Aquat. Living Resour. 13 (2) (2000) 121–128

S099074400000142X/FLA

Population structure of the deep-sea shrimp (*Pandalus borealis*) in the north-east Atlantic based on allozyme variation

Asbjørn Drengstig[(a)], Svein-Erik Fevolden[(a*)], Pierre E. Galand[(a)], Michaela M. Aschan[(b)]

[(a)] *The Norwegian College of Fishery Science, University of Tromsø, N-9037 Tromsø, Norway*

[(b)] *Norwegian Institute of Fisheries and Aquaculture, N-9291 Tromsø, Norway*

Received 15 November 1999; accepted 21 February 2000

Abstract — In order to elucidate the population structure of the deep-sea shrimp (*Pandalus borealis*) in the NE Atlantic, 32 subsamples and 3 865 individuals were analysed for allozymic variation. They were caught at various locations in the Barents Sea, in waters off Svalbard, Jan Mayen and Iceland, and in fjords along the Norwegian coast. Only three enzymes (malate dehydrogenase, phosphoglucomutase and glucosephosphate isomerase) of the 22 initially tested showed a combination of gel images that could be interpreted with confidence and allozymic variation. The locus coding for malate dehydrogenase was by far the most polymorphic. Samples caught within the Barents Sea and in the Svalbard area showed no significant heterogeneity in allele frequencies, supporting earlier suggestions of only one population of *P. borealis* in the Barents Sea. Genetic differentiation was found, however, between Norwegian fjords and the Barents Sea, and among fjords.

Genetic diversity / population genetics / enzymes / deep-sea shrimp / *Pandalus borealis*

Résumé — Structure de la population de *Pandalus borealis* en Atlantique nord-est basée sur la variation des alloenzymes. Afin d'étudier la structure de la population de la crevette *Pandalus borealis* de l'Atlantique nord-est, la variabilité enzymatique de 22 loci a été analysée dans 32 sous-échantillons de 3 865 individus. Les crevettes ont été capturées en différents points de la mer de Barents, au large de Svalbard, de Jan Mayen et de l'Islande, et dans des fjords de la côte norvégienne. Seuls, trois systèmes enzymatiques (malate deshydrogénase, phosphoglucomutase et l'isomérase glucose-phosphate) se sont avérés variables. Le locus correspondant à la malate deshydrogénase est, de loin, le plus polymorphe. Des échantillons capturés en mer de Barents et dans la zone du Svalbard n'ont pas montré de différence significative des fréquence d'allèles, confirmant des hypothèses antérieures selon lesquelles une seule population de *P. borealis* serait présente en mer de Barents. Cependant, des différenciations génétiques significatives ont été retrouvées entre les fjords norvégiens et la mer de Barents et entre fjords.

Diversité génétique / génétique des populations / enzymes / crevettes de grands fonds / *Pandalus borealis*

1. INTRODUCTION

The deep-sea shrimp, northern shrimp, or just shrimp (*Pandalus borealis* Krøyer, 1838) has a discontinuous circumpolar, boreal and subarctic distribution [18, 27]. Shrimp larvae exhibit a relatively long pelagic larval stage with a potential for extensive dispersal. It has been stated, however, that currents exposing pelagic shrimp larvae are crucial to their distribution upon settling [14, 23] and could thus act as an obstacle against panmixia over large geographic areas.

Norway, former USSR, Iceland and Greenland have been the most important shrimp fishery nations during the last decade [8]; in recent years Canada's catches have also become substantial. The shrimp fisheries in Norway commenced at the turn of this century and the species is today commercially harvested along the whole Norwegian coast and in the open Barents Sea, including Svalbard and Jan Mayen. The shrimp fishery is nowadays a substantial industry of vital economic importance in Norway with a commercial value in 1998 of more than 818 million Norwegian kroner [2].

* Corresponding author: sveinf@nfh.uit.no

Despite this importance, Norway is the only country without a total allowable catch quota (TAC) in the NE Atlantic [31]. Moreover, shrimp in the exploited areas has been harvested and managed as a single stock without taking into account possible consequences of a structuring into genetic discrete units.

The first efforts to substantiate population genetic differences of *P. borealis* by studying allozyme variation were made earlier this decade [16–18]. Whereas each of six gross regions (Barents Sea, Bering Sea, Gulf of Alaska, Gulf of Saint Lawrence, Okhotsk Sea, and Sea of Japan) seemed to be inhabited by different shrimp populations, shrimp within each of the regions were suggested to consist of only one panmictic population. In the Barents Sea/Svalbard region, accumulated knowledge has shown great variation, temporally and spatially, in growth performance and age at sex transition in shrimp [3, 12, 30]. Yet, using biological data, Berenboim [6] proposed that the Barents Sea shrimp consisted of only one super-population. In 1998, Jónsdóttir et al. [15] reported significant genetic differences between inshore shrimp on Iceland, and shrimp taken offshore and in the Denmark Strait.

