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Large-scale genetic structure and diversity of Arctic rainbow smelt *Osmerus dentex* Steindachner et Kner, 1870 throughout its distributional range based on microsatellites

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Abstract

Arctic rainbow smelt *Osmerus dentex* is one of the most abundant fish species widely distributed in the NW Pacific and Arctic seas. Studying this species can contribute to understanding the microevolutionary processes of the Arctic fauna in unstable climatic conditions and new habitats. However, little is known about the genetic structure and the mechanisms underlying its population dynamics. Ten microsatellite loci were used to genotype 822 individuals in 20 locations throughout a large part of the species' range in the Sea of Japan, Sea of Okhotsk, Bering, Kara, and White seas (across more than 11,000 km). *O. dentex* displayed substantial levels of genetic differentiation (overall $F_{ST} = 0.067$, $R_{ST} = 0.091$) and STRUCTURE identified eight distinct clusters. The significant regional variation was demonstrated in both genetic diversity and population structure, most notably between Arctic and Pacific basins. On a regional scale, contrasting patterns were revealed with limited gene flow between populations of the Arctic region ($F_{ST} = 0.117$) and high gene flow between the Bering Sea ($F_{ST} = 0.017$) or Sea of Okhotsk ($F_{ST} = 0.031$), which were probably associated with differences in larval distribution from the spawning grounds due to different oceanographic conditions of the studied areas. These results demonstrate the effect of local contemporary forces in shaping different patterns of genetic connectivity and diversity within *O. dentex*.

Keywords Genetic diversity · Population structure · Arctic (Pacific) rainbow smelt · *Osmerus dentex* · Arctic region · Pacific Ocean

Introduction

Pacific or Arctic rainbow smelt *Osmerus dentex* Steindachner and Kner, 1870 (Nellbring 1989) is a typical anadromous species widely distributed in estuaries and coastal waters of European and Siberian shores of the Arctic Ocean from the White Sea to Chukotka in eastern Siberia and from the Bering Sea to Korea and Northern Japan in the Pacific Ocean (Klyukanov 1975; Chereshnev 1998; Kottelat and Freyhof

2007). Spawning of smelt usually takes place in early spring, the upstream run is generally short, a maximum of a few km, but on some large rivers it can rise for very considerable distances. Smelt mature at 2–4 years of age, and the eggs attach to gravel; after hatching, larvae are immediately carried downstream and develop in estuaries. Adults return to estuaries after spawning and may move into shallow waters; however, they do not make long-distance migrations (Berg 1948; Nellbring 1989; Vasilets 2000; Chereshnev et al. 2002; Gritsenko 2002).

Arctic rainbow smelt can potentially be structured on a very small spatial scale up to individual river systems. They are philopatric, and their spatial migrations are limited. In different areas of the Sea of Okhotsk, Sakhalin, Kamchatka, Chukotka, and the White and Barents seas, *O. dentex* is distinguished by a certain number of ecological groups associated mainly with the timing and duration of spawning, the length of spawning and wintering migrations, and some morphometric traits (Kirpichnikov 1935; Podushko 1970; Vasilets et al. 2000; Chereshnev

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et al. 2002; Gritsenko 2002; Bugaev 2007). The investigation of populations within the White and Barents seas using allozymes (Sendek et al. 2005) and microsatellites (Semenova et al. 2019a) was fragmentary; however, some regional differences at the level of large bays have been revealed. The genetic difference has been observed using microsatellites between populations inhabiting rivers on the East and West sides of the Kamchatka Peninsula (Semenova et al. 2019b). Simultaneously, mtDNA-based studies have shown weak population structure of smelt in most of its range despite the high molecular diversity (Skurikhina et al. 2015).

Examination of genetic differentiation within related species of family Osmeridae, the rainbow smelt (*Osmerus mordax*) and the eulachon (*Thaleichthys pacificus*), which possess a similar life history, suggested that divergence may be very low across a wide geographic scale (McLean and Taylor 2001; Beacham et al. 2005; Bradbury et al. 2006; Kovach et al. 2013). At the same time, in some parts of the species' range, gene flow can be significantly limited (Bradbury et al. 2008a, b).

Arctic rainbow smelt is inferred to have expanded its range after the end of the latest Wisconsin glaciations from the main refuge in the NW Pacific (the Sea of Japan and the southern Sea of Okhotsk). In addition, it the existence of a small refuge in the White Sea (Skurikhina et al. 2018) has been proposed. Historical factors are thought to have played a significant role in the patterns of genetic variation in Arctic rainbow smelt. Meanwhile, contemporary mechanisms affecting the genetic structure of smelt remain largely unknown.

O. dentex is one of the most abundant fish species of the Osmeridae family, and it is important for commercial and sport fisheries in the Russian Far East waters (Andriashev and Chernova 1994; Bugaev et al. 2014). The economic importance of smelt clearly emphasises the need for a better understanding of the population structure of the species and the mechanisms underlying its population dynamics. Microsatellites can help identify cryptic population structure and distinguish historical and contemporary factors that influence the demographic histories of populations. Thus, understanding population structure based on neutral genetic variation has become a necessary step in the development of the conservation programs for many commercial exploited fish (Allendorf et al. 1987).

While earlier studies have identified the possibility of an additional small refuge in the White Sea, we reasoned that an investigation with nuclear markers might offer additional insights into this issue. It has been shown in several studies that the analyses of microsatellite data can be useful for resolving phylogenies at substantial divergence scales, including for estimating the number of post-glacial refugia that contributed to the re-colonisation of Northern Europe

(Koskinen et al. 2002; Tonteri et al. 2005; Peterson and Ardren 2009).

The purpose of this study was to investigate the population genetic structure of Arctic rainbow smelt across its range in the Arctic waters, eastern coast of Bering Sea, Sea of Okhotsk, and Sea of Japan using ten microsatellite loci. Unfortunately, in this paper and the literature, there are no data on smelt from the Arctic coast of Siberia due to the inaccessibility of this region. This greatly limits our ability to discuss smelt relationships throughout the Arctic coastline. Our specific goals were to (i) characterise the overall patterns of genetic diversity as well as regional and range-wide genetic structure of *O. dentex*; (ii) assess historical and contemporary drivers of population structure; and (iii) discuss conservation and management measures for *O. dentex* populations.

Materials and methods

Sample collection, microsatellite genotyping and descriptive genetic data

In this study, 20 locations of *O. dentex* from the White, Kara, Bering, Okhotsk, and Japan seas were analysed. These samples were collected in 2006–2019 at different periods of fish life cycles: in the rivers during spawning; in the mouth of the rivers and the estuaries during wintering, pre-spawning, or post-spawning migrations. We assume that all samples represent the populations of their specific rivers, since most of smelt in the range tend to adhere to local habitats for feeding or wintering (Table 1; Fig. 1).

