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Ichthyofauna of Russian Exclusive Economic Zone of the Bering Sea: 2. Ecological and Zoogeographical Characteristics

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Abstract—The ecological and zoogeographical characteristics of 344 species of Pisces and fish-like species comprising the ichthyofauna of the Bering Sea (Russian Exclusive Economic Zone) are presented for the study period of 1995–2012 (original studies) and those for previous findings in this area. The benthic species (elittoral, mesobenthic, and sublittoral; 216 species, or 62.8%) dominate if one takes into account the biotopic characteristics of the species; the majority belongs to the wide-boreal Pacific, wide-boreal Asiatic, and arctic-boreal species (255 species, or 74.1%) by the zoogeographic characteristics. The comparative analysis of the fish communities of the western Bering Sea evidences to the significant changes of the ichthyofauna within the depth southwards Navarin Cape. Arctic-boreal species can be considered as a specific faunistic "margin" between the northern and the southern ichthyofauna of the western Bering Sea due to their eurybiont characteristics.

Keywords: Bering Sea, ichthyofauna, biotopic structure, zoogeographic structure

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The first part of the publication series (Datsky, 2015a) covers the taxonomic diversity of the ichthyofauna of the Bering Sea within the Russian Exclusive Economic Zone (EEZ). It was found that the diversity of the ichthyofauna of the western Bering Sea, calculated under the ratio of species, genera, and families, was significantly higher that observed for the Arctic seas, the seas of the European part of Russia (except the Caspian Sea), and the Sea of Japan. It was similar to the diversity of the ichthyofauna of coastal waters of the northern Kuril Islands and the northern Sea of Okhotsk. The maximal diversity has been found for scorpion fishes and sculpins (Scorpaeniformes), perch-like fishes (Perciformes), salmons (Salmoniformes), flatfishes (Pleuronectiformes), and cods and hakes (Gadiformes); these families comprised 175 species out of 344 species, or 50.9% of the total species diversity.

The present study gives the ecological and zoogeographical characteristics of the ichthyofauna of the Bering Sea for the sea in total and for the certain areas, taking into account the ecological and zoogeographical peculiarities of the studied species. Detailed description of the materials and methods has been given in the first part of the publication series (Datsky, 2015a).

RESULTS AND DISCUSSION

Ecological Characteristics

The ecological characteristics of Pisces and fish-like species of the Bering Sea include the information of the peculiarities of the species life cycle and their belonging to the specific ichthyocenosis. Benthic and demersal fish species prevail in the Bering Sea (261 species out of 344 in total, or 75.9% of the species diversity); pelagic species comprise much less diversity (83 species, or 24.1%). Such biotopic distribution is usual for this area; it has been observed earlier (Andriashev, 1939; Datsky and Andronov, 2007; Balykin and Tokranov, 2010; Andronov and Datsky, 2014). The first group comprises littotal, sublittoral, elittoral, meso-, bathy-, and abyssobenthic fish species, as well as four freshwater species and one anadromous sublittoral species in regard to their ecological characteristics (Table 1; Datsky, 2015a. Table 3). The second group includes catadromous, neritic, epi-, meso-, and bathypelagic species, as well as anadromous neritic, epi-, and mesopelagic species. Regard must be paid to the high diversity of ichthyofauna (170 species) that may be found mostly in the upper pelagic zone (0–200-m depth) of the western Bering Sea (Ivanov, 2013) despite relatively low number of the true pelagic fish species.

In general, the ichthyofauna of the western Bering Sea may be divided into 16 ecological groups in regard

Table 1. Ecological characteristics of the ichthyofauna of the western Bering Sea

Family	Ecological group*																Species, total
	EL	MB	SL	MP	BB	BP	L	AEP	N	Cat	AN	AbB	EP	Fr	AMP	ASL	
Cottidae	25	5	13	–	1	–	2	–	–	–	–	–	–	1	–	–	47
Zoarcidae	10	18	6	–	4	–	1	–	–	–	–	3	–	–	–	–	42
Liparidae	5	18	1	2	4	–	5	–	–	–	–	–	–	–	–	–	35
Pleuronectidae	10	6	3	–	–	–	–	–	–	–	–	–	–	–	–	–	19
Stichaeidae	5	2	7	–	–	–	3	–	–	–	–	–	–	–	–	–	17
Agonidae	12	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	15
Arhynchobatidae	–	8	–	–	3	–	–	–	–	–	–	–	–	–	–	–	11
Salmonidae	–	–	–	–	–	–	–	8	–	–	3	–	–	–	–	–	11
Sebastidae	1	7	1	–	–	–	–	–	–	–	–	–	–	–	–	–	9
Cyclopteridae	6	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	8
Myctophidae	–	–	–	6	–	1	–	–	–	–	–	–	–	–	–	–	7
Psychrolutidae	3	3	–	–	1	–	–	–	–	–	–	–	–	–	–	–	7
Hemitripteridae	4	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	6
Macrouridae	–	–	–	–	5	–	–	–	–	–	–	1	–	–	–	–	6
Coregonidae	–	–	–	–	–	–	–	–		4	–	–	–	1	–	–	5
Gadidae	3	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	5
Hexagrammidae	2	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	5
Microstomatidae	–	–	–	5	–	–	–	–	–	–	–	–	–	–	–	–	5
Platytroctidae	–	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5
Bathymasteridae	1	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	4
Moridae	–	2	–	–	2	–	–	–	–	–	–	–	–	–	–	–	4
Oneirodidae	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	4
Osmeridae	–	–	–	–	–	–	–	–	2	1	1	–	–	–	–	–	4
Clupeidae	–	–	–	–	–	–	–	–	2	–	1	–	–	–	–	–	3
Gonostomatidae	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	3
Melamphaidae	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	3
Opisthoproctidae	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	3
Paralepididae	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	3
Petromyzontidae	–	–	–	–	–	–	–	1	–	–	–	–	–	1	1	–	3
Pholididae	–	–	1	–	–	–	2	–	–	–	–	–	–	–	–	–	3
Alepocephalidae	–	–		–	–	2	–	–	–	–	–	–	–	–	–	–	2
Anarhichadidae	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	2
Gasterosteidae	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	2
Malacosteidae	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	2
Melanostomiidae	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	2

Table 1. (Contd.)

Family	Ecological group*																Species, total
	EL	MB	SL	MP	BB	BP	L	AEP	N	Cat	AN	AbB	EP	Fr	AMP	ASL	
Notosudidae	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	2
Trichodontidae	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
Acipenseridae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
Alepisauridae	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1
Ammodytidae	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Anoplopomatidae	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Anotopteridae	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1
Bramidae	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1
Bythitidae	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1
Caristiidae	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Ceratiidae	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1
Cetomimidae	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1
Chauliodontidae	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1
Chiasmodontidae	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1
Engraulididae	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1
Icosteidae	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Lamnidae	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1
Nemichthyidae	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1
Neoscopelidae	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1
Notacanthidae	–	–	–		–	–	–	–	–	–	–	1	–	–	–	–	1
Oreosomatidae	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1
Ptilichthyidae	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Rajidae	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1
Scomberesocidae	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1
Scopelarchidae	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1
Somniosidae	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Squalidae	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Sternoptychidae	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1
Synaphobranchidae	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1
Zaproridae	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Total number of scpecies	93	79	44	29	21	19	13	9	8	6	6	6	5	4	1	1	344
Species ratio, %	27.0	23.0	12.8	8.4	6.1	5.5	3.8	2.6	2.3	1.7	1.7	1.7	1.5	1.2	0.3	0.3	100

* Here and in Table 2: EL—elittoral; MB—mesobenthic; SL—sublittoral; MP—mesopelagic; BB—bathybenthic; BP—bathypelagic; L—littoral; AEP—anadromous epipelagic; N—neritic; Cat—catadromous; AN—anadromous neritic; AbB—abyssal-benthic; EP—epipelagic; Fr —freshwater; AMP—anadromous mesopelagic; ASL—anadromous sublittoral.

to their reference to the certain biotope; benthic or pelagic (Table 1). The prevalence of the benthic species is supported mostly by the elittoral, mesobenthic, and sublittoral groups (216 species, or 62.8% of total species diversity). The tight contact between the shelf and the deep areas of the continental slope in the study area promotes the presence of the mesopelagic species (29 species, 8.4%), bethybenthic (21, 6.1%), bathypelagic (19, 5.5%), and abyssobethic species (6, 1.7%); in total, they comprise 75 species, or 21.8% of the total species diversity. The next groups are anadromous littoral species (13, 3.8%), anadromous epipelagic (9, 2.6%), neritic (8, 2.3%), catadromous neritic (6, 1.7%) and anadromous neritic (6, 1.7%), epipelagic (4, 1.5%), and freshwater species that can migrate to the brackish waters (4, 1.2%). Finally, one anadromous mesopelagic (0.3%) and one anadromous sublittoral (0.3%) species have been registered.