The present work was initiated to elucidate the possible genetic structuring of *P. borealis* spanning a larger area of the NE Atlantic. Of particular interest was to reveal a possible differentiation between shrimps in the open Barents Sea, and shrimps from Svalbard, Jan Mayen and Icelandic waters. We also wanted to examine possible genetic differences between inshore and offshore regions in Norway, and finally among different fjords along the Norwegian coast.

2. MATERIALS AND METHODS

A total of 3 865 specimens caught at 32 different sampling sites have been analysed (*figure 1*, *table I*). The shrimp were caught during a period of 4 years (1994–997), mainly on cruises with research vessels from the University of Tromsø using a Campelen 1800 Super bottom trawl. Shrimp caught during the 1994 and 1995 cruises were frozen at –20 °C, and transferred to –80 °C after the cruise, whereas during the 1996 and 1997 cruises newly caught shrimps were frozen in liquid nitrogen. Specimens from Icelandic waters were provided by The Marine Research Institute in Reykjavik and sample procedures are as in Jónsdóttir et al. [15]. Buffers and staining systems for the starch gel electrophoresis followed Fevolden and Ayala [11] and Fevolden [10], apart from the enzyme phosphoglucomutase, which was assayed as described by Jónsdóttir et al. [15]. Enzyme abbreviations and nomenclature followed Allendorf and Utter [1] and Shaklee et al. [26].

The statistical processing of data was performed using the computer programs BIOSYS-1 [29] and GENEPOP [24]. From the global estimate of Wright's [34] fixation index per locus [33], possible deviations from Hardy-Weinberg equilibrium were detected by using the exact Hardy-Weinberg test [24].

Contingency chi-square (χ^2) analyses were used to test heterogeneities in the total sample set and within each of six regions: the Barents Sea, Svalbard, Finnmark, Troms/Nordland, western Norway, and Iceland (cf. *table I*) for samples included in each region.

The program Phylip, release 3-57c [9], was used to calculate Nei's [20] genetic distances and Cavalli-Sforza's [7] chord measures. Nei's distances were used as coefficients to perform hierarchical cluster analysis using the unweighted pair-group method with arithmetic averaging (UPGMA) [28]. A dendrogram representing the linkages was then built. Cavalli-Sforza's chord measures were calculated after bootstrapping the original data set and a consensus dendrogram was then built.

3. RESULTS

Of the 22 enzymes initially tested only three, i.e. malate dehydrogenase (MDH), phosphoglucomutase (PGM) and glucosephosphate isomerase (GPI) showed a combination of adequate gel image interpretability and allozymic variation. (The others enzymes were: AAT, ADH, ADKIN, AO, EST, FUM, α-GPDH, HBDH, HK, IDH, LAP, LDH, MDH, ME, MPI, ODH, SDH, SOD and XDH.) *MDH** was by far the most polymorphic of the three corresponding loci; *GPI** and *PGM** were monomorphic at the majority of the sampling sites (*table II*). Moreover, *GPI** and *PGM** were only two-allelic, whereas *MDH** revealed additional but rare alleles in the southernmost samples off western Norway (*table II*).

The most conspiciuous observation that can be drawn from the allele–frequency data (*table II*) is the geographic diversity at the MDH* locus (*figure 2*). The most common *MDH**-allele in shrimp caught in the Barents Sea was assigned *MDH*-100*. Whereas coastal shrimp in the Troms/Nordland region had lower frequencies of the *MDH*-100* allele than the Barents Sea shrimp, the coastal shrimp from western Norway had higher frequencies of that allele. Shrimp from the Icelandic fjord sample exhibited *MDH**-allele frequencies resembling shrimp caught in the Troms archipelago, whereas *MDH**-allele frequencies of shrimp caught well off the coast of Iceland, plus in fjords of Finnmark, were comparable to those of shrimp from the open Barents Sea (*figure 2*).

Exact tests for Hardy-Weinberg equilibrium revealed deviations from random mating expectations at eight of 96 estimates (32 subsamples × 3 loci), and all but one was due to deficiencies of heterozygotes (positive F_{IS} values; *table II*).

