

Article

First Record of the Northern Wolffish *Anarhichas denticulatus* Krøyer, 1845 (Anarhichadidae: Zoarcoidei: Perciformes) in the Siberian Arctic: Further Evidence of Atlantification?

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Abstract: A single specimen of the northern wolffish *Anarhichas denticulatus* Krøyer, 1845, 393 mm in length, was documented for the first time in the Siberian Arctic (Laptev Sea, Russia). Species identification was confirmed by an integrative taxonomic approach that included examination of external morphology and DNA barcoding using the *COI* mtDNA gene. This species is widely distributed in the North Atlantic, but records in the Arctic Ocean are limited to the Canadian and US coasts. This record might represent a significant range extension of about 7500 km for the species and may be associated with the eastward transport of a pelagic juvenile specimen from the Northeastern Atlantic to the Laptev Sea by the North Atlantic current, consistent with the hypothesis of Atlantification of the Arctic Ocean. X-ray images of the Laptev Sea specimen and photographs showing ontogenetic variations of species' coloration are provided for reference. The Laptev Sea specimen had a more elongated shape, longer preorbital distance, and longer pectoral, dorsal, and anal fins, as well as a larger eye and wider caudal fin compared to North Atlantic samples. The size differences are likely associated with conditions experienced as a juvenile during the pelagic stage of the lifecycle.

Keywords: range extension; integrative taxonomy; morphometrics; *COI* mtDNA gene; Anarhichadidae; phylogeny; borealization; climate change; global warming; Laptev Sea; North Atlantic current



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1. Introduction

Climate changes, occurring in recent decades and most clearly manifested in the polar regions [1,2], are one of the most discussed environmental issues in recent years [3]. Warming in the Arctic Ocean has resulted in an increasing influence from the Atlantic Ocean, primarily through the transfer of heat by currents. The consequence of this influence is the elimination of differences in oceanic conditions between some Arctic areas and the North Atlantic [4–8]. This phenomenon has been described as Atlantification in the scientific literature [3,5,7,8], or less frequently, Atlantisation [9,10]. At the physical level, Atlantification manifests itself in the Arctic Ocean as increased advection of heat carried by

Atlantic Ocean waters, an increase in air and water temperature, a reduction of ice cover, earlier dates of ice retreat, a decrease in freshwater intake, and an increase in salinity [3,5,6]. In ecological terms, Atlantification leads to the transition of Arctic Ocean ecosystems to a more moderate state, also known as borealisation) [1,4,6,11,12]. This phenomenon is accompanied by a wide variety of effects, including a reduction in the species diversity of the Arctic fauna and the increased abundance of some invasive species. Ecosystems and communities may also become reorganized, with the change of dominant species from Arctic to boreal in most taxonomic groups from algae and invertebrates to higher vertebrates. Atlantification also results in the poleward extension of the ranges of boreal species and causes changes in food webs at all trophic levels [1–8,11–14]. The impact of Atlantification on individual fish species and fish communities in the Arctic has not been sufficiently studied. Most of the published information on this problem concerns the European Arctic (mainly the Barents Sea and Greenland waters) or the range extensions into Arctic waters of large boreal fish species capable of distant active migrations, such as Atlantic cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, beaked redfish *Sebastes mentella*, and Greenland halibut *Reinhardtius hippoglossoides* [3,12,15–18].

The family of wolffishes Anarhichadidae, according to modern concepts, includes two genera: *Anarhichas*, represented by four species, and *Anarrichthys*, represented by one species [19]. Two species, Bering wolffish *Anarhichas orientalis* and Pacific wolfeel *Anarrichthys ocellatus*, are widely distributed in the North Pacific. Atlantic (stripped) wolffish *Anarhichas lupus* and spotted wolffish *A. minor* are distributed exclusively in the North Atlantic and adjacent Arctic. Northern wolffish *A. denticulatus* is found in the North Atlantic and adjacent Arctic from Baffin Bay, Davis Strait, and off the northern Svalbard in the north to the Bay of Biscay in the south, and from the Gulf of St. Lawrence and New England in the west to Novaya Zemlya in the east. It is occasionally recorded in the Pacific Ocean sector of the Arctic in Chukchi and Beaufort Seas and off the western Canadian Arctic Archipelago [20].

The northern wolffish plays a significant role in the marine ecosystems of the North Atlantic. This species participates in trophic chains of various levels by feeding on planktonic organisms (mainly jellyfish and fish) during the pelagic period of life and consuming representatives of the bottom fauna (large benthos and bottom fish) as an adult [21–23].

In some areas, catches of this species can be quite significant, but its commercial value in comparison with other North Atlantic wolffishes is small due to the lower quality of the meat with high moisture content (90–92%) [20,21,24–26]. Nevertheless, the vitamin A content of the northern wolffish is higher compared to the spotted wolffish and Atlantic cod [21,25]. Currently, this species is fished only in Norway and Russia [20], but its fishing in the waters of Canada, where it is considered a threatened species, is prohibited [27–29]. In the past, the northern wolffish was caught as by-catch in trawl and longline fisheries and was discarded or used as bait in the Greenland halibut fishery [21,26].

