ISSN 1063-0740, Russian Journal of Marine Biology, 2023, Vol. 49, No. 5, pp. 361–374. © Pleiades Publishing, Ltd., 2023.
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ORIGINAL PAPERS

The Biological Features of the Atlantic Cod *Gadus morhua* L., 1758 (Gadiformes: Gadidae) of the Murmansk Coast: Race Composition and Fishing

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Received December 29, 2022; revised April 8, 2023; accepted June 8, 2023

Abstract—The biological features of Atlantic cod in the coastal zones of the Murman for 1999–2006 were studied. The age composition, growth rate and maturation, feeding habits, and structure of otoliths were analyzed. Histological and genetic studies were carried out. It has been shown that young cod mainly lives and spawns in Western Murman bays. Older cod leaves the bays due to insufficient food supply. The growth rate of young coastal cod is comparable to that of cod in the open part of the Barents Sea. With age, the cod of the open sea areas noticeably overtakes the cod that lives in the coastal zone in growth. It was noted that the cod spawns in the bays with both coastal and Atlantic types of otoliths. Studies of genetic polymorphisms indicate a high degree of genetic similarity between cod groups in the Norwegian and Barents Seas under the influence of currents (branches of the Norwegian Atlantic Current, the Murmansk Coastal Current) and against the background of migrations at different stages of ontogeny of cod from coastal and open water areas.

Keywords: cod, age, growth rate, maturation, nutrition, gametogenesis, otoliths structure, genetic studies

DOI: 10.1134/S1063074023050127

INTRODUCTION

At the beginning of the 20th century, the results of the Murmansk scientific fishing expedition indicated the existence of a local group of Atlantic cod *Gadus morhua* L., 1758 off the Murman coast, which stays and breeds here [7]. Very valuable observations on cod in the Murman coastal waters were made at the State Oceanographic Institute (now VNIRO) [9, 21, 24]. However, despite the extensive list of papers, some issues of biology remained debatable, including the racial composition of cod not only in the Murman coastal waters, but also within the entire Norwegian–Barents Sea region [4, 8, 13, 23, 42, 51, 52, 55, 60].

Starting from 1934, the Polar Institute began to study the raw stock of the Barents Sea, but the main efforts were directed to studying the biology of commercial fish in the open part of the sea, and insufficient attention was paid to studies of the Murman coastal zone. Attempts to resume the study of the resources of coastal waters were made in the second half of the 1970s, but the unsatisfactory material and technical support of these studies undermined the development of this direction.

In the current century, mainly to solve socio-economic problems, attempts were also made to revive the coastal fishery at the Murman; however, the shortcomings of the administrative and legal framework did not lead to a significant expansion of research and an increase in fishing, although there were some studies on the intraspecific variability of Atlantic cod using mitochondrial and nuclear DNA markers [12, 18]. At the same time, the issue of the rational exploitation of the cod stock is becoming relevant for the modern development of coastal fisheries. Under these conditions, it is important to conduct a comprehensive analysis of the materials obtained over several years on Atlantic cod, enabling one to identify general trends in changes in the study object.

The aim of this paper was to study the morphobiological and genetic characteristics of cod in the Murman coastal waters under the conditions of changing temperature of the Barents Sea waters and their comparison with cod groups in the Norwegian Sea.

MATERIALS AND METHODS

The materials were collected within the framework of PINRO research programs in 1999–2006 in the water area of Ura-Bay and Kislaya Bay (Western Murman, Motovsky Bay of the Barents Sea) during the spawning and post-spawning periods (Fig. 1, Table 1).

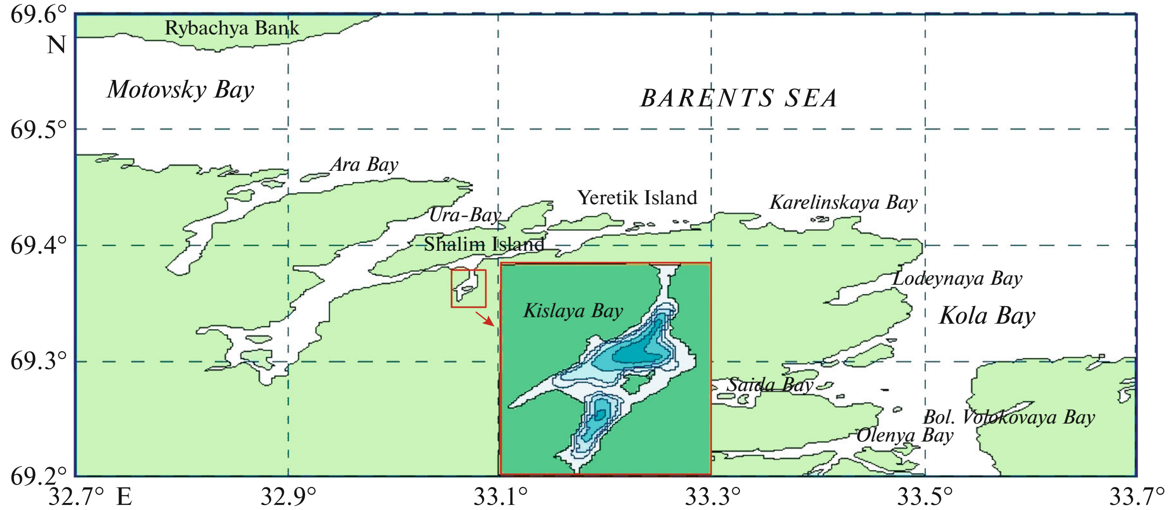

Fig. 1. The locations of Ura-Bay and Kislaya Bay (Western Murman).