Contingency chi-square analyses over the total sampling area revealed highly significant heterogeneity in allele frequencies at both *MDH** and *PGM** and over all three loci summarised (*table III*), giving evidence that the subsamples may belong to genetically different populations. For *MDH**, hierarchical *F*-statistics

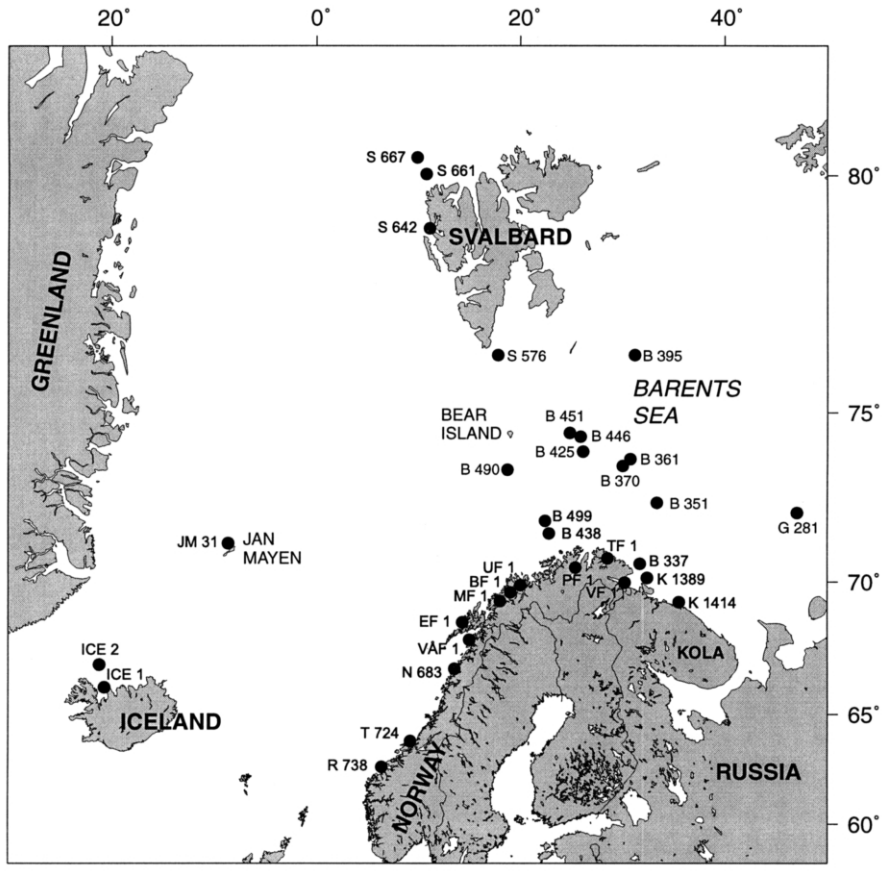


Figure 1. Approximate location of the 32 sampling sites.

showed that the variance among subsamples within regions is low, whereas the variance among subsamples and regions within the total sample set is substantial (*table IV*). Contingency chi-square analyses within each subregion revealed significant heterogeneity within three of them: Troms/Nordland, Finnmark and Iceland (*table V*). No significant heterogeneity was found in the Barents Sea proper (*table V*), but when the Jan Mayen sample (JM 31) was included in the Barents Sea sample set, a significant heterogeneity was revealed ($\chi^2 = 80.364$, df = 42, $P < 0.01$).

The cluster dendrogram based on Nei's genetic distance (*figure 3a*) reveals three main groupings represented by subsamples from 1) the Troms/Nordland region plus inshore Iceland, 2) western Norway, and 3) the Barents Sea (including Kola), Svalbard, Jan Mayen, offshore Iceland and Finnmark. The two western Norwegian samples (T724, R738) seem genetically more similar to Barents Sea shrimp than do shrimp caught in fjords in Troms.

When the frequency data are bootstrapped (which may be questionable with so few loci) and Cavalli-Sforza chord distance is utilised to construct trees, the same three main groupings can be seen (*figure 3b*). Subgroupings within each of the main nodes, however, differ between the two dendrograms, making it inappropriate to discuss real groupings on a smaller geographic scale.

4. DISCUSSION

To some extent the small number of loci hampers this study. In all allozymic studies of *P. borealis* reported so far, however, only a few polymorphic loci have been detected [15–18]. It is acknowledged that genetic studies of species with few polymorphic loci and low genetic variability are handicapped by the need for large sample sizes [13, 25], but most of the samples in this study were well within the recommendations made by these authors (*table I*). Rather early in the history of protein polymorhism it was suggested that marine crustaceans displayed low heterozygosity (e.g. [21]). The application of newer molecular techniques, however, has gradually challenged this view. Also for penaeid prawns, DNA-based markers have revealed far greater levels of variation compared with allozyme data ([5], but see below for *P. boralis*).

The present results reveal, first and foremost, genetic differentiation between populations from coastal

Table I. Details of the different subsamples. *n* = number of individuals analysed.

