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Walleye Pollock *Gadus chalcogrammus*, a Species with Continuous Range from the Norwegian Sea to Korea, Japan, and California: New Records from the Siberian Arctic

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Abstract: The first records of walleye pollock *Gadus chalcogrammus* Pallas, 1814 in the seas of the Siberian Arctic (the Laptev Sea, the Kara Sea, the southeastern Barents Sea), are documented. Information about the external morphology (morphometric and meristic characters), photos of sagittal otoliths and fish, and data on the sequences of the *CO1* mtDNA gene are presented. The results of a comparative analysis indicate that walleye pollock caught in the Siberian Arctic do not differ in principle from North Pacific and North Atlantic individuals. Previous conclusions about the conspecificity of the walleye and Norwegian pollock *Theragra finnmarchica* are confirmed. New captures of walleye pollock in the Siberian Arctic allow us to formulate a hypothesis about its continuous species' range from the coasts of Norway in the North Atlantic to the coasts of Korea, Japan, and California in the North Pacific. The few records of walleye pollock in the North Atlantic originate from the North Pacific due to the transport of early pelagic juveniles to the Arctic by currents through the Bering Strait and further active westward migrations of individuals which have switched to the bentho-pelagic mode of life.

Keywords: Norwegian pollock *Theragra finnmarchica*; size; maturity; morphology; mtDNA *CO1* gene; Arctic; North Atlantic; North Pacific

1. Introduction

Walleye pollock *Gadus chalcogrammus* Pallas, 1814 is the most widespread bentho-pelagic fish species of the North Pacific [1,2]. Its range extends from the Chukchi Sea in the north to the waters of Korea, Japan, and California in the south [3–5]. There are also occasional records of this species in the North Atlantic and adjacent Arctic, including the Norwegian and Barents seas [6,7]. Walleye pollock is a valuable commercial species, occupying a leading position in terms of catch both in the North Pacific and in world fisheries as a whole [8–12]. In addition, it plays an important role in the ecosystems of the

North Pacific, participating in various trophic chains from invertebrates as consumer to predatory fish, marine mammals and birds as prey [1,2,13].

For more than a century since the description of walleye pollock as a species, its taxonomic position has been repeatedly revised. Thus, it was originally described by Pallas [14] within the genus *Gadus* from a specimen from the Sea of Okhotsk off the coast of Kamchatka as *G. chalcogrammus*. About sixty years later, from the waters of Alaska near the Unalaska Island, Cope [15] described the species *Gadus periscopus*. Afterwards, Steindachner and Döderlein [16] described a new species *Gadus minor* from the waters of Japan near Tokyo. A few years later, Jordan and Gilbert [17] described a subspecies *Pollachius chalcogrammus fucensis* from the waters of Puget Sound (near Tacoma, Washington, USA), which Jordan and Evermann [18] subsequently placed in the genus *Thergara* and provided it with the status of a valid species *Theragra fucensis*. All these taxa were described from the waters of the North Pacific and are now recognized as junior synonyms of *Gadus chalcogrammus* [3,19,20]. In the mid-1950s, the Norwegian pollock *Theragra finnmarchica* Koefoed, 1956, was described from the waters of northern Norway (near Berlevåg) [21], which was long considered a valid species. Since its description, several dozen captures have been recorded in the Norwegian and Barents Seas [7,22–24]. Only with the widespread use of genetic analysis methods in ichthyology did it become possible to show the conspecificity of the walleye and Norwegian pollocks [25–29] and restore the validity of the *Gadus chalcogrammus* species.

Along with the change in taxonomic status, the ideas about the range of walleye pollock also changed. After the description of the Norwegian pollock, it was long believed that the genus *Theragra* is represented by two species (*T. chalcogramma* and *T. finnmarchica*) with ranges, respectively, in the North Pacific and the North Atlantic off the coast of Norway [30,31]. After the recognition of the Norwegian pollock as a junior synonym of the walleye pollock, it became clear that the range of this species is interrupted in the Siberian Arctic. At the same time, it is believed that there is an independent population in the Norwegian and Barents seas [6], which can be replenished by individuals from the North Pacific. However, there is another point of view [5], according to which the few records of walleye pollock in the North Atlantic are the result of the transport of its pelagic progeny by currents from the North Pacific to the Arctic through the Bering Strait and further active migrations into the Norwegian and Barents Seas. Thus, until now, there were no data on the occurrence of walleye pollock in the Siberian Arctic, so that it was not possible to draw reliable conclusions about the status of this species in the waters of the Northeast Atlantic. Meanwhile, this problem is important for understanding such evolutionary processes as speciation, distribution, population formation, etc.

The purpose of this paper is to document the first records of walleye pollock in the Siberian Arctic (southeastern Barents Sea, Kara Sea and Laptev Sea) testified with the data on external morphological characters, sequences of the *CO1* mtDNA gene, X-rays of fish, and photos of fish and sagittal otoliths.

2. Materials and Methods

This paper is based on new records of walleye pollock individuals in the southeastern Barents Sea in 2018, the Kara Sea in 2008, and the Laptev Sea in 2019 (Table 1) on board various Russian research and commercial fishing vessels. A total of 14 specimens were caught. New records of walleye pollock in the Siberian Arctic were obtained outside of its known range. One individual was caught in the southeastern Barents Sea to the north of the Kolguev Island (Figure 1). The capture of 9 more specimens was first recorded in the Kara Sea between the Franz Josef Land and Severnaya Zemlya archipelagos. Also, for the first time, this species was registered in the Laptev Sea to the northeast of the Taimyr Peninsula.