At the same time, the northern wolffish among all North Atlantic *Anarhichas* species is the least studied one, especially in the pelagic period of the lifecycle [30,31], and its life cycle remains absolutely unexplored. In the published literature, there is no information about basic biological features, such as the timing of spawning, the location of spawning grounds, age, growth, etc. [32–34]. Data on fecundity (23,000 eggs obtained for females between 112 and 134 cm long) are limited by solitary observations in the Barents Sea [25,27,33]. Information about diet and feeding habits is limited to a single publication [35]. It is known that eggs, larvae, and juveniles of the northern wolffish develop in the water column, becoming adults after reaching a length of about 70 cm and transit to a benthic way of life [25,30,36]; however, the duration of the pelagic stage of the lifecycle is still unclear. The early juveniles of the northern wolffish from spawning grounds are carried out by eastward currents and subsequently with a countercurrent system can return to the habitats of adult individuals, where they switch from pelagic to bottom lifestyle [37]. The captures of northern wolffish pelagic juveniles are quite rare [32], especially outside the known range.

Thus, the goals of the paper are (1) to document the first Siberian Arctic record of the northern wolffish, (2) to discuss the reasons for finding the species far beyond the known range and (3) to describe the variations in the coloration of individuals.

2. Materials and Methods

A single juvenile specimen (not sexed), with a total length of 393 mm and body weight of 622 g, was collected on 12 September 2019 in the Laptev Sea (Figure 1). The specimen was taken from a bottom trawl catch (station No. 115) at $77^{\circ}20'06''$ N and $120^{\circ}12'18''$ E at 452 m depth during the Transarctic expedition on board R/V “Professor Levanidov” [33–35,38–40]. The specimen (IORAS 04472, Figure 2) is deposited in the fish collection of the Institute of Oceanology, Russian Academy of Sciences (IO RAS), Moscow, Russia. After capture, the specimen was measured and weighed, and subsequently frozen. After completion of the expedition, it was transported from Murmansk to Moscow for further morphometric and genetic analyses in the VNIRO laboratory.

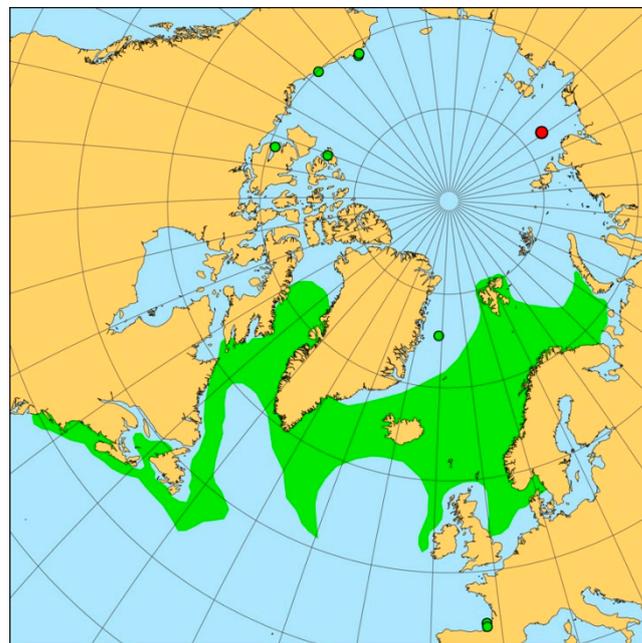


Figure 1. Range of the northern wolffish *Anarhichas denticulatus* (green shading) and occasional records outside of the main range (green circles) according to [20], and a new record of the species in the Laptev Sea (red circle, our data).

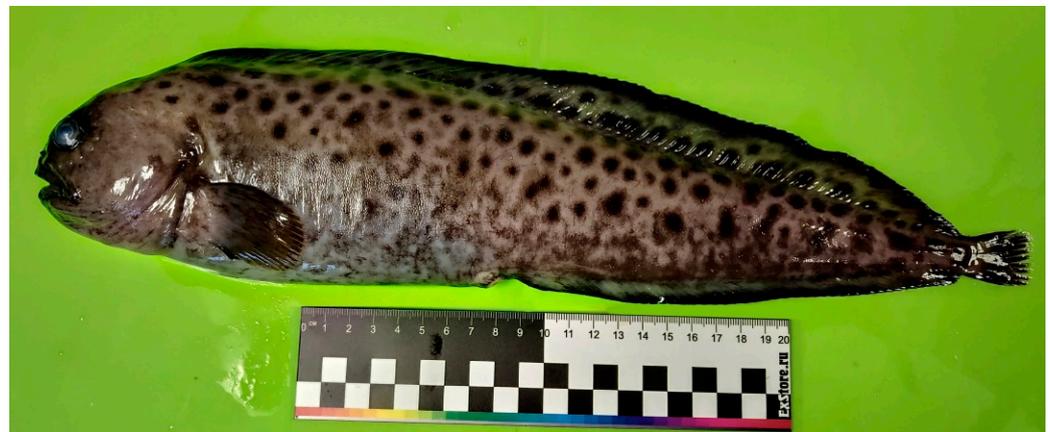


Figure 2. Specimen of the northern wolffish *Anarhichas denticulatus* with TL 393 mm (IORAS 04472) caught in the Laptev Sea (photo by A.M. Orlov, photographed just after capture).

Species identification was conducted with the use of an integrative taxonomic approach that included examination of external morphology and DNA barcoding. Identification of the specimen to species level was done using available ID keys and field guides [25,27,41]. Definitions of the morphological characters and measurements followed [28,42]. The following 17 morphometric characters were measured: total length, standard length, head length, preorbital length, postorbital length, interorbital distance, eye horizontal diameter, upper jaw length, body depth at dorsal-fin origin, body depth at anal-fin origin, predorsal length, caudal peduncle depth, dorsal fin length, pectoral fin length, pectoral fin width, anal fin length, caudal fin length, and caudal fin width. All measurements were taken on the thawed specimen using a digital caliper. The following five meristic characters were counted: dorsal fin rays, pectoral fin rays, caudal fin rays, anal fin rays, and total vertebrae. Rays in unpaired fins and vertebrae were counted from radiographs (Figure 3) produced on an EcoRay Orange 1040 HF Portable X-Ray Generator (EcoRay, Seoul, Republic of Korea).