Region	Locality	Station no.	Position	Depth (m)	Year	*n*
Barents Sea	Gåsbanken	G281	72°01'N 46°00'E	248	1994	240
	Barents Sea	B351	72°27'N 34°18'E	273	1995	118
	Barents Sea	B370	73°53'N 31°48'E	337	1995	120
	Barents Sea	B395	76°21'N 32°46'E	300	1995	120
	Barents Sea	B446	74°35'N 27°16'E	380	1995	50
	Barents Sea	B499	71°32'N 23°13'E	393	1995	34
	Barents Sea	B337	70°57'N 31°57'E	360	1996	60
	Barents Sea	B361	73°54'N 31°53'E	335	1996	109
	Barents Sea	B438	71°32'N 23°13'E	387	1996	120
	Barents Sea	B425	74°25'N 27°10'E	393	1996	70
	Barents Sea	B451	74°37'N 26°38'E	358	1996	120
	Barents Sea	B490	73°44'N 19°43'E	351	1996	119
	Kola Coast	K1389	70°12'N 32°52'E	316	1995	120
	Kola Coast	K1414	69°47'N 35°28'E	289	1995	240
	Jan Mayen	JM31	71°04'N 09°31'E	270	1995	317
Svalbard	Spitsbergen South	S576	76°29'N 18°05'E	260	1995	120
	Spitsbergen West	S642	79°04'N 11°43'E	339	1995	119
	Spitsbergen North	S661	80°02'N 10°41'E	406	1995	120
	Spitsbergen North	S667	80°11'N 10°12'E	554	1995	120
Finnmark	Varangerfjord	VF 1	69°57'N 30°06'E	321	1996	120
	Tanafjord	TF 1	70°36'N 28°16'E	233	1996	120
	Porsangerfjord	PF1	70°12'N 25°16'E	116	1997	66
Troms/Nordland	Eidsfjord/Vesterålen	EF 1	68°34'N 14°34'E	240	1995	136
	Balsfjord/Troms	BF 1	69°22'N 19°03'E	187	1995	215
	Malangen/Troms	MF 1	69°35'N 17°53'E	262	1996	150
	Vågsfjord/Harstad	VÅF 1	68°42'N 16°44'E	228	1996	120
	Skarholmen/Bodø	N683	67°45'N 14°05'E	314	1996	120
	Ullsfjord	UF1	69°46'N 19°47'E	270	1997	64
Western Norway	Romsdalsfjord	R738	62°39'N 06°40'E	200	1996	156
	Værøya/Trondheim	T724	63°56'N 09°06'E	140	1996	120
Iceland	Iceland/offshore	ICE 2	67°34'N 21°10'W	680	1994	36
	Iceland/inshore	ICE 1	66°13'N 16°47'W	176	1995	36

areas and populations from open ocean basins, in accordance with reports from Icelandic waters [15] and from far eastern seas [18]. When so few loci could be studied, selection cannot be rejected as a contributing effector to the offshore–inshore heterogeneity. There is reason to believe, however, that the profound variation that is found at *MDH** in shrimp is in part invoked by restricted gene flow between the open sea and fjords. Qualified support for this assumption can be found in analyses of some of the samples that are included in the present study using randomly amplified polymorphic DNA (RAPD) [19]. Evidence obtained from that assay also indicates genetic homogeneity in the Barents Sea/Spitsbergen region, but that shrimp from coastal areas in northern Norway are genetically different from shrimp caught offshore. The RAPD polymorphism displayed much more variation than the allozyme loci, but yet the major component of the total genetic diversity was attributable to individual diversity within the sampled stations [19].

The deep sea shrimp exhibits a long planktonic larval stage, up to 4 months [14, 23], which promotes high dispersal capacity and potentially extensive gene flow. Gene flow has been proposed to be the major contributing factor leading to genetic homogeneity in marine fishes [32]. It is well established today, however, that high dispersal capacity does not necessarily imply high rates of gene flow [22]. Behavioural mechanisms, selection against immigrants, complex oceanographic circulation processes and historical barriers may all counteract gene flow and panmixia. The coastline of Troms/Nordland consists of a high number of islands and fjords, which influence and complicate the current patterns in the area. It is plausible, therefore, that local oceanographic features may constrict gene flow, and thus allow for genetic differences between shrimps in fjords and those off the coast. When shrimp from fjords in eastern Finnmark are genetically indistinguishable from Barents Sea shrimp, this could reflect the open nature of the Finnmark fjords as compared to fjords further west.

The results from the present allozymic study and from the RAPD analyses of Martinez et al. [19] provide evidence of genetic differences also between shrimp caught near Jan Mayen and those from the Barents Sea proper. Apart from the possibility of mere sampling error (in the one Jan Mayen subsample), local circulation patterns around Jan Mayen may be thought to prevent extensive gene flow between nearshore shrimp and shrimp of the open ocean stock.

