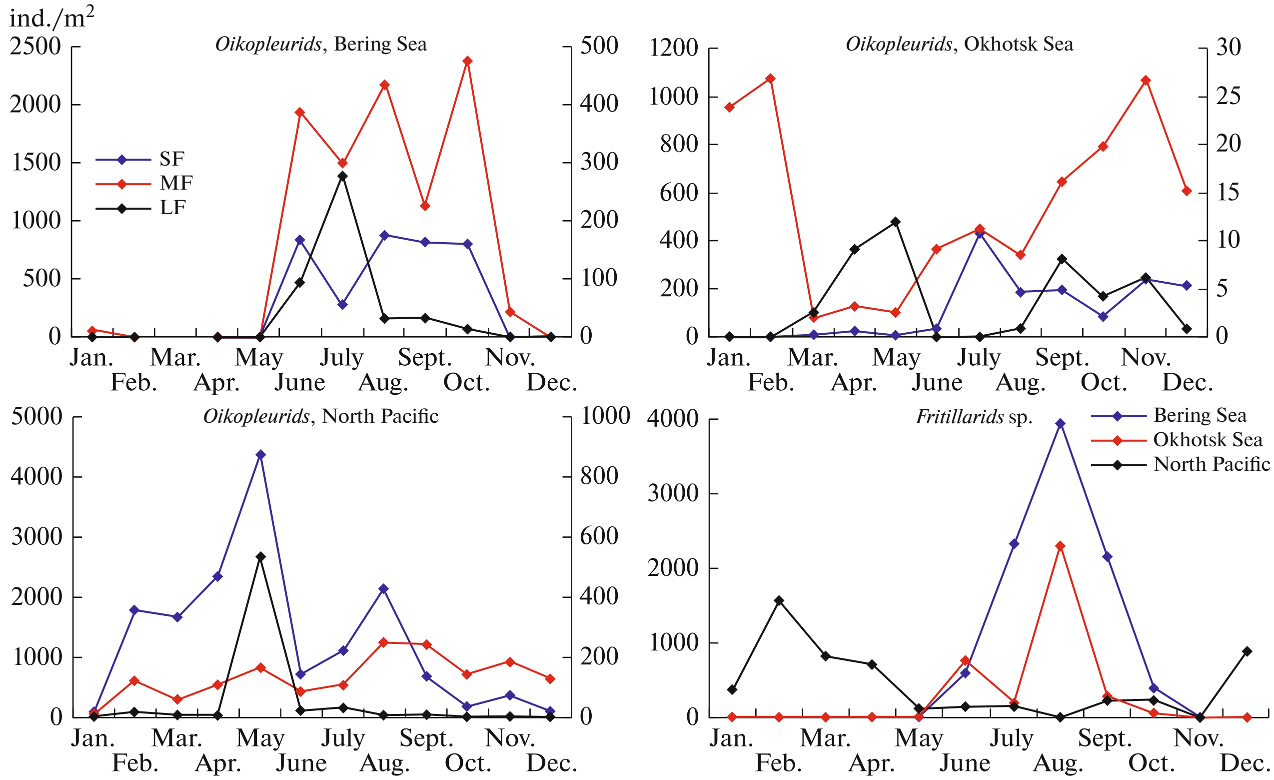

Fig. 7. The abundance of oikopleurids and fritillarids, ind./m^2 (SF, small fraction; MF, medium-sized fraction; LF, large fraction, right axis.

all three size fractions of oikopleurids are met mainly in summer–autumn, while the seasonal dynamics of the small- and medium-sized fractions coincide but the large fraction is the most abundant in July; its number then decreases sharply and large oikopleurids disappear by December. In the Okhotsk Sea, spawning of oikopleurids starts in February, when the first small individuals appear, but the peak of spawning occurs in June–December. Corresponding dynamics of the medium- and large oikopleurids are observed there. Both in the Bering and Okhotsk Seas, the highest abundance and biomass of all their size fractions are found in the shallowest waters (where they are accessible for the research vessels), and the number of oikopleurids decreases with the distance from the coast to the minimum in the deep sea (Table 4). This pattern is not traced for the North Pacific where all bathymetric zones, except the deep-sea one, are very narrow. Fritillarids are more abundant in the North Pacific in January–May and in the Bering and Okhotsk Seas in July–October.

