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Genetic differentiation of the Iceland scallop *Chlamys islandica* (Pectinidae) in the northern Atlantic Ocean

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ABSTRACT: Allozymic variation at gene loci encoding for glucosephosphate isomerase, phosphoglucomutase and superoxide dismutase was investigated in populations of *Chlamys islandica* from waters around Jan Mayen, Spitsbergen, Bear Island and northern Norway. The *Gpi* locus was particularly polymorphic with at least 12 different alleles and a mean heterozygosity of 84 %. Half the individuals were heterozygous at *Pgm-2* and between 30 and 40 % at *Sod*. The high polymorphism at *Gpi* runs counter to an earlier hypothesis suggesting a positive correlation between environmental variability and *Gpi* polymorphism of pectinids. *Pgm-2* and *Sod* revealed significant allele frequency heterogeneity among the different areas, *Gpi* only when the effective number of alleles was considered. The species has a large dispersal potential during a long planktonic larval stage, but information on the surface current system in the North Atlantic suggests that restricted gene flow, with possible contributions from selective constraints, account for the observed pattern in gene variability. It is suggested that the conservative approach of managing each area as if it contained discrete genetic units of the species should be adopted.

INTRODUCTION

The Iceland scallop *Chlamys islandica* (O. F. Müller) is an arctic/boreal bivalve with a circumpolar distribution. It is the most abundant species of scallop in Atlantic sub-Arctic and Arctic regions (Ekman 1953, Wiborg 1963, Luka et al. 1987). The scallop lives in cold water from below zero to between 8 and 10 °C on gravel or sandy bottoms at depths from 20 to 100 m (Ekman 1953, Wiborg 1963).

Since the mid-seventies, various pectinids have been studied for protein polymorphism using electrophoretic techniques (Wilkins & Mathers 1974, Mathers 1975, Wilkins 1975, 1978, Beaumont et al. 1980, Beaumont 1982a, b, Fujio et al. 1983, Beaumont & Beveridge 1984, Foltz & Zouros 1984, Macleod et al. 1985, Gosling & Burnell 1988). Biochemical genetic data has successfully been used to investigate the genetic population structure of pectinids (Beaumont 1982a, Macleod et al. 1985). Beaumont (1982a) investigated *Chlamys opercularis*, which has a more southerly distribution than *C. islandica*, and found genetically isolated populations around the British Isles despite a potentially large dispersal capacity through planktonic larvae. He argued that both random genetic drift and selection may be involved in the establishment and retention of large allele frequency differences between isolated populations.

In the absence of natural selection and genetic drift, gene flow through larval dispersal in marine invertebrates might be expected to generate uniform allele frequencies among conspecific populations over the dispersal area (see e.g. Gooch 1975, Scheltema 1975, Crisp 1978). However, Burton (1983) claimed that there is no strong support for a relationship between the length of the planktonic larval stage and the geographic boundaries of panmictic populations. Substantial population differentiation has been observed despite a high dispersal capacity, a situation which may partly be caused by natural selection, or physical barriers to dispersal (Burton 1983, see also Hedgecock 1986). As a spatially widespread organism with a long-lasting planktonic larval stage (up to 2 mo) *Chlamys islandica* was considered a suitable organism in which to study the effects of larval dispersal on genetic population structure.

Intensive exploitation of Iceland scallop started in Norway only 4 yr ago (in 1985). Fishing began on the

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scallop beds around Jan Mayen, which are already being heavily depleted, and later shifted to areas around Bear Island and off West Spitsbergen where the densest concentrations of commercial size are found (Rubach & Sundet 1987). For management purposes it is therefore important to determine the genetic structure of the species.

If the coastal current system in the northern Atlantic is considered, it is obvious that larval dispersal may be extensive. If larval behaviour does not result in the retention of self-sustaining stocks, it is quite possible that larvae spawned in one area are transported to and settle in regions far away from their origin. With this point in mind scallops were sampled from all major commercial scallop fishing grounds for Norwegian fishermen to elucidate the degree of differentiation in the population structure of the species.

High polymorphism has generally been reported in pectinids for the gene coding for glucosephosphate isomerase (references listed above). Early on, it was suggested that this locus is more polymorphic in species which experience high environmental variability (Mathers 1975, Wilkins 1975). During the course of this study, high variability at *Gpi* was also revealed in *Chlamys islandica*. Since the Iceland scallop is an inhabitant of what may appear to be an extremely stable environment (deep sublittoral habitats in cold regions), its allozymic variability will therefore be discussed in relation to the genetics of pectinids living in more temperate regions.

