Vol. 4: 221–227, 1981 | MARINE ECOLOGY – PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published February 27

Ecological Genetics of the Mussels *Mytilus edulis* and *M. galloprovincialis* on Irish Coasts

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ABSTRACT: Genetic polymorphism at the loci encoding the enzymes phosphoglucose isomerase, leucine aminopeptidase and phosphoglucomutase was investigated in Irish *Mytilus* populations. Allele frequencies and heterozygote proportions indicated that populations on exposed Atlantic coasts differed from those on sheltered Atlantic coasts, and from Irish Sea mussels. When compared with data on *M. edulis* collected in northern France and *M. galloprovincialis* from the Mediterranean these data indicate that in Ireland *M. galloprovincialis* occurs mainly at exposed sites, and hybridization with *M. edulis* occurs frequently. The systematic status of the two forms remains uncertain in the light of genetic evidence of hybridization and intergradation between them.

INTRODUCTION

Mytilus edulis L. and *Mytilus galloprovincialis* Lmk. occur on the coasts of Ireland (Baird, in Hepper, 1957; Kitching et al., 1959; Ebling et al., 1960). They are not, however, evenly distributed on all coasts; Seed (1974) reported that *M. edulis* alone occurred on the Irish Sea coast, whereas both mussels were found on the South, West and North coasts. Until recently, the two mussel types were distinguished by physiological and morphological characters alone (Seed, 1971). These characters are very variable in British and Irish mussels (Lewis and Seed, 1969), and accurate identification of populations of the two types based on these characteristics is difficult, especially at exposed sites (Seed, 1974). Biochemical genetic studies have indicated that they differ also at a small number of enzyme gene loci (Ahmad and Beardmore, 1976; Gosling and Wilkins, 1977; Skibinski et al., 1978) and in addition, suggest that some hybridization may occur between the two forms on the Atlantic coasts of Ireland and parts of Britain. The extent of hybridization varies from site to site, and it has been suggested (Skibinski and Beardmore, 1979) that in some environments hybrids and individuals of mixed ancestry may have fitness superior to that of the *edulis* form. The results of the present study, taken in conjunction with those from our preliminary report (Gosling and Wilkins, 1977), suggest that the *M. galloprovincialis* form favours the offshore habitat and hybridization with *M. edulis* is common there; in sheltered shore environments, *M. galloprovincialis* occurs only to a very limited extent and hybrids are consequently rarer.

MATERIALS AND METHODS

Approximately 4100 individual mussels were analysed in the period since October 1974. These were collected from 26 sites on the coasts of Ireland (Table 1). Mussels were collected from two types of habitat: exposed sites, located on headlands lacking protection from wave action and prevailing winds and sheltered sites located at the inner end of inlets and bays in fully saline waters. At four sites (2,5, 17 and 28) mussel populations were entirely sublittoral; these were classified as sheltered sites. For purposes of comparison pure samples of *Mytilus galloprovincialis* were analysed from Venice and Cannes on the Mediterranean coast and a single sample of *M. edulis* was analysed from San Vaast on the Channel coast of France.

Technical details of sample preparation, electrophoretic procedure and visualization of *Pgi* and *Pgm* have been described previously (Gosling and Wilkins, 1977). Staining for *Lap* was performed using the method of Murdock et al. (1975), but the *Lap* locus studied by us is not that studied by Murdock et al., nor the *Lap-1* locus described in Skibinski and Beardmore (1979).

The terminology used for all allozymes is as follows: *a* indicates the least anodal allozyme, and *b, c, d* etc.

0171-8630/81/0004/0221/$ 02.00

Table 1 Classification of the various sampling sites on the Irish, French and Italian coasts. E: exposed site; S: sheltered site; N: minimum number of individuals analysed for each of the 3 loci – *Pgi, Lap* and *Pgm*. Mussels from Sites 13 and 29 were not assayed for *Pgm*. Mussels from Sites 6, 11 and 13 were not assayed for *Lap*