Table II. Allele frequencies, observed and expected heterozygosity for the three polymorphic loci *MDH*, PGM** and *GPI**. The F_{IS} values are global estimates for all alleles at a locus; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Locus	Allele	G281	B351	B370	B395	B446	B499	B337	B361	B438	B425	B451	B490	K1389	K1414	JM 31	S576
*MDH**	100	0.569	0.551	0.517	0.542	0.484	0.512	0.592	0.592	0.523	0.579	0.572	0.534	0.617	0.558	0.647	0.617
	120	0.431	0.449	0.483	0.458	0.516	0.488	0.408	0.408	0.477	0.421	0.428	0.466	0.383	0.442	0.353	0.383
	140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	H_o	0.454	0.492	0.550	0.583	0.442	0.441	0.483	0.450	0.427	0.500	0.432	0.513	0.433	0.567	0.473	0.400
	H_e	0.499	0.497	0.502	0.499	0.503	0.507	0.487	0.485	0.501	0.491	0.492	0.500	0.475	0.494	0.458	0.475
	F_{is}	0.076	0.011	–0.097	–0.171	0.122	0.174	0.008	0.074	0.148	–0.018	0.121	–0.026	0.088	–0.147*	–0.034	0.158
PGM*	100	0.992	0.979	0.996	0.992	0.992	1.000	1.000	0.982	1.000	1.000	1.000	1.000	0.983	0.983	1.000	1.000
	120	0.008	0.021	0.004	0.008	0.008	0	0	0.018	0	0	0	0	0.017	0.017	0	0
	H_o	0.017	0.042	0.008	0.017	0.020	0	0	0.037	0	0	0	0	0.033	0.025	0	0
	H_e	0.017	0.042	0.008	0.016	0.020	0	0	0.036	0	0	0	0	0.033	0.025	0	0
	F_{is}	–0.006	–0.017	0	–0.004	0	0	0	–0.014	0	0	0	0	–0.013	–0.015	0	0
GPI*	100	0.998	1.000	1.000	1.000	1.000	0.988	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	120	0.002	0	0	0	0	0.012	0	0	0	0	0	0	0	0	0	0
	H_o	0.004	0	0	0	0	0.029	0	0	0	0	0	0	0	0	0	0
	H_e	0.004	0	0	0	0	0.029	0	0	0	0	0	0	0	0	0	0
	F_{is}	0	0	0	0	0	0.015	0	0	0	0	0	0	0	0	0	0

Locus	Allele	S642	S661	S667	VF 1	TF 1	PF 1	EF 1	BF 1	MF 1	VÅF 1	N683	UF 1	R738	T724	ICE2	ICE1
*MDH**	100	0.559	0.592	0.575	0.479	0.575	0.432	0.081	0.244	0.060	0.025	0.121	0.148	0.885	0.871	0.583	0.278
	120	0.441	0.408	0.425	0.521	0.425	0.568	0.919	0.756	0.940	0.975	0.879	0.852	0.090	0.083	0.417	0.722
	140	0	0	0	0	0	0	0	0	0	0	0	0	0.025	0.046	0	0
	H_o	0.496	0.500	0.450	0.442	0.517	0.379	0.118	0.302	0.120	0.050	0.142	0.265	0.090	0.150	0.611	0.278
	H_e	0.495	0.485	0.491	0.501	0.491	0.494	0.149	0.370	0.113	0.049	0.213	0.254	0.209	0.234	0.493	0.407
	F_{is}	–0.001	–0.031	0.083	0.119	–0.053	0.235	0.212**	0.183**	–0.060	–0.021	0.337**	–0.043	0.572***	0.359***	–0.244	0.320
PGM*	100	0.996	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.973	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	120	0.004	0	0	0	0	0	0	0	0.027	0	0	0	0	0	0	0
	H_o	0.008	0	0	0	0	0	0	0	0.013	0	0	0	0	0	0	0
	H_e	0.008	0	0	0	0	0	0	0	0.052	0	0	0	0	0	0	0
	F_{is}	0	0	0	0	0	0	0	0	0.745***	0	0	0	0	0	0	0
GPI*	100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	H_o	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	H_e	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	F_{is}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Considering the evidence from the present study of genetic divergence also on a smaller geographic scale, i.e. within the Troms/Nordland region, one may again seek causes among local current patterns. The possible role of random genetic drift, however, should not be neglected. Local fjord populations are deemed to be smaller than the oceanic populations and thus drift cannot be rejected as the appropriate null-hypothesis responsible for the differences observed. At odds with the present study, Martinez et al. [19] did not detect genetic differences within the same region (i.e. between the Balsfjord and Malangen) using the RAPD

Table III. Contingency χ^2 tests for heterogeneity of the three polymorphic loci over 32 sampling sites.

Locus	No. alleles	Chi-square	Degrees of freedom	*P*
*MDH**	3	1747.4	62	0.000
*PGM**	2	100.1	31	0.000
*GPI**	2	26.5	31	0.698
Total		1874.0	124	0.000

Table IV. Hierarchical *F*-statistics at the three polymorphic loci examined. Regions as in *table I*.