Walleye pollock captures in the Siberian Arctic were recorded in a wide range of depths from 42 to 603 m. The shallowest catch (42 m) was recorded in the southeastern Barents Sea, and the deepest (603 m) in the Laptev Sea. According to the capture depth, the Kara Sea (383 m) occupies an intermediate position.

Table 1. Data on new captures of walleye pollock *Gadus chalcogrammus* in the Siberian Arctic (M = male, F = female, na = not available).

Vessel/Gear	Date	Latitude, N	Longitude, E	Depth, m	Total Length, cm	Weight, g	Sex	Maturity Stage	Liver Weight, g	Gonad Weight, g	Food Weight, g	Age, Years
Barents Sea												
FV “Kotoyarvi”/longline	06.12.2018	69°31′50″	47°25′30″	42	77	2930	M	3–4	120	90	0	13+
Kara Sea												
RV “Obva”/bottom trawl	02.09.2008	82°00′00″	77°08′00″	383	35	310	F	3	18	8	12	5+
					43	530	F	4	21	16	17	7+
					41	452	F	3	14	8	8	6+
					41	495	F	4	16	34	5	7+
					40	474	F	4	36	27	4	6+
					42	420	F	4	12	14	2	6+
					37	360	M	4	18	13	19	5+
					34	250	F	3	12	4	0	5+
					33	230	F	2	9	2	4	4+
Laptev Sea												
RV “Professor Levanidov”/bottom trawl	12.09.2019	77°18′54″	122°44′12″	603	32	195	na	na	na	na	na	na
					34	247	na	na	na	na	na	na
		77°20′06″	120°12′18″	452	35	272	na	na	na	na	na	na
	13.09.2019	77°54′06″	115°52′36″	408	32	216	na	na	na	na	na	na

Figure 1. Map of walleye pollock *Gadus chalcogrammus* range (green shading) and its new records in the Barents Sea (★), Kara Sea (▲), and Laptev Sea (⊕).

All biological work was carried out in accordance with generally accepted methods [32,33]. In all fish, the total length (*TL*) and body weight were measured. In individuals from the Barents and Kara seas, the sex, the stages of gonad maturity, the weight of the liver, gonads, and stomach contents were additionally determined, and the age was examined by sagittal otoliths. Sagittae were extracted from freshly caught fish during the biological analyses onboard. The age determinations were carried out in the laboratory. Sagittae were broken transversely in half with a lancet and baked, then polished if necessary. They were burned in the flame of an alcohol burner. For the preparation of polished cross-sections of the sagittae, abrasive discs with aluminum-oxide- or silicon-carbide-coated grit of 0.1−0.9 µm (Buehler, Inc., Lake Bluff, IL, USA) were used. The readiness of each sagitta for further analysis was determined individually on the basis of visual observations. We used a trinocular microscope (Olympus SXZ12) with a DFPLAPO 1 × PF lens to view the cross-sections at 1 × 20–40 magnification. Otolith cross-sections were coated with glycerin and illuminated with reflected light [34,35]. The ratio between otolith length and otolith width [36] are based on the measurements made using digital caliper.

Gonadal maturity state of walleye pollock specimens were examined at macroscopic level based on a six-stage scale [37].

Four individuals from the Laptev Sea (specimens from the Kara and Barents Seas were discarded after dissection, examination of biological characteristics, and extraction of sagittae) were subjected to morphometric analysis with the measurement of characteristics previously used by various authors in the study of specimens from the North Pacific and the North Atlantic [23,24,28,30,38–41]. The following morphometric characteristics were measured: predorsal and preanal lengths, pectoral and pelvic fin lengths, body depth, depth of caudal peduncle, head length, upper jaw length, interorbital length, horizontal and vertical eye diameters, preorbital and postorbital lengths, lengths of *D1*, *D2* and *D3* bases, lengths of *A1* and *A2* bases. All measurements were carried out on individuals preserved in a 6% formalin solution using digital calipers. Counts of the number of *D1*, *D2*, *D3*, *A1*, *A2*, pectoral, pelvic, and caudal fin rays, and number of vertebrae were carried out according to radiographs produced on an EcoRay Orange 1040 HF Portable X-Ray Generator (EcoRay, Seoul, Republic of Korea). Individuals from the Laptev Sea were deposited in the ichthyological collection of the Shirshov Institute of Oceanology of the Russian Academy of Sciences under the catalog numbers IORAS 04464-04467.

The pectoral fins clips of walleye pollock specimens, preserved in alcohol, were registered and deposited in the Russian National Collection of Genetic Reference Materials in the Russian Federal Research Institute of Fisheries and Oceanography (VNIRO, Moscow, Russia) (Table 2). All tissue samples were fixed in volumes of 96% ethanol at least 5 times larger than sample volume. Fixed samples were stored at −20 °C; ethanol was changed approximately a month after collection, and again in a year.

Table 2. Information about *CO1* sequences and respective samples used for genetic analysis to identify walleye pollock *Gadus chalcogrammus* from various areas of species' range, its congeners and outgroup (na = not available).