In principle, some Appendicularia swim deeper than the epipelagic layer, but we note that all these species are fine-filterers with the food base located mainly in the photic layer. Their portion in the upper part of the epipelagic layer (0–50 m) is much larger than in its lower part occupying three-quarters of the layer (Table 5), with the exception of oikopleurids in the Bering Sea where their large fraction is distributed mainly in the lower epipelagic layer (83%).

Unfortunately, the interannual dynamics of Appendicularia cannot be analyzed in the plankton section of this study, although some long-term changes could be traced, which are possibly important for the food supply of nekton (Fig. 8).

Appendicularia in Nekton Food

Only medium-sized and large oikopleurids were found in the food of nekton, while small oikopleurids and fritillarids were almost completely absent, although they could be prey for small or young fish and squids that were not caught by large-mesh trawls. However, Appendicularia are presented in the diet throughout the whole area of their distribution, as it is shown based on example of six mass species of nekton in the Okhotsk Sea (on the Trophology database), so they are among preferable prey for these species (Fig. 9).

The role of Appendicularia in the food of fish and squid species is shown in detail in Tables 6–11 (with some averaged data in Tables 6 and 7).

All nekton species in the Trophology database with occurrence of larvaceans in their food are presented in Table 6. Out of 43 324 samples belonging to 151 nekton species, the larvaceans were found in 3061 samples

Table 3. The number of plankton stations and number of samples with Appendiculia, by months in 1984–2021

Stations	Month											
	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Bering Sea												
Total number of stations	1	2	0	106	80	597	678	926	1873	1060	262	106
Number of stations with findings of oikopleurids	1	0	0	1	1	328	215	322	627	464	27	1
Number of stations with findings of fritillarids	0	0	0	0	0	69	160	197	265	63	0	0
Okhotsk Sea												
Total number of stations	63	70	470	2290	2935	680	986	1117	669	1295	919	434
Number of stations with findings of oikopleurids	21	18	71	698	885	40	107	130	126	479	255	54
Number of stations with findings of fritillarids	0	0	0	0	0	0	11	7	15	23	3	0
North Pacific												
Total number of stations	109	71	675	222	46	763	476	242	152	109	199	129
Number of stations with findings of oikopleurids	9	37	279	142	41	455	139	69	72	29	51	17
Number of stations with findings of fritillarids	12	12	31	12	1	21	6	0	5	8	0	2

from 41 species, including such mass and commercially important species as walleye pollock, chum salmon, pink salmon, sockeye salmon, pacific herring, and northern smoothtongue (single Appendicularia in the food were regarded as occasions and the samples with their portion of less than 0.5% were not taken into account). The total portion of these nekton species in the database is very high, 41 507 samples (94.4%), and the percentage of Appendicularia in their food is significant in some cases (Table 8). Among the samples of stomachs from fish of different size classes with the highest portion of larvaceans, the index of stomach fullness with Appendicularia exceeded 200‱ for all size classes, although young of some mass fish species (pink salmon, chum salmon, walleye pollock) had a greater preference for larvaceans than their adults (Tables 9, 11). The role of Appendicularia in feeding fish decreases with the fish age, although it remains high for all size classes (see Table 11).

Thus, only 25% of all nekton species consume Appendicularia (on the Trophology database), but they include most of the mass species that form the basis of fishery, including pollock, polar cod, salmons,

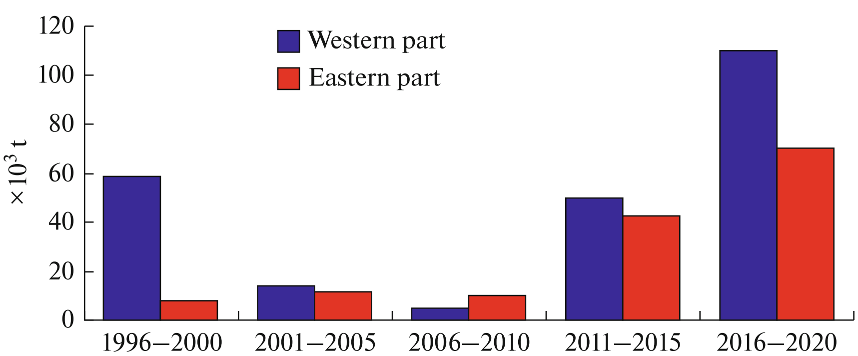

Fig. 8. Summary stock ($\times 10^3$ t) of oikopleurids in the biostatistical areas of the western (5–12, 19) and eastern (1–4, 13–18) parts of the northern Okhotsk Sea in spring, by 5-year periods. For better comparison, the total area of 420×10^3 km^2 is accounted for both parts, whereas the real area is 452×10^3 km^2 for the western part and 386×10^3 km^2 for the eastern part.