Locus	Subgroup/Total group	F_{ST}
*MDH**	subsample/region	0.018
	subsample/total	0.166
	region /total	0.150
*PGM**	subsample/region	0.011
	subsample/total	0.010
	region/total	0.001
*GPI**	subsample/region	0.000
	subsample/total	0.000
	region/total	0.001

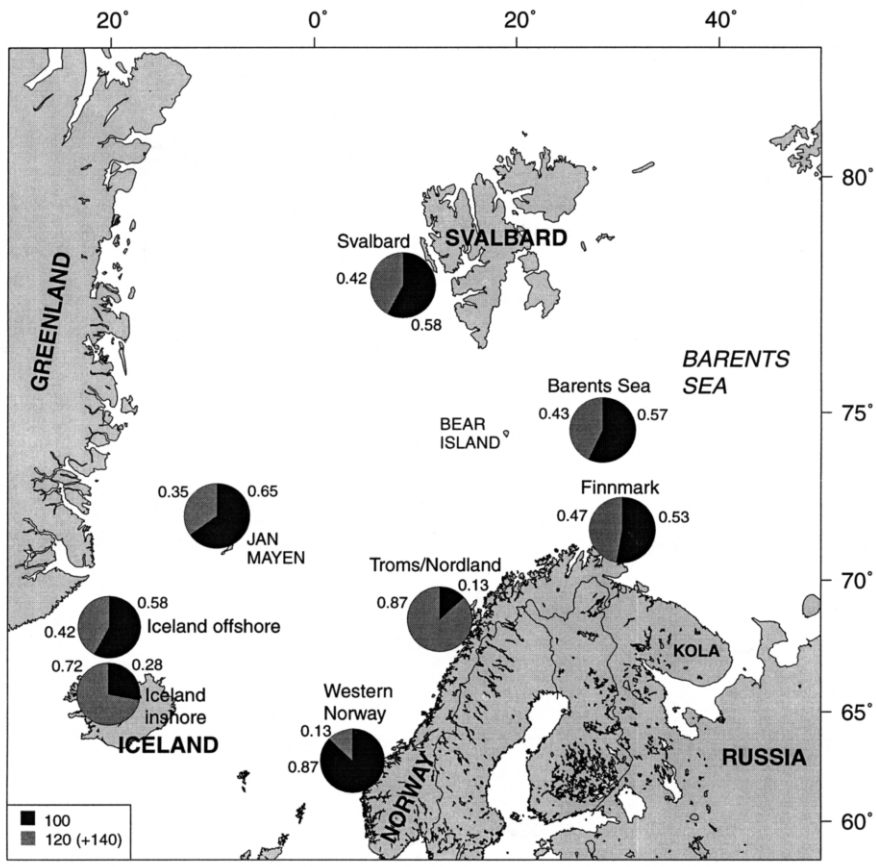


Figure 2. Pooled allele frequecies at the *MDH** locus in five regions defined under Material and methods (*table I*). Frequencies from Jan Mayen, and inshore and offshore Iceland are from the single subsamples taken at those localities.

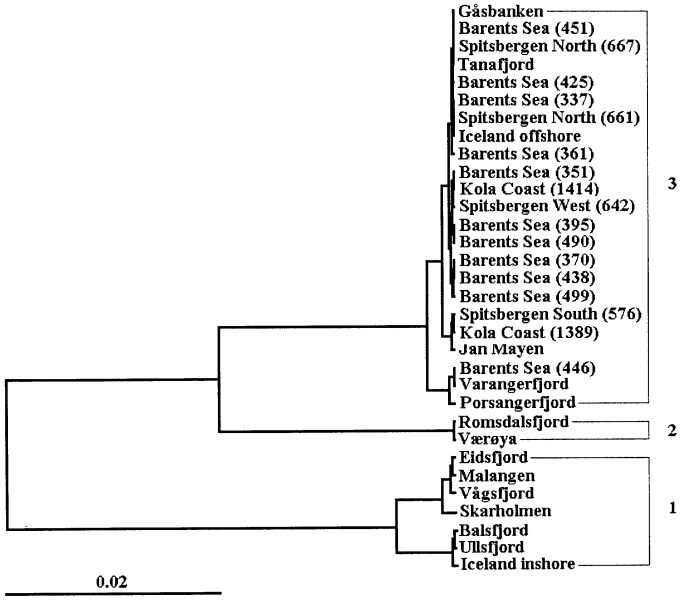
assay, which might imply dissimilar sensitivity of RAPDs and allozyme polymorphism.

Deficits of heterozygotes at single loci were revealed in eight subsamples, which is slightly more than expected by chance alone (5 % of 96 estimates). Common causes for Hardy-Weinberg deviations in samples are selection and Wahlund effect (sampling of mixed population with different allele frequencies). The fact that the sample sites that showed a deficit of heterozygotes were all but one taken near the coast, leaves the Wahlund effect a plausible contributor to the deviations.

