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ORIGINAL PAPERS

Consequences of the Impacts of a Harmful Algal Bloom on Benthic Invertebrates in the Eastern Kamchatka Shelf

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Abstract—Data of bottom trawl surveys conducted in the shelf zone of Kronotsky and Avachinsky Bays and off the southeastern coast of the Kamchatka Peninsula at depths of 65–210 m in 2018 and 2022, before and after the harmful microalgal bloom that occurred off the Kamchatka coast in the fall of 2020, were compared. The results indicate a significant decrease in the species diversity, population density, and biomass of benthic organisms in the lower sublittoral zone in 2022 compared to 2018. The least affected area was the northernmost region (Kronotsky Bay), while the most severely affected area was the southernmost region off the southeastern Kamchatka coast south of Cape Povorotny, where the biomass and species diversity dramatically decreased. This is consistent with the satellite monitoring data on chlorophyll *a* concentration off the Kamchatka coast in September 2020. According to these data, the area of the highest chlorophyll *a* concentration was the greatest in Avachinsky Bay and off the southeastern Kamchatka coast, where the strongest reduction in biodiversity of marine invertebrates was recorded.

Keywords: benthos, biomass, biodiversity, bottom trawl survey, red tide, intense microalgal bloom, depletion of fauna

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INTRODUCTION

An environmental emergency occurred off the coast of Kamchatka as a result of a harmful algal bloom (HAB), which led to a mass die-off of benthic animals in the fall of 2020 [18]. The main cause of the HAB was positive sea surface temperature anomalies observed in the coastal waters all along the Kamchatka Peninsula coast in July–September 2020, while anthropogenic or other natural factors could not have caused such an environmental emergency in this region [3]. In this case, the red tide was caused by the proliferation of dinoflagellates of the genus *Karenia* for the first time [23]. As a consequence, there was a mass die-off of benthic animals and a dramatic damage to benthic communities in the upper sublittoral zone off the southeastern Kamchatka coast [11, 14], without, however, affecting the littoral zone [7, 17]. Sufficient aeration of the littoral waters and *Karenia* dinoflagellate avoidance of coastal areas freshened by runoff [14, 23] prevented fish kills and mass die-offs of aquatic organisms.

A great difference was found in the biomass and species composition of benthic animals during the bottom trawl surveys in the Kamchatka shelf waters before and after 2020, when a mass die-off of benthic animals occurred in the upper sublittoral zone [14, 23]. In this study, we present data of trawl surveys conducted in the same regions in the lower sublittoral zone in June–July 2018 and 2022 to assess the consequences of the HAB in the fall of 2020 over the entire shelf zone off the southeastern Kamchatka coast.

MATERIALS AND METHODS

The research is based on data on the bycatch of invertebrates (excluding commercial crabs and king crabs) collected during two integrated bottom trawl surveys in the Eastern Kamchatka shelf from Cape Kronotsky to Cape Lopatka aboard the R/V MRTK *Inzhener Martynov* and R/V MRTK 316 in 2018 and 2022. An 18.8/28.5 m pr. 591 bottom trawl was used as fishing gear. The trawl has a four-panel front part with a length of 22.36 m along the belly line and a two-panel codend with a length of 11.5 m. The codend was equipped with a fine-mesh (10 × 10 mm) webbing liner. The trawl headrope was 18.8 m long and was equipped with floats with a total floating capacity of

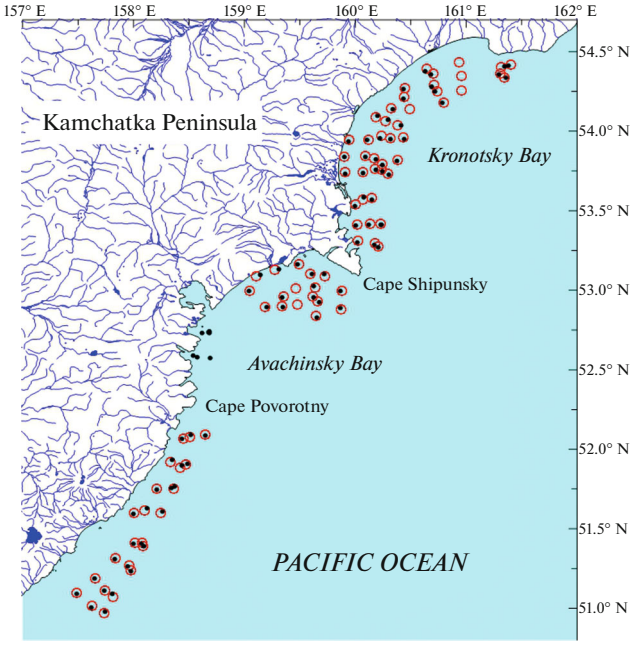

Fig. 1. A sampling map for the bottom trawl surveys; black opaque circles indicate trawl operation sites in 2018, and red transparent circles indicate trawl operation sites in 2022.

705 N. The trawl footrope was equipped with toggle chains and a groundrope chain with a total weight of 99.5 kg. The nominal trawl net opening was 3.5 m vertically and 16 m horizontally at a towing speed of 3.0 kn.The trawl was equipped with 2.5 m^2 oval trawl doors, trawl speed/symmetry sensors (Item ID: 109152), and with door position sensors (SS4 DoorSensor; Item ID: 109503) with temperature measurement (Item ID: 109148), depth (Item ID:109149-01), and angle detection (Item ID: 109147-01) functions.

Trawl hauls were conducted at a speed of 3.0 kn in the depth range of 65 to 210 m for 30 min in 2018 and for 15 min in 2022. A total of 86 trawl hauls were conducted in the Kronotsky and Avachinsky Bays and in the shelf waters of the southeastern part of the Kamchatka Peninsula south of Cape Povorotny in 2018; and 83 trawl hauls were conducted in the same areas in 2022 (Fig. 1). All invertebrates were collected from catches and, if possible, identified to the species level [4–6, 8–10, 12, 13, 15, 20, 22]. The numbers of individuals were counted and the total weight of each species was estimated. When it was impossible to sample a certain group of invertebrates (e.g., sea urchins) completely, a specified fraction of the catch was subsampled, identified to the species level, counted, weighed, and then recalculated to express the entire catch of the group in the trawl haul.

The population density (N) and biomass (M) of animal groups per unit of fished area (square kilometer) were calculated for each trawl station using the swept area method by the formulas:

$$N = \frac{n}{S} = \frac{n}{1.852vt0.001a} \text{ and } M = \frac{m}{S} = \frac{m}{1.852vt0.001a},$$

where n is number of individuals; m is weight (kg) of individuals of species or species group sampled; S is the area swept by the trawl (km^2); v is the trawling velocity (kn); t is the trawling time (h); and a is the horizontal opening of the trawl mouth (m) [1, 19]. The catchability coefficient for all groups was assumed to be 1 (100%). The calculations were performed using MS Excel. Distribution maps were composed in the Surfer 13 software by the Kriging method. The stock abundance (absolute biomass) was assessed using the KartMaster GIS program by spline approximation method of contouring a stock density, which is based on smoothing using a spline interpolation of the measurements at randomly located points and subsequent integration over the surveyed area [2, 16, 24, 25].

For the stock assessment in the KartMaster program, the following parameters were set: grid dimension was 500 × 500; smoothing parameter, 0; and water depth influence factor, 500.

Hydrological information (temperature, salinity) was collected using a CTD 48 profiler (Sea & Sun Technology) in 2018 and a JFE ASTD-102 profiler in 2022.

RESULTS AND DISCUSSION

Three study areas were included in the analysis: Kronotsky Bay (from Cape Kronotsky to Cape Shipunsky), Avachinsky Bay (from Cape Shipunsky to Cape Povorotny), and southeastern Kamchatka shelf extending south from Cape Povorotny (Fig. 1). Based on the results of trawl surveys conducted in 2018 and 2022, the average and maximum biomass per unit area (kg/km^2), average and maximum population density ($ind./km^2$), frequency of occurrence (relative number of samples where a species or group occurred, as a fraction of unity), absolute biomass (kg), and percentage in the average biomass (%) were calculated for 11 groups of benthic animals (at the rank of phylum, class, or order) in each area (Tables 1, 2). The distribution of biomass per unit area (kg/km^2) of aquatic organisms by group in each area in 2018 and 2022 is shown in Figs. 2–7. The range of surveyed depths was 65–204 m in 2018 and 75–210 m in 2022. The range of near-bottom temperatures was 1.55–4.97°C in 2018 and 0.69–2.61°C in 2022, with the highest temperatures observed in Avachinsky Bay. Salinity fluctuated within a range of 32.2–33.24 psu. The species composition with the frequency of occurrence in the three surveyed areas in 2018 and 2022 is given in Table 3.