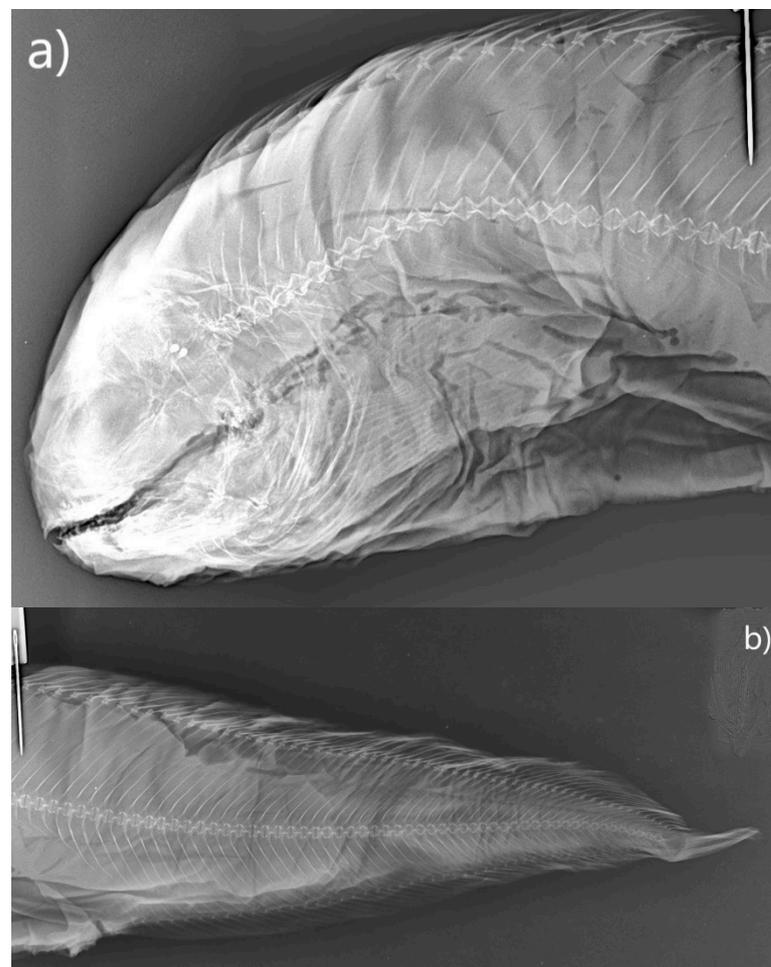


Figure 3. Radiograph of the Laptev Sea northern wolffish *Anarhichas denticulatus* specimen: (a) front part; (b) rear part.

The tissue samples used for genetic analysis are listed in Table 1. All tissue samples were preserved in volumes of 96% ethanol at least five times larger than the sample volume. Fixed samples were stored at $-20\text{ }^{\circ}\text{C}$; ethanol was changed approximately one month after collection and again after one year. DNA was extracted using the Wizard SV 96 Genomic DNA Purification System (Promega Corporation, Madison, WI, USA) according to the manufacturer's manual. All molecular genetic studies (DNA extraction, polymerase chain reaction (PCR), PCR product purification, and nucleotide sequencing) were per-

formed using standard molecular genetic techniques [43]. Cytochrome oxidase subunit I (COI) fragment was amplified with a primer complex of VF2_t1, FishF2_t1, FishR2_t1, and FR1d_t1 [43,44]. Amplification was conducted in a volume of 15 μL with 90 ng total DNA, buffer (1 \times) consisting of 2.5 mM MgCl₂, 0.2 mM dNTP, 0.5 mM of each primer, and 0.75 U μL^{-1} Color Taq polymerase. Cycling consisted of 5 min at 95 °C, followed by thirty-five cycles of 30 s each at 95 °C, 45 s at 52 °C, 60 s at 72 °C, and a final extension for 12 min at 72 °C. All resulting amplicons were purified by ethanol precipitation [45]. Purified fragments were sequenced from both strands by using Applied Biosystems BigDye Terminator v3.1. kit (Applied Biosystems, Foster City, CA, USA) with capillary electrophoresis on an ABI3500 Genetic Analyzer (Thermo Fisher Scientific, Waltham, MA, USA) in the VNIRO Laboratory of Molecular Genetics. The resulting sequences were assembled in Geneious 6.5.0 software (Biomatters, Auckland, New Zealand) and aligned using the “ClustalW” built-in algorithm [46]. The “postfix” was set to the maximum desired length after trimming off 615 bases, and any leading and trailing ambiguous bases were also removed. Any sequences whose lengths were less than 615 bp were considered failures and were removed from the analysis. Next, the bidirectional sequences were assembled into contigs (with default settings using dirty data algorithm, realigner, and prefer 3gap placement, as well as a 20-base minimum overlap and an 85% minimum match percentage). At this point, if any contig contained >2% ambiguities, those samples were also removed. Any remaining single-read sequences were used if their quality value was better than 98%. The resulting sequences were subsequently translated into the necessary format to construct a haplotype network in the PopArt program (Allan Wilson Centre Imaging Evolution Initiative, Otago, New Zealand) [47]. The FaBox 1.41 converter was used to convert the fasta file to the format required for calculation [48]. A network of haplotypes was constructed based on the maximum parsimony method using TCS v.1.21 software (Computational Science Laboratory, Provo, UT, USA). DnaSP v. 5.10.01 software (University of Barcelona, Barcelona, Spain) was used for the analysis of the average number of nucleotide substitutions and the number of haplotypes in samples [49].