Table 4. The abundance and biomass of Appendicularia in the epipelagic layer, by bathymetric zones

Bathymetric zone	*Oikopleurids* sp.						*Fritillarids* sp.			
	ind/m^3			mg/m^3			ind/m^3		mg/m^3	
	small fraction	medium-sized fraction	large fraction	small fraction	medium-sized fraction	large fraction	small fraction	medium-sized fraction	small fraction	medium-sized fraction
Bering Sea										
Coastal (25–50 m)	35.5	48.7	0.9	1.49	21.9	2.97	92.2	0.39	1.29	0.02
Internal shelf (50–100 m)	15.5	36.6	0.6	0.65	16.5	1.95	69.0	0.24	0.97	0.01
External shelf (100–200 m)	4.1	9.6	0.3	0.17	4.3	0.80	9.5	0.00	0.13	0.00
Continental slope (200–500 m)	1.1	9.8	0.2	0.05	4.4	0.53	3.0	0.00	0.04	0.00
Deep-water (>500 m)	2.3	5.5	0.5	0.10	2.5	1.76	2.9	0.15	0.04	0.01
Okhotsk Sea										
Coastal (< 50 m)	3.1	41.9	0.01	0.13	18.9	0.04	5.7	0	0.08	0
Internal shelf (50–100 m)	1.7	8.0	0.01	0.07	3.6	0.04	2.8	0	0.04	0
External shelf (100–200 m)	0.5	2.3	0.04	0.02	1.1	0.12	4.1	0	0.06	0
Continental slope (200–500 m)	0.1	1.5	0.05	0.01	0.7	0.17	0.5	0	0.01	0
Deep-water (>500 m)	1.0	5.1	0.03	0.04	2.3	0.11	0.1	0	0.00	0

Table 5. Appendicularia abundance in the entire epipelagic layer (0–200 m), in its upper part (0–50 m), and in its lower part (50–200 m)

Region	Fritillarids, small- and medium-sized fractions	Oikopleurids, small- and medium-sized fractions	Oikopleurids, large fraction	Fritillarids, small- and medium-sized fractions	Oikopleurids, small- and medium-sized fractions	Oikopleurids, large fraction	Fritillarids, small- and medium-sized fractions	Oikopleurids, small- and medium-sized fractions	Oikopleurids, large fraction
	entire epipelagic layer (0–200 m)			upper epipelagic layer (0–50 m)			lower epipelagic layer (50–200 m)		
Abundance, ind./m^3									
Bering Sea	6.4	9.3	0.61	24.70	24.8	0.42	0.29	4.1	0.67
Okhotsk Sea	0.3	9.6	0.06	0.74	22.4	0.14	0.13	5.4	0.03
North Pacific	3.2	11.7	0.10	8.34	37.8	0.30	1.53	3.0	0.03
Abundance, ind./m^2									
Bering Sea	1280	1861	122	1236	1241	21	44	620	101
Okhotsk Sea	56	1921	12	37	1118	7	19	803	5
North Pacific	647	2341	20	417	1891	15	230	450	5
Portion of the total abundance within the epipelagic layer, %									
Bering Sea	100	100	100	97	67	18	3	33	83
Okhotsk Sea	100	100	100	65	58	55	34	42	42
North Pacific	100	100	100	64	81	72	36	19	25