The absolute biomass of all groups of aquatic organisms caught at all stations from Cape Kronotsky to the southern tip of Kamchatka was 2 875 664.85 kg in 2018 and 1 048 455.57 kg in 2022 (Fig. 8), i.e., it decreased by 2.74 times (by 63.5%). The Kronotsky Bay shelf waters were the least adversely affected area;

Table 1. Taxonomic composition, median (Med) and maximum (Max) biomass per unit area (kg/km^2); median (Med) and maximum (Max) population density (ind./km^2); frequency of occurrence (as a fractions of unity); parameters of maximum catches (temperature, salinity, and depth); percentage in average biomass (%) and absolute biomass (kg) of invertebrates in the bycatch during bottom trawl surveys in three areas in the Eastern Kamchatka shelf waters from Cape Kronotskyto Cape Lopatka in 2018

Group	Biomass per unit area, kg/km^2		Population density, ind./km^2		Frequency of occurrence	Parameters of maximum catches			Percentage in average biomass, %	Absolute biomass, kg
	med	max	med	max		T, °C	salinity, psu	depth, m		
Kronotsky Bay shelf										
Porifera	0.13	4.63	–	–	0.05	1.89	32.98	88	<1	589.53
Actiniaria	3.23	34.16	49	584	0.5	1.58	33.06	204	1	16311.78
Cephalopoda	46.67	975.37	17	315	0.2	1.57	33.03	110	12	220230.4
Bivalvia	1.28	32.45	4	67	0.13	1.74	33.05	140	<1	–
Gastropoda	19.69	151.83	251	1952	0.7	1.55	33.04	170	5	134959.9
Asteroidea	23.3	137.63	298	4900	0.7	–	–	65	6	74970.8
Echinoidea	249.37	3208.92	11986	186174	0.63	–	–	80	64	800576.9
Holothuroidea	0.08	3.15	1	45	0.03	2.22	32.92	187	< 1	–
Ophiuroidea	12.27	347.45	223	4180	0.3	–	–	105	3	160406.9
Decapoda	9.05	80.87	2490	51555	0.8	–	–	147	2	67094
Ascidiacea	27.96	498.2	426	7839	0.38	2.022	32.98	70	7	194171.5
Avachinsky Bay shelf										
Porifera	0.505	5.49	–	–	0.14	2.1	32.9	76	<1	581.53
Actiniaria	0.85	11.05	14	104	0.36	4.5	32.38	95	<1	563.2
Cephalopoda	10.48	209.76	24	259	0.27	1.86	32.98	141	3	34702.5
Bivalvia	33.19	584.18	47	831	0.18	1.73	33	111	10	–
Gastropoda	10.71	108.75	128	934	0.45	4.5	32.38	95	3	7316.3
Asteroidea	19.5	225.4	112	1141	0.68	4.5	32.38	95	6	13795.1
Echinoidea	188.89	2037.64	8454	108674	0.73	1.86	32.98	141	59	342729.3
Holothuroidea	3.02	48.03	10	156	0.14	4.5	32.38	95	1	3002.71
Ophiuroidea	9.56	95.09	1846	25471	0.45	1.86	32.98	141	3	22900.1
Decapoda	6.17	76.22	1271	22361	0.68	2.33	32.87	111	2	3797.4
Ascidiacea	40.91	294.87	374	2270	0.59	4.97	32.2	93	13	65692.51
Southeastern Kamchatka shelf										
Porifera	1.55	16.95	–	–	0.23	1.67	33.06	155	<1	2674.39
Actiniaria	8.6	67.42	133	899	0.45	2.01	32.98	160	2	17189
Cephalopoda	62.76	613.54	30	157	0.4	1.81	33.03	105	16	138629.4
Bivalvia	0.12	1.39	6	67	0.08	1.67	33.06	155	<	–
Gastropoda	20.49	50.88	317	1167	0.58	–	–	190	5	41140.1
Asteroidea	11.19	167.15	102	359	0.58	1.95	33.15	118	3	21681.1
Echinoidea	258.24	2562.03	9546	70119	0.48	1.67	33.06	155	67	445718
Holothuroidea	0	0	0	0	0	–	–	–	0	0
Ophiuroidea	5.67	43.64	277	1236	0.38	2.37	33.24	134	2	10324.1
Decapoda	13.24	56.83	1008	5900	0.6	2.37	33.24	134	4	28352.5
Ascidiacea	3.14	57.93	104	2045	0.13	2.37	33.24	134	1	5863.9

Table 2. Taxonomic composition, median (Med) and maximum (Max) biomass per unit area (kg/km^2); median (Med) and maximum (Max) population density (ind./km^2); frequency of occurrence (as a fractions of unity); parameters of maximum catches (temperature, salinity, and depth); percentage in average biomass (%), and absolute biomass (kg) of invertebrates in the bycatch during bottom trawl surveys in three areas in the Eastern Kamchatka shelf waters from Cape Kronotsky to Cape Lopatka in 2022

Group	Biomass per unit area, kg/km^2		Population density, ind./km^2		Frequency of occurrence	Parameters of maximum catches			Percentage in average biomass, %	Absolute biomass, kg
	med	max	med	max		*T*, °C	salinity, psu	depth, m		
Kronotsky Bay shelf										
Porifera	0	0	0	0	0	–	–	–	–	–
Actiniaria	2.03	45.17	25	405	0.23	1	32.83	80	1	9219.91
Cephalopoda	2.63	112.37	2	45	0.05	1.45	33.13	210	2	119979.6
Bivalvia	0.7	29.89	3	135	0.02	0.99	32.88	101	1	–
Gastropoda	9.14	111.34	101	1169	0.35	–	–	140	6	81 504.08
Asteroidea	22.33	148.96	73	854	0.47	1.52	33.06	121	15	54176.13
Echinoidea	87.18	2010.97	3515	68 321	0.4	1.03	32.94	86	60	542 571.4
Holothuroidea	0	0	0	0	0	–	–	–	–	–
Ophiuroidea	+	+	+	+	+	–	–	–	+	+
Decapoda	4.5	32.14	498	11 552	0.44	1.08	33.06	147	3	17 205
Ascidiacea	16.66	583.15	96	3057	0.16	1.16	33.04	89	12	124 388.3
Avachinsky Bay shelf										
Porifera	0.04	0.67	5	90	0.06	1.36	33.11	106	< 1	344.27
Actiniaria	0	0	0	0	0	–	–	–	0	0
Cephalopoda	12.69	215.75	8	135	0.06	1.73	32.59	98	51	33 185.6
Bivalvia	1.02	13.48	5	45	0.12	0.75	32.83	94	4	1349.4
Gastropoda	1.52	12.1	24	270	0.24	2.61	32.54	144	6	1641.58
Asteroidea	1.55	26.34	5	90	0.06	1.73	32.59	98	6	4051.4
Echinoidea	2.09	15.28	90	539	0.53	–	–	75	8	2689.48
Holothuroidea	+	+	+	+	0.06	–	–	–	+	+
Ophiuroidea	0	0	0	0	0	–	–	–	0	0
Decapoda	5.39	42.61	278	2203	0.71	1.36	33.11	106	22	19017.49
Ascidiacea	0.72	8.09	42	360	0.29	1.36	33.11	106	3	1455.26
Southeastern Kamchatka shelf										
Porifera	3.68	26.83	68.4	449	0.43	0.83	32.99	161	21	8248.84
Actiniaria	0	0	0	0	0	–	–	–	0	0
Cephalopoda	0.12	2.79	4	45	0.08	0.78	32.94	210	1	285.2
Bivalvia	0	0	0	0	0	–	–	–	0	0
Gastropoda	0	0	0	0	0	–	–	–	0	0
Asteroidea	0	0	0	0	0	–	–	–	0	0
Echinoidea	0	0	0	0	0	–	–	–	0	0
Holothuroidea	0	0	0	0	0	–	–	–	0	0
Ophiuroidea	0	0	0	0	0	–	–	–	0	0
Decapoda	13.1	86.89	1233	6787	0.95	0.69	32.92	198	76	26 620.8
Ascidiacea	0.31	583.15	4	3057	0.16	0.75	32.82	89	2	521.83

Plus sign (+) means occurrence of single, very small specimens that were not taken for measurements.