Site		Shore exposure	N
IRELAND			
East coast			
1	Belfast	S	142
2	Drogheda	S	79
3	Baldoyle	S	99
4	Dublin	S	100
5	Wicklow	S	37
6	Cahore Point	E	70
South coast			
7	Wexford	E	425
8	Waterford	S	142
9	Cork	E	73
10	Cork	S	88
11	Kinsale	S	59
12	Lough Ine	S	162
13	Bantry	S	82
West coast			
14	Kilkee	E	96
15	Blackhead	E	194
16	Nimmo's Pier	S	213
17	Lough Atalia	S	198
18	Salthill	S	28
19	Carna	E	76
20	Glinsk	S	124
21	Killary	S	1054
22	Achill	E	63
23	Donegal	E	86
24	Donegal	S	69
North coast			
25	Melmore Head	E	46
26	Portrush	E	79
NORTH FRANCE AND MEDITERRANEAN AREA			
27	San Vaast	S	92
28	Cannes	S	68
29	Venice	S	54

are used for progressively more anodal allozymes. Alleles Pgi^f, Pgi^d and Pgi^b in this paper correspond to alleles Pgi^A, Pgi^B and Pgi^C respectively in Gosling and Wilkins (1977) and to alleles Pgi^5, Pgi^3 and Pgi^1 of Ahmad and Beardmore (1976).

RESULTS

Pgi, Pgm and *Lap* migrated towards the anode in all individuals and multiple zones of activity were observed for each enzyme.

At the *Pgi* locus 7 alleles were observed in Irish populations of *Mytilus*. The three most common alleles were designated Pgi^f, Pgi^d and Pgi^b. The less common alleles were Pgi^a, Pgi^c, Pgi^e and Pgi^g. All of these, with the exception of Pgi^a and Pgi^g, were also observed – though at different frequencies – in *M. galloprovincialis* from the Mediterranean area.

At the *Lap* locus, 3 common (Lap^b, Lap^c and Lap^d) and 2 rare alleles (Lap^a and Lap^e) were observed in both forms. At the *Pgm* locus also both forms exhibited three common (Pgm^b, Pgm^c and Pgm^d) and two rare alleles (Pgm^a and Pgm^e). At each locus all alleles which exhibited a frequency ≥ 0.05 in at least one sample were treated separately for statistical analyses. Alleles with frequencies < 0.05 have been pooled where necessary.

Irish Sea Sites

527 individuals were analysed from 6 separate sites, all but one of which were sheltered or sublittoral. Table 2 summarizes the allele frequency data for the common alleles at each enzyme locus in these samples. Genotype proportions and allele frequency data for each of the samples analysed in the present study are available on request.

Pgi: At the *Pgi* locus 3 alleles Pgi^b, Pgi^d and Pgi^f were common with mean frequencies of 0.05, 0.30 and 0.61 respectively; 2 other alleles Pgi^a and Pgi^g each occurred at frequencies of approximately 0.01. The alleles Pgi^e and Pgi^c were entirely absent in these samples, all of which were in Hardy-Weinberg equilibrium with D_t values close to 0 (D_t was calculated as $[H_o-H_e]/H_e$, where H_o is the total number of heterozygotes observed per sample, and H_e the total number expected from the estimated allele frequencies). Allele frequencies were homogeneous over all sites analysed.

Lap: At the *Lap* locus 3 common alleles, Lap^b, Lap^c,

Table 2. Mean frequencies and standard deviation of the major alleles of *Pgi, Lap* and *Pgm* in samples of mussels from Irish coastal sites. N: number of sites sampled

Loci	IRISH SEA COAST Sheltered N = 5	ATLANTIC COAST Sheltered N = 9	ATLANTIC COAST Exposed N = 9
Pgi^b	0.05 ± 0.01	0.05 ± 0.02	0.04 ± 0.02
Pgi^d	0.30 ± 0.01	0.37 ± 0.05	0.44 ± 0.06
Pgi^e	0.0 ± 0.0	0.02 ± 0.03	0.16 ± 0.07
Pgi^f	0.61 ± 0.02	0.52 ± 0.07	0.29 ± 0.05
Lap^b	0.11 ± 0.03	0.10 ± 0.02	0.09 ± 0.04
Lap^c	0.61 ± 0.05	0.57 ± 0.04	0.48 ± 0.04
Lap^d	0.26 ± 0.03	0.30 ± 0.07	0.41 ± 0.05
Pgm^b	0.13 ± 0.05	0.13 ± 0.02	0.14 ± 0.04
Pgm^c	0.64 ± 0.03	0.60 ± 0.03	0.57 ± 0.04
Pgm^d	0.21 ± 0.02	0.25 ± 0.04	0.28 ± 0.04

and Lap^d and 2 rare alleles Lap^a and Lap^e were observed. The mean frequency of Lap^c (0.61) was considerably higher than Lap^d (mean frequency 0.26). All samples were in Hardy-Weinberg equilibrium and allele frequencies were homogeneous over localities.