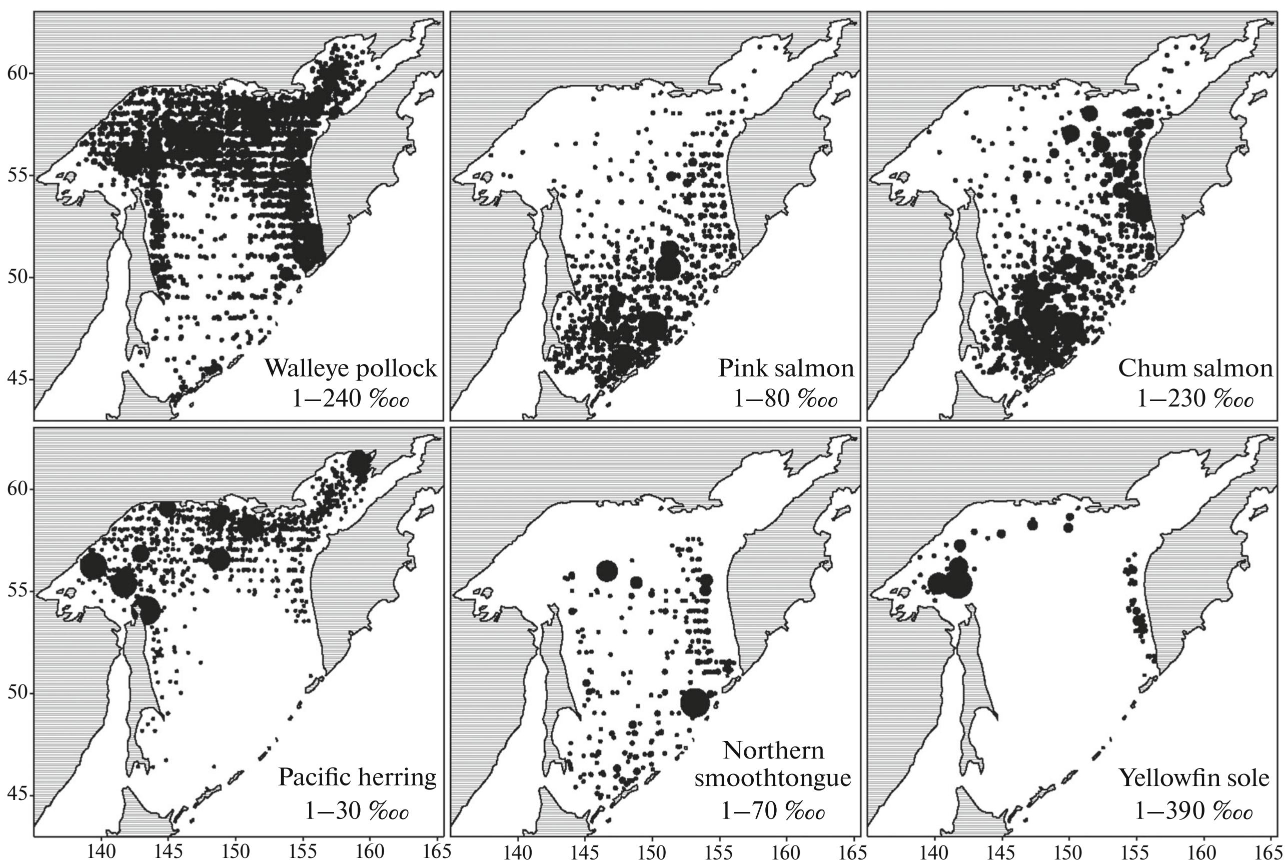

Fig. 9. Oikopleurids in food of mass fish species in the Okhotsk Sea.

Table 6. The rank of Appendicularia in food of nekton by number of samples with their findings in food of nekton, by number of samples with their findings

Nekton species	Index of stomach fullness, ‱	Index of stomach fullness for oikopleurids, ‱	Percentage of oikopleurids in the food in stomach	Total number of samples	Number of samples with oikopleurids	Percentage of samples with oikopleurids
Theragra chalcogramma	89	19	21	12819	1457	11.4
Oncorhynchus keta	89	37	42	8730	951	10.9
Oncorhynchus gorbuscha	92	22	24	5191	122	2.4
Oncorhynchus nerka	76	22	29	4058	73	1.8
Clupea pallasii	121	21	17	2642	55	2.1
Average indices and total number of samples for the top-5 species	**93**	**24**	**26**	**33440**	**2658**	**7.9**
Oncorhynchus tschawytscha	103	10	10	1819	1	0.1
Oncorhynchus kisutch	65	32	49	1144	4	0.3
Mallotus villosus	121	27	22	536	7	1.3
Leuroglossus schmidti	41	10	25	526	96	18.3
Gadus morhua macrocephalus	120	52	43	419	1	0.2
Oncorhynchus masou	104	33	32	394	1	0.3
Gonatopsis borealis	93	6	6	345	2	0.6
Scomber japonicus	160	46	29	331	48	14.5
Reinchardtius hippoglossoides	132	22	17	288	2	0.7
Boreogadus saida	125	31	25	209	26	12.4
Average indices and total number of samples for the 6–15 species	**106**	**27**	**25**	**6011**	**188**	**3.1**
Salvelinus malma	71	25	35	174	1	0.6
Limanda sakhalinensis	146	85	58	165	29	17.6
Stenobrachius leucopsarus	80	4	5	152	4	2.6
Berryteuthis magister	35	10	30	150	1	0.7
Pleurogrammus monopterygius	98	20	20	140	4	2.9
Sardinops melanostictus	98	35	36	136	22	16.2

Table 6. (Contd.)

