Population structure of *Chlamys islandica* in the Northeast Atlantic – northern stocks compared with a southern relict population

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To gain a better understanding of the genetic relations that may exist between populations of *Chlamys islandica* in different regions of the northern Atlantic, the geographic range of earlier studies was extended to include populations sampled further east (Kap Kanin in Russia) and west (Breidarfjordur on Iceland), plus a relict population from the southwest coast of Norway (Fauskangerpollen). The patterns of variation that were found at selected allozyme loci support the suggestion that populations of *C. islandica* in the Northeast Atlantic are genetically structured. The relict population from Fauskangerpollen was genetically most distinct from any of the other populations.

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INTRODUCTION

The Iceland scallop, *Chlamys islandica* (O.F. Müller), with its subarctic or northern boreal occurrence, is the northernmost species of the family Pectinidae and the most abundant scallop in Arctic regions. It occurs in the southwest Kara Sea, the White Sea, the Barents Sea, along the western coast of Novaya Zemlya and around Bear Island, in the Svalbard Archipelago, along the coast of northern Norway south to Lofoten, all around Jan Mayen and Iceland, and on the west and east sides of southern Greenland (Ekman 1953; Ockelman 1958; Wiborg 1963; Luka & al. 1987; Lubinsky 1980). In southern Norway relict populations are found near Bergen and in the Stavanger fjord (Greve & Samuelsen 1971). The species is found at depths of 10-250 m although the greatest concentrations occur above 100 m depth. The scallop thrives in water associated with strong currents and with temperatures of about –1.5 to 8 °C (Wiborg 1963; Wiborg & Bøhle 1974). Sexual maturation occurs at three to six years of age, depending on the surrounding temperature (Sundet & Vahl 1981; Vahl 1982). The larvae spend up to 10 weeks in the planktonic stage before they settle (Gruffydd 1976; Wallace 1982) and thus have a relatively high potential for dispersal.

A fishery of *C. islandica* started in 1969 in Icelandic waters (Parsons & al. 1991). In Norway, a large scale commercial exploitation began in 1985 with harvesting of scallop beds initially around Jan Mayen. This site was closed in 1987 after having shown signs of over-exploitation, and the fishery shifted to beds off Bear Island and western Spitsbergen. In late 1988, areas off those islands were also closed (Parsons & al. 1991). The short profitable exploitation periods reflected the lack of proper management regimes; thus, it was acknowledged that information about the genetic structure of the species was needed. Two previous reports concluded that *C. islandica* populations in the region comprised of northern Norway, Jan Mayen, Bear Island, and Spitsbergen (Svalbard), may be at least partially isolated from one another (Fevolden 1989, 1992). The aim of the present study has been to extend the geographical range of populations in the previous studies. Some of the populations examined in the earlier studies were resampled and assayed together with populations sampled further east (off Kap Kanin in Russia) and west (Breidarfjordur in Iceland), plus one relict population from the west coast of southern Norway (Fauskangerpollen).

Correlations between fitness-related traits, such as growth, and heterozygosity have been the subject of several studies in various bivalve species (see reviews by Zouros & Pogson 1994). In an attempt to estimate possible correlations between growth and heterozygosity in *C. islandica,* one particularly large sample (from Moffen) was subjected for such comparisons.

MATERIAL AND METHODS

The various sample sites are shown in Fig. 1. Scallops from Moffen (sampled in August 1994), Kap Kanin (September 1994) and Breidarfjordur (September 1996) were collected by a triangular dredge, with approximately 1 m

