**Spatial variation in the frequency of left-sided morph in flounder**

**Spatial variation in the frequency of left-sided morph in European flounder *Platichthys flesus* (Linnaeus, 1758) from the marginal Arctic (the White Sea)**

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**ABSTRACT**

The European flounder, *Platichthys flesus*, is a polymorphic flatfish exhibiting large population variation in proportion of left-sided and right-sided morphs across its range. Detailed studies of flounder populations within its geographic range can provide valuable information for analyzing spatial patterns of frequencies of the two morphs. We have examined the frequencies of left-sided individuals of flounder in the White Sea (Kandalaksha, Onega, Dvina, and Mezen bays), the region in the northeastern part of species’ range adjacent to the Arctic. The proportion of the two morphs in the populations of the White Sea flounders demonstrated high variability and specific regional characteristics. The highest frequency of left-sided individuals was observed in the northwestern (Kandalaksha Bay) and southwestern (Onega Bay) parts of the White Sea. Flounders living in the eastern part of the White Sea (Dvina and Mezen bays) showed much lower frequency of this trait. No consistent pattern of geographic variation in proportion of the morphs was observed across flounder’s geographic range. Geographic variation in proportion of left-sided individuals in flounder populations is likely to be determined by a set of biotic and abiotic factors whose selective influence acting through trophic relationships of this species with other hydrobionts can differ in different parts of flounder’s geographic range.

**Keywords:** geographical variation, left-sided morph, *Platichthys flesus*,population polymorphism, White Sea

**INTRODUCTION**

The European flounder *Platichthys flesus* (Linnaeus, 1758) (Pleuronectidae) is a marine and brackish species distributed across a wide geographic area that ranges from the western part of the Mediterranean, through the Atlantic coast of Europe, around the British isles and Ireland, across the North, Baltic, Barents and White seas and eastward to the southwestern part of Novaya Zemlya archipelago and Kara Bay of the Kara Sea (Berg, 1932; Andriashev, 1954; Fuks, 2021; Mecklenburg *et al*., 2018). Individuals of this species can be either left-sided or right-sided depending on the side of the body on which the eyes lie at the early developmental stages following the metamorphosis. In the left-sided (reversed) flounders, both eyes are on the left side of the body, while in the right-sided individuals they lie on the right side. Both morphs are present in populations of this species in varying proportions. Crossbreeding studies conducted on the starry flounder *P. stellatus* (Pallas, 1787)*,* a polymorphic congeneric species of *P. flesus*, have shown that body asymmetry direction is under moderate genetic control (Polycansky, 1982; Boklage, 1984).

The studies of lateral polymorphism in the populations of the European flounder are still rather scarce and the majority of information on the frequency of morphs was obtained from the flounders caught in the Baltic Sea off the coasts of Sweden, Germany and Estonia (Apstein, 1905; Duncker, 1900; Fornbacke *et al.*, 2002; Mikelsaar 1958). Fornbacke *et al*. (2002) have reported a clinal change in proportion of left-sided individuals in flounder catches along the coast of Sweden, but the results of other authors on Baltic and North Sea flounders have shown a very high variation in proportion of morphs in different populations (Duncker, 1900; Galleguillos, Ward, 1982; Mikelsaar, 1958; Redeke, 1915; *etc.*). In the White Sea, the relative frequency of reversed individuals was measured for some most numerous flounder populations from Kandalaksha (Velikaya Salma Strait), Onega, Dvina and Mezen bays (Dietrich, 2009; Nikolaev, 1949; Semushin *et al.,* 2015; Shatunovsky, 1964). However, for the White Sea flounders our knowledge of regional variation in this trait remains incomplete because of the paucity of information on the flounder populations inhabiting the western part of the sea and because of the lack of statistical estimation of the observed variation in this trait among the samples studied by different authors. Кроме того, изучение особенностей фенотипического разнообразия у камбалы, обитающей на краю северо-восточной части ареала на границе с Арктикой представляет особый интерес с точки зрения анализа адаптивной роли латерального полиморфизма у *P.flesus* в экстремальных habitats. No analysis has yet been conducted to date of the geographic patterns of variation in frequency of lateral morphs in *P.flesus* populations across the species range. Such data are necessary to study various mechanisms of maintaining lateral polymorphism in fishes this species.

The primary goals of the present study were: 1) to analyse spatial variation in proportion of the two morphs in flounders from different bays of the White Sea; 2) to evaluate large-scale geographic variation in proportion of left- and right-sided morphs in flounder populations across the geographic range of the species.

