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The genetic population structure

of the blue whiting (Micromesistius poutassou)

Jarle Mork & Marianne Giæver [1]

Biological Station, N-7018 Trondheim, Norway

ABSTRACT

The genetic population structure of the blue whiting was studied by means of enzyme electrophoresis. Most of the Eastern Atlantic distribution range of the species was covered by samples from the Barents Sea in the north to the inner Mediterranean (Greece) waters in the south-east.

Genetic heterogeneity was generally low between samples from the spawning areas west of the British Isles. Inner Mediterranean blue whiting deviated somewhat genetically, and a genetic substructure on a west-east axis north of the British Isles was also indicated. However, the most striking trait in the material was the deviating gene frequencies of the blue whiting from northern Norway and the Barents Sea, which showed very significant signs of being a reproductively isolated stock.

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[1]) Authorship equal

INTRODUCTION

The blue whiting (Micromesistius poutassou Risso 1810) is a pelagic marine gadoid with a widespread distribution along the continental slopes of the North Atlantic. In the western Atlantic it is found patchwise from West Greenland to 40°N (SE of Newfoundland) and on the eastern side continuosly from Spitsbergen (82°N) to the Canary Islands (26°N) (Zilanov 1980; Fig. 1). The blue whiting is also present in the Mediterranean to about 27°E. In terms of biomass the blue whiting is one of the most abundant teleosts in the North Atlantic, and it's commercial significance has been increasing. In 1979 and 1980 annual landings exceeded one million tonnes, and from 1980 and on they have regularly been on more than half a million tonnes (Monstad 1990).

Depending on latitude, spawning takes place from February (in the south) to April. The largest spawning aggregations are found along the continental slope and on the banks west of The British Isles. In 1992 the spawning stock in that area was assessed to 4,3 million tonnes (Monstad et al. 1992). Smaller spawning aggregations has also been reported, e.g. in the Mediterranean and in Norwegian fjords (Froglia & Gramitto 1981; Bailey 1982). Eggs and larvae are pelagic and are carried by currents to the nursery areas, which appear to be in shallower areas at the fringes of the adult population's range (Bailey 1982).

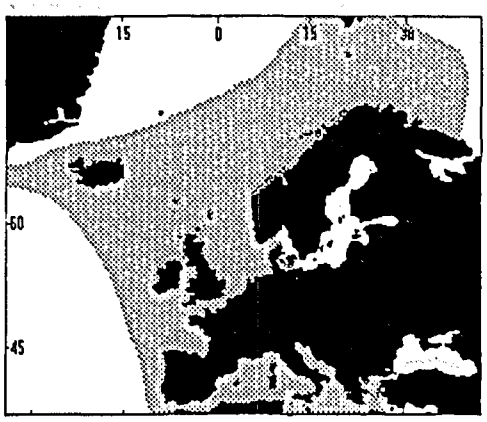

Figure 1. Blue whiting distribution in the eastern Atlantic and the Mediterranean (modified from Zilanov (1984)).

The eastern Atlantic blue whiting reaches maturity between 2 and 8 years of age. Body length can be up to 50 cm although the largest specimens in spawnings stock samples usually measure 35-40 cm. Adult blue whiting feeds mainly on pelagic crustaceans and fishes (Bailey 1982).

Resource management of the atlantic blue whiting has been complicated by insufficent knowledge about its population structure. Apparently, the group- or shoal affinity of blue whiting is size- and/or sex-dependent and hence, common sampling methods tend to give biased measures of stock parameters like growth rates and maturity age (Bailey 1982).

Studies particularly devoted to the population structure problem have focused on comparison of parasite types and infestation rates (Karasev 1990), morphometrics and meristic characters (Aloncle & Colignon 1964; Kandler & Kieckhafer 1966; Cendrero 1967; Robles 1968; Sahrage & Schøne 1975; Schultz et al. 1978; Isaev & Seliverstov 1991), and frequencies of certain eye lense proteins in electrophoretic analyses (Bussman 1985). The conclusions in these studies can be summarized as followes:

* **The "Karasev model"** assumes three separate blue whiting stocks in the areas (1) Spitzbergen, Barents Sea, and Iceland, (2) Norwegian Sea, Faroes, and Hebrides, (3) Porcupine Bank, Celtic Sea, Bay of Biscay, and Shetland.
* **The "Zilanov model"** suggests four stocks: (1) The Mediterranean, (2) the west Atlantic, (3) the Bay of Biscay, (4) the Hebrido-Norwegian stock.
* **The "Isaev & Seliverstov model"** recognizes five stocks: (1) The Mediterranean, (2) the west Atlantic, (3) the Bay of Biscay, (4) the Porcupine, (5) the Hebridean stock.