For a comparative analysis of the characteristics of growth (Rybachya Bank, year 2000, 110 specimens) and nutrition (Rybachya Bank, year 2004, 167 specimens), cod samples from open water areas of the Barents Sea were used.

In the course of biological analysis of cod, the full length, weight, sex, stage of maturity, and fat content (hepatosomatic index) were recorded, otoliths were taken to identify the age and type, and color features were noted.

When identifying the ages of cod, otoliths broken into two halves in the center were examined with shading of the fracture surface at a magnification of 16x under a binocular. The otoliths were not subjected to additional processing (staining, firing, etc.). Based on the analysis of the structure of the otoliths, the data were obtained on the spawning activity of cod, and on the identification of coastal and marine groups. The study of the structure of otoliths was carried out using the methodological recommendations by Mankevich [19, 20].

The maturity of gametes was identified on a 6-point scale [30, 31]. To obtain information on the structural changes in the gonads during the spawning period, their histological studies were performed. To fix the material, a part about 1 cm^3 in size was taken from the middle part of the gonad. Bouin's solution was used as a fixative. Camera processing of gonads was carried out according to standard histological methods [27].

The composition of food and its quantitative characteristics were analyzed according to the methodological recommendations for the study of fish nutrition [5, 15, 38]. As indicators, we used the stomach filling index and the food similarity index (FS-coefficient), as well as data on the composition of food, expressed by the frequency of occurrence of food objects (% of the total number of analyzed stomachs with food) and the mass of individual food objects (%). Statistical analysis of data was carried out according to standard methods [14, 26].

For genetic studies, samples of the white muscles were taken. The work was done by a comprehensive

Table 1. The number of processed samples of *Gadus morhua* in the bays of Western Murman (69°21′55″ N, 33°04′15″ E), ind

Year	Complete biological analysis	Otolith studies	Genetic studies	Histological studies	Quantitative nutrition analysis
1999	55	55	55	–	–
2000	28	–	28	–	–
2003	99	99	99	–	–
2004	124	124	50	13	124
2005	31	31	31	–	–
2006	31	31	31	–	–
Total	368	340	294	13	124

"–", no data.

method using the study of allozymes and DNA polymorphisms (microsatellites), which provides a fairly detailed characterization of the genetic status of individual populations within the range of the species [1, 39]. We analyzed unified enzyme systems used for population genetic studies of Atlantic cod both in Russia and abroad [45, 48, 49]: α-glycerophosphate dehydrogenase (*AGP**), phosphoglucoisomerase (*PGI-1**, *PGI-2**), lactate dehydrogenase (*LDH**), isocitrate dehydrogenase (*IDH**), and phosphoglucomutase (*PGM**). DNA analysis was carried out according to standard methods; the microsatellite loci *Gmo3*, *Gmo8*, *Gmo-G12*, *Gmo-G18*, *Gmo19*, *PGmo32*, *Gmo34*, and *Gmo35* were used [32, 44, 47].

It should be noted that in connection with the fact that in the basin of the Norwegian and Barents Seas, coastal and oceanic groups of Atlantic cod are distinguished on the basis of the otolith structure [33, 54], regarding the degree of reproductive independence, on which the opinions of researchers differ to a large extent, and compared the samples represented by individuals with the same type of otolith: either oceanic or coastal. This approach, when analyzing the structure of the Norwegian–Barents Sea populations of Atlantic cod, is used by both domestic and foreign researchers [2, 55, 60]. To obtain the required sample size for the analysis of multiallelic allozyme and, especially, microsatellite loci in samples separated by otolith type from Ura-Bay and Kislaya Bay, samples from different samples were combined with a preliminary test for heterogeneity using the *METROP* software package [43, 63].

Using the *GDA* [46] and *Arlequin* software packages, version 3.1 [41], we identified the average allele frequency per locus (*Ap*) for the sample, corresponding to the Hardy–Weinberg distribution (the distribution of genotypes in all variants was equilibrium at the significance level $p > 0.05$; only in in two variants with allozymes and in three variants with microsatellites, the distribution of genotypes was balanced at $0.05 > p > 0.01$), heterozygosity expected (H_E) and observed (H_O) (differences between expected and observed heterozygosity were insignificant in all cases), genetic identity (I) , coefficients of genetic differentiation F_{ST} and θ [50, 59]. An analysis of the intensity of gene flows *Nm* (the number of migrants per generation) was carried out by the method based on an analysis of genetic differentiation using the Wright equation [61]: $Nm = (1/ F_{ST} - 1)/4$.

When analyzing the materials for the purpose of comparison, we also used the data obtained in the course of joint Russian–Norwegian studies and partially published data on the variability of loci in cod samples from the Barents and Norwegian Seas for 2002–2006 [55]. A brief description of the samples is presented in Table 4.

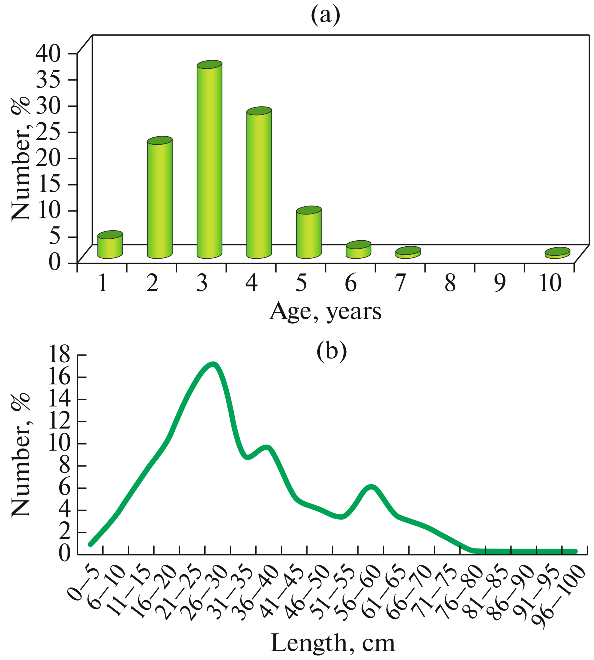

Fig. 2. The age (a) and size (b) compositions of *Gadus morhua* in the bays of Western Murman in 1999–2006.