**MATERIALS AND METHODS**

Specimens of *Platichthys flesus* for this study were collected in different bays of the White Sea during regular expeditions made by the Polar branch of the VNIRO and the Zoological Institute of the Russian Academy of Sciences (May-August 2013-2021). In Kandalaksha Bay, fish were caught in the Chupa Inlet, totaling 584 individuals (Fig.1). In Onega Bay, flounders were collected in two locations - at the head of the bay near Kyi island, situated in the mouth of Onega river (n=1310), and in the mouth of Nyukhcha river (n=1144). In Dvina and Mezen bays, fish were caught in the estuarine zones of Northern Dvina (n=2613) and Mezen rivers (n=905). For the generalized comparative analysis, the material collected during the present study was supplemented by data on previous catches made in 2001-2012 in Onega, Dvina and Mezen bays (collections of G.Fuks and other staff of the SevPINRO (Arkhangelsk); Semushin *et al*., 2015). Flounders were collected in rivers and coastal waters at different depths using variable mesh gillnets (mesh size of 30-50 mm) and traps.

The total body length (*TL*) of all freshly caught flounders was measured to the nearest 0.1 cm. The number of left- and right-sided individuals was counted in all samples. The sex of flounders was determined visually after their dissection. Student's t-test was used to compare mean body sizes of fish. Bonferroni's correction was applied to adjust the significance level for multiple comparisons (Quinn & Keough, 2002). Comparison between proportions of morphs for flounders caught at different collection points was performed using χ2 test (Quinn, Keough, 2002). Because the males and females showed no difference in frequency of morphs (Semushin *et al*., 2015), the comparison of samples was performed without differentiating for sex.

**RESULTS**

The proportion of left-sided individuals in flounder samples from different bays of the White Sea ranged from 3.3% to 28.4% (Fig. 1). The highest frequencies of left-sided flounders were recorded in a population from Kandalaksha Bay (Chupa Inlet). The frequencies of reversed individuals in the samples taken from two different places in southern part of Onega Bay varied from 19.8% (Nyukhcha river area) to 21.0 % (Kyi island area, Onega river) and had equal values (χ2=0.64, *р*>0.05). For further analysis, the data on flounder catches from these locations in Onega Bay were pooled into a single dataset. The comparison of populations from the northwestern (Chupa Inlet, Kandalaksha Bay) and southwestern (Nyukhcha river, Kyi island area and Onega river; Onega Bay) parts of the White Sea revealed the difference in morph proportions between these two regions (28.4% and 20.7%, respectively; χ2=18.33, *р*<0.01). The frequencies of reversed individuals in the populations from the eastern part of the White Sea (Dvina and Mezen bays) were several times lower and ranged from 3.3% to 5.2% (Fig. 1). Differences between populations from these regions were statistically significant (χ2=11.89, *р*<0.01). Left-sided individuals were least frequent in the population from Mezen Bay.

The sex ratios in the population of Mezen and Kandalaksha bays were equal (1:1), but other two populations were dominated by females (Onega Bay, χ2= 53.8, *p*<0.05; Dvina Bay, χ2= 200.7, *p*<0.05). In all samples, the sex ratio among left-sided individuals was not significantly different from that of right-sided individuals (0.34<χ2<3.61, *р*>0.05).

In each region, the average body lengths of the individuals of the same sex were not significantly different between the left- and right-sided flounders (Table 1, *t*-test, *p*>0.05). The body length ranges of flounders from studied populations in the White Sea were similar.

Fig. 2 shows the frequencies of reversed individuals in the populations of the European flounder from the White Sea and other parts of its geographic distribution. In Kandalaksha Bay, flounders from Chupa Inlet differed significantly from those of the Velikaya Salma Strait (χ2=12.18, *р*<0.01; Fig.2, Table 2, # 1, 5). Flounders from two different areas of Onega Bay (Fig.2, Table 2, # 32, 33) were similar in frequency to one another and also to the flounders from Chupa Inlet (0.38<χ2<0.48, *р*>0.05). ). Flounders from two close locations at the western coast of Onega Bay – Kuz Inlet and Kolezhma river (Fig.2, Table 2, # 32, 33) were similar in frequency of left-sided morph to one another and also to the flounders from Chupa Inlet (0.38<χ2<0.48, *р*>0.05). Besides, frequencies of left-sided individuals in samples from Kuz Inlet and Kolezhma river were significantly higher than in samples taken in the southern part of the same bay (Fig.2, Table 2, # 2).

Камбалы из двух участков западного побережья Онежского залива – Куз-губы и р.Колежма (там же, № 2, 32, 33), продемонстрировали сходство между собой и с камбалой из губы Чупа по рассматриваемому признаку (0.38<χ2<0.48, *р*>0.05). Вместе с тем, у камбал из популяций, обитающих в южной части Онежского залива (р.Нюхча, район р.Онега), левосторонние особи встречались гораздо реже. Полученные нами данные по камбале Двинского и Мезенского заливов не отличались достоверно от опубликованных сведений по доле реверсивных особей в этих популяциях (0.20<χ2<0.80, *р*>0.05; там же, № 3, 4, 24, 34, 35).