DNA was extracted from the fin by the following standard methods using the Diatom DNA Prep kits (IsoGene, Russia). Ten microsatellite loci isolated from Pacific smelt or relative species were tested (Kaukinen et al. 2004; Coulson et al. 2006; Fisch et al. 2009). We designed new primers for six loci using the Primer-BLAST (Ye et al. 2012) (Online Resource 1). DNA amplification and separation of the PCR products were carried out according to the procedure described in Semenova et al. (2019b).

The genotype data were analysed with MICRO-CHECKER 2.2.3 to check for null alleles and scoring errors (Van Oosterhout et al. 2004). The populations were tested for deviations from HW equilibrium and linkage disequilibrium using GENEPOP 3.4 (Raymond and Rousset 1995).

The GDA 1.0 software (Lewis and Zaykin 2001) was used for calculating allele frequencies, the expected and observed heterozygosities (H_E, H_O), allelic diversity (A), and the number of private alleles (A_{PR}). The allelic richness (A_R), corrected for the minimum sample size, was calculated using FSTAT 2.9.3 (Goudet 2001). Estimates of genetic variability were calculated for all localities and clusters revealed by

Table 1 Sample information for Arctic rainbow smelt from the White, Kara, Bering seas, Sea of Okhotsk and Sea of Japan

N pop	Code	Location	Area, region	Sampling date	Stage of the life cycle	Latitude (N)/longitude (E)	n
1	TUM	Tumnin River	Sea of Japan, Tatar Strait, Pacific Basin	04.2019	Spawning	49°17′/140°12′	30
2	AMU	Amur River	Sea of Okhotsk, Western coast, Pacific Basin	03.2019	Spawning	53°11′/140°22′	49
3	SAH	Naiba River	Sea of Okhotsk, Southern coast of Sakhalin Island, Pacific Basin	02.2019	Pre-spawning	47°41′/142°83′	37
4	AMH16	Amakhton Bay	Sea of Okhotsk, Northern coast, Pacific Basin	07.2016	Post-spawning	59°53′/150°47′	50
5	AMH18	Amakhton Bay	The same	04.2018	Spawning		41
6	KOV	Kovran River	Sea of Okhotsk, Northeastern part; Kamchatka Peninsula (Western coast), Pacific Basin	06.2014	Spawning	57°22′/156°84′	50
7	HAI	Khairyuzova River	The same	05.2014	Spawning	57°10′ /156°69′	50
8	BEL	Belogolovaya River	The same	07.2014	Post-spawning	57°07′ /156°67′	50
9	KRU	Krutogorova River	Sea of Okhotsk, Eastern part; Kamchatka Peninsula (Western coast), Pacific Basin	03.2011	Pre-spawning	55°07′/155°37′	40
10	KOL	Kol River	The same	05.2006	Spawning	53°82′/155°93′	12
11	BOL	Bolshaya River	Sea of Okhotsk, Southeastern part; Kamchatka Peninsula (Western coast), Pacific Basin	01.2014	Wintering	52°73′/156°17′	50
12	AVA	Avacha River	Pacific Ocean, Avacha Bay; Kamchatka Peninsula (Eastern coast), Pacific Basin	01.2014	Wintering	52°86′/158°69′	32
13	NER14	Lake Nerpich'e	Bering Sea; Kamchatka Peninsula (Eastern coast), Pacific Basin	02.2014	Wintering	56°21′/162°58′	50
14	NER16	Lake Nerpich'e	The same	12.2016	Wintering		55
15	UKA	Uka River	The same	05.2017	Spawning	57°85′/162°20′	39
16	KAR	Tazovskaya Inlet	Kara Sea, Arctic Region	10.2018	Wintering	68°90′/74°58′	32
17	MEZ	Mezen Bay	White Sea, Arctic Region	12.2016	Wintering	66°57′/43°96′	42
18	DVI	Dvina Bay	The same	12.2018	Wintering	64°57′/39°65′	48
19	KAB	Nikolskaya Inlet	White Sea, Kandalaksha Bay, Arctic Region	06.2016	Post-spawning	66°55′ /33°04′	21
20	KAN	Rugozerskaya Inlet	The same	06.2015	Post-spawning	66°55′/33°10′	44

STRUCTURE (see below). The differences in the average number of alleles (A_R) and heterozygosity (H_O) between sites were tested using a randomisation test (1000 permutations) in FSTAT.

Bottleneck events

To detect indications for a recent bottleneck or a reduction in population size, we used BOTTLENECK 1.2.02 (Piry et al. 1999) with the Wilcoxon test, based on 100,000 iterations using a stepwise mutation model (SMM), an infinite allele model (IAM), and a two-phase mutation model (TPM) (set at 70% SMM, 30% IAM). For each population, only polymorphic loci in HWE were used. We also used the *M*-ratio

method with the critical value of $M = 0.68$ following Garza and Williamson (2001).

Population structure and connectivity

Population differentiation was estimated per population pair and overall using F_{ST} (θ) and R_{ST} (Weir and Cockerham 1984; Slatkin 1995) in GENEPOP and GDA. Fisher's exact test in GENEPOP was used to test for significant differences in allele frequencies between populations. We compared the levels of variation among locations based on allele identity (F_{ST}) and allele size (R_{ST}). A permutation test (1,000 permutations) used to determine whether stepwise-like mutations contributed to genetic differentiation ($R_{ST} = F_{ST}$) was carried out using SPAGEDi 1.2 (Hardy and Vekemans 2002;
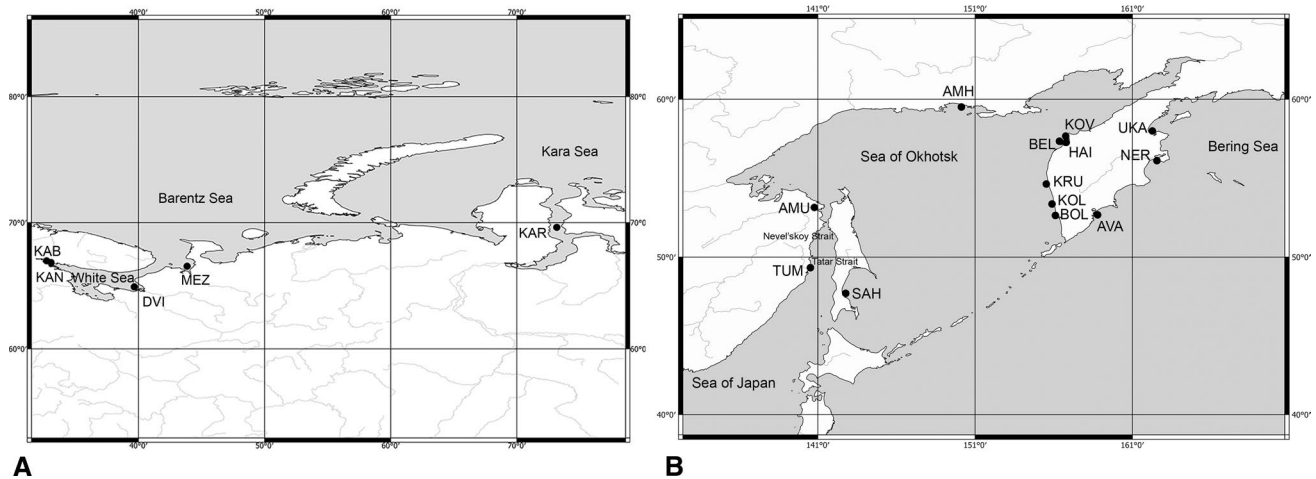
Fig. 1 Map of sampling locations of Arctic rainbow smelt *O. dentex* used in the present study. **a** Geographic location of the populations from the Arctic area. **b** Geographic location of the populations from the Pacific area

