VERTICAL STRUCTURE OF THE FISH COMMUNITY IN THE PACIFIC ZONE NEAR THE NORTHERN KURIL ISLANDS

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Seasonal bathymetric movements of fish in the subarctic waters of the Far Eastern seas have a significant impact on the distribution of all fish and make important changes in the structure of the species composition of the ichthyofauna on the shelf and continental slope. The purpose of this work was to determine the vertical structure of bathymetrical communities of fish in the Pacific waters of the northern Kuril Islands and its seasonal changes. The main material for the article was the data collected during trawl surveys in the period 1987–2021. It is shown that the boundary between the elittoral and mesobenthal communities in the cold season of the year was in nearly 350 m, in the warm period of the year it shifted to a depth of 100 m. The new information makes it possible to assess the characteristic features of elittoral and mesobenthal communities and seasonal changes in the intermediate boundaries between them and clarifies the scale of migration processes during annual life cycle of fish in the area.

Keywords: northern Kuril Islands, bathymetrical communities of fish, seasons, species similarity, ecosystem’s parameter.

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The general pattern of the bathymetric distribution of fish in the oceanic shelf and landfill zone off the northern Kuril Islands follows characteristic patterns related to the biology and life cycle of different species (Orlov, 1998, 2001, 2010; Orlov et al., 2000, 2006; Orlov, 2003, 2005; Tokranov et al., 2005; Tokranov, Orlov, 2012, 2013; Ulchenko, Orlov 2013; Orlov, Tokranov, 2014). The ecological characteristics of fish largely determine whether each species is confined to a certain range of depths. At the same time, in the subarctic seas, the spatial boundaries of individual vertical groupings are significantly influenced by periodic seasonal migrations of fish associated with their wintering, breeding and feeding. The bathymetric boundaries of the groupings also change during the interannual fluctuations in the thermal regime of the reservoir, which regulate the immediate timing of these migrations.

The vertical distribution of demersal fish communities is studied in various regions of the World Ocean, including the Sakhalin-Kuril region (Yamamura et al., 1993; Blaber et al., 1994; Fujita et al., 1995; Farina et al., 1997; Gaertner et al., 1998; Mahon et al., 1998; Robards et al., 1999; Kim, Shelepova, 2001; Mueter, Norcross, 2002; Kim, 2004; Kim, 2004, 2005; Busalacchi et al., 2010; Causse et al., 2011; Amsler et al., 2016; Kim, Kim, 2019; Zhang et al., 2022). At the same time, published information on species diversity and quantitative structure of vertical fish assemblages, considered in seasonal and interannual aspects, remains extremely scarce.

An exception is a large-scale study that addressed many aspects of seasonal distribution, biology, and stocks of marine fish in the Pacific waters off the northern Kuril Islands and Southeast Kamchatka, conducted in the 1990-2000s during year-round scientific expeditions on Japanese fishing vessels as part of the long-term Research Program on understudied fish of the continental slope of the Far Eastern seas (Fishery-biological..., 2000). Research in these years significantly expanded existing knowledge about the systematics, zoogeography, biology, and stocks of the ichthyofauna in the Kuril waters (Orlov, 1998, 1996, 2004, 2005; Orlov, Moiseev, 1999; Orlov et al., 2000, 2011; Orlov, Nesin, 2000; Orlov, Abramov, 2001; Orlov, Mukhametov, 2001; Tokranov, Orlov, 2002; Tokranov, Orlov, 2003; Tokranov et al., 2003; Orlov et al., 2006; Orlov, Tokranov, 2007, 2008; Orlov, 2010). Numerous publications, especially by researchers such as A.M. Orlov (Institute of Oceanology RAS) and A.M. Tokranov (Kamchatka Branch of the Pacific Institute of Geography, Far Eastern Branch of RAS), were dedicated to the specifics of spatial distribution, size and age indicators, patterns of sexual maturation, and feeding habits of a wide range of common but poorly studied fish species of the Pacific shelf and slope of the northern Kuril Islands. Despite the extreme inaccessibility of most areas of the Kuril Islands slope due to the widespread presence of rocky-stony substrates, sharp changes in bottom topography, and steep bottom inclines, the nearly decade-long accumulated biological information currently makes this area the most studied in the Russian Far East region in terms of ichthyofauna species diversity and comprehensive research on local fish biology.

The total species richness and dominant components of ichthyofauna in the study area within different bathymetric zones, including according to the vertical zonation scheme (Parin, 1968), were previously studied by Orlov (Orlov, 2005). He compiled a detailed list of fish by biotopes, as well as their species composition by individual sublittoral zones (inner, middle, and outer shelves) and bathyal zones (meso-, bathy-, and abyssobenthic) in the bottom and near-bottom horizons. The depth distribution of dominant, common, rare, and very rare species was characterized based on occurrence in catches, and the author used catch per unit effort values to describe the relative species richness. Bathymetric fish communities were correlated with the above-mentioned zones.

The similarity in seasonal behavior of benthic and near-bottom fish species, due to characteristic changes in the main environmental conditions, suggests the existence of multi-species demersal communities, primarily sequentially distributed in areas from the coast toward the open part of the ocean (continental slope). The subarctic structure of water masses should form the spatial pattern of fish distribution, and the adaptation of sublittoral, elittoral, or mesobenthic fish to certain environmental conditions in various depth ranges of shelf and slope areas of the sea significantly limits the available zone of their distribution. In this regard, the features of bathymetric separation of sublittoral, elittoral, and mesobenthic groups are of considerable interest, especially in the seasonal aspect. This information has both scientific and practical significance, allowing the determination of relationships between different ecological groups of fish, as well as regulating the species composition of the necessary bycatch of various objects during fishing operations.

However, bathymetric boundaries of communities can be determined not by depth ranges schematically indicated based on vertical division of the seabed (Orlov, 2005), but by analyzing the overall species similarity of fish in different studied areas of the sea. In this case, during seasonal rearrangements in fish distribution, the boundaries of multispecies communities undergo periodic changes. The purpose of this work is to characterize the seasonal dynamics of composition and distribution of demersal fish communities in the Pacific subzone near the northern Kuril Islands, to evaluate ecosystem parameters of shelf (elittoral) and slope (mesobenthic) fish communities when the boundary between them changes.

MATERIAL AND METHODOLOGY

The main material used was the results of eight trawl surveys in the area of the Pacific coast of the northern Kuril Islands in 1987-2021 (Table 1). The selection of specific surveys was determined by the completeness of their coverage of the study area, the maximum range of surveyed depths, as well as their implementation in different seasons of the year. During multi-year studies, surveys covered most months of the year, but a characteristic feature of the general database was the absence of observations in the typical summer period (July-September).

Table 1. List of trawl surveys off the Pacific coast of the northern Kuril Islands in 1987-2021, the results of which were used in the work

No.	Months, year	Vessel	Number of stations	Depths, m	Trawl type
1	January-February, 1987	SRTM "Shursha"	93	42-500	DT 28.0 m

2	February-March, 2002	R/V "Dmitry Peskov"	68	50-600	DT 34/26 m
3	March, 2011	R/V "Professor Probatov"	83	47-491	DT 30/25 m
4	March-April, 2015	R/V "Dmitry Peskov"	61	65-420	Same
5	May, 2021	Same	63	50-480	DT 27.1 m
6	May-June, 2006	R/V "Professor Probatov"	105	45-498	DT 34/25 m
7	May-June, 2007	Same	114	60-348	DT 64.8 m
8	October, 1987	BMRT "Tikhookeansky"	87	35-350	DT 43.0 m

Note. SRTM - medium fishing freezer trawler, NIS - research vessel, BMRT - large freezer fishing trawler.