The maximal number of the littoral species belongs to Liparidae (five species); sublittoral, to Cottidae (13), elittoral, to Cottidae (25), Agonidae (12), Zoarcidae (10), and Pleuronectidae (10); mesobenthic, to Zoarcidae (18) and Liparidae (18). The species of Myctophidae family (six) prevail in the mesopelagic group; Macrouridae (five), in the bathybenthic group; Oneirodidae, in the bathypelagic group; Salmonidae, in the groups of catadromous epipelagic fish (eight) and neritic fish (three); Coregonidae (four), in the catadromous group; and Zoarcidae, in the abyssobenthic group (three). In the other ecological groups, there was no dominating family (Table 1).

The majority of the diverse elittoral group of the fishes of the Bering Sea (93 species, or 27.0% of the total species diversity) is presented by the species belonging to the families of Cottidae, Zoarcidae, Pleuronectidae, and Agonidae. The most typical representatives are saffron cod *Eleginus gracilis*, walleye pollock *Theragra chalcogramma,* Pacific cod *Gadus macrocephalus*, Atka mackerel *Pleurogrammus monopterygius*, Arctic staghorn sculpin *Gymnocanthus tricuspis*, armorhead sculpin *G. galeatus*, butterfly sculpin *Hemilepidotus papilio*, spatulate sculpin *Icelus spatula*, great sculpin *Myoxocephalus polyacanthocephalus,* warty sculpin *M. verrucosus*, ribbed sculpin *Triglops pingelii*, crested sculpin *Blepsias bilobus*, Arctic alligatorfish *Aspidophoroides olrikii*, sturgeon poacher *Podothecus accipenserinus*, veteran poacher *P. veternus,* longnose poacher *Sarritor leptorhynchus*, Okhotsk snailfish *Liparis ochotensis*, marbled eelpout *Lycodes raridens*, Canadian eelpout *L. polaris,* wattled eelpout *L. palearis*, stout eelblenny *Anisarchus medius*, daubed shanny *Leptoclinus maculatus,* Pacific sand lance *Ammodytes hexapterus,* Sakhalin sole *Limanda sakhalinensis*, Alaska plaice *Pleuronectes quadrituberculatus*, yellowfin sole *L. aspera,* Bering flounder *Hippoglossoides robustus,* flathead sole *H. elassodon*, and Pacific halibut *Hippoglossus stenolepis*. The majority of the listed species belong to the numerous or common species under the classification by Sheiko and Fedorov (2000). These species have been found in the trawl catches widely in the whole study area. The fish of this group comprise the ecologically flexible species (walleye pollock and Pacific halibut) that perform long-distance horizontal and vertical migrations within the deep-sea areas and in the coastal waters (Shuntov et al., 1993; Chikilev and Pal'm, 1999; Datsky and Andronov, 2007).

Some specimens of the numerous mesobenthic group (shortfin eelpout *Lycodes brevipes*, Alaska skate *Bathyraja parmifera*, and Greenland halibut *Reinhardtius hippoglossoides*) have been found sporadically in the catches performed in the upper shelf of the Bering Sea (depths of 20–40 m); however, most of them tended to occupy the depths of more than 150–200 m and areas of silty sediments. The shelf areas are more attractive for the young specimens of the Greenland halibut, while the adults are usually found at the continental slope. However, in certain years, the mature specimens of Pacific sleeper shark *Somniosus pacificus*, Okhotsk skate *Bathyraja violacea*, mud skate *B. taranetzi*, microdisk snailfish *Careproctus ostentum*, Kamchatka flounder *Atheresthes evermanni,* arrowtooth flounder *A. stomias*, and darkfin sculpin *Malacocottus zonurus* are registered at the depths of 80–90 m (Datsky and Andronov, 2007). The Aleutian skate *B. aleutica*, white-blotched skate *B. maculata*, shortraker rockfish *Sebastes borealis,* Pacific ocean perch *S. alutus*, shortspine thornyhead *Sebastolobus alascanus,* broadbanded thornyhead *S. macrochir,* sablefish *Anoplopoma fimbria*, blacknose sculpin *Icelus canaliculatus,* wide-eye sculpin *I. euryops*, spinyhead sculpin *Dasycottus setiger*, slender snailfish *Paraliparis grandis*, Alaska snailfish *Careproctus colletti*, salmon snailfish *C. rastrinus*, blotched snailfish *Crystallichthys mirabilis*, blackmouth eelpout *Lycodapus fierasfer*, and longsnout prickleback *Lumpenella longirostris* may be named as the typical representatives of the mesobenthic group in the study area. In general, the majority of the mesobenthic ichthyofauna of the Bering Sea belongs to Liparidae, Zoarcidae, Arhynchobatidae, and Sebastidae families: 51 species, or 64.6% of the species diversity of the mesobenthic group (Table 1).

The third numerous group comprises 44 sublittoral species (or 12.8% of species diversity) inhabiting the depths of less than 50 m. This group is presented mostly by the families of Cottidae, Zoarcidae, and Stichaeidae (Table 1). The common species are whitespotted greenling *Hexagrammos stelleri,* masked greenling *H. octogrammus*, hamecon *Artediellus scaber*, threaded sculpin *Gymnocanthus pistilliger*, fourhorn sculpin *Myoxocephalus quadricornis*, Bering poacher *Occella dodecaedron*, snake prickleback *Lumpenus sagitta,* pighead prickleback *Acantholumpenus mackayi*, banded gunnel *Pholis fasciata*, Arctic shanny *Stichaeus punctatus*, longhead dab *Limanda proboscidea*, Arctic flounder *Liopsetta glacialis,* and starry flounder *Platichthys stellatus*. The species belonging to this group usually do not form large schools or stocks, and

they prefer gravel-pebble and sandy bottom sediments and rarely migrate deeper than 100–150 m. Most of these species are stenobionts, they are characterized by a number of morphological adaptations (small body size, flatten or vermiform body, reduction or modification of the fins, thickening and/or additional armoring of the teguments, cryptic coloration, and adverse buoyancy) for the successful life in the shallow waters (Andriyashev, 1939, 1954; Borets, 1997).

The characteristics given above may also be applied for the fish species of the littoral group that inhabit mostly the tidal zone (rocky bottom or the macrophytes beds). Some species of this group may migrate down to 150 m, for example, stippled gunnel *Rhodymenichthys dolichogaster* (Sheiko and Fedorov, 2000). Only the most strong and ecologically flexible fish species can survive these harsh environmental conditions of the littoral (storms, tidal events, etc.) (Borets, 1997). The list of these species in the western Bering Sea comprises 13 species (3.8%); the most common are brightbelly sculpin *Microcottus sellaris*, pored sculpin *Porocottus mednius*, stone cockscomb *Alectrias alectrolophus*, spotted snailfish *Liparis callyodon,* and stippled gunnel.