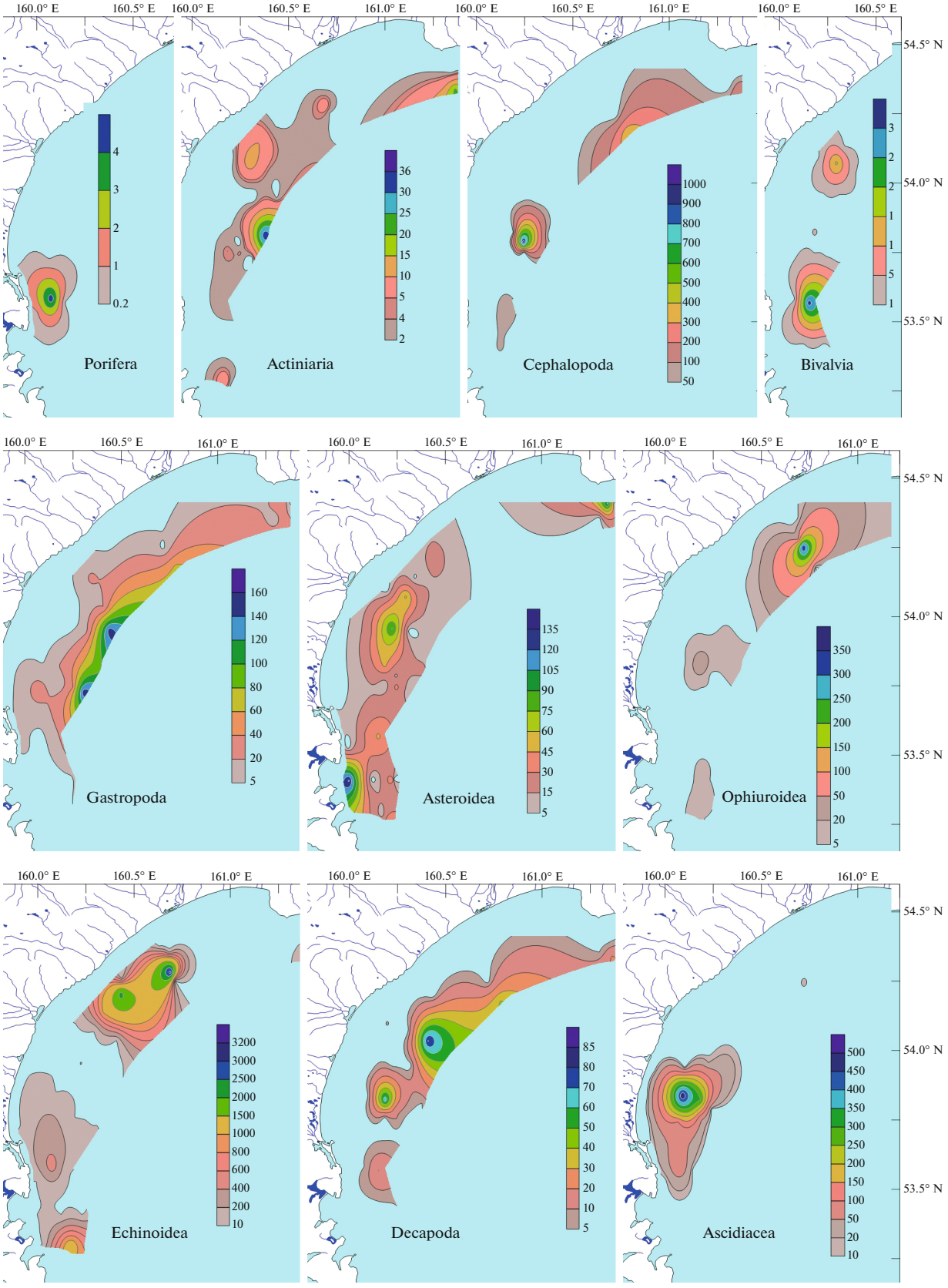

Fig. 2. The distribution of biomass per unit area (kg/km^2) of aquatic organisms by group in the Kronotsky Bay shelf waters in 2018.

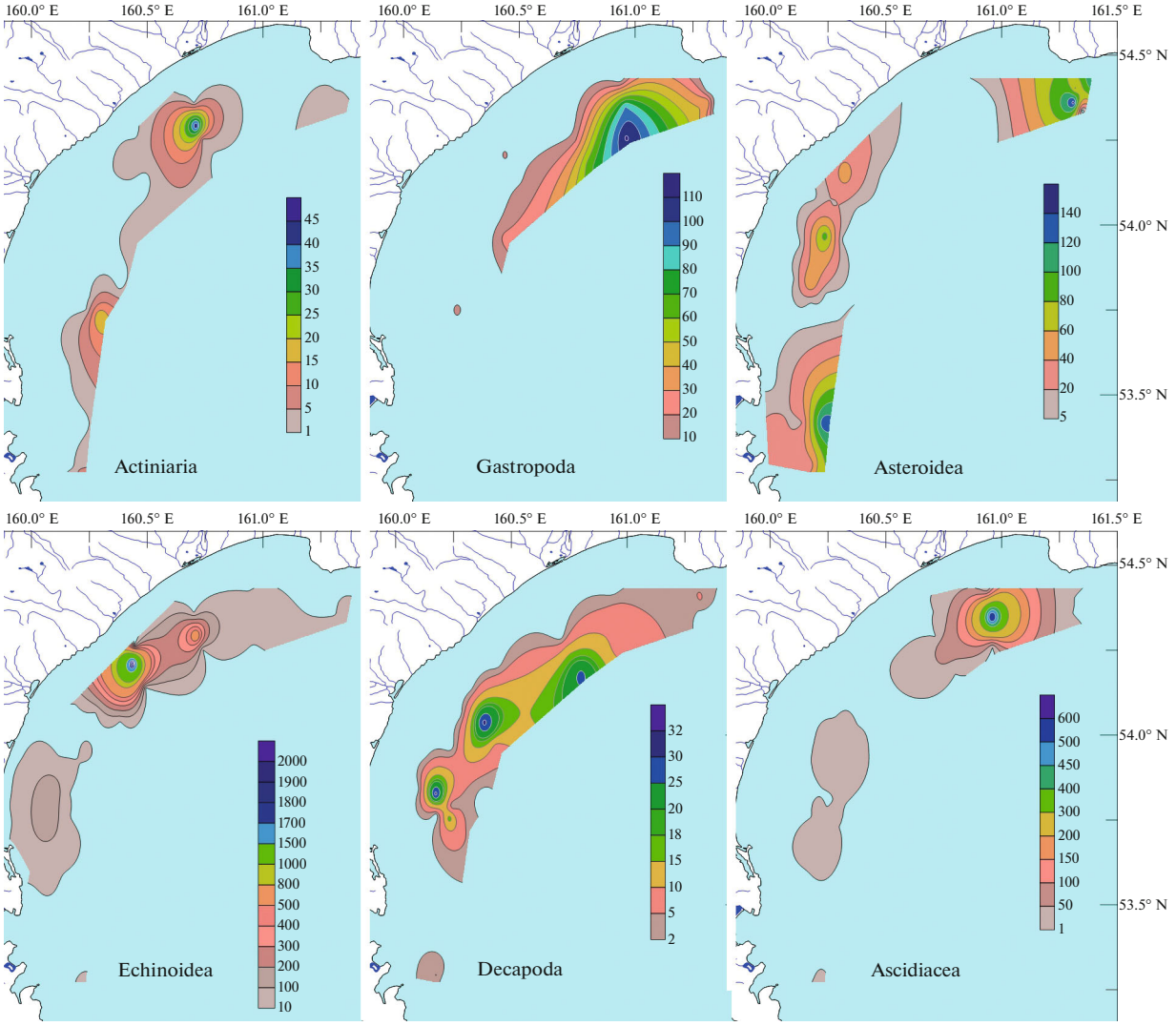

Fig. 3. The distribution of biomass per unit area (kg/km^2) of aquatic organisms by group in the Kronotsky Bay shelf waters in 2022.

the biomass of benthic invertebrates decreased by 1.76 times there in 2022 compared to 2018, and the loss was slightly more than 43%. In Avachinsky Bay, the biomass decreased by 7.77 times in 2022 compared to 2018; 87% of the benthic invertebrates died. The most catastrophic losses were observed in the southernmost study area, in the southeastern Kamchatka shelf waters south of Cape Povorotny, where the biomass of benthic invertebrates decreased by almost 20 times in the lower sublittoral zone, and 95% of the macrozoobenthos that had been recorded from bycatch of trawl surveys previously, died.