RESULTS

An analysis of the biological data of cod samples from the coastal waters of Western Murman showed the presence of individuals aged from 1 to 10 years (full body length from 5 to 97 cm). The samples were based on individuals aged 2, 3, and 4 years (22, 36, and 27%, respectively) and two size groups of 21–25 and 26–30 cm (15 and 17%, respectively) (Figs. 2a, 2b). The cod weight varied from 19 to 5124 g, with the average being 341 g.

The difference in size–weight (mean values) characteristics between the cod of coastal and offshore water areas was shown, while there was a tendency for these differences to increase with age (Fig. 3). Thus, for example, if at the age of 6 years the length of the cod caught in the bays of Western Murman was 25% less than that of the cod from the offshore areas of the Barents Sea (Rybachya Bank), the 10-year-old coastal cod were almost half as long.

More than 20% of the specimens from Kislaya Bay had a bright brownish-red coloration (Fig. 4). Such cod were mentioned for the first time in [34] where it was given the name “turyanka” from the word “tura” meaning seaweed, kelp [10, 37]. The specific coloration is apparently a consequence and evidence of habitation in the sublittoral, in the zone of macrophytes, especially brown algae, due to which the cod acquires a protective brownish color.

The analysis of food composition demonstrated some differences in cod from coastal and offshore areas. In the bays, cod mainly feed on benthic organ-

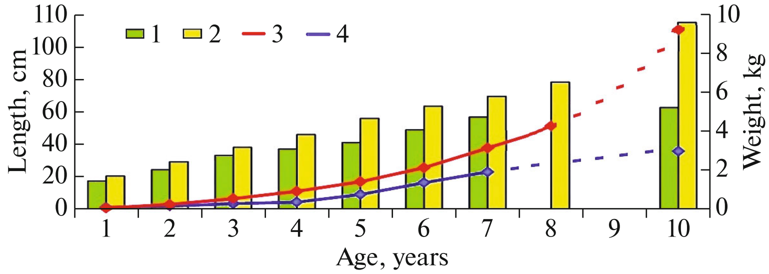

Fig. 3. The length (histogram) and weight (line graph) of *Gadus morhua* caught in the bays of Western Murman and cod from the Barents Sea ((1 and 3) Western Murman, (2 and 4) Barents Sea, Rybachya Bank) in 1999–2006.

Fig. 4. *Gadus morhua* with a brownish-red color (turyanka).

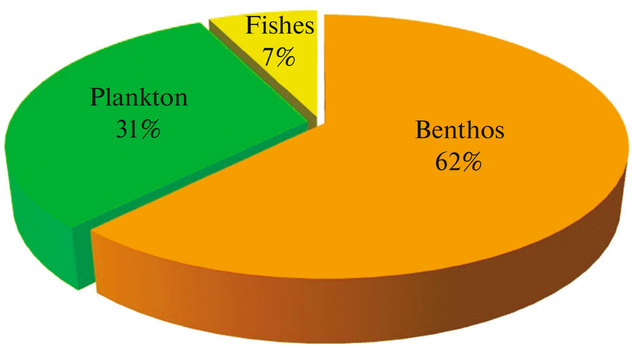

Fig. 5. The food composition of *Gadus morhua* in the bays of Western Murman in 2004 (% of the weight of the food bolus).

isms (62%) (Fig. 5), among which the hermit crabs *Pagurus pubescens*, Polychaeta, shrimp, and *Ophiura* sp. (from 24 to 50%) (Table 2) were the most frequent; the total proportion of these objects in the weight of the food bolus was more than 32%. Of secondary importance in the diet of Atlantic cod is plankton (about 31%), which, according to our data, was dominated by the copepods *Calanus finmarchicus* and Euphausiacea. Fish objects in the composition of cod food in the bays of Western Murman did not exceed 7% (Fig. 5). Fish objects prevailed in the stomachs of cod from offshore areas of the Barents Sea (Rybachya Bank) (more than 82% of the weight of the food bolus) (Table 2). The food similarity index between coastal and offshore cod was only 17%. At the same time, cod fed quite actively in the bays. Here, the proportion of feeding fish was 95%, which was almost 1.4 times higher than that for the cod in Rybachya Bank (Table 2). At the same time, the index of stomach filling and fat content of coastal cod were two times lower than those of offshore cod.

The majority of individuals in the bays of Motovsky Bay were immature with gonads of maturity stage II (Fig. 6). At the age of 1–2 years, females dominated in number, and in older groups, the number of fish of different sexes were approximately the same (Fig. 7). In the bays of Western Murman, a small part of individuals were mature already at a body length of 25–30 cm at the age of 3 years, while on the whole individuals become sexually mature by 5–6 years, reaching 51–60 cm (Fig. 8).