Nekton species	Index of stomach fullness, ‱	Index of stomach fullness for oikopleurids, ‱	Percentage of oikopleurids in the food in stomach	Total number of samples	Number of samples with oikopleurids	Percentage of samples with oikopleurids
Scomber australicus	89	26	29	136	13	9.6
Pleurogrammus azonus	68	22	32	131	7	5.3
Eleginus gracilis	292	86	29	110	13	11.8
Limanda aspera	140	28	20	91	1	1.1
Diaphus theta	203	35	17	78	10	12.8
Ammodytes hexapterus	212	66	31	70	6	8.6
Bathylagus ochotensis	31	16	54	59	29	49.2
Tarletonbeania crenularis	207	114	55	58	5	8.6
Gymnocanthus detrisus	232	110	47	56	7	12.5
Stenobrachius nannochir	12	4	28	55	2	3.6
Engraulis japonicus	98	7	7	54	5	9.3
Symbalophorus californiensis	92	6	7	43	5	11.6
Sebastes borealis	155	81	52	37	2	5.4
Lipolagus ochotensis	33	12	37	35	25	71.4
Coryphaenoides cinereus	78	7	9	34	8	23.5
Onychoteuthis banksii	55	11	20	25	6	24.0
Salvelinus leucomaenis	50	17	33	20	2	10.0
Myoxocephalus jaok	274	164	60	19	1	5.3
Ceratoscopelus warmingii	138	41	30	16	1	6.3
Pseudobathylagus milleri	19	11	60	12	3	25.0
Average indices and total number of samples for the 6–41 species	**116**	**40**	**35**	**2056**	**212**	**10.3**

Table 7. Appendicularia in food of seven nekton species with the highest number of samples

Nekton species	Number of samples with oikopleurids	Total number of samples	Percentage of samples with oikopleurids	Index of stomach fullness for oikopleurids, ‱	Index of stomach fullness, ‱	Percentage of oikopleurids in the food in stomach
Bering Sea						
Oncorhynchus keta	604	4848	12	34	86	39
Oncorhynchus nerka	47	2929	2	22	76	30
Oncorhynchus gorbuscha	38	1816	2	36	121	30
Theragra chalcogramma	216	1688	13	33	162	21
Clupea pallasii	24	506	5	28	106	27
Leuroglossus schmidti	17	49	35	11	20	56
Bathylagus ochotensis	23	31	74	16	25	62
Top-7 dominant species	**969**	**11867**	**8**	**26**	**85**	**30**
Sub-dominant species (11)	**34**	**1209**	**3**	**18**	**93**	**19**
Okhotsk Sea						
Theragra chalcogramma	1186	10499	11	17	77	22
Clupea pallasii	28	2093	1	11	138	8
Oncorhynchus keta	183	1605	11	42	94	44
Oncorhynchus gorbuscha	46	1553	3	15	65	23
Leuroglossus schmidti	67	427	16	8	41	20
Limanda sakhalinensis	29	137	21	85	146	58
Lipolagus ochotensis	23	29	79	13	31	41
Top-7 dominant species	**1562**	**16343**	**10**	**27**	**85**	**32**
Sub-dominant species (16)	**47**	**1513**	**3**	**37**	**99**	**37**
North Pacific						
Oncorhynchus keta	161	2249	7	44	94	47
Oncorhynchus gorbuscha	35	1798	2	17	84	20
Oncorhynchus nerka	20	979	2	24	68	35
Theragra chalcogramma	55	608	9	9	80	11
Scomber japonicus	48	331	15	46	160	29
Sardinops melanostictus	22	116	19	35	98	36
Scomber australicus	13	136	10	26	89	29
Top-7 dominant species	**354**	**6217**	**6**	**29**	**96**	**30**
Sub-dominant species (9)	**41**	**485**	**8**	**26**	**119**	**22**
Chukchi Sea						
Boreogadus saida	22	131	17	34	117	29
Eleginus gracilis	13	39	33	86	292	29
Ammodytes hexapterus	3	31	10	88	299	30
Clupea pallasii	3	30	10	55	86	64
Oncorhynchus keta	3	28	11	85	176	48
Mallotus villosus	2	27	7	34	76	45
Oncorhynchus gorbuscha	3	24	13	20	205	10
Top-7 dominant species	**49**	**310**	**16**	**58**	**179**	**32**
Sub-dominant species (2)	**2**	**11**	**18**	**26**	**113**	**23**