Table 1. Information about COI sequences and respective samples used for molecular analysis.

Specimen Number	Group	Species	GenBank Accession Number	Capture Area
1	Main group	<i>Anarhichas denticulatus</i>	NBMF210-17	Norway, Svalbard
2			GLF059-14	Greenland
3			CMNAF082-06	Canada, Davis Strait
4			OQ913876	Laptev Sea
5		<i>Anarhichas lupus</i>	DSFIB479-13	Barents Sea
6			GLF062-14	Greenland
7			SCFAD157-09	Canada, Davis Strait
8	Sister group	<i>Anarhichas minor</i>	CMNAF004-06	Canada, Davis Strait
9			SCAFB970-07	NW Atlantic, Flemish Cap
10			NBMF071-15	Norway, Svalbard
11			<i>Anarhichas orientalis</i>	DSFIB108-11
12			DSFIB278-13	USA, Chukchi Sea
13		<i>Anarrichthys ocellatus</i>	FMV172-08	USA, Washington
14			GBMNE4254-21	USA, Washington
15	Outgroup	<i>Lycodes toyamensis</i>	GBGCA4720-13	Korea

Data processing was performed, and genetic distances and percent identity were calculated using Geneious 6.0.5 software (Biomatters, Auckland, New Zealand) based on the Bayesian Inference method with *Lycodes toyamensis* as the outgroup [50] with the use of a Substitution Model HKY85; 1,100,000 chain length; and 100,000 burn-in-length [51].

Data on the *COI* sequences of the congeners and outgroup of a Laptev Sea specimen were taken from the open BOLD Systems database (<https://www.boldsystems.org/>, accessed on 14 March 2023).

3. Results

Morphological description

Morphometrics and meristics are presented in Table 2. The body is strongly flattened. The head is large (more than 19% SL) and noticeably pointed to the snout. The eye is large, its diameter is 3.5% SL. The dorsal and anal fins are long, their length is 89.7% and 50.4% SL, respectively, the number of rays is 80 and 49, respectively, and the ends of unpaired fins are almost closely adjacent to the base of the caudal fin. The pectoral fins are rounded, relatively small, with 19 rays, and their length is 12.3% SL. The caudal fin is almost truncated, almost twice as short as the head (8.3% SL), with 22 rays.

Table 2. Morphometrics and meristics of northern wolffish specimens collected in the Laptev Sea and North Atlantic (NA—not available; characters of the Laptev Sea specimen deviated from those known from the literature are shown in bold).

Character	Northwestern Atlantic [52]	Northwestern Atlantic [31]	Bay of Biscay [42]	Barents Sea [24]	Barents Sea [25]	Laptev Sea [This Study]
Total length, mm	265	48–350	1095–1110	NA	NA	393.0
Total weight, g	NA	NA	12,751–14,360	NA	NA	622
Standard length (SL), mm	NA	NA	1035–1055	NA	NA	359.0
			Morphometrics, % SL			
Head length	19.6	20.08–26.1	20.7–20.8	NA	16.8–18.0	19.4
Preorbital length	NA	NA	4.2–4.8	NA	NA	6.2
Postorbital length	NA	NA	12.9–14.1	NA	NA	13.4
Interorbital distance	NA	NA	3.0–5.3	NA	NA	4.9
Eye horizontal diameter	NA	NA	2.4–3.0	NA	NA	3.5
Upper jaw length	NA	NA	NA	NA	NA	9.3
Body depth at D origin	20.0	19.1–28.4	NA	NA	NA	25.8
Body depth at A origin	18.1	13.5–24.0	NA	NA	NA	23.9
Predorsal length	17.4	16.7–24.2	16.2–20.3	NA	14.9–18.2	20.6
Preanal length	51.0	43.0–56.9	50.2–52.0	NA	49.1–55.2	49.3
Caudal peduncle depth	4.0	3.3–6.1	NA	NA	NA	3.6
Dorsal fin length	NA	NA	81.1–84.1	NA	NA	89.7
Pectoral fin length	10.6	10.3–14.4	NA	<12.0	NA	12.3
Pectoral fin width	NA	NA	13.0–13.8	NA	NA	10.8
Anal fin length	NA	NA	40.8–42.5	NA	NA	50.4
Caudal fin length	7.4	7.8–10.9	NA	NA	NA	8.3
Caudal fin width	NA	NA	6.8–8.7	NA	NA	6.1
			Meristics			
Dorsal fin rays	79	NA	77	77–80	76–81	80
Pectoral fin rays	20	NA	22	20–22	19–21	19
Caudal fin rays	21	NA	18	NA	19–22	22
Anal fin rays	49	NA	42	45–47	46–50	49
Total vertebrae	81	NA	NA	79–81	78–82	78

The teeth on the jaws are pointed and widely spaced (Figure 4). The lateral teeth of the outer row on the lower jaw and the palate are canine-shaped, with curved tops. The vomerine row of teeth is short.



Figure 4. Front view of the head of the Laptev Sea northern wolffish *Anarhichas denticulatus* specimen (photo by A.M. Orlov).

Coloration

The specimen caught in the Laptev Sea has a spotted coloration (Figure 2). The main background of the body is gray. Dark brown spots of irregular shape and various sizes are randomly distributed mainly in the upper part of the trunk from the origin of the base of the dorsal fin to the end of the caudal peduncle. The lower part of the body has marble stains, lighter than the spots in the front part of the body, and of the same intensity in the rear part. There are no spots on the head, anal, pectoral, and caudal fins. A dark border runs along the outer edge of the dorsal and anal fins. There are spots in the central and lower part of the dorsal fin, which sometimes merge with each other. The caudal fin is monotonously dark. The base of the pectoral fins is lighter as compared to the distal part. The front part of the head is colored darker than its rear part.