A generalized scheme of the research area with a total number of 674 trawl stations is shown in Fig. 1. The total range of surveyed depths was 35-600 m. The temperature of the bottom water layer was recorded by an ATD-HR #0663 logger ("JFE Advantech Co., Ltd.", Japan).

Maps of the spatial distribution of fish were created using the Surfer software (https://www.goldensoftware.com/products/surfer). For the interpolation of unified catch data (t/mile ^{2}), the kriging method was used (Koshel, Musin, 2001), and a grid file was built with a step of 0.01° (Tarasyuk et al., 2000). The number of nearest points in the sector for interpolation was chosen to be equal to the maximum, the minimum - 1; maximum search radius - 0.5, minimum - 0.3 latitude degrees; the point search ellipse was positioned along the isobaths at an angle of 35°.

The study used SakhNIRO archival materials obtained during numerous field works by different researchers who used fish identification guides for the Far Eastern seas and an illustrated fish atlas for field identification of fish to species level (Taranets, 1937; Lindberg, Krasyukova, 1975, 1987; Lindberg, Fedorov, 1993; Amaoka et al., 1995). Latin and Russian names of species and families are given in accordance with catalogs and annotated lists of fish, including those of the Far Eastern seas (Orlov, 1998; Borets, 2000; Fedorov, 2000; Sheiko, Fedorov, 2000; Fedorov et al., 2003; Parin et al., 2014; Fricke et al., 2024).

For vertical fish grouping, the Morisita-Horn coefficient was used (Krebs, 1999). As the main units of measurement, indices of relative fish abundance (catch density) were used, expressed in t/mile^2. Data for all species were standardized, i.e., brought to 1. For community identification, the database was used without considering walleye pollock *Gadus chalcogrammus* , but in the final species composition of communities, walleye pollock is presented. The proportion of walleye pollock was calculated separately based on the total fish biomass. It should be noted that adult walleye pollock predominantly concentrates in the near-bottom horizon of the sea, which influences the assessment of species significance in communities where it is present. The total bathymetric range of the study area was divided into 50-meter intervals, between which species composition similarity was identified. Similarity dendrograms were constructed using Ward's method (Ward, 1963) in R environment, and for data visualization, the *k* -means clustering method (*k* -means) from the fviz_cluster package was used (Gorban, Zinovyev, 2010).

The main parameters of fish groupings in the identified zones were: species richness, entropy, abundance evenness, and species composition heterogeneity (Krebs, 1999). The similarity of species structure was assessed using the Morisita coefficient in Horn's interpretation, recognized as one of the best similarity indicators for ecological calculations (Wolda, 1981, Krebs, 1999): $CH = 2\Sigma X_{ij}X_{ik}/((\Sigma X_{ij}^2 / N_j^2) + (\Sigma X_{ik}^2 / N_k^2)) N_j N_k$, where CH is the Morisita-Horn coefficient, X_{ij} and X_{ik} are the proportions of the *i* th species by weight in samples *j* and *k* , respectively, $N_j = \Sigma X_{ij}$ is the total weight of the species in sample *j* , $N_k = \Sigma X_{ik}$ is the total weight of the species in sample *k* .

Entropy (H) or the measure of community orderliness was determined using Brillouin's formula (Brillouin, 1962 - cited by: Smetanin et al., 1983): $H = \Sigma p_i \log_2 p_i$, where p_i is the proportion of the *i* th species in the community.

Species richness was calculated using the jackknife estimate method (Krebs, 1999): $S = s + (n - 1)/n)k$, where S – is the measure of species richness (number of species); s – is the observed number of species in n trawls, n – is the total number of trawls, k – is the number of unique species (recorded only in one catch).

Species abundance evenness was determined using Simpson's index (Krebs, 1999): $E_{1/D} = 1/D/s$, where $E_{1/D}$ – is Simpson's evenness index, D – is Simpson's heterogeneity index, s – is the number of species in the entire sample.

Species composition heterogeneity was calculated using Simpson's indices (Krebs, 1999): $D = \Sigma\ p_i^2$, where D – is Simpson's index, equal to the probability that two individuals randomly taken from a community belong to different species; p_i – is the proportion of the i-th species in the community; $1 - D = 1 - \Sigma\ p_i^2$, where $1 - D$ – is Simpson's diversity index, interpreted as the probability that two selected individuals belong to the same species; $1/D = 1/\Sigma\ p_i^2$, where $1/D$ – is the reciprocal Simpson's index, interpreted as the number of equally significant species required to create the observed heterogeneity in the sample.

RESULTS

Winter, January – February 1987. A total of four clusters were identified (Fig. 2). The first and second groupings were distributed in the isobath zone of 51–100 m and 101–150 m, respectively (Table 2). A distinctive feature of these groupings was the weak presence of walleye pollock, whose average proportion in the total ichthyomass did not exceed 0.021 and 0.014, respectively. Both groupings were characterized by a similar composition of dominant members, represented by the same species of mass elittoral fish. However, the overall species composition of fish in them differed noticeably. The first grouping was formed predominantly by Pacific cod *G. macrocephalus* (its proportion 0.678), northern rock sole *Lepidopsetta polyxystra* (0.155), and whitespot Irish lord *Hemilepidotus jordani* (0.044), whereas in the second grouping these same species were arranged in a different order – rock sole (0.404), whitespot Irish lord (0.249), and Pacific cod (0.227). While the second grouping was dominated only by elittoral species, the first unexpectedly included some mesobenthic fish, among which were unidentified representatives of the Arhynchobatidae and snailfish Liparidae families.

The third, most extensive, grouping, represented predominantly by elittoral species with some presence of mesobenthal fish, was distributed in the zone of isobaths 151-350 m. The dominant 10 species constituted 0.974 of the total biomass. The basis of the grouping was formed by mass elittoral species that migrated here for wintering. Walleye pollock clearly dominated over all other members (0.681). The dominant group, as in the previous groupings, included Pacific cod, rock sole, and bigmouth sculpin. The fourth grouping (depth 351-500 m) was typically mesobenthal, which was also determined by its specific species composition. Of the elittoral species, only walleye pollock was found here, but its share was very substantial (0.900 of the total biomass). The dominant 10 species (excluding walleye pollock) formed the predominant share of biomass - 0.997. The two most significant taxa were unidentified mesobenthal fish attributed to *Raja* sp. (apparently, *Bathyraja* or *Arctoraja* (Orlov et al., 2006)) and Liparidae gen. sp. Their total share was high - 0.745. They were followed by Greenland halibut *Reinhardtius hippoglossoides* .

Judging by the species composition of the groupings, in winter, typical shelf species occupied the entire sublittoral and elittoral zone - up to a depth of 350 m. The elittoral was the preferred sea zone, while the mesobenthal following it was predominantly inhabited by slope species. The only elittoral species widely distributed at all surveyed depths was walleye pollock, and as the depth increased, its concentrations only increased.

Table 2. Species structure of dominant species in bathymetric fish groupings off the Pacific coast of the northern Kuril Islands in winter 1987.