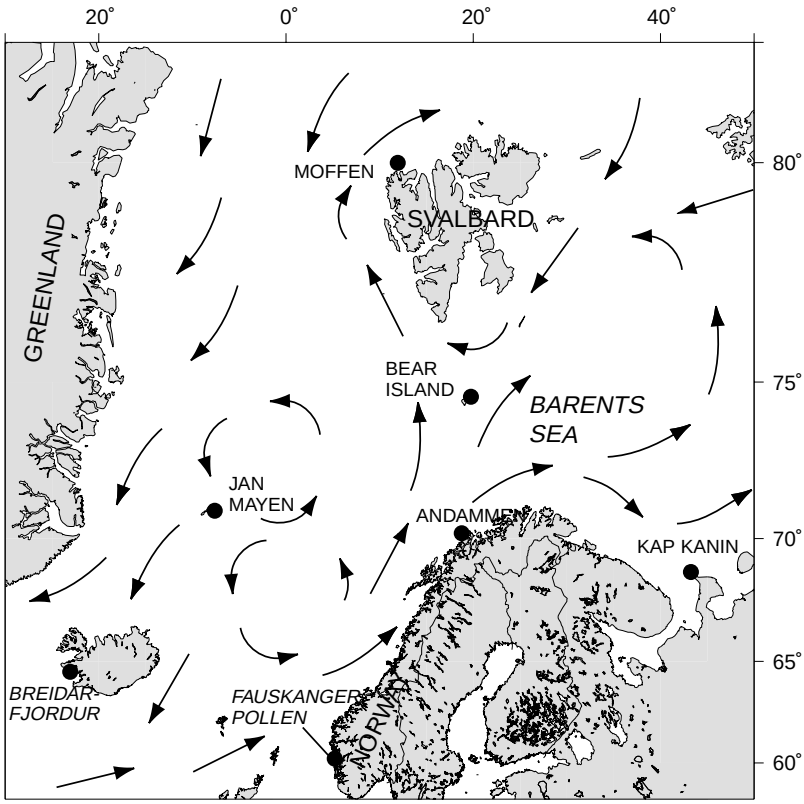

Fig. 1. *Chlamys islandica.* Sampling sites (black dots) of *Chlamys islandica*. Arrows indicate main current systems in the NE Atlantic.

frame edge. The specimens used for biochemical genetic analyses were randomly collected from the dredges to ensure a non-biased size and age distribution. The scallops from Fauskangerpollen (August 1995) were sampled by divers.

Adductor muscles and gonads (Moffen and Breidarfjordur), or whole animals (Kap Kanin and Fauskangerpollen) were immediately frozen at –25 °C and stored at –80 °C in the laboratory until analysis.

The age of individual scallops was estimated by counting growth rings in the shell hinge ligament as described by Johannesen (1973). Because of the uncertainty when reading the age of the youngest and oldest individuals, only five year-classes (ages 7 to 11) were used in the analyses of age-genetics correlations. Those were also the most numerous of the age groups.

The enzymes chosen for the study were found by Fevolden (1989, 1992) to be polymorphic in this species, and thus with a potential use for population structure analyses. They were phosphoglucomutase (PGM; monomeric), superoxide dismutase (SOD; dimeric), malate dehydrogenase (MDH; dimeric) and glucose phosphate isomerase (GPI; dimeric). All four enzyme-loci produced consistent gel resolution, but some low-frequency alleles at *Gpi* were difficult to score with certainty because they had positions on the gel very close to other alleles. To avoid bias they were pooled with their neighbouring alleles. The procedures for electrophoretic assays and for enzyme staining are as in Fevolden (1989). Nomenclature of loci and alleles follows the recommendation of Allendorf & Utter (1979).

Data were analysed with the population genetics computer program Genepop (Raymond & Rousset 1995; release 1.2). Phylip (Felsenstein 1993; release 3.57c) was used to bootstrap the gene frequencies data, calculate Nei's (1972) genetic distance and Cavalli-Sforza's chord measure (1967) and to draw consensus cluster dendrograms.

From the global estimate of Wright's (1965) fixation index per locus (Weir & Cockerman 1984), possible deviations from Hardy-Weinberg equilibrium were detected by using the exact Hardy-Weinberg test (Raymond & Rousset 1995).

Data from four samplings of *C. islandica* surveyed in

a recent study (Fevolden 1992) were compiled for inter-region heterogeneities and cluster analyses. Those were from Moffen (Spitsbergen), Jan Mayen, Bear Island and Andammen (north of Tromsø; cf. Fig. 1). Since no differences in allele frequencies (Fisher exact test) were found between the previous and the present Moffen samplings, the two data sets from this area were pooled together. Inter-region heterogeneities in allele frequencies were tested using the Fisher exact test. The original data sets were bootstrapped and Nei's (1972) genetic distance and Cavalli-Sforza's chord measure (1967) were calculated to visualise the genetic structuring of the species. The distances were used as coefficients to perform hierarchical cluster analysis using the unweighted pair-group method with arithmetic averaging (UPGMA algorithm described by Sneath & Sokal 1973). Consensus dendrograms representing the linkages were then built.