Our results on flounders from Dvina and Mezen bays were not significantly different from published data on frequency of reversed individuals in these populations (0.20<χ2<2.15, *р*>0.05; Fig.2, Table 2, # 3, 4, 24, 34, 35). По обобщенным данным (опубликованные + наши оригинальные) популяции камбалы из этих заливов достоверно различаются по частотам морф (χ2=10.33, *р*<0.01)

χ2=21.61, *р*<0.01 кут – колежма, куз

χ2=0.12, *р>*0.05 чупа- колежма, куз

The analysis of the published data on frequency of reversed individuals from flounder’s geographic range has shown that all the studied populations were polymorphic and the frequency of left-sided individuals was not higher than 50% (Table 2). The highest frequency of left-sided individuals was found for the sample from the Murmansk coast of the Barents Sea (44.5%; table 2, # 14) and the southwestern (42.7%; German coast, Kiel, Eckernforde; # 6) and eastern (39.5%; Estonian coast; # 12) parts of the Baltic Sea (Fig. 2). In addition to the flounder populations from Dvina and Mezen bays of the White Sea, the lowest frequencies of this trait (4.7-7.5%) were also observed in some areas of the coastal waters of Great Britain and Ireland (Table 2; # 11, 15, 17, 19, 22, 37). No apparent geographic trend was found for the changes in proportion of left-sided individuals in flounder populations.

**DISCUSSION**

The comparison between the results of the present study and previously published data (Shatunovsky, 1964; Dietrich, 2009) has revealed differences in proportion of left-sided individuals in flounders living in different parts of Kandalaksha Bay of the White Sea (Chupa Inlet and the Velikaya Salma Strait), with this proportion being significantly higher in flounders from the Velikaya Salma Strait located about 30 km northwest of Chupa Inlet (Table 2). Previously, the flounders from these populations have also been shown to differ in certain meristic characters: the number of fin rays and lateral line pores (Yershov, Matvienko, 2018). The spatial isolation and morpho-ecological differentiation of flounders in Kandalaksha Bay of the White Sea is determined to a significant extent by geomorphological and hydrological characteristics of the region (numerous inlets, rivers with estuarine zones, shallow-water areas, etc.) which provide variety of habitats for fish and restrict gene flow between populations around the coast.

Flounders from Kuz Inlet (Nikolaev, 1949) and the Kolezhma river (Mikelsaar, 1958) from the one side and the fishes from other studied areas of Onega Bay - Nyukhcha river and Kiy island area the other (our data) showed clear difference in morph frequencies (χ2=21.61, *р*<0.01 кут – колежма, куз). This gives evidence that two separated populations of flounder exist in these two studied areas of Onega Bay. Most probably local cyclonic currents and skerry nature of the costline on the western side of bay favour separation of populations. Это свидетельствует о наличии обособленных популяций камбалы в рассматриваемых двух районах Онежского залива. Скорее всего, обособлению популяций камбал способствуют локальные циклонические течения в исследованных акваториях (……….), а также шхерный характер береговой линии на западном побережье залива. Alongside with that, it is likely that some flounder populations in Onega Bay experience intensive genetic exchange as a result of the overlap between extensive nursery grounds for immature fish during the summer, especially in the head region of the bay. Moreover, significant intermixing of individuals from different populations is further facilitated by the characteristics of the hydrological regime of the bay. This area is known to have strong tidal currents (Filatov, Terzhevik, 2007), that disperse pelagic eggs of flounders over significant distances after the spring-summer spawning period. According to the ichthyoplankton surveys conducted in different years in Onega Bay, the eggs of the European flounder are encountered over the major portion of this area (Altukhov, 1980; Mishin *et al*., 2018; Parukhina 2007, 2015).

Камбала, обитающая в водах западного побережья Онежского залива - Куз-губа (Nikolaev 1949), р. Колежма (Mikelsaar 1958), достоверно отличалась по соотношению морф от камбал из южной части этого же залива (р. Нюхча, р.Онега, Кий-остров, наши данные). Между локальными популяциями камбалы в каждом из этих районов Онежского залива, по-видимому, происходит довольно интенсивный обмен генами вследствие общности обширных нагульных площадей для неполовозрелых рыб в летний период. Кроме того, значительному перемешиванию особей из разных популяций способствуют и особенности гидрологического режима залива в целом. Известно, что для данной акватории Белого моря характерны сильные приливные течения (Filatov and Terzhevik 2007), которые разносят пелагические икринки камбалы на значительные расстояния после весенне-летнего нереста рыб. По данным ихтиопланктонных съемок, сделанных в Онежском заливе в разные годы, икринки речной камбалы встречаются на большей части площади его акватории (Altukhov 1980; Mishin *et al*. 2018; Parukhina 2007, 2015).