Table 8. The portion of oikopleurids in food of nekton species (the portions >0.5‰ are taken into account), ‰

Number of samples with oikopleurids	Portion of samples with oikopleurids in the total number of samples	Index of stomach fullness for oikopleurids		Index of stomach fullness	
		minimum value	maximum value	minimum value	maximum value
6	0.2	327.0	556	329	556
6	0.2	254.0	294	254	392
22	0.7	205.0	252	220	493
23	0.8	153.0	199	153	526
97	3.2	100.0	150	101	1020
310	10.1	50.0	100	50	625
700	22.9	20.0	50	20	659
534	17.4	10.0	20	10	765
1364	44.5	0.6	10	1	514

Table 9. The highest portions of Appendicularia in food of certain size-classes of nekton (top-20 samples), ‰

Rank of sample	5–10 cm		10–20 cm		20–30 cm		30–40 cm		40–60 cm		60–80 cm	
	Index of stomach fullness for oikopleurids	Index of stomach fullness	Index of stomach fullness for oikopleurids	Index of stomach fullness	Index of stomach fullness for oikopleurids	Index of stomach fullness	Index of stomach fullness for oikopleurids	Index of stomach fullness	Index of stomach fullness for oikopleurids	Index of stomach fullness	Index of stomach fullness for oikopleurids	Index of stomach fullness
1	425	567	371	382	556	556	327	503	252	280	294	327
2	270	365	329	329	388	400	282	352	233	480	220	220
3	244	305	265	316	239	239	275	392	214	428	197	241
4	227	227	254	254	237	493	209	419	213	426	136	169
5	210	233	235	264	233	333	207	220	206	254	87	134
6	182	460	227	267	228	397	170	213	199	209	80	114
7	168	526	218	242	227	268	157	175	180	401	76	76
8	136	169	188	406	225	225	136	272	180	401	73	182
9	128	233	175	183	211	281	131	187	172	391	62	62
10	111	222	173	173	207	261	130	131	170	213	61	81
11	100	250	171	263	165	172	127	181	169	338	60	66
12	84	241	170	191	164	274	119	239	156	157	58	194
13	58	115	167	167	153	153	117	260	154	193	53	68
14	57	381	166	166	149	173	111	556	147	227	50	50
15	56	94	150	191	149	152	111	333	146	146	48	119
16	54	105	136	379	142	178	109	109	144	146	47	121
17	52	120	132	331	141	141	107	182	143	286	46	154
18	48	323	131	194	138	138	107	153	139	232	45	227
19	46	56	130	131	136	136	106	125	139	201	45	135
20	45	451	123	154	135	180	104	190	137	195	44	63
Total number of samples	102		389		506		679		1214		172	

herring, mackerels, sardine, and some others (see Tables 7, 10). In some cases, Appendicularia form the basis or significant part of their food (Tables 6, 7, 10).

We note that trophologists (the author among them) frequently find a soup-like liquid in fresh stomach samples that presumably is the result of the Appendicularia house disintegration. Obviously, the houses, in particular, abandoned ones remained in plankton for a time due to their neutral buoyancy and have some contents that are attractive for consumers,

Table 10. The portion of oikopleurids in food of some fish species (number of cases with certain percentage)

Fish species	Percentage of oikopleurids in the food in stomach											Total number of samples	Percentage of samples with oikopleurids
	100	90–100	80–90	70–80	60–70	50–60	40–50	30–40	20–30	10–20	0.5–10.0		
Oncorhynchus gorbuscha	3	2	4	5	3	6	9	12	11	24	43	5191	2.4
Oncorhynchus keta	60	64	63	80	90	79	93	115	91	133	83	8730	10.9
Theragra chalcogramma	10	16	26	31	47	56	100	120	176	343	532	12819	11.4
Oncorhynchus nerka	2	4	1	0	3	5	8	9	14	10	17	4058	1.8
Boreogadus saida	0	1	2	0	0	0	1	4	2	8	8	209	12.4
Clupea pallasii	2	5	0	0	0	2	2	2	5	14	23	2642	2.1
Leuroglossus schmidti	3	2	3	2	4	4	9	11	18	20	20	526	18.3
Summary occurrence	80	94	99	118	147	152	222	273	317	552	726	34175	8.1