Inter-year-class heterogeneities for the present Moffen scallops were tested by contingency table chi-square analyses and the results of these tests were considered as unbiased since the average expected frequency in each table was at least 6.0; $n/(rc) > 6.0$ where n is the sum of

Table 1. *Chlamys islandica*. Allele frequencies for individual alleles at 4 polymorphic loci in the four sampling areas. 2N: number of genomes (twice the number of scallops scored), H_o and H_e: observed and expected heterozygosities at each locus; The F_{IS} values are global estimates for all alleles at a locus.

Locus	Allele	Fauskangerpollen	Kap Kanin	Breidarfjordur	Moffen
Gpi	(2N)	190	214	236	2254
	33	0.032	0.009	0.008	0.018
	62	0.153	0.093	0.081	0.060
	71	0.242	0.107	0.169	0.122
	85	0.000	0.000	0.000	0.006
	88	0.158	0.182	0.178	0.164
	96	0.000	0.000	0.000	0.008
	100	0.216	0.332	0.297	0.333
	108	0.111	0.145	0.131	0.181
	117	0.079	0.117	0.106	0.094
	122	0.011	0.014	0.030	0.015
H_o (H_e)		0.716 (0.831)	0.664 (0.805)	0.703 (0.819)	0.770 (0.904)
F_{IS}		0.140	0.177*	0.142*	0.039*
Mdh	(2N)	190	218	234	2228
	42	0.000	0.000	0.004	0.001
	100	0.605	0.683	0.624	0.633
	171	0.316	0.183	0.222	0.215
	207	0.005	0.000	0.000	0.001
	214	0.074	0.133	0.150	0.149
H_o (H_e)		0.526 (0.531)	0.450 (0.484)	0.590 (0.541)	0.497 (0.531)
F_{IS}		0.009	0.071	–0.090	0.063*
Sod	(2N)	190	226	238	2368
	40	0.137	0.084	0.134	0.117
	71	0.042	0.071	0.063	0.073
	100	0.821	0.845	0.794	0.810
	125	0.000	0.000	0.008	0.001
H_o (H_e)		0.305 (0.307)	0.310 (0.275)	0.353 (0.348)	0.324 (0.385)
F_{IS}		0.005	–0.127	–0.012	0.003
Pgm-2	(2N)	192	228	240	2344
	87	0.005	0.000	0.017	0.001
	89	0.333	0.211	0.171	0.202
	95	0.005	0.004	0.008	0.004
	100	0.552	0.689	0.671	0.659
	105	0.099	0.096	0.133	0.133
	110	0.005	0.000	0.000	0.001
H_o (H_e)		0.510 (0.577)	0.360 (0.474)	0.467 (0.505)	0.476 (0.595)
F_{IS}		0.116	0.242*	0.076	0.062*

* F_{is} is significant at the 5% level.

all expected frequencies in the $r \times c$ table (Roscoe & Byars 1971).

Differences between mean growth of heterozygotes and homozygotes at single loci for the Moffen sample was tested by Students t-test, whereas differences in growth among scallops of the five heterozygosity classes (0 to 4 heterozygous loci), were tested by 1-way analysis of variance (ANOVA). The ratio (length × width × thickness)/age was used as an index of growth.

RESULTS

Allele frequencies and observed and expected heterozygosities at each sampling site are in Table 1. Global estimates of F_{IS} (Weir & Cockerman 1984) for all alleles at a locus showed six significant deviations from Hardy-Weinberg expectations. Three of those deviations were detected at the *Gpi* locus. All indicate a deficit of heterozygotes (positive F_{IS} values).

Fisher's exact test on the sampling sites from this study and those of Fevolden (1992) showed highly significant inter-region heterogeneity in allele frequencies at all four loci (Table 2); the differences are significant also when a sequential Bonferroni correction for multiple tests is used (see Rice 1989 for calculation of new significance levels). When the relict population from Fauskangerpollen is excluded from the test, significant geographic heterogeneity in the remaining regions appeared at *Mdh*, *Sod* and *Pgm-2* (both with and without sequential Bonferroni correction).

Two consensus cluster dendrograms, also compiling data from the previous survey (Fevolden 1992), both indicate that the Kap Kanin and Bear Island populations cluster together and that the Moffen and Jan Mayen populations constitute another cluster group. The Fauskangerpollen population is unambiguously the genetically most distinct (Fig. 2). The Andammen population on the other hand, does not hold the same position in the two consensus trees. When Cavalli-Sforza chord distance is used, Andammen groups with Jan Mayen and Moffen, whereas when Nei's distance is used, Andammen clusters with Kap Kanin and Bear Island.