Genetic analysis

The results of a comparative genetic analysis of the sequences of northern wolffish mtDNA *CO1* gene fragments from different regions show that there were no principal differences between various samples (Figure 5). *Lycodes toyamensis* selected as an outgroup represented a separate branch from all representatives of the Anarhichadidae family. Individuals of northern wolffish, Atlantic wolffish, spotted wolffish, and Bering wolffish formed independent clusters that were well-separated from the monotypic genus *Anarrichthys* represented by the single species of Pacific wolfeel. At the same time, northern wolffish and Bering wolffish were both well-differentiated from clusters consisting of Atlantic and spotted wolffishes. It should be noted that northern wolffish samples did not form separate clusters according to the geographical principle and were mixed with each other. Thus, the nucleotide sequences of samples from Svalbard (Norway), Davis Strait (Canada), Greenland, and the Laptev Sea were very close to each other. Genetic similarities between them were 99.8–100.0%.

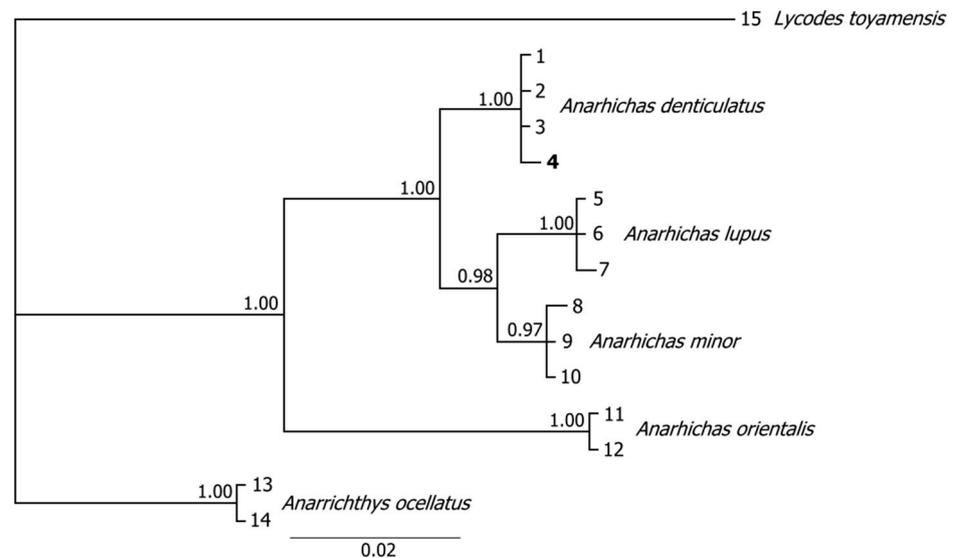


Figure 5. Tree topology reconstruction of the Laptev Sea northern wolffish *Anarhichas denticulatus* specimen, its congeners, sister group, and outgroup based on the Bayesian Inference Substitution Model HKY85; 1,100,000 chain length; and 100,000 burn-in-length for mitochondrial cytochrome oxidase subunit I (*COI*) genes. Numbers beside each branch indicate bootstrap values. The Laptev Sea specimen is shown in bold. Numbers to the right of the branches correspond to the number of specimens in Table 1.

4. Discussion

Morphology

The specimen from the Laptev Sea, as a whole, according to its external morphological characters, corresponds well to the descriptions given in many published sources [20,24–27,30,31,41,42,52–54]. At the same time, some morphometric features of our specimen go beyond those known in the literature (Table 2). In comparison with large individuals that are 1095–1110 mm long [37], it has a larger preorbital distance (6.2% SL vs. 4.2–4.8% SL) and an eye diameter (3.5% vs. 2.4–3.0%), longer dorsal (89.7% vs. 81.1–84.1%) and anal (50.4% vs. 40.8–42.5%) fins, but the pectoral fin was shorter (10.8% vs. 13.0–13.8%) and the caudal fin was narrower (6.1% vs. 8.7%). The most probable and main reason for such differences is the change in the proportions of the body during ontogenesis due to the change of biotope, specifically the transition from a pelagic to a benthic lifestyle. Barsukov [52] noted that in the juveniles of the species considered, the head, pectoral fin, and eye diameter are slightly larger in comparison with adults. Grigor'ev [31] also pointed out the change in some morphometric characters with body length. Another possible reason for the differences between the data we received and the published ones might be associated with the fact that we carried out all morphometric measurements on a defrosted specimen, not preserved in formalin. Meanwhile, it is known [37] that due to the watery consistency of northern wolffish tissues, its size significantly decreases after preservation with formalin (on average by 16.7%) in contrast to freezing (on average by 5.9%).

Coloration

The body coloration of the northern wolffish has been described in a number of publications [20,21,24,25,30,31,37,52,55,56]. However, the description of coloration there, as a rule, is presented for some single stages of the lifecycle (early pelagic juveniles or benthic adults). The description of the coloration of a one-year-old adolescent juvenile 26.5 cm long is only presented in a single paper [52].