On background of the substantial uncertainty about the true genetic population structure of blue whiting, the management recommendations by ICES have been based on a very simple ad hoc model considering only two stocks; the "southern" and the "northern" stock, with a somewhat arbitrary separation line drawn along the 50th latitude. Thus,

* **the "ICES" model** considers two stocks with a separation line at 50°N.

Bussman (1984), who compared blue whiting from Spitzbergen, Iceland, the Faroes, and west of the British Isles, concluded that all these stocks were reproductively isolated.

Population genetic studies on blue whiting stock structure are few. The study of Bussman (1984) on frequencies of certain eye-lense proteins is not really genetic since a genetic basis for the variation was not established. That restriction does not apply to the study by Møller & Nævdal (1969) which described a haemoglobin polymorphism in blue whiting. However, the allele frequencies reported in their study where from only one location (the northern North Sea).
The present study applied population genetics methods on samples from most parts of the species' range. The object was to investigate the potential of tissue enzyme polymorphisms for revealing the genetic population structure of the blue whiting, and to test various biologically based models of it's stock structure against genetic data.

MATERIALS AND METHODS

Samples of blue whiting were obtained from 18 areas by bottom and pelagic trawl during cruises with the Norwegian vessels R/V "Johan Hjort", R/V "G.O.Sars", R/V "Johan Ruud" and the Greek vessel R/V "Ioannis Rossos" (Fig. 2 and Table 1). Most samples consisted of specimens from only one trawl hawl. However, the samples Ba1 and Ba2 contained fish from several hawls, and the Gibraltar and Biscay samples were from commercial catches bought on the fish markets in Marbella and Santander, respectively. Length, weight, sex and age (otolith readings done by staff at the Institute of Marine Research, Bergen) were recorded for each specimen. For the blue whiting taken in the spawning areas west of the British Isles the maturity stage was determined by examination of the gonads according to Anon. (1979). Tissue samples (liver and muscle) for starch gel electrophoresis were cut out immediately after catch and brought to the laboratory in a frozen state.

Tissue extracts were prepared by mincing equal volumes of muscle and liver tissue in destilled water. The homogenate was then centrifuged for 10 minutes at 10.000g in a refrigerated centrifuge (4°C). Starch gel electrophoresis followed Allendorf et al. (1977) using the buffer system of Ridgway et al. (1970). Enzyme staining were carried out according to Abersold et al. (1987). Based on a recent study on blue whiting tissue enzymes which reports a generally low level of genetic variability in the species (Mork & Giæver 1993), two polymorphic loci (*PGM-1** and *IDHP-2**) were chosen for routine screening. Biological and genetic data were analysed using Statgraphics 5.0 (STSC, Inc.), Biosys 1.7 (Swofford & Selander 1981) and various inhouse software for genetic analyses (Mork 1992). The conformity of various models to our genetic data was tested by varying the hierarchical subdivision in Biosys 1.7 F-statistic analyses.