Contingency chi-square analyses revealed no significant differences in allele frequencies at any locus among five year-classes (7 - 11 yr) at Moffen ($p \geq 0.372$). Moreover, there was no differences between mean growth of heterozygotes and homozygotes at any locus in the same sample set (t-test; $p \geq 0.275$; from 1113 to 1183 individuals compared for the different loci), and no differences for growth among scallops having from 0 to 4 heterozygous loci (ANOVA; $F = 1.013$, $p = 0.399$; 1030 specimens compared).

Table 2. *Chlamys islandica*. Fisher exact test for inter region heterogeneity in allele frequencies (H_0: the allelic distribution is identical across populations) at four polymorphic loci for seven regions: Fauskangerpollen, Kap Kanin, Breidarfjordur, Moffen, Bear Island, Andammen and Jan Mayen. The latter four include data from Fevolden (1992). p = significance level, s.e. = standard error. In parenthesis: values when Fauskangerpollen is excluded from the test. Sample sizes are given in Table 2.

Locus	No. of alleles	p	s.e.
Gpi	10	0.000 (0.061)	0.000 (0.017)
Mdh	6	0.002 (0.003)	0.002 (0.001)
Sod	4	0.036 (0.022)	0.011 (0.009)
Pgm-2	6	0.001 (0.000)	0.000 (0.001)

DISCUSSION

More significant deviations from Hardy-Weinberg distributions of genotypes were found than expected by chance alone. All Hardy-Weinberg deviations were due to deficits of heterozygotes (i.e. positive F_{IS} values, Table 1); an observation which is in accordance with a series of other bivalves (e.g. Zouros & Foltz 1984). The heterozygote deficit revealed at *Gpi* could in part be caused by misscoring of genotypes. Due to the high number of alleles found close to one another at this locus, some heterozygotes could have been scored as homozygotes. A variety of explanations for deficits of heterozygotes has been advanced, and the observations have been enigmatic because large panmictic populations are often expected for bivalves, and several of these species exhibit positive correlations between allozyme heterozygosity and fitness related traits (e.g. growth rate; see Hare 1996 and references therein). The latter enigma does not arise from the present study since no correlation between growth and single-locus or multiple-locus heterozygosity was found.

As visualised by the consensus dendrograms (Fig. 2), scallops from the relict population in Fauskangerpollen are genetically most distinct from the other populations. This locality houses one of the southernmost populations of *C. islandica* known in the eastern Atlantic, separated by at least 1000 km from populations further north. The poll is small, inshore, and although it communicates with a fjord the scallops are restricted to the poll itself (Greve & Samuelsen 1971). Thus, the possibility for extensive larval dispersal is low. An influx of southwardly migrating larvae from the distant northern populations is impossible due to the northerly direction of the coastal currents. Transport of larvae from Fauskangerpollen northwards is also unlikely since the larvae would then have to reach the offshore coastal currents and drift hundreds of kilometres. A plausible explanation for the deviant genetic structure of this population is, therefore, its geographic isolation with restrictions on gene exchange. It

is not known how many years the Fauskangerpollen population has been isolated from the other populations in the Northeast Atlantic. It is assumed that historically the whole coast of Norway was inhabited by *C. Islandica* and that the disappearance of stocks south of Lofoten was caused by a gradual increase of the water temperature since the last ice age. The discreteness of the Fauskangerpollen population is comparable to the distinctness recently found in a similarly closed population of the scallop *Pecten maximus* off northern Eire (Wilding & al. 1997; Heipel & al. 1998).

Patterns of variation were found also among the remaining sampling sites, with three of four loci (*Mdh*, *Pgm-2*, and *Sod*) showing significant inter-region heterogeneity (Table 2). Thus, there is reason to suggest, as did Fevolden (1989, 1992), that populations of *C. Islandica* in the Northeast Atlantic are at least partially isolated from one another. The non-consistent positioning of Andammen in the two dendrograms, however, renders it difficult to establish the real groupings of populations.

Fevolden (1989, 1992) developed several arguments discounting genetic drift as the main cause of observed heterogeneity in *C. Islandica*; the large population sizes and the long life span (> 20 years) being the most obvious. The fact that no differences in allele frequencies between year-classes was shown in the present study (at Moffen) is in accordance with results published by Lewis & Thorpe (1994) on temporal stability of allele frequencies in *Chlamys opercularis.* This could theoretically indicate that random genetic drift is an unlikely explanation for the spatial variations observed. However since no evidence for selection can be provided and the time period covered is limited (five consecutive year classes), drift can still not be rejected as the appropriate null hypothesis responsible for the differences observed. Over such a large geographic area however, restricted gene flow must be considered a likely contributor to the observed genetic diversity.