MATERIAL AND METHODS

The scallops were dredged from RV 'Johan Ruud' during summer 1987, except for the Thomsø sample which was taken in November 1986. Samples for electrophoresis were randomly collected from the dredges to ensure a non-biased size or age distribution. The 8 sample sites are shown in Fig. 1 and other details given in Table 1.

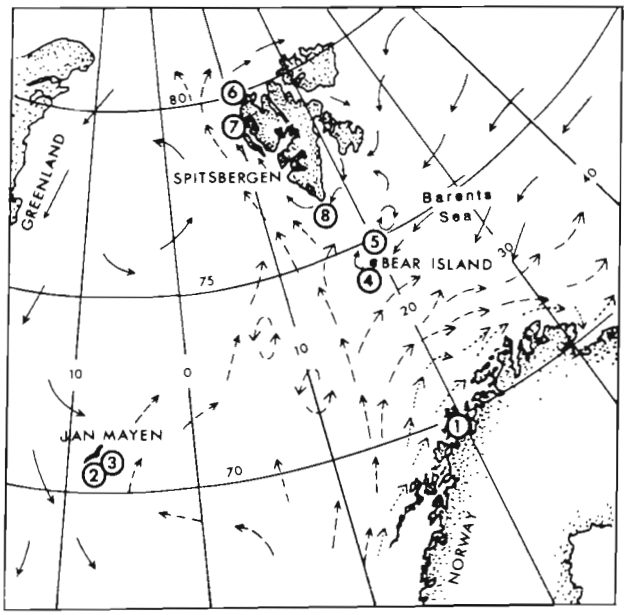

Fig. 1. Sampling sites of *Chlamys islandica*. Arrows indicate surface currents in the North Atlantic. ---> = Atlantic currents, —> = polar currents, ···> = Norwegian Coastal Current

The adductor muscles and gonads were dissected out from fresh specimens and immediately frozen at −80 °C. Before electrophoresis approximately equal amounts of muscle and gonad were homogenized in a solution containing 100 µl Triton X-100, 100 µl β-mercaptoethanol, and 10 mg NADP per 100 ml distilled water The homgenates were centrifuged at 12 000 *g* for 15 min and supernatants were saved for electrophoresis. Altogether nearly 1700 scallops were analysed using starch gel electrophoresis (as in Ayala et al. 1973).

The reaction of 28 different enzyme stains plus one general protein stain was initially tested, but only the 3 most polymorphic systems will be dealt with in detail here. They are: glucosephosphate isomerase (GPI, E.C. 5.3.1.9), phosphoglucomutase (PGM, E.C. 2.7.5.1), and

Table 1. *Chlamys islandica*. Sampling stations with depth of highest shell concentration and approximate temperature during the summer season (Sundet pers. comm.)

Locality	Depth of maximum concentrations (m)	Temperature (°C)
1. Tromsø, Berg	30–50	2–6
2. Jan Mayen, Straumflaket	70–100	0.5–1.2
3. Jan Mayen, north of Straumflaket	70–100	0.5–1.2
4. Bear Island South	70–110	ca 2.3
5. Bear Island North, Kveitehola	70–110	ca 2.3
6. Spitsbergen, Breibogen	40–70	3.8–4.8
7. Spitsbergen, Sjubreflaket	30–100	3.4–5.8
8. Spitsbergen, Sørkapp	60–100	ca 1

superoxide dismutase (SOD, E.C. 1.15.1.1). The staining of GPI and PGM followed Fevolden & Ayala (1981) with modifications as in Haug & Fevolden (1986). SOD bands were visualized in a solution containing 5 mg riboflavin, 75 mg EDTA, and 10 mg NBT (nitroblue tetrazolium) in 100 ml of 0.05 *M* Tris-HCl pH 8.0. After incubation in the dark for 20 min gels were exposed to strong light leaving oxidase activity as white bands. Staining of the remaining systems (listed under 'Results') followed Fevolden & Ayala (1981).

