Heredity 57 (1986) 171–180

Received 4 November 1985

Growth rate and heterozygosity in the plaice, *Pleuronectes platessa*

B. J. McAndrew,*
R. D. Ward† and
J. A. Beardmore

Department of Genetics,
University College of Swansea,
Singleton Park, Swansea, SA2 8PP, U.K.

Samples of young plaice were examined to see if there was any relationship between growth rate and individual heterozygosity, screened across five polymorphic enzyme loci (*Pgm*-1, *Ada*, *Mdh*-2, *Pgi*-2, *αGpdh*-1). Two out of 46 samples showed a significant negative correlation between growth rate and multi-locus heterozygosity; none showed a significant positive correlation. There was no overall tendency to negative or positive correlations. The largest sample ($N = 689$) showed no relationship between multi-locus heterozygosity and growth rate, although one of the five loci, *αGpdh*-1, showed a significant positive correlation. The only significant correlation in the next largest sample ($N = 248$) was between multi-locus heterozygosity and growth rate, and that was negative. Fish of intermediate growth rate were not significantly different in heterozygosity from faster or slower growing fish. There was no relationship between variability in growth rate and multi-locus heterozygosity. These findings are discussed in the context of similar surveys from other species, and the conclusion drawn that the universality of a positive relationship between growth rate and multi-locus heterozygosity remains to be established.

INTRODUCTION

In recent years, a number of papers have been published examining the relationship between growth rate and individual heterozygosity. A variety of plant and animal species have been investigated, for a limited number of polymorphic loci, and the majority of these studies point to the existence of a positive correlation (Mitton and Grant, 1984).

The first study associating individual multi-locus heterozygosity and growth rate came from Singh and Zouros (1978) and Zouros *et al.*, (1980), working on the American oyster, *Crassostrea virginica*. Positive associations have subsequently been reported from natural populations of some other bivalves: *Mytilus edulis* (Koehn and Gaffney, 1984, although the relationship changed in older samples from the same cohort, Diehl and Koehn, 1985), *Mulinia lateralis* (Garton *et al.*, 1984), and for one of two populations of *Macoma balthica* (Green *et al.*, 1983). However, Foltz and Zouros (1984) and Beaumont *et al.* (1985) were unable to detect any such relationship in two species of scallops, *Placopecten magellanicus* and *Pecten maximus* respectively. Furthermore, Beaumont *et al.* (1983) also observed no effect of multi-locus heterozygosity on growth rate in 1 year old sibships of *M. edulis* reared in the laboratory.

Positive correlations between heterozygosity and length were reported in 5 out of 7 populations of young larvae of the salamander, *Ambystoma tigrinum* (Pierce and Mitton, 1982), and laboratory experiments suggested that the length differences were due to differential growth rates. Older larvae did not show the relationship. King (1985) found little evidence of a correlation between heterozygosity and growth rate in the herring, *Clupea harengus*, although there was a positive correlation between multi-locus heterozygosity and length. Beacham and Withler (1985) could not detect a difference in growth rate between homozygous and heterozygous pink salmon, *Oncorhynchus gorbuscha*. Cothran *et al.* (1983) observed a positive relationship between individual heterozygosity and foetal growth rate in the white-tailed deer, *Odocoileus virginianus*. Bottini *et al.* (1979) had earlier described a similar relationship in man,

Present addresses:
* Institute of Aquaculture, University of Stirling, Stirling, FK9 4LA, U.K.
† Department of Human Sciences, Environmental Biology Unit, Loughborough University, Loughborough, Leicestershire, LE11 3TU, U.K.

although Ward *et al.* (1985) were unable to detect such an effect in a larger study of human birth weight, albeit from a different population.

In plants, heterozygosity and growth rate was found to be associated in quaking aspen, *Populus tremuloides* (Mitton and Grant, 1980), but this species reproduces primarily vegetatively and the population has a clonal structure. Significant positive correlations were found in 3 of 8 stands of the pitch pine, *Pinus rigida*, but one stand showed a significant negative correlation (Ledig *et al.*, 1983). In neither ponderosa pine (*Pinus ponderosa*) nor lodgepole pine (*Pinus contorta*) is heterozygosity related to mean growth rate of mature trees (Grant *et al.*, 1982; Knowles and Mitton, 1980; Knowles and Grant, 1981; Mitton, 1983; Mitton *et al.*, 1981).