Bathybenthic species dominate in the group of the deep-sea ichthyofauna of the Bering Sea (Table 1). Regard must be paid to the five species of Macrouridae family: giant grenadier *Albatrossia pectoralis*, popeye grenadier *Coryphaenoides cinereus*, Pacific grenadier *C. acrolepis*, filamented rattail *C. filifer,* and longfin grenadier *C. longifilis*. The first two species are the most common (especially the first one); the other three are found much more rarely. These five species dominate in the benthic ichthyocenoses of the continental slope of Olyutorsko-Navarin region (Borets et al., 2001; Gavrilov and Glebov, 2013). In addition to the Macrouridae family, a large role belongs to the bathybenthic species of the other families: Zoarcidae (snakehead eelpout *Embryx crotalinus*, Kamchatka eelpout *Lycenchelys camchatica*, behemoth eelpout *L. hippopotamus*, and soft eelpout *Bothrocara molle*) and Liparidae (spiny snailfish *Acantholiparis opercularis*, falcate snailfish *Careproctus cypselurus,* blacktail snailfish *C. melanurus*, and ebony snailfish *Paraliparis holomelas*). Most of these species inhabit the depths of 500 m and deeper (Datsky, 2015a. Table 3); that are why they are found rarely in the trawl catches performed in this area.

The abyssobenthic species are found even more rarely in the Bering Sea; they are abyssal grenadier *Coryphaenoides armatus*, longnose tapirfish *Polyacanthonotus challengeri*, deepwater arrowtooth eel *Histiobranchus bathybius*, as well as three representatives of Zoarcidae family: manytoothed eelpout *Lycenchelys micropora*, keeled eelpout *L. plicifera,* and longnape eelpout *L. volki*. All these species, except abyssal grenadier, prefer to inhabit the depths of 2000 m and more, so they are found in the catches very rarely.

The group of the pelagic fish of the western Bering Sea comprises mostly meso- and bathypelagic species (48 species; or 14.0% of the species diversity) (Table 1; Datsky, 2015a. Table 3). Due to the preference of these species to the pelagic environment and the depths of 200 m and more, they have been mostly found in the deep-sea southwestern Bering Sea (Olyutorsky-Navarin and Olyutorsky-Karaginsky regions), with some exceptions.

High biomass of the mesopelagic fish species allows concluding on their great role in the ecosystem, where they are responsible for the transport of the matter and energy in the pelagic zone of the Bering Sea (Balanov, 1995; Shuntov and Sviridov, 2005; Shuntov and Temnykh, 2008a, 2008b). The families of Myctophidae and Microstomatidae dominate in this group, some species of these families (California headlightfish *Diaphus theta*, northern smoothtongue *Leuroglossus schmidti*, slender blacksmelt *Bathylagus pacificus*, and stout blacksmelt *Pseudobathylagus milleri*) are quite numerous in the epi- and mesopelagic zone of the Bering Sea; northern lampfish *Stenobrachius leucopsarus,* Alaska pollock, and Pacific viperfish *Chauliodus macouni* are the major components of the nekton communities of the mesopelagic zone of the study area. The last three species dominate by biomass (Balanov, 1995; Shuntov and Sviridov, 2005). The majority of the mesopelagic fish species have been presented in the catches by large-size immature specimens, except northern lampfish, stout blacksmelt, slender blacksmelt, and barreleye fish *Macropinna microstoma*. Probably, they use the pelagic area of the Bering Sea (200–800-m depths) as feeding grounds but reproduce in the southern regions of the Northern Pacific (Balanov, 1995).

Nineteen fish species have been registered in the catches performed at the depths of 500 m and more in the western Bering Sea; they all belong to the bathypelagic group (Table 1; Datsky, 2015a. Table 3). Common species are the representatives of the families of Oneirodidae, Melamphaidae, and Gonostomatidae, including bulb-fish *Oneirodes bulbosus*, Alaska dreamer *O. thompsoni*, deep-water bristlemouth *Cyclothone atraria,* slender bristlemouth *C. pseudopallida*, slender fangjaw *Sigmops gracilis*, crested bigscale *Poromitra crassiceps*, and highsnout melamphid *Melamphaes lugubris*. Opposite to the mesopelagic fish species, the fish of this group do not perform diel vertical migrations, when they move up to several hundreds meters in the nighttime as the component of the migrating sound scattering layer (i.e., the complex of the macroplankton and micronecton animals performing diel vertical migrations). These species do not change their depth greatly within the day and night. Despite their small body size (up to 30–40 cm), the bathypelagic group comprises the predator species also, such as longfin dragonfish *Tactostoma macropus* Pacific viperfish (Parin, 1988).

Epipelagic fish species characterized by low abundances and frequency of occurrence in the catches also prefer southwestern areas of the Bering Sea; they inhabit mostly the pelagic zone of the shelf (depth of less than 200 m). Such species as salmon shark *Lamna ditropis*, North Pacific daggertooth *Anotopterus nikparini*, long-snouted lancetfish *Alepisaurus ferox*, Pacific saury *Cololabis saira,* and Pacific pomfret *Brama japonica* (Datsky, 2015a. Table 3) usually spend the whole life cycle in the epipelagic zone of the Pacific Ocean, and the northern catches of these species may be preconditioned by either sporadical transport with the currents (Pacific pomfret) during the anomalous warm years, or/and the shifting of the northern margin of their range during the years of their extremely high abundance (Pacific saury) (Savinykh, 1995; Baitalyuk, 2004; Filatov, 2007; Shuntov and Temnykh, 2008a; *Saira-2014...*, 2014), or by the food-searching migrations of salmon shark, North Pacific daggertooth, and long-snouted lancetfish (Mel'nikov, 1997; Balanov and Radchenko, 1998; Savinykh and Glebov, 2003; Golub', 2007). Regard must be paid to the most pronounced northward migrations of the salmon shark that penetrates even to the Chukchi Sea, while the other epipelagic species found in the western Bering Sea do not perform such distant migrations (*Atlas...*, 2006; Chernova, 2011; Mecklenburg et al., 2011; Datsky, 2015b).

The tightest relationships are observed for the epipelagic and neritic fish species; these relationships are characterized by mutual (regular or sporadic) penetration of the representatives of both groups to the "alien" biotopes. However, a common feature is observed for the fish that belong or relate to the neritic pelagic zone but migrate from the shelf to the open sea; particularly, they must return back to the coastal or even fresh waters to finish their life cycle successfully (Parin, 1988). Eight neritic species inhabiting the pelagic zone of the Bering Sea have been registered (Table 1); the most common among them are Pacific herring *Clupea pallasii*, Pacific capelin *Mallotus villosus catervarius*, polar cod *Boreogadus saida,* and smooth lumpfish *Aptocyclus ventricosus* (Datsky, 2015a. Table 3). These four species have been registered regularly in the trawl catches; they all reproduce or feed within the continental shelf close to the coastal waters (Nikol'sky, 2013).

The presence of the other representatives of the neritic ichthyofauna in the western Bering Sea (Japanese sardine *Sardinops melanostictus*, Japanese anchovy *Engraulis japonicus*, Japanese smelt *Hypomesus japonicus*, and spinous lumpfish *Eumicrotremus soldatovi*) is a result of the shifting of the geographical ranges of these species northwards during anomalously warm years of the late 1990s–early 2000s. Such events are common in the ichthyocenoces and are the most pronounced during the periods of climate warming, as it was also observed in the late 1930s–early 1950s (Shuntov and Temnykh, 2008a). Regard must be paid to cold-water polar cod, which is the dominant fish species in the Chukchi Sea and in the Bering Strait; however, this species has shrunk the distance of its feeding migrations, as well as the abundance of the migrating stock nowadays in the Bering Sea (Nikolaev et al., 2008).

