ISSN 2079-0864, Biology Bulletin Reviews, 2024, Vol. 14, No. 3, pp. 376–393. © Pleiades Publishing, Ltd., 2024.
Russian Text © The Author(s), 2023, published in Zhurnal Obshchei Biologii, 2023, Vol. 84, No. 4, pp. 327–344.

Ecological-Parasitological Method in Studies of Population Biology of Beaked Redfish *Sebastes mentella* (Scorpaeniformes: Sebastidae) in the Irminger Sea

Y. I. Bakay[a, *], S. P. Melnikov[b], and A. I. Glubokov[b]

[a] *Polar Branch of the Russian Federal Research Institute of Fisheries and Oceanography (PINRO Knipovich PINRO), Murmansk, 183038 Russia*

[b] *Russian Federal Research Institute of Fisheries and Oceanography, Moscow, 105187 Russia*

**e-mail: bakay@pinro.ru*

Received January 27, 2023; revised June 23, 2023; accepted August 3, 2023

Abstract—The results of the analysis of the data set obtained in the course of long-term studies of the population biology of beaked redfish *Sebastes mentella* are used as an interdisciplinary approach in the study of its geographical, biotopic, ontogenetic, and phylogenetic features and population structure in the pelagic zone of the Irminger Sea and the adjacent bathyal zone of Greenland and Iceland. The approach is based on the ecological-parasitological method, which involves the use of data on the composition of parasite communities and the occurrence of their individual species as biomarkers for understanding the features of the ecology of hydrobionts. The results obtained, which include information on the spatial distribution, functional subdivision of the area, ontogenetic migrations, maturation and growth rate, underwater marking, and phenetic, genetic, and other features of beaked redfish, made it possible to identify the conditions for divergent formation and significant isolation of its pelagic and benthic groupings constituting the North Atlantic population. The colonization by this species of great depths of the oceanic pelagic zone and the near-bottom layer of the bathyal zone, accompanied with an increase in the rate of sexual maturation and migratory activity in the pelagic zone, characterizes the direction of the current stage of its phylogenesis. The unity of the pelagic grouping of beaked redfish in the vast water area and throughout the depth of its distribution in the Irminger and Labrador seas is substantiated. It is shown that significant differences in infestation rate between males and females of beaked redfish, stable in time and space, with the only species-specific parasite (the copepod *Sphyrion lumpi*) serve as a phene of the pelagic grouping of the North Atlantic population of the host.

DOI: 10.1134/S2079086424030022

INTRODUCTION

Of the four species of North Atlantic redfish, *Sebastes* Cuvier, 1829 is of greatest interest from the point of view of population organization of beaked redfish *Sebastes mentella* Travin, 1951, being the most widespread and phylogenetically young. It is characterized by high ecological plasticity, expressed in its adaptability to living both in the bottom layer of the shelf and bathyal and in the mesopelagic zone in a wide range of depths in the water area from the Barents, Greenland, and Norwegian seas to the coast of Canada (Population structure..., 2004; Melnikov and Bakai, 2009a, 2009b, 2021; Melnikov, 2016; Melnikov and Glubokov, 2017; Rolsky et al., 2017; Karamushko and Christiansen, 2021).

Despite the efforts of scientists from different countries, a unified idea of the species structure of the beaked redfish has not been formed. The results of our many years of research and analysis of published data allowed us to conclude that this species in its vast range has formed three populations relatively isolated from each other by a system of constant sea currents: the North Atlantic, the Norwegian-Barents Sea, and the Flemish Cap (Melnikov, 2016; Bakay, 2021). However, debates about the structure of the first of them, inhabiting the Irminger Sea and adjacent waters, do not wane. Thus, since the 1980s, fishing regulation of this population has been based on the concept of its unity (Saborido-Rey et al., 2004; Bakai and Melnikov, 2008; Melnikov and Bakai, 2009a). However, in 2010, it was changed owing to the hypothesis adopted by ICES (International Council for the Exploration of the Sea) about the existence of three "types" ("populations") of beaked redfish in the Irminger Sea (Population structure..., 2004) and the corresponding decision of the NEAFC (North-East Atlantic Fisheries Commission) on separate regulation of fishing for the two "pelagic populations." To confirm this hypothesis, studies were carried out using genetic markers: mtDNA (Schmidt, 2005), allozymes (Daníelsdóttir et al., 2008), RAPD markers (Johansen and Dahle, 2004), microsatellites (Pampoulie and Danielsdottir, 2008; Stefansson et al., 2009).

In the work summarizing the results of these studies (Cadrin et al., 2010), four units of the beaked redfish stock in the seas of the North Atlantic are identified: "pelagic shallow-water" (lives in the pelagic zone at a depth of less than 500 m), "pelagic deep-water" (at a depth of more than 500 m), "slopes of Iceland" (in the bottom layer of the bathyal of Iceland), and "western" (off the coast of Canada). Richter (1996), having discovered differences in the rate of sexual maturation and several meristic characters, suggested the existence of two "populations" of beaked redfish: "oceanic" (in the pelagic zone of the Irminger Sea) and "coastal" (off the coast of Greenland and Iceland). Other authors (Roques et al., 2002), according to the results of studies of microsatellite DNA sequences, on the contrary, indicate the presence of a single "panoceanic" population of beaked redfish inhabiting the pelagic zone of the Irminger and Labrador Seas, the bathyal waters of the Grand Banks of Newfoundland (GBN), and off the Labrador Peninsula and the islands of Greenland, Iceland, and the Faroes.

However, the differentiation of beaked redfish "populations" in these publications was based only on the identified variability in frequency individual markers and biological indicators. Here, ecological and population confirmation of such differentiation and information about the internal structure of the identified "populations" were absent, and upon sampling, the features of the spatial and bathymetric distribution, age, and sex of the redfish were often not taken into account, which led to inconclusive conclusions regarding its population structure.

Considering the ecological plasticity of the beaked redfish, which inhabits different biotopes over a wide range of depths, it seems advisable to use an ecological approach in the study of its population biology, which involves, in particular, the analysis of parasite–host relationships (Yablokov, 1987). The ecological-parasitological method involves the use of data on the composition and specificity formation communities of parasites, the occurrence of individual species as biomarkers of differences/similarities in living and nutritional conditions, migrations, and intraspecific, interspecific, and phylogenetic characteristics of their hosts (Konovalov, 1971; Gaevskaya and Kovaleva, 1986; MacKenzie and Abaunza, 2005; Catalano et al., 2014; MacKenzie and Hemmingsen, 2015). Specific parasites can also serve as indicators of the "relatedness" of the host (Bakai, 2021).

Some researchers (Williams et al., 1992; MacKenzie, 2002) believe that the use of parasitological data may have advantages over other approaches in population biology (morphometric, genetic-biochemical, analysis of otolith structure), where the accumulation of differences in the variability and frequencies of individual traits is a much more conservative and lengthy process. In addition, the presence of interspecific hybridization among redfish of the genus *Sebastes* (Roques et al., 2001; Makhrov et al., 2011; Artamonova et al., 2011, 2013) limits the use of morphometric and genetic-biochemical data in population studies of these fish. Therefore, we took the ecological-parasitological method as the basis for using an integrated approach (providing the acquisition and analysis of mutually complementary data aimed at studying the spatial, population structure, and phylogeny of the species (Begg and Waldman, 1999; Catalano et al., 2014)).

Goal of the work was to identify ecological-geographical, biotopic, bathymetric, population, and phylogenetic features of beaked redfish living in the Irminger Sea and adjacent waters through analysis parasitological data and materials received other methods for studying fish population biology.

MATERIALS AND METHODS

We used the results of a complete parasitological dissection (Bykhovskaya-Pavlovskaya, 1985) and a study of parasites of various taxa of 1528 beaked redfish individuals aged 5–25 years obtained from trawl catches in the 0–500 m and 501–900 m layer in the pelagic zone of the Irminger Sea and the bottom layer of the bathyal (depth 235–1040 m) of Greenland and Iceland during more than 40 expeditions during domestic ichthyoplankton surveys in April–May 1985–1995 and domestic (1982–1998, 2021) and international (1999–2018) trawl-acoustic surveys to assess the stock of this species in June–July and during voyages of fishing vessels in April–October 1981–2022. In these regular expeditions, in most of which the authors took part, the reproductive and feeding areas, the routes of distribution of larvae, the conditions for the formation of aggregations, the size and age composition, the rate of sexual maturation, the ratio of immature and sexually mature fish, and linear and weight growth, and feeding characteristics and composition of parasite communities of beaked redfish were determined. The collection and processing of biological material was carried out according to accepted methods (*Instruktsii i nastavleniya*, 1980; *Instruktsii i metodicheskie*..., 2001), and its volume is presented in Table 1. The age of fish is determined by their scales (Pavlov et al., 1992). Processing of genetic samples and analysis of its results were carried out at the Severtsov Institute of Ecology and Evolution (IEE) of the Russian Academy of Sciences and at VNIRO.

The taxonomic composition of parasite communities is presented according to the World Register of Marine Species (http://www.marinespecies.org/). To indicate in the tables the parasites that belong to certain classes, the following designations are accepted: My—Myxozoa, Mo—Monogenea, Ce—Cestoda,

Table 1. Volume of collected and processed material on beaked redfish in the Irminger Sea and adjacent waters

Types of research	Number of fish, specimens
Complete parasitological necropsy	1528
Partial parasitological dissection	425
Registration of ectolesions*	123 885
Body length measurement (*TL*), cm	152 611
Age determination	17 876
Determination of the rate of puberty	100 066
Determination of the growth rate	4244
Nutrition analysis	121 525
Protein polymorphism analysis	3803
DNA microsatellite sequence analysis	613

* Includes determination of the degree and characteristics of infestation with copepod *Sphyrion lumpi* and occurrence and localization of skin pigment formations (Bakai and Karasev, 1995).

Tr—Trematoda, Ch—Chromadorea, Pa—Palaeacanthocephala, He—Hexanauplia. Long-term features of infestation of beaked redfish with copepods *Sphyrion lumpi* have been revealed according to the developed methodology (Bakai and Karasev, 1995).

The indicators of parasite infestation indicators were as follows: extent of invasion (EI) is the proportion (%) of fish infected with a parasite of a given species out of the number studied; abundance index (AI) is the number of parasites of a given species per fish studied (Bush et al., 1997). The second indicator was not determined for Myxozoa. The EI confidence interval was estimated as an interval covering the parameter with a given reliability (Roitman and Lobanov, 1985). Significance of differences (p) in EI by parasites and the occurrence of skin pigment spots in beaked redfish was determined using a significance criterion test (χ^2) at significance level $p < 0.05$ (Breev, 1976). To identify the geographical features of parasite communities, calculations of the measure of similarity (L_0) of their composition based on the Sørensen–Chekanovsky coefficient using the “weighted pair-group method” were used (Bailey, 1970; Andreev and Reshetnikov, 1978). It is accepted that the degree of isolation of the compared groups of beaked redfish has an inverse relationship to the values of L_0 and direct dependence on the magnitude of differences in the rate of puberty of their individuals (Hall et al., 2015).

To assess the belonging of parasites to zoogeographical and ecological complexes, we used published data (Andriyashev, 1979; Zubchenko, 1993; Lile et al., 1994; Hemmingsen and MacKenzie, 2001) and the results of our own research. These complexes have the following designations in the tables: AB—arctic-boreal, AamB—arctic-amphiboreal, atB—Atlantic-boreal, amB—amphiboreal, K—cosmopolitans, PZ—polyzonal, MP—mesopelagic, MB—mesobenthal, EC—epicontinental. The “core” of parasite communities is formed by the dominant species found in beaked redfish in all or most areas. The “component community” of parasites is considered as a set of infracommunities of parasites of all age groups of a population or group host (Dugarov and Pronin, 2013). The occurrence of male and female redfish with skin pigmented formations was assessed, using them as a reasonable phene (Bakai, 2015).