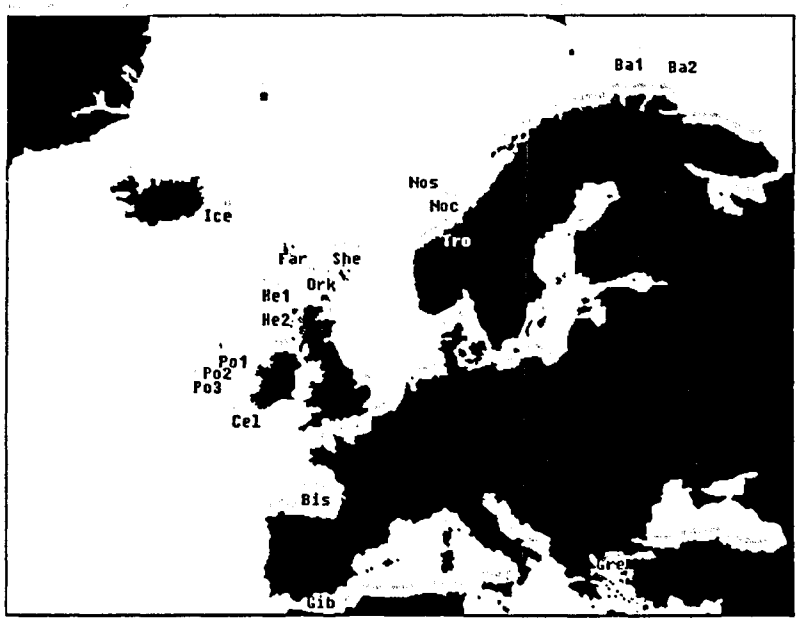

Figure 2. Blue whiting sampling locations.

Table 1. Sample code, vessel, date, catch gear (w/mesh size in mm), cruise station no., position, and sample size (N). BT=bottom trawl, PT=pelagic trawl, FM=fine-meshed net insert.

Sample	Vessel/date	Catch gear	Station	Position	N
Ba1	F/F "G. O. Sars" 27.02.1992	BT (40 mm) FM	101	N 71°35' Ø 26°30'	15
	F/F "G. O. Sars" 25.02.1992	BT (40mm) FM	89	N 71°17' Ø 29°27'	14
	F/F "G. O. Sars" 01.03.1992	BT (40 mm) FM	107	N 71°35' Ø 25°35'	12
	F/F "G. O. Sars" 25.02.1992	BT (40mm) FM	86	N 71°56' Ø 30°12'	8
	F/F "G. O. Sars" 28.02.1992	BT (40mm) FM	105	N 73°27' Ø 23°27'	2
	F/F "G. O. Sars" februar 1992	BT (40mm) FM	79	N 70°48' Ø 31°30'	13
Ba2	F/F "Johan Ruud" 28.08.1992	BT (35mm) FM (10mm)	1331	N 70°17' Ø 31°29'	18
	F/F "Johan Ruud" 29.08.1992	BT (35mm) FM (10mm)	1343	N 70°47' Ø 30°33'	20
	F/F "Johan Ruud" 30.08.1992	BT (35mm) FM (10mm)	1349	N 70°58' Ø 29°42'	30
Bis	Commercial November 1990	BT (40-65mm)		N 44°00' V 02°30'	102
Cel	F/F "Johan Hjort" 18.03.1992	PT (20mm) FM (11mm)	157	N 50°00' V 11°04'	100
Far	F/F "Johan Hjort" 02.04.1992	BT (40mm) FM (11mm)	185	N 61°13' V 05°14'	100
Gib	Commercial November 1990	BT (40-65mm)		N 35°90' V 15°03'	100
Gre	F/F "Ioannos Rossos" 25./28.08.1992	BT FM		N 39°50' Ø 23°14'	68
He1	F/F "Johan Hjort" 31.03.1992	PT (20mm) FM (11mm)	182	N 58°30' V 09°17'	100
He2	F/F "Johan Hjort" 29.03.1992	PT (20mm) FM (11mm)	180	N 56°39' V 09°16'	100
Ice	11.03.1992	BT		N 64°11' V 11°45'	135
Noc	F/F "M. Sars" 01.05.1992	BT (40mm) FM (11mm)	157	N 64°06' Ø 09°36'	100
Nos	F/F "M. Sars" 29.04.1992	BT (40mm) FM (11mm)	148	N 65°27' Ø 05°55'	100
Ork	F/F "Johan Hjort" 01.04.1992	BT (40mm) FM (11mm)	184	N 59°57' V 05°02'	100
Po1	F/F "Johan Hjort" 27.03.1992	PT (20mm) FM (11mm)	174	N 54°11' V 11°43'	100
Po2	F/F "Johan Hjort" 26.03.1992	BT (40mm) FM (11mm)	171	N 53°39' V 13°59'	100
Po3	F/F "Johan Hjort" 25.03.1992	PT (20mm) FM (11mm)	167	N 52°29' V 14°42'	100
She	F/F "Johan Hjort" 03.04.1992	PT (20mm) FM (11mm)	187	N 61°07' V 02°21'	100
Tro	September 1992	Lure		N 63°76' V 10°23'	92
Sum					1723