Studies of cod gonads in the coastal waters of Western Murman showed that all individuals in the sample taken for histology (late March–April 2004) were sexually mature (Table 3). In females, the state of the ovaries was characterized mainly as pre-spawning and spawning (maturity stages: IV, IV–V, and V), males of maturity stage VI were also noted. The gonadosomatic index varied from 0.8 to 19%. In the ovaries of spawning females, hydrated oocytes were found ready for spawning, as well as postovulatory follicles, indicating that some of the mature germ cells had already been spawned. The ovary of the smallest mature cod contained the last portion of hydrated oocytes and numerous remnants of postovulatory follicles from previous portions (Figs. 9a, 9b). Male gonads were in the spawning and post-spawning states. In the vas defer-

Table 2. The composition of the food bolus of *Gadus morhua* caught in the bays of Western Murman (69°21′55″ N, 33°04′15″ E) and on Rybachya Bank (69°44′00″ N, 32°30′00″ E) of the Barents Sea in 2004

Object	Bays of the Western Murman		Rybachya Bank	
	f	*m*	*f*	*m*
	Planktonic organisms			
Calanus finmarchicus	28.21	0.98	–	–
Euphausiacea	17.09	0.25	18.42	11.11
Calanus hyperboreus	9.40	0.04	–	–
Hyperiidea	6.84	0.02	–	–
Larval fish	5.13	0.38	–	–
Nauplii Cirripedia	4.27	0.01	–	–
Mysida	2.56	+	–	–
Cirripedia larvae	2.56	0.20	–	–
Ctenophora	1.71	+	4.39	0.62
Paralithodes camtschaticus larvae	1.71	+	–	–
Chaetognatha	0.85	0.01	–	–
	Bottom organisms			
Pagurus pubescens	50.43	10.04	–	–
Polychaeta	41.88	8.59	–	–
Shrimps	27.35	2.59	31.58	5.53
Ophiura sp.	23.93	11.70	–	–
Gammaridea	7.69	0.18	–	–
Nemertea	4.27	0.83	–	–
Paralithodes camtschaticus	3.42	15.98	1.75	0.17
Isopoda	2.56	0.11	1.75	0.08
Bivalvia	2.56	0.05	–	–
Strongylocentrotus droebachiensis	1.71	0.03	–	–
	Fishes			
Ammodytes hexapterus marinus	7.69	3.68	–	–
Mallotus villosus	4.27	10.65	30.70	51.16
Young *Pollahius virens*	2.56	13.09	–	–
Pisces remnants	1.71	0.01	–	–
Pholis gunnellus	1.71	2.58	–	–
Clupea harengus harengus	0.85	0.06	–	–
Young *Gadus morhua*	0.85	5.36	1.75	3.99
Myoxocephalus scorpius	0.85	12.37	–	–
Digested Pisces	–	–	11.40	4.68
Maurolicus sp.	–	–	0.88	0.04
Young *Melanogrammus aeglefinus*	–	–	9.65	19.78
Young *Sebastes*	–	–	0.88	0.55
Lumpenus sp.	–	–	2.63	1.21
Hippoglossoides platessoides	–	–	3.51	1.07
Stomach filling index, %	115.2		231.3	
Fatness, %	2.07		3.88	
Proportion of feeding individuals, %	95.2		68.3	

Legend: *f* , frequency of occurrence, % of the number of fed fish; *m*, share of object, % by weight of the food bolus; "–" no data.

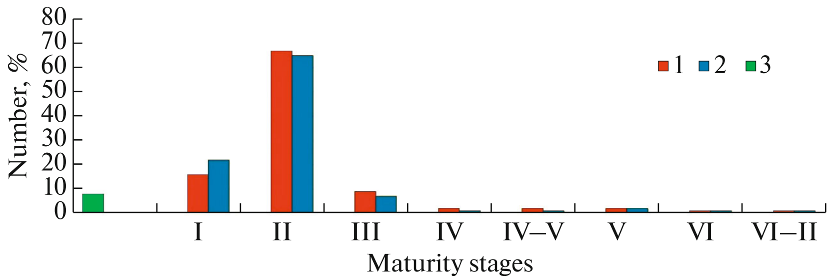

Fig. 6. The maturity stages of *Gadus morhua* gonads in the bays of Western Murman in 1999–2006. Designations: (1) females (177 specimens); (2) males (147 specimens); (3) immature (27 specimens).

ens of spawning fish, numerous mature sperm cells were noted, and there were some signs indicating that some of the sperm had already been spawned (Figs. 10a, 10b). In post-spawning specimens, it was possible to observe regenerative processes in the testicles and residual, unspawned spermatozoa, which were subjected to resorption.

The study of the structure of otoliths showed that cod with otoliths of the coastal, Atlantic, and intermediate types were present in the bays of Western Murman (Fig. 11). The numbers of these fish in different years were not the same. The cod with coastal type otoliths were the most numerous (from 60 to 85% in different years). Less common were cod with Atlantic type otoliths (up to a maximum of 25% in 2004). The lowest presence was noted in cod with intermediate type otoliths (no more than 5%).

The results of the genetic studies demonstrated different levels of variability of allozyme and microsatellite loci, which, for example, was reflected by the values of H_O and Ap (Table 4). All microsatellite loci were highly polymorphic, while out of six allozyme markers, only two loci showed a high level of variability: *PGI-1** and *LDH**.

The level of differentiation of the tested samples of Atlantic cod differed in selective and neutral markers. Despite a higher level of selective impact of environmental factors in the coastal waters of the Barents and Norwegian Seas against the background of their seasonal changes, which is expressed, among other things, in the structure of otoliths, a rather high similarity in the studied allozyme loci between the samples was revealed, regardless of localization and type of otolith. This was confirmed by a high level of identity between the samples (I = 0.994–0.999) and low insignificant values of the coefficient of genetic differentiation θ both in the samples with coastal and oceanic types of otoliths and between the groups of samples with Atlantic and coastal types (Table 5).