The high genetic variability found at the investigated loci corroborates the idea that *C. islandica* is an organism with exceptionally high intra-population genetic diversity at specific loci. Whether there is an adaptive strategy to this is of course an intriguing question and was discussed in some details by Fevolden (1989, 1992). Due to the complexity, however, of the dynamic interactions that occur between the environment and the species, and the difficulties in imagining how a species perceives its environment, single models which can fully explain why this pectinid has higher genetic variability than other bivalve species at the same loci (Fevolden 1992) are still unattainable, or at least speculative.

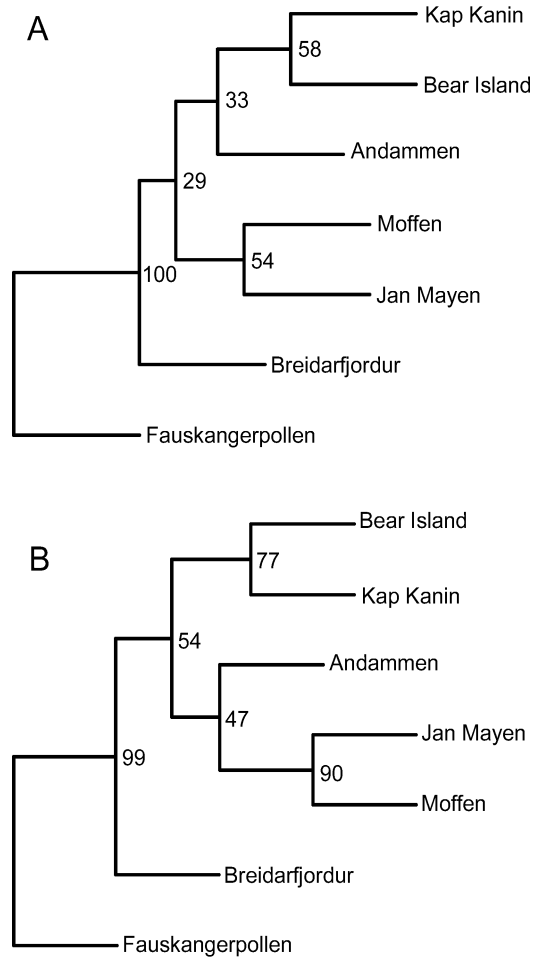

Fig. 2. *Chlamys islandica*. Consensus UPGMA dendrogram based on Nei's (1972) genetic distance (A) and Cavalli-Sforza's (1967) chord measure (B) using bootstrapped data. The number at the nodes indicate the number of times (out of 100) the groupings occurred. 4 polymorphic loci were used for pairwise comparison of the 4 samples from this study (Fauskangerpollen, Kap Kanin, Breidarfjordur, and Moffen) added to 4 samples from Fevolden (1992; Bear Island, Moffen, Andammen, and Jan Mayen).

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REFERENCES

Allendorf FW, Utter FM. 1979. Population genetics. In: Hoar WS, Randall DJ, Brett J, editors. *Fish physiology, bioenergetics and growth*. New York: Academic Press. p 407-454.

Cavalli-Sforza LL, Edwards AWF. 1967. Phylogenetic analysis: models and estimation procedures. *Evolution* 32:550-570.

Ekman S. 1953. Zoogeography of the Sea. London: Sidgewick and Jackson. 417 p.

Felsenstein J. 1993. *PHYLIP* (Phylogeny Inference Package) version 3.5c. Distributed by the author. Department of Genetics, University of Washington, Seattle.

Fevolden SE. 1989. Genetic differentiation of the Iceland scallop *Chlamys islandica* (Pectinidae) in the northern Atlantic Ocean. *Marine Ecology Progress Series* 51:77-85.

Fevolden SE. 1992. Allozymic variability in the Iceland scallop *Chlamys islandica*: geographic variation and lack of growth- heterozygosity correlations. *Marine Ecology Progress Series* 85:259-268.

Greve L, Samuelsen TJ. 1971. A population of *Chlamys islandica* (O. F. Müller) found in western Norway. *Sarsia* 45:17-24.