Species	Density, t/mile ^{2}	Relative share	EH	Species	Density, t/mile ^{2}	Relative share	EH
First grouping, 22 species, depth 51–100 m				Third grouping, 29 species, depth 151–350 m			
Gadus chalcogrammus	0.092	0.021	el	*Gadus chalcogrammus*	24.734	0.681	el
Gadus macrocephalus	2.901	0.678	el	*Gadus macrocephalus*	6.284	0.543	el
Lepidopsetta polyxystra	0.663	0.155	el	*Lepidopsetta polyxystra*	2.848	0.246	el
Hemilepidotus jordani	0.187	0.044	el	*Hemilepidotus jordani*	0.669	0.058	el
Pleuronectes quadrituberculatus	0.147	0.034	el	*Bathyraja* sp.	0.627	0.054	mb
Gymnocanthus sp.	0.094	0.022	el	*Myoxocephalus jaok*	0.213	0.018	el
Myoxocephalus polyacanthocephalus	0.073	0.017	el	Liparidae gen. sp.	0.202	0.017	mb
Liparidae gen. sp.	0.065	0.015	mb	*Hexagrammos lagocephalus*	0.172	0.015	el
Bathyraja sp.	0.063	0.015	mb	*Gymnocanthus* sp .	0.102	0.009	el
Hippoglossus stenolepis	0.029	0.007	el	*Reinhardtius hippoglossoides*	0.092	0.008	mb
Limanda aspera	0.014	0.003	el	*Hemitripterus villosus*	0.069	0.006	el
Second grouping, 26 species, depth 101–150 m				Fourth grouping, 14 species, depth 351–500 m			
Gadus chalcogrammus	0.204	0.014	el	*Gadus chalcogrammus*	37.234	0.900	el
Lepidopsetta polyxystra	5.728	0.404	el	Liparidae gen. sp.	1.975	0.478	mb
Hemilepidotus jordani	3.524	0.249	el	*Bathyraja* sp.	1.104	0.267	mb
Gadus macrocephalus	3.215	0.227	el	*Reinhardtius hippoglossoides*	0.465	0.112	mb
Gymnocanthus sp.	0.603	0.043	el	*Somniosus pacificus*	0.313	0.076	mb
Myoxocephalus jaok	0.251	0.018	el	*Clidoderma asperrimum*	0.087	0.021	mb
Raja sp.	0.166	0.012	el	*Sebastolobus macrochir*	0.049	0.012	mb
Hippoglossoides elassodon	0.159	0.011	el	*Atheresthes evermanni*	0.049	0.012	mb
Gymnocanthus detrisus	0.093	0.007	el	*Malacocottus zonurus*	0.045	0.011	mb
Pleurogrammus monopterygius	0.068	0.005	el	*Lycodes* sp.	0.021	0.005	mb
Pleuronectes quadrituberculatus	0.057	0.004	el	*Crystallias matsushimae*	0.011	0.003	mb

Note. Here and in Tables 3-9: EC - ecological characteristic; type: el - elittoral, mb - mesobenthic.

Winter, February-March 2002 . This year, four clusters were identified at depths from 50 to 600 m (Fig. 3). The first coastal grouping was localized at a depth of 50 m and apparently extended to shallow waters (Table 3). Regarding abiotic environmental factors, the water temperature in the bottom layer averaged 0.28°C. Sandy-pebble grounds were most common (37.5%). The species composition of the grouping was represented by 15 species, and the dominant group was mainly formed by elittoral species with the presence of two mesobenthic skates (Aleutian skate *Arctoraja parmifera* and Taranetz's skate *Bathyraja taranetzi*). Rock sole, helmet sculpin *Gymnocanthus galeatus* and Aleutian skate were characterized by maximum relative biomass. Walleye pollock was absent.

The second elitoral grouping was located at depths of 51-200 m. The average water temperature in the zone was 0.65°C. Sandy-pebble substrates predominated - 38.8%. There were 69 species in total. In this zone, the density of walleye pollock concentrations was already high, which in this indicator was second only to rock sole. When excluding walleye pollock, the basis of biomass was formed by rock sole, white-belly eelpout, Pacific cod, and other elitoral species. Mesobenthic fish species were absent in the dominant group.

The third grouping was distributed at depths of 201-450 m, it already differed significantly from the previous ones in its species structure and was generally represented by 76 species. Within the dominant group, there were both elitoral and mesobenthic species. The average water temperature was 2.04°C. The substrate was most often formed by sandy-pebble fractions (33.3%). The biomass of walleye pollock significantly exceeded that of all other members of the grouping, followed by Pacific cod, broadhead careproct *Careproctus furcellus* , flathead sole *Hippoglossoides elassodon* , Aleutian skate *Bathyraja aleutica* , and shortfin elassodiscus *Elassodiscus tremebundus* . It should be noted that in this sea zone there were no clear leaders in biomass except for walleye pollock, and all species of the dominant group were comparable in terms of concentration density.

Table 3. Species structure of dominant species in bathymetric fish groupings off the Pacific coast of the northern Kuril Islands in winter 2002

Species	Density, t/mile ^{2}	Relative proportion	EC	Species	Density, t/mile ^{2}	Relative proportion	EC
First grouping, 15 species, depth 1 - 50 m, bottom water temperature 0.28°C				Third grouping, 76 species, depth 201 - 450 m, bottom water temperature 2.04°C			
Gadus chalcogrammus	0	0	el	*Gadus chalcogrammus*	2.270	0.289	el
Lepidopsetta polyxystra	0.912	0.685	el	*Gadus macrocephalus*	0.539	0.097	el
Gymnocanthus galeatus	0.145	0.109	el	*Careproctus furcellus*	0.475	0.085	mb
Arctoraja parmifera	0.094	0.070	mb	*Hippoglossoides elassodon*	0.388	0.070	el
Podothecus accipenserinus	0.051	0.038	el	*Bathyraja aleutica*	0.323	0.058	mb
Bathyraja taranetzi	0.051	0.038	mb	*Elassodiscus tremebundus*	0.303	0.054	mb
Pleuronectes quadrituberculatus	0.032	0.024	el	*Lepidopsetta polyxystra*	0.291	0.052	el
Gymnocanthus detrisus	0.017	0.013	el	*Bathyraja violacea*	0.283	0.051	mb
Aptocyclus ventricosus	0.013	0.010	n	*Hemilepidotus jordani*	0.242	0.043	el
Limanda sakhalinensis	0.009	0.006	el	*Hexagrammos lagocephalus*	0.234	0.042	el
Sarritor leptorhynchus	0.003	0.002	el	*Gymnocanthus galeatus*	0.228	0.041	el
Second grouping, 69 species, depth 51 - 200 m, bottom water temperature 0.65°C				Fourth grouping, 66 species, depth 451 - 600 m, bottom water temperature 2.38°C			
Gadus chalcogrammus	0.960	0.139	el	*Gadus chalcogrammus*	2.173	0.159	el
Lepidopsetta polyxystra	1.695	0.284	el	*Rastrinus scutiger*	2.185	0.191	mb
Hemilepidotus jordani	0.797	0.134	el	*Bathyraja maculata*	2.116	0.185	mb
Gadus macrocephalus	0.652	0.109	el	*Bathyraja aleutica*	0.861	0.075	mb
Gymnocanthus detrisus	0.309	0.052	el	*Hippoglossoides elassodon*	0.814	0.071	el
Gymnocanthus galeatus	0.274	0.046	el	*Atheresthes evermanni*	0.606	0.053	mb
Hemilepidotus gilberti	0.269	0.045	el	*Coryphaenoides pectoralis*	0.521	0.045	bb
Sarritor frenatus	0.246	0.041	el	*Bothrocara soldatovi*	0.494	0.043	mb
Triglops scepticus	0.224	0.038	el	*Lycodes albolineatus*	0.474	0.041	mb
Myoxocephalus polyacanthocephalus	0.220	0.037	el	*Careproctus furcellus*	0.381	0.033	bb
Pleurogrammus monopterygius	0.166	0.028	el	*Malacocottus zonurus*	0.353	0.031	mb

Note. Type: bb - bathybenthic; here and in tables 4, 8: n - neritic.