The anadromous Pisces and fish-like (17 species, 4.9%) found in the western Bering Sea may be divided into epipelagic group (six species of *Oncorhynchus* genus, Dolly Varden trout *Salvelinus malma*, Kamchatkan rainbow trout *Parasalmo penshinensis,* and Arctic lamprey *Lethenteron camtchaticum*), neritic group (three species of *Salvelinus* genus, Pacific rainbow smelt *Osmerus mordax dentex*, three-spined stickleback *Gasterosteus aculeatus,* and American shad *Alosa sapidissima*), mesopelagic group (Pacific lamprey *Entosphenus tridentatus*), and sublittoral group (green sturgeon *Acipenser medirostris*). It is obvious that salmonids (11 species) dominate in this list. All these species grow in the ocean but spawn in the rivers, migrating upstream by hundreds of kilometers. The most common species of salmonids in the study area were chum salmon *Oncorhynchus keta* and sockeye salmon *O. nerka*; pink salmon *O. gorbuscha*, Chinook salmon *O. tshawytscha,* and coho salmon *O. kisutch* have rarely been registered. Petromyzontidae family has been presented by two species, while Osmeridae, Clupeidae, and Gasterosteidae families by one species each (Table 1).

In the brackish waters (bays, inlets, lagoons, and estuaries), catadromous species have been registered (pond smelt *Hypomesus olidus*, broad whitefish *Coregonus nasus*, sardine cisco *C. sardinella*, sharpnose whitefish *C. anaulorum*, inconnu *Stenodus leucichthys nelma*, and ninespine stickleback *Pungitius pungitius*). The species of Coregonidae family dominate in this group; these species feed and grow in the summer–autumn season in the brackish waters (the period of their lowest salinity) and return back to the rivers for winter and spring when the water salinity in these areas is maximal. The fluctuations of the water salinity may be one of the factors that precondition the seasonal chages in the fish communities, as was found for the Gulf of Anadyr, the Bering Sea (Andronov et al., 2014), the Gulf of Ob, the Kara Sea, and the Laptev Sea (Kuznetsov et al., 2011; Kuznetsov, 2014).

Typically freshwater species, such as humpback whitefish *C. lavaretus pidschian*, burbot *Lota lota leptura*, slimy sculpin *Cottus cognatus cognatus,* and Far Eastern brook lamprey *L. reissneri*, are rarely found even in the brackish waters. In general, the representatives of the last two groups tend to inhabit rivers and lakes; they migrate to the brackish waters mostly during the growth period (Chereshnev et al., 2001; Chereshnev, 2008).

Four regions have been defined in accordance with the ratio and distribution of the ichthyofauna of numerous fish families (Andriashev, 1939, 1954): the

eastern Bering Sea, the western Bering Sea, the northern Bering Sea, and the Chukchi Sea. These studies have also found the similarity of the last two regions and allowed defining the Anadyr faunistic barrier that split the northern Bering Sea from its eastern and western parts (Andriyashev, 1939). Later, it was found that the ecological characteristics of Pisces and fish-like species of the Chukchi Sea and the shallow waters of the northwestern Bering Sea (upper shelf, depths < 100 m, between Olyutorsky Cape and Dezhnev Cape) were rather similar (Datsky, 2015b). If one does not pay much attention to the absolute number of the species, which is predictably lower in the Arctic sea due to the total decline of elittoral, sublittoral, and mesobenthic fish species, then the ratio of the species belonging to certain groups is quite similar in both seas due to the shallow depths and harsh environmental conditions. Significant differences have been observed only in the Chukchi Sea; there were, particularly, the decrease of the ratio of the mesobenthic species and the total absence of the anadromous mesopelagic species (Pacific lamprey).

In the present study, when taking into account the scheme of the biogeographical areas (Datsky, 2015a. Fig. 1), it is obvious that the most northern part of the Bering Sea (Chirikov Basin) is quite similar to the Chukchi Sea by the ratio of certain ecological groups of ichthyofauna (Table 2). Earlier, such similarity of ichthyofauna of this region was found both with the northern Bering Sea (Andriyashev, 1939) and with its shallow areas (depths < 100 m) up to Cape Olyutorsky (Datsky, 2015b). This is preconditioned mostly by the shallow depths of both areas and severe temperature regime. In general, the comparative analysis of the fish communities of the western Bering Sea evidences that the composition of ichthyofauna changes vertically when moving southwards only in the Gulf of Anadyr and differs significantly from the northern areas of the sea southwards off Navarin Cape. Similar changes in the fish communities of these areas have been reported earlier (Andronov and Datsky, 2014a; Andronov and Datsky, 2014b). The presence and vicinity of the continental slope and deep-sea areas promote regular findings of meso-, bathy- and abyssobenthic fish species, as well as epi-, meso-, and bathypelagic species in Olyutorsky-Navarin and Olyutorsky-Karaginsky regions. Similar explanation may be suggested for the general increase of the absolute number of sublittoral and elittoral species southwards and the decrease of their relative abundance meantime in the fish communities.

Zoogeographic Characteristics

The Bering Sea contacts the Pacific Ocean at its southern margin and the Chukchi Sea at its northern margin. The Bering Sea combines two different faunistic regions of the Pacific Ocean (Asian and American); thus, the ichthyofauna of the Bering Sea is mixed. The boreal fish species form the basis (approximately 92%) of the ichthyofauna of the Bering Sea (Andriashev, 1939); i.e., the representatives of the northern Pacific temperate fauna are usually found southwards of Bering Strait. This regularity is true for the nekton communities of the western Bering Sea, where the ratio of such species reaches 90% (Ivanov, 2013). The original data of the present and previous studies support these conclusions; particularly, only 24 fish species (7.0%) belong to the Arctic fauna, and 320 species (93.0%) are boreal (Table 3; Datsky, 2015a. Table. 3).

Generally, 18 zoogeographic groups of Pisces and fish-like species have been defined in the fish communities of the western Bering Sea taking into account their geographical ranges (Table 3); warm-water and stenobiont species dominate (218 species, or 63.4% of species diversity). There are 126 (36.6%) cold-water species of panarctic, arctic, arctic-boreal, subarctic palearctic, high-boreal Pacific, high-boreal American, high-boreal Asiatic, circumboreal, Anadyr–Beringian, and Anadyr–Koryak ranges. Undoubtedly, relatively easy water exchange with the Pacific Ocean through the deep-water straits of the Aleutian Volcanic Arc largely preconditions forming such structure of the ichthyofauna of the Bering Sea; the waters of the Pacific origin comprise 90% of the water volume of the Bering Sea (Istoshin, 1969). The severe conditions of the Chukchi Sea, which is affected by the cold-water masses of the Arctic Ocean and receiving the water masses from the Bering Sea through the Bering Strait, promote domination here of the arctic ichthyofaun that comprises 62.7% of the species diversity (Datsky, 2015b).

The margin position of the Bering Sea in the system of the Pacific Ocean and its large size, and significant role of the water masses of the Pacific origin here promote the presence of the numerous wide-boreal Pacific fish species (90 species from 40 families, 26.2% of the species diversity) and wide-boreal Asiatic fish species (72 species from 20 families, 20.9%). These two groups are followed by high-boreal Pacific (42 species from 13 families, 12.2%), arctic-boreal (34 species from 14 families, 9.9%), cosmopolitan (24 species from 20 families, 7.0%), high-boreal Asiatic (17 species from 5 families, 4.9%), arctic (15 species from 4 families, 4.4%), and wide-boreal American (ten species from five families, 2.9%). The low-boreal groups (Pacific and Asiatic) are presented by 17 species from 15 families (4.9% of the species diversity). The representatives of the other zoogeographic complexes are rare and have nearly no effect on the ichthyofauna of the Bering Sea.