Gruffydd LlD. 1976. The development of the larvae of *Chlamys islandica* in the plankton and its salinity tolerance in the laboratory (Lamellibranchia, Pectinidae). *Astarte* 8:61-67.

Hare MP, Karl SA, Avise JC. 1996. Anonymous nuclear DNA markers in the American Oyster and their implications for the heterozygote deficiency phenomenon in marine bivalves. *Molecular Biology Evolution* 13:334-345.

Heipel DA, Bishop JDD, Brand AR, Thorpe JP. 1998. Population genetic differentiation of the great scallop *Pecten maximus* in western Britain investigated by randomly amplified polymorphic DNA. *Marine Ecology Progress Series* 162:163-171.

Johannesen OH. 1973. Age determination in *Chlamys islandica* (O. F. Müller). *Astarte* 6:15-20.

Lewis RI, Thorpe JP. 1994. Temporal stability of gene-frequencies within genetically heterogeneous populations of the queen scallop *Aequipecten* (*Chlamys*) *opercularis*. *Marine Biology* 121:117-126.

Lubinsky I. 1980. Marine Bivalve Molluscs of the Canadian central and eastern Arctic: Faunal composition and zoogeography. *Canadian Bulletin of Fisheries and Aquatic Sciences* 207:1-111.

Luka GI, Mukhin AI, Ponomarenko VP. 1987. Living resources of the Arctic and Sub-Arctic regions and their exploitation. *ICES Council Meeting* 1987/D. 32 p.

Nei M. 1972. Genetic distance between populations. *American Nature* 106:283-292.

Ockelmann WK. 1958. The zoology of East Greenland. 4. Marine Lamellibranchiata. *Meddelelser om Grønland* 122(4):1-256.

Parsons GJ, Dadswell MJ, Rodstrom EM. 1991. Fisheries and aquaculture: Scandinavia. In: Shumway SE, editor. *Scallops: biology, ecology and aquaculture*. Amsterdam: Elsevier Amsterdam. 763 p.

Raymond M, Rousset F. 1995. Genepop (version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity* 86:248-249.

Rice WR. 1989. Analysing tables of statistical tests. *Evolution* 43:223-225.

Roscoe JT, Byars JA. 1971. Sample size restraints commonly imposed on the use of the chi-square statistic. *Journal of the American Statistic Association* 66:755-759.

Sneath PHA, Sokal RR 1973. *Numerical taxonomy, the principles and practice of numerical classification*. San Francisco: Freeman W H. 573 p.

Sundet JH, Vahl O. 1981. Seasonal changes in the dry weight and biochemical composition of the tissues of sexually mature and immature Iceland scallop, *Chlamys islandica*. *Journal of the Marine Biology Association of the United Kingdom* 61:1001-1010.

Vahl O. 1982. Long term variation in the recruitment of the Iceland scallop, *Chlamys islandica* from northern Norway. *Netherland Journal for Sea Research* 16:80-87.

Wallace JC. 1982. The culture of the Iceland scallop, *Chlamys islandica* (O.F. Müller). I. Spat collection and growth during the first year. *Aquaculture* 26:311-320.

Weir BS, Cockerman CC. 1984. Estimating F-statistics for the analysis of population structure. *Evolution* 38:1358-1370.

Wiborg KF 1963. Some observations on the Iceland scallop *Chlamys islandica* (O.F. Müller) in Norwegian waters. *Fiskeridirektoratets Skrifter Serie Havundersøkelser* 13:38-53.

Wiborg KF Bøhle B. 1974. Occurrence of edible shellfish (bivalves) in Norwegian coastal waters (with a selection of marine gastropods). *Translation Series Fisheries and marine service Canada* no. 2978. p 34.

Wilding CS, Beaumont AR, Latchford JW. 1997. Mitochondrial DNA variation in the scallop *Pecten maximus* (L) assessed by a PCR-RFLP method. *Heredity* 79:178-189.

Wright S. 1965. The interpretation of population structure by F-statistics with special regard to systems of mating. *Evolution* 19:395-420.

Zouros E, Foltz DW. 1984. Possible explanations of heterozygote deficiency in bivalve molluscs. *Malacologia* 25:583-591

Zouros E, Pogson GH. 1994. The present status of the relationship between heterozygosity and heterosis. In: Beaumont AR, editor. *Genetics and evolution of aquatic organisms*. London: Chapman and Hall. p 135-146.

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