An interdisciplinary (integrated) approach in population studies (Begg and Waldman, 1999; Catalano et al., 2014) included the use of our previously published results of studies of the composition of parasites and substantiated phenes of beaked redfish living in the Irminger Sea and adjacent waters. To study the characteristics of the population biology of the beaked redfish, data on its size and age composition, rate of sexual maturation and growth, reproduction, functional structure of the area, ontogenetic and seasonal migrations, oceanological conditions for the formation of aggregations, genetic and biochemical characteristics, results of underwater tagging, and other parameters were used (Saborido-Rey et al., 2004; Melnikov, 2006, 2007, 2008, 2013, 2016; Melnikov and Bakai, 2006, 2009a, 2009b; Sigurðsson et al., 2006; Bakai and Melnikov, 2008; Melnikov and Popov, 2009; Melnikov et al., 2009; Makhrov et al., 2010, 2011; Bakai, 2015). There are no reports on the results of studies of the composition of parasites of beaked redfish in this area by other authors in literary sources.

The Irminger Sea is located southeast of Greenland. In the southwest, it borders with the Labrador Sea along a line from the southern tip of Greenland to the southeast of the Labrador Peninsula; in the north, it borders with the Greenland Sea along the line northwest of Iceland–Cape Nansen in Greenland. In the south and east, the Irminger Sea is limited by a spatially and temporally variable convergence zone, which extends (conventionally) from the south of Iceland to the southeast of Newfoundland (Fairbridge, 1974). The accepted designations of the North-East Atlantic Fisheries Commission (NEAFC) and the Northwest Atlantic Fisheries Organization (NAFO) are indicated.

RESULTS AND DISCUSSION

Oceanographic features of the area are determined by the macrocirculatory system of currents in the form of the Subpolar Cyclonic Gyre (SCG). It can be traced in the surface and intermediate layers of the Irminger and Labrador seas, formed by the North Atlantic (NAC), Irminger, East and West Greenland, and Labrador currents (Bulatov, 1971). The boundaries of the SCG are determined by the bottom topography: in the east, the Reykjanes Ridge; in the west, the slopes of Greenland, Canada, and the island of Newfoundland; in the north, the Greenland-Iceland threshold. Subarctic waters of the East Greenland Current, following south along Greenland, mix with the flow of the western branch of the warm Irminger Current, a derivative of the NAC. The West Greenland Current, formed near South Greenland, together with the Labrador Current, form the western periphery of the SCG. Part of the waters of the Labrador Current, turning northeast at the GBN, replenishes the NAC and closes the SCG (*Atlas okeanov*, 1977).

Owing to the interaction of water masses of Atlantic and subarctic origin at depths of up to 1000 m under conditions of specific bottom topography (the Reykjanes Ridge is associated with bathyal areas of Iceland and Greenland), frontal zones are formed—the polar front (along the southeastern coast of Greenland) and the subpolar front (from Iceland to GBN) with temperature gradients of 0.5–1.5°C over 10 miles. Here, complex processes of subsidence and rise of waters and the formation of upwellings, meanders, and eddies occur, contributing to the formation of areas of increased biological productivity in the pelagic zone of the Irminger Sea (Dubravin, 2001; Pedchenko, 2001; Sutton et al., 2008). This ensures the concentration of zooplankton, on which the beaked redfish and other numerous representatives of the ichthyofauna of the mesopelagic complex feed, creating aggregations (Pavlov, 1992; Melnikov and Bakai, 2006, 2009a, 2009b; Melnikov and Popov, 2009; Melnikov et al., 2009; Dolgov, 2015). Such topographical, oceanological, and biotopic features of the Irminger and Labrador seas created favorable conditions for the North Atlantic redfish population after the end of the Last Glacial Maximum (Brochmann et al., 2003). Within the range of this population, there are no oceanological barriers that prevent the ontogenetic and seasonal migrations of the beaked redfish (Pedchenko, 2001).

Functional subdivision of the area of the North Atlantic of the redfish population has been studied on the basis of the results of many years of domestic and international research. It has been determined that aggregations of beaked redfish distributed in the pelagic zone of the Irminger and Labrador seas in a water area of more than 420000 square miles (Fig. 1, areas 1–6) and in the bottom layer of the adjacent water areas of the bathyal and shelf of Greenland, Iceland, and Canada (regions 7–9) are parts of this population. From a single reproduction center located in the pelagic zone (regions 4–6), juveniles are carried out in the stream of the western branch the Irminger Current and settle on the southern sections of the Greenland shelf and Baffin Island, which, together with the waters of the Labrador shelf, serve as a breeding area for this population (Magnusson, J. and Magnusson, J.V., 1985; Pavlov, 1992; Stransky, 2000; Population structure..., 2004; Saborido-Rey et al., 2004; Melnikov and Bakai, 2009a, 2009b; Melnikov and Popov, 2009; Cadrin et al., 2010; Melnikov, 2013, 2016; Melnikov and Glubokov, 2015; Bakai, 2020b, 2021).

We have established that, in the North Atlantic population of beaked redfish, there are two groups that differ in ecological and physiological parameters: pelagic (consists of early maturing individuals and inhabits the pelagic zone of the Irminger Sea in the layer of 100–900 m) and bottom (late-maturing individuals dominate, living mainly in the bottom layer of the adjacent bathyal waters of Greenland, Iceland, and Canada at a depth of 600–1200 m) (Melnikov, 2006, 2008, 2016; Melnikov and Bakai, 2006, 2009b; Melnikov and Glubokov, 2017; Bakai, 2020a). In the first group, the bulk of redfish (50% of individuals) becomes sexually mature at a body length of 29–33 cm and an age of 9–12 years; in the second group, at a length of 35–43 cm and an age of 14–19 years. Their biological differentiation is associated with the beginning of return migrations of fish from the areas where juveniles live when they reach sexual maturity. Thus, early-maturing beaked redfish individuals are the first to leave the breeding area on the shelf of Greenland and Canada, entering the oceanic pelagic zone of the North Atlantic. Late-maturing individuals, as they grow during a long (up to 5–7 years) migration, replenish their benthic accumulations in the bathyal waters.

In the pelagic zone of the Irminger and Labrador seas in June–August, beaked redfish measuring 23–32 cm in size are distributed near the breeding area off the coast of Greenland. With distance from Greenland, the size (age) of fish increases (Melnikov and Bakai, 2009a). Feeding migration of beaked redfish from places where prelarvae are deposited by females in April–May over the Reykjanes Ridge passes in two main directions. So, the redfish mostly 30–35 cm in length, following the westward shifting northern subpolar front, migrates to the Greenland fishing zone and NAFO regulation areas, where its preferred planktonic crustaceans are concentrated in areas of increased bioproductivity in the upper 500-m layer. Individual redfish with size of 36–46 cm shift north along the western slope of the Reykjanes Ridge, where

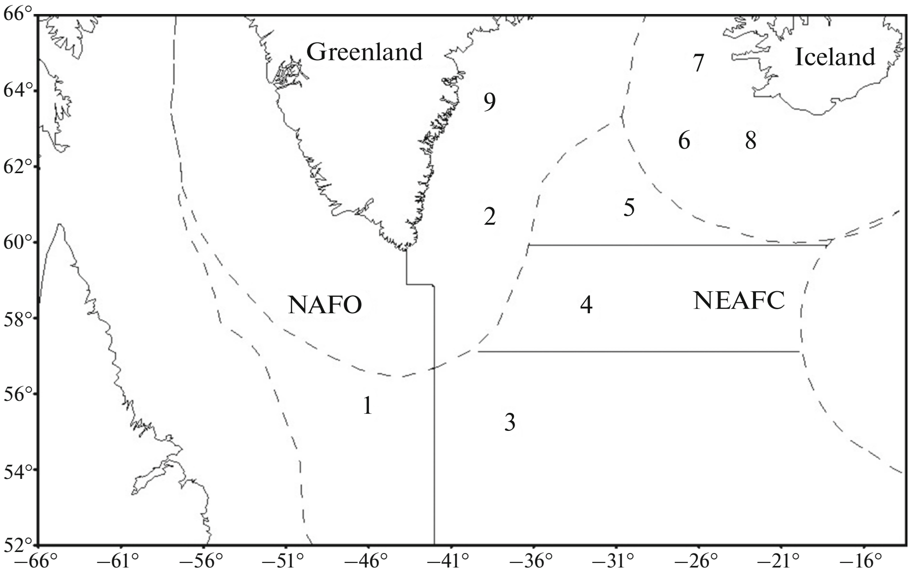

Fig. 1. Zoning of the water area of distribution of pelagic (1–6) and bottom (7–9) beaked redfish in the seas of the North Atlantic. Dotted line—boundaries of 200-mile zones. (1) NAFO regulatory areas, (2) East Greenland, (3, 4, 5) southern, central, and northern open parts of the Irminger Sea (NEAFC regulation areas), (6) Iceland zone, (7, 8) bathyal zone of Iceland, (9) bathyal zone of Greenland.

their preferred shrimp, mesopelagic fish, and juvenile cephalopods are distributed at depths greater than 500 m.

Most beaked redfish individuals in the pelagic zone are sexually mature. The proportion of immature fish decreases from 10.0–13.6% in the waters south and southeast of Greenland to 3.0–4.5% in the northeast of the range (above the Reykjanes Ridge). The beginning of redfish maturation in all regions occurs at the same length. The observed minor differences in the length of fish during mass and full maturation in the northeast of the range are due to the migration of some slowly maturing individuals from the bathyal zone of Iceland to the pelagic zone of the Irminger Sea (Melnikov and Bakai, 2009a).

The rates of linear and weight growth and sexual maturation of beaked redfish are the same in layers of 100–500 and 501–900 m pelagic zone of the Irminger Sea (Bakai and Melnikov, 2008). This indicates that the recruitment of the spawning part of its North Atlantic population in both layers occurs at the same length and age of fish.

In the pelagic zone of the northeastern part of the Irminger Sea, the size and age groups of beaked redfish are vertically segregated. Thus, the upper 500-meter layer is inhabited by individuals aged 5–18 years. At greater depths, the age of the fish was 6–25 years, of which about a third are over 18 years old (Bakai and Melnikov, 2008). This distribution is due to the vertical zonality of the distribution of food organisms of the mesopelagic complex. The beaked redfish diet exhibits age selectivity, which is maintained by daily vertical migrations following the rise or fall of its preferred food organisms.

Research parasite communities made it possible to identify 24 species belonging to 7 classes: four species of Myxozoa, one of Monogenea, six of Cestoda, four of Trematoda, four of Chromadorea, two of Palaeacanthocephala, three of Hexanauplia (Table 2). Most of them are widespread heteroxenous ecologically plastic species. Three species of Myxozoa (*Leptotheca adeli*, *Myxidium obliquelineolatum*, *Pseudoalataspora sebastei*), monogenean *Microcotyle caudata*, and copepod *Chondracanthus nodosus* are specific to genus *Sebastes*, whose representatives live in the seas of the North Atlantic and the adjacent region of the Arctic Ocean. Only copepod *Sphyrion lumpi* is specific to beaked redfish (Bakai, 2021).