No. Sample	Number in VNIRO Genetic Database	Genbank Accession Number	Sampling Date	Locality	Country	Source
			European hake *Merluccius* (outgroup)			
1	na	KX782815	11.06.2013		Germany	NCBI
			Greenland cod *Gadus ogac* (sister group 1)			
2	na	LC146707	26.07.2016		Greenland	NCBI
			Atlantic cod *Gadus morhua* (sister group 2)			
3	na	KJ204879	2010–2012	North Sea	na	NCBI
4	na	KJ204880	2010–2012	North Sea	na	NCBI
			Pacific cod *Gadus macrocephalus* (sister group 3)			
5	na	ABCBF117-10	na	na	Canada	BOLD Systems
6	na	ABCBF118-10	na	na	Canada	BOLD Systems
			Walleye pollock *Gadus chalcogrammus* (main group)			
7	na	ABFJ129-06	09.10.2005	Hachinohe	Japan	BOLD Systems
8	na	DSFAL234-07	12.09.2007	N Bering Sea	USA	BOLD Systems
9	na	DSFAL479-08	09.08.2008	W Beaufort Sea	USA	BOLD Systems
10	na	DSFAL480-08	09.08.2008	W Beaufort Sea	USA	BOLD Systems
11	na	DSFAL481-08	09.08.2008	W Beaufort Sea	USA	BOLD Systems
12	na	FHAK128-19	02.08.2018	British Columbia	Canada	BOLD Systems
13	na	FHAK129-19	02.08.2018	British Columbia	Canada	BOLD Systems
14	na	FMV085-08	29.04.2003	Puget Sound, Washington	USA	BOLD Systems
15	na	FMV086-08	29.04.2003	Puget Sound, Washington	USA	BOLD Systems
16	na	FMV441-09	02.02.2009	Puget Sound, Washington	USA	BOLD Systems
17	na	GBGC4810-08	na	Finnmark	Norway	BOLD Systems
18	na	GBGC4811-08	na	Finnmark	Norway	BOLD Systems
19	na	GBGC4812-08	na	Finnmark	Norway	BOLD Systems
20	na	NBMF027-15	14.08.2011	Svalbard	Norway	BOLD Systems
21	na	SDP113001-13	03.08.2012	Aleutian Islands	USA	BOLD Systems
22	na	SDP113002-13	03.08.2012	Aleutian Islands	USA	BOLD Systems
23	na	SDP131037-14	03.08.2012	Aleutian Islands	USA	BOLD Systems
24	THE5962	MZ750950	11.09.2019	E Chukchi Sea	USA	NCBI
25	THE5980	MZ750951	11.09.2019	E Chukchi Sea	USA	NCBI
26	lapLevArk88	MZ750942	12.09.2019	Laptev Sea	Russia	NCBI
27	lapTHE5897	MZ750943	13.09.2019	Laptev Sea	Russia	NCBI
28	LevArk89	MZ750944	12.09.2019	Laptev Sea	Russia	NCBI
29	THE5896	MZ750948	13.09.2019	Laptev Sea	Russia	NCBI
30	THE5898	MZ750949	13.09.2019	Laptev Sea	Russia	NCBI
31	barTHE2842	MZ750938	06.12.2018	SE Barents Sea	Russia	NCBI
32	chuk1THE5881	MZ750939	23.08.2019	W Chukchi Sea	Russia	NCBI
33	chuk1THE5884	MZ750940	23.08.2019	W Chukchi Sea	Russia	NCBI
34	chuk2THE5983	MZ750941	11.09.2019	W Chukchi Sea	Russia	NCBI
35	THE5882	MZ750945	23.08.2019	W Chukchi Sea	Russia	NCBI
36	THE5885	MZ750946	23.08.2019	W Chukchi Sea	Russia	NCBI
37	THE5889	MZ750947	23.08.2019	W Chukchi Sea	Russia	NCBI

DNA was extracted with 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 performed using standard molecular genetic techniques [42]. Cytochrome oxidase subunit I (*CO1*) fragment of 510 b.p. was amplified with a primer complex of *VF2_t1*, *FishF2_t1*, *FishR2_t1*, *FR1d_t1* [42,43]. Amplification was conducted in a volume of 15µL with 90 ng total DNA, buffer 1x, 2.5 mM $MgCl_2$, 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 [44].

Purified fragments were sequenced from both strands by Applied Biosystems BigDye Terminator v3.1. kit (Applied Biosystems, Foster City, CA, USA) with capillary electrophoresis on ABI3500 Genetic Analyzer in VNIRO Laboratory of Molecular Genetics.

Resulting sequences were assembled in Geneious 6.5.0 (Biomatters, Auckland, New Zealand) [45] and aligned with "ClustalW" built in algorithm. They were subsequently translated into the necessary format for constructing a haplotype network in the PopArt program (Allan Wilson Centre Imaging Evolution Initiative, Otago, New Zealand) [46]. The FaBox 1.41 converter was used to convert the fasta file to the format required for calculation [47]. A network of haplotypes was constructed on the basis of 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 number of haplotypes in samples [48].

Data processing was performed, and a molecular genetic tree was constructed by using Geneious 6.0.5 software (Biomatters, Auckland, New Zealand) based on the Neighbor–Joining method with European hake *Merluccius merluccius* as an outgroup [49] with the use of Genetic Distance HKY model and 1000 bootstrap replicates [50].

Data on *CO1* sequences of walleye pollock from various parts of species' range and its congeners represented by Greenland cod *Gadus ogac*, Atlantic cod *G. morhua* and Pacific cod *G. macrocephalus* (sister groups involved in the analysis for comparative purposes [51]) were taken from the open BOLD (https://www.boldsystems.org/) (accessed on 24 September 2021) and NCBI (https://www.ncbi.nlm.nih.gov/) (accessed on 24 September 2021) databases.

3. Results

The records considered were represented by individuals of various lengths and physiological state (Figure 2). The smallest walleye pollock with a length of 32–35 cm (on average 33.3 cm) was recorded in the Laptev Sea. In the Kara Sea, the fish was noticeably larger with a length of 33–43 cm (on average, 38.4 cm). The largest individual with a length of 77 cm was caught in the Barents Sea. The body weight of walleye pollock varied between 195–272 g (on average 232.5 g) in the Laptev Sea and from 230 to 530 g (on average 391.2 g) in the Kara Sea. The weight of an individual from the Barents Sea was 2930 g.