If there is a general relationship between growth rate and individual heterozygosity, as determined by screening between 4 and 10 polymorphic loci (most of the above studies falling into this range), this has clear theoretical implications for the current neutralist-selectionist controversy, and important practical implications for those engaged in animal and plant breeding. Yet the generality of the relationship seems to us not clearly established, and, as is so often the case, more work is required on further species.

In this paper, we examine the relationship between growth rate and multiple and single locus heterozygosity in a fish, the plaice. *Pleuronectes platessa.* In order to do this, we have restricted ourselves to examination of data from young plaice (less than 460 days of age), for which we have numerous large samples of known age.

MATERIALS AND METHODS

Young fish were collected by pushnetting in shallow water on the sandy beaches of South Wales, with by far the greatest number coming from Pendine Sands, Carmarthen Bay. Other beaches were sampled at Swansea Bay and Oxwich Bay. These fish are spawned off Trevose Head, Cornwall (Simpson, 1959), and the young fish are carried by ocean currents to the nursery beaches where they were sampled. Spawning takes place in late January, February, and March, probably peaking around mid-February (Simpson, 1959). In our calculations of fish age, we have assumed a nominal fertilisation date of February 14 for each year. Cushing (1969) has estimated the standard error of the mean date of spawning in the North Sea as 2·5 days.

Fish were weighed to the nearest 0·01 g and measured in length (from tip of head to tip of caudal fin) to the nearest mm. Each fish was then screened electrophoretically for five polymorphic loci, whose products were detectable in muscle tissue, and, depending on the number of heterozygous loci, assigned a heterozygosity score of 0, 1, 2, 3, 4, or 5. These loci were phosphoglucomutase-1 (*Pgm*-1), adenosine deaminase (*Ada*), malate dehydrogenase-2 (*Mdh*-2), phosphoglucose isomerase-2 (*Pgi*-2) and glycerophosphate dehydrogenase (α*Gpdh*-1). Details of gene and genotype frequencies and electrophoretic procedures followed are given in Ward and Beardmore (1977). Cross-tabulations and some of the statistical tests were performed using the SPSS computer package (Nie *et al.*, 1975).

RESULTS

In this analysis, we have chosen length as the parameter by which to estimate growth rate: weight is subject to greater short-term variation. Forty-six samples of young fish were analysed, 29 from Pendine, nine from Swansea, and eight from Oxwich, providing a total of 3964 fish. Information on sampling dates, ages, sample sizes, mean lengths and mean numbers of loci heterozygous is presented in table 1.

Fig. 1 shows graphically the age-related changes in mean length of the two most thoroughly sampled cohorts, Pendine 1975 and Pendine 1977. The youngest "O" group fish (those in their first year of life) were collected at the end of May or beginning of June. Growth continued through the summer months, ceased in the winter, and resumed in the spring. Patterns of growth were similar in the two cohorts, although the 1977 cohort was on average somewhat smaller than that of 1975. Density of O-group fish, estimated from catch/effort returns, was probably greater in 1977, and increased competition may have retarded growth slightly in this cohort.

Several tests were carried out to uncover any possible relationships between growth rate and heterozygosity.

First, both the Pearson (parametric) and Spearman (non-parametric) correlation coefficients were calculated for each sample. These two sets of values were generally very similar to each other; the Pearson values are given in table 1. It can be seen that of the 46 samples, 20 had a positive value for r and 26 a negative value. This is not significantly different from a random distribution ($X = 0{\cdot}78$, $P = 0{\cdot}38$), and hence this analysis fails

Table 1 Sample ages, numbers, sizes, heterozygosities, and correlation coefficients between heterozygosity score and Length