Pgm: 3 common alleles Pgm^b ($\bar{p}$ 0.13), Pgm^c ($\bar{p}$ 0.64) and Pgm^d ($\bar{p}$ 0.21) and 2 rare alleles Pgm^a and Pgm^e were observed at this locus. Allele frequencies were homogeneous over localities. There is no evidence at the 3 loci that the mussels in the Irish Sea constitute anything except a single panmictic population. The single exposed shore sample did not differ greatly in allele frequency from the sheltered shore samples from this area.

Atlantic Coast Sites

Approximately 3400 individuals were analysed from 9 exposed and 9 sheltered sites on the Atlantic coasts (North, West and South coasts) of Ireland. The data obtained are summarized in Table 2.

In both sheltered and exposed shore samples four common *Pgi* alleles (Pgi^b, Pgi^d, Pgi^e and Pgi^f), 3 common *Lap* alleles (Lap^b, Lap^c, Lap^d) and 3 common *Pgm* alleles (Pgm^b, Pgm^c and Pgm^d) were observed. However, the frequencies of these alleles differed considerably between the 2 groups of samples.

Pgi: In sheltered sites Pgi^f had a mean frequency of 0.52, and Pgi^e – which was entirely absent from the Irish Sea sites – had a mean frequency of 0.02. At exposed sites the mean frequency of Pgi^f was significantly smaller ($\bar{p}$ 0.29) and that of Pgi^e ($\bar{p}$ 0.16) significantly greater than in sheltered sites. Within each group – exposed and sheltered – interlocality heterogeneity in allele frequency was greater than that observed in the Irish Sea samples. The majority of the sheltered shore samples were in Hardy-Weinberg equilibrium, whereas all exposed shore populations, with one exception, exhibited significant deficiencies of heterozygotes.

Lap: In sheltered sites the mean frequency of Lap^c (0.57) was higher and that of Lap^d (0.30) lower than in exposed shores (0.48 and 0.41 respectively). All samples with the exception of two sheltered shore sites were in Hardy-Weinberg equilibrium.

Pgm: The mean frequencies of the 3 common alleles were very similar in the 2 groups. In general, the frequency of Pgm^d was higher and that of Pgm^c lower than those observed in the Irish Sea samples. At 6 sites significant deficiencies of heterozygotes were observed. When the mean allele frequencies at the 3 groups of sites (Irish Sea, Atlantic sheltered and Atlantic exposed) were compared by single-factor analysis of variance, the differences between them were statistically significant ($p < 0.05$ or less) for the most common alleles at all loci. Of the 3 loci, *Pgi* exhibited the greatest degree of differentiation in all intergroup comparisons. The major component of the overall heterogeneity can be attributed to differences between exposed Atlantic sites and sheltered (both Atlantic and

Table 3. Frequency of Pgi^e together with D_t values at the *Pgi* locus in samples of *Mytilus* from exposed and sheltered sites on the Atlantic coasts of Ireland. D_t = deviations of observed heterozygote numbers from Hardy-Weinberg expectations formulated as: $D_t = (H_0 - H_e)/H_e$, where H_0 = total number of heterozygotes observed and H_e = total number expected from the estimated allele frequencies. Site numbers in parentheses correspond to those in Table 1. H^{min} and H^{max}: minimum and maximum proportions of hybrid genotypes in each population. (See text for calculation procedure). Probability that observed genotype proportions within each population depart from Hardy-Weinberg expectations given after D_t value as follows: N.S. = deviation not significant; • = significant at the 5% level; •• = significant at the 1% level; ••• = significant at the 0.1% level