Walleye pollock catches in the Barents and Kara Seas were mainly represented by females with gonads at various stages of maturity from immature (stage 2) to maturing (stage 3) and mature (stage 4).

The age of walleye pollock in the Kara Sea ranged from 4+ to 7+ years (on average 5.7 years). The age of the largest fish from the Barents Sea was 13+ years. At the same time, walleye pollock in the Kara Sea actively fed, and the stomach of a large male from the Barents Sea was empty.

Walleye pollock specimens from the Laptev Sea were characterized by the following (Table 3) external morphological characteristics (average values in percent of standard length, % *SL*): predorsal length 44.9, preanal length 29.0, pectoral fin length 17.5, pelvic fin length 14.9, body depth 17.0, depth of caudal peduncle 4.3, pectoral fin length 25.0, upper jaw length 10.5, interorbital length 6.3, horizontal eye diameter 6.3, vertical eye diameter 5.7, preorbital length 7.9, postorbital length 11.9, length of *D1* base 10.4, length of *D2* base 15.8, length of *D3* base 15.0, length of *A1* base 18.3, length of *A2* base 15.1. The average values of the meristic characteristics of these individuals were as follows (Figure 3): number of *D1* fin rays 12.8, number of *D2* fin rays 16.3, number of *D3* fin rays 19.0, number of *A1* fin rays 20.8, number of *A2* fin rays 20.0, number of pectoral fin rays 18.5, number of pelvic fin rays 6.8, number of caudal fin rays 50.5, number of vertebrae 51.5.

The sagittal otoliths of walleye pollock caught in the Kara Sea (Figure 4) have the following morphological characteristics. The lateral surface (side opposite the sulcus) is distinctly concave. It is flat or almost flat. Otolith width is less than 44% of otolith length and usually less than 40%. Lobulations on ventral margin do not extend up to the longitudinal midline.

The results of a comparative genetic analysis of the sequences of walleye pollock mtDNA *CO1* gene fragment (Figure 5) from different regions show that there were no principal differences between various samples. European hake *Merluccius* (outgroup) represented a separate branch from all representatives of *Gadus* genus. Individuals of Greenland cod *Gadus ogac*, Atlantic cod *G. morhua* and Pacific cod *G. macrocephalus* (sister groups), which formed independent clusters, were well differentiated from walleye pollock samples. Nine substitutions with site positions 69, 84, 123, 219, 270, 324, 399, 408 and 486 were found within the walleye pollock samples, all of them were synonymous. No non-synonymous substitutions were found within the group of walleye pollock and cod sequences. Only four non-synonymous substitutions were found in the European hake sample in relation to all other samples in positions 56, 209, 272 and 368. At the same time, walleye pollock samples did not form separate clusters according to the geographical principle and were mixed with each other. Thus, the nucleotide sequences of samples from the North Atlantic (Barents and Norwegian Seas and waters of Svalbard) were close to those from the Beaufort, Chukchi and Laptev Seas, and the Pacific waters of the United States and Canada. At the same time, samples from the Laptev Sea were close to those from the Beaufort and Chukchi Seas, the North Atlantic and the waters of the Pacific coast of the United States and Canada.

Figure 2. Photographs of walleye pollock *Gadus chalcogrammus* caught outside of native range (from the Laptev Sea (**a**,**b**), the Kara Sea (**c**,**d**), the Barents Sea (**e**)) and viscera of specimen from the Barents Sea (**f**).

Table 3. Morphometric and meristic characteristics of walleye pollock *Gadus chalcogrammus* from various parts of species' range.

Character/Source	**North Atlantic**						**North Pacific**				**Laptev Sea**		
											11		
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**Min.**	**Max.**	**Mean**
Total length (*TL*), mm	620	585				422					322	352	333.0
Standard length (*SL*), mm	550	555		507	309						292	320	302.5
Morphometrics													
% *TL*													
Predorsal length	40.0	42.6				40.7			40.4–44.1		39.6	41.2	40.8
Preanal length	27.1	29.9				29.4			27.3–29.2		25.0	28.6	26.3
Pectoral fin length	16.1	15.0							17.5–21.4		15.0	16.3	15.9
Pelvic fin length	14.7	15.6							9.5–11.8		12.6	15.1	13.6
Body depth	15.5	22.6	16.7–18.2						9.8–15.2		15.2	15.9	15.5
Depth of caudal peduncle	4.0	4.2	4.4–4.5						3.0–3.5		3.6	4.2	3.9
Head length	21.8	24.6	25.0–26.7						21.8–24.2		22.2	23.4	22.7
% *SL*													
Predorsal length				47.2	45.7						43.9	45.3	44.9
Preanal length				31.2	32.4						27.5	31.4	29.0
Pectoral fin length	20.0			18.4	17.7						16.6	18.0	17.5
Pelvic fin length	18.7			15.7	15.9						13.8	16.6	14.9
Body depth											16.7	17.4	17.0
Depth of caudal peduncle	4.5			4.2	4.6						4.0	4.6	4.3
Pectoral fin length	24.5			25.7	26.4						24.5	25.8	25.0
Upper jaw length	11.1										9.7	11.1	10.5
Interorbital length	29.6										5.7	6.8	6.3
Horizontal eye diameter				4.9	5.8						5.9	6.6	6.3
Vertical eye diameter											5.3	6.0	5.7
Preorbital length				8.4	8.6						7.5	8.5	7.9
Postorbital length				12.9	12.6						11.4	12.9	11.9
Length of *D1* base				12.1	12.1						9.0	11.5	10.4
Length of *D2* base				17.5	17.6						14.8	16.8	15.8
Length of *D3* base				16.0	15.9						13.8	15.6	15.0
Length of *A1* base				20.7	21.4						17.2	20.2	18.3
Length of *A2* base				16.8	16.6						11.4	17.2	15.1
Meristics													
Number of *D1* fin rays	13	12	13	12.8	12.5		12–14	12–14	12–14	13–14	12	14	12.8
Number of *D2* fin rays	16	15	16–17	16.1	16.3		12–18	12–18	12–18	15–19	14	18	16.3
Number of *D3* fin rays	17	16	18–20	18.4	18.1	17.5	20–21	17–21	20–21	18–23	18	20	19.0
Number of *A1* fin rays	17	20	19–20	19.7	20.8		19–23	19–23	19–23	19–24	18	22	20.8
Number of *A2* fin rays	20	19 (21)	19–20	18.9	19.4		21–23	20–23	21–23	20–23	19	21	20.0
Number of pectoral fin rays	19	16	19	18.8	18.8			18–19			16	20	18.5
Number of pelvic fin rays	6	7		6.1	6.2			5–6			6	7	6.8
Number of caudal fin rays				45.5	42.2						50 *	52 *	50.5
Number of vertebrae							50	50–52	50	50–52	51	52	51.5