	Site	Date	Age	Length *N*	Mean	*SD*	*H*	*r*
1	Pendine	14.10.73	242	109	74·85	18·108	1·422	−0·131
2	Pendine	25.10.73	253	186	80·60	21·571	1·435	−0·006
3	Pendine	11.7.74	147	95	45·93	4·389	1·232	0·106
4	Pendine	18.8.74	185	53	61·79	9·214	1·453	−0·233*
5	Pendine	25.5.75	100	30	29·73	5·839	1·533	0·071
6	Pendine	11.6.75	117	83	38·21	8·391	1·518	−0·013
7	Pendine	10.7.75	146	29	57·24	9·736	1·345	0·009
8	Pendine	7.8.75	174	77	63·78	7·643	1·312	−0·017
9	Pendine	8.9.75	206	96	73·84	10·807	1·448	−0·245†
10	Pendine	6.10.75	234	137	72·47	13·847	1·416	−0·094
11	Pendine	4.11.75	263	102	68·85	9·221	1·510	−0·006
12	Pendine	2.12.75	291	57	69·89	10·789	1·649	0·037
13	Pendine	19.1.76	339	83	68·92	12·536	1·554	0·028
14	Pendine	19.2.76	370	32	76·00	9·509	1·625	−0·221
15	Pendine	16.3.76	396	31	78·22	10·852	1·613	−0·074
16	Pendine	15.4.76	426	28	89·11	22·076	1·250	0·228
17	Pendine	13.5.76	454	16	106·31	7·228	1·562	0·074
18	Pendine	1.6.77	107	33	25·09	3·527	1·636	−0·150
19	Pendine	16.6.77	122	248	36·33	6·976	1·440	−0·041
20	Pendine	4.7.77	140	689	39·75	10·290	1·478	−0.011
21	Pendine	15.9.77	213	149	62·31	11·547	1·597	0·115
22	Pendine	12.10.77	240	42	65·55	11·350	1·310	−0·254
23	Pendine	12.11.77	271	171	71·08	16·110	1·567	0·009
24	Pendine	13.12.77	302	91	68·02	13·498	1·286	−0·049
25	Pendine	11.1.78	331	132	66·46	12·121	1·538	−0·102
26	Pendine	10.2.78	361	162	71·20	11·672	1·475	0·010
27	Pendine	9.3.78	388	120	69·21	10·505	1·500	0·010
28	Pendine	24.4.78	434	31	74·74	9·126	1·387	−0·012
29	Pendine	8.5.78	448	37	87·46	13·960	1·514	0·255
30	Swansea	12.6.75	118	96	43·09	8·543	1·562	−0·084
31	Swansea	27.6.75	133	71	50·40	10·055	1·254	−0·186
32	Swansea	25.7.75	161	34	59·18	8·371	1·176	−0·096
33	Swansea	12.8.75	179	22	57·59	11·350	1·364	0·247
34	Swansea	7.9.75	205	29	64·17	12·033	1·552	−0·094
35	Swansea	4.12.75	293	29	82·00	12·381	1·448	0·178
36	Swansea	21.1.76	341	87	77·03	12·213	1·494	0·137
37	Swansea	17.2.76	368	27	82·74	16·870	1·741	−0·205
38	Swansea	18.3.76	398	26	84·88	12·193	1·423	0·128
39	Oxwich	30.8.73	197	73	77·06	14·259	1·315	0·105
40	Oxwich	27.9.73	225	78	87·59	22·597	1·462	0·039
41	Oxwich	8.8.75	175	65	62·46	12·022	1·554	0·068
42	Oxwich	9.9.75	207	32	66·00	16·184	1·406	−0·133
43	Oxwich	8.10.75	236	23	68·57	11·832	1·565	0·106
44	Oxwich	18.2.76	369	27	68·15	12·152	1·222	−0·008
45	Oxwich	14.4.76	425	56	77·77	16·322	1·429	−0·035
46	Oxwich	12.5.76	453	40	92·90	10·619	1·600	−0·120

Note: H is the mean number of heterozygous loci per fish. r has $N-2$ df. * $P = 0{\cdot}05$–$0{\cdot}01$, † $P = 0{\cdot}01$–$0{\cdot}001$.

to support the hypothesis of a positive relationship between growth rate and heterozygosity. Only two of the correlation coefficients are significantly different from zero, and both of these are negative.