Holothurians and brittle stars almost completely disappeared from catches in 2022, with the exception of one small specimen of *Cucumaria* sp. and two very small young brittle star specimens, whose weights were not taken into account separately. Of the remaining groups, the most significant reduction in absolute biomass was recorded for sea anemones (by 3.7 times) and sea urchins (by 2.9 times). The decrease in absolute biomass was by more than two times in cephalopods (by 2.6 times), gastropods (by 2.2 times), and ascidians (by 2.1 times). The absolute biomass of starfish also decreased by almost two times (by 1.9 times), while the smallest decrease (by 1.6 times) was recorded for decapods without commercial crabs and king crabs. The absolute biomass of sponges showed an increase (by 2.2 times) in general, but only due to a three-fold increase in their numbers in bycatches in the southernmost area off the southeastern Kamchatka south of Cape Povorotny. However, the absolute biomass of sponges decreased by 1.7 times in the neighboring region, in the Avachinsky Bay shelf waters, and sponges were not found at all in the Kronotsky Bay shelf waters in 2022. Sea anemones completely disappeared from the bycatch in Avachinsky

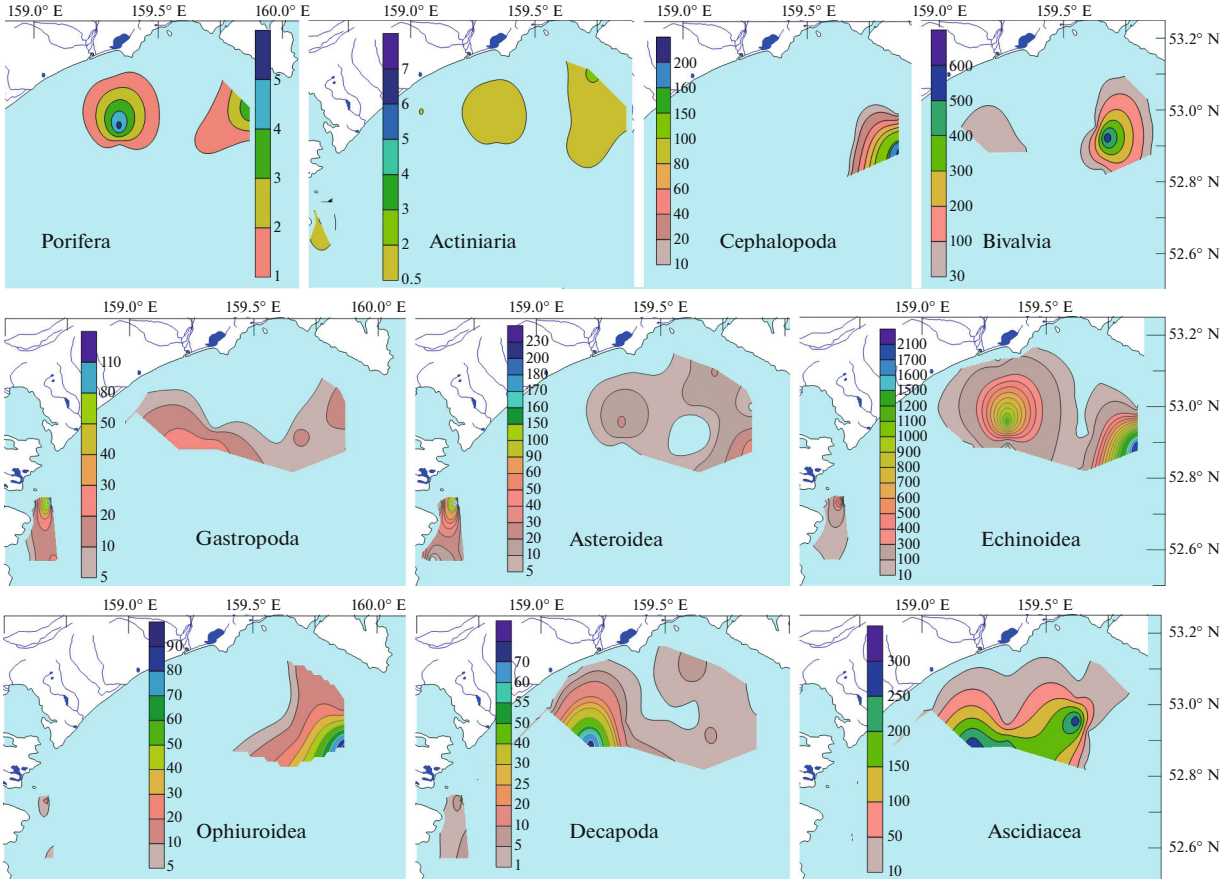

Fig. 4. The distribution of biomass per unit area (kg/km^2) of aquatic organisms by group in the Avachinsky Bay shelf waters in 2018.

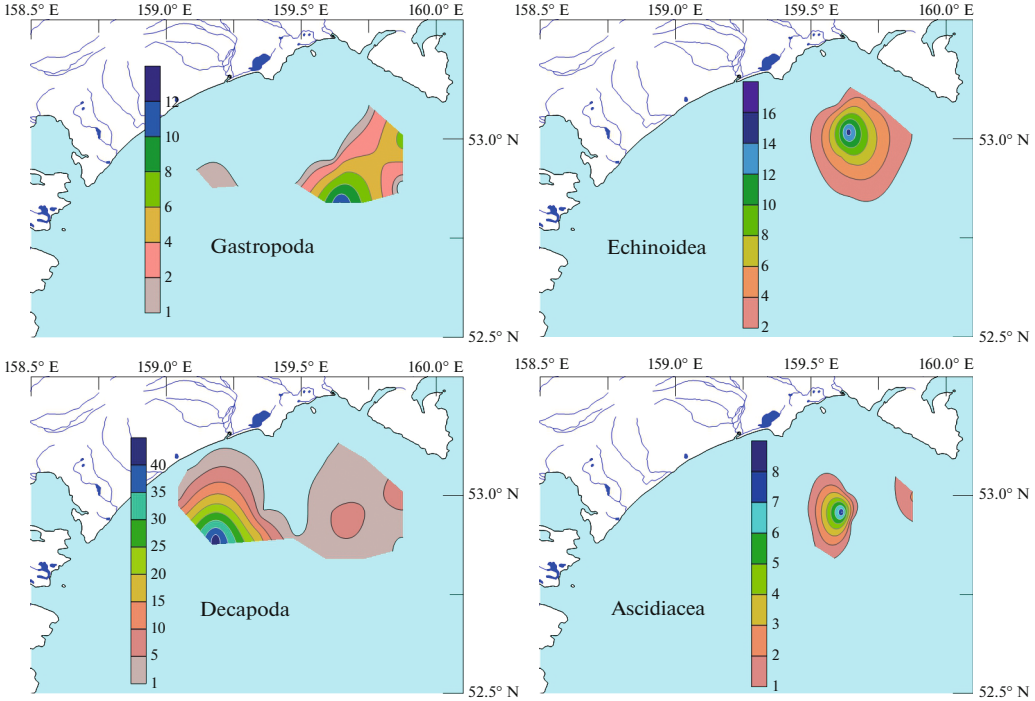

Fig. 5. The distribution of biomass per unit area (kg/km^2) of aquatic organisms by group in the Avachinsky Bay shelf waters in 2022.