RESULTS

Analyses of about 1723 specimens revealed a total of five alleles at *PGM-1** and three at *IDHP-1** (Table 2). With few exception the samples were in Hardy-Weinberg equilibrium at both loci. Exceptions were observed for *PGM-1** in sample He1 (chi-square Goodness-of fit test, P=0.042) and Ba2 (P=0.003). Both deviations were due mostly to an overrepresentation of the rare heterozygote *PGM-1*88/110*. Furthermore, samples He1 and Po3 showed an excess of *PGM-1** heterozygotes (P=0.044 and 0.037, respectively). However, considering the number of Goodness-of-fit tests actually performed and adjusting the significance level accordingly (i.e., approximately 0.05/36=0.0014), none of these deviations are formally significant.
The within-sample allele frequencies showed no significant heterogeneity between sex-, age-, or gonadic stage groups, and there was no significant linkage disequilibrium in any sample.

There was, however, a highly significant heterogeneity of allele frequencies between samples (contingency table tests of allelic proportions yielded a chi-square of 88.150 (df=68, P=0.051) for *PGM-1** and 71.351 (df=34, P<0.001) for *IDHP-2*). The total chi-square of 159.501 (df=102, P<0.001) strongly suggests that the material includes samples from reproductively isolated populations.

Table 2. Blue whiting allele frequencies at *PGM-1** and *IDHP-2**.

Sample	*PGM-1**					*IDHP-2**		
	*100	*110	*88	*78	*116	*100	*78	*139
Ba1	0.887	0.105	0.008	0.000	0.000	0.632	0.368	0.000
Ba2	0.856	0.106	0.038	0.000	0.000	0.633	0.367	0.000
Bis	0.843	0.142	0.015	0.000	0.000	0.784	0.216	0.000
Cel	0.816	0.168	0.015	0.000	0.000	0.808	0.192	0.000
Far	0.775	0.215	0.000	0.010	0.000	0.783	0.217	0.000
Gib	0.820	0.160	0.015	0.000	0.005	0.825	0.175	0.000
Gre	0.879	0.121	0.000	0.000	0.000	0.889	0.111	0.000
He1	0.845	0.140	0.015	0.000	0.000	0.790	0.210	0.000
He2	0.790	0.200	0.010	0.000	0.000	0.813	0.187	0.000
Ice	0.826	0.152	0.022	0.000	0.000	0.794	0.202	0.004
Noc	0.792	0.202	0.006	0.000	0.000	0.823	0.177	0.000
Nos	0.840	0.145	0.015	0.000	0.000	0.820	0.180	0.000
Ork	0.837	0.158	0.005	0.000	0.000	0.828	0.172	0.000
Po1	0.805	0.190	0.005	0.000	0.000	0.816	0.184	0.000
Po2	0.805	0.180	0.010	0.000	0.005	0.859	0.141	0.000
Po3	0.830	0.150	0.020	0.000	0.000	0.825	0.175	0.000
She	0.835	0.160	0.005	0.000	0.000	0.853	0.147	0.000
Tro	0.773	0.210	0.017	0.000	0.000	0.803	0.197	0.000

F-statistic analyses using the Biosys 1.7 program revealed only moderately large F_{st}-values at both of the two polymorphic loci (Table 3). It is apparent from the table that *IDHP-2** has the greatest statistical power in population discrimination of the two.

Table 3. Blue whiting F-statistics for *PGM-1** and *IDHP-2**.

Locus	F_{IS}	F_{IT}	F_{ST}
*PGM-1**	0.018	0.025	0.007
*IDHP-2**	-0.002	0.024	0.026
Average	0.008	0.025	0.017

The allele frequencies in Table 2 were used to calculate pairwise genetic distances (D of Nei 1972) between samples. The D-values were used for UPGMA cluster analysis and dendrogram construction. The dendrogram is shown in Fig. 3.