Secondly, the mean lengths of fish having a heterozygosity score of 0, 1, 2, 3, 4 and 5 were calculated for each of the 46 samples (see appendix), and the data analysed in one of two ways. In method A, each of the heterozygosity classes in each sample was assigned a rank of 1, 2, 3, 4 or 5. The class with the smallest mean length was assigned a rank of 1, the next shortest class in that sample assigned a value of 2, and so on. The very small number of fish heterozygous at all five loci was ignored. These data were then subjected to an analysis of variance by ranks (Meddis, 1984), using a specific test that there should be a monotonically ascending trend of ranks from the homozygous

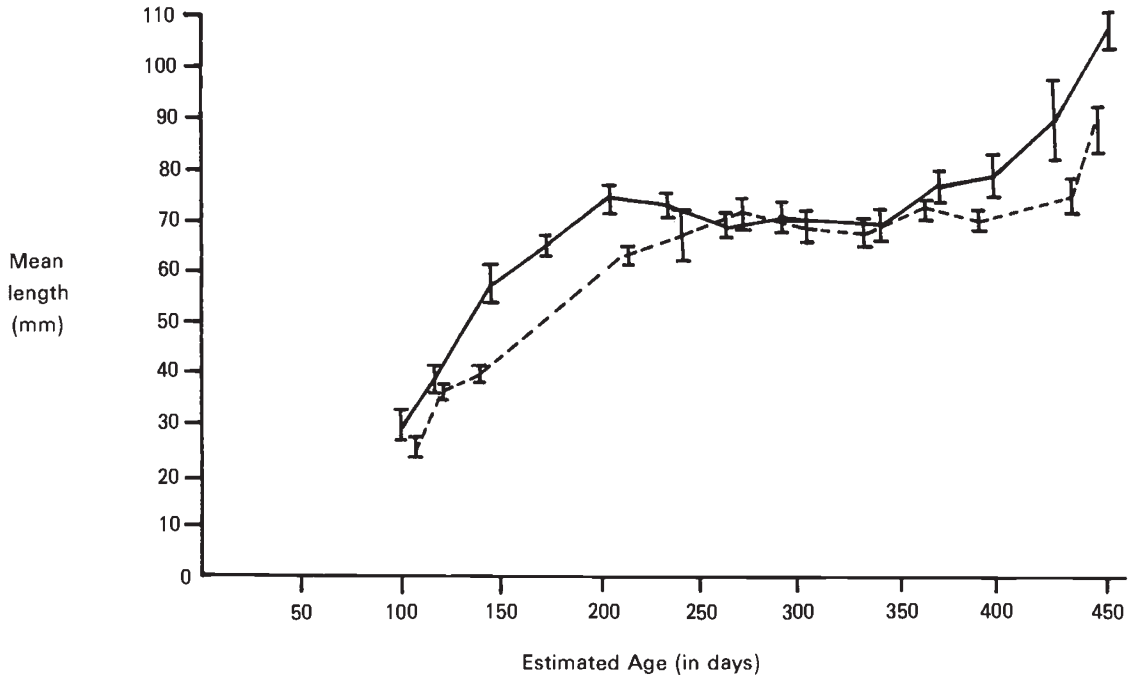

Figure 1 Mean length of fish plotted against estimated age in days. Solid lines (——) indicate the 1975 cohort, dashed lines (- - - - -) the 1977 cohort. 95 per cent confidence limits are given.

fish to those with a heterozygosity score of 4. The results of this test are given in table 2. It can be seen that there is no evidence to support the view that increasing multi-locus heterozygosity is associated with growth rate.

In method B, the small numbers of fish having scores of 4 and 5 were pooled with those having scores of 3, and if the mean length of fish with a particular heterozygosity score (0, 1, 2 or 3+) was greater than the overall mean length of that sample, that group was assigned to a "+" category, if less, to a "−" category. If heterozygosity is associated with increased growth rate, then groups of fish having heterozygosity scores of 2 and 3+ should primarily fall into the "+" category: conversely, groups of homozygous fish should fall into the "−" category. In fact, as table 3 shows, there is no evidence of "+" groups predominating in the multiply heterozygous fish, and no evidence of "−" groups predominating in the homozygous fish. No groups within a particular heterozygosity class deviate from a 1:1 distribution of "+" and "−". Thus this analysis also fails to support the hypothesis that multiply heterozygous fish grow more rapidly.