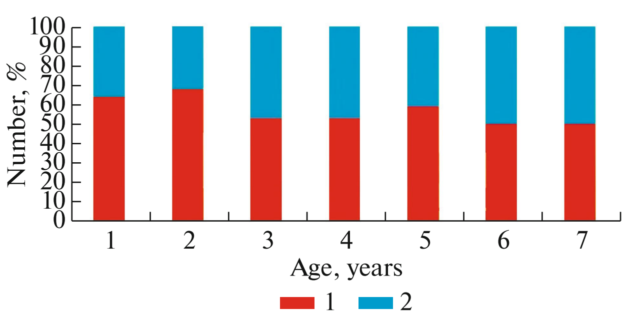

Fig. 7. The ratio of females (1) and males (2) among the Atlantic cod of the bays of Western Murman in 1999–2006.

For microsatellite markers, the results when comparing groupings with Atlantic and coastal types of otoliths were similar to the results for allozymes: the differentiation coefficient turned out to be low and insignificant (Table 6). A high degree of genetic similarity, reflecting to a certain extent the genetic unity of the cod of the Norwegian–Barents Sea stock [11], is evidenced by the low values of genetic differentiation, both within the group with the coastal type of otolith and the group with the oceanic type (Tables 7, 8).

The intensities of gene migration between cod groups with oceanic and coastal types of otoliths obtained on the basis of differentiation by allozyme and microsatellite markers had similar high values (66.8 and 52.9 migrants per generation, respectively), reflecting the intensive exchange of genetic material between Atlantic cod groups in open and coastal water areas of both the Barents and Norwegian Seas.

DISCUSSION

This paper presents a comprehensive description of the group of Atlantic cod living in the coastal waters of Western Murman.

A comparison of the growth characteristics of cod from Western Murman coast and the open part of the Barents Sea showed that the cod from open waters significantly exceeds those living in the coastal zone, in terms of both linear and weight indicators. These differences are especially noticeable as the fish mature. It is interesting to note that similar tendencies are also

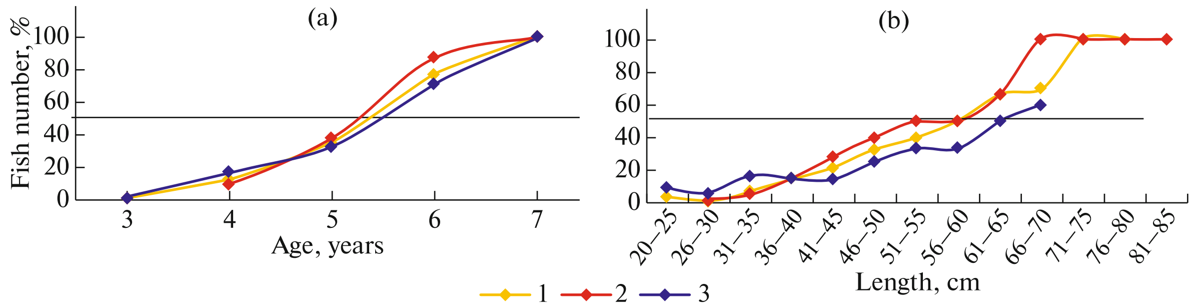

Fig. 8. Maturation ogives of *Gadus morhua* in the bays of Western Murman depending on age (a) and length (b) in 1999–2006. ((1) females and males, (2) females, (3) males).

described for the waters of the Norwegian Sea: the oceanic cod has a higher growth rate compared to individuals from the coast and fjords [40].

According to the data we obtained, the differences in growth rate between coastal and open water cod show a tendency to increase with age. This may be explained by the fact that with a relatively equal food supply, cod juveniles in offshore areas and in the coastal zone grow fairly evenly, and the differences in growth rates observed with age are caused by the detected differences in nutrition. A better food supply (as evidenced by the results presented above on a higher value of the stomach fullness index) and higher calorie content of the fish diet (compared to benthic invertebrates that prevail in the diet of cod in the coastal zone) [17] contribute to the higher growth rate of cod of open water areas of the Barents Sea.

The feeding characteristics and growth rates also seem to influence the differences in the timing of sexual maturation of cod in open and coastal waters: against the background of a higher growth rate, later maturation of cod in open waters was noted. In the bays of Western Murman cod begin to mature at the age of 3 years, and on the whole it becomes sexually mature by 5–6 years, while in the Barents Sea (sea waters) only a small part of the cod mature at this age, and most individuals become sexually mature at 8–10 years [35].

It is known that the main spawning grounds for cod of the Norwegian–Barents Sea stock are located off the coast of Norway. The optimal conditions for

Table 3. The biological characteristics of *Gadus morhua* (Western Murman) sampled for histological analysis in 2004

Fish No.	Length, cm	Weight, g	Age, years	Otolith type	Sex	Maturity stage	Gonads weight, g	Gonadosomatic index, %
1	29	246	3	Coastal	M	V	8.62	3.5
2	105	12440	–	Atlantic	F	IV	2358	19.0
3	83	5124	11	Coastal	F	V	258	5.0
4	65	2925	10	Coastal	F	IV	410	14.0
5	44	812	4	Coastal	F	V	22.07	2.7
6	36	452	5	Atlantic	M	VI	3.83	0.8
7	31	300	4	Coastal	M	V	3.33	1.1
8	50	1170	5	Atlantic	F	IV	68.23	5.8
9	45	984	5	Coastal	F	IV–V	159	16.2
10	45	794	5	Atlantic	M	VI	13.09	1.6
11	36	474	4	Coastal	F	V	59.44	12.5
12	40	695	4	Coastal	F	IV–V	107	15.4
13	37	498	4	Coastal	M	V	5.88	1.2

"–", no data.