The coloration of fishes may vary very much and can change due to stress, background color matching, and death [55]. Some fishes manifest ontogenetic changes of coloration as

well [56]. The lifecycle of the northern wolffish is characterized by the pelagic stage of eggs, larvae, and juveniles with the subsequent transition of adults to a benthic way of life after reaching about 70 cm in length [25,30,36]. Naturally, during such a long period of time and the change of biotopes, the coloration of individuals of the northern wolffish should undergo significant changes. The material at our disposal from the waters of the North Atlantic (Greenland, the Mid-Atlantic Ridge) and the Arctic (the Laptev Sea), along with the published data, allows us to present the ontogenetic and other changes in the coloration of the northern wolffish in great detail. In early juveniles 2.5–2.6 cm long, there are no spots on the body [25,53]. The coloration of young northern wolffish is similar to that of adult individuals [31,37]. The spots are not pronounced in juveniles 5–9 cm long [20,31]; however, they appear on the back and flanks after fixation with formalin, sometimes forming transverse stripes on the trunk and in the front half of the tail [31]. According to [37], the formation of spots in juvenile northern wolffish occurs when reaching a length of 8–9 cm, which is not confirmed by a photograph of an individual 8.1 cm long [20] that has a monotonous, almost black, coloration without spots and with transparent pectoral and caudal fins. The young specimen caught by us in the waters of Greenland about 11 cm long (Figure 6a) had a general brownish coloration with a darker head, back, and belly. On the back and the rear side of the body, there were rare irregularly shaped spots of slightly darker color as compared to the main body coloration. The pectoral and caudal fins were transparent. A dark transverse stripe was clearly visible in the front half of the tail.

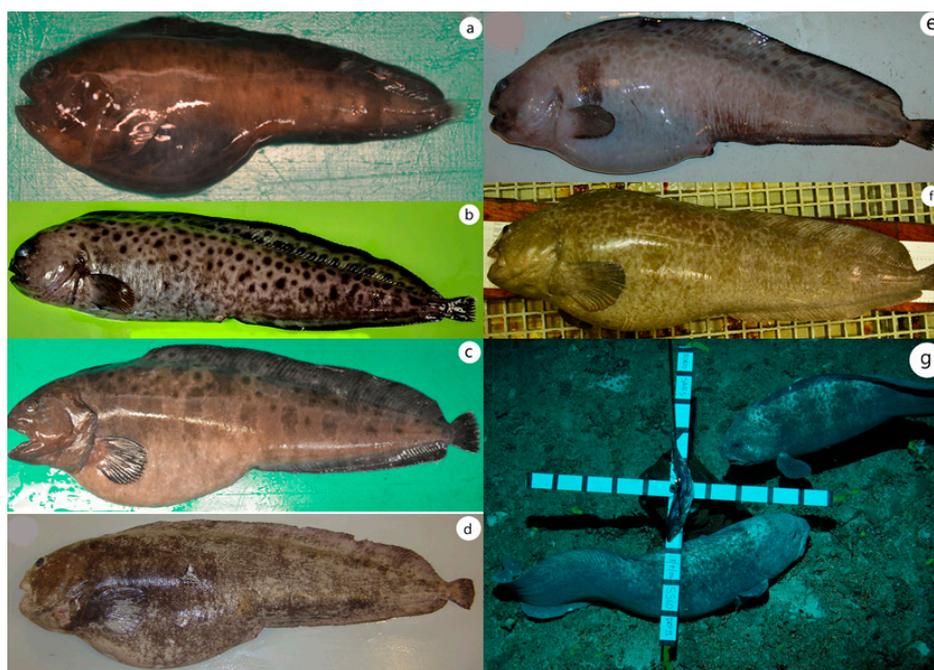


Figure 6. Specimens of the northern wolffish *Anarhichas denticulatus*: (a,c,d) caught by bottom trawl in Greenland waters in 2013 onboard R/V “Paamiut” 11.4, 55.8 and ~98 cm long, respectively (photos by A.M. Orlov, photographed just after capture); (b) specimen 39.3 cm long from the Laptev Sea (photo by A.M. Orlov, photographed just after capture); (e,f) caught by fish trap during 2004 MAR-ECO cruise on board R/V “G.O. Sars” off the Mid-Atlantic Ridge weighed 18.3 kg and ~30 kg, respectively (photos from MAR-ECO project archive, photographed just after capture); (g) photographed underwater by “ROBIO” lander ~100 cm long (photo courtesy Oceanlab, the University of Aberdeen, Scotland).

The coloration of our specimen from the Laptev Sea (Figures 2 and 6b) turned out to be very close to that of an individual with a length of 26.5 cm [52] and two specimens with a length of 51–66 cm [20], with some differences. In the specimens mentioned above, the spots are comparable in size to the eye diameter, while in our specimen, spots of such size were very rare (in the central part of the posterior half of the trunk). In an individual

26.5 cm long, the distal edges of the pectoral and caudal fins were light [52], in contrast to individuals with a length of 39–66 cm [20] [our data], whose pectoral and caudal fins were dark. Another characteristic phenetic feature of our specimen and individual 66 cm long [20] was the presence of marble coloration of the abdomen and the remaining lower part of the trunk, which is also occasionally observed in adults [30].

It is believed that individuals of the species considered spend a very long time in the water column [57], and transition to a benthic lifestyle occurs once reaching 60–70 cm in length [21,25,30,36]. Nevertheless, the coloration of the pelagic juveniles can vary significantly. Thus, a specimen caught by us in the waters of Greenland about 56 cm long (Figure 6c), in addition to spots in the upper part of the trunk, had ten more transverse stripes on the flanks.