Finally, the fourth grouping consisted of 66 species at depths of 451-600 m. The average water temperature increased to 2.38°C. The predominant substrate type was sand (silt-sand) (66.6% in total). Even at these depths, walleye pollock was the second most abundant species by biomass. Excluding it, mainly mesobenthic species dominated, among which the armored sculpin *Rastrinus scutiger* , the spotted skate *Bathyraja maculata* , the Aleutian skate, and the flathead sole were prominent.

Winter, March 2011 . In March, three clusters or separate vertical groupings were identified. The first (coastal) grouping, consisting of 41 species, was localized at depths of 51-100 m; the second, elittoral, included 53 species and concentrated in the 101-250 m isobath zone; the third – upper mesobenthic – consisted of 46 species and occupied depths of 251-500 m (Fig. 4). The coastal grouping was characterized by a minor presence of walleye pollock, while in the other groupings this species significantly dominated (Table 4). As we moved to greater depths, the density of walleye pollock aggregations increased. When excluding walleye pollock from the analysis, the coastal grouping was dominated (in descending order of density values) by: rock sole, white-bellied eelpout, broad-browed helmet-head *Gymnocanthus detrisus* , and Pacific cod. The elittoral grouping was dominated by the same species: rock sole, white-bellied eelpout, Pacific cod, and broad-browed helmet-head. Along with them, mesobenthic skate species – Aleutian and spotted – appeared in the dominant group. In the mesobenthic grouping, the presence of abundant elittoral species (walleye pollock, Pacific cod, rock sole) continued to have a strong influence, but traditional slope inhabitants were also abundantly represented: the violet skate *Bathyraja violacea* , the rough snailfish *Careproctus rastrinus* , Taranetz's skate, shortfin elassodiscus, and Kamchatka flounder *Atheresthes evermanni* .

Table 4. Species structure of dominant fish species in bathymetric groupings off the Pacific coast of the northern Kuril Islands in winter 2011.

Species	Density, t/mile ^{2}	Relative proportion	EH
First grouping, 41 species, depth 51–100 m			
Gadus chalcogrammus	0.079	0.024	el
Lepidopsetta polyxystra	1.257	0.399	el
Hemilepidotus jordani	0.723	0.229	el
Gymnocanthus detrisus	0.520	0.165	el
Gadus macrocephalus	0.164	0.052	el
Myoxocephalus polyacanthocephalus	0.163	0.052	el
Hippoglossus stenolepis	0.063	0.020	el
Gymnocanthus sp .	0.039	0.012	el
Podothecus veternus	0.038	0.012	el
Hemilepidotus gilberti	0.030	0.010	el
Limanda aspera	0.029	0.009	el
Second grouping, 53 species, depth 101-250 m			
Gadus chalcogrammus	8.940	0.417	el
Lepidopsetta polyxystra	4.873	0.390	el
Hemilepidotus jordani	2.639	0.211	el
Gadus macrocephalus	2.440	0.195	el
Gymnocanthus detrisus	0.861	0.069	el
Myoxocephalus polyacanthocephalus	0.398	0.032	el
Hippoglossoides elassodon	0.203	0.016	el
Hippoglossus stenolepis	0.158	0.013	el
Gymnocanthus galeatus	0.090	0.007	el
Bathyraja aleutica	0.089	0.007	mb
Bathyraja maculata	0.083	0.007	mb
Third grouping, 46 species, depth 251-500 m			
Gadus chalcogrammus	11.116	0.771	el
Bathyraja violacea	0.372	0.113	mb
Gadus macrocephalus	0.330	0.100	el
Lepidopsetta polyxystra	0.274	0.083	el
Careproctus rastrinus	0.254	0.077	mb
Bathyraja taranetzi	0.225	0.068	mb
Elassodiscus tremebundus	0.176	0.053	mb
Atheresthes evermanni	0.162	0.049	mb
Aptocyclus ventricosus	0.154	0.047	n
Lycodes albolineatus	0.124	0.038	mb

Hippoglossus stenolepis	0.121	0.037	el

In March, there is active movement of migrating schools traveling along the slope of the North Kuril Islands in a southwestern direction for subsequent entry into the coastal waters of Paramushir Island. At the same time, the preservation of the boundary between elitoral and mesobenthal species at the 250 m isobath indicates the absence of mass vertical movements of fish in March.

The examined winter survey results showed that in the cold season, the boundary between elitoral and mesobenthic fish assemblages ran between isobaths of 200 and 350 m. Up to a depth of 100-150 m near the shore, shelf assemblages were present, consisting predominantly of elitoral species. Among them, three mass species dominated: cod, northern rock sole, and narrow-headed sculpin. Walleye pollock was relatively scarce in this zone.

Between the coastal and mesobenthic assemblages, there was an extensive elitoral community which formed after wintering migrations of shelf species to the upper areas of the slope at depths from 100-150 to 200-350 m. This assemblage was represented, besides walleye pollock, predominantly by rock sole, white-belly eelpout, and cod. However, here individual mass representatives of the continental slope were already encountered, among which skates, liparids, and Greenland halibut were notable.

In the mesobenthal, one or two assemblages formed, one observed at depths of 201-450 m, the second at 450-600 m. The first can be called transitional, intermediate, upper mesobenthic, as it was dominated by the same mass elitoral species - walleye pollock, cod, rock sole and flathead sole, white-belly eelpout. At the same time, the proportion of mesobenthic species here was clearly increased, and the dominant species included Aleutian skate, purple skate, and shortfin snailfish. In the deepest assemblage (lower mesobenthic), exclusively mesobenthic fish were represented, and typical slope species dominated, such as spotted and Aleutian skates, thorny sculpin, Greenland and Asian arrowtooth halibuts.

It should be noted that from the localization zone of elitoral assemblages to the zone of mesobenthic assemblages, there was a characteristic change in the average water temperature, which steadily increased. At the same time, the predominant character of the sandy-pebble substrate for different zones remained unchanged, which is important for the demersal way of life for most dominant species in vertical assemblages.

Spring, March-April 2015 . This year, three groupings were sequentially identified (Fig. 5). The first coastal grouping, consisting of 33 species, was located at depths of 51-100 m (Table 5). All species were elittoral. Walleye pollock, by relative biomass, was inferior to three dominant species - rock sole, white-bellied eelpout, and Pacific cod.

Table 5. Species structure of dominant species in bathymetric fish groupings off the Pacific coast of the northern Kuril Islands in spring 2015.