The dominance of helminths (67% of the total number of species) indicates that the ecological-trophic factor is decisive in the formation of the composition of parasites of beaked redfish in the Irminger Sea, which are largely characteristic of planktivorous fish. This is due to the presence of both dominant polyzonal nematodes *Anisakis simplex* and *Hysterothylacium aduncum* and mesobenthal trematodes *Podocotyle reflexa*, forming the "core" of parasite communities this host, and many rarer helminths, *Bothriocephalus scorpii* and *Scolex pleuronectis* and other cestodes, *Anomalotrema koiae* and *Lecithophyllum botryophoron*, and other trematodes. The beaked redfish acquires them by consuming planktonic invertebrates (euphausiids, calanids, hyperiids, mysids, chaetognaths), serving as the first intermediate hosts in the life cycles of these helminths, as well as planktivorous fish (mainly Mycthophidae and Paralepididae)

Table 2. The structure of component communities of parasites and the significance of differences in the extent of parasite infection of beaked redfish in the pelagic and bathyal zones of the Irminger Sea

Parasite, indicator*** (class)	Species complex		Bathyal zone of Southeast Greenland		Pelagic zone		Significance of differences $(p)^a$	Pelagic zone of the northern part of the sea	Bathyal zone of southwest Iceland	Significance of differences $(p)^b$
	ecological	zoogeographical			East Greenland	open part				
			depth, m					depth, m		
			235–580	700–1040	170–410	150–430		501–900	430–880	
			L_{av}, cm (n, ind.)					L_{av}, cm (n, ind.)		
			29.1 (80)	34.5 (59)	33.2 (107)	36.7 (850)		39.9 (115)	38.5 (158)	
*Leptotheca adeli**** (My)	MB	AB	26.2/+	23.7/+	2.8/+	1.0/+	$p < 0.05$	6.1	7.0	$p > 0.05$
Myxidium incurvatum (My)	MB	amB	12.5/+	18.6/+	8.4/+	4.9/+	$p < 0.05$	10.4	22.2	$p < 0.05$
*M. obliquelineolatum**** (My)	MB	AB	8.8/+	11.9/+	7.5/+	4.5/+	$p < 0.05$	4.3	8.2	$p > 0.05$
*Pseudoalataspora sebastei**/*** (My)	MB	AB	20.0/+	23.7/+	6.5/+	2.1/+	$p < 0.05$	6.1	10.1	$p > 0.05$
*Microcotyle caudata**** (Mo)	MB	AB	–	–	–	–		–	17.1/0.48	$p < 0.05$
Bothriocephalus scorpii (Ce)	MP	AamB	–	–	5.6/0.08	10.1/0.20	$p < 0.05$	4.3/0.04	6.3/0.06	$p > 0.05$
Diphyllobothrium sp. pl. (Ce)	MP	atB	–	–	–	0.5/0.01	$p > 0.05$	2.6/0.03	–	$p < 0.05$
Grillotia erinaceus pl. (Ce)	PZ	amB	–	–	0.9/0.01	0.9/0.01	$p > 0.05$	3.5/0.04	–	$p < 0.05$
Hepatoxylon trichiuri pl.*** (Ce)	MP	atB	–	–	1.9/0.02	0.7/0.01	$p > 0.05$	4.3/0.04	–	$p < 0.05$
Phyllobothrium sp. pl. (Ce)	MB	amB	–	–	1.9/0.03	1.3/0.03	$p > 0.05$	0.9/0.01	0.6/0.01	$p > 0.05$
Scolex pleuronectis pl. (Ce)	PZ	K	2.5/0.03	1.7/0.03	14.9/0.40	11.4/0.30	$p < 0.05$	7.8/0.08	–	$p < 0.05$
Anomalotrema koiae (Tr)	MB	AB	3.8/0.06	11.9/0.30	1.9/0.02	1.0/0.01	$p < 0.05$	0.9/0.01	3.8/0.04	$p > 0.05$
Derogenes varicus (Tr)	PZ	K	2.5/0.13	1.7/0.02	0.9/0.01	0.7/0.01	$p < 0.05$	–	–	$p > 0.05$
Lecithophyllum botryophoron (Tr)	MP	AamB	1.3/0.01	3.4/0.03	0.9/0.01	1.2/0.02	$p > 0.05$	2.6/0.04	1.9/0.03	$p > 0.05$
*Podocotyle reflexa** (Tr)	MB	AamB	16.3/0.25	36.0/0.40	1.9/0.03	1.6/0.02	$p < 0.05$	2.6/0.03	5.7/0.06	$p > 0.05$
Anisakis simplex l.*/*** (Ch)	PZ	K	50.0/1.20	66.1/3.10	78.5/4.40	90.1/8.30	$p < 0.05$	90.4/7.03	72.8/4.68	$p < 0.05$
Hysterothylacium aduncum l.* (Ch)	PZ	amB	21.3/0.30	6.8/0.09	7.5/0.10	6.8/0.10	$p < 0.05$	3.5/0.04	13.3/0.29	$p < 0.05$
Pseudoterranova decipiens l. (Ch)	PZ	AamB	1.3/0.01	–	–	–	$p > 0.05$	–	–	$p > 0.05$
Spinitectus oviflagellis (Ch)	EC	atB	1.3/0.01	–	–	–	$p > 0.05$	–	3.2/0.11	$p < 0.05$
Corynosoma strumosum l. (Pa)	EC	AamB	2.5/0.05	5.1/0.05	0.9/0.01	0.2/0.002	$p < 0.05$	–	1.3/0.02	$p > 0.05$
Echinorhynchus gadi (Pa)	PZ	amB	1.3/0.01	1.7/0.14	–	–	$p < 0.05$	–	1.3/0.02	$p > 0.05$
*Chondracanthus nodosus**** (He)	MB	AB	–	–	–	–		–	0.7/0.01	$p > 0.05$
Pennella sp. (He)	MB	AB	–	1.7/0.02	–	–	$p < 0.05$	–	–	$p > 0.05$
*Sphyrion lumpi**/**/*** (He)	MP	amB	1.0/0.02*[1]	23.4/0.40*[2]	41.1/1.00*[3]	45.1/1.10*[4]	$p < 0.05$	42.9/0.88*[5]	17.9/0.28*[6]	$p < 0.05$
Occurrence of pigment spots, %			0.2	3.8	16.8	20.1	$p < 0.05$	15.0	3.0	$p < 0.05$

n—number of fish examined, specimens. Before the line, EI, %; after the line, AI, specimens (+ not determined for Myxozoa). * Types of "core" communities. ** *n*—taking into account the remains of the invasion, specimens. *[1]—609, *[2]—731, *[3]—781, *[4]—10770, *[5]—662, *[6]—1077; *** indicators of environmental features. $(p)^a$—the significance of the differences was established for the EI values in the bathyal zone (depth of 235–580 m—first column) and the open part of the pelagic zone of the Irminger Sea (fourth column); $(p)^b$—the significance of the differences was established for EI values in the pelagic zone of the northern part of the Irminger Sea and the bathyal zone of Iceland.

infected with these parasites (Polyansky, 1958; Køie, 1981, 2000; Smith, 1983; Marcogliese, 1992; etc.).

Communities of parasites of beaked redfish in the waters of the North Atlantic, as well as in the seas of the Arctic Ocean (Bakai, 2011), are formed mainly by Arctic-boreal (50.0%) and to a lesser extent boreal species (37.5%) and cosmopolitan species (12.5%) (Table 2). The dominance of species of the Arctic-boreal complex is stable. So, of the 12 species of parasites of this complex encountered in the bathyal of Greenland and Iceland, nine (75.0%) species are common for beaked redfish; five of them (55.6%) represent the "core" of the community. The predominance of parasites of mesobenthal (41.7%), polyzonal (29.2%), and mesopelagic (20.8%) ecological complexes in the beaked redfish of the Irminger Sea has been established.

On the basis of the results of an analysis of the geographical and biotopic features of the composition of the beaked redfish parasites, eight species were identified that largely meet the requirements for indicators of ecological and population characteristics fish (Gaevskaya and Kovaleva, 1986; MacKenzie, 2002; MacKenzie and Hemmingsen, 2015; etc.). These include species specific to genus *Sebastes* (mesobental monogenean *Microcotyle caudata* and copepod *Chondracanthus nodosus*) and mesopelagic species-specific copepod *Sphyrion lumpi* and cestode *Hepatoxylon trichiuri* defined as indicator based on the principle of alternative infection (Konovalov, 1971). Specific to genus *Sebastes*, myxosporidians *Leptotheca adeli*, *Myxidium obliquelineolatum*, and *Pseudoalataspora sebastei* and polyzonal nematode *Anisakis simplex*, found everywhere, were used on the basis of the presence of significant differences in the degree of infection by them (see Table 2).

Throughout the entire range of beaked redfish in the pelagic zone of the Irminger and Labrador seas, which we divided into six regions (Fig. 1), the same level of infection has been established ($p > 0.05$) by parasites of most (17 out of 18 detected) species (Table 3). Higher incidence of myxosporidian *L. adeli* in the beaked redfish in area 1 (9% compared to 1–4% in other areas) is due to a significant proportion of maturing fish that have recently entered the pelagic zone from the breeding area on the Greenland shelf, where the center of invasion by Myxozoa is located (Melnikov and Bakai, 2009b).

In all areas of the pelagic zone of the North Atlantic, a stable specificity in time (since 1981) and space of the localization and occurrence of pigment spots on the body of male and female beaked redfish has been recorded (Melnikov and Bakai, 2009a). So, in 97% of cases, such spots are localized in female redfish on the sides of the body and in males on the head and less often on the fins. Everywhere, at all depths (Bakai and Melnikov, 2008), in all years, the occurrence of spots is greater in females than in males, by 1.4–3.0 (average 1.8) times. Such features of the occurrence of skin pigment spots were absent in other areas of the beaked redfish range, which made it possible to substantiate this phenomenon as a phene of the pelagic group of its North Atlantic population (Bakai, 2015).

Results of calculations of the similarity measure (L_0) show high similarity ($L_0 = 93–100\%$) of the composition of beaked redfish parasites (Fig. 2) in all (1–6) pelagic regions of the North Atlantic seas, even hundreds of miles apart (regions 1 and 5–6). On the contrary, significant differences were found ($L_0 = 78–81\%$) of the composition of beaked redfish parasite communities in the pelagic zone (regions 1–6) and in the bathyal waters of Iceland/Greenland (regions 7–9) (Melnikov and Bakai, 2006). Thus, even for adjacent areas of the Irminger Sea pelagic zone (regions 5–6) and the bathyal of Iceland (regions 7–8), of the 21 species of parasites found here, only 12 (57.1%) species were common, and significant differences were also found in the degree of parasite infestation of ten common species (see Table 2), of which four are classified as indicators of the ecological and population characteristics of this host.

Among the latter, significant differences were identified in the degree of infection of beaked redfish with the dominant nematode *A. simplex*, localized on the internal organs and muscles of fish. Thus, its infestation of redfish in the Icelandic bathyal waters turned out to be significantly less than in the adjacent pelagic region (see Table 2). This property is manifested in redfish of all size groups (Fig. 3), which is determined by the characteristics of its diet in these biotopes that differ in trophic conditions (Melnikov and Bakai, 2006). Significant differences in the occurrence of fish with pigment spots on the skin have also been established (see Table 2).

Identified features point to isolation of aggregations of beaked redfish in the bathyal zone of Iceland/Greenland and in the pelagic zone of the Irminger Sea. These clusters are formed, respectively, by late- and early-maturing individuals from a single growing area on the Greenland shelf (Melnikov and Bakai, 2006, 2009a, 2009b). The second of them are characterized by permanent residence in the pelagic zone and increased migratory activity, expressed in extended (up to several hundred miles) migrations, determined by the reproductive cycle of the beaked redfish and seasonal feeding (Melnikov and Popov, 2009), as well as in significant (up to 200 m) daily vertical feeding migrations (Bakai and Melnikov, 2008).