More is known about the coloration of adult northern wolffish; however, even among individuals with a benthic lifestyle, there are specimens with uncharacteristic coloration. The coloration of adults is most often described as monophonic dark (Figure 6d) from grayish-brown to almost chocolate, sometimes with obscure vague dark spots [20,21,24,25,27,30]. A rather rare exception is spotted individuals or those with marble coloration [30,54]. At the same time, Barsukov [30] notes that the spots in adults are less bright compared to juveniles. A specimen with such coloration was, for example, caught in the waters of the Mid-Atlantic Ridge (Figure 6f). Spotted individuals of the northern wolffish 65–73 cm long caught in the northwestern Atlantic at a depth of 450–460 m [54] had bright small spots on their bodies. Since this paper did not specify the fishing gear that captured these specimens, judging by their size and coloration, it is most likely that they had not yet transitioned to a benthic lifestyle. Another rare variation of color is marble [30], as, for example, documented in a 98 cm long specimen from the waters of the Mid-Atlantic Ridge (Figure 6e). Finally, the rarest variation in the coloration of an adult northern wolffish, which is not reported in published sources, is the presence of transverse stripes on the body. Such stripes, along with spots, are clearly visible on the body of one of the wolffish about 1 m long in an underwater photograph taken by the ROBIO lander in the waters of the Mid-Atlantic Ridge (Figure 6g).

Distribution

Among the North Atlantic wolffishes, the northern wolffish is the most widely distributed species [30]. It is found in the North Atlantic and adjacent Arctic from Baffin Bay, Davis Strait, and off the northern Svalbard in the north to the Bay of Biscay in the south, and from the Gulf of St. Lawrence and New England in the west to Novaya Zemlya in the east [20,58]. It is occasionally recorded in the Pacific Ocean sector of the Arctic in Chukchi and Beaufort Seas and off the western Canadian Arctic Archipelago [20]. Our specimen caught in the Laptev Sea represents the first record of the species in the Siberian Arctic, at a distance of about 7500 km from the border of the known range.

Among all the North Atlantic wolffishes, the northern wolffish is found at the greatest depths [21], possibly down to 1500 m [27]. It is believed that juveniles spend a long time in the water column [57], but there are different points of view regarding its specific habitats. Barsukov [25] believed that it inhabits great depths above the continental slope, while Ponomarenko [36] suggested that during this period of its lifecycle, it lives in a bathypelagial at great depths far from the coasts. The results of recent studies [58] have shown that juvenile northern wolffishes with a length of 2.5–60 cm are found in trawl catches in a wide range of depths from the surface to 1483 m, mainly above the continental slope, but also occasionally observed far from the coasts. However, there is no certainty that these specimens were not caught at shallower depths during the lifting of the trawl since the catches were carried out with non-locking fishing gear. Our specimen in the Laptev Sea was also caught at a great distance from the coast at a depth of 452 m. However, given that the trawling was carried out by a bottom trawl, it is quite likely that this specimen was caught in the water column during the lifting of the fishing gear. Thus, the habitat depths of the juvenile northern wolffish remain not fully understood, which requires additional research with the use of closing mid-water trawls.

One of the possible reasons for the record of juvenile northern wolffish in the Laptev Sea may be through ballast water discharge, which is one of the main vectors of invasion of alien species [59,60]. However, in our opinion, this reason for the northern wolffish record is highly unlikely. The shipping traffic in the Laptev Sea and the neighboring Kara Sea is significantly lower in comparison with the Barents Sea and the North Atlantic. In addition, the vast majority of the vessels operating in the Siberian Arctic are Russian and, as a rule, do not make long cruises between the North Atlantic and the seas of the Siberian Arctic [61,62]. In the future, with the intensification of navigation along the Northern Sea Route, the invasion of alien species into the Siberian Arctic with ballast water may become quite real.

The main reason for the captures of pelagic juveniles far from the coasts is considered to be their north-eastward transport by currents from spawning grounds, the localization of which is not fully understood [37]. Atlantic waters in the Arctic Basin move from west to east. The inflow of waters from the Atlantic occurs in two branches: through the Barents Sea and the Fram Strait [63,64]. The Barents Sea branch of the Atlantic waters runs between Novaya Zemlya and Franz Josef Land, from where it enters the Kara Sea and then through St. Anna Trench into the Arctic Basin. Meeting north of the Kara Sea, these branches interact with each other, gradually mixing and forming the Arctic Circumpolar Boundary Current [63,64]. The distribution of Atlantic waters from the Fram Strait to the Novosibirsk Islands takes about two years, and in the area of the Lomonosov Ridge, their age is estimated at three years [65]. There are no data on the age of the northern wolffish in the literature [34], and its spawning grounds are unknown [37]. Therefore, it is impossible to determine how much time a juvenile northern wolffish can spend in the water column during transportation by currents. Based on the age of Atlantic waters and the fact that pelagic juveniles are most often observed east of Greenland over the continental slope from Svalbard to the Norwegian coast [58], it can be assumed that they can reach the Laptev Sea from the northeastern Atlantic for several (at least three) years. We hypothesize that the specimen caught in the Laptev Sea could have been carried out from the spawning grounds by the North Atlantic current as a result of the recent climate change, which has significantly increased in intensity since 2000, transferring more heat to the northeastern Atlantic and the adjacent Arctic [6]. Thus, the discovery of pelagic juvenile northern wolffish in the Laptev Sea could serve as confirmation of the ongoing Atlantification of the Arctic. Shevelev and Kuz'michev [37] noted that as pelagic juveniles grow, they can return to the nursery and spawning grounds with countercurrents. It is premature to judge whether the Siberian Arctic should be considered a sterile zone of eviction of North Atlantic species. This requires further research and data accumulation.

Genetics

The results of genetic studies of the Anarhichadidae family representatives are few and have been performed using various genetic markers [50,66–69]. At the same time, most of the previous phylogenetic studies did not involve all five valid species of the family. An exception in this regard is the paper [67], in which all representatives of the family were analyzed using the control region of mtDNA (*D-loop*) and the nuclear gene *ND1* as genetic markers.