The Tris-citric acid (pH 8.5; gel) and lithium hydroxide boric acid (pH 8.1; electrode) butter system of Ridgway et al. (1970) gave best resolution of the GPI and SOD bands and also good resolution for the faster of 2 polymorphic PGM bands. PGM was also analysed in the following system: gel buffer 5.9 m*M* $K_2HPO_4 \cdot 3H_2O$, 1.2 m*M* citric acid, pH 7.0; bridge butter 160.7 m*M* $K_2HPO_4 \cdot 3H_2O$, 27.1 m*M* citric acid, pH 6.7 (modified after Selander & Yang 1969). This system yielded wider separation of the different allelic bands in the faster *Pgm* locus, and also showed activity in the slower *Pgm* locus. The latter locus is highly polymorphic, but uneven migration makes interpretation difficult.

The different alleles are assigned figures where 100 designates the commonest allele. The designation of the remaining alleles indicates their percentage mobility relative to the 100 allele. Since there was a large number of alleles at the *Gpi* locus, the effective number of alleles was calculated using the formula $n_e = 1/\Sigma p_i^2$ where p_i is the frequency of the *i*th allele.

Conformity to Hardy-Weinberg expectations of genotype distribution in a random mating population was tested by calculating Wright's F_{IS} value (fixation index of subpopulations; Wright 1965). Positive and negative values of F_{IS} indicate excess and deficit of homozygotes. The significance of F_{IS} was tested by calculating χ^2 as F_{IS}^2 N, where N is sample size (Li 1955, Brown 1970). Inter-sample heterogeneity in allele frequencies was tested by contingency table analyses. To reveal similarities between samples cluster analysis was performed on matrices of Nei's (1972) genetic distances using unweighted pair group method with arithmetic averages.

RESULTS

Loci coding for 11 proteins were monomorphic (*aldolase, esterase-1, fumarase, hexokinase-1, isocitrate dehydrogenase, malic enzyme, 6-phosphogluconate dehydrogenase, xanthine dehydrogenase*, plus 3 unidentified protein loci). For cost-efficiency reasons and because they were considered less likely to provide information on stock structuring, these loci were examined only for the Tromsø sample. Nine enzyme stains produced variable gel bands that could not be consistently scored (adenyl kinase, esterase, glucose-6-phosphate dehydrogenase, glyceraldehyde-3-phosphate, α-glycerophosphate dehydrogenase, hydroxybutyrate dehydrogenase, mannosephosphate isomerase, octanol dehydrogenase, and sorbitoldehydrogenase). Enzyme stains for 8 systems produced no visible, or very weak bands (acid phosphatase, alkaline phosphatase, aldehyde oxidase, aspartate aminotransferase, glucose dehydrogenase, lactate dehydrogenase, leucine aminopeptidase and malate dehydrogenase).

Only 3 of the polymorphic enzyme systems showed consistent gel resolution. The dimeric GPI was the most variable. This enzyme is encoded at a single locus and at least 12 different alleles were observed. Seven samples contained no less than 10 alleles; 9 alleles were observed in the Tromsø locality alone (Table 2). Additional low-frequency alleles had positions so close to other alleles that they could not be scored with certainty. They were therefore pooled with their neighbouring alleles. The effective number of alleles, which takes into account the reduced contribution to variability by low-frequency alleles, varied between 4.79 and 5.97 (Table 2). As a result of the high number of codominant alleles as many as 50 different genotypes were actually scored. More than 80 % of the individuals in any one sample were heterozygous at this locus (Table 2).

The monomeric enzyme PGM is encoded at 2 loci. *Pgm-2* showed 5 alleles, 2 of which were rare (Table 3). Half the individuals were heterozygous for this locus. The slower migrating bands representing *Pgm-1* were also highly polymorphic ($\geq$ 4 alleles), but the locus could not be scored with confidence.

The dimeric SOD is also encoded at a locus with 5 different alleles of which 2 were rare (Table 4). Between 28 and 43 % of the individuals in any one sample were heterozygous at this locus.

Average heterozygosity over the 3 polymorphic loci plus the 11 monomorphic was estimated at 0.116 (Tromsø sample).