*—total number of caudal fin rays (principal and procurrent); sources: 1—Barents Sea [24]; 2—Barents Sea [23]; 3—North Atlantic [40]; 4—Norwegian and Barents seas [28]; 5—waters off Alaska [28]; 6—Bering Sea [23]; 7—North Pacific [39]; 8—North Pacific [41]; 9—North Pacific [30]; 10—North Pacific [38]; 11—Laptev Sea (our data).

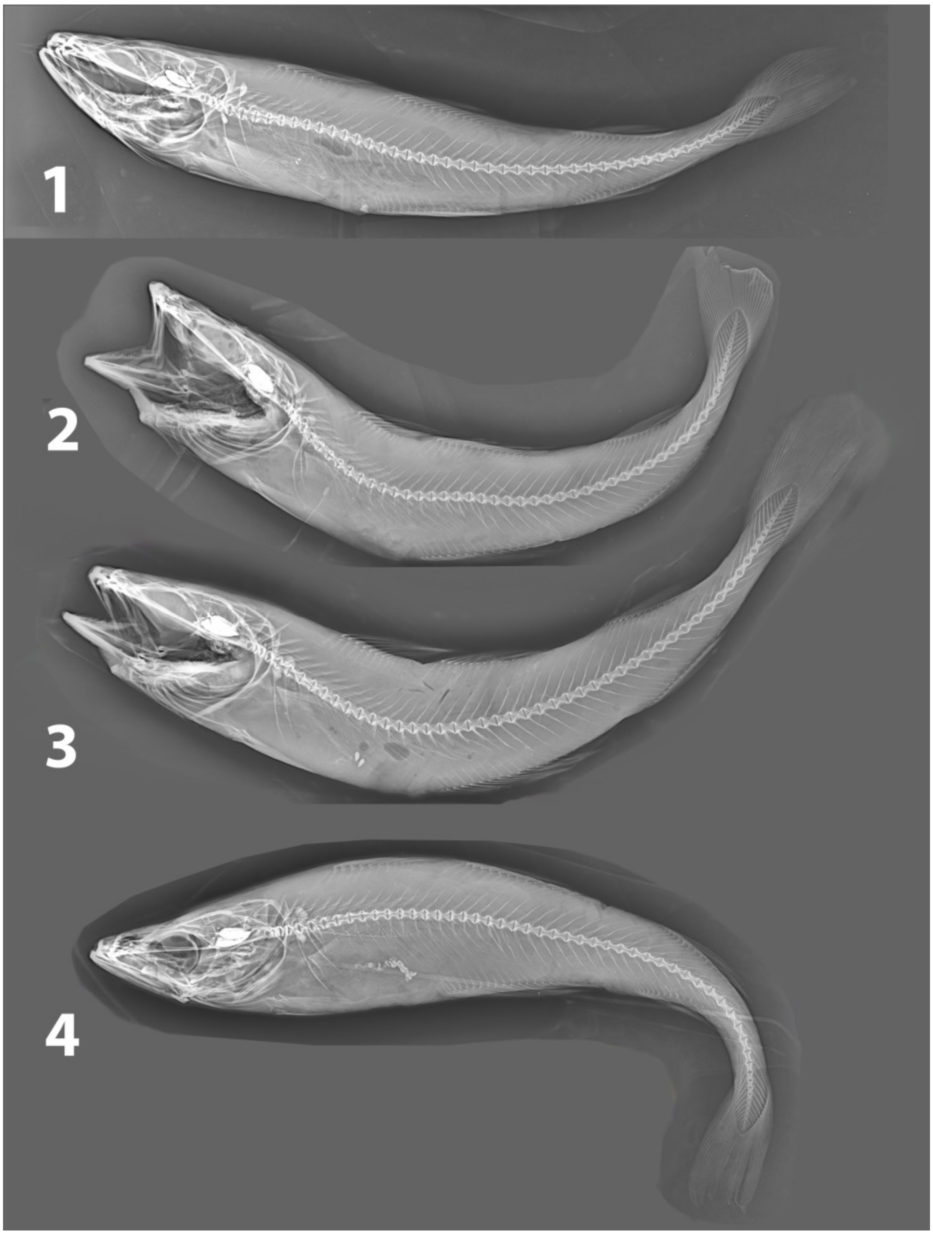

Figure 3. X-ray images of walleye pollock *Gadus chalcogrammus* from the Laptev Sea: (**1**): IORAS 04464, (**2**): IORAS 04465, (**3**): IORAS 04466, (**4**): IORAS 04467.