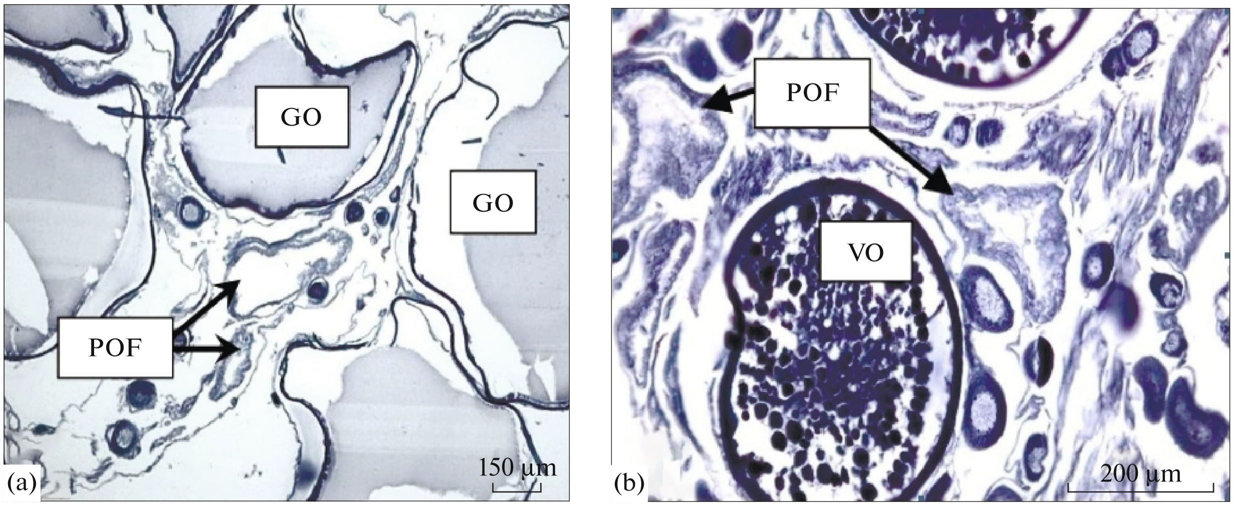

Fig. 9. Fragments of ovaries of spawning *Gadus morhua* females, fish length 36 (a) and 44 (b) cm. One can see hydrated (GO, maturity stage V) and vitellogenous (VO, maturity stage IV) oocytes, as well as postovulatory follicles (POF).

reproduction are considered to be the temperature of the bottom layer from 4 to 6°C [29, 35]. At the same time, the water temperature in this region is subject to cyclical changes. Thus, during the 20th century, there were two cold (1900–1920 and 1960–1970) and two warm (1930–1950 and from the mid-1980s) periods [56]. During periods of warming in the western part of the Barents Sea, temperature conditions develop that promote active spawning of cod in the waters of Western Murman as well (the bays and fjords of Motovsky Bay) [6, 22, 35, 36]. It is believed that mainly young first maturing cod spawn in the bays of Western Murman, while older, repeat spawning individuals leave the smaller bays and bays of the Kola Peninsula, preferring spawning grounds near the Lofoten Islands [22]. At the same time, the results of histological studies allow clarification of the understanding of the composition of the cod spawning group in West Murman coast. It has been shown that 77% of the entire sample was cod in immediate spawning or post-spawning state. In fact, this was mostly first-time spawning cod at the ages of 3–4 years, while 11-year-old cod were also in the spawning state. Another important observation is that the fourth portion of the spawning group from Ura-Bay fjord was made up of individuals with the Atlantic type of otolith, which indicated their habitation in the open waters of the Barents Sea and coming to spawning grounds in the coastal zone.

The results of the study of allozyme variability and nuclear DNA polymorphism apparently indicate the genetic similarity of cod from coastal and open water areas. Thus, in terms of protein markers, we did not reveal significant differences either between the samples with the coastal type of otolith, or with the Atlantic type, or between the groups of samples with the Atlantic and coastal types of otoliths. This is quite consistent with the results of studies previously carried out according to a similar scheme [2, 3], although our version used a larger number of polymorphic marker loci.

The results we obtained using microsatellite markers when comparing cod from open and coastal waters (with Atlantic and coastal types of otoliths, respectively) were similar to the data on allozymes. As noted above, genetic studies have been expanded by additionally using cod samples from coastal and open areas of the Norwegian Sea to cover the entire Norwegian–Barents Atlantic cod stock. The obtained low values of genetic differentiation within the group with the coastal type of otolith, within the group with the oceanic type, between the groups with the coastal and oceanic (Atlantic) types of otoliths indicate the similarity, unity at the genetic level of Atlantic cod of the Norwegian–Barents Sea stock [11].

Thus, a study using two groups of characteristics (biological and genetic) provided, at first glance, contradictory results: differentiation in terms of a set of biological parameters and similarity in terms of both selective and neutral genetic markers. To a certain extent, the contradiction may be resolved by considering the indicator of gene migration. Its high value indicates an intense level of exchange of genetic material between Atlantic cod groups, which evens out even small differences at the genetic level. This is consistent with the results of ichthyoplankton sampling at spawning grounds, which demonstrate a gradual removal of pelagic eggs and larvae of Atlantic cod (denatant migrations) from fjord and coastal waters to open areas in the spring months with subsequent mixing of cod from oceanic and coastal populations