ATLANTIC SITES									
	Exposed					Sheltered			
Site	P^e	D_t	H^{min}	H^{max}	Site	P^e	D_t	H^{min}	H^{max}
(7)	0.15	– 0.31•••	4.3	20.0	(8)	0.0	– 0.29•••	0.0	0.0
(9)	0.16	– 0.17••	9.6	25.0	(10)	0.06	– 0.25••	4.9	9.0
(14)	0.16	– 0.33•••	7.6	11.0	(11)	0.02	+ 0.08 N.S.	3.4	7.0
(15)	0.28	– 0.17••	8.0	25.0	(13)	0.05	– 0.19 N.S.	4.9	6.0
(19)	0.13	– 0.17•••	5.3	14.0	(16)	0.0	– 0.10 N.S.	0.0	0.5
(22)	0.17	– 0.03•	9.5	25.0	(17)	0.01	– 0.09 N.S.	1.0	2.0
(23)	0.13	– 0.30•••	5.8	14.0	(18)	0.0	– 0.01 N.S.	0.0	0.0
(25)	0.19	– 0.09 N.S.	6.5	24.0	(21)	0.02	– 0.08 N.S.	0.8	3.0
(26)	0.09	– 0.38•••	6.7	11.0	(24)	0.06	– 0.11 N.S.	4.3	9.0
Mean	0.16	– 0.22	7.03	18.78		0.02	– 0.11	2.14	4.05
S.D.±	0.05	0.11	1.71	5.88		0.02	0.11	2.06	3.53

Note: In populations with D_t values close to 0, individual genotype proportions can be significantly out of Hardy-Weinberg equilibrium

Table 4. *Pgi, Lap* and *Pgm* allele frequencies together with χ^2 and D_t values in samples of *Mytilus* from Lough Ine and Glinsk. χ^2: goodness-of-fit of observed to expected values from Hardy-Weinberg equilibrium; N.S. = $P > 0.05$; $^{\bullet}$ = $P < 0.05$; $^{\bullet\bullet}$ = $P < 0.01$; $^{\bullet\bullet\bullet}$ = $P < 0.001$

Pgi										
Lough Ine	N	a	b	c	d	e	f	g	χ^2	D_t
M. gallopr.	162	0.01	0.07	0.04	0.45	0.17	0.24	0.02	$29.2^{\bullet\bullet\bullet}$	− 0.22
Glinsk										
M. edulis	40	0.0	0.09	0.05	0.46	0.06	0.34	0.00	4.7 N.S.	− 0.02
M. gallopr.	116	0.0	0.02	0.06	0.42	0.24	0.25	0.00	$49.6^{\bullet\bullet\bullet}$	− 0.22
Lap										
Lough Ine	N	a	b	c	d	e			χ^2	D_t
M. gallopr.	230	0.01	0.07	0.55	0.37	0.01			$24.3^{\bullet\bullet\bullet}$	− 0.22
Glinsk										
M. edulis	39	0.0	0.06	0.51	0.42	0.0			$9.6^{\bullet\bullet}$	− 0.40
M. gallopr.	124	0.0	0.14	0.47	0.38	0.01			6.9 N.S.	− 0.15
Pgm										
Lough Ine	N	a	b	c	d	e			χ^2	D_t
M. gallopr.	231	0.01	0.12	0.57	0.29	0.01			4.9 N.S.	− 0.02
Glinsk										
M. edulis	39	0.0	0.14	0.54	0.31	0.01			1.2 N.S.	− 0.12
M. gallopr.	132	0.0	0.17	0.53	0.27	0.03			8.3 N.S.	− 0.14

Irish Sea) sites. Sheltered Atlantic sites are not identical to sheltered Irish Sea sites although the differences between them are significant for only 4 allelic comparisons and then only at the 5 % level.

Three special features of the data for the *Pgi* locus are presented in Table 3: (a) Pgi^e which is entirely absent in all Irish Sea samples, both sheltered and exposed (527 individuals), occurs at a low mean frequency (0.02) in sheltered Atlantic sites and at relatively high mean frequency (0.16) in exposed Atlantic sites. (b) The high frequency of Pgi^e is positively correlated with high negative D_t values (i. e., large deficiencies of heterozygotes) in these samples. The D_t values in Table 3 refer to total heterozygote deficiency, not to those involving Pgi^e alone; they measure the extent to which the total number of heterozygotes depart from Hardy-Weinberg expectations. (c) If hybridization is taking place between the 2 types of mussel one method of estimating its amount is to calculate the frequencies of individuals heterozygous for two different alleles, each of which is common in one form of mussel but uncommon in the other. At the *Pgi* locus such genotypes occur at an average frequency of 7–19 % on exposed Atlantic sites and at 2–4 % on sheltered sites, depending on which genotypes are used in the calculation (Table 3). The minimum value is calculated using *Pgi* genotypes a/c, a/e, b/c, b/e, c/f, c/g, e/f and e/g alone. The maximum value includes the genotypes c/d and e/d which may represent either hybrids or pure *Mytilus galloprovincialis* heterozygotes.