Previous studies [50,67,69] have shown a greater genetic proximity to each other of *A. minor* and *A. lupus* than each of these two species to *A. denticulatus* (Figure 5). In all the above publications on phylogenetic trees, the northern wolffish forms a cluster separate from other North Atlantic species, which is confirmed by our results. At the same time, *A. minor* and *A. lupus* differ in nine nucleotide substitutions (the level of genetic similarity 98.2–98.5%), and the closest species to *A. denticulatus* is *A. minor* separated by 13 mutations (similarity 97.6–97.9%) (Figure 7). The Bering Sea wolffish *A. orientalis* on similar schemes is genetically well-separated from North Atlantic species [55], which is confirmed by our results. The nucleotide sequences of all North Atlantic wolffish have a very similar composition to those of *A. orientalis* (93.3–94.5%), but the most genetically close to the latter species is probably *A. minor* separated by 34 nucleotide substitutions. The monophyletic

genus *Anarrichthys* with a single species *A. ocellatus* stands apart from the genus *Anarhichas* representatives [67,69], which is also reflected in our results. At the same time, according to the results of a phylogenetic analysis based on the mtDNA control region and the *ND1* nuclear gene [67], it was concluded that the wolfeel is genetically closer to the North Pacific Bering wolffish than to the North Atlantic wolffishes. This conclusion is not confirmed by our results since the level of genetic similarity between *Anarrichthys ocellatus* and *Anarhichas orientalis* is 92.2–92.7%, while the similarity between the first species and North Atlantic wolffishes is from 92.5 to 92.8%. At the same time, the minimum number of nucleotide substitutions (44) is recorded between *Anarrichthys ocellatus* and *Anarhichas lupus*.

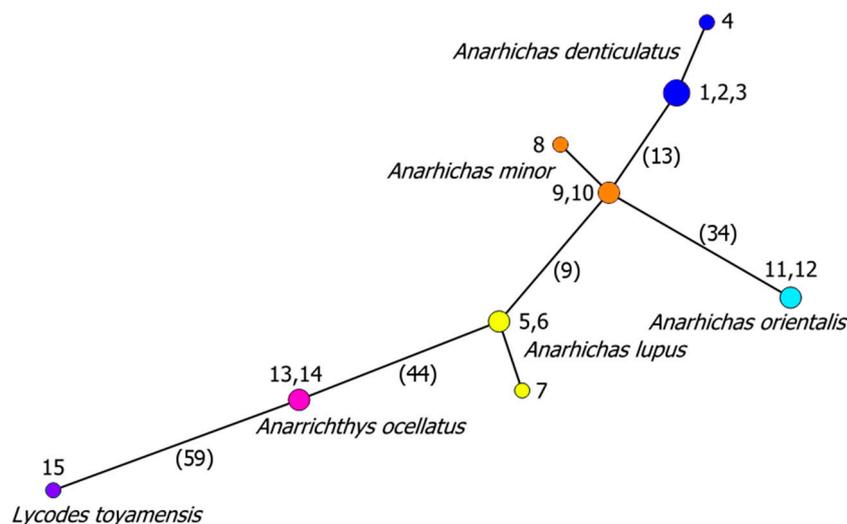


Figure 7. Phylogenetic relationships of the Anarhichadidae family by *COI* mtDNA sequences. Numbers indicate specimens (see Table 1 for explanation), numbers of substitutions are given in parentheses, and the size of circles corresponds to the number of specimens.

It should be noted that North Atlantic wolffishes are characterized by low genetic diversity and low population differentiation [67,68], which is not typical for many other marine fishes (e.g., [70–73]). The materials analyzed by us, although few in number, confirm the previous conclusions [68]. Intraspecific differences in the nucleotide sequences of *A. minor* and *A. lupus* from remote parts of the ranges did not exceed one mutation. The nucleotide sequences of the *A. denticulatus* specimen from the Laptev Sea also differed from those from the waters of Svalbard, Greenland, and Davis Strait by only a single substitution. The reason for such a low mtDNA polymorphism of the northern wolffish is associated with the peculiarities of its population structure, which in turn is due to the lifestyle of the species considered [74]. According to [37], the early juveniles of the northern wolffish from spawning grounds are carried out eastward and subsequently with a countercurrent system can return to the habitats of adult individuals, where they switch from pelagic to bottom lifestyle. Such a scheme, in our opinion, could lead to the presence of panmixia (e.g., [75–78]). However, McCusker and Bentzen [67] using microsatellite loci showed the presence of genetic differences between samples from the Barents Sea and the rest of the North Atlantic. This may probably mean the presence of at least two separate populations in this region. Our study did not reveal any differences between samples since mitochondrial DNA has a lower resolution in population structure analysis as compared to microsatellite loci [79–81].

5. Conclusions

The results of our study document the first discovery of a northern wolffish in the Siberian Arctic (Laptev Sea, Russia) far beyond the known range. This record might represent a significant range extension of about 7500 km for the species. It is unlikely that this capture is accidental. Most likely this record is caused by the transfer of pelagic

juvenile northern wolffish from spawning grounds in the northeastern Atlantic to the Arctic by Atlantic waters, the intensity of which has increased significantly in recent years due to climatic changes. Thus, this capture could serve as confirmation of the ongoing Atlantification of the Siberian Arctic. This process is accompanied by the penetration of boreal species into the Arctic not only from the Atlantic but also from the Pacific Ocean, including a decrease in the abundance of native species, an increase in the number of invasive species, structural rearrangements of communities and trophic chains. Further warming in the Arctic is fraught with the extinction of some species of Arctic fauna and a partial loss of global biodiversity.

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