From a management point of view the results obtained in the present study suggest that shrimp from coastal areas, where appropriate, should conservatively be treated as separate harvest units. A total allowable catch quota (TAC) for shrimp fisheries in the Barents Sea, including Svalbard and Jan Mayen, may be quantified based on being treated as a panmictic population. Nevertheless, caution ought to be exercised when determining harvest units and a total allowable catch quota of shrimp, in accordance with conclusions based upon classical population characteristics 4].

Table V. Contingency χ^2 tests for the six different regions.

Region	Number of subsamples within each region	Chi-square	Degrees of freedom	*P*
Barents Sea	15	53.901	39	0.057
Iceland	2	13.709	1	0.000
Svalbard	4	4.833	6	0.565
Finnmark	3	8.168	2	0.017
Troms/Nordland	6	140.553	10	0.000
Western Norway	2	1.700	2	0.427



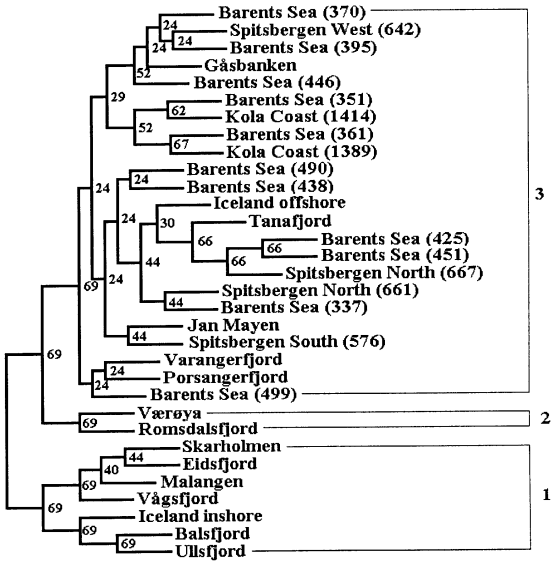


Figure 3. UPGMA dendrogram based on Nei's (1972) genetic distance (A) and consensus dendrogram based on Cavalli-Sforza's (1967) chord measure using bootstrapped data (B). The numbers at the nodes indicate the number of times (out of 100) the groupings occurred.

Acknowledgements. This study was part of a cooperative project between The Norwegian Institute of Fisheries and Aquaculture (Tromsø) and The Norwegian College of Fishery Science, University of Tromsø. The work was supported by grants from The Norwegian Research Council (project no. 108151/120; to M.M.A.). Ólöf D.B. Jónsdóttir is highly acknowledged for providing shrimp from Icelandic waters.

REFERENCES

[1] Allendorf F.W., Utter F.M., Population genetics, in: Hoar W.S., Randall D.J., Brett J.R. (Eds.), Fish Physiology, Bioenergetics and Growth, Academic Press, New York, 1979, pp. 407–454.

[2] Anonymous, Statistikk, Norges Fiskerier (1998), Norges Råfisklag, in Norwegian, 1999.

[3] Aschan M., Spatial variability in length frequency distribution and growth of shrimp *Pandalus borealis* in the Barents Sea, presented at the International Pandalid Symposium, September 1999, J. Northwest Atl. Fish. Sci. (2000) in press.

[4] Aschan M., Sunnanå K., Evaluation of the Norwegian Shrimp Surveys conducted in the Barents Sea and the Svalbard area 1980–1997, ICES CM 1997/Y 7, 1997.

[5] Benzie J.A.H., Population genetic structure in penaeid prawns, Aquacult. Res. 31 (2000) 95–119.

[6] Berenboim B.I., Reproduction of the populations of the shrimp *Pandalus borealis* in the Barents Sea, Oceanology 22 (1982) 85–89.

[7] Cavalli-Sforza L.L., Edwards A.W.F., Phylogenetic analysis: models and estimation procedures, Evolution 32 (1967) 550–570.

[8] FAO, Yearbook of Fishery Statistics, Catches and Landings 1995, FAO Vol. 80, 1997.

[9] Felsenstein J., PHYLIP (Phylogeny Inference Package) version 3.5c, Department of Genetics, Univ. Washington, Seattle, 1993.

[10] Fevolden S.E., Genetic differentiation of the Iceland scallop *Chlamys islandica* (Pectinidae) in the northern Atlantic ocean, Mar. Ecol. Prog. Ser. 51 (1989) 77–85.

[11] Fevolden S.E., Ayala F.J., Enzyme polymorphism in Antarctic krill (*Euphausiacea*); genetic variation between populations and species, Sarsia 66 (1981) 167–181.