Thirdly, the largest sample (number 20, comprising 689 individuals), collected from Pendine in July 1977, was subjected to special scrutiny and

Table 2 Rank analysis of the relationship between heterozygosity class and mean length

Het. class	*N*	Rank sum	Rank mean	Assigned coefficient
0	46	133·0	2·891	1
1	46	136·5	2·967	2
2	46	141·5	3·076	3
3	46	112·0	2·435	4
4	29	82·0	2·828	5

Coefficients assigned to represent the expected ordering of the samples. The agreement between the pattern of coefficients and sample means is non-significant ($P > 0{\cdot}10$, $L = 1688{\cdot}5$, $Z = 1{\cdot}410$).

Table 3 Numbers of groups of fish of specified heterozygosity score with mean lengths longer (+) and shorter (−) than the overall mean length of their sample

Het. score	*N*	+	−	X^2	*P*
0	46	22	24	0·043	ns
1	46	25	21	0·174	ns
2	46	26	20	0·783	ns
3+	46	19	27	1·391	ns

X^2 tests the hypothesis that frequency of + equals frequency of −.

analysed using procedures similar to those of Koehn and Gaffney (1984). Individuals ranged in size from 16 to 70 mm, with a mean of 39·75 (+0·39) mm. There is no correlation between length and heterozygosity score (Pearson's $r = -0{\cdot}015$, Spearman's $r = -0{\cdot}0017$, $df = 687$, $P > 0{\cdot}05$). There is no significant variation in mean length with heterozygosity score (table 4), and the correlation of mean length with heterozygosity is non-significant ($r = -0{\cdot}210$, $df = 4$, $P > 0{\cdot}05$). Pooling fish with heterozygosity scores of 4 and 5 also produces a non-significant correlation coefficient ($r = 0{\cdot}533$, $df = 3$, $P > 0{\cdot}05$). The variance in growth rate, as measured by the coefficient of variation, is not correlated with heterozygosity ($r = 0{\cdot}329$, $df = 4$, $P > 0{\cdot}05$, or, following pooling, $r = -0{\cdot}103$, $df = 3$, $P > 0{\cdot}05$).

Table 4 Relationship between heterozygosity score and length in sample 20

Het. score	*N*	Mean length	*SE*	*CV*
0	105	40·02	0·94	24·13
1	273	39·47	0·64	26·95
2	213	39·71	0·67	24·44
3	75	40·33	1·36	29·24
4	21	40·29	1·95	22·78
5	2	39·00	8·0	29·01

r for mean length against heterozygosity score = −0·015, df = 4, n.s.

Next, each fish in this sample was placed into one of 11 size classes, ranging from 15 to 70 mm in 5 mm intervals. The mean number of heterozygous loci per fish per interval was determined, as was the mean heterozygosity per fish per interval for each of the five loci. The results are given in table 5, together with the correlation coefficients between mean length and heterozygosity. It will be seen that there is no significant correlation between multi-locus heterozygosity and length, and of the five single locus tests, only one, that for *αGpdh*-1, proved statistically significant ($0.05 > P > 0{\cdot}01$). This correlation was positive, showing that for this locus, increased growth rate did appear to be associated with increasing heterozygosity. In order to check this finding, the next largest sample (number 19) was analysed in a similar way (table 5). In this instance, the only significant correlation was between multi-locus heterozygosity and length, and this correlation was negative. Thus, the conclusion from these analyses is again that there is no general relationship between heterozygosity and growth rate.