Wright's fixation index revealed a general conformity to Hardy-Weinberg expectations with the few significant exceptions shown in Tables 2 to 4. For *Gpi*, significant F_{IS} values in populations 3 and 5 were caused by deficits of homozygotes of specific alleles. The mean of F_{IS}, however, is negative in 7 of 8 samples of *Gpi* and 6 of 8 samples of *Sod* (Tables 2 and 4), indicating a slight, but general excess of heterozygotes. At *Pgm-2*, significant F_{IS} values in populations 2 and 6 were caused by a surplus of homozygotes. In population 2, however, the significance was due to the observation of one rare homozygote with a low expected value (0.011) and this result is presumably not biologi-

Table 2. *Chlamys islandica*. Allelic variation and Wright's fixation index, F_{IS} (e.g. Wright 1965), for the locus *Gpi*. A: allele designation (relative mobility); p: allele frequency; X: pool of rare alleles; $\bar{F}_{IS}$: weighted mean of F_{IS} over alleles; n_e: effective number of alleles; *2N*: number of genomes (twice the number of animals); *H*: observed (left figure) and expected (right figure) heterozygosity for each population

	Population															
	1		2		3		4		5		6		7		8	
A	p	F_{IS}	p	F_{IS}	p	F_{IS}	p	F_{IS}	p	F_{IS}	p	F_{IS}	p	F_{IS}	p	F_{IS}
33	0.025	−0.026	0.008	−0.008	0.012	−0.012	0.018	−0.019	0.032	−0.033	0.017	−0.017	0.020	−0.024[a]	0.042	−0.043
62	0.050	0.064	0.036	−0.037	0.047	−0.049	0.070	−0.075	0.058	−0.061	0.063	0.076	0.057	−0.061	0.049	−0.052
71	0.101	0.012	0.099	−0.110	0.127	−0.146*	0.147	−0.055	0.128	−0.147	0.094	0.044	0.130	−0.012	0.109	−0.069
85	–	–	–	–	0.005	−0.005	0.004	−0.004	0.006	−0.006	0.010	−0.011	0.005	−0.005	0.003	−0.003
88	0.159	−0.106	0.189	0.001	0.147	0.062	0.169	−0.047	0.179	−0.132	0.160	−0.067	0.164	−0.006	0.174	−0.031
96	0.017	−0.017	0.008	−0.008	0.012	−0.012	0.015	−0.015	0.013	−0.013	0.019	−0.019	0.013	−0.013	0.008	−0.008
100	0.285	−0.124	0.327	−0.067	0.326	−0.037	0.257	0.038	0.253	−0.203*	0.300	−0.052	0.315	0.023	0.281	−0.005
108	0.198	−0.037	0.196	0.079	0.201	−0.068	0.213	−0.096	0.202	−0.054	0.221	−0.041	0.161	0.038	0.214	−0.054
117	0.140	−0.023	0.120	0.057	0.113	0.069	0.081	−0.088	0.099	0.105	0.110	−0.039	0.107	−0.010	0.107	−0.010
122	0.025	−0.026	0.018	−0.018	0.010	−0.010	0.019	−0.026[a]	0.029	−0.030	0.006	−0.006	0.023	−0.024	0.010	−0.013[a]
X	–		–		–		0.007		–		–		0.003		0.003	
$\bar{F}_{IS}$		−0.055		−0.010		−0.029		−0.042		−0.095		−0.029		0.003		−0.033
n_e	5.587		4.789		5.043		5.790		5.974		5.274		5.449		5.507	
2N	358		392		408		272		312		480		384		384	
H	0.866	0.823	0.801	0.795	0.824	0.802	0.860	0.828	0.910	0.834	0.833	0.812	0.813	0.817	0.844	0.819

[a] Estimate for this allele and X pooled

* $p < 0.05$; other values insignificant

Table 3. *Chlamys islandica*. Allelic variation and Wright's fixation index, F_{IS} at the locus *Pgm-2*. Designations as in Table 2

	Population															
	1		2		3		4		5		6		7		8	
A	p	F_{IS}	p	F_{IS}	p	F_{IS}	p	F_{IS}	p	F_{IS}	p	F_{IS}	p	F_{IS}	p	F_{IS}
89	0.244	0.098	0.148	−0.054	0.131	0.114	0.126	−0.077	0.146	0.037	0.222	0.106	0.183	−0.008	0.217	0.128
95	0.019	−0.020	0.008	0.664[a]	0.010	−0.010	0.019	−0.019	0.019	−0.020	0.004	−0.004	0.003	−0.003	0.011	−0.011
100	0.653	0.056	0.643	0.010	0.636	0.040	0.700	−0.041	0.721	0.097	0.646	0.175••	0.664	−0.024	0.635	0.155
105	0.083	0.127	0.198	0.101	0.220	0.072	0.152	−0.006	0.114	0.001	0.127	0.045	0.151	−0.051	0.138	0.019
110	–	–	0.005	−0.005	0.003	−0.003	0.004	−0.004	–	–	–	–	–	–	–	–
$\bar{F}_{IS}$		0.079		0.031		0.065		−0.039		0.053		0.123		−0.026		0.113
2N	360		400		396		270		308		472		372		378	
H	0.467	0.508	0.510	0.528	0.499	0.531	0.489	0.472	0.422	0.447	0.453	0.518	0.516	0.504	0.471	0.532