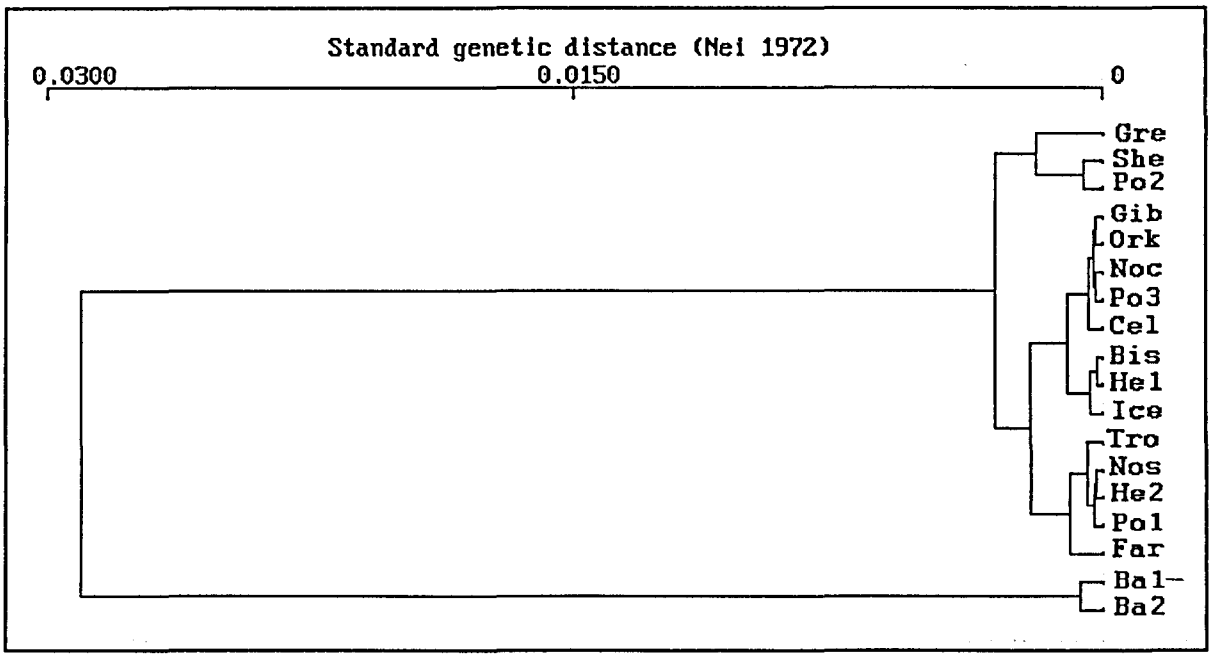

Figure 3. UPGMA dendrogram of genetic distances (D of Nei 1972) based on allele frequencies in Table 2.

The main bifurcation in the dendrogram is between samples from the Barents Sea (Ba1 and Ba2) and all others. This bifurcation is statistically very significant ($P << 0.001$; pooled chi-square from contingency table tests at both loci). Also the Greek sample (Gre) stands out somewhat from the others in the dendrogram. Testing its allele frequencies against all others except She, Po2, Ba1, and Ba2 yields a significant chi-square ($P=0.02$). Excluding these three samples (i.e. Ba1, Ba2, and Gre) which come from the fringes of the species range, the rest of the samples show no significant heterogeneity in allele frequencies ($P=0.479$).

Among the four models of blue whiting population structure considered in "Introduction" only the "Karasev model" showed a reasonable fit to the genetic observations in this study (Table 4). For the other models, the inclusion of the Barents Sea together with the other areas created a very significant heterogeneity in allele frequencies between locations within "stocks". Even for the "Karasev model", as much as 33% of the total variability fell between locations within "stocks" (Table 4; last column). An "empirical" stock structure based on the genetic data from the present study would be an inner Mediterranean, a central, and a northeastern blue whiting (Table 4).

Table 4. Hierarchical F-statistics analyses (Biosys 1.7) used to test how well the different models of blue whiting population structure conform with the genetic observations in this study.

Model	χ^2-test of heterogeneity in allelic proportions within "stocks"				Hierarchical F-statistics: Variation within levels in % of of the total variation.
	"Stocks"	χ^2	df	P	
Zilanov	1. Biscaya (Cel, Bis)	0.855	3		
	2. Mediterranean (Gib,Gre)	6.007	4		Between samples within "stocks": 100%
	3. Hebrido-Norwegian (all others except Tro)	128.985	72		Between "stocks" within total: 0%
	Sum	135.847	79	< 0.001	
Isaev & Seliverstov	1. Porcupine (Po1,Po2,Po3)	6.438	8		
	2. Biscaya (Cel,Bis)	0.855	3		Between samples within "stocks": 100%
	3. Mediterranean (Gib,Gre)	6.007	4		Between "stocks" within total: 0%
	4. Hebridean (all others except Tro)	97.553	45		
	Sum	110.853	60	< 0.001	
ICES	1. Southern (Cel,Bis,Po1,Po2,Po3)	12.168	16		Between samples within "stocks": 100%
	2. Northern (all others except Gib,Gre,Tro)	97.553	45		Between "stocks" within total: 0%
	Sum	109.721	61	< 0.001	
Karasev	1. Northern (Ba1,Ba2,Ice)	22.145	8		
	2. Southern (Cel,Bis,Po1,Po2,Po3)	12.168	16		Between samples within "stocks": 33%
	3. Central (all others except Gib,Gre,Tro,She)	23.274	20		Between "stocks" within total: 67%
	Sum	57.587	44	0.082	
Empirical (this study)	1. Northeastern (Ba1,Ba2)	2.479	3		
	2. Inner Mediterranean (Gre)	0	0		Between samples within "stocks": 20%
	3. Central (all others)	83.877	84		Between "stocks" within total: 80%
	Sum	86.374	87	0.499	