Loss of connection between the beaked redfish and benthic biocenoses as a result of the migration of its early-maturing individuals from the Greenland shelf to the pelagic zone of the North Atlantic causes a depletion in the composition of trematodes, nematodes, and acanthocephalans (see Table 2) owing to the exclusion of bottom crustaceans from its diet. As one moves away from the coast, the occurrence of

Table 3. Structure of parasite communities and the significance of differences in the extent of infection of beaked redfish by them in the pelagic zones of the seas of the North Atlantic

Parasite (class)	Species complex		Labrador Sea	Irminger Sea					Significance of differences (p)
				East Greenland	open part			Iceland zone	
					south	center	north		
	ecological	zoogeographical	district 1 ($n = 199$)	district 2 ($n = 107$)	district 3 ($n = 183$)	district 4 ($n = 218$)	district 5 ($n = 449$)	district 6 ($n = 75$)	
Leptotheca adeli (My)	MB	AB	9.0/+	2.8/+	1.1/+	0.9/+	1.1/+	4.0/+	<0.05
Myxidium incurvatum (My)	MB	amB	6.5/+	8.4/+	3.3/+	6.0/+	5.1/+	6.6/+	>0.05
M. obliquelineolatum (My)	MB	AB	9.5/+	7.5/+	4.9/+	3.2/+	4.9/+	4.0/+	>0.05
*Pseudoalataspora sebastei** (My)	MB	AB	5.0/+	6.5/+	2.2/+	2.3/+	2.0/+	5.3/+	>0.05
Bothriocephalus scorpii (Ce)	MP	AamB	12.3/0.19	5.6/0.09	12.6/0.21	8.3/0.19	10.1/0.11	5.3/0.09	>0.05
Diphyllobothrium sp. pl. (Ce)	MP	atB	0.5/0.01	–	0.5/0.01	0.5/0.01	0.5/0.01	1.3/0.01	>0.05
Grillotia erinaceus pl. (Ce)	PZ	amB	1.1/0.01	0.9/0.01	1.1/0.01	0.9/0.01	0.9/0.01	1.3/0.01	>0.05
Hepatoxylon trichiuri pl. (Ce)	MP	atB	0.5/0.01	1.9/0.01	1.6/0.02	0.5/0.01	0.5/0.01	2.6/0.03	>0.05
Phyllobothrium sp. pl. (Ce)	MB	amB	1.6/0.02	1.9/0.03	2.2/0.06	1.4/0.03	0.9/0.02	1.3/0.01	>0.05
Scolex pleuronectis pl. (Ce)	PZ	K	8.9/0.25	14.9/0.37	15.3/0.55	13.8/0.3	8.8/0.14	8.0/0.08	>0.05
Anomalotrema koiae (Tr)	MB	AB	2.2/0.05	1.9/0.02	1.1/0.01	1.4/0.01	0.9/0.01	1.3/0.01	>0.05
Derogenes varicus (Tr)	PZ	K	1.1/0.01	0.9/0.01	1.6/0.02	0.5/0.01	0.5/0.01	–	>0.05
Lecithophyllum botryophoron (Tr)	MP	AamB	2.2/0.02	0.9/0.01	3.3/0.07	0.5/0.01	0.7/0.01	2.6/0.04	>0.05
*Podocotyle reflexa** (Tr)	MB	AamB	2.8/0.03	1.9/0.03	2.2/0.02	2.8/0.03	0.9/0.01	2.6/0.02	>0.05
Anisakis simplex l.* (Ch)	PZ	K	78.8/6.2	78.5/4.4	78.7/6.0	83.9/6.6	79.0/6.3	74.7/6.0	>0.05
*Hysterothylacium aduncum** (Ch)	PZ	amB	7.8/0.09	7.5/0.09	7.8/0.13	8.7/0.12	5.5/0.13	5.3/0.07	>0.05
Corynosoma strumosum l. (Pa)	MB	atB	0.5/0.01	–	0.5/0.01	0.5/0.01	–	–	>0.05
*Sphyrion lumpi**/** (He)	MP	amB	39.7/0.89*^{1}	34.6/0.73*^{2}	46.2/1.08*^{3}	46.9/0.92*^{4}	42.7/0.98*^{5}	48.0/1.08*^{6}	>0.05

For the numerical designation of regions, see Fig. 1. n—number of fish examined, specimens. Before the line, EI, %; after the line, AI, specimens (+ not determined for Myxozoa). * Types of the "core" of the parasite community. ** Taking into account the remains of the invasion (n, specimens): *^{1}—991, *^{2}—781, *^{3}—1108, *^{4}—1902, *^{5}—8501, *^{6}—662. (p)—the significance of differences in EI waas established for its values in adjacent pairs of regions.

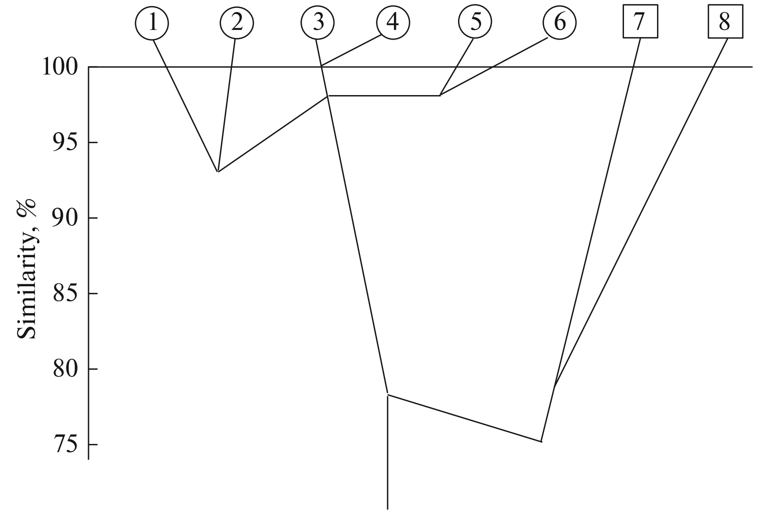

Fig. 2. Dendrogram of similarity (L_0) of the composition of parasites of beaked redfish in the pelagic zone of seas of the North Atlantic (regions 1–6) and the bathyal zone of Iceland (districts 7–8).

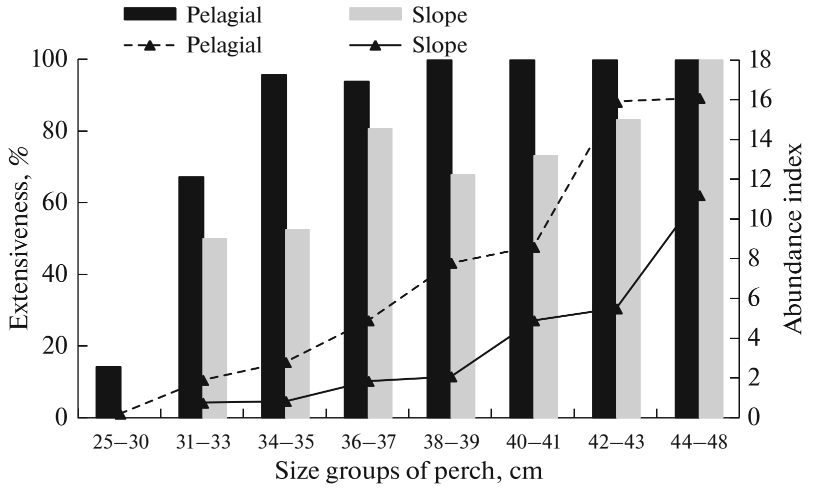

Fig. 3. Dynamics of extensiveness (columns) and abundance index (lines) of infestation of beaked redfish with nematode *Anisakis simplex* in the bathyal zone of Iceland and the adjacent pelagic region of the Irminger Sea.

myxosporidians significantly decreases. With an increase in diet associated with the growth (maturation) and entry of redfish into the pelagic zone, it acquires new helminths (cestodes of four species) with an increase in infection with existing ones (*A. simplex*, *Scolex pleuronectis*). This change in the composition of parasites is due to the expansion of the food spectrum due to copepods, an increase in the role euphausiids, hyperiids, pelagic shrimp, planktivorous fish, pteropods, and cephalopods (Melnikov and Bakai, 2009b).

Late-maturing individuals of beaked redfish do not make such migrations, moving to a depth of more than 600 m in the bathyal of Greenland and Iceland and emerging only into nearby pelagic zones, where they produce offspring (Melnikov, 2016). Absence of mass exchange between pelagic and benthic aggregations of beaked redfish off Iceland was confirmed by the results underwater tagging carried out by Icelandic researchers (Sigurðsson et al., 2006). This life strategy is consistent with the “pace of life hypothesis,” which explains differences in the rate of puberty and migration activity of individuals of the same population (species) by the presence of “slow and fast pace of life” (Hall et al., 2015).

There are no significant differences in the degree of infection of the majority (15 out of 16 detected) species of beaked redfish parasites throughout the depth of its habitat (100–900 m) in the pelagic zone of the Irminger Sea, despite differences in the average length (age) of the studied individuals. This is demonstrated by the results of a comparative analysis of the composition of parasites in samples of beaked redfish

Table 4. Composition of parasite communities of beaked redfish in successive samples from two layers of the pelagic zone of the Irminger Sea (57°57′ N, 36°42′ W, June 27, 1999)

Parasite (class)	Layer of pelagic zone of sea				Significance of differences (p)
	190–290 m ($n = 25$) $l = 30$–38 cm ($L_{\text{avg}} = 35.2$ cm)		550–805 m ($n = 30$) $l = 40$–47 cm ($L_{\text{avg}} = 42.4$ cm)		
	indicators of the degree of invasion				
	EI, %	AI, spec.	EI, %	AI, spec.	
Leptotheca adeli (My)	8.0 (0.8–21.9)*	+	6.7 (0.6–18.4)	+	>0.05
Myxidium incurvatum (My)	8.0 (0.8–21.9)	+	6.7 (0.6–18.4)	+	>0.05
M. obliquelineolatum (My)	4.0 (0.0–15.3)	+	6.7 (0.6–18.4)	+	>0.05
Pseudoalataspora sebastei (My)	4.0 (0.0–15.3)	+	3.3 (0.0–12.8)	+	>0.05
Bothriocephalus scorpii (Ce)	8.0 (0.8–21.9)	0.08	16.7 (5.6–32.2)	0.17	>0.05
Diphyllobothrium sp. pl. (Ce)	4.0 (0.0–15.3)	0.04	3.3 (0.0–12.8)	0.03	>0.05
Grillotia erinaceus pl. (Ce)	4.0 (0.0–15.3)	0.04	6.7 (0.6–18.4)	0.07	>0.05
Hepatoxylon trichiuri pl. (Ce)	4.0 (0.0–15.3)	0.04	3.3 (0.0–12.8)	0.03	>0.05
Phyllobothrium sp. pl. (Ce)	8.0 (0.8–21.9)	0.20	26.7 (12.4–44.0)	0.67	>0.05
Scolex pleuronectis pl. (Ce)	8.0 (0.8–21.9)	0.08	6.7 (0.6–18.4)	0.10	>0.05
Anomalotrema koiae (Tr)	4.0 (0.0–15.3)	0.04	3.3 (0.0–12.8)	0.03	>0.05
Lecithophyllum botryophoron (Tr)	4.0 (0.0–15.3)	0.04	26.7(12.4–44.0)	0.40	<0.05
Podocotyle reflexa (Tr)	4.0 (0.0–15.3)	0.04	3.3 (0.0–12.8)	0.03	>0.05
Anisakis simplex l. (Ch)	100 (88.7–100)	11.00	100 (90.5–100)	12.02	>0.05
Hysterothylacium aduncum (Ch)	8.0 (0.8–21.9)	0.08	6.7 (0.6–18.4)	0.07	>0.05
*Sphyrion lumpi*** (He)	46.0 (28.7–67.6)	1.17	51.7 (35.3–70.9)	1.05	>0.05

n —number of fish examined, specimens. * Confidence interval of EI (+ not determined for Myxozoa). l—range of lengths of fish. L_{avg}—average length of fish. ** Taking into account the remains of the invasion.

obtained from successive catches at one position in the upper (<500 m) and lower (>500 m) layers (Table 4).