The polar cod is a representative of the panarctic group between the numerous components of the arctic ichthyofauna. This species is common in the Arctic Ocean; it is a eurybiont species that can live at a wide range of salinity; it may even migrate to the brakish

Table 2. Ecological characteristics of the ichthyofauna of the western Bering Sea and the Chukchi Sea

District	Ecological group															Species, total
	EL	MB	SL	MP	BB	BP	L	AEP	N	Cat	AN	AbB	EP	Fr	AMP	ASL	
Chukchi Sea*	49 44.5	7 6.4	25 22.7	0 0	2 1.8	0 0	3 2.7	7 6.4	3 2.7	6 5.5	4 3.6	0 0	1 0.9	3 2.7	0 0	0 0	110
Bering Sea (western part), including:	93 27.0	79 23.0	44 12.8	29 8.4	21 6.1	19 5.5	13 3.8	9 2.6	8 2.3	6 1.7	6 1.7	6 1.7	5 1.5	4 1.2	1 0.3	1 0.3	344
– Chirikov Basin	59 48.4	10 8.2	28 23.0	0 0	1 0.8	0 0	2 1.6	7 5.7	4 3.3	3 2.5	4 3.3	0 0	1 0.8	2 1.6	1 0.8	0 0	122
– Gulf of Anadyr	75 43.6	28 16.3	35 20.3	3 1.7	2 1.2	0 0	2 1.2	7 4.1	4 2.3	6 3.5	4 2.3	0 0	1 0.6	4 2.3	1 0.6	0 0	172
– Olyutorsky-Navarin region	78 30.5	61 23.8	30 11.7	22 8.6	18 7.0	13 5.1	4 1.6	7 2.7	6 2.3	3 1.2	5 2.0	2 0.8	4 1.6	2 0.8	1 0.4	0 0	256
– Olyutorsky-Karaginsky region	82 27.7	70 23.6	30 10.1	28 9.5	19 6.4	17 5.7	13 4.4	9 3.0	8 2.7	2 0.7	5 1.7	5 1.7	5 1.7	1 0.3	1 0.3	1 0.3	296

Here and in Table 4: numbers above the line indicate the number of species; below the line, the ratio of the total number of the species for the indicated area, %; * according to Datsky, 2015b.

Table 3. Zoogeographic characteristics of the ichthyofauna of the western Bering Sea

	Zoogeographic group																		Species, total
	WBPac	WBAs	HBPac	ArcB	Cos	HBAs	Arc	WBAm	LBPac	LBAs	HBAm	SArcPal	AtlPac	Pac	AnKor	AnBer	CB	PanArc	
Cottidae	5	16	10	6	–	5	4	–	–	–	–	–	–	–	–	1	–	–	47
Zoarcidae	5	7	11	1	–	6	7	4	–	1	–	–	–	–	–	–	–	–	42
Liparidae	8	11	8	1	–	–	3	1	–	1	2	–	–	–	–	–	–	–	35
Pleuronectidae	5	3	1	5	–	1	–	3	–	1	–	–	–	–	–	–	–	–	19
Stichaeidae	1	7	1	6	–	–	–	–	–	–	1	–	1	–	–	–	–	–	17
Agonidae	3	5	3	2	–	–	1	1	–	–	–	–	–	–	–	–	–	–	15
Arhynchobatidae	3	7	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11
Salmonidae	5	2	–	3	–	1	–	–	–	–	–	–	–	–	–	–	–	–	11
Sebastidae	4	2	2	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	9
Cyclopteridae	1	1	1	–	–	4	–	–	–	–	1	–	–	–	–	–	–	–	8
Myctophidae	6	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7
Psychrolutidae	3	2	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	7
Hemitripteridae	4	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	6
Macrouridae	4	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	6
Coregonidae	–	–	–	–	–	–	–	–	–	–	–	4	–	–	1	–	–	–	5
Gadidae	2	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	1	5
Hexagrammidae	2	1	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	5
Microstomatidae	4	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	5
Platytroctidae	1	–	–	–	2	–	–	–	–	–	–	–	1	1	–	–	–	–	5
Bathymasteridae	1	1	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	4
Moridae	1	1	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	4
Oneirodidae	2	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	4
Osmeridae	–	1	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4
Clupeidae	–	1	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	3
Gonostomatidae	1	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	3
Melamphaidae	1	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	3
Opisthoproctidae	1	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	3
Paralepididae	–	–	–	–	2	–	–	–	1	–	–	–	–	–	–	–	–	–	3
Pholididae	–	–	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
Petromyzontidae	1	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	3
Alepocephalidae	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	2
Anarhichadidae	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
Gasterosteidae	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	2
Malacosteidae	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	2
Melanostomiidae	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	2
Notosudidae	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	2

Table 3. (Contd.)

	Zoogeographic group																		Species, total
	WBPac	WBAs	HBPac	ArcB	Cos	HBAs	Arc	WBAm	LBPac	LBAs	HBAm	SArcPal	AtlPac	Pac	AnKor	AnBer	CB	PanArc	
Trichodontidae	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	2
Anoplopomatidae	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Acipenseridae	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1
Alepisauridae	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Ammodytidae	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Anotopteridae	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1
Bramidae	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Bythitidae	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1
Caristiidae	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Ceratiidae	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Cetomimidae	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Chauliodontidae	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Chiasmodontidae	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1
Engraulididae	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Icosteidae	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Lamnidae	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Nemichthyidae	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Neoscopelidae	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Notacanthidae	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Oreosomatidae	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Ptilichthyidae	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Rajidae	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Scomberesocidae	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Scopelarchidae	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Somniosidae	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Squalidae	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Sternoptychidae	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Synaphobranchidae	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Zaproridae	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Number of species	90	72	42	34	24	17	15	10	9	8	8	6	3	2	1	1	1	1	344
Species ratio, %	26.2	20.9	12.2	9.9	7.0	4.9	4.4	2.9	2.6	2.3	2.3	1.7	0.9	0.6	0.3	0.3	0.3	0.3	100

Zoogeographic groups here and in Table 4: WBPac—wide-boreal Pacific; WBAs—wide-boreal Asiatic; HBPac—high-boreal Pacific; ArcB—arctic-boreal; Cos—cosmopolitan; HBAs—high-boreal Asiatic; Arc—arctic; WBAm—wide-boreal American; LBPac—low-boreal Pacific; LBAs—low-boreal Asiatic; HBAm—high-boreal American; SArcPal—subarctic palearctic; AtlPac—Atlantic–Pacific; Pac—Pacific; AnKor—Anadyr–Koryak; AnBer—Anadyr-Beringian; CB—circumboreal; PanArc—panarctic.

waters (Manteifel', 1943; Korotaev and Chikilev, 2000; Chernova, 2011). High abundance and large-scale migrations of the polar cod from the Chukchi Sea to the Bering Sea are usually observed during the cold years (Nikolaev et al., 2008). In the Bering Sea, the polar cod is a common species in the northwestern areas (northern Gulf of Anadyr), but it forms large stocks here only sporadically. Probably, such migrations occur due to the expanding of the geographical range of this species; the latter event, in turn, is preconditioned by the rapid increase of the abundance of the polar cod in the Chukchi Sea (Fadeev, 1986). In certain years, this species may reach Olyutorsky Bay (Andriashev, 1939, 1954; Borets et al., 2001); this area may be considered as the southern margin of this species in the Bering Sea.