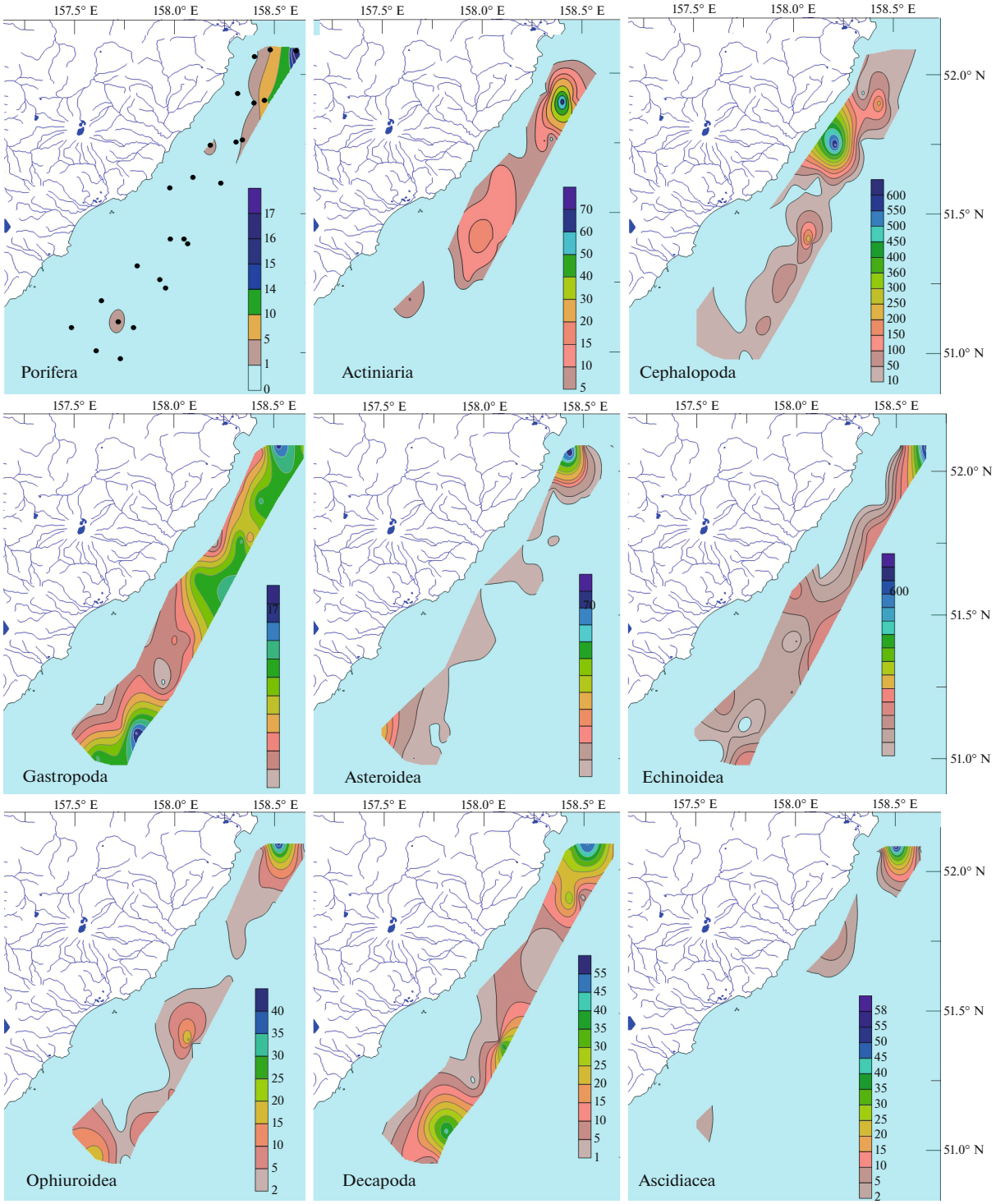

Fig. 6. The distribution of biomass per unit area (kg/km^2) of aquatic organisms by group in the southeastern Kamchatka shelf waters south of Cape Povorotny in 2018.

Bay and in an area to the southern tip of Kamchatka, while their biomass decreased by 1.8 times (by 43.5%) in the Kronotsky Bay shelf waters. The absolute biomass of cephalopods remained almost unchanged in Avachinsky Bay, decreased by 1.84 times (by 47.5%) in Kronotsky Bay, and catastrophically decreased, by 486 times (by 99.8%), in the southeastern Kamchatka shelf waters south of Cape Povorotny in 2022 compared to 2018 data. The absolute biomass of bivalve mollusks was not estimated. The absolute biomass of

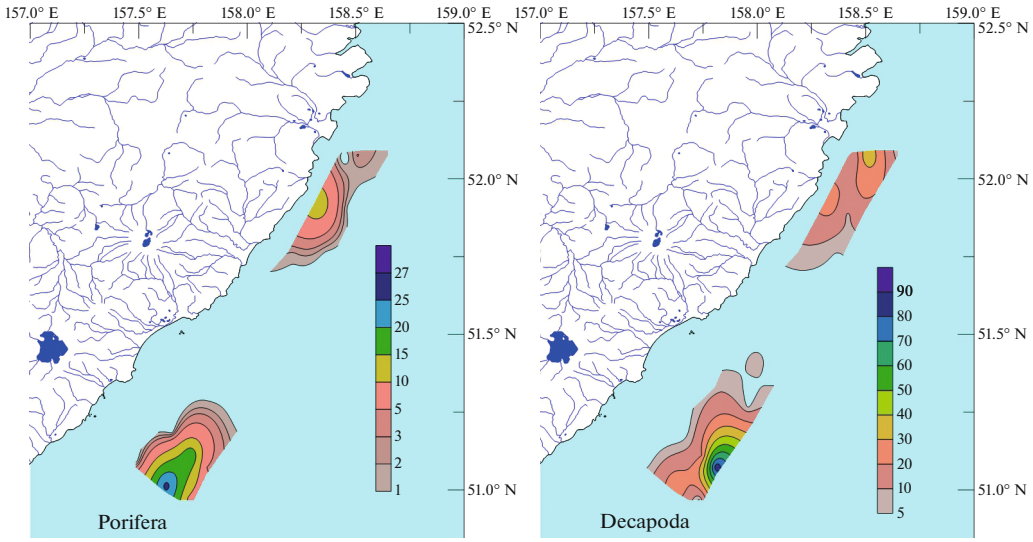

Fig. 7. The distribution of biomass per unit area (kg/km^2) of aquatic organisms by group in the southeastern Kamchatka shelf waters south of Cape Povorotny in 2022.