At 2 sites (Lough Ine and Glinsk) mussels were found which morphologically resembled *Mytilus galloprovincialis*. Because of this, allele frequency data for these samples were treated separately and are presented in Table 4. The Lough Ine sample was collected from the site at which Kitching et al. (1959), Ebling et al. (1960) and Seed (1974) had observed a high incidence (58–77 %) of *M. galloprovincialis*. At all 3 loci, allele frequencies closely resembled those characteristic of Atlantic exposed shore mussels (Table 2). A significant deficiency of heterozygotes was observed at the *Pgi* and *Lap* loci. Individuals bearing some resemblance in shell morphology to *M. edulis* were subsequently separated from this sample. These constituted approximately one third of the total sample. No statistically significant differences in allele frequencies were observed at any of the three loci between these individuals and the remainder of the sample. At the *Pgi* locus the '*eduls* group' was in Hardy-Weinberg equilibrium whereas a significant deficiency of heterozygotes was observed in the remainder. The opposite was observed at the *Lap* locus where a significant deficiency of heterozygotes was observed only in the '*edulis* group'.

In the Glinsk sample also, the mussels resembled *Mytilus galloprovincialis* morphologically. Allele frequencies at the 3 loci again closely resembled those characteristic of Atlantic exposed shore mussels (Table 2). A significant deficiency of heterozygotes was observed only at the *Pgi* locus. This sample was compared with mussels collected from the same shore but which did not obviously resemble *M. galloprovincialis* in shell characteristics. The 2 samples differed significantly at the *Pgi* locus and the frequency of Pgi^e

Table 5. *Pgi, Lap* and *Pgm* allele frequencies together with χ^2 values in samples of *Mytilus edulis* and *M. galloprovincialis* from San Vaast and Cannes (France) and from Venice (Italy)

Pgi		N	d	e	f	Others*	χ^2
San Vaast	*M. edulis*	92	0.26	0.0	0.64	0.10	5.5 N.S.
Cannes	*M. gallopr.*	80	0.79	0.13	0.03	0.05	1.4 N.S.
Venice	*M. gallopr.*	74	0.87	0.12	0.0	0.01	0.4 N.S.
Lap		N	b	c	d	Others*	χ^2
San Vaast	*M. edulis*	102	0.14	0.66	0.20	0.0	0.4 N.S.
Cannes	*M. gallopr.*	95	0.02	0.53	0.45	0.0	35.2***
Venice	*M. gallopr.*	54	0.07	0.51	0.40	0.02	1.1 N.S.
Pgm		N	b	c	d	Others*	χ^2
San Vaast	*M. edulis*	104	0.12	0.66	0.22	0.0	4.3 N.S.
Cannes	*M. gallopr.*	68	0.10	0.53	0.34	0.03	6.5 N.S.

* Pooled uncommon alleles Pgi^a, Pgi^b and Pgi^g in *M. edulis*; Pgi^b and Pgi^c in *M. galloprovincialis*; Lap^e; Pgm^a and Pgm^e

was significantly higher in the sample resembling *M. galloprovincialis*. The *M. edulis* sample was in Hardy-Weinberg equilibrium at the *Pgi* and *Pgm* loci but not at the *Lap* locus. The *M. galloprovincialis* sample was in Hardy-Weinberg equilibrium at the *Pgm* and Lap loci but not at the *Pgi* locus.

Sites Outside Ireland

Mussels identified morphologically as either *Mytilus edulis* or *M. galloprovincialis* were collected from sites in France and Italy; their allele frequency data are presented in Table 5. Contingency χ^2 tests indicated that allele frequencies at the *Pgi* locus were significantly different in the 2 forms ($p < 0.001$). Pgi^d was the commonest allele in *M. galloprovincialis* ($\bar{p} = 0.83$); the frequency of Pgi^f was high in *M. edulis* ($\bar{p} = 0.64$) and extremely low in *M. galloprovincialis* ($\bar{p} = 0.02$); Pgi^e, which was absent in *M. edulis*, occurred at a mean frequency of 0.13 in *M. galloprovincialis*. The mean frequency of Lap^d (0.43) was significantly higher ($p < 0.001$) and that of Lap^c (0.52) significantly lower ($p < 0.001$) in *M. galloprovincialis* than in *M. edulis*. At the *Pgm* locus also allele frequencies in the two species differed significantly but only at the 5 % level.