The results of the genetic analysis reveal 12 different haplotypes among the walleye pollock samples studied (Table 4). The haplotype H2 was the most frequent among them, which was found in 15 walleye pollock samples from the Bering, Beaufort, Chukchi, and Laptev Seas, the waters of British Columbia, Puget Sound, Norway, Svalbard and the Aleutian Islands. The remaining haplotypes were observed in 1–3 cases. At the same time, haplotype H1 was found in walleye pollock from the waters of Japan and the Chukchi Sea, i.e., in remote areas from each other.

The *CO1* haplotype network, constructed on the basis of all walleye pollock samples, its congeners and outgroup (Figure 6), demonstrates that walleye pollock haplotypes form a star-shaped structure with the main central haplotype H2, from which the remaining haplotypes are separated by 1–2 mutations. At the same time, various haplogroups are formed by haplotypes belonging to individuals from different geographical areas.

Figure 4. Walleye pollock *Gadus chalcogrammus* whole sagittal otoliths of from the Kara Sea (**a**,**b**) and sagitta cross-section of the specimen from the Barents Sea (**c**).

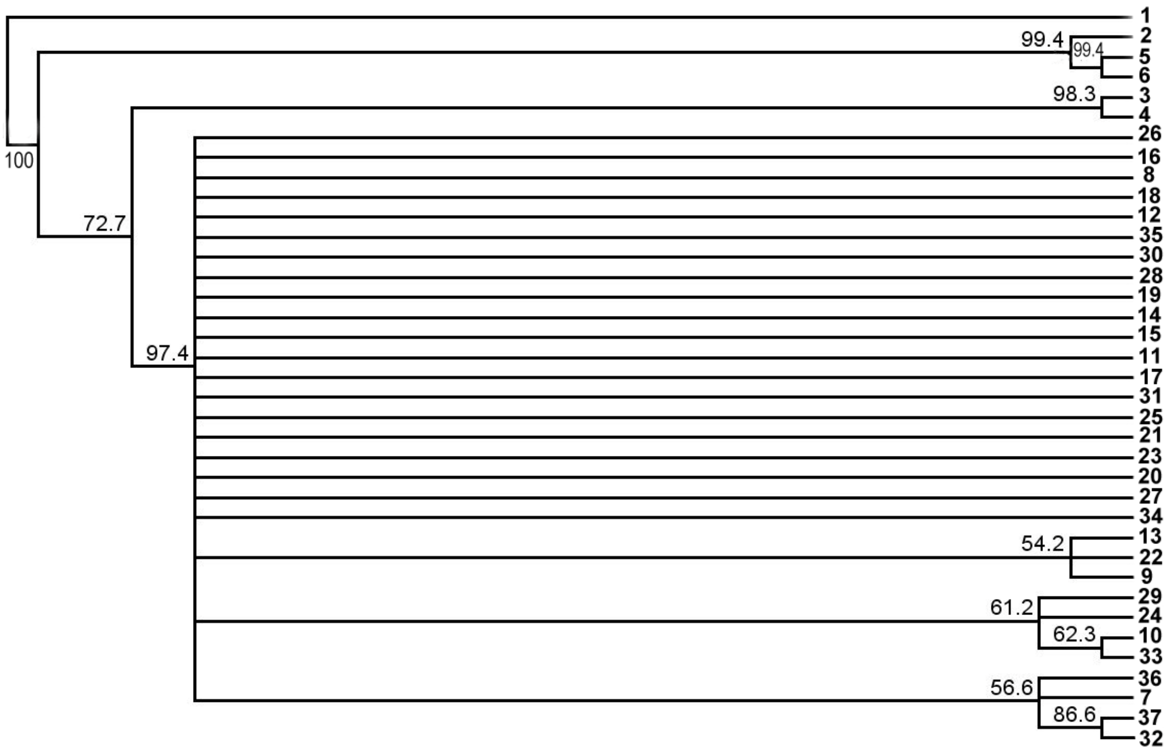

Figure 5. Tree topology reconstruction of 35 selected walleye pollock *Gadus chalcogrammus* specimens from the entire species range based on the Neighbor–Joining method, Kimura 2-parameter model and 1000 bootstrap replicates for mitochondrial cytochrome oxidase subunit I (*CO1*) genes. Numbers beside each branch indicate bootstrap values above 50%. Numbers to the right of the tree correspond to the number of specimens in Table 2.

Table 4. Composition of *CO1* haplotypes in the studied walleye pollock *Gadus chalcogrammus* samples. Numbers of samples correspond to Table 2.

No. Sample	No. Haplotype												Country, Locality
	1	2	3	4	5	6	7	8	9	10	11	12	
7	■												Japan, Hachinohe
8		■											USA, Bering Sea
9				■									USA, Beaufort Sea
10			■										USA, Beaufort Sea
11		■											USA, Beaufort Sea
12		■											Canada, British Columbia
13					■								Canada, British Columbia
14		■											USA, Puget Sound
15		■											USA, Puget Sound
16		■											USA, Puget Sound
17		■											Norway, Finnmark
18		■											Norway, Finnmark
19						■							Norway, Finnmark
20		■											Norway, Svalbard
21									■				USA, Aleutians
22				■									USA, Aleutians
23		■											USA, Aleutians
24											■		USA, Chukchi Sea
25		■											USA, Chukchi Sea
26							■						Russia, Laptev Sea
27		■											Russia, Laptev Sea
28								■					Russia, Laptev Sea
29											■		Russia, Laptev Sea
30												■	Russia, Laptev Sea
31		■											Russia, Barents Sea
32	■												Russia, Chukchi Sea
33			■										Russia, Chukchi Sea
34		■											Russia, Chukchi Sea
35		■											Russia, Chukchi Sea
36										■			Russia, Chukchi Sea
37	■												Russia, Chukchi Sea
Total number of particular haplotype	3	15	2	2	1	1	1	1	1	1	2	1	