[a] The significant value ($p < 0.001$) is caused by the observation of one rare 95/95 homozygote
•• $p < 0.01$; other values insignificant

Table 4. *Chlamys islandica*. Allelic variation and Wright's fixation index, F_{IS}, for the locus *Sod*. Designations as in Table 2

	Population															
	1		2		3		4		5		6		7		8	
A	p	F_{IS}	p	F_{IS}	p	F_{IS}	p	F_{IS}	p	F_{IS}	p	F_{IS}	p	F_{IS}	p	F_{IS}
40	0.117	−0.133	0.112	−0.024	0.137	−0.066	0.136	−0.095	0.110	0.074	0.121	0.025	0.136	−0.022	0.122	0.006
62	–	–	–	–	–	–	–	–	–	–	0.002	−0.002	–	–	–	–
71	0.042	0.095	0.138	−0.031	0.093	−0.103	0.074	−0.079	0.058	0.056	0.084	−0.036	0.078	0.140	0.096	0.013
100	0.841	0.019	0.750	−0.088	0.769	0.010	0.787	−0.140	0.828	0.066	0.792	−0.078	0.783	0.039	0.781	−0.067
110	–	–	–	–	–	–	0.004	−0.004	0.003	−0.003	–	–	0.003	−0.003	–	–
$\bar{F}_{IS}$		−0.026		−0.056		−0.039		−0.112		0.066		−0.037		0.039		−0.026
2N	358		392		364		272		308		462		374		384	
H	0.285	0.278	0.429	0.427	0.396	0.382	0.397	0.358	0.279	0.300	0.364	0.351	0.348	0.363	0.375	0.366

Table 5. *Chlamys islandica*. Contingency chi-square analysis of inter-sample and inter-area heterogeneity at the 3 polymorphic loci. Alleles with expected values less than 1 are pooled with alleles having the next highest value

Locus	Inter-sample			Inter-area		
	Chi-square	df	p	Chi-square	df	p
Gpi	69.108	63	0.279	36.346	27	0.112
Pgm-2	78.142	21	<0.001	71.130	9	<0.001
Sod	28.734	14	<0.02	20.829	6	<0.005
Additive	175.984	98	<0.001	128 305	42	<0.001

cally significant. Nevertheless, the mean of F_{IS} over alleles at *Pgm-2* in 6 of 8 populations is positive (Table 3), as is the mean of F_{IS} over populations (0.051), indicating a small overall escess of homozygotes.

Contingency table analyses revealed no inter-sample heterogeneity at the highly polymorphic *Gpi* locus, but significant heterogeneity both at *Pgm-2* and *Sod* (Table 5). No significant heterogeneity was found among samples within any of the different regions ($p \geq 0.12$). Pooling samples within each geographical region – Jan Mayen, Spitsbergen, Bear Island, Tromsø (only one sample) – revealed highly significant inter-region heterogeneity at *Pgm-2* and *Sod* (Table 5). No inter-region heterogeneity was seen at *Gpi* using normal procedures for pooling classes with low expectations. However, the exceptionally high number of alleles at *Gpi* produces high degrees of freedom. When only 6 allele classes were used – the 5 most frequent (according to the calculated effective number of alleles) plus a pool of the remaining alleles – a slightly significant inter-area heterogeneity is seen even at this locus ($\chi_{15}^2 = 26.757$; $0.05 > p > 0.025$).

The dendrogram based on Nei's (1972) genetic distance averaged across the 3 polymorphic loci (Fig. 2) shows that populations sampled within each of the different areas are clustered together, leaving the Jan Mayen samples as genetically most distant from any other sample.