Fifteen fish species that prefer to inhabit the adjacent arctic seas (i.e., of the arctic geographic range) have been registered in the western Bering Sea; particularly, they belonged to Zoarcidae (seven species), Cottidae (four species), Liparidae (three species), and Agonidae (one species) (Table 3). These species belong to sublittoral and elittoral groups only: rough hamecon, Arctic staghorn sculpin, Arctic alligatorfish, Canadian eelpout, saddled eelpout *Lycodes mucosus,* polar eelpout *L. turneri*, fish doctor *Gymnelus viridis*, and fourhorn sculpin (found periodically in the trawl catches), as well as Arctic seasnail *Liparis bathyarcticus*, gelatinous seasnail *L. fabricii,* kelp snailfish *L. tunicatus*, Chukot fringed sculpin *Porocottus quadrifilis*, halfbarred pout *G. platycephalus*, Barsukov's pout *G. barsukovi*, and Knipowitsch pout *G. knipowitschi*, included into the list by the references (Fedorov, 1973; Sheiko and Fedorov, 2000; Chernova, 2008, 2011; *Ryby...*, 2013; Parin et al., 2014). All the species belonging to this group prefer the water masses of high dissolved oxygen concentration, and most of them spawn in autumn and winter (Nikol'sky, 1980, 2013). The southern margin of their range belongs to the Gulf of Anadyr; only the first six species of this list have been registered southwards, and the Arctic staghorn sculpin has been found in the catches from Olyutorsky-Karaginsky region (Datsky, 2015a. Table 3).

The actic-boreal zoogeographical complex comprises numerous species mostly belonging to Cottidae family (six species) and Stichaeidae family (six species), as well as Pleuronectidae family (five); the other 11 families are presented by 17 species in total (Table 3; Datsky, 2015a. Table 3). This group combines the representatives of different ecological groups: elittoral (saffron cod, warty sculpin, ribbed sculpin, Veteran poacher, Atlantic poacher, marbled eelpout, dusky snailfish *Liparis gibbus*, stout eelblenny, sand lance, Bering flounder, yellowfin sole, Pacific halibut, etc.), sublittoral (threaded sculpin, snake prickleback, slender eelblenny *Lumpenus fabricii*, Arctic flounder, starry flounder, etc.), littoral (stippled gunnel), neritic (capelin, herring), anadromous neritic (Pacific rainbow smelt, Arctic char, Taranetz char *Salvelinus taranetzi*, three-spined stickleback), anadromous epipelagic (Arctic lamprey, Dolly Varden trout), and catadromous fish (pond smelt *Hypomesus olidus*). Most of these species prefer the water temperature range around zero Celsius, so they dominate in the fish communities of the western Bering Sea in winter and in spring; in the cold years, they may stay until mid-summer (Glebov et al., 2003).

Arctic-boreal species are well adapted to the extreme environment; they are found in both the warmest coastal areas (water temperature higher than 6–8°C) and in the cold water masses (temperature below zero Celsius). They comprise the species that prefer the temperature regime of the Arctic zone, but that can be found in the temperate boreal conditions, and the fish species that inhabit the waters of the temperatures above zero Celsius and migrating to the cold waters. The first group comprises capelin, marbled eelpout, daubed shanny, threaded sculpin, Pacific sand lance, and warty sculpin; the second group comprises saffron cod, yellowfin sole, Pacific halibut, Veteran poacher, and herring. Most of these species are characterized by relatively wide temperature range (i.e., they are eurytherm species), but the temperature optimum in the first group is shifted to the Arctic environment, while that in the second group is shifted to the boreal conditions (Andronov and Datsky, 2014a).

High-boreal species are presented in three groups: Pacific (42 species), Asiatic (17), and American (eight). Zoarcidae, Cottidae, and Liparidae form the basis of the first group; Zoarcidae, Cottidae, and Cyclopteridae form the basis of the second group; and Liparidae forms the basis of the third group. The species of this type of geographical range are distributed widely in the Bering Sea and in the Gulf of Alaska; they belong to the most cold-water species among the boreal fish. In some cases, their distribution is similar to the distributional pattern of the arctic-boreal ichthyofauna; thus, they are considered as the transitional forms from the arctic species to the boreal species (Datsky and Andronov, 2007; Andronov and Datsky, 2014a).

The maximal diversity of the high-boreal ichthyofauna belongs to the Pacific species; they are presented mostly by elittoral (17 species) and mesobenthic species (12); sublittoral (six species), littoral (six species), and abyssobenthic species (one) have also been registered (Table 3). Interestingly, in Chirikov Basin and Gulf of Anadyr, only three species belong to this group: fatlip pout *Gymnelis bilabrus*, dark pout *G. obscurus*, and decorated warbonnet *Chirolophis decoratus*. An opposite pattern is observed in the southwestern Bering Sea (Olyutorsky–Navarin and Olyutorsky–Karaginsky regions), where 22 high-boreal Pacific species have been found. The most common littoral species here are spotted snailfish *Liparis callyodon*, Commander snailfish *L. mednius*, thumbtack snailfish *L. micraspidophorus,* Kussakin's

snailfish *L. kussakini*; sublittoral species: large-plate sculpin *Stelgistrum concinnum*; elittoral species: dusky rockfish *Sebastes ciliatus*, small-plate sculpin *S. beringianum*, roughspine sculpin *Triglops macellus*, highbrow sculpin *T. metopias*, scalybreasted sculpin *T. xenostethus*, biporous pout *Gymnelus diporus*; mesobenthic species: mud skate *Bathyraja taranetzi*, northern rockfish *Sebastes polyspinis*, whitetail sculpin *Malacocottus aleuticus*, longnose eelpout *Lycenchelys longirostris,* manypore eelpout *L. ratmanovi*, slender eelpout *Lycodapus leptus,* and variform eelpout *L. poecilus*. Regard must be paid to the rare occurrence of most species listed above in the trawl catches; their findings refer here mostly to the published data. Another seventeen species belonging to different ecological groups have been registered widely in the study area: Atka mackerel, red Irish lord *Hemilepidotus hemilepidotus*, thorny sculpin *Icelus spiniger*, bigmouth sculpin *Hemitripterus bolini*, fourhorn poacher *Hypsagonus quadricornis*, tubenose poacher *Pallasina barbata,* longnose poacher *Sarritor leptorhynchus*, Pacific spiny lumpsucker *Eumicrotremus orbis*, blotched snailfish *Crystallichthys mirabilis*, wattled eelpout, ebony eelpout *Lycodes concolor*, and northern rock sole *Lepidopsetta polyxystra*.

High-boreal Asiatic species also form a relatively abundant group in the study area (Table 3; Datsky, 2015a. Table 3). They are presented mostly by elittoral species (nine) with small impact (one to two species) of mesobenthic, littoral, sublittoral, neritic, anadromous epipelagic, and abyssobenthic species. Such species as pimpled lumpsucker *Eumicrotremus andriashevi*, bumpy lumpsucker *Cyclopteropsis inarmatus*, smallhook sculpin *Artediellus miacanthus*, spinyhook sculpin *A. gomojunovi,* hookhorn sculpin *A. pacificus*, halfbarred pout *Gymnelus hemifasciatus,* and longhead dab are relatively common and are found in the trawl catches widely in the study area. The rest of this zoogeographic group, i.e., such species as Kamchatka steelhead, whitespotted sculpin, Berg's lumpsucker *Cyclopteropsis bergi*, Soldatov's lumpsucker, keeled eelpout *Lycenchelys plicifera*, poorpore pout *Gymnelus pauciporus*, Alaska eelpout *Bothrocara pusillum*, Derjugin's slipskin *Lycodapus derjugini*, Pavlovski's eelpout *Krusensterniella pavlovskii*, and plumed sculpin *Archistes plumarius*, have been registered exclusively in the southwestern Bering Sea; rare findings of this species refer to the published data only (Fedorov, 1973; Borets 1997, 2000; Sheiko and Fedorov, 2000; Mecklenburg and Sheiko, 2003; Anderson et al., 2009; Parin et al., 2014).