Hardy et al. 2003). Sequential Bonferroni adjustments were applied to correct for the effect of multiple tests. We conducted a Mantel test to evaluate isolation by distance (IBD) using the standardised genetic distance ($F_{ST}/1 − F_{ST}$) and the logarithm of the geographic distance among locations, with 10,000 permutations, in the IBD 1.52 program (Jensen et al. 2005).

Bayesian analysis was implemented in STRUCTURE 2.3.4 (Pritchard et al. 2000), assuming the admixture model and correlated allele frequencies between clusters. STRUCTURE was run using MCMC simulations of 9,00,000 iterations, with a burn-in period of 1,00,000. Runs were conducted for the number of putative populations (i.e. *K*), set at 1–15, with each having 20 iterations. The optimum *K* value was assessed by analysing the Ln *P*(*K*) distribution, and the Evanno method Δ*K* (Evanno et al. 2005), as well as the bar plots showing individual assignments. All parameters were received on the STRUCTURE HARVESTER webpage (Earl and vonHoldt 2012). To study the intricate population structure within clusters, we used the 'hierarchical STRUCTURE analysis' (Vähä et al. 2007). Firstly, we estimated the optimal *K*-value at the uppermost hierarchical level of structure, delineating large-scale differences in our data set. Then we examined whether substructure existed within each of the populations identified at the uppermost level by estimating *K* within each of those populations. We used the CLUMPAK webserver (Kopelman et al. 2015) to align and visualise bar plots at multiple *K* values.

We performed an analysis of molecular variance (AMOVA; Excoffier et al. 1992) in ARLEQUIN 3.5 (Excoffier and Lischer 2010) to estimate the amount of genetic variation present at the following hierarchical levels: among major sea basins (Japan, Okhotsk, Bering, Kara, and White seas), among sites within major sea basins, and within

sites (analysis #1). We conducted AMOVA analysis #2 at the hierarchical levels based on eight clusters previously identified by STRUCTURE: among major clusters, among sites within these clusters, and within sites.

BARRIER 2.2 (Manni et al. 2004) was used to highlight the geographical areas with pronounced genetic discontinuity between the sites, i.e. barriers. Geographical coordinates were supplied for each site and connected by Delauney triangulation, such that each connection had an association. Within the analysis, barriers were set from 1 to 5. To test the significance of the detected barriers, 1000 resampled bootstrapped (population pairwise) DA genetic distance matrices (Nei's chord distance) were calculated in MICROSATELLITE ANALYSER (MSA) software (Dieringer and Schlötterer 2003).

Results

Data quality check, Hardy–Weinberg equilibrium, and linkage disequilibrium

A table of allele frequencies by populations is presented in Online Resource 2. MICROCHECKER suggested a possible null allele at the *MGPL-Omo*9 locus in six locations: AMU, KRU, BEL, BOL, NER14, and DVI. No other loci showed signs of possible null alleles. There was no evidence for scoring error due to shuttering or large allele drop-out for any microsatellite loci. Locus *MGPL-Omo*9 was discarded from further analyses of population structure.

Of the 200 single-locus tests for conformation to HWE, five had significant departure from the expectations following Bonferroni corrections (Online Resource 3). Four of them for the *MGPL-Omo*9 locus could be explained by the

presence of null alleles. When the results of all loci were combined for each population, only BEL departed from HWE after correction ($p = 0.000$). Evidence for linkage disequilibrium was detected between *MGPL-Omo*3 and *MGPL-Omo*16 with all populations pooled ($p < 0.0001$). Therefore, *MGPL-Omo*16 was removed from the dataset.

Microsatellite diversity and tests for bottleneck

The mean number of alleles per location ranged from 3.1 to 6.7. The levels of observed heterozygosity (H_O) and allelic richness (A_R) per location ranged from 0.365 to 0.567 and from 2.6 to 4.9, respectively (Table 2; Online Resource 3). No private alleles (A_{PR}) with $p > 0.05$ were found in any of the localities. The lowest genetic diversity was shown in the smelt of the inner part of the White Sea (Kandalaksha and Dvina bays). H_O and A_R were declines in the direction from the Sea of Japan and Sea of Okhotsk to the Bering Sea, then to the Kara Sea and the White Sea. Measures of genetic diversity (A_R, H_O) significantly differed among sites (A_R, $p = 0.004$; H_O, $p = 0.032$).

There were no indications of bottlenecks in any of the populations for the IAM, TPM, or SMM models ($0.461 < p < 1.000$). Moreover, in all populations excluding BEL, we identified a deviation from mutational drift equilibrium and a significant heterozygosity deficit (Wilcoxon test, $p < 0.0003$–0.019). No evidence of bottleneck effects were detected by the *M*-ratio tests, as estimated *M* values ranging in locations from 0.709 to 0.888 were above the critical $M = 0.68$.

Population genetic structure

The global $F_{ST} = 0.067$ (95% CI: 0.038–0.099) revealed a significant level of genetic structuring among all locations. Individual locus F_{ST} varied considerably, from 0.021 at *MGPL-Omo2* to 0.116 at *MGPL-Omo4*, all associated exact tests of global differentiation were significant ($p < 0.05$). The overall $R_{ST} = 0.091$ (95% CI 0.078–0.103) was also significant, as were all locus-specific tests (Online Resource 4).