Species	Density, t/mile ^{2}	Relative share	EH
First grouping, 33 species, depth 51-100 m			
Gadus chalcogrammus	2.197	0.085	el
Lepidopsetta polyxystra	9.013	0.383	el
Hemilepidotus jordani	6.291	0.267	el
Pleurogrammus monopterygius	2.577	0.110	el
Gadus macrocephalus	1.162	0.049	el
Myoxocephalus polyacanthocephalus	1.044	0.044	el
Gymnocanthus detrisus	1.024	0.044	el
Hemilepidotus gilberti	0.899	0.038	el
Limanda aspera	0.423	0.018	el
Hemitripterus villosus	0.259	0.011	el
Myoxocephalus jaok	0.198	0.008	el
Second grouping, 51 species, depth 101-300 m			
Gadus chalcogrammus	8.595	0.261	el
Hemilepidotus jordani	14.367	0.590	el
Lepidopsetta polyxystra	4.456	0.183	el

Gadus macrocephalus	2.161	0.089	el
Gymnocanthus detrisus	0.611	0.025	el
Hexagrammos lagocephalus	0.390	0.016	el
Myoxocephalus polyacanthocephalus	0.305	0.013	el
Bathyraja violacea	0.266	0.011	mb
Hippoglossoides elassodon	0.246	0.010	el
Bathyraja taranetzi	0.244	0.010	mb
Hemitripterus villosus	0.206	0.008	el
Third grouping, 31 species, depth 301-400 m			
Gadus chalcogrammus	8.758	0.549	el
Gadus macrocephalus	1.199	0.166	el
Bathyraja violacea	1.095	0.152	mb
Lepidopsetta polyxystra	0.838	0.116	el
Careproctus furcellus	0.792	0.110	mb
Lycodes brunneofasciatus	0.690	0.096	mb
Bathyraja taranetzi	0.590	0.082	mb
Careproctus roseofuscus	0.456	0.063	mb
Careproctus rastrinus	0.399	0.055	mb
Malacocottus zonurus	0.171	0.024	mb
Hippoglossus stenolepis	0.148	0.020	mb

The second elitoral grouping, consisting of 51 species, was located at depths of 101-300 m. In terms of biomass, walleye pollock was second only to the white-belly Irish lord, which noticeably dominated over all members of the community. The top ten species were led by the white-belly Irish lord, rock sole, and Pacific cod, while among mesobenthic species, the violet skate and Taranetz's skate stood out.

The third upper mesobenthal grouping, represented by 31 species with primarily mesobenthal lifestyle, formed in the range of 301-400 m. Walleye pollock absolutely dominated here; additionally, Pacific cod and rock sole were among the mass species. Along with them, slope fish were widely distributed, such as purple skate, broadhead careproctus, and brown-banded eelpout *Lycodes brunneofasciatus* . It should be noted that the boundary between elittoral and mesobenthal groupings still ran along the 300 m isobath during the early spring period.

Spring, May 2021 . In this year, two groupings were identified, classified by species structure as elittoral and upper mesobenthal (Fig. 6). The first one was located on the shelf with depths up to 100 m and consisted of 36 species, predominantly elittoral (Table 6). In this grouping, walleye pollock absolutely dominated, with rock sole, white-belly eelpout, and Pacific cod leading the top ten species.

The second grouping was distributed across a wide depth range of 101-500 m and was formed by 79 species, represented by mass elittoral fish and numerous representatives of mesobenthal individuals. The noticeably dominant walleye pollock formed aggregations here with approximately three times lower density than on the shelf, followed by Pacific cod, white-belly eelpout, and rock sole. Despite the fact that the grouping was dominated by mass representatives of the elittoral, mesobenthal fish predominated in the general list by number of species, primarily shortfin elassodiscus, purple skate, and white-lined eelpout *L. albolineatus* . In May, the boundary between elittoral and mesobenthal groupings shifted toward the shore and already ran along the 100 m isobath, i.e., was located at the edge of the shelf. This boundary location persisted in May-June in all subsequent surveys examined.

Spring, May-June 2006 . During these months, two groupings were identified, as in May 2021 (Fig. 7). The elittoral grouping, consisting of 33 species, was distributed at depths of 51-100 m (Table 7). The dominant fish group was represented exclusively by elittoral species, with walleye pollock absolutely predominating; besides it, white-belly eelpout, Pacific cod, and Atka mackerel *Pleurogrammus monopterygius* were among the mass species.

The second, upper mesobenthic grouping was distributed at depths of 101-500 m and consisted of 69 species. The dominant fish group was formed mainly by elittoral species, but mesobenthic fish (shortfin elassodisc; spotted skate, violet skate, Taranetz's skate; Greenland halibut) were also widely distributed. The grouping was absolutely dominated by walleye pollock;

other mass species included northern rock sole, Pacific cod, white-bellied eelpout, and rock sole. The boundary between elittoral and mesobenthic groupings ran along the 100 m isobath.

Table 6. Species structure of dominant species in bathymetric fish groupings off the Pacific coast of the northern Kuril Islands in spring 2021.

Species	Density, t/mile ^{2}	Relative proportion	EA	Species	Density, t/mile ^{2}	Relative proportion	EA
First grouping, 36 species, depth 51–100 m				Second grouping, 79 species, depth 101–500 m			
Gadus chalcogrammus	12.747	0.611	el	*Gadus chalcogrammus*	4.544	0.383	el
Lepidopsetta polyxystra	3.530	0.434	el	*Gadus macrocephalus*	1.315	0.180	el
Hemilepidotus jordani	2.037	0.251	el	*Hemilepidotus jordani*	1.025	0.140	el
Gadus macrocephalus	0.809	0.100	el	*Lepidopsetta polyxystra*	0.695	0.095	el
Gymnocanthus detrisus	0.390	0.048	el	*Elassodiscus tremebundus*	0.674	0.092	mb
Pleurogrammus monopterygius	0.273	0.034	el	*Bathyraja violacea*	0.362	0.050	mb
Hemitripterus villosus	0.198	0.024	el	*Lycodes albolineatus*	0.321	0.044	mb
Hexagrammos lagocephalus	0.185	0.023	el	*Careproctus furcellus*	0.312	0.043	mb
Myoxocephalus polyacanthocephalus	0.163	0.020	el	*Malacocottus zonurus*	0.283	0.039	mb
Hippoglossoides elassodon	0.144	0.018	el	*Pleurogrammus monopterygius*	0.263	0.036	el
Hippoglossus stenolepis	0.089	0.011	el	*Atheresthes evermanni*	0.228	0.031	mb

Table 7. Species structure of dominant fish species in bathymetric groupings off the Pacific coast of the northern Kuril Islands in spring-summer 2006

Species	Density, t/mile ^{2}	Relative share	EC	Species
First grouping, 33 species, depth 51–100 m, bottom water temperature 1.73°C				Second grouping, 69 spe bottom water tem
Gadus chalcogrammus	3.380	0.853	el	*Gadus chalcogrammus*
Hemilepidotus jordani	1.257	0.317	el	*Pleurogrammus monopterygius*
Gadus macrocephalus	0.973	0.245	el	*Gadus macrocephalus*
Pleurogrammus monopterygius	0.888	0.224	el	*Hemilepidotus jordani*
Lepidopsetta polyxystra	0.224	0.057	el	*Lepidopsetta polyxystra*
Hexagrammos lagocephalus	0.214	0.054	el	*Elassodiscus tremebundus*
Myoxocephalus polyacanthocephalus	0.111	0.028	el	*Bathyraja maculata*
Hemilepidotus gilberti	0.056	0.014	el	*Bathyraja violacea*

Hippoglossus stenolepis	0.053	0.013	el	*Reinhardtius hippoglossoides*
Gymnocanthus detrisus	0.049	0.012	el	*Bathyraja taranetzi*
Hippoglossoides elassodon	0.028	0.007	el	*Gymnocanthus galeatus*

This year, the bottom water temperature was estimated, which on average in the elitoral grouping habitat zone was 1.73°C, and in the rest of the zone – 3.12°C. In February-March 2002, in the habitats of this grouping, the average water temperature at depths of 51-200 m reached significantly lower values (0.65°C). It should be assumed that throughout the year, the water temperature at the bottom, apparently, cannot serve as a parameter that unambiguously determines the nature of the vertical distribution of individual groupings.