Semushin *et al*. (2015) have reported that the proportion of left-sided individuals in the flounder populations inhabiting the White Sea region decreases from west to east. Additional data provided by the present study have shown that the left-sided individuals are most common in the northwestern part of the White Sea (Velikaya Salma, Kandalaksha Bay). In Chupa Inlet located more to the south along the Karelian coast of Kandalaksha Bay and in Onega Bay, the proportion of left-sided fish in the populations is somewhat lower. ВСТАВКА A significant decrease in proportion of left-sided flounders is observed in Dvina Bay, and the lowest proportion of reversed individuals occurs in Mezen Bay. Given the quantitative characteristics of this trait, it can be concluded that the frequency of left-sided individuals is much higher in the flounder populations from Kandalaksha and Onega bays than in those from Dvina and Mezen bays. It is noteworthy that changes in frequency between these two groups of populations occur abruptly rather than in a gradual fashion. It should be also noted that along the coast of the White Sea between estuaries of the large rivers Northern Dvina, Onega and Mezen the flounder is not numerous and is encountered in small numbers mostly on shoals near estuaries of small rivers.

Another pattern of geographic variation in this trait was found by Fornbacke *et al*. (2002) for the flounders living in the western part of the Baltic Sea. The frequency of left-sided flounders in the 6 samples studied decreased gradually from the western coast of Sweden (27.5%), across its southeastern part (22.4%) and then in the northern direction (20.1%). The authors concluded that variation in this trait showed a biogeographic cline along the coast of Sweden. In our opinion, however, this statement calls for further research, because of the uneven sampling across the study area. For instance, this study lacks any data for the coastal waters of the vast part southern coast of Sweden. Four samples taken from different points along the eastern coast of Sweden showed no statistically significant difference (0.1<χ2<0.51, *р*>0.05; our calculations). The only differences in proportion of reversed individuals that were statistically significant were found between 2 samples from the western coast of Sweden (Stromstad, Lysekil) and one sample from the eastern coast (island Oland) (calculated from Fornbacke *et al*., 2002), which indicates above all the existence of populational differences between flounders from these two sampling areas.

Data on variation in frequency of reversed individuals in catches from the eastern part of the Baltic Sea has been provided by Mikelsaar (1958). The frequency of left-sided individuals in the 15 samples from the Estonian coast (n ≥ 200 ind. each) ranged from 22.5% to 39.5%, with an average value of 36.6% of total number of the individuals studied. Mikelsaar (1958), however, has not revealed any consistent pattern of variation in frequency of reversed individuals caught in different parts of the study area. It should be noted that local variability in frequency of left-sided flounders along the Estonian coast was much higher than in the coastal waters of Sweden.

The analysis of morphological polymorphism across the geographic range of European flounder has demonstrated a high populational variation in proportion of reversed individuals. No consistent geographic trend has been observed for variation in this trait among the studied populations from the coastal waters of North Europe. Judging from the available information, however, the reversed individuals are least frequent in the populations living on the western and eastern margins of flounder’s geographic range (Fig.2).

Possible causes producing interpopulation variation in proportion of morphs of the European flounder remain little explored. Fornbacke *et al.* (2002) have suggested that variation in frequency of left-sided individuals in the samples of flounders along the coast of Sweden is associated with interspecific interactions of young individuals of this species with those of the European plaice *Pleuronectes platessa* Linnaeus, 1758. These authors have argued that food competition of plaice fry on nursery grounds of the Skagerrak Strait is more intense with the right-sided individuals of flounder than with the left-sided individuals. This results in increased survival of the left-sided individuals on the west coast of Sweden, where the numbers of plaice fry in shallow water are high. The authors regarded a larger body size of left-sided fry compared to the right-sided individuals as indirect evidence of the advantage that the left-sided individuals have in using food resources. However, the results of the present study and previously published data suggest that variation in proportion of morphs in some other parts of flounder’s geographic range cannot be explained by the possible influence of competition with the European plaice. The average frequency of reversed individuals in flounders inhabiting the eastern part of the Baltic Sea (Estonian coast), where the plaice is rare (Mikelsaar, 1958; Ojaveer *et al*., 2003), is much higher than in flounders from the western coastline of Sweden, where the plaice is abundant in shallow water. In the White Sea, the highest frequency of left-sided flounders was recorded in Kandalaksha and Onega bays, where the plaices are only sporadically caught by fishing gears and their numbers are extremely low (Nikolaev, 1951; Mukhomedyarov, 1963; our observations). It is clear that increased survival of left-sided flounders in these parts of the geographic range is caused by some other factors. As regards the differences in size of fry between left- and right-sided individuals (Fornbacke *et al*., 2002), they can, in our opinion, be associated not only with differences in their growth rates as a result of the interspecific competition with plaice fry, but also with different hatching times due to a more extended spawning season in flounder. The spawning period of flounder normally lasts about 1 month and its duration varies in different parts of the Baltic Sea (Berg, 1949; Florin, 2005; Nissling, Dahlman, 2010; Ojaveer *et al.,* 2003).