Mesopelagic copepod infestation *Sphyrion lumpi*—a parasite specific to beaked redfish—occurs for the first time in its early-maturing individuals as a result of return migration to the pelagic seas of the North Atlantic (NA). The results of our long-term (1981–2022) research indicate the similarity and consistency of the characteristics of infestation of redfish by copepod *S. lumpi* throughout the pelagic zone of the NA, absent in other areas of the range (Bakai, 2020b, 2021). So, only in the pelagic zone of the NA was infestation by *S. lumpi* found significantly more often in female redfish (by 1.3–1.5 times for EI and 1.8–2.0 times according to AI) without significant interannual fluctuations in the degree of invasion (Fig. 4). When assessing the latter, it is necessary to take into account all traces of invasion in the form of remains of the copepod cephalothorax, which remain in the fish, probably until the end of its life, and therefore serve as a reliable marker (Bakai and Karasev, 1995).

Such time-stable indicators of the degree of invasion by copepod *S. lumpi* recorded in males and females of beaked redfish in all areas (Table 5) and at all depths (Fig. 5) of its distribution in the pelagic zone of the Irminger and Labrador seas are justified as a phene (in the understanding of Yablokov (1982)) of the pelagic group of its North Atlantic population (Bakai, 2013). The likely reason for the persistence of sex differences in infection, characteristic of this host in all its size groups (Fig. 6), may be a putative selection for resistance to invasion by copepod *S. lumpi*, dominant among male redfish of this population (Makhrov et al., 2011). Older individuals are characterized by an increase in the degree of infestation by copepod *S. lumpi* due to the significant (up to 26 years) life expectancy of redfish, which contributes to repeated infection with this parasite.

The presence of remains of infestation with *S. lumpi* in late-maturing beaked redfish in the bathyal zone of Greenland at a depth of 700–1040 m (see Table 2) are caused by their periodic release into the nearby pelagic zone during the reproduction period. The absence of invasion by this copepod at a depth of less than 580 m indicates the nonreturn of redfish from the pelagic and deep-water areas of the bathyal to the breeding area.

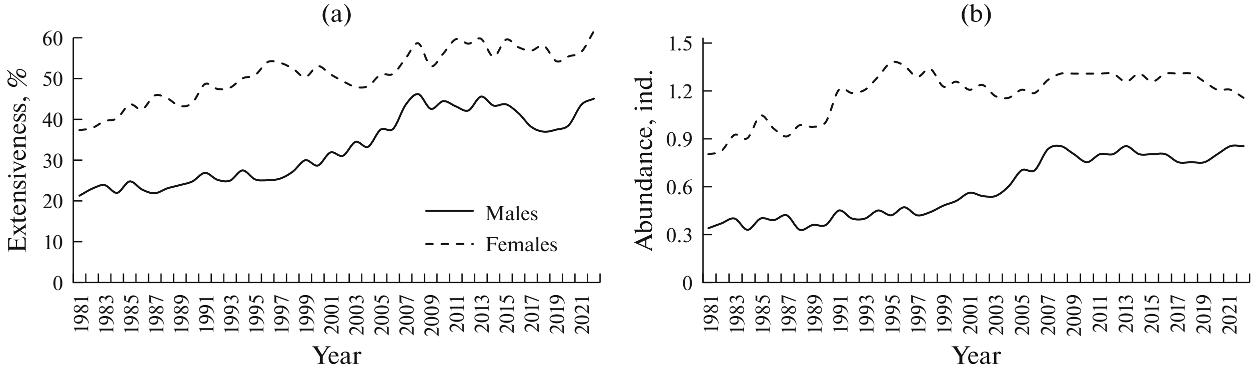

Fig. 4. Interannual dynamics of extensiveness (a) and abundance index (b) of infestation of beaked redfish with copepod *Sphyrion lumpi* (taking into account traces of invasion) in the pelagic zone of the Irminger Sea in the layer of 100–500 m in 1981–2022.

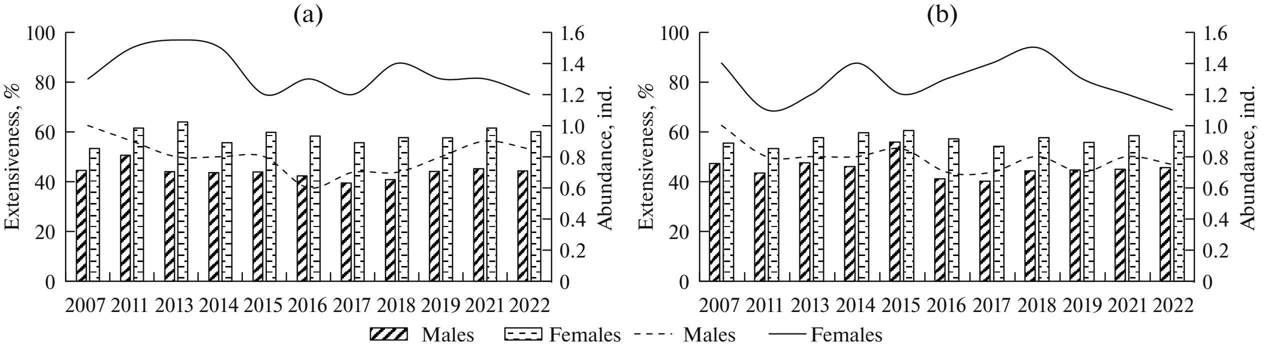

Fig. 5. Interannual dynamics of EI (bars) and AI (lines) of infestation of males and females of beaked redfish with copepod *Sphyrion lumpi* (taking into account traces of its invasion) at a depth of less than 500 m (a) and more than 500 m (b) in the pelagic zone of the Irminger Sea in 2007–2022.

Some researchers (Magnusson, J. and Magnusson, J.V., 1995; Cadrin et al., 2010; Klapper et al., 2017) erroneously indicated that the beaked redfish in the pelagic zone of the Irminger Sea is less infested by copepods *S. lumpi* at a depth of more than 500 m, where large (older) individuals dominate. Their misconception is due to noncompliance of techniques registration of invasion by this copepod (Bakay and Karasev, 2001) adopted by ICES and NAFO and providing for the recording of all traces of its parasitism. Less infestation is observed when taking into account invasion by living individuals of *S. lumpi*, since at a

Table 5. Degree of infestation of beaked redfish with copepods *Sphyrion lumpi* in six regions of the pelagic zone of the seas of the North Atlantic (according to international trawl-acoustic surveys in June–July 2001)

Degree of infestation with copepod *S. lumpi*		Irminger Sea				Labrador Sea	Significance of differences (*p*)
		Iceland zone	open part of the Irminger Sea		Southeast Greenland		
			north	south			
Extensiveness, %	Males	43.4	38.2	37.9	28.9	31.2	>0.05
	Females	59.9	49.5	58.4	44.1	44.3	>0.05
	Both sexes	52.3	42.7	46.2	36.6	37.1	>0.05
Abundance index, specimens	Males	0.6	0.6	0.6	0.5	0.6	>0.05
	Females	1.6	1.3	1.4	1.0	1.2	>0.05
	Both sexes	1.1	1.0	1.0	0.8	0.9	>0.05

Degree of infestation is given taking into account traces of infestation with copepod *S. lumpi*.

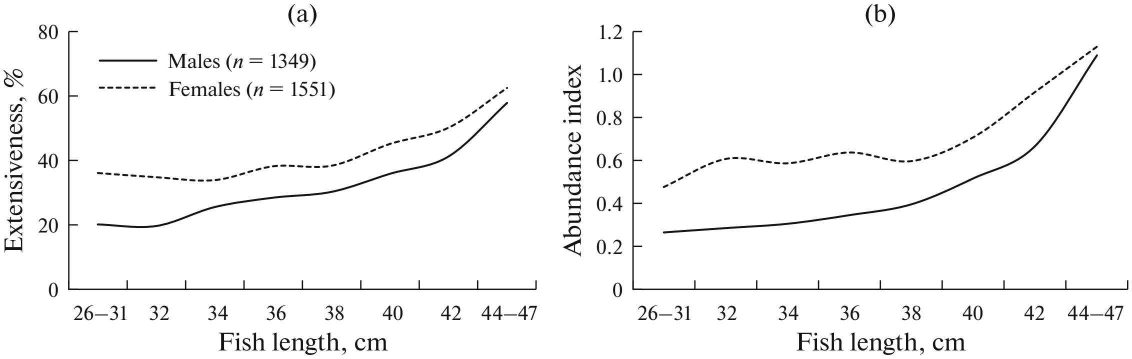

Fig. 6. Rates of infestation of beaked redfish of various size groups with copepod *Sphyrion lumpi* in the pelagic zone of the Irminger Sea in April–July 2006.

depth of 600–1000 m there is a rise in deep waters caused by the vertical component of the Irminger Current and upwellings on the slopes of the Reykjanes Ridge (Pedchenko, 1992). This leads to the removal of copepod metanauplii into the so-called sound-scattering layer located above (350–600 m), where they are eaten by numerous organisms inhabiting it (fish of the families Mycthophidae and Paralepididae, cephalopods, jellyfish, ctenophores, etc.). Moreover, at a depth of more than 500 m, beaked redfish aggregations are less dense, which reduces the possibility of dispersal of sedentary metanauplii of females of the parasite.

An example of underestimation of traces of infestation with copepod *S. lumpi*, not detected in beaked redfish by manual scanning (palpation) of the fish body, used by researchers from Germany and Iceland during international surveys in the Irminger Sea, is that the overall infestation of redfish from depths of more than 500 m with the parasite became slightly lower (Klapper et al., 2017). This noncompliance with the methodology adopted by ICES and NAFO particularly affected the results of registering infestation with copepod *S. lumpi* for 2001–2007 presented by authors from Germany only by the share (%) of infested fish (Klapper et al., 2017). With this approach to recording copepod infestations, the proportion (%) of traces of its invasion not taken into sufficient account by palpation increases in older beaked redfish specimens that dominate at greater depths, significantly underestimating the objective indicators of overall infestation.

Absence of significant differences in the indicators of overall infestation with copepod *S. lumpi* of males and females of the beaked redfish in the presented materials, which are constant in time and space (see Fig. 4 and Table 5), indicates the incorrectness of the data included in the calculations of the German authors (Klapper et al., 2017) and, as a consequence, the unreliability of their conclusions. Thus, on the basis of the differences identified in this way in the total proportion (%) of copepod-infected fish, they expected to confirm the hypothesis about the existence of “shallow and deep-water reserves” of beaked redfish, living respectively at a depth of <500 m and >500 m in the pelagic zone of the Irminger Sea.

Stability in time (no later than the beginning of the 1980s) and space (aquatic area of more than 420 000 sq. miles) of the parasitic system of “copepods *S. lumpi*—beaked redfish” and parasitocenosis of this host (Bakai and Melnikov, 2008; Melnikov and Bakai, 2009a) indirectly indicates the equilibrium state of the biocenosis of the pelagic zone of seas of the North Atlantic. This equilibrium is observed against the background of alternating cold and abnormally cold years (1981–1995, 2016–2018) with warm and abnormally warm years (1998–2013 and 2019) in terms of the thermal state of the waters of the active layer (Melnikov and Glubokov, 2015; *Sostoyanie syr’evykh*..., 2020) and a 42-year-old press of the international redfish fishery.

Discussions about the **vertical structure of pelagic aggregations of beaked redfish** began in the 1990s, when Icelandic researchers (Magnusson, J. and Magnusson, J.V., 1995) to substantiate the presence of two “types” (reserves) of redfish in the pelagic zone of the Irminger Sea (“oceanic” and “pelagic deep-sea”) reported its differences at depths of more and less than 500 m in six characteristics: size composition, body shape, length at puberty, intensity of red color, degree of infestation with copepod *S. lumpi*, and occurrence of pigment spots on the body. We have shown that differences in many of these characteristics are due to changes in the age of fish and violations of the methodology for assessing the last two (Bakai, 2015, 2021). It has also been established that sexual maturation of beaked redfish at different depths occurs at a similar age, and living at different depths over a wide range is caused by its age-related food selectivity (Bakai and Melnikov, 2008).