Spring, May–June 2007. This year, four groupings have already been identified (Fig. 8). The coastal grouping was represented by 27 species inhabiting depths of 51–100 m (Table 8). It was formed by elittoral species, among which walleye pollock absolutely dominated, followed by blackbelly eelpout, northern rock greenling, Pacific cod, and rock sole.

The elittoral grouping included 51 species and was located at depths of 101–200 m. It was dominated by elittoral species with a small presence of mesobenthic fish, represented mainly by skates – mud and Okhotsk. Pacific ocean perch *Sebastes alutus* was noted in smaller quantities. The grouping was absolutely dominated by northern rock greenling, followed by walleye pollock. The next dominant members of the grouping were broadhead sculpin, Pacific cod, and narrowhead sculpin.

The upper mesobenthic grouping, consisting of 41 species, was found at depths of 201–300 m, consisted mainly of mesobenthic species, over which the density was dominated by mass elittoral fish, such as walleye pollock, Pacific cod, and rock sole. Walleye pollock was unrivaled and clearly prevailed over all other species. Among mesobenthic fish, only various species of skates were abundant: mud, Okhotsk, and Taranetz's.

Table 8. Species structure of dominant species in bathymetric fish groupings off the Pacific coast of the northern Kuril Islands in spring–summer 2007.

Species	Density, t/mile ^{2}	Relative share	EH	Species	Density, t/mile ^{2}	Relative share	EH
First grouping, 27 species, depth 51 – 100 m				Third grouping, 41 species, depth 201–300 m			
Gadus chalcogrammus	10.795	0.718	el	*Gadus chalcogrammus*	19.124	0.795	el
Hemilepidotus jordani	2.881	0.679	el	*Gadus macrocephalus*	1.991	0.404	el
Pleurogrammus monopterygius	0.488	0.115	el	*Bathyraja violacea*	0.510	0.103	mb
Gadus macrocephalus	0.342	0.081	el	*Lepidopsetta polyxystra*	0.346	0.070	el
Lepidopsetta polyxystra	0.241	0.057	el	*Bathyraja maculata*	0.259	0.053	mb
Gymnocanthus detrisus	0.136	0.032	el	*Bathyraja taranetzi*	0.253	0.051	mb
Myoxocephalus polyacanthocephalus	0.032	0.008	el	*Pleurogrammus monopterygius*	0.195	0.039	el
Hemilepidotus gilberti	0.020	0.005	el	*Lycodes albolineatus*	0.165	0.034	mb
Gymnocanthus galeatus	0.017	0.004	el	*Careproctus rastrinus*	0.143	0.029	mb
Aptocyclus ventricosus	0.014	0.003	n	*Malacocottus zonurus*	0.135	0.027	mb
Hippoglossus stenolepis	0.013	0.003	el	*Arctoraja parmifera*	0.123	0.025	mb
Second grouping, 51 species, depth 101–200 m				Fourth grouping, 43 species, depth 301–350 m			
Gadus chalcogrammus	12.136	0.178	el	*Gadus chalcogrammus*	4.926	0.541	el
Pleurogrammus monopterygius	53.025	0.946	el	*Bathyraja violacea*	0.794	0.190	mb
Gymnocanthus detrisus	0.827	0.015	el	*Bathyraja taranetzi*	0.401	0.096	mb
Gadus macrocephalus	0.464	0.008	el	*Elassodiscus tremebundus*	0.385	0.092	mb
Gymnocanthus galeatus	0.407	0.007	el	*Hippoglossoides elassodon*	0.375	0.090	el
Lepidopsetta polyxystra	0.248	0.004	el	*Lycodes albolineatus*	0.279	0.067	mb
Hemilepidotus jordani	0.204	0.004	el	*Gadus macrocephalus*	0.279	0.067	el
Bathyraja violacea	0.146	0.003	mb	*Arctoraja parmifera*	0.216	0.052	mb
Bathyraja maculata	0.086	0.002	mb	*Careproctus furcellus*	0.186	0.044	mb
Hippoglossus stenolepis	0.072	0.001	el	*Malacocottus zonurus*	0.162	0.039	mb
Sebastes alutus	0.071	0.001	mb	*Bathyraja maculata*	0.135	0.032	mb

The lower mesobenthic grouping is represented by 43 species and was formed at depths of 301-350 m. This was a typical mesobenthic grouping, but walleye pollock continued to dominate. Following it, the main components of the community were violet skate, Taranetz's skate, and shortfin smooth lumpsucker. Of the remaining elitoral species, only flathead sole and Pacific cod were present in the grouping.

In the considered year, the boundary separating elitoral and mesobenthic groupings was located at a greater isobath – 200 m.

Autumn, October 1987 . The autumn survey was conducted up to 350 m, but even with this, four groupings were identified (Fig. 9). The first coastal grouping of 36 species was located at depths of 35-100 m, covering the entire strip of coastal waters near the islands (Table 9). The grouping was represented primarily by elitoral species with a small presence of the mesobenthic shield skate. Although walleye pollock had high abundance in the grouping, it was inferior to cod in relative biomass. In the dominant group, Pacific cod, Sakhalin flounder *Limanda sakhalinensis* and white-belly eelpout prevailed.

In the elitoral grouping, consisting of 54 species and located at depths of 101-250 m, predominantly mesobenthic species were present with a high proportion of mass elitoral species. Aleutian and violet skates, Pacific cod, and a number of mesobenthic fish dominated with a clear predominance of walleye pollock. The elitoral species, besides the aforementioned species, included the northern rock sole, represented in small numbers but ranked among the top ten species.

The subsequent mesobenthic groupings were formed by species preferring to inhabit greater depths of the slope. In the upper mesobenthic grouping, consisting of 32 species and localized at depths of 251-300 m, walleye pollock absolutely dominated, followed by Pacific cod, rock sole, and a number of mesobenthic fish, headed by spotted skate, rough careprocte, and violet skate.

Table 9. Species structure of dominant species in bathymetric fish groupings off the Pacific coast of the northern Kuril Islands in autumn 1987.