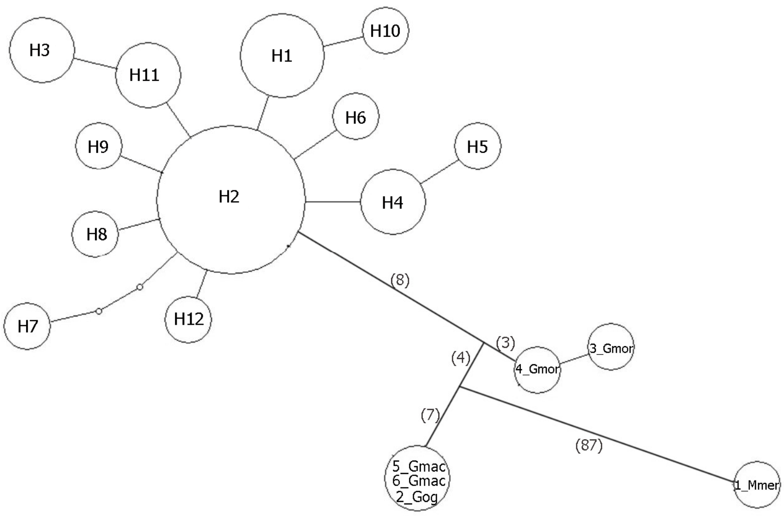

Figure 6. *CO1* haplotype network of walleye pollock, its congeners and outgroup. Numbers of haplotypes correspond to Table 4, numbers of substitutions are given in brackets, Mmer = European hake, Gmor = Atlantic cod, Gog = Greenland cod, Gmac = Pacific cod, numbers before species acronyms correspond to number of samples in Table 2. The diameters of the circles are proportional to the number of samples, smallest circle corresponds to single sample.

4. Discussion

Until recently, nothing was known about the occurrence of walleye pollock in the Siberian Arctic. It was believed that walleye pollock could not be found in the Chukchi Sea [3,52,53]. Its presence in this area was only recently reported, but the abundance of this species was considered insignificant [6]. In August 2019, adult walleye pollock were found in large amounts in the western Chukchi Sea, and in September 2019 several specimens were caught in the Laptev Sea [5,54–57]. However, there was no detailed description of the records in the latter area.

The depths of walleye pollock captures in the Siberian Arctic (42–603 m) fit into the known range of its occurrence in the North Pacific, which is 0–1280 m [58] and well corresponds to the range of their preferred habitat depths (30–590 m).

Walleye pollock can reach a total length of 91 cm [53,59], but fish of this length are extremely rare in catches. The catches are usually dominated by medium-sized individuals, and the size composition depends on the geographical area, season, depth, and fishing gear [1,52]. Our catches of walleye pollock by bottom trawls in the Kara and Laptev Seas were mainly represented by medium-sized individuals, which is typical for trawl catches in other areas [52,60–62]. A large male in the Barents Sea was caught by the bottom longline that is associated with the feeding habits of an adult walleye pollock, which, as it grows, turns to a predatory lifestyle [1,63].

The body weight of walleye pollock can reach 3.9 kg [64]. The body weight of walleye pollock individuals caught in the Siberian Arctic did not differ in principle from that of individuals from the eastern Bering Sea [63]. Thus, the eastern Bering Sea walleye pollock with a length of 33 cm has an average body weight of 250 g, with a length of 39 cm—410 g, with a length of 43.5 cm—565 g and with a length of 72 cm—2537 g. These values are quite comparable to those of our specimens.

The maximum age of walleye pollock is estimated to be from 15 years [63] to 28 years [65]. At the same time, the catches in the Bering Sea are dominated by fish aged from 2+ to 5+ years, which account for about 90% in the western Bering Sea and more than half of the catches in the eastern Bering Sea [66]. Fish under the age of 7+ years predominate in other parts of the range [60–62]. In this respect, the age composition of our catches does not principally differ from that in the native range, since a significant part of the individuals from the Kara Sea were over the age of 5+ years, and the individual from the Barents Sea was 13+ years old.

The predominance of females in our samples may be due to a small sample size, although there is information about the prevalence of females in catches at spawning grounds, for example, in the Korean waters of the Sea of Japan [67]. In the eastern Bering Sea, 50% of the females and males become sexually mature at a length of 35 and 32 cm, respectively [63]. Off the coast of Hokkaido, the southern Kuril Islands and the western Kamchatka, the corresponding values are 40.7–45.3 cm and 37.5–43.1 cm [68]. All females and males become sexually mature depending on the area at a length of 41–53 cm [66]. In our samples from the Kara Sea, all walleye pollock individuals with a length of 34 cm or more were sexually mature, which fully corresponds to the published data for the northern parts of its range.

Walleye pollock spawning lasts for 2–7 months [3]. In the northern parts of the range, it occurs in the winter–spring period, while in the southern regions it is shifted to the winter [1,52]. The period of walleye pollock captures in the Kara Sea (September) fell on the feeding period, when the fish actively feeds, which explains the good filling of their stomach with food. In the Barents Sea, a large male with an empty stomach was caught in December, during the pre-spawning period, when the feeding activity of this species decreases [1,52]. Unfortunately, the analysis of the diet composition of walleye pollock individuals caught in the Siberian Arctic was not carried out. Nevertheless, through the X-ray of a single specimen from the Laptev Sea (no. 3, Figure 3), sagittal otoliths are clearly visible in the stomach. In shape, they certainly belong to a representative of the family

Gadidae [69], most likely to the polar cod *Boreogadus saida*, which is the most abundant fish in this area [55,70–73].