The high-boreal American group is the smallest; it comprises only eight species belonging mostly to sublittoral and elittoral species. They inhabit the eastern Bering Sea and the Gulf of Alaska; in the study area, they have been mostly found southwards Navarin Cape, except docked snailfish *Lethotremus muticus* caught in Gulf of Anadyr (Table 3; Datsky, 2015a. Table 3). In the trawl catches, the only shortmast sculpin *Nautichthys robustus* has been found. The other species of this group (fringed greenling *Hexagrammos superciliosus*, soft sculpin *Psychrolutes sigalutes*, polydactyl snailfish *Paraliparis dactylosus*, lobefin snailfish *Polypera greeni*, Alaskan ronquil *Bathymaster caeruleofasciatus*, pearly prickleback *Bryozoichthys marjorius*) have been included into the list in accordance with the previously published data (Fedorov, 1973; Sheiko and Fedorov, 2000; Zolotov, 2012; Parin et al., 2014).

Relatively cold-water, freshwater, and catadromous fish species form a separate group. They are nine species belonging to four types of geographical ranges. These species tend to inhabit the river basins of the northwestern Bering Sea and the eastern Chukchi Sea; they are found rarely in the trawl catches, and all the findings of these species have been made in the brackish waters. The only two species, eastern burbot and ninespined stickleback, that are characterized by a wide range in the Arctic and boreal seas of the Northern Hemisphere (Chernova, 2011) have been registered southwards Cape Olyutorsky. Generally, the other species are not found southwards 174° E; they inhabit mostly the coastal waters of the Gulf of Anadyr (Chereshnev, 2008; *Macrofauna*..., 2012; Andronov et al., 2014). The maximal species diversity was observed for the Coregonidae family that is presented by subarctic palearctic range (humpback whitefish, broad whitefish, Siberian white salmon, and least cisco) and Anadyr–Koryak range (sharpnose whitefish) (Table 3; Datsky, 2015a. Table 3). Alongside with that, sharpnose whitefish and least cisco, together with Arctic rainbow smelt, are among the common species of the summer ichthyocenoses of the estuarine brackish waters of Anadyrskiy Liman, or Anadyr Estuary (Kuznetsova and Kuznetsov, 1988; Andronov et al., 2014). The Asiatic brook lamprey has been found exclusively in the estuary of Anadyrsky Liman (Parin et al., 2014).

Wide-boreal species is presented in the western Bering Sea by a large and diverse group of 172 species (50.0%) belonging to three geographical groups: Pacific (90 species), Asiatic (72), and American (ten). Within this zoogeographical group, mesobenthic species dominate (53 species), followed by elittoral (39), bathybental (20), mesopelagic (15), and sublittoral (15) species. Most of the species of this group have been found in the trawl catches (116 species) and were abundant or common (frequency of occurrence in the catches was 10% and more). These are relatively warm-water species belonging mostly to the families of Cottidae (21 species), Liparidae (20), Zoarcidae (16), Pleuronectidae (11), and Arhynchobatidae (10). The frequency of occurrence of this species obviously increases from north southwards: in the Chukchi Sea, there are 39 species of this group; in Chirikov Basin, 49; in Gulf of Anadyr, 82; in Olyutorsky-Navarin region, 149; and in Olyutorsky-Karaginsky, 161 (Table 3, 4; Datsky, 2015a. Table 3). Alongside with that, 87 species have not been registered northwards

Navarin Cape. Generally, one can conclude here that boreal elements are quite diverse in regard to the faunistic characteristic. In the other words, there are species that are distributed widely in the study area, but most of the species are characterized by local ranges. That is why the second (geographical) characteristic is necessary for this group (Pacific, Asiatic, or American). This was first suggested by Andriashev (Andriashev, 1939) during his studies of ichthyofauna of the Bering Sea.

Wide-boreal Pacific complex includes twelwe ecological groups; the dominating groups are mesobenthic (21 species), elittoral (16), bathybental (15), and mesopelagic (14) species belonging to several families: Liparidae (eight species), Myctophidae (six), Salmonidae (five), Pleuronectidae (five), Zoarcidae (five), and Cottidae (five species). The most usual representatives of this complex are abundant or common in the study area (61 species); they perform long-distance migrations and inhabit vast areas. For example, 41 species has been found in the Gulf of Anadyr; 26 species reached Chirikov Basin during their feeding and other types of migrarions, and 22 species have been even registered in Chukchi Sea (Tables 3 and 4; Datsky, 2015a. Table 3).

The common species belonging to wide-boreal Pacific group and that have been found regularly in the trawl catches were salmon shark, Pacific sleeper shark, walleye pollock, Pacific cod, five specis of *Oncorhynchus* genus, northern lampfish, garnet lampfish, gianr grenadier, Pacific grenadier, popeye grenadier, Pacific ocean perch, shortraker rockfish, shortspine thornyhead, sablefish, masked greenling, whitespotted greenling, armorhead sculpin, yellow Irish lord, antlered sculpin, darkfin sculpin, spinyhead sculpin, shaggy sea raven *Hemitripterus villosus*, smooth lumpsucker, sturgeon poacher, blackfin starsnout *Bathyagonus nigripinnis*, searcher, Alaska plaice, flathead sole, and Greenland halibut. In addition, seventeen species found in the western Bering Sea have been included into this list in accordance with the published data only (Fedorov, 1973; Borets, 1997, 2000; Sheiko and Fedorov, 2000; Love et al., 2005; D'yakov, 2011; Parin et al., 2014), and the locations of their rare catches was limited by the area stretching south-westwards Navarin Cape.

Wide-boreal Asiatic ichthyofauna is characterized by less species diversity belonging to ten ecological groups; mesobenthic (26 species), elittoral (21), sublittoral (ten) species dominate. Compared to wide-boreal Pacific zoogeographical complex, a significant decrease of mesopelagic (14 vs. 1), bathybentic (15 vs. 5), and bathypelagic (7 vs. 1) species is observed, which may occur due to the absence of the deep-sea ichthyofauna of the northern Pacific Ocean in this list. The abundant species of the Asiatic ichthyofauna are Aleutian skate, rock greenling *Hexagrammos lagocephalus*, purplegray sculpin *Gymnocanthus detrisus*, banded Irish lord *Hemilepidotus gilberti*, great sculpin, blacknose sculpin, spectacled sculpin *Triglops scepticus*, hawk poacher *Podothecus sturioides,* sawback poacher *Sarritor frenatus*, salmon snailfish, dimdisk snailfish *Elassodiscus tremebundus*, slender snailfish, stone cockscomb, Sakhalin sole, and Kamchatka flounder. The warm-water species are presented mostly by the families of Cottidae (16 species), Liparidae (11), Stichaeidae (seven), Zoarcidae (seven), and Arhynchobathydae (seven species). In comparison to the Pacific ichthyofauna, the penetration of the wide-boreal Asiatic species northwards is less pronounced due to their lower diversity; however, 38, 21, and 16 species have been registered in the Gulf of Anadyr, in Chirikov Basin, and in Chukchi Sea, respectively (Tables 3, 4; Datsky, 2015a. Table 3).

Wide-boreal American zoogeographic complex is only presented by ten species, mostly by mesobenthic species belonging to Zoarcidae family (four species) and Pleuronectidae family (three species). Their distribution in the western Bering Sea is limited by the area of the Gulf of Anadyr, except shortfin eelpout and Kamchatka flounder. Shortfin eelpout was found in Chirikov Basin and the young specimens of Kamchatka flounder were found in the southern Chukchi Sea (Datsky, 2015b). This complex also includes gray starsnout *Bathyagonus alascanus*, green sturgeon, manytoothed eelpout, blackmouth eelpout, black eelpout *Lycodes diapterus*, swellhead snailfish *Paraliparis cephalus*, rex sole *Glyptocephalus zachirus,* and Dover sole *Microstomus pacificus*. All these species tend to inhabit the eastern Bering Sea and the Gulf of Alaska (Allen and Smith, 1988; Mecklenburg et al., 2002); their findings in the western Bering Sea may evidence to the margins of their geographical ranges here.