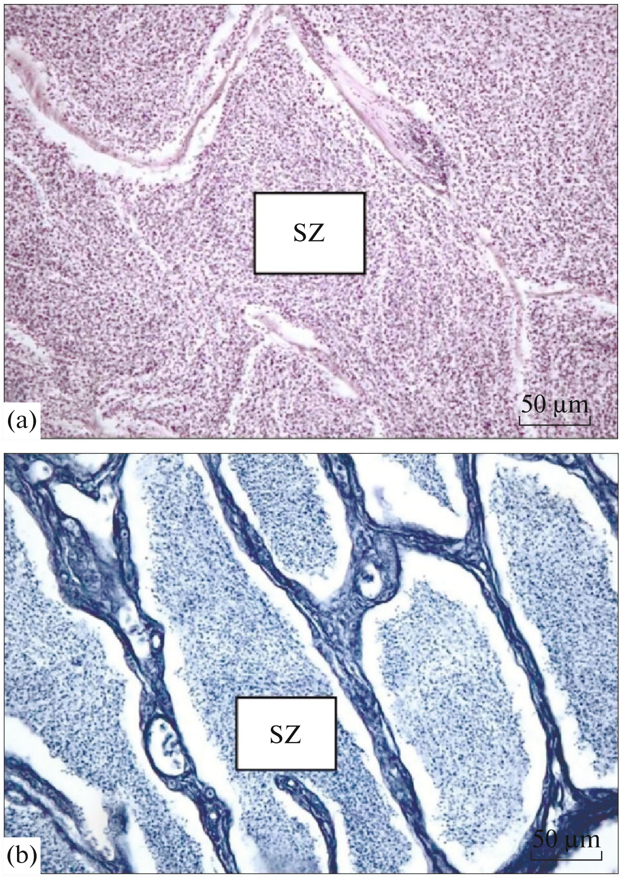

Fig. 10. Fragments of testicles of spawning male *Gadus morhua*, fish length 29 (a) and 31 (b) cm. Numerous mature spermatozoa (SZ) are visible.

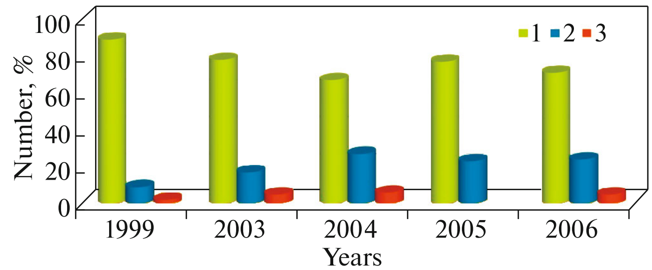

Fig. 11. Correlation of *Gadus morhua* with otoliths of various types in the bays of Western Murman ((1) coastal, (2) Atlantic, and (3) intermediate types of otoliths).

[25, 56], as well as active migrations of juveniles and adults between coastal and open areas [49].

The success of cod fishing in the coastal zone of the Kola Peninsula depends on many factors, the main of which are the states of populations and the nature of fish migrations, depending on the hydrological conditions in a particular year, which contribute to or prevent the formation of dense and stable concentrations of the food base [28]. PINRO studies have shown that the raw stock of the Murman coastal water area allows rational long-term fishing for bottom fish, while the cod biomass varies from 22 to 43 thousand tons in different seasons [16].

In cold years in the spring, cod migrate eastward mainly along the Coastal branch of the Murmansk current, forming dense commercial concentrations near the coast; in warm weather cod migrate along the Main Branch, when cod fishing in the coastal zone is usually ineffective [28]. In addition, powerful approaches of capelin to the coast in years of different thermal state of water masses are the reason for the active migration of wintering accumulations of cod to the coastal zone.

Currently, cod catching in the coastal zone of the Kola Peninsula is possible using trawl, longline, and line fishing. Features of the distribution of fish in different hydrological years and seasons can be a determining factor in the choice of fishing gear [28].

Thus, these studies have shown that off the coast of Murman, mainly Atlantic cod of younger and middle age classes live, with large cod of older age groups being less common. The most likely reason for the shorter life span of cod in the waters of Murman is the migration of older fish to sea areas to improve their feeding conditions, which contribute to an increase in the growth rate of cod in open waters. Although the cod in the study area are feeding quite actively, the basis of the diet is still low-calorie benthic organisms, resulting in a relatively low growth rate.

During the study period, the majority of individuals off the coast of Murman were immature. Nevertheless, pre-spawning, spawning, and post-spawning fish were also present here. A high percentage of mature fish of younger age groups was noted. It is probable that first-time maturing individuals mainly spawn here. At the same time, repeatedly spawning individuals, apparently as a result of searching for better conditions for feeding, leave the bays and gulfs of the Kola Peninsula, preferring open water areas, and subsequently migrate to spawning grounds near the Lofoten Islands. It can be assumed that the number of young mature fish in the spawning stock of cod in the coastal waters of Western Murman against the background of favorable temperature conditions will be determined by the yield of generations.

The presence of cod with otoliths of both coastal and Atlantic types in the bays of Western Murman indicates the absence of strict confinement of these fishes to particular habitats and the presence of a constant exchange of genetic material between them as a result of migrations. This can be confirmed by spawning in the bays of cod with Atlantic-type otoliths, which, in turn, proves the origin of coastal cod not only from the individuals of the coastal group living here, but also from the cod of the open sea areas.