In summary, *Pgi* proved to be the most effective locus in differentiating samples which were identified morphologically as either pure *Mytilus edulis* or pure *M. galloprovincialis*. Highly significant differences ($p < 0.001$) in both genotypic and allelic distributions at this locus were observed when populations of the 2 forms were compared. The other 2 loci were not as useful in differentiating between them.

Table 6 summarizes the allele frequency data for Irish mussel populations and compares these with the data on *Mytilus edulis* and *M. galloprovincialis* from France and Italy. The overall resemblance of the Irish Sea and sheltered Atlantic data to those of *M. edulis* from northern France is apparent. The Atlantic exposed shore mussels, on the other hand, are very different from French *M. edulis*, and from the Irish Sea samples, and their allele frequencies at all 3 loci are intermediate to those of *M. edulis* and *M. galloprovincialis*.

Table 6. Mean frequency of the major *Pgi, Lap* and *Pgm* alleles in pure *Mytilus edulis* from France, in Irish coastal mussels and in pure *M. galloprovincialis*

Mytilus edulis	Pgi^b	Pgi^d	Pgi^e	Pgi^f	Lap^b	Lap^c	Lap^d	Pgm^b	Pgm^c	Pgm^d
France	0.04	0.26	0.0	0.64	0.14	0.66	0.20	0.12	0.66	0.22
Mytilus										
Irish Sea	0.05	0.30	0.0	0.61	0.11	0.61	0.26	0.13	0.64	0.21
Atlantic sheltered	0.05	0.37	0.02	0.52	0.10	0.57	0.30	0.13	0.60	0.25
Atlantic exposed	0.04	0.44	0.15	0.29	0.09	0.48	0.41	0.14	0.57	0.28
M. gallopr.										
Mediterranean	0.01	0.83	0.13	0.02	0.05	0.52	0.43	0.10	0.53	0.34

DISCUSSION

The study of genetic variation in European populations of mussels is complicated by the occurrence of two morphologically distinct forms, *Mytilus edulis* and *M. galloprovincialis*. While some authorities regard *M. galloprovincialis* as a good species, others consider it a variety of the larger *M. edulis* superspecies (see review by Lubet, 1973). Whether they are regarded as separate species or not, they do differ biochemically at a number of loci (Ahmad and Beardmore, 1976, Gosling and Wilkins, 1977 and Skibinski et al., 1978). These biochemical differences are confirmed and extended in this study and can be summarized as follows: *M. galloprovincialis* is characterised by a high frequency of Pgi^d and an intermediate frequency of Pgi^e. *M. edulis* is characterised by a high frequency of Pgi^f and the absence or very low frequency of Pgi^e. When samples of the 2 forms are compared at this locus, statistically significant differences in both genotypic and allelic proportions are observed. At the *Lap* and *Pgm* loci while both forms share the same alleles, each exhibits its own characteristic allele frequencies and these are significantly different between the two. Of the three loci analysed *Pgi* appears to be the most useful in differentiating between the two types of mussels. Mussels on the Irish Sea coast of Ireland exhibit allele frequencies at all 3 loci which are very similar to those of the pure *M. edulis* population collected at San Vaast and to pure samples of *M. edulis* collected elsewhere by others (Ahmad and Beardmore, 1976; Ahmad et al., 1977). This fact, together with the homogeneity in allele frequency observed throughout the Irish Sea samples and their morphological appearance, is consistent with the view (Seed, 1974) that mussels in this region constitute a single panmictic population of *M. edulis* alone.