A pairwise population analysis of *O. dentex* detected a significant difference in allele frequencies for 175 of the 190 possible tests (Exact tests, $p < 0.05$), with multilocus

Table 2 Mean genetic diversity estimates of *O. dentex* per location and per clusters revealed by STRUCTURE

Cluster by STRUCTURE	Location	N	A	A_R	H_O	H_E
(1) The Sea of Japan and southern and western parts of the Sea of Okhotsk	Mean per cluster	115.4	7.5	4.49	0.540	0.516
	TUM	30	6	4.7	0.554	0.533
	AMU	49	6.7	4.5	0.525	0.512
	SAH	36.4	5.9	4.4	0.567	0.544
(2) Northern part the Sea of Okhotsk	Mean per cluster	88.3	7.7	4.38	0.519	0.529
	AMH16	49.7	6.4	4.4	0.541	0.538
	AMH18	38.7	6.6	4.4	0.490	0.523
(3) Western coast of Kamchatka Peninsula (the Sea of Okhotsk)	Mean per cluster	282.1	5.9	4.27	0.561	0.561
	KOV	48.5	6.5	4.4	0.558	0.544
	HAI	47.6	6.5	4.9	0.570	0.596
	BEL	48.2	6.0	4.5	0.573	0.536
	KRU	39.6	6.3	4.7	0.598	0.554
	KOL	11.8	3.9	3.8	0.533	0.595
	BOL	50	6.5	4.5	0.545	0.524
	AVA	18.2	4.1	3.8	0.519	0.504
(4) Eastern coast of Kamchatka Peninsula (the Bering Sea)	Mean per cluster	142.5	6.9	4.14	0.504	0.500
	NER14	49.8	6.2	4.3	0.543	0.507
	NER16	54.5	6.2	4.2	0.515	0.500
	UKA	38.4	5.6	4.1	0.482	0.505
(5) The Kara Sea	KAR	30.5	4.5	3.6	0.543	0.551
(6) The White Sea, Mezen Bay	MEZ	41.2	4.4	3.4	0.486	0.568
(7) The White Sea, Dvina Bay	DVI	45.9	5.1	3.4	0.385	0.370
(8) The White Sea, Kandalaksha Bay	Mean per cluster	63	3.4	2.66	0.355	0.358
	KAN	21	3.1	2.6	0.369	0.385
	KAB	42	3.6	2.6	0.365	0.362

N collection sizes, *A* number of alleles, A_R allelic richness, H_E expected heterozygosity, H_O observed heterozygosity

F_{ST} ranging from 0.0004 to 0.1781 (Table 3). Pairwise F_{ST} for collections in consecutive years (AMH16 and AMH18; NER14 and NER16) were not significant, so yearly collections from the same locations were pooled in further analyses. The genetic differentiation was also not significant between locations of the Tumnin and Amur rivers, between sites of Kandalaksha Bay from the White Sea, and between the majority of the sites from the western coast of Kamchatka. After correcting for multiple testing, nine more tests were found to be non-significant, including all sites of Western Kamchatka except BEL and smelt from Lake Nerpich'e vs the Uka River of Eastern Kamchatka. The highest levels of genetic differentiation were revealed in comparisons of smelt from the Arctic region (the White and Kara seas) vs the Pacific Basin (the Sea of Japan, Sea of Okhotsk, and Bering Sea), with pairwise F_{ST} that ranged from 0.056 to 0.199. However, among Arctic populations, pairwise F_{ST} were quite high (0.055–0.170), except the F_{ST} between KAN and KAB sites in the Kandalaksha Bay in the White Sea.

Pairwise R_{ST} followed a similar pattern and were significant in 135 out of 190 comparisons before Bonferroni adjustments and in 128 cases after it, ranging from 0.0020 to 0.4130 (Table 3). The greatest differences in F_{ST} and R_{ST} were shown between the smelt of the White Sea and the smelt of Pacific Basin.

The allele size permutation test found significant differences between all F_{ST} and R_{ST} estimates ($R_{ST} > F_{ST}$, $p = 0.0013$) and supported the existence of a population structure within *O. dentex* formed not only by drift and gene migration but also by the contribution of the SMM. Sixty-one out of 190 pairwise comparisons between locations resulted in a significant phylogeographic signal (R_{ST} significantly larger than F_{ST}; Table 3). These significant comparisons were generally population pairs from Kandalaksha Bay, the White Sea (KAR, KAB), and the remaining locations, except DVI vs KAB. Also, about 50% of the pairwise tests between populations from the Eastern Kamchatka (the Bering Sea) vs the Western Kamchatka (the Sea of Okhotsk) were considerable. In addition, some comparisons between the Sea of Japan and the southwestern part of the Sea of Okhotsk vs the populations of the Western Kamchatka were substantial. When testing the Arctic region or the Pacific Basin separately, there were no differences between the F_{ST} and R_{ST} indices.

Bayesian analysis in STRUCTURE of the first hierarchical level detected by ΔK test indicated two clusters corresponding with: (1) all location from the Pacific Basin and the Kara Sea, and (2) smelt of the White Sea. The likelihood of the data Ln $P(K)$ was lowest at $K = 13$ and indicated the possibility of a deeper structuring of the smelt (Online Resource 5).At the second round of hierarchical analysis the White Sea initial cluster was separated into the three groups: the Mezen Bay, Dvina Bay, and Kandalaksha Bay. Also,

there were two clusters detected within 'the Pacific Basin' cluster: (1) the Sea of Japan and Sea of Okhotsk, and (2) the Bering Sea and the Kara Sea. Most individual genotypes of AVA (the eastern coast of Kamchatka, the Pacific Ocean) indicated admixture between these clusters. However, > 50% genotypes referred to the cluster 1. A third round of analysis found further structuring within two groups, where the Sea of Japan-Sea of Okhotsk cluster was again divided into two clusters: (1) Tumnin and Amur rivers, and Sakhalin and Amakhton Bay; and (2) the western coast of Kamchatka and AVA. The Bering Sea and the Kara Sea were also separated into discrete clusters: (1) NER and UKA, and (2) KAR. Finally, the fourth round of STRUCTURE revealed TUM-AMU-SAH and AMH as a separated cluster, while no subdivision was indicated within Western Kamchatka-AVA cluster. The finest population structure detected by STRUCTURE therefore consisted of eight geographical groups (Fig. 2): (1–3) three groups among the White sea (the Kandalaksha, Dvina, and Mezen bays); (4) the Kara Sea; (5) the eastern coast of Kamchatka (the Bering Sea); (6) the western coast of Kamchatka (the Sea of Okhotsk) and a sample from Pacific Ocean (AVA); (7) Amakhton bay (the Sea of Okhotsk); and (8) Sakhalin, Amur River (the Sea of Okhotsk), and Tumnin River (the Sea of Japan).