Some authors (Pampoulie and Danielsdottir, 2008; Stefansson et al., 2009; Cadrin et al., 2010), justifying the validity of the above hypothesis, showed that indi-

Table 6. The main results of the analysis of the results of genetic studies supporting the hypothesis of the presence of two populations beaked redfish in the pelagic zone of the Irminger Sea (according to Makhrov et al., 2011)

Markers used	Compliance with conditions for use as a method for identifying population structure (Hedgecock, 1994; Waples, 1998)		
	are the samples collected from depths above and below 500 meters?	is the genetic structure stable over time?	are there any data on selection?
Protein-coding genes	NO	UNSTABLE	YES
mtDNA	Yes/NO	NOT STUDIED	YES
Microsatellites	Yes/NO	UNSTABLE	ANALYSIS IS INCORRECT
RAPD analysis	Yes	NOT STUDIED	NOT STUDIED
AFLP analysis	NO	UNSTABLE	NOT STUDIED

In capital letters, data on incorrect application of the method.

vidual “forms” of beaked redfish may differ in the frequencies of a number of genes, which, in their opinion, indicates the presence of “two populations” of this species living at different depths in the pelagic zone of the Irminger Sea. For explanations of the possible reasons for such differences by the staff of the Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences and VNIRO, the reliability of the results presented in these works (Table 6) was analyzed, using our own data (Makhrov et al., 2010, 2011; Artamonova et al., 2011, 2013; Zelenina et al., 2011). The results of the analysis indicate the impossibility of using the data presented in the publications of foreign researchers to substantiate the hypothesis of the existence of “two populations” of beaked redfish in the Irminger Sea.

Thus, the results of a comparative analysis of the data presented in the mentioned works revealed, in some cases, statistically significant differences in the frequencies of gene variants (alleles, haplotypes) in samples obtained in different years, which indicates the instability of the genetic structure over time. Detection of significant differences in the frequencies of variants encoding protein genes (for example, malic enzyme—MEP) and mtDNA, between samples from the same locality, but differing in biologically important indicators, indicates that these variants are subject to selection in the North Atlantic population beaked redfish (Makhrov et al., 2011).

At the Institute of Ecology and Evolution, Russian Academy of Sciences, an analysis of new data was also carried out explaining possible genetic differences in beaked redfish in samples from different depths of the Irminger Sea. It is shown that, in the discussed works (Pampoulie and Danielsdottir, 2008; Stefansson et al., 2009; Cadrin et al., 2010), the presence of interspecific hybrids of the genus *Sebastes* is not taken into account in this region (Makhrov et al., 2011; Artamonova et al., 2011, 2013) and off the coast of Canada (Roques et al., 2001). Even the coauthors of the “two populations” hypothesis recognized the influence of interspecific hybridization on genetic heterogeneity beaked redfish (Saha et al., 2017).

The differences in allele frequencies of the gene encoding the malic enzyme (MEP-2*) cannot serve as a basis for identifying “two populations” of beaked redfish (Danielsdottir et al., 2008) and, since this gene is subject to selection (Rolsky et al., 2011) and the change in its frequency with depth occurs gradually (Melnikov et al., 2007). This may be a consequence of differences in the migratory activity of early- and late-maturing individuals of beaked redfish (Melnikov and Bakai, 2009b).

The discovery of differences in allele frequencies of microsatellite loci (Stefansson et al., 2009) also does not serve as a strong argument in favor of the “two populations” hypothesis of redfish, since other proponents (Pampoulie and Danielsdottir, 2008), having studied the frequencies of the same nine loci, noted that the data for at least four of them do not correspond to the assumption of their neutrality. In addition, Russian researchers (Zelenina et al., 2011) found no differences in microsatellites of beaked redfish in samples from different depth layers pelagic zone of the Irminger Sea.

Other authors indicated a morphometrically uniform population beaked redfish in this region (Garabana, 2005) and no differences in the structure and chemical composition of otoliths between samples from different depths and samples from benthic and pelagic groups in the Iceland region (Stransky et al., 2005). High similarity was also established for 19 morphometric characteristics in the samples of beaked redfish from various deep layers of the pelagic zone of this area (Population structure..., 2004). Thus, the available evidence does not support the existence of “two populations” of this species in the pelagic zone of the Irminger Sea.

CONCLUSIONS

Thanks to the current system of currents of Atlantic and subarctic origin in the conditions of the specific bottom topography in the waters of the central and western parts of the North Atlantic, a zone of increased biological productivity is formed and favorable conditions for the functioning of North Atlantic redfish population emerge. Its reproductive part is distributed in the pelagic zone of the Irminger and Labrador seas in layer of 100–900 m, from a single center of reproduction in which pelagic juveniles are carried out and settle in the breeding area located in the bottom layer of the adjacent areas of the shelf and bathyal zone of Greenland and Canada.

The features of the evolution of the beaked redfish reflect the strategy inherent in this phylogenetically young species aimed at expanding its range by populating the mesopelagic and bottom layer of the bathyal zone of the seas of the North Atlantic Ocean in a wide range of depths, reducing the tension of competitive relations of various ranks. The development of stable pelagic and benthic groups of beaked redfish formed respectively by early-maturing individuals with increased migratory activity and late-maturing individuals from a single breeding area indicates the continuation of the speciation process.

The ecological-trophic factor is the leading one in the formation of the “core” and the general composition of the beaked redfish parasites, which are dominated by common helminths. The component community of parasites of the beaked redfish population of the North Atlantic population is formed by predominantly Arctic-boreal and, to a lesser extent, boreal and cosmopolitan species. It is dominated by species of mesobenthic, mesopelagic, and polyzonal ecological complexes. The identified features characterize this host as a benthic-pelagic species of the subpolar and temperate zones of the seas of the North Atlantic.

Stable in time and space, significant differences in the degree of invasion of males and females of beaked redfish by the only species-specific parasite (copepod *Sphyrion lumpi*) are a phene of the pelagic group of its North Atlantic population. Features of invasion by this parasite indicate absence of a massive return of redfish from the pelagic and bathyal zones to the Greenland breeding area and that species-specific parasites can serve indicators not only of the ecology of the host but also of its “kinship.”

The results of the analysis of a complex of ecological, parasitological, and population characteristics indicate the unity of the pelagic group of the North Atlantic beaked redfish population throughout the entire water area and the depth of its distribution, as well as its isolation from a benthic group living in adjacent areas of the bathyal zone of Greenland and Iceland. Spatial variability of individual population parameters of beaked redfish in the pelagic zone of the Northern seas is due to the peculiarities of its life and migration cycles.

The results of the conducted studies indicate the great potential of the ecological-parasitological method in studying the population and phylogenetic characteristics of fish. The use of parasitological data to study the population biology of beaked redfish is most conclusive in a comparative analysis of the features of the spatial structure of communities of its parasites, and not of their individual species. An interdisciplinary approach that included the results of such an analysis, the spatial characteristics of the identified phenes, the functional structure of the area, population and genetic data, tagging of the beaked redfish, and the oceanological conditions of the area allowed us to form an idea of the structure of its North Atlantic population. It is largely consistent with the hypothesis of the existence of a single “panoceanic” population in the Irminger and Labrador seas.

Inherent beaked redfish interspecific hybridization, selection, and differences in migratory activity explain the possible manifestations of genetic differences in its samples from different deep layers of the pelagic zone of the Irminger Sea. The results of the analysis of the ecological, parasitological, and population characteristics of the beaked redfish indicate an incorrect interpretation of data on the variability of individual characteristics (differences in parasite infestation of individual species, possible genetic differences) as a justification for population differentiation. To do this, one should take into account modern ecological and population data, the specifics of the life cycle, the spatiotemporal distribution of the object, and abiotic factors.

ACKNOWLEDGMENTS

We express great gratitude to our colleagues from the Polar Branch of VNIRO, with whom we shared the hardships of long sea expeditions to distant regions of the Arctic. We especially thank M.Yu. Kalashnikov and V.I. Popov for their invaluable assistance in collecting and processing the analyzed materials. We are grateful to the anonymous reviewers for relevant critical comments and recommendations, the implementation of which contributed to improving the initial version of the article.

FUNDING

The materials were prepared within the framework of budgetary funding of research work according to thematic plans of the Polar Branch of the Russian Federal Research Institute of Fisheries and Oceanography (PINRO).

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

All applicable international, national, and institutional guidelines for the care and use of animals were followed.

CONFLICT OF INTEREST

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

REFERENCES

Aleksandrov, D.I., Amel'kin, A.V., Bakai, Yu.I., et al., *Sostoyanie syr'evykh biologicheskikh resursov Barentseva, Belogo i Karskogo morei i Severnoi Atlantiki v 2020 g.* (The State of Primary Biological Resources of the Barents, White, and Kara Seas and the North Atlantic in 2020), Pestrikova, L.I., Ed., Murmansk: PINRO im. N.M. Knipovicha, 2020.

Andreev, V.L. and Reshetnikov, Yu.S., Analysis of the composition of freshwater ichthyofauna of the Northeastern part of the USSR based on set theory methods, *Zool. Zh.*, 1978, vol. 57, no. 2, pp. 165–174.

Andriyashev, A.P., On some questions of vertical zonality of marine benthic fauna, in *Biologicheskie Resursy Mirovogo Okeana* (Biological Resources of the World Ocean), Moscow: Nauka, 1979, pp. 117–138.

Artamonova, V., Karabanov, D., Makhrov, A., Rolskiy, A., Bakay, Yu., and Popov, V., Hybridization of redfish (genus *Sebastes*) in the Irminger Sea and its significance for studies of population structure of beaked redfish, *S. mentella*, in *ICES Annual Science Conference. ICES CM/A:06*, 2011.

Artamonova, V., Makhrov, A., Karabanov, D., Rolskiy, A., Bakay, Yu., and Popov, V., Hybridization of beaked redfish (*Sebastes mentella*) with small redfish (*S. viviparus*) and diversification of redfishes (Scorpaeniformes) in the Irminger Sea, *J. Nat. Hist.*, 2013, vol. 47, nos. 25–28, pp. 1791–1801. https://doi.org/10.1080/00222933.2012.752539

Atlas okeanov, Atlanticheskii i Indiiskii okeany (Ocean Atlas, Atlantic and Indian Oceans), Leningrad: GUNiO, 1977.

Bailey, N.T.J., *The Mathematical Approach to Biology and Medicine*, London: John Wiley and Sons, 1967.

Bakay, Yu.I., Ecologal and parasitological chracteristics of redfish *Sebastes mentella* (Scorpaeniformes: Sebastidae) from the Norwegian Sea and adjacent waters, *J. Ichthyol.*, 2011, vol. 51, no. 1, pp. 90–97. https://doi.org/10.1134/S0032945211010036

Bakay, Yu.I., Infection by copepod *Sphyrion lumpi* as a phenomenon of the North Atlantic population of beaked redfish *Sebastes mentella* (Sebastinae), in *Parazitologiya v izmenyayushchemsya mire. Mat-ly V S"ezda Parazitol. ob-va RAN: Vseros. konf. s mezhdunar. uchastiem (ISiEZh SO RAN)* (Parasitology in a Changing World, Proc. V Congr. Parasitol. Soc. RAS, All-Russ. Conf. with Int. Participation (Inst. Syst. Ecol. Animals Sib. Otd. Russ. Acad. Sci.)), Novosibirsk: Garamond, 2013, p. 20.