Species	Density, t/mile ^{2}	Relative share	EH	Species	Density, t/mile ^{2}	Relative share	EH
First grouping, 36 species, depth 35-100 m				Third grouping, 32 species, depth 251-300 m			
Gadus chalcogrammus	228.133	0.261	el	*Gadus chalcogrammus*	1155.784	0.687	el
Gadus macrocephalus	373.299	0.578	el	*Gadus macrocephalus*	118.153	0.224	el
Limanda sakhalinensis	146.826	0.227	el	*Lepidopsetta polyxystra*	101.944	0.193	el
Hemilepidotus jordani	43.726	0.068	el	*Bathyraja maculata*	69.723	0.132	mb
Lepidopsetta polyxystra	39.963	0.062	el	*Careproctus rastrinus*	38.420	0.073	mb

Myoxocephalus polyacanthocephalus	8.253	0.013	el	*Bathyraja violacea*	38.078	0.072	mb
Pleurogrammus monopterygius	7.314	0.011	el	*Lycodes brunneofasciatus*	36.723	0.070	mb
Limanda aspera	4.527	0.007	el	*Careproctus furcellus*	27.744	0.053	mb
Pleuronectes quadrituberculatus	3.085	0.005	el	*Bathyraja aleutica*	15.586	0.030	mb
Arctoraja parmifera	2.976	0.005	mb	*Careproctus phasma*	13.100	0.025	mb
Trichodon trichodon	1.901	0.003	el	*Crystallias matsushimae*	12.573	0.024	mb
Second grouping, 54 species, depth 101-250 m				Fourth grouping, 29 species, depth 301-350 m			
Gadus chalcogrammus	3501.313	0.836	el	*Gadus chalcogrammus*	631.393	0.530	el
Bathyraja aleutica	509.434	0.740	mb	*Bathyraja aleutica*	138.984	0.248	mb
Bathyraja violacea	60.563	0.088	mb	*Bathyraja violacea*	122.166	0.218	mb
Gadus macrocephalus	33.158	0.048	el	*Gadus macrocephalus*	67.446	0.120	el
Careproctus furcellus	10.471	0.015	mb	*Careproctus furcellus*	62.784	0.112	mb
Bathyraja maculata	9.547	0.014	mb	*Bathyraja maculata*	37.901	0.068	mb
Reinhardtius hippoglossoides	7.492	0.011	mb	*Reinhardtius hippoglossoides*	31.247	0.056	mb
Bathyraja taranetzi	5.975	0.009	mb	*Bathyraja taranetzi*	27.274	0.049	mb
Lycodes brunneofasciatus	5.421	0.008	mb	*Lycodes brunneofasciatus*	23.171	0.041	mb
Hippoglossoides elassodon	5.371	0.008	el	*Hippoglossoides elassodon*	11.370	0.020	el
Arctoraja parmifera	5.214	0.008	mb	*Arctoraja parmifera*	10.164	0.018	mb

In the lower mesobenthic grouping, observed at depths of 301-350 m, walleye pollock continued to dominate despite the significant depths. Among elitoral fish, Pacific cod was present here with flathead sole following far behind. The dominant group was represented by Aleutian skate, violet skate, broadhead careproctus, spotted skate, and Greenland halibut.

In the autumn period, the boundary between typical shelf and slope groups ran along the 250 m isobath.

DISCUSSION

Previous decades of research have yielded detailed seasonal maps of the spatial distribution of demersal fish species in the waters of the northern Kuril Islands (Orlov, 2010). They demonstrated the characteristic variability in the locations of individual fish aggregations during their annual life cycle.

An earlier attempt to identify the species composition and quantitative ratio of fish of different species in the sublittoral and benthal communities was based on pre-defined boundaries of separate sections of the sea floor – sublittoral (inner shelf 0-50 m, intermediate shelf 51-100 m, outer shelf 101-200 m) and benthal (mesobenthal 201-500 m, bathibenthal 501-2500 m, abyssobenthal 2501-4000 m) -according to already published information (Orlov, 2005). The methodology for selecting bathymetric zones in that work differs significantly from the present one in that, firstly, there is no linkage to the seasonal pattern of fish migrations in subarctic seas; secondly, it does not demonstrate the variability of community boundaries, which affects the results of identifying the species composition characteristics and quantitative structure of the distinguished vertical communities. This creates significant difficulties for comparative characterization of the results of both studies. Other publications devoted to the analysis of vertical fish communities in the study area are absent.

The data obtained in this study show that in the shelf zone and upper slope sections of the northern Kuril Islands, separate bathymetric groupings are formed, represented predominantly by elittoral or mesobenthic species, but more often with mixed species composition. The characteristic species structure of the groupings is determined during seasonal movements of both elittoral and mesobenthic fish. The boundary between vertical groupings with predominantly elittoral or mesobenthic ichthyofauna periodically shifts, positioning between the isobaths of 100 and 350 m and following seasonal patterns of fish distribution (Fig. 10). During the cold period of the year, from October to April, this boundary is noted at a considerable distance from the coast, according to available data, reaching maximum in January-February. From May to September, with warming of coastal waters, the boundary apparently shifts up to the 100 m isobath and then with cooling returns again to depths of 300-350 m.

In the North Kuril shelf zone, the presence of a coastal or sublittoral grouping (up to 100 m depth) should be noted, which is formed exclusively by elittoral fish species. The most numerous in species composition and extensive in distribution area is the proper elittoral grouping, the name of which corresponds well to its location in the elittoral zone up to 350 m. The subsequent groupings are divided into upper and lower mesobenthic, located in the surveyed mesobenthic zone of 350-600 m. Almost everywhere, including in the lower mesobenthic grouping, mass elittoral species dominate in different seasons of the year, among which walleye pollock, Pacific cod, northern rock sole, and white-bellied eelpout stand out. These species create their aggregations as widely as possible in both the shelf zone and continental slope, which is possible due to their large-scale seasonal bathymetric migrations. Despite the similarity of dominant species in the groupings, the overall species composition of fish in different areas varies significantly, which allows distinguishing various-depth vertical groupings.

The available data (Table 10) show that the elittoral assemblage can be characterized by significant similarity in its species composition across different years and seasons. In 33% of the recorded cases, the similarity coefficient reached 0.83–0.97. The similarity of the adjacent upper mesobenthic assemblage can also be relatively high, although the maximum values of the similarity coefficient, observed in 22% of cases, were slightly lower (0.61–0.77) than for the elittoral assemblages. In the remaining comparison cases, the similarity coefficients were noticeably lower.

Table 10. Similarity matrices of the elitoral (above the diagonal) and upper mesobenthic (below the diagonal) fish assemblages at the Pacific coast of the northern Kuril Islands for different seasons and years of research

Season, year	Winter, 1987	Winter, 2002	Winter, 2011	Spring, 2015	Spring, 2021	Spring, 2006	Spring, 2007	Autumn, 1987
Winter, 1987		0.0306	0.0266	0.4553	0.5591	0.5731	0.2291	0.9264
Winter, 2002	0.5669		0.7693	0.8759	0.8849	0.5549	0.3982	0.3345
Winter, 2011	0.7114	0.9095		0.9185	0.9699	0.6061	0.5066	0.4764
Spring, 2015	0.0004	0.2166	0.1958		0.9717	0.6373	0.6132	0.2129
Spring, 2021	0.0187	0.7408	0.7174	0.4975		0.5719	0.5548	0.3033
Spring, 2006	0.0061	0.3684	0.3527	0.3704	0.6491		0.7532	0.5243
Spring, 2007	0.0001	0.0177	0.0047	0.0149	0.0756	0.5411		0.1884
Autumn, 1987	0.0113	0.6071	0.6827	0.2305	0.6818	0.5244	0.0064	

Ecosystem parameters of the elitoral and upper mesobenthic assemblages in different years follow a certain pattern (Table 11). Species diversity (number of species) of the elitoral assemblage ranged from 41.5-81.7 and decreased to 33.9-38.1 only in winter 1987 and in May-June 2007. The underestimated values could have been caused by serious deficiencies in taxonomic species identification (1987) and the presence of a rigid ground rope on the bottom trawl (2007). The entropy assessment of the assemblages showed its high level during the cold period of the year with a maximum value in February-March 2002. The greatest decrease in entropy was observed in May-October, which apparently can be associated with a greater degree of separation between elitoral and mesobenthic fish and, consequently, with greater orderliness of the corresponding assemblages during the warm period. The evenness of assemblages increased in spring and, apparently, in summer periods and decreased towards the cold period, when mass fish species formed dense single-species feeding aggregations. As for the heterogeneity of the species structure of assemblages, its dynamics is opposite to changes in evenness and intensifies towards the cold season, when the difference in the quantitative ratio of dominant species is not as significant as in the warm period of the year.

