ISSN 1022-7954, Russian Journal of Genetics, 2017, Vol. 53, No. 12, pp. 1350–1357. © Pleiades Publishing, Inc., 2017.
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ANIMAL GENETICS

Toward *Gadus* (Gadidae) Genus Taxonomy: Development of Modern Structure

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Received February 14, 2017; in final form, April 4, 2017

Abstract—According to the results of analysis of genetic differentiation and Bayesian hierarchical cluster analysis of polymorphism in microsatellite loci, it was demonstrated that the development of marginal groups represented by subspecies level taxa (Greenland (*Gadus macrocephalus ogac*) and White Sea (*Gadus morhua marisalbi*) cod) occurred in the late Holocene in a similar scenario, but in different regions and from different initial forms. The development of these reproductively independent cod groups was a result of physiological adaptations to arctic conditions in coastal northern water areas that developed under global cooling in the Subboreal.

Keywords: White Sea cod (*Gadus morhua marisalbi*), Greenland cod (*Gadus macrocephalus ogac*), microsatellite loci, taxonomic status

DOI: 10.1134/S1022795417120122

INTRODUCTION

The members of the *Gadus* genus are marine (forming accumulations), bottom, and bottom-pelagic fishes that mastered the shelf and upper bathyal of arctic and high-boreal regions of the Arctic, Atlantic, and Pacific oceans. Cod at the species, subspecies, and population levels produce a number of forms, including those that are of great national economic value [1].

Cod not only inhabits almost all shelf boreal water areas in the Northern Hemisphere, but also spreads into arctic waters. Thus, "demonstrating" a good con-
1 firmation of the ideas about zoogeographic faunistic complexes [2, 3], cod moves to the arctic complex by the formation of individual taxa specialized by a number of characteristics: White Sea and Greenland.

Different living conditions and high biological variability of the cod generate a variety of forms and lead to certain difficulties in interpretation of the status of individual taxa. No less complex problems arise during the analysis of the cod population structure, ways of its resettlement, and peculiarities of formation.

For more than a century, researchers suggested different modifications of its structure using different approaches to systemization in the *Gadus* genus, applying different methods (from the fixation of the appearance and morphobiological characteristics and study of migrations to the study of features of the genome structure). Thus, Greenland and White Sea cod were considered to be different species [4]; they represented subspecies of a single species [1] and were reduced to a synonymy inside a single taxon [5]. At present, despite long-term efforts, the situation remains ambiguous. Thus, for example, their position was clarified using, among other things, the results of morphogenetic studies [6, 7], based on materials of Svetovidov [8]. This was reflected in the last version of electronic fish catalog of the California Academy of Sciences [9], where White Sea and Greenland cod are presented as subspecies level taxa: *Gadus morhua marisalbi* and *Gadus macrocephalus ogac*, respectively. However, international Internet resources (FishBase, FAO FishFinder, ITIS), based on the materials of Walters [10] and Cohen et al. [11], still do not recognize White Sea cod as an independent taxon, but perceive it as Greenland cod expanding its range in the eastern direction. Accordingly, there is no single sufficiently detailed idea about the peculiarities of the development of these taxa, stages, chronology, and factors and mechanisms of the effect on them.

The aim of the present work is to detect peculiarities of the development of modern structure of the *Gadus* genus based on the analysis of polymorphism of microsatellite loci using the methods of studying of genetic differentiation and Bayesian cluster analysis, taking into account the consideration of history of

ciers of areas in Greenland and the White Sea depression, all this speaks in favor of the fact that both White Sea cod and Greenland cod as reproductively independent groups were developed in the Late Holocene exactly under conditions of Subboreal cooling with colder conditions as compared with modern ones.

Discussing the level of gene differentiation from initial forms of Greenland and White Sea cod, one should note an almost double excess of this indicator in Greenland cod. As is known, two factors can be responsible for the gene differentiation value in the above listed populations: divergence time and gene migration level [50]. The first of the factors should not have a perceptible influence because of the similarity of the time of development of marine conditions and possible settlement of both Greenland fjords and the White Sea depression. Thus, higher values of the gene migration are responsible for a decrease in the gene differentiation between White Sea cod and its initial form (Atlantic cod). The effect of the Norwegian coastal current distributed in the northeast direction and passing through the mouth zones of Norwegian fjords and coastal waters of Western Murman and falling into White Sea in a complex with the Barents Sea feeding current (Deryugin current) can be one of the physical mechanisms of the gene migration on the basis of the limited transfer of the genetic material of Atlantic cod from the Norwegian–Barents Sea stock to the White Sea [51, 52].

Thus, using the genetic and hierarchical analyses, the scenario of the development of marginal groups of Greenland and White Sea cod, the development of the gene migration level, etc., was clarified; this makes it possible to confirm their taxonomic heterogeneity and subspecies status (*G. macrocephalus ogac* and *G.morhua marisalbi*, respectively).

Along with data on genetic analysis, the development of a reasonable scenario of the formation linked to geochronological, geological, climatic, and oceanological changes is an important moment during the establishment of taxonomic status. The presented results of genetic analysis not only support the scenario of the development of a two-species *Gadus* genus structure but also provide an opportunity to detail the peculiarities of the development of taxonomic hierarchy levels and to clarify the chronology of individual events. Thus, at the beginning of the Pliocene (initially after the first opening of the Bering Strait over the past 100 million years), the cod supergroup, which unites the North Atlantic, Arctic, and North Pacific populations, was apparently developed. Middle Pliocene regression, which led to the closing of the Bering Strait and a gap in the single range of cod, is a starting point (approximately 3.2–3.0 million years ago) of evolution of North Atlantic and North Pacific cod populations independent of each other. The presented materials deny other existing scenarios of the development of the *Gadus* genus: with monotypic and three-species structures [1, 9].

According to the results of genetic analysis, it was demonstrated that the formation of marginal groups adapted to arctic conditions represented by the subspecies level taxa (Greenland cod (*G. macrocephalus ogac*) and White Sea cod (*G. morhua marisalbi*)) occurred in the Late Holocene in a similar scenario, but in different regions and from different initial forms.

ACKNOWLEDGMENTS

This work was supported in part by the Russian Foundation for Basic Research (project no. 16-05-00317) (the laboratory processing of material, preparation of summary tables and manuscript); the laboratory analysis of the samples was supported by the Russian Science Foundation (project no. 14-50-00029 “Scientific Bases of Creation of National Depositary Bank of Living Systems”).

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