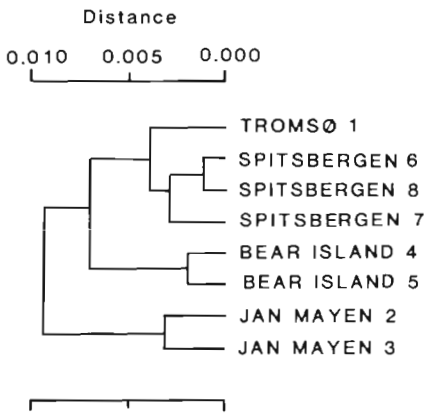

Fig. 2. *Chlamys islandica*. Cluster dendrogram based on Nei's (1972) genetic distance for pairwise comparison of samples across the three polymorphic loci *Gpi*, *Pgm-2*, and *Sod*. Unweighted pair-group method with arithmetic averaging has been used to construct the dendrogram

DISCUSSION

Intra-sample allozyme variation

The 3 polymorphic loci all show high intra-sample variability. Although the different alleles have not been confirmed by breeding trials, the consistency in banding patterns with characteristics as expected for mono- and dimeric enzymes, and general conformity to Hardy-Weinberg expectations, suggest that the isozyme variants are genetically based and inherited in simple Mendelian fashion.

High variability at *Gpi* in terms of number of alleles and heterozygosity has also been found in other and more southerly distributed pectinids (Wilkins & Mathers 1974, Mathers 1975, Wilkins 1975, 1978), although only in *Pecten maximus* of the same magnitude as in *Chlamys islandica* (Wilkins & Mathers 1974, Wilkins 1978, Beaumont & Beveridge 1984). Beaumont & Beveridge (1984) measured a *Pgm* heterozygosity in *Chlamys opercularis* similar to that reported here for *C. islandica*, even higher values for *C. distorta*, but significantly lower values for *C. varia* and *Pecten maximus*. All 4 species were sampled in the Irish Sea. SOD has been much less studied in bivalves than GPI and PGM, but there appears to be generally lower polymorphism at this locus than found here for *C. islandica*. Beaumont & Beveridge (1984) found *Sod* to be monomorphic in *C. varia* and *C. distorta*, and to show inconsistent resolution in *C. opercularis* and *P. maximus*, although with unquantified variability in the latter.

There has been a great deal of speculation about the ecological/biological significance of differentiated gene variation among marine organisms, that is whether or not there is an adaptive strategy to the variation. Despite difficulties in classifying the interactions between the environment and the species and the different species' perception of the environment (see Nelson & Hedgecock 1980, Nevo et al. 1984), substantial contributions to the neutral-selection controversy are still

frequently published (e.g. Mitton & Grant 1984, Nevo et al. 1984, Hedrick 1986, Koehn & Hilbish 1987, Lavie et al. 1987, Noy et al. 1987).

At an early stage, it was postulated that bivalves which experience greater environmental variability are more polymorphic, particularly at *Gpi*, than those living in more constant environments (Levinton 1973, Mathers 1975, Wilkins 1975); polymorphism should enhance fitness in variable environments (in accordance with the niche-width hypothesis; van Valen 1965). On comparing the inter-tidal *Chlamys varia* with the sub-littoral *C. opercularis*, it was concluded that at least as long as species within the same genus are compared, a more stable environment (sublittoral) is typical for more monomorphic species (Mathers 1975). The high variability observed in the relatively deep living *Pecten maximus* did not fit this model, but could be related to the species' ability to swim, resulting in opportunities for experiencing a more variable environment (Wilkins 1975). Both *C. opercularis* and *C. islandica* swim, live on similar substrates, and at similar depths, but *C. islandica* lives in much colder water – presumably in a more stable environment, or a narrower niche. It is interesting, therefore, to observe that *C. islandica* shows significantly higher *Gpi* polymorphism than *C. opercularis*, in fact the highest found in any member of the genus *Chlamys*. Also the variability at *Pgm* and *Sod* in *C. islandica* is equal to or greater than that of pectinids from environments which are presumably spatiotemporally more heterogeneous.