Finally, a reasonable alternative hypothesis to an increase in growth rate with heterozygosity is that fish of intermediate growth rate have the highest heterozygosity. In order to test this hypothesis, the fish analysed in table 4 were separated into three categories, those with decreased growth rates, those with average growth rates, and those with increased growth rates. For each of the two samples, the numbers of heterozygous and homozygous loci in each category were calculated, both for the multi-locus comparison and for each of the five individual loci taken separately. Chi squared tests were performed, first by comparing the numbers of heterozygous and homozygous loci between the three categories of fish (giving 2df per test), and secondly by pooling fish with increased and decreased growth rates and comparing these fish with fish of intermediate growth rates (giving 1df per test). The results are given in table 6, 24 tests were performed, and two were significant at the 5 per cent level. In sample 19, fish of intermediate growth rate had higher average heterozygosity for *Mdh*-2 than other fish, and in sample 20, fish of intermediate growth rate had higher average heterozygosity for *Ada* than other fish. These deviations from the null hypothesis may be explained through sampling error, and there is thus very little evidence that fish of intermediate growth rate have increased heterozygosity.

DISCUSSION

The plaice provides an excellent species in which to examine any hypothesised relationships between quantitative traits and enzyme heterozygosity. The Bristol Channel population we have sampled is a very large, randomly mating population, without significant deviations from Hardy-Weinberg expectations at loci taken singly or in pairs (Ward and McAndrew, 1985), and with little immigration from neighbouring populations (Macer, 1972; note that such populations are in any case likely to be genetically very similar to the Bristol Channel population, Ward and Beardmore, 1977).

No relationship has been found in the plaice between multi-locus heterozygosity and morphological variability, as assayed by caudal, anal, and dorsal fin ray numbers (McAndrew *et al.*, 1982), and the results presented here indicate that there is also no relationship between multi-locus heterozygosity and variability in growth rate. Thus the reduction in growth rate variability with increasing individual heterozygosity observed in

Table 5 The relationship between size category of fish and multiple and single locus heterozygosity within the two largest samples

Size category	*N*	Mean length	Mean number of loci heterozygous per fish: Multi locus	Single locus: *Pgm*-1	*Ada*	*Mdh*-2	*Pgi*-1	*Gpdh*-1
Sample 19, sample size = 248								
15–20	4	19·75	1·25	0·50	0·25	0·00	0·25	0·25
21–25	19	22·68	1·63	0·32	0·58	0·37	0·11	0·26
26–30	23	28·61	1·48	0·57	0·61	0·04	0·09	0·17
31–35	60	33·91	1·48	0·40	0·43	0·27	0·15	0·23
36–40	63	37·73	1·41	0·43	0·44	0·30	0·11	0·21
41–45	58	42·52	1·28	0·43	0·36	0·16	0·14	0·19
46–50	20	47·39	1·35	0·35	0·45	0·15	0·10	0·30
51–55	1	51·00	3·00	1·00	1·00	0·00	0·00	1·00
Sample 20, sample size = 689								
15–20	16	18·94	1·69	0·56	0·44	0·25	0·25	0·19
21–25	51	23·31	1·39	0·41	0·45	0·28	0·08	0·18
26–30	70	27·88	1·41	0.40	0·41	0·17	0·14	0·29
31–35	87	33·14	1·47	0·47	0·40	0·24	0·10	0·25
36–40	142	38·25	1·55	0·51	0·49	0·17	0·11	0·28
41–45	135	42·64	1·47	0·39	0·47	0·21	0·23	0·19
46–50	74	47·74	1·47	0·50	0·37	0·22	0·15	0·24
51–55	68	52·63	1·39	0·49	0·34	0·18	0·10	0·28
56–60	26	57·42	1·73	0·42	0·50	0·42	0·08	0·31
61–65	18	62·67	1·60	0·33	0·39	0·22	0·22	0·44
66–70	2	69·00	1·00	0·50	0·00	0·00	0·00	0·50
Pearson correlation coefficients between mean length and heterozygosity:								
Sample 19:		*r*, 4 df,	−0·915*	−0·117	−0·778	−0·338	0·158	0·248
Sample 20:		*r*, 8 df,	0·219	−0·411	−0·195	0·184	−0·051	0·718*

* $P = 0{\cdot}05$–$0{\cdot}01$

Note: in the calculation of *r*, samples of less than 10 fish were ignored.