In different parts of flounder’s geographic range, the interspecific competition resulting in preferential selection of morphs can also be associated with fish species other than plaice. In the shallow coastal waters of the White Sea, the flounder is known to cohabit with other benthophagous species: the Arctic flounder *Liopsetta glacialis* (Pallas, 1776) and the dab *Limanda limanda* (Linnaeus, 1758) (Altukhov *et al*., 1958; White Sea, 1995). Shatunovsky & Chestnova (1970) have shown that in the inlets of Kandalaksha Bay, where the Arctic flounder is relatively abundant, the young European flounder (*TL*<20 cm) compete with this species for food, and the food spectra of fishes of the two species can overlap by 60-70%. However, the information about possible differences in composition of food consumed by different morphs of the European flounder compared to the Arctic flounder is still lacking. Further studies of dietary habits and behavior in shared nursery areas are needed to evaluate the possible influence of competition with the plaice and other species of flatfish on survival of morphs of the European flounder during their first years (0+ and 1+) of life.

Another factor that is likely to influence spatial variation in flounder polymorphism is ecological selection between morphs in individual populations. Russo *et al*. (2012), for example, have revealed intrapopulation differences in food spectra between left- and right-sided individuals of flounders in Dublin Bay (Ireland). The morphs also showed some morphological differences in relative sizes of the premaxillare, the length of the tail peduncle and the position of eyes, i.e. the characters that play a role in targeting and capturing prey items. The authors have argued that the frequency of morphs can be dependent to a certain extent on characteristics of benthic food resources and the accessibility of certain food organisms, because the left- and right-sided individuals showed preference toward different dietary objects. It remains to be determined to what extent these differences in the composition of prey organisms are important for survival, growth, and fecundity of fish and whether there are ecological differences between two morphs in various regions of flounder geographic range. It should be noted that morphological differences in feeding habits, behavior and swimming have previously been found between the morphs of the starry flounder *P. stellatus* (Pallas, 1787), which suggested the existence of trophic specialization in the right- and left-sided individuals (Bengstrom, 2007; Bengstrom, Palmer, 2007; Bergstrom *et al.,* 2019).

Fornbacke *et al*. (2002) have noted that variation in proportion of left-sided adult flounders along the coast of Sweden correlates with the salinity gradient of the coastal waters. Over the last two decades, the basin of the Baltic Sea experienced major ecological changes due to eutrophication, intensive fishing, global climate change and other factors (Elmgren, 2001; Korpinen *et al.*, 2012; Olsson *et al.,* 2012). Negative trends in ecological health result in degradation of habitats of many fish species including the European flounder. In the early 2000s, a dramatic fall in numbers and biomass of the European flounder was observed in the northern part of the Baltic Sea (Jokinen et al., 2015). It is clear that in this situation the similarity in trends observed for changes in biological traits of fish and certain hydrological data do not necessarily imply any consistent relationship between these factors in the study area and the observed correlations should be treated with caution. Experimental studies are required to confirm the presumed relationship and determine the direction of natural selection. In our opinion, variations in water temperature and salinity can undoubtedly influence mortality of flounder in coastal waters, but the main influence of these factors is indirect, i.e. through qualitative changes in those environmental conditions that play a role in successful fish spawning, feeding and growth.

To sum up, it should be stressed that populations of *P. flesus* living in the White Sea and other parts of flounder’s geographic range are likely to be affected by factors of natural selection specific for each area that influence the proportion of left- and right-sided fish.

Подводя итог сказанному следует подчеркнуть, что в бассейне Белого моря и других частях ареала, по-видимому, действуют свои специфические факторы естественного отбора, влияющие на соотношение лево- и правосторонних рыб в популяциях *P. flesus*.

Future studies should therefore be aimed at the analysis of adaptive strategy and ecological segregation of flounder morphs as a result of dynamic relationships with the environment and competitive biotic interactions with other fish species in different parts of flounder’s geographic range.