Low-boreal Pacific and Asiatic species (17 species, or 4.9% of species diversity) together with Atlantic-Pacific and Pacific species (5, 1.5%) penetrate from the tropical climatic zone to the boreal climatic zone in summer and autumn only. In the western Bering Sea, they may be considered as rare species taking into account low frequency of occurrence in the trawl catches (0.03–9.27%). For most of them, the area of the Far East seas is the expatriation zone or the region where pseudo-populations are formed; however, some species use this area as the feeding grounds during the season of the optimal water temperature regime (Ivanov, 2013). In the study area, these species are American shad, brownsnout spookfish *Dolichopteryx longipes*, streaklight tubeshoulder *Holtbyrnia latifrons*, longfn dragonfish, longfin waryfish *Scopelosaurus adleri,* scaly waryfish *Scopelosaurus harryi*, slender barracudina *Lestidiops ringens*, North Pacific daggertooth, longfin codling *Laemonema longipes*, pelagic brotula *Thalassobathia pelagica*, spikehead dreamer *Bertella idiomorpha*, Japan-sea eelpout *Bothrocara hollandi*, Japanese sandfish *Arctoscopus japonicus*, scaly-eye plaice *Acanthopsetta nadeshnyi*, and longsnout prickleback. Most of these species have been found only in the southern Bering Sea (Olyu-

Table 4. Zoogeographic characteristics of the ichthyofauna of the western Bering Sea and the Chukchi Sea

Area	Zoogeographic group																		Species, total
	WBPac	WBAs	HBPac	ArcB	Cos	HBAs	Arc	WBAm	LBPac	LBAs	HBAm	SArcPal	AtlPac	Pac	AnKor	AnBer	CB	PanArc	
Chukchi Sea*	22 20.0	16 14.5	5 4.5	33 30.0	2 1.8	4 3.6	18 16.4	1 0.9	0 0.0	0 0.0	0 0.0	6 5.5	0 0.0	0 0.0	0 0.0	1 0.9	1 0.9	1 0.9	110
Bering Sea (western part), including:	90 26.2	72 20.9	42 12.2	34 9.9	24 7.0	17 4.9	17 4.9	15 4.4	10 2.9	9 2.6	8 2.3	8 2.3	6 1.7	3 0.9	2 0.6	1 0.3	1 0.3	1 0.3	344
– Chirikov Basin	26 21.3	21 17.2	11 9.0	34 27.9	1 0.8	7 5.7	2 1.6	15 12.3	0 0.0	0 0.0	0 0.0	2 1.6	0 0.0	0 0.0	0 0.0	1 0.8	1 0.8	1 0.8	122
– Gulf of Anadyr	39 22.7	38 22.1	20 11.6	34 19.8	2 1.2	7 4.1	15 8.7	5 2.9	0 0.0	0 0.0	1 0.6	0 0.0	1 0.6	0 0.0	1 0.6	1 0.6	1 0.6	1 0.6	172
– Olyutorsky–Navarin region	81 31.6	60 23.4	25 9.8	33 12.9	14 5.5	10 3.9	6 2.3	8 3.1	5 2.0	4 1.6	2 0.8	2 0.8	2 0.8	1 0.4	0 0.0	1 0.4	1 0.4	1 0.4	256
– Olyutorsky–Karaginsky region	85 28.7	68 23.0	36 12.2	30 10.1	22 7.4	17 5.7	1 0.3	8 2.7	8 2.7	8 2.7	5 1.7	1 0.3	3 1.0	2 0.7	0 0.0	0 0.0	1 0.3	1 0.3	296

torsky–Karaginsky region), except the last one (registered in Gulf of Anadyr also). Fifteen species (>68%) out of 22 species belonging to 18 families are mesobenthic and mesopelagic in accordance to their ecological characteristics (Table 3; Datsky, 2015a. Table 3).

Cosmopolitan species are grouped separately in a relatively large complex; the area of their distribution covers vast areas of Pacific, Atlantic, and Indian oceans and adjacent seas. In the western Bering Sea, there are 24 species belonging to 20 families (7.0% of species diversity). Twenty-two species have been found southwards Cape Navarin in the southwestern Bering Sea, except North Pacific spine dogfish *Squalus suckleyi* and arctic skate *Amblyraja hyperborea*, which were found widely in the western Bering Sea. Bathy- and mesopelagic species dominate (15 species), followed by mesobenthic species (four). The typical representatives of ichthyofauna are deep-water arrowtooth eel, avocet snipe eel *Avocettina infans*, teardrop tubeshoulder *Holtbyrnia innesi*, phantom bristlemouth *Cyclothone pseudopallida*, lowcrest hatchetfish *Argyropelecus sladeni*, white barracudina *Arctozenus risso*, longnose lancetfish, Pacific blackchin *Scopelengys tristis*, smooth abyssal grenadier, twopole dreamer *Oneirodes eschrichtii*, Kroyer's deep-sea angler fish *Ceratias holboelli*, crested bigscale, and coster dory. None of these species have been found in the trawl catches; here, they refer only to the published data (Fedorov, 1973; Sheiko and Fedorov, 2000; *Atlas*..., 2006; *Makrofauna*..., 2012, 2014; Parin et al., 2014; Tuponogov and Kodolov, 2014).

A vast area of the Bering Sea characterized by a variety of environment promotes high diversity of the ichthyofauna in the study area. A shallow northern part of the sea is affected by the cold Arctic water masses coming from the Chukchi Sea, and the strong penetration of the warm Pacific waters is observed in the southern Bering Sea. That is why warm-water fish species dominate in the southwestern Bering Sea, and the number of the arctic species increases northwards (Table 4). The number of the wide-boreal Pacific species increases from 22 up to 85 species when moving southwards from Chukchi Sea to Olyutorsky–Karaginsky region of the Bering Sea; wide-boreal Asiatic, from 16 up to 68; wide-boreal American, from 1 up to 8; high-boreal Pacific, from 5 up to 36; high-boreal Asiatic, from 4 up to 17; cosmopolitan, from 2 up to 22 species. Low-boreal species appear southwards Cape Navarin. The relative increase of the ratio of the warm-water species (cosmopolitan, low-boreal Pacific and Asiatic, Atlantic-Pacific, and Pacific) is observed in the marginal areas of the Gulf of Anadyr and Olyutorsky-Navarin region.

The opposite pattern is observed for the arctic species, when the decrease of their diversity southwards is the most obvious at the margin between Gulf of Anadyr and Olyutorsky-Navarin region. Such opposite tendencies in distribution of the boreal Pacific species and arctic species in the Bering Sea has been reported earlier (Andriashev, 1939; Datsky and Andronov, 2007; Andronov and Datsky, 2014a). Relatively steep continental slope carrying ridges and hollows, relatively narrow shelf of Olyutorsky-Navarin region, vast shallow plateau of the Gulf of Anadyr and Chirikov Basin, effect of warm Central Bering Sea Current, interaction of the water masses, and other environmental factors promote the natural separation of the ichthyofauna. Such separation of the benthic ichthyofauna is quite complex, when five fish communities are defined (sublittoral, elittoral, transitional shelf-bathyal, α-bathyal, and β-bathyal), referring to different depth ranges (Andronov and Datsky, 2014b).

It seems possible that arctic-boreal species due to their eurybiont features (especially regarding water temperature) may serve specifically as a faunistic "margin" between the northern and the southern ichthyofaunas of the western Bering Sea (Andronov and Datsky, 2014a). Despite the relative substitution of these species southwards by the other faunistic complaexes, the absolute number of species is stable from the northern to the southern margin of the study area (30–33 species). Zoogeographical complexes "adjacent" to the arctic-boreal group (high-boreal and arctic) exhibit the opposite tendencies: the number of the warm-water species decreases northwards, the number of the cold species increases at the north (Table 4). Generally, the up-to-date margins between the faunistic complexes coincide with the scheme of the faunistic regions of the Bering Sea developed 75 years ago (Andriashev, 1939) and given in detail later (Datsky and Andronov, 2007; Andronov and Datsky, 2014a; Andronov and Datsky, 2014b).

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