Table 6 The relationship between growth rate of fish and multiple and single locus heterozygosity within the two largest samples

Growth rate	Size category	*N*	Mean number of loci heterozygous per fish: Multi locus	Single locus: *Pgm*-1	*Ada*	*Mdh*-2	*Pgi*-1	*Gpdh*-1
Sample 19								
A, decreased	<31 mm	46	1·521	0·457	0·565	0·174	0·109	0·217
B, intermediate	36–40 mm	123	1·488	0·415	0·439	0·285	0·130	0·220
C, increased	>40 mm	79	1·316	0·418	0·392	0·152	0·127	0·228
X^2, 2 df, A *v.* B *v.* C			1·750	0·256	3·584	5·654	0·143	0·026
X^2, 1 df, B *v.* (A+C)			0·555	0·077	0·072	5·573*	0·058	0·007
Sample 20								
A, decreased	<36 mm	224	1·451	0·442	0·418	0·228	0·121	0·241
B, intermediate	36–45 mm	277	1·513	0·451	0·477	0·188	0·166	0·231
C, increased	>45 mm	188	1·495	0·468	0·372	0·229	0·138	0·287
X^2, 2 df, A *v.* B *v.* C			0·464	0·286	5·096	1·622	2·148	2·017
X^2, 1 df, B *v.* (A+C)			0·276	0·004	4·163*	1·621	1·885	0·855

* $P = 0{\cdot}05$–$0{\cdot}01$

the bivalves *Crassostrea virginica* (Zouros *et al.*, 1980) and *Mytilus edulis* (Koehn and Gaffney, 1984) is not a universal phenomenon.

The major question addressed here is whether multi-locus heterozygosity, as assessed by screening five polymorphic loci, is related to growth rate in the plaice. We find no significant evidence for such a relationship, so the question then becomes one of why we failed to detect such a relationship, when it is apparently so strong in some other species (Mitton and Grant, 1984).

In this paper, length at time t is equated with growth rate. There are two problems with making such an equation. The first is that, as with species examined by other investigators, spawning is spread over a period of time, and thus the fish collected at time t must in reality comprise a range of ages. However, this variation in age relative to the mean age at time t is probably small (and decreases as t increases), and since every collection of fish included a wide range of sizes, it seems likely that age differentiation within a sample accounts for only a small proportion of the size differentiation. The second problem is that we may not be sampling randomly the entire cohort at any given date. In particular, there is a tendency for larger O-group fish to be found in deeper water than smaller fish (Gibson, 1973), and since we were routinely sampling in water less than 1 m deep, it is likely that the largest, most rapidly growing, fish were under-represented. Thus the mean lengths of our samples, especially for the older fish, are likely to be underestimates of the population means.

Mitton and Grant (1984) suggest that relationships between heterozygosity and growth rate are most likely to be detected in young stages of animals and plants, since such stages put most of their surplus energy into growth with very little being put into reproduction. We have studied plaice from the time they arrive on the nursery beaches, aged about 3 months, to the time they move off into deeper water, a period of about a year. Thus we have restricted ourselves to the examination of young, immature, fish, the stage Mitton and Grant feel would be most likely to reveal such a relationship. Of course, it is possible that heterozygosity and growth rate are related in very young fish (<100 days) or even in older fish (where our samples are very much smaller and do not permit critical testing of the hypothesis), but this is an unsatisfactory conclusion. There are no reasonable grounds for not expecting the relationship to be found in the age range sampled: the fish are growing during the majority of months sampled, especially during the summer when the two largest samples were collected, and at this time competition for food and predator avoidance on the nursery beaches is intense. It is estimated that by the time that metamorphosed fish have reached the nursery beaches, less than 1 per cent of spawned eggs have survived (Harding, 1973), and mortality of "O" group plaice on nursery grounds has been estimated at 50 per cent per month after recruitment is complete (July), gradually dropping to 15 per cent per month by December (Macer, 1967; Steele and Edwards, 1970).

Another explanation for our failure to find significant positive correlations might be that we were simply "unlucky" in our choice of loci, and that had we picked other loci positive correlations might have been forthcoming. Yet this also seems a poor explanation, for in those studies that have reported a positive relationship, and which have partitioned out the effect between loci, virtually all loci analysed, regardless of function, appear to contribute to the trend (Zouros *et al.*, 1980; Green *et al.*, 1983; Koehn and Gaffney, 1984). Furthermore, some of the loci we screened, such as *Pgm* and *Pgi*, are common to many of these surveys.