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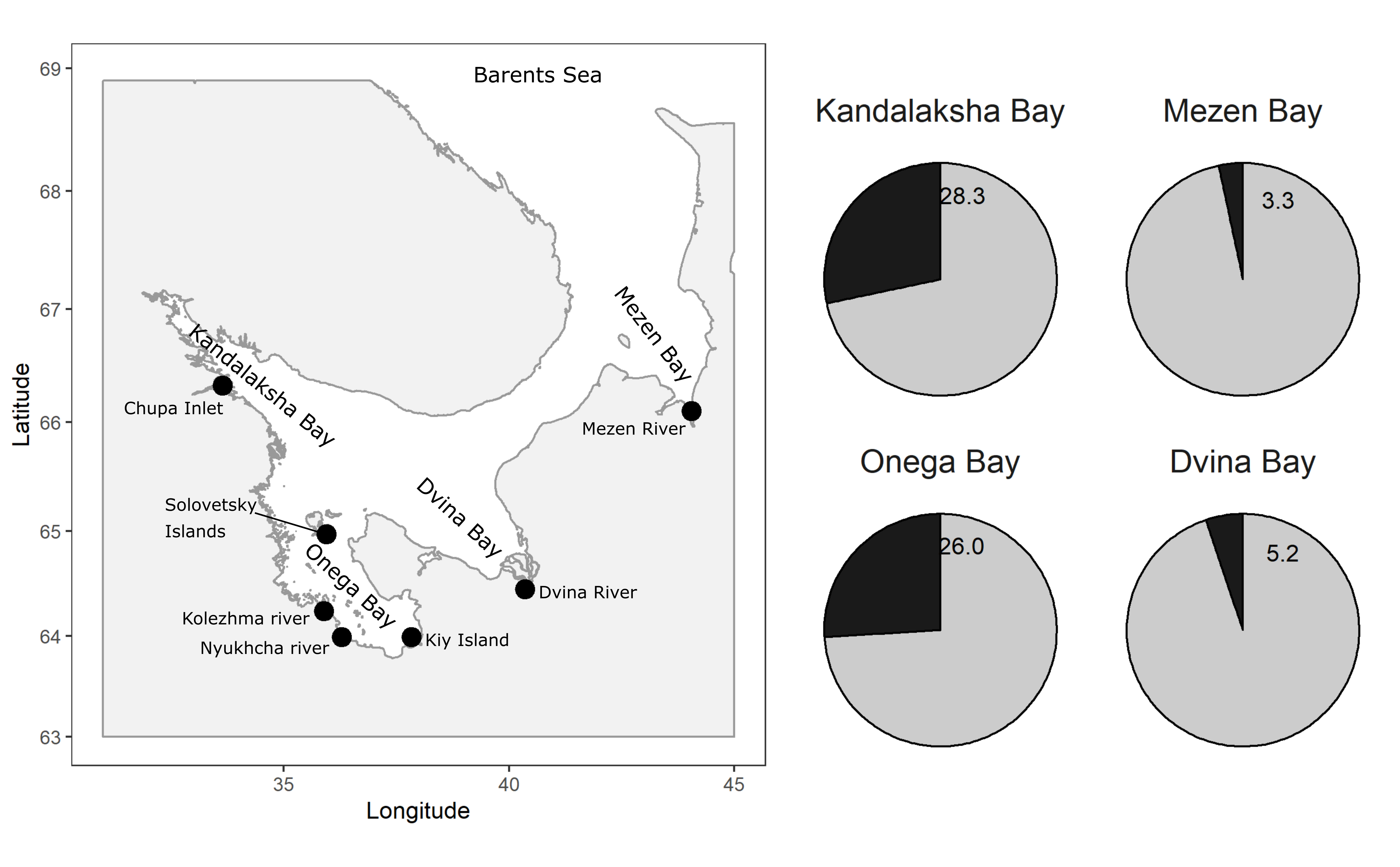
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**FIGURE CAPTIONS**