The data on morphometric characteristics of individuals from the Laptev Sea, as a whole, are within the limits of intraspecific variability of walleye pollock from the waters of the North Atlantic and North Pacific [23,24,28,30,38–41]. Minor differences in our data from previously published research may be related to the shorter length of our fish, since walleye pollock is characterized by age-related variability of external morphological features [74,75]. As for the meristic characters, the overwhelming majority of them also are within the limits of intraspecific variability. The only exception is the number of rays in the pectoral fin, which in one case (20) slightly exceeds the known range (16–19) from published sources [23,24,28,39,40].

Walleye pollock sagittal otoliths from the Kara Sea had a typical shape for sagittae of gadid fishes [61] and did not differ in any way in shape or proportions from those of North Pacific walleye pollock individuals [69,76,77].

The results of our genetic analysis (composition of haplotypes, haplotype network, and tree topology reconstruction) clearly show that throughout the vast range from the Norwegian and Barents Seas to waters of Japan, Korea and California, including the Arctic, there is a single species, walleye pollock *Gadus chalcogrammus*. This is in good agreement with the results of previous studies [25–29], which indicate the conspecificity of the walleye and Norwegian pollocks and do not support the opinion of individual scientists [23,24] about the validity of the latter species.

The new data obtained by us on the records of walleye pollock in the Siberian Arctic allow us to present a hypothetical scheme of its dispersion from the North Pacific. The distribution of walleye pollock in the North Atlantic is limited to the coastal waters of the Norwegian Sea from the west, to the north of the Kolguev Island from the east, and to the waters north of the Svalbard from the north [6,78], according to our data. At the same time, records of this species in this area are extremely rare [7] and are mainly represented by large adult fish [22–24,28]. Until recently, there was no information about the occurrence of adult walleye pollock in the Chukchi Sea [52,53]. Only recently there was information about its presence in this area, but the abundance of this species was considered insignificant here [6]. In recent years, adult pollock has been found in large numbers in the western Chukchi Sea [5,54–57]. New captures of medium-sized walleye pollock in the Laptev and Kara Seas suggest that individuals of this species at the early life stages from the Bering Sea through the Bering Strait with Pacific inflow [79] are transported to the Chukchi and East Siberian Seas. This possibility is evidenced by the appearance in recent years, along with adult walleye pollock, of a noticeable number of juveniles in the Chukchi Sea [54]. It can be further assumed that, after reaching a certain length, walleye pollock can perform active lengthy migrations, which are an integral part of its lifecycle [5,80–82]. At the same time, shifting gradually westward as it grows, it moves against the currents that in the Laptev, Kara and Barents Seas have a general eastward direction [83,84]. This assumption is supported by the size composition of walleye pollock, which in the Laptev Sea is represented by individuals with a length of 32–35 cm, in the Kara Sea by fish with a length of 33–43 cm, and in the Barents and Norwegian Seas reaches a length of over 43 cm, on average over 50 cm [22–24,28]. Judging by the age of the fish in the samples, such migrations can take several years. However, it should be noted that recently a walleye pollock with a length of 36.5 cm was caught in the waters north of Svalbard [78], which does not quite fit into the hypothesis we proposed. Nevertheless, based on the morphological features, the authors assume the North Pacific origin of this individual. It can be assumed that this specimen was transported to Svalbard by another way, namely, by a current that carries surface waters from the Laptev Sea to Svalbard through the central Arctic [83,84]. It is possible that with the warming in the Arctic basin, the survival of early walleye pollock progeny became possible, and the record of this specimen is the result of the spawning of large-sized walleye pollock individuals migrated to the Barents and Norwegian Seas from the North Pacific. This possibility is indicated by the physiological state of specimens caught in the Barents Sea, whose gonads were in a pre-spawning or post-spawning condition [23,24], according to our data. In any case, their abundance here is very low and therefore there are no reasons to assume the presence of a self-reproducing population in this area yet. Thus, the waters of the North Atlantic and the adjacent Arctic should probably be considered as a zone of sterile walleye pollock eviction.

5. Conclusions

The data presented here clearly indicate that the few records of walleye pollock in the North Atlantic have their origin from the North Pacific, and its range extends almost continuously from the coast of Norway in the North Atlantic to the coasts of Korea, Japan, and California in the North Pacific. Walleye pollock has not yet been found in the East Siberian Sea, since research there is extremely rare and limited in that area [85,86]. However, the discovery of walleye pollock in the East Siberian Sea, in our opinion, is a matter of the near future. The warming in the Arctic, accompanied by a decrease in the ice cover, provides good opportunities for the intensification of scientific research both in terms of expanding the geographical coverage of water areas previously closed by ice, and of the seasonal duration of work.

Undoubtedly, research in the seas of the Siberian Arctic and the northeastern Atlantic will continue in the future, accompanied by new records of walleye pollock. In this regard, the comparison of individuals from different geographical areas in order to determine their macro- and microevolutionary histories and relationships seems very promising. This requires carrying out research in the following areas:

- comparative analysis of fossil records, modern distribution and variability of mtDNA genes (see e.g., [87]);
- comparative analysis of the shape of otoliths (see e.g., [88,89]);
- comparison of the chemical composition of otoliths (see e.g., [90]);
- comparative analysis of the diet composition and feeding habits (see e.g., [91]), including evaluation of microplastic, macroplastic and other marine litter content in the stomach and its impact on the biological condition of fish (see e.g., [92–94]) since pollution of the Siberian Arctic in recent years become a serious ecological problem [95,96].

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