The global AMOVA, analysis # 1, indicated that a significant majority of genetic variation was located within sites (F_{ST}: 92.2%; R_{ST}: 89.8%). Significant variation was also attributable to differences between sea basins and between sites within sea basins. Analysis #2 revealed a similar genetic variation within sites. Between eight STRUCTURE clusters were 6.3% genetic variation by F_{ST} and 9.1% by R_{ST}, whereas a small remainder of the variation was attributable to differences among sites within the clusters (Table 4).

BARRIER identified five discontinuities in gene flow across the species' range supported with more 88% bootstrap level. The main barriers (1) delimited the Kandalaksha Bay populations (KAN, KAB) with the highest bootstrap support of 100%. Another strong barrier (2) (with up to 100% support) separated populations of smelt from the Kara and White seas from the remainder of the species' range. Between the Kara Sea and the White Sea, the barrier (3) had 88% bootstrap support, and between Mezen Bay and Dvina Bay, the barrier (4) had 99% bootstrap support. TUM and AMU populations showed genetic isolation, with a 100% supported barrier (5) (Online Resource 6).

There was significant support for an overall isolation by distance both in F_{ST} and in R_{ST}. Significant IBD was also evidenced among the Arctic populations, as well as among the Pacific Basin populations. On a smaller spatial scale, within the western coast of Kamchatka, the eastern coast of Kamchatka or the Sea of Japan and Southwestern Sea of Okhotsk, IBD was observed only among the Eastern Kamchatka locations (Online Resource 7).

Table 3 Pairwise F_{ST} (below diagonal) and R_{ST} (above diagonal) among all locations of *O. dentex*

	Sea of Japan	Sea of Okhotsk										Pacific Ocean	Bering Sea			Kara Sea	White Sea			
	TUM	AMU	SAH	AMH16	AMH18	KOV	HAI	BEL	KRU	KOL	BOL	AVA	NER14	NER16	UKA	KAR	MEZ	DVI	KAN	KAB
TUM	–	-0.006	-0.002	0.003	0.029	0.032	0.056	0.056	0.041	0.017	0.035	-0.001	-0.002	-0.001	0.011	0.053	0.062	0.085	0.223	0.240
AMU	0.000	–	0.008	0.014	0.023	0.060	0.089	0.087	0.072	0.047	0.067	0.014	0.009	0.017	0.014	0.074	0.065	0.081	0.214	0.218
SAH	0.011	0.031	–	0.027	0.046	0.061	0.100	0.100	0.074	0.054	0.078	0.017	0.021	0.021	0.010	0.052	0.046	0.088	0.189	0.204
AMH16	0.007*	0.012	0.027	–	0.015	0.009	0.043	0.045	0.017	-0.009	0.021	0.011	0.022	0.018	0.028	0.082	0.109	0.081	0.260	0.267
AMH18	0.010*	0.012	0.046	0.006	–	0.052	0.102	0.099*	0.052	0.029*	0.074	0.047	0.051	0.052	0.0460	0.124	0.132	0.042	0.236	0.231
KOV	0.025	0.036	0.057	0.009	0.021	–	0.019	0.026	-0.001	-0.019	0.004	0.024	0.046	0.032	0.062	0.076	0.141	0.106	0.284	0.299
HAI	0.021	0.029	0.053	0.005	0.021	0.001	–	-0.007	0.009	0.005	-0.002	0.067	0.077	0.072	0.107	0.128	0.176	0.193	0.346	0.373
BEL	0.041	0.046	0.076	0.022	0.037	0.008*	0.009	–	0.009	0.011*	0.005	0.074	0.074	0.069	0.104	0.139	0.174	0.191	0.357	0.381
KRU	0.039	0.053	0.079	0.017	0.037	0.003	0.004*	0.012	–	-0.021	0.001	0.049	0.064	0.051	0.080	0.119	0.167	0.125	0.312	0.334
KOL	0.051	0.057	0.084	0.012	0.035	0.002	0.009*	0.015	0.006	–	-0.012	0.036	0.038*	0.029*	0.066	0.113	0.177	0.116	0.410	0.414
BOL	0.015	0.019	0.054	0.003*	0.009*	-0.000	-0.002	0.015	0.009*	0.012	–	0.048	0.056	0.047	0.088	0.109	0.165	0.156	0.324	0.344
AVA	0.055	0.071	0.098	0.029	0.054	0.026	0.028	0.026	0.037	0.011	0.031	–	0.030	-0.001	-0.001	0.035	0.062	0.064	0.266	0.255
NER14	0.068	0.074	0.115	0.048	0.079	0.048	0.044	0.025	0.048	0.044	0.056	0.055	–	-0.006	0.007	0.047	0.045	0.074	0.209	0.219
NER16	0.092	0.101	0.123	0.072	0.101	0.064	0.059	0.031	0.069	0.057	0.078	0.047	0.005	–	0.012*	0.047	0.061*	0.076	0.241	0.247
UKA	0.068	0.066	0.116	0.039	0.059	0.047	0.040	0.040	0.054	0.045	0.049	0.035	0.012	0.019*	–	0.053	0.017	0.067	0.197	0.203
KAR	0.096	0.109	0.124	0.087	0.102	0.065	0.072	0.064	0.071	0.090	0.081	0.107	0.101	0.101	0.099	–	0.067	0.122	0.199	0.219
MEZ	0.078	0.080	0.111	0.065	0.085	0.071	0.067	0.058	0.078	0.091	0.077	0.089	0.047	0.055	0.029	0.087	–	0.1268	0.172	0.181
DVI	0.104	0.091	0.166	0.073	0.093	0.088	0.091	0.076	0.101	0.1104	0.086	0.080	0.048	0.067	0.033	0.171	0.055	–	0.162	0.142
KAN	0.076	0.086	0.089	0.103	0.111	0.131	0.131	0.151	0.162	0.199	0.127	0.169	0.156	0.174	0.149	0.161	0.111	0.154	–	-0.007
KAB	0.092	0.100	0.109	0.109	0.112	0.139	0.139	0.159	0.173	0.198	0.135	0.172	0.161	0.178	0.166	0.145	0.106	0.156	-0.008	–