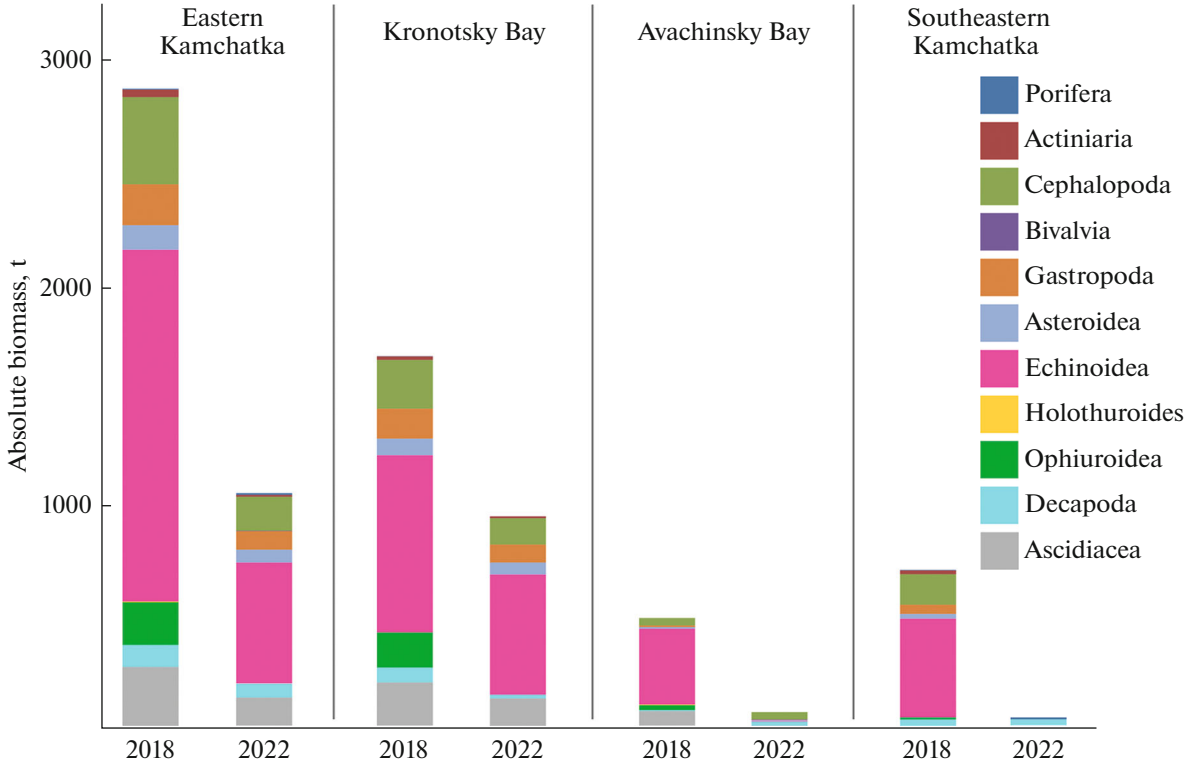

Fig. 8. The absolute biomass of invertebrate groups recorded from the bycatch of the bottom trawl surveys in 2018 and 2022.

gastropods decreased by 1.66 times (almost by 40%) in the Kronotsky Bay, by 4.5 times (by 77.5%) in Avachinsky Bay in 2022 compared to 2018, and this group disappeared completely from the southeastern Kamchatka shelf waters south of Cape Povorotny. A similar situation occurred with starfish and sea urchins: the absolute biomass of starfish decreased by 1.4 times (by 27%) and that of sea urchins decreased by 1.5 times (by 32%) in Kronotsky Bay; and by 3.4 times (by 70.6%) and by 127.4 times (by 99.2%) in Avachinsky Bay, respectively. Off the southeastern Kamchatka coast south of Cape Povorotny, echinoderms com-

Table 3. The frequency of occurrence of species (as a fraction of unity) in the bycatch of bottom trawl surveys in 2018 and 2022 in three areas in the Eastern Kamchatka shelf waters from Cape Kronotsky to Cape Lopatka

Species	2018			2022		
	Kronotsky Bay	Avachinsky Bay	Southeastern Kamchatka	Kronotsky Bay	Avachinsky Bay	Southeastern Kamchatka
Porifera						
Porifera varia	0.05	0.14	0.38	–	0.06	0.43
Actiniaria						
Actiniaria varia	0.5	0.32	0.75	0.23	–	–
Liponema brevicorne	0.05	–	0.04	–	–	–
Metridium cf. *farcimen*	–	0.05	0.17	–	–	–
Cephalopoda						
Enteroctopus cf. *dofleini*	0.2	0.05	0.5	0.05	0.06	0.08
Rossia pacifica	0.03	0.23	0.21	–	–	–
Bivalvia						
Chlamys behringiana	–	–	0.08	–	–	–
Serripes groenlandicus	–	–	–	0.02	0.12	–
Keenocardium californiense	0.03	–	0.04	–	–	–
Hiatella arctica	–	0.05	–	–	–	–
Musculus niger	0.05	–	–	–	–	–
Panomya ampla	0.05	0.18	–	–	–	–
Gastropoda						
Fusitriton oregonensis	0.05	0.09	0.21	–	–	–
Beringius behringii	–	–	0.08	–	–	–
Beringius sp.	–	–	0.04	–	–	–
Buccinum cristatum	0.1	–	–	–	–	–
Buccinum beringense	0.38	0.18	0.38	–	0.06	–
Buccinum cnismatum	0.03	–	–	–	–	–
Buccinum polare	0.18	0.05	0.13	0.28	0.06	–
Buccinum rossicum	–	–	0.04	–	–	–
Buccinum shiretokoense	–	–	0.04	–	–	–
Buccinum sp.	–	–	0.13	–	–	–
Neptunea cf. *excelsior*	0.08	–	0.04	0.23	–	–
Neptunea behringiana	0.13	0.05	–	–	0.18	–
Neptunea ventricosa	0.03	0.14	0.08	–	–	–
Neptunea lamellosa	0.1	–	0.04	–	–	–
Neptunea laticostata	0.05	0.14	0.42	–	–	–
Neptunea lyrata	0.05	–	0.33	–	–	–
Neptunea pribiloffensis	0.2	–	–	–	–	–
Neptunea multistriata	0.18	0.05	0.42	–	–	–
Neptunea vinosa	0.03	–	–	–	–	–
Neptunea convexa	0.1	–	0.04	–	–	–
Neptunea sp.	0.03	–	–	–	–	–
Clinopegma decora	0.03	0.05	0.13	–	–	–
Clinopegma chikaoi	0.03	0.23	0.04	–	–	–
Neancistrolepis beringiana	0.28	0.14	0.08	–	–	–
Neancistrolepis glabra	–	–	0.04	–	–	–

Table 3. (Contd.)

Species	2018			2022		
	Kronotsky Bay	Avachinsky Bay	Southeastern Kamchatka	Kronotsky Bay	Avachinsky Bay	Southeastern Kamchatka
Neoberingius frielei	0.15	0.09	0.08	–	–	–
Lussivolutopsius hydractiniferus	–	–	0.04	–	–	–
Plisifusus kroyeri	0.08	0.05	0.21	–	–	–
Pyrulofusus deformis	0.03	–	–	–	–	–
Pyrulofusus harpa	–	0.05	0.08	–	–	–
Volutopsius castaneus	0.13	0.14	0.33	–	–	–
Colidaespp.	–	–	0.08	–	–	–
Crepidula sp.	0.03	–	–	–	–	–
Cryptonatica aleutica	0.05	–	0.04	–	–	–
*Euspira*sp.	–	0.09	–	–	–	–
Boreotrophon sp.	–	–	0.13	–	–	–
Trichotropis bicarinata	0.03	–	–	–	–	–
Asteroidea						
Evasterias echinosoma	–	0.05	–	0.42	–	–
Asterias rathbuni	0.08	–	–	–	–	–
Leptasterias polaris	0.13	0.05	0.01	–	–	–
Leptasterias arctica	–	0.05	0.05	–	–	–
Lethasterias nanimensis	0.55	0.45	0.02	0.02	0.05	–
Crossaster papposus	–	–	0.02	0.05	–	–
Leptychaster sp.	–	0.09	–	–	–	–
Ctenodiscus crispatus	0.03	0.05	–	–	–	–
Trophodiscus uber	0.23	0.32	0.2	–	–	–
Diplopteraster multipes	0.1	–	–	–	–	–
Pteraster militaris	–	–	0.01	–	–	–
Pteraster octaster	–	0.09	0.09	–	–	–
Henricia spp.	0.18	0.05	0.12	0.09	–	–
Hippasterias phrygiana	0.05	0.05	0.06	–	–	–
Ceramaster patagonicus	–	0.05	–	–	–	–
Echinoidea						
Echinarachnius parma	0.5	0.64	0.08	0.23	0.35	–
Strongylocentrothus pallidus	0.5	0.32	0.21	0.21	0.18	–
Holothuroidea						
Cucumaria sp.	–	0.14	–	–	0.06	–
Synallactes nozawai	0.03	–	–	–	–	–
Ophiuroidea						
Gorgonocephalus eucnemis	0.23	0.41	0.1	0.05	–	–
Ophiura sarsii	0.1	0.09	0.09	0.02	–	–
Decapoda						
Sclerocrangon boreas	–	–	–	–	0.09	–
Argis lar	0.18	0.32	0.08	0.02	0.47	0.3
Argis ochotensis	–	–	0.06	–	–	–
Neocrangon communis	0.13	0.23	0.05	0.05	–	0.17

Table 3. (Contd.)