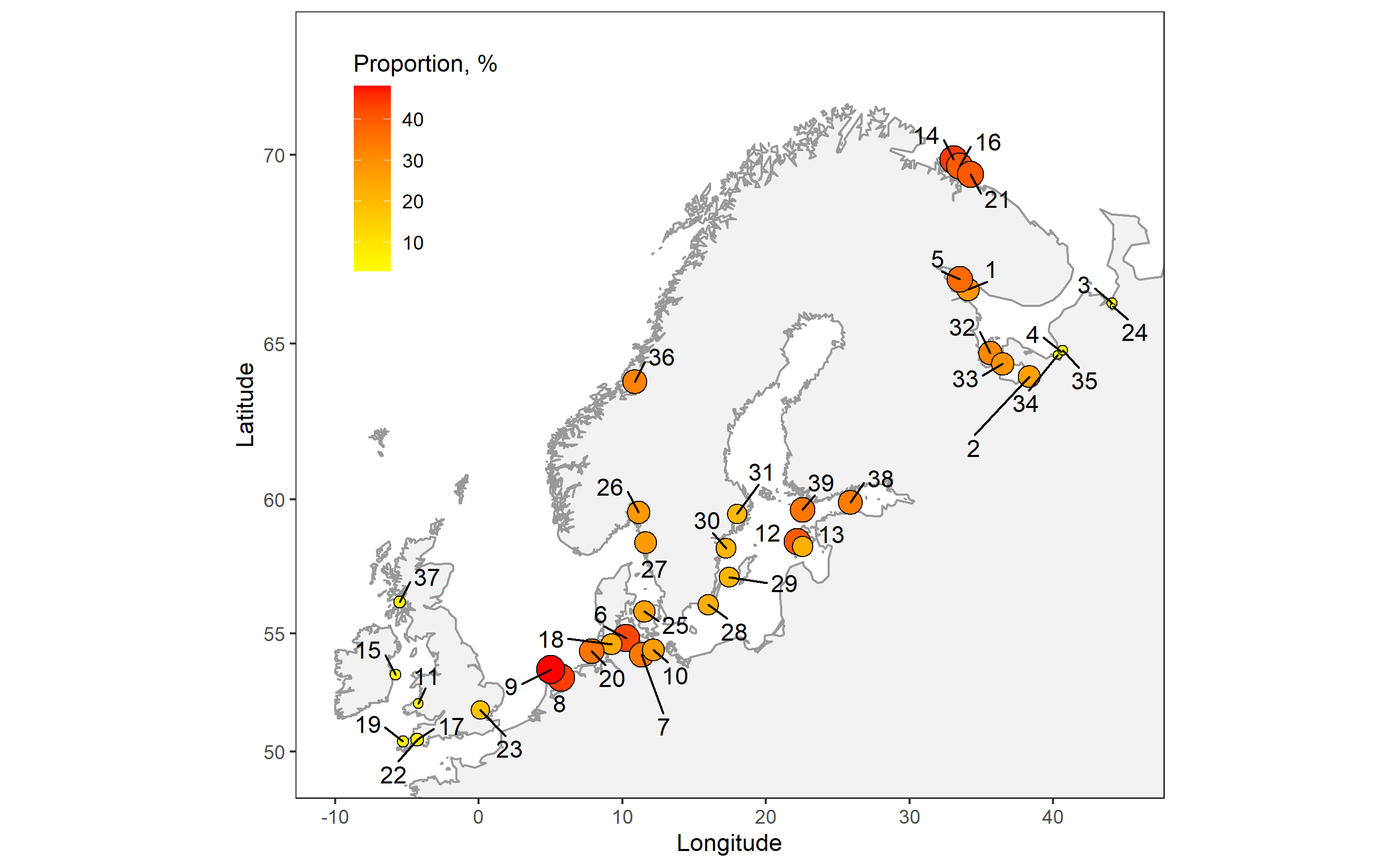
**Fig. 1.** Map showing the sampling areas in the White Sea. Frequency of left-sided *Platichthys*

*flesus* (%, black sectors) morph from the four bays of the White Sea.



**Fig. 2.** Geographical variation in the proportions of left-sided *Platichthys flesus* morph across

its range. The size of the circles corresponds to the proportion of left-sided individuals in a sample. Data sources are given in Table 2.



**TABLES**

**Тable 1.** Length (cm) of *Platichthys flesus* morphs of different sexes from four bays of the White Sea (Mean ± SE and range (min – max))

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Bay | Female Left | Female Right | Male Left | Male Right |
| Kandalaksha Bay | 27.6 ± 1.03  16.0 – 38.2 | 26.3 ± 0.60  16.6 – 42.5 | 23.0 ± 0.44  14.3 – 32.4 | 22.5 ± 0.37  13.0 – 34.1 |
| Onega Bay | 20.4 ± 0.26  7.0 – 41.1 | 19.5 ± 0.15  7.1 – 44 | 17.3 ± 0.23  6.9 – 33.6 | 16.4 ± 0.13  6.6 – 34.2 |
| Dvina Bay | 21.3 ± 0.37  9.4 – 35.1 | 21.9 ± 0.10  5.1 – 48.3 | 18.5 ± 0.39  9.3 – 28.2 | 18.1 ± 0.07  7.5 – 36.7 |
| Mezen Bay | 20.2 ± 0.97  10.8 – 34.0 | 18.7 ± 0.17  7.2 – 41.2 | 16.7 ± 0.52  10.6 – 25.0 | 16.9 ± 0.11  9.1 – 30.4 |