Significance of tests before (asterisk) and after (bold) corrections for multiple tests are indicated. Italics indicate tests of $R_{ST} > F_{ST}$ statistically significant at $P < 0.05$
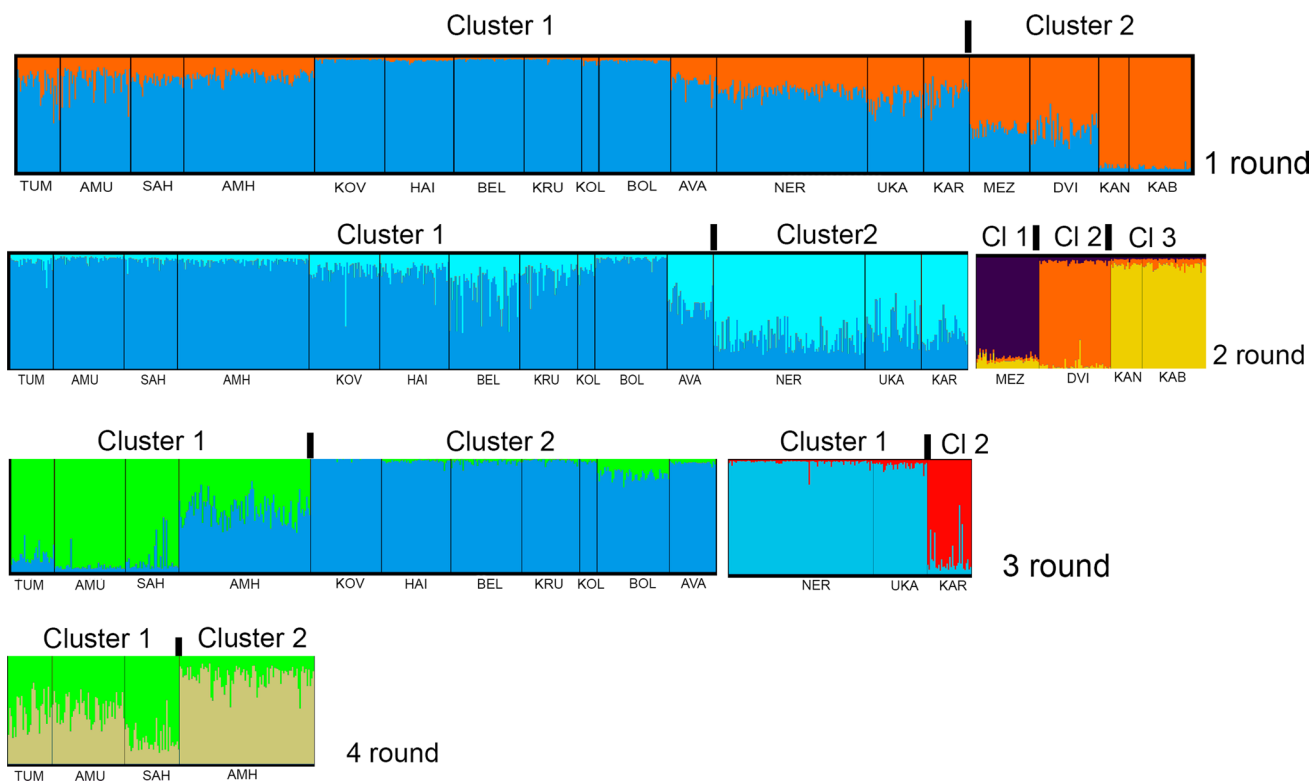
Fig. 2 Population structure of *O. dentex* as estimated from four levels of hierarchical STRUCTURE analysis with $K = 2$ initial clusters. Rows represent the hierarchical approach with subsets of populations separated and re-analysed

Table 4 Analysis of molecular variance (AMOVA) from collections of *O. dentex*

Analysis	Significance test (P-value)		Percentage variation		Fixation indices	
	F_{ST}	R_{ST}	F_{ST}	R_{ST}	F_{ST}	R_{ST}
Analysis #1 Grouping of sea basins						
Among groups	0.000	0.000	4.56	6.07	0.077	0.102
Among population within groups	0.000	0.000	3.23	4.12	0.034	0.043
Within populations	0.000	0.000	92.2	89.8	0.045	0.061
Analysis #2 Grouping of STRUCTURE clusters ($K = 8$)						
Among groups	0.000	0.000	6.31	9.08	0.073	0.096
Among population within groups	0.000	0.071	0.99	0.54	0.010	0.005
Within populations	0.000	0.000	92.7	90.3	0.063	0.091

Discussion

In this study, we revealed considerable genetic diversity and population differentiation in Arctic smelt, following a hierarchical geographic pattern. Genetic differentiation was most pronounced between the Arctic region, and, especially, the population from Kandalaksha Bay (the White Sea), vs the smelt inhabiting basins of the Pacific Ocean. Lower levels of genetic variation within populations from the Kara and White seas were also revealed.

Genetic differentiation among Arctic smelt was considerably stronger than among Pacific populations. The regional differences in gene flow and connectivity within smelt populations of the Arctic and Pacific basins were mainly associated with differences in larval distribution from the spawning grounds due to different oceanographic conditions of the studied areas. These results demonstrate the effect of local contemporary forces in shaping different patterns of genetic connectivity and diversity within *O. dentex*.

Genetic variation within sampling locations

The genetic variation in the Kandalaksha and Dvina bays (the White Sea) were among the lowest we observed, whereas estimates in the Sea of Okhotsk were almost two times greater. A decrease in the molecular diversity in the Arctic region has also been reported in mtDNA-based studies suggesting that the ancestral population had undergone an effective size reduction or a founder effect during re-colonisation (Skurikhina et al. 2015, 2018). These patterns are largely consistent with those of the Pacific herring *Clupea pallasii* and species of the family Osmeridae, *Hypomesus olidus*, which have similar geographic distributions in the Pacific Ocean and the Arctic waters (Semenova et al. 2015; Skurikhina et al. 2019).

The history of glaciations in the Northern hemisphere, environmental conditions, and the species life history appear to have an important influence on the level of genetic variation within *O. dentex*. It has typically shown increased genetic variation within populations located in or near areas of former glacial refuge compared to populations from glaciated areas presumably founded by small numbers of individuals (Bernatchez and Wilson 1998; Costello et al. 2003; Stamford and Taylor 2004). The movement *O. dentex* from the main refuge after the retreat of the glaciers was in the direction from the Sea of Okhotsk to the Bering Sea, and then, to the Kara Sea and occurred through the Bering Strait about < 15 Kya (Taylor and Dodson 1994; Gladenkov and Gladenkov 2004; Dodson et al. 2007; Skurikhina et al. 2018). Decreases in the effective number of smelt populations may have occurred and in modern time, due to the species' habitation in the harsh climate of the Arctic, subject to periodic fluctuations.