Species	2018			2022		
	Kronotsky Bay	Avachinsky Bay	Southeastern Kamchatka	Kronotsky Bay	Avachinsky Bay	Southeastern Kamchatka
Crangon dalli	0.08	0.09	0.01	–	0.12	–
Lebbeus groenlandicus	0.03	–	–	–	–	–
Hyas coarctatus	0.18	0.05	0.02	0.09	0.18	0.3
Oregonia gracilis	–	0.14	–	–	–	–
Pandalus borealis	0.03	–	0.02	–	–	0.13
Pandalus goniurus	0.15	0.41	0.07	0.05	0.06	0.26
Labidochirus splendescens	0.03	–	–	–	–	0.3
Pagurus rathbuni	–	–	–	–	0.29	–
Pagurus brandti	0.68	0.41	0.27	0.37	0.47	0.74
			Ascidiacea			
Ascidiacea varia	0.23	0.45	0.04	0.07	–	0.08
Boltenia ovifera	0.15	0.41	0.13	–	–	–
Boltenia echinata	0.03	0.09	0.04	–	0.18	–
Chelyosoma orientale	0.05	–	–	–	–	–
Halocynthia aurantium	0.28	0.41	0.17	0.14	–	–
Total number of species	61	49	60	20	18	10
Number of species in the year		85			30	

pletely disappeared from the bycatch in 2022. The ascidian fauna was the most adversely affected in Avachinsky Bay, where the absolute biomass of this group decreased by 45 times (by 97.8%); it also decreased by 11 times (by 91%) off the southeastern Kamchatka coast south of Cape Povorotny and by 1.6 times (by 36%) in Kronotsky Bay. For crustaceans, as represented in the bycatch by decapods (excluding commercial crabs and king crabs, which we do not consider here), the situation was quite different: the absolute biomass increased by five times (by 400%) in Avachinsky Bay, remained almost unchanged off the southeastern Kamchatka coast south of Cape Povorotny, and decreased by almost four times (by 74%) in Kronotsky Bay. The percentage of decapods in the average biomass increased in all three areas in 2022, but most significantly in the southeastern Kamchatka shelf waters south of Cape Povorotny (by 19 times) and in Avachinsky Bay (by 11 times). It increased in the Kronotsky Bay shelf waters to a lesser extent (by 1.5 times).

The average biomass per unit area was lower in 2022 than in 2018 in most groups, except for cephalopods in Avachinsky Bay (it was 1.2 times higher) and sponges off the southeastern Kamchatka coast south of Cape Povorotny (it was 2.4 times higher). The maximum biomass per unit area increased significantly only in three groups off the southeastern Kamchatka coast south of Cape Povorotny: by 1.6 times for sponges, by 1.53 times for crustaceans, and by 10 times for ascidians. Sea urchins were the most abundant in all three shelf areas in 2018: the average biomass per unit area was about 200–250 kg/km^2, and the maximum value was about 2000–3000 kg/km^2. In 2022 these parameters decreased by 2.9 and 1.6 times in Kronotsky Bay, by 65 and 133 times in Avachinsky Bay, and decreased to zero in the southeastern Kamchatka shelf waters south of Cape Povorotny, respectively.

The average and maximum population density (ind./km^2) significantly decreased (from 1.5–2 times to several orders of magnitude) in all groups in 2022 compared to 2018, except for Porifera and Decapoda in the southeastern Kamchatka shelf waters south of Cape Povorotny (Fig. 9). A 1.5-fold increase in the maximum population density of Ascidiacea was also recorded there, while a 2-fold increase in the maximum population density of Bivalvia occurred in the Kronotsky Bay shelf waters (Tables 1, 2).

The frequency of occurrence decreased in all groups, except for Decapoda in the Avachinsky Bay shelf waters and off the southeastern Kamchatka coast south of Cape Povorotny, where the frequency of occurrence of Porifera and Ascidiacea also increased.

Thus, two groups of benthic invertebrates completely disappeared from bycatch in Kronotsky and Avachinsky Bays after 2020; only 9 out of 11 groups remained. Off the southeastern Kamchatka coast, 4

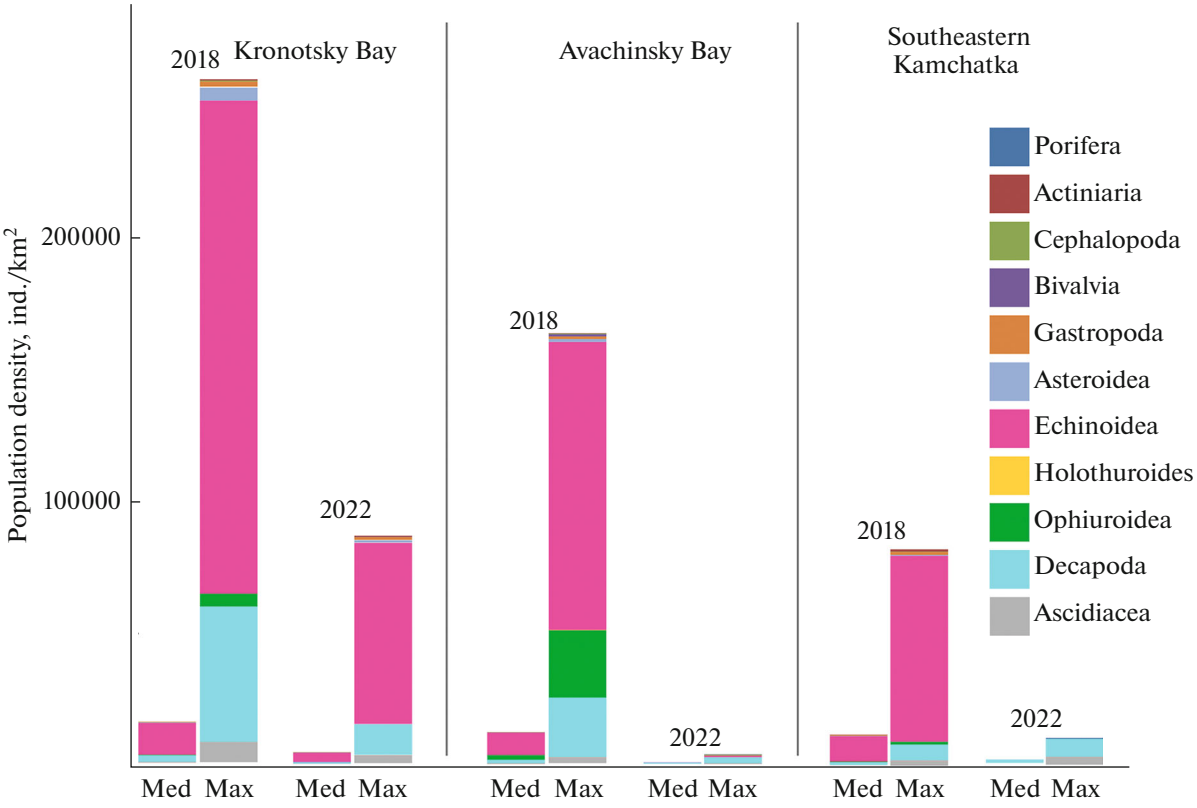

Fig. 9. The median (Med) and maximum (Max) population density of invertebrate groups recorded from the bycatch of the bottom trawl surveys in 2018 and 2022.

out of 10 groups remained: Porifera, Cephalopoda, Decapoda, and Ascidiacea.

Only 30 species out of those in the species list compiled based on the results of surveys in all three study areas were found in 2022 (see Table 3 with a total of 88 species or groups of species) while 85 species were recorded in 2018. The species diversity decreased by almost 3 times (Fig. 10), in particular, by 3 times (67% of species disappeared) in Kronotsky Bay, by 2.7 times (more than 63% of species disappeared) in Avachinsky Bay, and by 6 times (more than 83% of species disappeared) off the southeastern Kamchatka coast south of Cape Povorotny. The greatest losses of species diversity were observed in mollusks (86.4% of species), especially in gastropods (89%) and bivalves (80%), as well as in starfish (73.3%) and sea anemones (67%). More than 92% of gastropod species disappeared in Kronotsky Bay, 80% in Avachinsky Bay, and 100% off the southeastern Kamchatka coast south of Cape Povorotny. The starfish diversity was the least adversely affected in Kronotsky Bay, 50% of species disappeared from the bycatch there in 2022. Only one species, *Lethasterias nanimensis*, was caught at one station in Avachinsky Bay out of the 11 species recorded in 2018, i.e., 91% of species disappeared, while 100% of starfish species disappeared off the southeastern Kamchatka coast.