Table 11. Ecosystem parameters of elittoral and mesobenthic fish assemblages in the Pacific waters near the northern Kuril Islands in different seasons and years of research

Parameter	Winter, 1987	Winter, 2002	Winter, 2011	Spring, 2015	Spring, 2021	Spring, 2006	Spring, 2007	Autumn, 1987
Elittoral assemblages								
S	33.9	81.7	75.7	41.5	44.3	44.9	38.1	69.7
$E_{1/D}$	0.095	0.116	0.063	0.127	0.104	0.139	0.076	0.033
D	0.363	0.125	0.242	0.239	0.267	0.218	0.485	0.558
$1-D$	0.637	0.875	0.758	0.761	0.733	0.782	0.515	0.442
$1/D$	2.8	8.0	4.1	4.2	3.8	4.6	2.1	1.8
H	2.114	3.869	2.656	2.639	2.596	2.642	1.727	1.744
Number of species	29	69	66	33	36	33	27	54
Mesobenthic assemblages								
S	19.6	91.7	60.8	68.5	107.4	87.8	60.8	41.2
$E_{1/D}$	0.224	0.280	0.374	0.050	0.153	0.072	0.022	0.247
D	0.319	0.047	0.058	0.391	0.083	0.202	0.896	0.127
$1-D$	0.681	0.953	0.942	0.609	0.917	0.798	0.104	0.873
$1/D$	3.1	21.3	17.2	2.6	12.1	5.0	1.1	7.9
H	2.093	4.817	4.445	2.159	4.249	3.078	0.492	3.475
Number of species	14	76	46	51	79	69	51	32

Note. S - a measure of species richness (number of species), $E_{1/D}$ - evenness by species abundance, D - heterogeneity of species composition according to Simpson's index, 1 - D - Simpson's diversity index, 1/ D - inverse Simpson's index, H - entropy.

The species diversity of the mesobenthic assemblage, in turn, demonstrates the following pattern (Table 11). The minimum species diversity (number of species) was observed in the autumn-winter period of 1987, as well as in months close to winter, and ranged from 19.6 to 41.2. In other cases, this indicator fell within the range of 60.8-107.4 (79.5 on average). Probably, this difference is objective, since in the cold season of the year, mesobenthic assemblages are formed by a smaller number of species-members, while in the warm period, the species composition expands due to migrants from adjacent bathymetric ranges.

The entropy assessment of mesobenthic assemblages was characterized by the highest indicators in the winter and near-summer seasons of the year and slightly decreased during transitional periods. This showed that in the mesobenthal, winter and spring assemblages are less ordered, which is probably due to the mutual influence of shelf or slope fish during their mass seasonal migrations. The evenness of species composition is high in the cold period of the year, while the heterogeneity of species structure, on the contrary, increases in the warm season.

CONCLUSION

Thus, the characteristic vertical structure of the demersal ichthyofauna community in the Pacific waters of the Northern Kuril region is closely related to periodic migratory movements of fish and seasonal dynamics of their spatial distribution. Sublittoral, elittoral, and mesobenthic groups undergo important changes in their distribution across isobaths, species structure, and values of ecosystem parameters in both seasonal and interannual aspects. At the same time, it should be noted that the boundary between elittoral and mesobenthic groups generally runs within the 100-350 m isobaths, gradually shifting throughout the year. A significant role in the reformation of these communities is played by the most abundant elittoral fish - walleye pollock, Pacific cod, yellowfin sole, and white-bellied eelpout, which through their seasonal migrations strongly influence the spatial-temporal structure and intra-annual dynamics. The information obtained can serve as a basis for ecosystem research in the area and needs to be supplemented with new data during subsequent trawl surveys covering all seasons of the year.

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COMPLIANCE WITH ETHICAL STANDARDS

This work uses existing results from previously conducted ichthyofauna studies. Permission for such analytical research is not required.

CONFLICT OF INTEREST

The author of this work declares that he has no conflict of interest.

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FIGURE CAPTIONS

Fig. 1. Scheme of the study area with stations (●) of the trawl surveys from 1987-2021; (—) – isobaths.

Fig. 2. Dendrogram of similarity of species composition of bathymetric fish groupings (a) at the surveyed depths of 42-500 m off the Pacific coast of the northern Kuril Islands and visualization of clusters (b) in the space of the first two principal components (PC) according to data from January-February 1987. Clusters (groupings): (▲) – *1* , (■) – *2* , (●) – *3* , (+) – *4* . Here and in Fig. 3-9: A-K – 50-meter depth ranges (A – 1-50 m, B – 51-100 m, and so on).

Fig. 3. Dendrogram of similarity of species composition of bathymetric fish groupings (a) at the surveyed depths of 50-600 m off the Pacific coast of the northern Kuril Islands and visualization of clusters (b) in the space of the first two principal components (PC) according to data from January-February 2002. Here and in Fig. 8, 9: clusters (groupings): (●) – *1* , (▲) – *2* , (■) – *3* , (+) – *4* .

Fig. 4. Dendrogram of similarity of species composition of bathymetric fish groupings (a) at the surveyed depths of 47-491 m off the Pacific coast of the northern Kuril Islands and visualization of clusters (b) in the space of the first two principal components (PC) according to data from March 2011. Clusters (groupings): (▲) – *1* , (●) – *2* , (■) – *3* .

Fig. 5. Dendrogram of similarity of species composition of bathymetric fish groupings (a) at the surveyed depths of 65-420 m off the Pacific coast of the northern Kuril Islands and visualization of clusters (b) in the space of the first two principal components (PC) according to data from March-April 2015. Clusters (groupings): (●) – *1* , (▲) – *2* , (■) – *3* .

Fig. 6. Dendrogram of similarity of species composition of bathymetric fish groupings (a) at the surveyed depths of 50-480 m off the Pacific coast of the northern Kuril Islands and visualization of clusters (b) in the space of the first two principal components (PC) according to data from May 2021. Clusters (groupings): (▲) – *1* , (●) – *2* .

Fig. 7. Dendrogram of similarity of species composition of bathymetric fish groupings (a) at the surveyed depths of 45-498 m off the Pacific coast of the northern Kuril Islands and visualization of clusters (b) in the space of the first two principal components (PC) according to data from May-June 2006. Clusters (groupings): (▲) – *1* , (●) – *2* .

Fig. 8. Dendrogram of similarity of species composition of bathymetric fish groupings (a) at the surveyed depths of 60-348 m off the Pacific coast of the northern Kuril Islands and visualization of clusters (b) in the space of the first two principal components (PC) according to data from May-June 2007.

Fig. 9. Dendrogram of similarity of species composition of bathymetric fish groupings (a) at the surveyed depths of 35-350 m off the Pacific coast of the northern Kuril Islands and visualization of clusters (b) in the space of the first two principal components (PC) according to data from October 1987.

Fig. 10. Depth of the boundary (■) between the elitoral and mesobenthic fish groupings off the Pacific coast of the northern Kuril Islands in different seasons and years of research: (⌶) – range of surveyed depths.