Bakay, Yu.I., Pigment spots on the skin as a phene of the North Atlantic population of the beaked redfish, *Sebastes mentella* Travin, 1951 (Scorpaenidae), *Russ. J. Mar. Biol.*, 2015, vol. 41, no. 2, pp. 136–139. https://doi.org/10.1134/S1063074015020030

Bakay, Yu.I., Ecological and population features of beaked redfish *Sebastes mentella* (Sebastidae) in the Northwest Atlantic based on the analysis of its parasite fauna, *J. Ichthyol.*, 2020b, vol. 60, no. 3, pp. 475–484. https://doi.org/10.1134/S0032945220030030

Bakay, Yu.I., Parasites and maturation rate as indicators of population structure in the beaked redfish *Sebastes mentella* (Sebastidae), *J. Ichthyol.*, 2020a, vol. 60, no. 2, pp. 289–298. https://doi.org/10.1134/S0032945220020010

Bakay, Yu.I., Parasite communities as indicators of ecology, intra-species, and supra-species structure of marine redfishes of the genus *Sebastes* (Scorpaeniformes: Sebastidae) of the Atlantic and Arctic Oceans, *Extended Abstract of Doctoral (Biol.) Dissertation*, Moscow: VNIRO, 2021.

Bakay, Yu.I. and Karasev, A.B., *Diagnostika i registratsiya ektoporazhenii morskikh okunei (metodicheskoe rukovodstvo)* (Diagnostics and Registration of Ectolesions of Marine Redfishes (Methodical Guide)), Murmansk: PINRO, 1995.

Bakay, Yu.I. and Karasev, A.B., Registration of ectolesions of redfish *Sebastes* genus in the North Atlantic (methodical guidelines), in *NAFO SCR Doc., Ser. no. 4401*, 2001.

Bakay, Yu.I. and Mel'nikov, S.P., Biological and ecological characteristics of deepwater redfish *Sebastes mentella* (Scorpaenidae) at different depths in the pelagial of the Irminger Sea, *J. Ichthyol.*, 2008, vol. 48, no. 1, pp. 68–80. https://doi.org/10.1134/S0032945208010074

Begg, G. and Waldman, J., A holistic approach to fish stock identification, *Fish. Res.*, 1999, vol. 43, no. 1, pp. 35–44. https://doi.org/10.1016/S0165-7836(99)00065-X

Breev, K.A., Application of mathematical methods in parasitology, *Tr. Gos. Nauchno-Issled. Inst. Ozern. Rechn. Rybn. Khoz.*, 1976, vol. 105, pp. 109–126.

Brochmann, P., Gabrielsen, V., Nordal, I., Landvik, J., and Elven, R., Glacial survival or *tabula rasa*? The history of North Atlantic biota revisited, *Taxon*, 2003, vol. 52, no. 3, pp. 417–450. https://doi.org/10.2307/3647444

Bulatov, R.P., Research on the circulation and water transfer in the Atlantic Ocean, *Okeanol. Issled.*, 1971, no. 22, pp. 7–93.

Bush, A., Lafferty, K., Lotz, J., and Shostak, A., Parasitology meets ecology on its own terms: Margolis et al. revisited, *J. Parasitol.*, 1997, vol. 83, no. 4, pp. 575–583. https://doi.org/10.2307/3284227

Bykhovskaya-Pavlovskaya, I.E., *Parazity ryb. Rukovodstvo po izucheniyu* (Fish Parasites, A Study Guide), Leningrad: Nauka, 1985.

Cadrin, S., Bernreuther, M., Daníelsdóttir, A., Hjörleifsson, E., Johansen, T., et al., Population structure of beaked redfish, *Sebastes mentella*: Evidence of divergence associated with different habitats, *ICES J. Mar. Sci.*, 2010, vol. 67, no. 8, pp. 1617–1630. https://doi.org/10.1093/icesjms/fsq046

Catalano, S.R., Whittington, I.D., Donnellan, S.C., and Gillanders, B.M., Parasites as biological tags to assess host population structure: Guidelines, recent genetic advances and comments on a holistic approach, *Int. J. Parasitol.: Parasites Wildlife*, 2014, vol. 3, no. 2, pp. 220–226. https://doi.org/10.1016/j.ijppaw.2013.11.001

Daníelsdóttir, A., Gíslason, D., Kristinsson, K., Stefánsson, M., Johansen, T., and Pampoulie, C., Population structure of deep-sea and oceanic phenotypes of deepwater redfish in the Irminger Sea and Icelandic continental slope: Are they cryptic species?, *Trans. Am. Fish. Soc.*, 2008, vol. 137, pp. 1723–1740. https://doi.org/10.1577/T07-240.1

Dolgov, A.V., Composition and structure of the mesopelagic fish communities in the Irminger Sea and adjacent waters, *J. Ichthyol.*, 2015, vol. 55, no. 1, pp. 53–68. https://doi.org/10.1134/S0032945215010026

Dubravin, V.F., *Poverkhnostnye vodnye massy i formirovanie zon biologicheskoi produktivnosti Atlanticheskogo okeana* (Surface Water Masses and Formation of Zones of Biological Productivity in the Atlantic Ocean), St. Petersburg: Gidrometeoizdat, 2001.

Dugarov, Z.N. and Pronin, N.M., Dynamics of parasite communities in an age series of Baikal omul *Coregonus migratorius* (Georgi, 1775), *Biol. Bull. Russ. Acad. Sci.*, 2014, vol. 41, no. 3, pp. 264–275. https://doi.org/10.1134/S1062359013050038

Gaevskaya, A.V. and Kovaleva, A.A., Parasitological method in population studies of fish of the Atlantic Ocean and its seas, in *Biologicheskie resursy Atlanticheskogo okeana* (Biological Resources of the Atlantic Ocean), Moscow: Nauka, 1986, pp. 329–338.

Garabana, D., The genus *Sebastes* Cuvier, 1829 (Pisces, Scorpaenidae) in the North Atlantic: Species and stock discrimination using traditional and geometric morphometrics, *PhD Thesis*, Vigo, Spain: Univ. of Vigo, 2005.

Hall, M., Asten, T., Katsis, A., Dingemanse, N., Magrath, M., et al., Animal personality and pace-of-life syndromes: Do fast-exploring fairy-wrens die young?, *Front. Ecol. Evol.*, 2015, vol. 3, p. 28. https://doi.org/10.3389/fevo.2015.00028

Hedgecock, D., Does variance in reproductive success limit effective population sizes of marine organisms?, in *Genetics and Evolution of Aquatic Organisms*, Beaumont, A.R., Ed., London: Chapman & Hall, 1994, pp. 122–134.

Hemmingsen, W. and MacKenzie, K., The parasite fauna of the Atlantic cod, *Gadus morhua, Adv. Mar. Biol.*, 2001, vol. 40, pp. 1–80. https://doi.org/10.1016/S0065-2881(01)40002-2

Instruktsii i nastavleniya (Instructions and Guidelines), Murmansk: PINRO, 1980.

Johansen, T. and Dahle, G., Discrimination among species of the genus *Sebastes* in the North Atlantic by random amplified polymorphic DNA, *Sarsia*, 2004, vol. 89, no. 6, pp. 478–483. https://doi.org/10.1080/00364820410002695

Karamushko, O.V. and Christiansen, J.S., New data on the distribution of beaked redfish *Sebastes mentella* (Sebastidae) in the Greenland Sea, *J. Ichthyol.*, 2021, vol. 61, no. 1, pp. 96–102. https://doi.org/10.1134/S0032945221010082

Klapper, R., Bernreuther, M., Wischnewski, J., and Klimpel, S., Long-term stability of *Sphyrion lumpi* abundance in beaked redfish *Sebastes mentella* of the Irminger Sea and its use as biological marker, *Parasitol. Res.*, 2017, vol. 116, pp. 1561–1572. https://doi.org/10.1007/s00436-017-5433-y

Køie, M., On the morphology and life-history of *Podocotyle reflexa* (Creplin, 1825) Odhner, 1905, and a comparison of its developmental stages with those of *P. atomon Odhner*, 1905 (Trematoda), *Ophelia*, 1981, vol. 20, no. 1, pp. 17–43. https://doi.org/10.1080/00785236

Køie, M., Metazoan parasites of teleost fishes from Atlantic waters off the Faroe Islands, *Ophelia*, 2000, vol. 52, no. 1, pp. 25–44. https://doi.org/10.1080/00785236.1999.10409417

Konovalov, S.M., *Differentsiatsiya lokal'nykh stad nerki Oncorhynchus nerka (Walbaum)* (Differentiation of Local Stocks of Sockeye Salmon *Oncorhynchus nerka* Walbaum), Leningrad: Nauka, 1971. http://dspace.vniro.ru/handle/123456789/7039.

Lile, N., Halvorsen, O., and Hemmingsen, W., Zoogeographical classification of the macroparasite faunas of four flatfish species from the northeastern Atlantic, *Polar Biol.*, 1994, vol. 14, pp. 137–141. https://doi.org/10.1007/BF00234976

MacKenzie, K., Parasites as biological tags in population studies of marine organisms, *Parasitology*, 2002, vol. 124, pp. 153–163. https://doi.org/10.1017/s0031182002001518

MacKenzie, K. and Abaunza, P., Parasites as biological tags, in *Stock Identification Methods: Applications of Fisheries Science*, Cadrin, S., Friedland, K., and Waldman, J., Eds., New York: Elsevier Academic Press, 2005, pp. 211–226. https://doi.org/10.1016/B978-012154351-8/50012-5

MacKenzie, K. and Hemmingsen, W., Parasites as biological tags in marine fisheries research: European Atlantic waters, *Parasitology*, 2015, vol. 142, no. 1, pp. 54–67. https://doi.org/10.1017/S0031182014000341

Magnusson, J. and Magnusson, J.V., Oceanic redfish (*Sebastes mentella*) in the Irminger Sea and adjacent waters, *Sci. Mar.*, 1995, vol. 59, nos. 3–4, pp. 241–254.

Makhrov, A., Artamonova, V., Popov, V., Rolskiy, A., and Bakay, Yu., Single population of beaked redfish (*Sebastes mentella*) in the Irminger Sea: Biological characteristics and dynamics of gene pool, in *NEAFC 29th Annual Meeting Document AM 2010/30*, 2010.

Makhrov, A., Artamonova, V., Popov, V., Rolskiy, A., and Bakay, Yu., Comment on: Cadrin et al. (2010) "Population structure of beaked redfish, Sebastes mentella: evidence of divergence associated with different habitats. ICES Journal of Marine Science, 67: 1617–1630," *ICES J. Mar. Sci.*, 2011, vol. 68, no. 10, pp. 2013–2015. https://doi.org/10.1093/icesjms/fsr132

Marcogliese, D., *Neomysis americana* (Mysidacea) as an intermediate host for sealworm, *Pseudoterranova decipiens* (Nematoda: Ascaridoidea), and spirurid nematodes (Ascaridoidea), *Can. J. Fish Aquat. Sci.*, 1992, vol. 49, pp. 513–515. https://doi.org/10.1139/f92-060

Mel'nikov, S.P., *Okeanicheskii okun'-klyuvach Severnoi Atlantiki: biologiya i promysel* (Oceanic Beaked Redfish of the North Atlantic: Biology and Fishery), Murmansk: PINRO, 2006.

Melnikov, S.P., The use of information on parameters of the life cycle in the management of *Sebastes mentella* fisheries in the Irminger Sea, in *ICES CM/L:03*, 2007.

Mel'nikov, S.P., Identification of beaked redfish stock in the Irminger Sea based on recruitment information, *Voprosy Rybolovstva*, 2008, vol. 9, no. 1, pp. 138–153.

Mel'nikov, S.P., Beaked redfish *Sebastes mentella* of the Atlantic and Arctic Oceans (population structure, biology, fishery), *Extended Absract of Doctoral (Biol.) Dissertation*, Moscow: VNIRO, 2013.