Comparisons of F_{ST} and R_{ST} estimates

The results showed that some populations of *O. dentex* were isolated from each other long enough for mutations to cause genetic differences between them (Hardy et al. 2003). It is especially true for the sites from Kandalaksha Bay, and there is a possibility this is caused by a long time of divergence. One likely reason for this may be post-glacial colonisation by ancestral smelt of the White Sea from more than one glacial refuge. The existence of small refuges in the White Sea, in the Late Pleistocene, was previously assumed by Skurikhina et al. (2018). Colonisation from two refuges has also been detected for Atlantic salmon in the White Sea (Tonteri et al. 2005). Moreover, it has been recently reported that a pond smelt, *H. olidus* inhabiting the Barents and Kara seas, might have survived in glacial refuge of the Polar Ural region (Skurikhina et al. 2019).

However, other locations from the Arctic basin demonstrated from one (KAR) to three (MEZ) pairwise R_{ST} larger than F_{ST} compared to the Pacific sites. Also, some locations from the Pacific Basin have significant permutation tests compared to other Pacific populations (Table 3). Estoup and Angers (1998) argued that mutations are expected to have a substantial effect on population divergence only after 2000 generations. Generation lengths for smelt are usually about 2–4 years (Chereshnev et al. 2002; Bugaev 2007), which can be transformed in no less than 4000–8000 years of interspecies divergence. Thus, it can be assumed that the duration of the phylogenetic history of smelt already exceeds the time required to the mutation process to become significant in genetic differentiation and, therefore, the R_{ST} larger than F_{ST} does not necessarily indicate the origin of populations from different refuges.

Genetic population structure of *O. dentex* across the entire range

There were signals of IBD observed for the entire geographical range, as within the Arctic and Pacific basins separately. However, with these analyses, it is difficult to make an inference regarding migration-drift equilibrium, because these results may be due to the restricted gene flow (barrier effect), which contribute a strong IBD pattern (Hutchinson and Templeton 1999; Koizumi et al. 2006). At the small spatial scale, there was no correlation between genetic and geographical distances, excluding Eastern Kamchatka. However, these analyses involved too few populations (from three to seven), so the power of detecting IBD signal may be limited (Jenkins et al. 2010). Nevertheless, it can be assumed that geography (or distance) is one of the main factors determining the population structure of *O. dentex* throughout its large-scale range.

Genetic differentiation was particularly pronounced between populations of the Arctic region and other populations located in the Pacific (Table 3). At the same time, genetic differentiation among the Arctic populations was considerably stronger than among the populations from the Pacific Basin. So, the overall F_{ST} estimate of the Arctic region ($F_{ST} = 0.117$, $R_{ST} = 0.144$) was significantly ($p < 0.001$) greater than for the Sea of Japan/Okhotsk ($F_{ST} = 0.031$, $R_{ST} = 0.031$) or the Bering Sea ($F_{ST} = 0.017$, $R_{ST} = 0.002$).

The overall level of genetic differentiation we observed was similar to that found in related species with analogous life histories, namely *O. mordax*, across the broad-scale including Newfoundland and mainland Canada (Bradbury et al. 2011) and corresponded to the differentiation indices for groups with a moderate genetic structure (Zhivotovsky 1991). Moreover, we demonstrated the various patterns of genetic differentiation within the Arctic and the Pacific geographical areas. A similar spatial genetic structure was also found in *O. mordax*. So, the microsatellite divergence within

the mainland Canada and the USA was an order of magnitude lower than in Newfoundland due to the re-colonisation of the island by two glacial races (Bradbury et al. 2006, 2011; Kovach et al. 2013). Within other anadromous osmerid species the level of geographic differentiation was usually low (McLean and Taylor 2001; Beacham et al. 2005).

The differentiation of smelt in the Pacific Basin

The microsatellites showed significant differences on a large geographic scale between groups from the western coast of Kamchatka (north-eastern Sea of Okhotsk), and the northern (AMH) and southwestern populations that were consistent with the division based on mtDNA (Skurikhina et al. 2015, 2018). The isolation of the southwestern Sea of Okhotsk cluster is also supported by the results of the BARRIER analysis (Online Resource 6). Interestingly, the most considerable mtDNA separation was observed for the Sea of Japan, whereas in our study, the microsatellite differentiation of smelt from the Sea of Japan versus the Sea of Okhotsk was low. According to mtDNA data, the boundary between the diverged populations of the Sea of Japan and the Sea of Okhotsk probably passes in the Nevelskoy Strait (the northern part of Tatar Strait) connecting these seas. The smelt collection areas from the Sea of Japan analysed by Skurikhina et al. (2018) are located almost 400 km to the south of the site (TUM) from our study, which belongs to the Tatar Strait. It can be assumed that the biogeographic border between the seas is located south of the Tatar Strait; however, a more extensive sampling program is needed to clarify the genetic structure and geographical boundaries of *O. dentex* distribution in the Sea of Japan.

The locations collected along the western coast of Kamchatka separated by more than 500 km demonstrated a low level of genetic differentiation and did not follow an IBD pattern. Only the Belogolovaya River (BEL) had significant pairwise F_{ST} and R_{ST} with other Western Kamchatka sites and was differentiated from even its nearest neighbours. According to fisheries statistics and certain morphometric traits of smelt in Western Kamchatka two geographically distinct population groups were defined: the 'northern' group has the main breeding centre in the rivers of the Northwestern Kamchatka [Kovran (KOV), Khairyuzova (HAI), Belogolovaya (BEL), and Moroshechnaya], and the 'southern' group has the main breeding centre in the Bolshaya (BOL) and Kol' (KOL) rivers in the Southwestern Kamchatka (Vasilets et al. 2000; Bugaev et al. 2014). However, the assumption about the independence of smelt groups in the northern and southern areas of the Western Kamchatka was not supported by our data. Moreover, the genetic differentiation between sites in SW and NW Kamchatka was lower in certain cases than differentiation within the locations from the NW coast.