The frequency of occurrence of the surviving species decreased in 2022 in most cases (Table 3), except for 20 species, whose occurrence increased in one, and less often in two, study areas. Half of the species whose occurrence increased in 2022 were crustaceans (the order Decapoda) caught in the Avachinsky Bay area and off the southeastern Kamchatka coast south of Cape Povorotny, where the loss of other groups of benthic animals was the greatest. Out of three species found in Avachinsky Bay in 2022, while not being listed in 2018, two also belong to decapods. The mesh size of the fishing gear did not allow surveying smaller crustaceans, e.g., from the order Amphipoda, whose outbreak was recorded from the upper sublittoral zone of Avachinsky Bay in 2021 and 2022 [14]. However, a five-fold increase in absolute biomass and occurrence of crustaceans in the lower sublittoral zone in Avachinsky Bay are consistent with the data of Sanamyan et al. [14], who showed that crustaceans in general were not greatly affected by the effects of an HAB, and some of them significantly increased in abundance, probably due to a reduced predation pressure, an increase in food supply, and reduced competition between hermit crabs for gastropod shells [21] which became available due to the mass mortality of mollusks [14]. Thus, the entire Avachinsky Bay shelf saw an increase in abundance and biomass of crustaceans

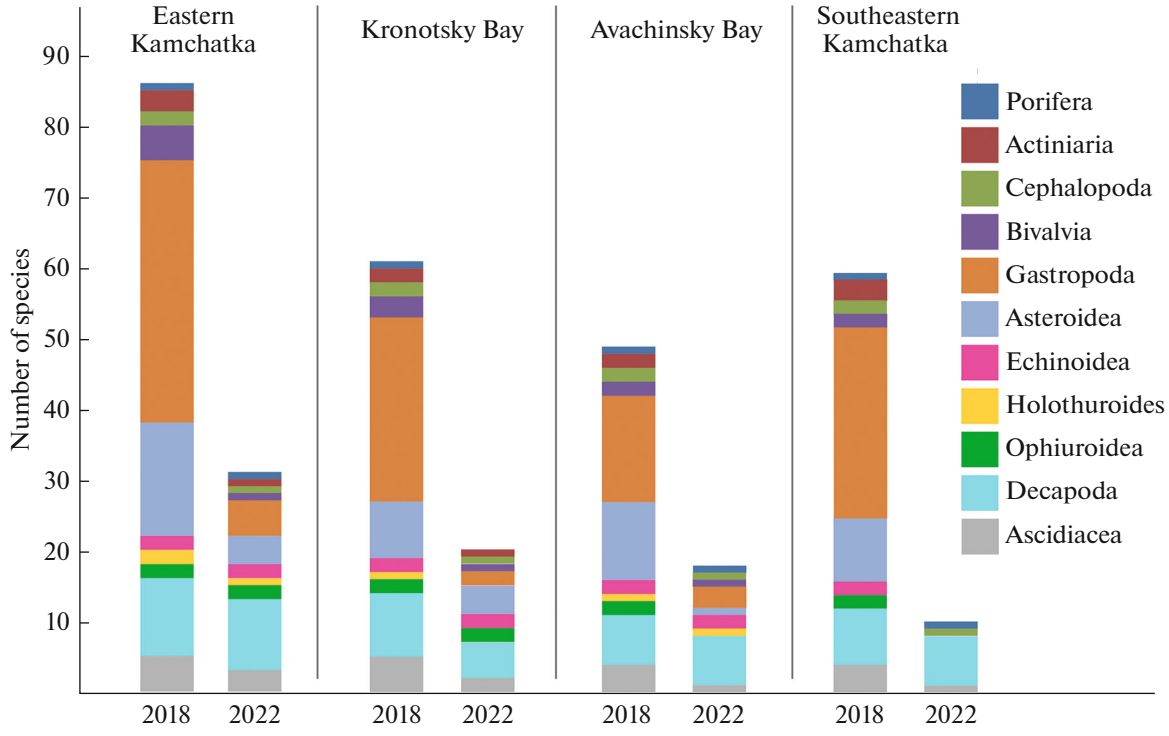

Fig. 10. The number of species in main taxa recorded from the bycatch of the bottom trawl surveys in 2018 and 2022.

against the background of a decrease in biodiversity of other groups of benthic invertebrates. The 87% reduction in benthos biomass in the lower sublittoral zone of Avachinsky Bay was consistent with the visual estimate of an 80–90% loss in the upper sublittoral zone made earlier by Sanamyan et al. [14]. The previously reported two-fold reduction in the species composition of marine invertebrates in the upper sublittoral zone of Avachinsky Bay after the HAB in 2020 [14] is also close to the current estimate of 2.7 times in the lower sublittoral zone. Thus, the biodiversity all over the Avachinsky Bay shelf zone suffered a 2–3-fold loss in species composition and a reduction in abundance and biomass of benthic animals by 80–90% after the HAB in 2020. These values are intermediate between such data for Kronotsky Bay and the shelf waters of the southeastern Kamchatka coast south of Cape Povorotny.

The data of satellite-based chlorophyll *a* monitoring off the Kamchatka coast showed the largest area of the highest chlorophyll *a* concentration in Avachinsky Bay and in the area off the southeastern Kamchatka coast in September 2020 [3]. This suggests that the mass die-off of benthic organisms was associated with the HAB impact caused by dinoflagellates of the genus *Karenia* in the fall of 2020 [23].

CONCLUSIONS

Both the biomass and the species diversity of the benthic fauna decreased by almost three times in the shelf zone of eastern Kamchatka from Cape Kronotsky to the southern tip of Kamchatka following the die-off that occurred as a result of the HAB in the fall of 2020. Crustaceans can be considered as the least affected group: despite the mortality of crustaceans recorded after the HAB in the fall of 2020, their losses were lower than those in other groups of invertebrates, and the absolute biomass of decapods in Avachinsky Bay shelf increased by five times in 2022 compared to 2018. The most adversely affected area was the southernmost region from Cape Povorotny to Cape Lopatka, where an almost 20-fold decrease in the absolute biomass of benthic invertebrates occurred in the lower sublittoral zone, i.e., 95% of the zoobenthos that had been recorded from bycatch during trawl surveys previously, died. Out of ten animal groups recorded in 2018, less than half survived. In 2022, a complete absence of representatives of six high-ranking taxa was recorded from this area: the order Actiniaria and such classes as Bivalvia, Gastropoda, Asteroidea, Echinoidea, and Ophiuroidea (the entire phylum Echinodermata). The species diversity decreased by 6 times (more than 83% of the species disappeared). The least affected area was the northernmost part of the shelf zone, in Kronotsky Bay; the absolute biomass decreased by 1.76 times (by 43%); 2 out of the 11 groups of benthic invertebrates recorded in 2018

disappeared in 2022, the phylum Porifera and the class Holothuroidea; the species diversity decreased by 3 times (67% of the species disappeared). The shelf waters of Avachinsky Bay suffered significantly and occupied an intermediate position in terms of estimated damage between the northern and southern areas; the absolute biomass decreased by 7.77 times (by 87%); 2 out of the 11 groups of benthic invertebrates disappeared: the order Actiniaria and the class Ophiuroidea; the species diversity decreased by 2.7 times (63% of the species disappeared).

Considering such criteria as the wide diversity of taxa exposed to the HAB impact (almost all groups of benthic invertebrates were affected, up to disappearance of high-ranking taxa, from orders to phyla) and the high percentage of species that disappeared (65% for all three areas), the consequences of HAB were catastrophic for the entire eastern Kamchatka shelf from Cape Kronotsky to Cape Lopatka.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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