The outstanding feature of the Atlantic coast data is the marked difference observed between exposed-shore mussels and those from sheltered sites. We believe that this difference reflects the occurrence in exposed shore samples of significant proportions of both *Mytilus galloprovincialis* and *M. edulis*, whereas *M. galloprovincialis* does not occur to any great extent on sheltered shores. Our reasoning is as follows: Allele frequencies, especially at the *Pgi* locus are significantly different between pure *M. edulis* and pure *M. galloprovincialis* (see Table 5). Samples which are mixtures of these 2 forms will exhibit intermediate allele frequencies (depending on the relative proportions in the mixture) and, in addition, will exhibit overall deficiencies of heterozygotes (the Wahlund effect) at those loci where allele frequencies differ greatly. This is precisely what is observed in Atlantic exposed shore samples. When the frequencies of the 10 major alleles are compared (Table 6), exposed-shore populations exhibit values which are either similar to those of *M. galloprovincialis* or are intermediate between *M. edulis* and *M. galloprovincialis* in 8 of the 10 comparisons. At the *Pgi* locus, where *M. edulis* and *M. galloprovincialis* differ most in allele frequencies, all the exposed shore populations exhibit relatively high frequencies of the *M. galloprovincialis* allele Pgi^e and all have statistically significant total heterozygote deficiencies. Sheltered Atlantic shore populations, on the other hand, have allele frequencies which resemble more closely those of *M. edulis* and, with only two exceptions, are all in Hardy-Weinberg equilibrium at the *Pgi* locus. They are not, however, identical to the *M. edulis* population of the Irish Sea (Table 2).

We reject the hypothesis that the genetic differences observed between exposed and sheltered shore mussels are due to selection for the following reasons: Mussels from the single exposed shore site sampled on the Irish Sea coast did not differ appreciably in allele frequency from the sheltered shore samples, and did not exhibit deficiencies of heterozygotes at the *Pgi* locus. In the two sheltered Atlantic sites, i. e., L. Ine and Glinsk where the mussels resembled *Mytilus galloprovincialis* in morphological features, and at one of which (L. Ine) *M. galloprovincialis* has been confirmed by a number of independent authors, the allele frequencies and genotype proportions resemble exposed rather than sheltered shore mussels. Finally, if selection is acting against heterozygotes in exposed shore populations, a greater deficiency of heterozygotes might be expected among larger (older) individuals than in smaller (younger) individuals. In our earlier report (Gosling and Wilkins, 1977) we showed that heterozygote deficiency at the *Pgi* locus is neither correlated with absolute nor relative size of individual mussel nor is it correlated with position of the mussels on the shore, i. e., mussels in the higher, more exposed regions of the shore do not differ in allele frequency or genotype proportions from samples collected sublittorally in the same area.

The factors which result in the virtual absence of *Mytilus galloprovincialis* from most of the sheltered shore sites are at present unknown, as are those which exclude it from the Irish and British coasts (Seed, 1974; Skibinski and Beardmore, 1979) of the Irish Sea. Indeed, genetic evidence shows that in Britain *M. galloprovincialis* occurs only along the Cornish peninsula, the extreme north and north east of Scotland and along the coast of Yorkshire (Skibinski and Beardmore, 1979). It would be valuable to know whether these represent the more exposed of the sites sampled in Britain.

On the coasts of Ireland and Britain, the 2 forms are not easily distinguished morphologically. Features

normally confined to one or other of the forms often occur together in single individuals, and intermediate forms occur commonly, making accurate identification difficult and sometimes impossible. Difficulties of this nature have been experienced by Lewis and Powell (1961), Seed (1974), Ahmad and Beardmore (1976) and by us in this study. An explanation for this high degree of morphological intermediacy may lie in hybridization and introgression between the 2 forms. Skibinski and Beardmore (1979) have indicated that hybridization and introgression occur at certain localities and the degree of intergradation differs from locality to locality. We have observed that hybrid genotypes occur at frequencies of about 7 % in exposed shore samples and at 2 % in those from sheltered sites. Our results indicate that hybridization occurs at all exposed shore sites on the Atlantic coasts of Ireland and is not restricted to a small number of isolated localities. Whether the 2 forms should continue to be regarded as good biological species despite the evidence for such extensive hybridization and integradation (Skibinski and Beardmore, 1979) is doubtful. Indeed, when they are compared at a total of 13 loci, and the extent of their genetic identity is computed, the value obtained is similar to the mean value obtained in comparisons of subspecies of other taxa (Skibinski et al., 1980).

Acknowledgements. We thank B. Ashe, B. Beatty and M. Staunton for technical assistance and all those who helped in the collection of samples. We thank Professor Pierre Lubet, Université de Caen, Normandy, France for the generous use of the facilities in his laboratory. This research was supported by a grant from the National Board of Science and Technology, Ireland.

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This paper was presented by Dr J. Mauchline; it was accepted for printing on December 15, 1980