**Table 2.** Proportions of left-sided *Platichthys flesus* morph in various populations based on the

published and original data

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| No | **Locality** | **Sample size** | **Left, %** | **Author** |
| 1 | Chupa Inlet, Kandalaksha Bay, White Sea, Russia | 584 | 28,4 | Present study |
| 2 | Onega Bay, White Sea, Russia | 4403 | 20,7 | Present study |
| 3 | Mezen river, Mezen Bay, White Sea, Russia | 2272 | 3,3 | Present study |
| 4 | Delta of the Northern Dvina river, Dvina Bay, White Sea, Russia | 5007 | 5,2 | Present study |
| 5 | Velikaya Salma Strait, Kandalaksha Bay, White Sea, Russia | 957 | 37,1 | Shatunovsky, 1964; Dietrich, 2009 |
| 6 | Eckernforde Bay; Laboe (Kiel), Baltic Sea, Germany | 3331 | 42,7 | Apstein, 1905 |
| 7 | Neustadt Bay, Baltic Sea, Germany | 90 | 34,4 | Duncker, 1900 |
| 8 | Zuiderzee, North Sea, Netherlands | 50 | 44 | Redeke, 1915 |
| 9 | Den Helder, North Sea, Netherlands | 75 | 48 | Redeke, 1915 |
| 10 | Rostock, Baltic Sea, Germany | 15 | 26,7 | Momigliano *et al*., 2018 |
| 11 | Loughor estuary, South Wales, UK | 64 | 4,7 | Galleguillos & Ward, 1982 |
| 12 | Sorve peninsula, Saaremaa, Baltic Sea, Estonia | 200 | 39,5 | Mikelsaar, 1958 |
| 13 | Mandjala, Saaremaa, Baltic Sea, Estonia | 200 | 22,5 | Mikelsaar, 1958 |
| 14 | Murman coast, Barents Sea, Russia | 475 | 44,5 | Sych, 1930 |
| 15 | North Bull Island, Dublin Bay, Irish Sea | 590 | 5,6 | Russo *et al.*, 2012 |
| 16 | Murman coast, Barents Sea, Russia | no data | 39,6 | Suvorov, 1926 |
| 17 | English Channel, Plymouth, UK | 1120 | 5,4 | Duncker, 1900 |
| 18 | Elbe river mouth, North Sea, Germany | 225 | 23,6 | Duncker, 1900 |
| 19 | Mevagissey harbour, UK | 192 | 5,7 | Duncker, 1900 |
| 20 | Langeoog, Wadden Sea, North Sea, Germany | 26 | 35 | Voronina, 1999 |
| 21 | Murman coast, Barents Sea, Russia | 25 | 40 | Voronina, 1999 |
| 22 | English Channel, Plymouth, UK | 40 | 7,5 | Galleguillos & Ward, 1982 |
| 23 | Thames estuary, London, UK | 50 | 18 | Galleguillos & Ward, 1982 |
| 24 | Mezen Bay, White Sea, Russia | 1367 | 3,1 | Semushin *et al.*, 2015 |
| 25 | Danish Belt Sea | 49 | 25,4 | Galleguillos & Ward, 1982 |
| 26 | Stromstad, Skagerrak, Sweden | 455 | 27,5 | Fornbacke *et al*., 2002 |
| 27 | Lysekil, Skagerrak, Sweden | 653 | 27 | Fornbacke *et al*., 2002 |
| 28 | Karlskrona, Baltic Sea, Sweden | 631 | 22,4 | Fornbacke *et al.,* 2002 |
| 29 | Oland, Baltic Sea, Sweden | 1673 | 21,1 | Fornbacke *et al.*, 2002 |
| 30 | Vastervik, Baltic Sea, Sweden | 193 | 21,2 | Fornbacke *et al*., 2002 |
| 31 | Nynashamn, Baltic Sea, Sweden | 186 | 20,1 | Fornbacke *et al.*, 2002 |
| 32 | Kuz Inlet, Onega Bay, White Sea, Russia | 187 | 31,3 | Nikolaev, 1949 |
| 33 | Kolezhma river, Onega Bay, White Sea, Russia | 358 | 28,5 | Mikelsaar, 1958 |
| 34 | Delta of the Northern Dvina river, White Sea, Russia | 897 | 4 | Dietrich, 2009 |
| 35 | Delta of the Northern Dvina river, White Sea, Russia | 2394 | 4,7 | Semushin *et al*., 2015 |
| 36 | Trondheimsfjord, Norway | 269 | 32,3 | Nordgaard, 1915 |
| 37 | Millport, Cumbrae, Scottish coast, UK | no data | 6,7 | Elmhirst, 1911 |
| 38 | Pudisoo, Baltic Sea, Estonia | 1271 | 33,1 | Mikelsaar, 1958 |
| 39 | Hiiumaa, Baltic Sea, Estonia | 800 | 35 | Mikelsaar, 1958 |