Table 11. Portion of oikopleurids in food of some common fish species, by size-classes

Fish species	Size class, cm	Index of stomach fullness, ‱	Index of stomach fullness for oikopleurids, ‱	Percentage of oikopleurids in the food in stomach	Number of samples
Oncorhynchus gorbuscha	10–20	167	48	28	24
	20–35	78	19	24	50
	35–50	77	15	20	41
Oncorhynchus keta	10–20	147	69	47	73
	20–30	104	53	51	132
	30–40	75	37	49	125
	40–50	89	33	37	201
	50–60	86	33	39	265
	60–75	67	23	34	145
Theragra chalcogramma	5–10	182	36	20	20
	10–20	156	28	18	48
	20–30	100	17	17	177
	30–40	82	18	22	400
	40–50	85	20	24	411
	50–70	107	23	21	197

although the nutritional value of a house itself is low. Unfortunately, it is impossible to count the number of abandoned houses both in plankton and fish food, and, accordingly, to determine their significance in the nekton diet.

An indicative case was noted in the summer of 1988 when sexually mature walleye pollock with the stomachs filled with larvaceans and liquid from their houses were sampled in mass in the Okhotsk Sea at Kamchatka, sometimes with stomach contents of more than 10% of the body weight [3]. Possibly, the abnormal feeding of these pollock was due to sharp decrease of Euphausia abundance in this area, on the background of a high abundance of Appendicularia (which was not registered, perhaps because of active consumption by pollock). In all subsequent years, such an anomaly of pollock feeding was not observed.

CONCLUSIONS

The significance of Appendicularia in the plankton community and for the nekton food supply is still underestimated in the Far-Eastern Seas and North Pacific, partially because of insufficient knowledge about these species and lack of scientific literature, in particular, Russian. They could be ranked by biomass (stock) immediately behind the dominant groups of large zooplankton (Copepoda, Euphausia, Chaetognatha, Amphipoda, and Coelenterata), even if one counts only the animals, without their houses, while with the houses they should be added to the list of the dominant groups. In the entire studied area, Appendicularia are represented by three species: *Oikopleura vanhoeffeni*, *O. labradoriensis*, and *Fritillaria borealis*; *Fritillaria* sp. (possibly *F. pacifica*) dwell in the southern periphery of the North Pacific. The larger and more numerous oikopleurids prevail by their abundance and biomass. Fritillaris are presented mostly in the small fraction of zooplankton and insignificantly in the middle-sized fraction. Appendicularia form the densest accumulations in the upper epipelagic layer (from 55 to 97% of their number in the entire epipelagic layer), where they find the highest concentration of their prey.

In the Bering and Okhotsk Seas, the abundance and biomass of Appendicularia are higher in the coastal zone (with the depths of less than 50 m) and decrease in the order shelf–continental slope–deep waters. In the surveyed parts of the North Pacific and Chukchi Sea, the deep-water and coastal areas prevail, accordingly.

Appendicularia are a significant part of the diet for many nekton species (41 out of 151 species in the Trophology database), including the main commercial fishes (pollock, salmons, herring, polar cod, mackerels, sardine, and others), even without the houses, whose portion cannot be evaluated. Beyond some nutritional value, their mucus houses, glowing at night, with an animal inside whose tail vibrates constantly, attract many plankton eaters. High indices of the stomach fullness with Appendicularia (>200‱) are observed for all size classes of nekton, although the averaged indices for the young of some mass fish species (pink salmon, chum salmon, and walleye pollock) are higher than for their adults.