[12] Hansen H., Aschan M., Growth performance, size and age at maturity of shrimp *Pandalus borealis* in the Svalbard area related to environmental parameters, J. Northwest Atl. Fish. Sci. (2000) in press.

[13] Hartl D.L., A Primer of Population Genetics, Sinauer Associates, Inc., Sunderland, MA, USA, 1988.

[14] Horstedt S.A., Smidt E., The deep sea prawn (*Pandalus borealis* Kr.) in Greenland waters, Meddelelser fra Danmarks fiskeri- og havundersøgelser, Biancos Lunos Bogtrykkeri A/S. Bind 1 11 (1956) 1–118.

[15] Jónsdóttir Ö.D., Imsland A.K., Nævdal G., Population genetic studies of Northern shrimp (*Pandalus borealis* Krøyer) in Icelandic waters and Denmark Strait, Can. J. Fish. Aquat. Sci. 55 (1998) 770–780.

[16] Kartavtsev Y.P., Wide-scale genetic differentiation among pink shrimp *Pandalus borealis* populations, in: Beaumont A.R. (Ed.), Genetics and Evolution of Aquatic Organisms, Chapman and Hall, 1994, pp. 41–51.

[17] Kartavtsev Y.P., Berernboim B.I., Zgurowsky K.I., Population genetic differentiation of pink shrimp *Pandalus borealis* Krøyer 1838, from the Barents and Bering Seas, J. Shellfish Res. 10 (1991) 333–339.

[18] Kartavtsev Y.P., Zgurowsky K.A., Fedina Z.M., Spatial structure of the pink shrimp *Pandalus borealis* Krøyer 1838 from the far-eastern seas as proved by methods of population genetics and morphometrics, J. Shellfish Res. 12 (1993) 81–87.

[19] Martinez I., Skjerdal T., Dreyer B., Aljanabi S.M., Genetic structuring of *Pandalus borealis* in the North Atlantic, II: RAPD analysis, ICES C.M. 1997/T:24, 1997.

[20] Nei M., Genetic distance between populations, Am. Nat. 106 (1972) 283–292.

[21] Nelson K., Hedgecock D., Enzyme polymorphism and adaptive strategy in the decapod Crustacea, Am. Nat. 116 (1980) 238–280.

[22] Palumbi S.R., Genetic divergence, reproductive isolation, and marine speciation, Annu. Rev. Ecol. Syst. 25 (1994) 547–572.

[23] Rasmussen B., On the geographical variation in growth and sexual development of the deep sea prawn (*Pandalus borealis* Kr.), Serie havundersøkelser 10 (Reports on Norwegian fishery and marine investigations), A.s. John Griegs Boktrykkeri, Bergen, 1953.

[24] Raymond M., Rousset F., GENEPOP (version 1.2), A population genetics software for exact tests and ecumenicism, J. Hered. 86 (1995) 248–249.

[25] Shaklee J.B., The utilisation of isozyme as gene markers in fisheries management and conservation, Isozyme 11 (1983) 213–247.

[26] Shaklee J.B., Allendorf F.J., Morizot D.C., Whitt G.S., Gene nomenclature for protein coding loci in fish, Trans. Am. Fish. Soc. 119 (1990) 2–15.

[27] Shumway S.E., Perkins H.C., Schick D.F., Stickney A.P., Synopsis of biological data on the pink shrimp, *Pandalus borealis* Krøyer 1838, NOAA Technical Report NMSFK 30 FAO Fisheries Synopsis No. 144, 1985.

[28] Sneath P.H.A., Sokal R.R., Numerical taxonomy, the principles and practice of numerical classification, in: Kennedy D., Park R.B. (Eds.), W.H. Freeman, San Francisco, 1973.

[29] Swofford D.L., Selander R.B., BIOSYS-1: A Computer Program for the Analysis of Allelic Variation in Population Genetics and Biochemical Systematics, release 1.7., Champaign, Illinois: Natural History Survey, 1989.

[30] Teigsmark G., Populations of the deep-sea shrimp (*Pandalus borealis Krøyer*) in the Barents Sea, Fisk. Dir. Skr. Ser. Havunders 17 (1983) 377–430.

[31] Toresen R., Mehl S., Johnsen A.L., Jørgensen T., Toft K.Ø., Havets ressurser 1998, FiskenHav, Særnr. 1, in Norwegian, 1998.

[32] Ward R.D., Woodwark M., Skibinski D.O.F., A comparison of genetic diversity levels in marine, freshwater and anadromous fishes, J. Fish Biol. 44 (1994) 213–232.

[33] Weir B.S., Cockerman C.C., Estimating F-statistics for the analysis of population structure, Evolution 38 (1984) 1358–1370.

[34] Wright S., The interpretation of population structure by F-statistics with special regard to systems of mating, Evolution 19 (1965) 395–420.