Table 4. The characteristics of the analyzed samples of *Gadus morhua*

Localization, geographic coordinates and sample index	Otolith type	Marker: allozymes	Marker: microsatellites
Barents Sea (2002–2006)			
Kislaya bay (BKG) 69°21′55″ N, 33°04'15″ E	Atlantic	–	$n = 28$ $H_O = 0.633$ $Ap = 9.37$
Kislaya bay (BKG) 69°21′55″ N, 33°04′15″ E	Coastal	–	$n = 55$ $H_O = 0.651$ $Ap = 10.37$
Ura-bay (BUG) 69°21′29″ N, 32°56′02″ E	Atlantic	$n = 30$ $H_O = 0.127$ $Ap = 2.00$	–
Ura-bay (BUG) 69°21′29″ N, 32°56′02″ E	Coastal	$n = 107$ $H_O = 0.177$ $Ap = 2.75$	–
Kildin Island area (BK) 69°18′20″ N, 34°09′40″ E	Atlantic	$n = 23$ $H_O = 0.184$ $Ap = 2.00$	$n = 23$ $H_O = 0.640$ $Ap = 8.62$
Kildin Island area (BK) 69°18′20″ N, 34°09′40″ E	Coastal	$n = 21$ $H_O = 0.198$ $Ap = 2.50$	$n = 20$ $H_O = 0.618$ $Ap = 7.75$
Norwegian Sea (2002–2003)			
Lofoten Islands (NL1) 68°04′20″ N, 14°27'40″ E	Atlantic	$n = 39$ $H_O = 0.179$ $Ap = 2.33$	–
Lofoten Islands (NL2) 68°04′20″ N, 14°27'40″ E	Atlantic	–	$n = 82$ $H_O = 0.563$ $Ap = 10.50$
Vikna area (NV) 65°39′43″ N, 11°45′14″ E	Coastal	$n = 94$ $H_O = 0.168$ $Ap = 2.75$	$n = 47$ $H_O = 0.645$ $Ap = 10.37$
Vega area (NVg) 65°40′31″ N, 11°57′28″ E	Coastal	$n = 53$ $H_O = 0.198$ $Ap = 2.25$	$n = 48$ $H_O = 0.644$ $Ap = 9.75$
Smorfjord (NS) 70°32′31″ N, 25°11′28″ E	Coastal	$n = 85$ $H_O = 0.186$ $Ap = 2.50$	$n = 40$ $H_O = 0.674$ $Ap = 9.00$

Legend: n, sample size; Ap, number of alleles per locus; H_O, observed heterozygosity; –, no data.

Table 5. The level of differentiation of *Gadus morhua* in the basins of the Norwegian and Barents Seas (according to six allozyme loci) at the main levels of the population hierarchy (values of the index θ, %)

Statistics	Samples of cod with coastal type of otolith	Samples of cod with Atlantic type of otolith	Between cod with coastal and Atlantic types of otoliths
Differentiation level, θ	–0.007 insignificant	–1.457 insignificant	0.372 insignificant
95% confidence bootstrap interval	[0.516; –0.211]	[–0.516; –1.539]	[0.882; –0.178]
Most differentiating loci	*PGM** (1.1673)	*PGM** (–0.0002)	*LDH** (0.9461)

Table 6. The level of differentiation of *Gadus morhua* in the basins of the Norwegian and Barents Seas (according to eight microsatellite loci) at the main levels of the population hierarchy (values of the index θ, %)

Statistics	Samples of cod with coastal type of otolith	Samples of cod with Atlantic type of otolith	Between cod with coastal and Atlantic types of otoliths
Differentiation level, θ	0.585 reliable	1.465 reliable	0.471 insignificant
95% confidence bootstrap interval	[0.140; 1.194]	[0.326; 3.254]	[1.610; −0.109]
Most differentiating loci	*Gmo-G12* (0.020)	*Gmo34* (0.090)	*Gmo34* (0.047)

Table 7. Estimates for eight microsatellite loci of genetic identity (*I*) [50] (above diagonal) and genetic differentiation based on (F_{ST}) (below diagonal) among the samples of *Gadus morhua* with Atlantic otolith type in the Norwegian and Barents Seas basins

Samples	NL2	BKG	BK
NL2		0.952	0.972
BKG	**0.015**		0.940
NS	0.002nd	**0.022**	

According to F_{ST} values: values in bold type are significant, taking into account the Bonferroni correction; nd, values are insignificant.

Table 8. Estimates for eight microsatellite loci of genetic identity (*I*) [50] (above diagonal) and genetic differentiation based on F_{ST} (below diagonal) among the samples of *Gadus morhua* with coastal otolith type in the Norwegian and Barents Seas basins

Samples	NVg	NV	NS	BKG	BK
NVg		0.975	0.965	0.979	0.950
NV	0.003nd		0.959	0.975	0.975
NS	**0.009**	**0.013**		0.976	0.951
BKG	0.002nd	0.005*	0.003nd		0.961
BK	**0.014**	0.001nd	0.007nd	0.006nd	

* Values are significant at $p < 0.05$. According to F_{ST} values: values in bold type are significant, taking into account the Bonferroni correction; nd, values are insignificant.

Comparative population-genetic studies of the coastal and oceanic groups of Atlantic cod in the basins of the Norwegian and Barents Seas have demonstrated their relatively high similarity at the genetic level. Thus, the study of the genetic polymorphisms of cod in the offshore areas and bays of the Western Murman (as an integral part of the Barents Sea cod population) in comparison with the cod populations of the Norwegian Sea indicates a high level of genetic unity, which is formed as a result of both joint spawning of cod with the Atlantic and coastal types of otoliths in water areas of the Western Murman, and of the mixing of oceanic and coastal (fjord) cod during denatant and contranatant migrations at different stages of ontogeny in the waters of the Norwegian and Barents Seas [6, 23, 57, 58, 62].

ACKNOWLEDGMENTS

The authors are grateful to the colleagues from the Polar Branch of the Russian Federal Research Institute of Fisheries and Oceanography: N.N. Trostyansky, V.B. Matyushkin, and S.V. Dolgov for their assistance in collecting materials in Western Murman bays and to N.V. Zuikova and N.A. Lepesevich for the participation and assistance in processing materials.

FUNDING

The study was carried out within the framework of the State Assignments of the the Polar Branch of the Russian Federal Research Institute of Fisheries and Oceanography and the Moscow State University.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflicts of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Animal-related experiments were approved by the Bioethics Committee of Moscow State University, protocol dated February 16, 2023.

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Translated by V. Petrakovl