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REFERENCES

1. Volkov, A.F., Opportunities and techniques of using the databases of TINRO “Zooplankton of the North Pacific, Okhotsk, Bering, and Chukchi Seas”, “Nekton trophology”, and “Marine biology”, *Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr.*, 2019, vol. 198, pp. 239–261. https://doi.org/10.26428/1606-9919-2019-198-239-261
2. Volkov, A.F., Technique of collecting and processing the samples of plankton and the samples on nekton feeding (step-by-step instructions), *Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr.*, 2008, vol. 154, pp. 405–416.
3. Volkov, A.F., Gorbatenko, K.M., and Efimkin, A.Ya., Feeding ways of pollock, *Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr.*, 1990, vol. 111, pp. 123–132.
4. Naumov, N.P. and Kartashev, N.N., *Zoologiya pozvonochnykh. 1. Nizshiye khordovyye, beschelyustnyye, ryby, zemnovodnyye* (Zoology of Vertebrates, Part 1: Lower Chordates, Jawless, Fish, Amphibians), Moscow: Vysshaya Shkola, 1979.
5. Shuntov, V.P., Volkov, A.F., Temnykh, O.S., and Dulepova, E.P., *Mintai v ekosistemakh dal’nevostochnykh morei* (Walleye Pollock in Ecosystems of the Far-Eastern Seas), Vladivostok: Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr., 1993.
6. Alldredge, A.L., Abandoned larvacean houses: A unique food source in the pelagic environment, *Science*, 1972, vol. 177, no. 4052, pp. 885–887. https://doi.org/10.1126/science.177.4052.885
7. Alldredge, A.L., Discarded appendicularian houses as sources of food, surface habitats, and particulate organic matter in planktonic environments, *Limnol. Oceanogr.*, 1976, vol. 21, no. 1, pp. 14–24. https://doi.org/10.4319/lo.1976.21.1.0014
8. *An Illustrated Guide to Marine Plankton in Japan*, Chihara, M. and Murano, M., Eds., Tokyo: Tokai Univ. Press, 1997.
9. Choe, N. and Deibel, D., Life history characters and population dynamics of the boreal larvacean *Oikopleura vanhoeffeni* (Tunicata) in Conception Bay, Newfoundland, *J. Mar. Biol. Assoc. U. K.*, 2011, vol. 91, no. 8, pp. 1587–1598. https://doi.org/10.1017/S0025315410001876
10. Gorsky, G. and Fenaux, R., The role of Appendicularia in marine food webs, in *The Biology of Pelagic Tunicates*, Bone, Q., Ed., Oxford: Oxford Univ. Press, 1998, pp. 161–169.
11. Knoechel, R. and Steel-Flynn, D., Clearance rates of Oikopleura in cold coastal Newfoundland waters: a predictive model and its trophodynamic implications, *Mar. Ecol.: Prog. Ser.*, 1989, vol. 53, pp. 257–266.
12. Lohmann, H., Die Appendicularien, *Nordisches Plankton*, 1901, vol. 2, no. 3, pp. 11–21.
13. Lohmann, H., *Die Appendicularien der Plankton-Expedition: Ergebnisse der Plankton-Expedition der Humboldt-Stiftung 1889*, Kiel: Lipsius und Tischer, 1896, vol. 2.
14. Maekakuchi, M., Abe, Y., Matsuno, K., Hirawake, T., and Yamaguchi, A., Horizontal and vertical distribution of the appendicularian community and population

structure in the Bering and Chukchi Seas during the summer of 2007, *Bull. Fish. Sci. Hokkaido Univ.*, 2018, vol. 68, no. 3, pp. 43–49. https://doi.org/10.14943/bull.fish.68.3.43

15. Paffenhöfer, G.A., On the biology of Appendicularia of the south-eastern North Sea, in *Proc. 10th Eur. Symp. Mar. Biol.*, Wetteren: Univ. Press, 1976, pp. 437–455.
16. Shiga, N., Maturity stages and relative growth of *Oikopleura labradoriensis* Lohmann (Tunicata, Appendicularia), *Bull. Plankton Soc. Jpn.*, 1976, vol. 23, pp. 81–95.
17. Shiga, N., Regional and annual variations in abundance of an Appendicularian, *Oikopleura labradoriensis* in the Bering Sea and the northern North Pacific Ocean during summer, *Bull. Plankton Soc. Jpn.*, 1982, vol. 29, no. 2, pp. 119–128.
18. Shiga, N., Regional and vertical distributions of *Oikopleura vanhoeffeni* on the northern Bering Sea shelf in summer, *Bull. Plankton Soc. Jpn.*, 1993, vol. 39, no. 2, pp. 117–126.
19. Shiga, N., Seasonal and vertical distributions of Appendicularia in the Volcano Bay, Hokkaido, Japan, *Bull. Mar. Sci.*, 1985, vol. 37, no. 2, pp. 425–439.
20. Shiga, N., Takagi, S., and Nishiuchi, K., Interannual variation and vertical distribution of appendicularians in the south of St. Lawrence Island, northern Bering Sea shelf, in summer, *Mem. Fac. Fish., Hokkaido Univ.*, 1998, vol. 45, no. 1, pp. 48–51.

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