Melnikov, S.P., Intraspecies structure of beaked redfish *Sebastes mentella* of the Atlantic and Arctic oceans, *J. Ichthyol.*, 2016, vol. 56, no. 1, pp. 52–71. https://doi.org/10.1134/S0032945216010082

Mel'nikov, S.P. and Bakai, Yu.I., Biological and ecological justification for the regulation measures of beaked redfish fishing in the area of Iceland, *Rybn. Khoz.*, 2006, no. 1, pp. 48–50.

Melnikov, S.P. and Bakay, Y.I., Structure of aggregations and principal populational characteristics of redfish *Sebastes mentella* (Scorpaeniformes: Scorpaenidae) in the pelagic zone of the Irminger Sea and adjacent waters, *J. Ichthyol.*, 2009a, vol. 49, no. 2, pp. 170–182. https://doi.org/10.1134/S0032945209020040

Melnikov, S.P. and Bakai, Y.I., Recruitment of stock of deepwater redfish *Sebastes mentella* (Scorpaeniformes, Scorpaenidae) in the pelagial of the Irminger Sea and adjacent waters, *J. Ichthyol.*, 2009b, vol. 49, no. 8, pp. 650–661. https://doi.org/10.1134/S0032945209080098

Mel'nikov, S.P. and Glubokov, A.I., The impact of climate variability on the distribution and dynamics of beaked redfish population in the pelagic zone of the Irminger Sea and adjacent waters, *Rybn. Khoz.*, 2015, no. 3, pp. 84–88.

Melnikov, S.P. and Glubokov, A.I., Trends of intraspecific differentiation in the beaked redfish *Sebastes mentella* (Scorpaenidae) from the Atlantic Ocean and adjacent waters, *Biol. Bull. Rev.*, 2019, vol. 9, no. 1, pp. 83–91. https://doi.org/10.1134/S2079086419010067

Melnikov, S.P. and Popov, V.I., The distribution and specific features of the biology of deepwater redfish *Sebastes mentella* (Scorpaenidae) during mating in the pelagial of the northern Atlantic, *J. Ichthyol.*, 2009, vol. 49, no. 4, pp. 300–312. https://doi.org/10.1134/S0032945209040031

Melnikov, S.P., Shibanov, V.N., Stroganov, A.N., and Novikov, G.G., On the issue of biological and genetic studies of *Sebastes mentella* in the open areas of the North East Atlantic, in *ICES CM 2007/L:02*, 2007.

Melnikov, S.P., Karsakov, A.L., Popov, V.I., Tretyak, V.L., and Tretyakov, I.S., The impact of variations in oceanographic conditions on distribution, aggregation structure and fishery pattern of redfish (*Sebastes mentella* Travin) in the pelagial of the Irminger Sea and adjacent waters, in *ICES CM 2009/E:15*, 2009.

Pampoulie, C. and Danielsdottir, A., Resolving species identification problems in the genus *Sebastes* using nuclear genetic markers, *Fish. Res.*, 2008, vol. 93, pp. 54–63. https://doi.org/10.1016/j.fishres.2008.02.007

Pavlov, A.I., Biology, stock status, and fishery of beaked redfish (*Sebastes mentella* Travin) in the Irminger Sea, *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Moscow: VNIRO, 1992.

Pavlov, A.I., Oganin, I.A., and Vaganova, M.V., Age structure and growth features of beaked redfish in the Irminger Sea, in *Issledovanie bioresursov Severnoi Atlantiki* (Study of the Biological Resources of the North Atlantic), Murmansk: PINRO, 1992, pp. 82–95.

Pedchenko, A.P., The condition of redfish aggregations for motion in spring in the Irminger Sea, in *ICES CM 1992/G:58*, 1992.

Pedchenko, A.P., Oceanographic conditions of the Irminger Sea and their influence on the distribution of beaked redfish, *Extended Abstract of Cand. Sci. (Geogr.) Dissertation*, Murmansk: PINRO, 2001.

Polyanskii, Yu.I., Parasitofauna and environment. Some questions of the ecology of parasites of marine fish, in *Osnovnye problemy parazitologii ryb* (Major Problems of Fish Parasitology), Leningrad: Leningrad. Gos. Univ., 1958, pp. 55–89.

Population structure, reproductive strategies and demography of redfish (genus *Sebastes*) in the Irminger Sea and adjacent waters (ICES V, XII and XIV, NAFO 1), in *REDFISH QLK5-CT1999-01222 Final Report*, 2004.

Rikhter, V.A., On population structure of beaked redfish (*Sebastes mentella* Travin) in the Irminger Sea as related to larval drift, *NAFO Scientific Council Studies*, 1996, no. 27, pp. 49–56.

Roitman, V.A. and Lobanov, A.L., A method for estimating the abundance of parasite hemipopulations in the host population, in *Issledovaniya po morfologii, taksonomii i biologii gel'mintov ptits* (Research on the Morphology, Taxonomy, and Biology of Bird Helminths), Moscow: Nauka, 1985, pp. 102–123.

Rol'skii, A.Yu., Artamonova, V.S., Makhrov, A.A., et al., Pelagic beaked redfish of the Irminger Sea. One population or multiple populations?, in *Mat-ly 29 konf. molodykh uchenykh, posvyashch. 140-letiyu so dnya rozhdeniya G.A. Klyuge "Morskie issledovaniya ekosistem Evropeiskoi Arktiki"* (Proc. 29th Conf. of Young Scientists Dedicated to the 140th Anniversary of the Birth of G.A. Klyuge "Marine Research of the European Arctic Ecosystems"), Murmansk: Murmansk. Mor. Biol. Inst. Kol'sk. Nauch. Tsentr Ross. Akad. Nauk, 2011, pp. 180–185.

Rol'skii, A.Yu., Makhrov, A.A., and Artamonova, V.S., Speciation processes of marine redfish of the genus *Sebastes* in the Atlantic and Arctic oceans, in *Sovremennye problemy biologicheskoi evolyutsii: Mat-ly III Mezhdunar. konf. k 130-letiyu N.I. Vavilova i 110-letiyu Gosudarstvennogo Darvinovskogo muzeya* (Current Problems of Biological Evolution, Proc. III Int. Conf. to the 130th Anniversary of N.I. Vavilov and the 110th Anniversary of the State Darwin Museum), Moscow: Gos. Darvinovskii Muzei, 2017, pp. 101–104.

Roques, S., Sevigny, J.-M., and Bernatchez, L., Evidence for broadscale introgressive hybridization between two redfish (genus *Sebastes*) in the Northwest Atlantic: A rare marine example, *Mol. Ecol.*, 2001, vol. 10, pp. 149–165. https://doi.org/10.1046/j.1365-294X.2001.01195.x

Roques, S., Sevigny, J.-M., and Bernatchez, L., Genetic structure of deep-water redfish, *Sebastes mentella*, population across the North Atlantic, *J. Mar. Biol. Assoc. U. K.*, 2002, vol. 140, pp. 297–307. https://doi.org/10.1007/s002270100705

Saborido-Rey, F., Garabana, D., Stransky, C., Melnikov, S., and Shibanov, V., Review of the population structure and ecology of *Sebastes mentella* in the Irminger Sea and adjacent waters, *Rev. Fish Biol. Fisheries*, 2004, vol. 14, pp. 455–479.
https://doi.org/10.1007/s11160-005-3585-9

Saha, A., Johansen, T., Hedeholm, R., et al., Geographic extent of introgression in *Sebastes mentella* and its effect on genetic population structure, *Evol. Appl.*, 2017, vol. 10, no. 1, pp. 77–90.
https://doi.org/10.1111/eva.12429

Schmidt, C., Molecular genetic studies on species and population structure of North Atlantic Redfish (genus *Sebastes*; Cuvier 1829), *PhD Thesis*, Hamburg: Univ. of Hamburg, 2005.

Shevelev, M.S., Bakai, Yu.I., Gotovtsev, S.M., et al., *Instruktsii i metodicheskie rekomendatsii po sboru i obrabotke biologicheskoi informatsii v raionakh issledovanii PINRO* (Instructions and Methodological Recommendations for Collecting and Processing Biological Information in PINRO Research Areas), Murmansk: PINRO, 2001.

Sigurðsson, T., Thorsteinsson, V., and Gustafsson, L., *In situ* tagging of deep-sea redfish: Application of an underwater, fish-tagging system, *ICES J. Mar. Sci.*, 2006, vol. 63, pp. 523–531.
https://doi.org/10.1016/j.icesjms.2005.05.023

Smith, J.W., Larval *Anisakis simplex* (Rudolphi, 1809, det. Crabbe, 1978) and larval *Hysterothylacium* sp. (Nematoda: Ascaridoidea) in euphausiids (Crustacea: Malacostraca) in the North-East Atlantic and northern North Sea, *J. Helminthol.*, 1983, vol. 57, pp. 167–177.
https://doi.org/10.1017/S0022149X00009433

Stefansson, M., Reinert, J., Sigurðsson, P., and Kristinsson, K., Depth as a potential driver of genetic structure of *Sebastes mentella* across the North Atlantic Ocean, *ICES J. Mar. Sci.*, 2009, vol. 66, pp. 680–690.
https://doi.org/10.1093/icesjms/fsp059

Stransky, C., Migration of juvenile deep-sea redfish (*Sebastes mentella* Travin) from the East Greenland shelf into the central Irminger Sea, in *ICES CM 2000/N:28*, 2000.

Stransky, C., Gudmundsdóttir, S., Sigurdsson, T. et al., Age determination and growth of Atlantic redfish (*Sebastes marinus* and *S. mentella*): Bias and precision of age readers and otolith preparation methods, *ICES J. Mar. Sci.*, 2005, vol. 62, pp. 655–670.
https://doi.org/10.1016/j.icesjms.2005.01.018

Sutton, T., Porteiro, F., Heino, M., et al., Vertical structure, biomass and topographic association of deep-pelagic fishes in relation to a mid-ocean ridge system, *Deep Sea Res., Part II*, 2008, vol. 5, pp. 161–184.
https://doi.org/10.1016/j.dsr2.2007.09.013

The Irminger Sea, in *Oceanographic Encyclopedia*, Fairbridge, R.W., Ed., New York: Reinhold Publishing Corporation, 1966.

Waples, R., Separating the wheat from the chaff: Patterns of genetic differentiation in high gene flow species, *J. Hered.*, 1998, vol. 89, no. 5, pp. 438–450.
https://doi.org/10.1093/jhered/89.5.438

Williams, H., MacKenzie, K., and McCarthy, A., Parasites as biological indicators of the population biology, migrations, diet, and phylogenetics of fish, *Rev. Fish Biol. Fisheries*, 1992, vol. 2, pp. 144–176.
https://doi.org/10.1007/BF00042882

Yablokov, A.V., The state of research and some problems of population phenetics, in *Fenetika populyatsii* (Phenetics of Populations), Moscow: Nauka, 1982, pp. 3–14.

Yablokov, A.V., *Populyatsionnaya biologiya: Ucheb. posobie dlya biol. spets. vuzov* (Population Biology: A Textbook for Biological Specialties of Universities), Moscow: Vysshaya Shkola, 1987.

Zelenina, D., Shepetov, D., Volkov, A., Barmitseva, A., Melnikov, S., and Miuge, N., Population structure of beaked redfish (*Sebastes mentella* Travin, 1951) in the Irminger Sea and adjacent waters inferred from microsatellite data, *Genetica*, 2011, vol. 47, no. 11, pp. 1501–1513.
https://doi.org/10.1134/S1022795411110202

Zubchenko, A.V., Vertical zonality and peculiarities of parasite fauna formation in deep-sea fish of the North Atlantic, in *Parazitologicheskie issledovaniya ryb Severnogo basseina: sb. nauch. tr.* (Parasitol. Res. of Fish in the Northern Basin: Proceedings), Murmansk: PINRO, 1993, pp. 39–60.