Despite the overall impression of genetic homogeneity in blue whiting from the central parts of its distribution area, some local substructure might be indicated by the samples from north of the British Isles. Thus, the Faroe sample contained two copies of an allele not found elsewhere, and contingency test comparisons of allele proportions between the Faroe sample (Far) and the nearby location Shetland (She) showed a pooled chi-square value (two loci) of 5.454 (df=2, P=0.065).

On background of the different opinions regarding the stock structure of the Hebridean and the Porcupine blue whiting in various models (cf "Introduction"), their genetic relationship was of special interest in this study. We found, however, no indication of reproductive isolation between blue whiting from the Hebrides (He1 and He2) and from the Porcupine (Po1, po2, and Po3). Testing pooled Hebridean samples against pooled Porcupine samples yielded a pooled chi-square (two loci) of 6.694 (df=4, P=0.153) for genotypes, and chi-square=2.699 (df=2, P=0.259) for alleles.

DISCUSSION

As reported by Mork & Giæver (1993), the blue whiting shows a relatively low level of genetic variability. The tissue enzyme loci employed in this study are the most polymorphic ones known in blue whiting at present.

We found no effect of age, sex or gonadic maturity stage on allele frequencies in any sample in this study, and no significant genetic disequilibrium. Thus, under the assumption that the employed genetic characters are selectively neutral or nearly so, the significant geographical heterogeneity in allele frequencies demonstrated at both *PGM-1** and *IDHP-2** indicates a clear genetic structure in blue whiting.

The main feature of this structure appears to be that blue whiting from the northeastern and southeastern parts of the species range are reproductively separated from spawning groups in the central parts of it's distribution. The genetic homogeneity observed in the central parts ranged from Iceland/Norwegian Sea to southern Spain, without any obvious geographical clines or shifts. Only 1.5% of the "between-component" of the total genetic variation stemmed from differences between samples in this area. This does not rule out the existence of smaller local stocks in that region; that is quite possible and may e.g. have been responsible for some signs of genetic heterogeneity observed in the Faroe-Shetland area. It is also important to be aware that similarity in allele frequencies does not necessarily mean that samples are from the same population.

Hierarchical F-statistic analyses were employed to test the conformity of various models of stock structure to the genetic data. In general, models which did not postulate a separate population in the norteast showed bad fits. Among the models listed introductory, that of Karasev (1990) conformed reasonably well, although the present genetic data do not support a lumping of Iceland together with the Barents Sea in a "northern" stock.

Our present data do not allow estimates of the actual ranges and sizes of the separate stocks indicated in Barents Sea region and in the inner Mediterranean. The representativity of our single sample from Greece waters (Gre) for larger groupings in the inner Mediterranean may be questioned. However, the Barents Sea subsamples were drawn from a wide geographic area (cf Ba1 and Ba2 in Table 1), and their intrinsic genetic homogeneity indicate a substantial geographic range of the stock.

By and large, the level of genetic differentiation in blue whiting appear to be similar to that in its relative, the Atlantic cod. Based on a study covering most of the distribution range of cod, Mork *et al.* (1985) reported that 2.1% of the total genetic variation could be assigned to differences between areas (for blue whiting 1.7%, cf Table 3). In cod, too, it was the samples from the fringes of the species range which showed the most deviating genetic characteristics. Considering the biology of these species, e.g. their extensive feeding/spawning migrations and the pelagic drift of eggs and larvae, this pattern is, maybe, not unexpected.

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