It has been shown for *O. mordax* that gene flow was limited beyond to approximately 200 km (Kovach et al. 2013; Bradbury et al. 2008a). Fish species of the genus *Osmerus* are characterised by short upstream migrations and small pelagic marine larvae that exit the river within hours of hatching (Berg 1948; Nellbring 1989); however, even among the osmerids, the level of gene flow observed in *O. dentex* along the western coast of Kamchatka is high. This indicates that extensive mixing occurs either in the feeding grounds or during larval drift from the spawning site. It is assumed that adult smelt, both *O. mordax* and *O. dentex*, do not make long feeding migrations and population structure is largely determined by the distribution of the early life studies (Baby et al. 1991; Bernatchez and Martin, 1996; Bradbury et al. 2006; Kovach et al. 2013). The number of genetically distinct populations results from the number of distinct larvae retention zones (Baby et al. 1991), which may be determined by geographical, physical, or oceanographic factors. So the genetic similarity of smelt from the Western Kamchatka may be explained by hydrographic factors influenced on larvae dispersal. There is a main West Kamchatka Current (WKC) along the western coast of Kamchatka. The scheme of water circulation in the Sea of Okhotsk is subject to inter-annual dynamics, and in addition to the WKC, in some years an intense shelf current in the South direction is formed (Compensation Current) (Chernyavsky 1981; Khen et al. 2019). The dynamics of currents determine the spatial distribution of fish larvae, so it has been shown that capelin *Mallotus villosus* and pollock *Theragra halcogramma* larvae can be carried far from the coast and widely distributed along the coast of Kamchatka in years of intense WKC action (Varkentin et al. 2001; Naumova and Kolomeitsev 2015). The high similarity of smelt between the sites along the Western Kamchatka is likely due to the intensive circulation patterns.

The differentiation of smelt in the Arctic Region

The Arctic rainbow smelt are characterised by high morpho-ecological variability: several local shoals or even geographic races of smelt are distinguished based on growth and maturation rates, meristic and morphometric indices, and habitats: Kandalaksha, Onega, Dvina, and Czech groups (Kirpichnikov 1935; Altukhov and Yerastova 1974). An early allozymes-based study described genetic isolation for the smelt from Onega Bay of the White Sea, on the one hand, and from Dvina Bay and the South-Eastern Barents Sea, on the other hand (Sendek et al. 2005).

The pairwise estimates among the five locations from the Arctic region using microsatellites were high, and significant allele frequency differences were observed among all sites excluding KAN vs KAB. These data suggest that each location from the different bays of the White and Kara seas represents a genetically distinct population and that the

Kandalaksha Bay contains a single population. The main discontinuities in gene flow defined by BARRIER between each of the bays, well-defined STRUCTURE clustering and the high pairwise F_{ST} and R_{ST} estimates, indicate that little genetic exchange occurs among the population of Arctic basins.

The observed patterns of divergence may indicate that some groups of smelt have colonised Kandalaksha Bay from another ice-age refuge and may represent historically isolated populations preserved at glacial margins during the Pleistocene glaciations. Probably, during the colonisation, the ancient population could be distributed not across the entire White Sea, but along some rivers, such as the rivers in the Kandalaksha Bay. The hypothesis that relict smelt populations inhabit only the Kandalaksha Bay was partially confirmed by the microsatellite data. Thus, the other locations in the White Sea from the Dvina and Mezen bays revealed pairwise estimates of F_{ST} and R_{ST} with populations from the Bering Sea almost three times smaller than those between the Kandalaksha Bay population vs the Bering Sea.

However, historically isolated populations often contain private alleles not observed in other populations (Slatkin 1985; Allendorf and Luikart 2007). But no private alleles were observed in the Kandalaksha Bay population as we might expect if this was a relict population. Furthermore, the distribution of allele size of smelt in the Kandalaksha Bay was consistent with other sites and didn't reveal evidence of a multimodal size distribution for any loci that could also indicate distinct historical origin (Lu et al. 2001; Saint-Laurent et al. 2003).

The combination of low genetic variability in populations of the White Sea and high levels of their interpopulation differentiation could also arise if the populations originated from the same ancestral refuge due to a founder effect and ancient bottleneck (McCauley 1993; Costello et al. 2003). In addition, the patterns of genetic differentiation may be influenced by contemporary factors, such as migration barriers. It has been shown, for example, that for European grayling (*Thymallus thymallus*) post-colonisation divergence of populations could also be effective in the absence of the homogenising effect of migration (Koskinen et al. 2002).

There is almost no possibility for modern mixing between the studied smelt populations in the White Sea. Thus, a very limited distribution of adults from spawning grounds has been shown (Kirpichnokov 1935; Berger 2007). It can also be assumed that there is a limited distribution of smelt larvae from estuarine areas of their native rivers. Unfortunately, large-scale studies of the distribution of smelt larvae in the White Sea have not been carried out; however, for White Sea herring, the restriction of larvae dispersion from the spawning ground was shown (Evseenko and Mishin 2011; Kobylyanskii et al. 2014). The retention of larvae in the shallow waters is due to the specific hydrological characteristics

of the White Sea—the coastal structural frontal zones of increased gradients of the hydrophysical properties. These front zones are quasi-stationary, have different causes of occurrence and are usually expressed only in the spring and summer periods (Pantyulin 2003, 2012), the time of their existence just coincides with the time of stay of smelt larvae in sea waters (Parukhina 2009, 2016). The most obvious role of frontal zones is the barrier function, i.e. the retention of fish larvae within the water area bounded by the front (Sabates and Olivar 1996; Grioche and Koubbi 1997). The important role of frontal zones in forming aggregations of larvae of various species of pelagic fish and their development has been shown in several papers (e.g. Munk et al. 1999). That is largely consistent with the member-vagrant hypothesis (Iles and Sinclair 1982) that the number of genetically distinct populations is determined by the number of distinct larval retention areas. So, barriers to migration of smelt in the early stages of development appear to be an important factor influencing patterns of genetic variability among populations of *O. dentex*.

Stock management

Arctic rainbow smelt is a commercial fish species in the Pacific Ocean, so this genetic data will serve as a basis for making informed decisions on the management of this species in Russia. Our results determine that smelt shows high levels of population subdivision and genetic structure in the Arctic region. Such a high level of genetic subdivision suggests a high level of demographic independence. In addition, low rates of genetic variability of smelt populations in the White Sea may mean a small effective size of these populations and their particular vulnerability to external influences, including anthropogenic factors. Currently, the activity of the fishing industry in the White, Kara, and Laptev seas is reduced due to the socio-economic processes taking place in the country (Stasenkov et al. 2011; Ulchenko et al. 2016; Filatov et al. 2019). Nevertheless, the White Sea fishery should be carefully conducted to conserve the diversity of smelt in each particular bay, because genetically divergent populations are increasingly being recognised as appropriate units for conservation. The state of smelt stocks in different parts of the Pacific Basin is not currently a concern, but there is no doubt that the state of smelt populations needs to be assessed considering the geographic unit that may be genetically distinct (Bugaev et al. 2014; Burlak 2018).

Declarations

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

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