Yet, the whole enigma again ends up with speculations about how the Iceland scallop actually perceives its environment, and whether its niche is in fact narrow or wide compared to those of the more temperate species. Although the arctic/subarctic environment of *Chlamys islandica* is stable in theory with, for instance, only minor temporal and spatial variation in temperature, other factors like food supply vary during the year. Moreover, by videomonitoring the species' habitat we have seen (unpubl.) that it seems so thrive on a wide variety of substrates, from crevices between large rocks to flat, sandy, and occasionally almost muddy bottom. Considering also its wide geographical distribution, it could thus be argued that the scallop's niche is in fact wide. This argumentation illustrates one problem of relating specific gene variability to a species' fitness. Rating environments according to heterogeneity is still a very subjective process.

Inter-sample variation, gene flow and population structuring

The variability at both *Pgm* and *Sod* was significantly heterogeneous over the sampling area, whilst the highly polymorphic *Gpi* locus showed significant inter-area heterogeneity only when the effective number of alleles was considered. The pattern of variation was such that each geographical area formed a cluster. Due to the large population sizes, and the long life span of the species ($\geq$ 20 yr), which meant that many age cohorts were sampled, random genetic drift is not considered likely to account for the inter-area differentiation. Other models, selective and neutral, can better explain this observation, e.g.: (1) The long larval stage of *Chlamys islandica* has a potential for extensive gene flow and panmixia, but local adaptive selection may act on the settling larvae causing inter-area gene diversity among the adult populations; (2) the differentiated allele frequency variability is a result of reduced gene flow and the existence of more or less reproductively isolated stocks.

If environmental selection acts upon the settling larvae (or upon spat after settling) one might expect the adult population to be in Hardy-Weinberg disequilibrium. The surplus of homozygotes frequently seen at the *Pgm* locus could of course theoretically indicate that homozygotes are fitter than the corresponding heterozygotes, but alternative explanations like mixing of different genetic units (Wahlund effect) must also be considered (unless all the immigrant larvae are selected against before maturation). Such a surplus of homozygotes seems to be a common feature among marine bivalves (Fujio et al. 1983, Beaumont & Beveridge 1984, Foltz & Zouros 1984, Zouros & Foltz 1984), although no unambiguous explanation for the phenomenon has been found. Moreover, the pattern of variability for *Gpi* and *Sod* revealed frequent excesses of heterozygotes, opposite to that of *Pgm* and indicative of heterosis. Thus, the possibility that some of the diversity observed among the geographic regions is retained by natural selection cannot be discounted – a selection which of course could act upon loci linked to those studied.

On the other hand, considering the rather complex current system in the northern Atlantic, it is quite possible that the gene diversity is mainly of a neutral pattern, i.e. physical factors restrict larval dispersal and gene flow between areas. The behaviour of Iceland scallop larvae is to a large extent unknown, but presumably they are dispersed through the upper part of the water column where they will be subject to transport with the surface water currents. Dispersal of larvae with surface currents from N Norway to Bear Island, and as far north as Spitsbergen, is only possible if larvae spawned along the coast of N Norway reach the Norwegian Atlantic Current outside the Norwegian Coastal Current (Fig. 1). The latter, however, is likely to transport larvae into the eastern Barents Sea, which may in fact be the normal regime. If the larvae did reach the Atlantic current, they are likely to pass Bear

Island too far off the west coast to settle in the scallop beds there. Moreover, the local current system around Bear Island is very complex. A surface gyre NE of the island, and certainly within reach of locally spawned larvae, could restrict larval dispersal, and possibly engender a self-sustaining stock. The scallops growing off the coast of Spitsbergen, on the other hand, seem to be dependent on an influx of larvae since locally spawned larvae are likely to drift north and out of the region. However, scallops from the coast of Norway do not seem a very likely source. There is no reason to believe that there is extensive gene exchange between Jan Mayen and the remaining areas since there are prevailing northerly currents both east of Jan Mayen and west of Norway/Bear Island/Spitsbergen. Physical barriers could thus account for the distinct difference in allozyme variability between Jan Mayen and the remaining areas.

The information now available on *Chlamys islandica* is in itself insufficient to discriminate between diversifying selective constraints and restricted gene flow, although one must assume that neutral factors contribute significantly to the gene diversity that has been observed. Gene flow can of course be stepwise and a gross circulatory pattern may exist that over generational time ties some of the different geographical populations in the North Atlantic together; however, this gene flow is apparently insufficient to create a genetically homogeneous stock. For management purposes, therefore, the data suggest that the conservative approach of considering each area as if it was inhabited by semi-discrete genetic units, which should be managed independently of one another, should be adopted.

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