Perhaps there is no general relationship between multi-locus heterozygosity, at least when assessed from 5 to 10 loci, and growth rate, and those species exhibiting such a relationship are the exception, not the rule. It is well recognised that heterozygosity over half a dozen loci is only very weakly correlated with real individual heterozygosity, measured across the entire genome (Mitton and Pierce, 1980; Chakraborty, 1981), and thus such a general relationship is perhaps not to be expected. So how can the phenomenon be explained in those species exhibiting it? Perhaps only a few loci are concerned in determining growth rate, and by chance some studies happen to sample from this small pool. This seems an unlikely explanation, especially bearing in mind that this pool would have to vary between species, since those studies that have failed to find correlations have loci in common with those giving positive correlations. A second explanation might be that in the latter group of species, heterozygosity at 5 to 10 loci is highly correlated with genomic heterozygosity, perhaps through some aspect of population structure. For example, if the individuals sampled were the progeny of random matings between and within two inbred populations, then the more outbred, more heterozygous, progeny might well grow faster. Cothran *et al.* (1983) attributed their results on foetal growth rate in deer to such a population structure. Population subdivision will generate heterozygote deficiencies

through the Wahlund effect, and although such deficiencies were not recorded by Cothran *et al.*, deficiencies have been recorded in some of the species exhibiting positive correlations, such as *Crassostrea gigas* (Singh and Zouros, 1978) and *Mytilus edulis* (Koehn and Gaffney, 1984). However, it should be pointed out that such deficiencies are not necessarily the result of population structure, and that several species showing positive correlations do not show deviations from Hardy–Weinberg expectations (*e.g.*, *Odocoileus virginianus*, Cothran *et al.*, 1983; *Mulinia lateralis*, Garton *et al.*, 1984; *Pinus rigida*, Ledig *et al.*, 1983).

Implicit in the hypothesis of a positive correlation between growth rate and heterozygosity, is the notion that increased growth rate is associated with increased fitness. If this were generally true, then directional selection for increased growth rate would be ubiquitous. This seems unlikely, and indeed those individuals growing very rapidly (or very slowly) may well be imbalanced in some physiological way and thus have decreased fitness. Growth rate is a quantitative trait, and in natural populations might be expected to be under stabilising selection.

A clear example of stabilising selection operating on growth rate comes from the classic work of Karn and Penrose (1951, see also Gordon, 1977) on human birth weight: newborn infants of intermediate birth weights had higher viabilities than those of more extreme weights. Since, in man at least, birth weight is more dependent on maternal genotype and maternal environment than on foetal genotype (which contributes about 24 per cent of birth weight variance, Robson, 1978), it is likely to be a poor character to use in man (and probably other mammals) in searches for heterozygosity/growth rate correlations. Notwithstanding, Cothran *et al.* (1983) for deer and Bottini *et al.* (1979) for man have reported such associations, although a study by Ward *et al.* (1985) failed to confirm the results of Bottini *et al.*

Under stabilising selection, and if increasing heterozygosity confers increasing fitness, one might expect individuals of intermediate growth rate to be highly heterozygous. If it is assumed that growth rate in the plaice is subject to stabilising selection, then the results presented in the present paper also fail to support this hypothesis.

To conclude, growth rate in young plaice is not significantly correlated with multi-locus heterozygosity (at 5 loci), nor is it significantly correlated with heterozygosity at the five loci taken individually.

Acknowledgement This work was supported by N.E.R.C. grant GR3/1558 and by the award of a N.E.R.C. research studentship to B. J. McAndrew. We thank Andy Beaumont for comments on an earlier draft of this paper.

REFERENCES

BEACHAM, J. D. AND WITHLER, R. E. 1985. Heterozygosity and morphological variability of pink salmon (*Oncorhynchus gorbuscha*) from southern British Columbia and Puget Sound. *Can. J. Genet. Cytol., 27,* 571-579.

BEAUMONT, A. R., BEVERIDGE, C. M. AND BUDD, M. D. 1983. Selection and heterozygosity within single families of the mussel *Mytilus edulis.* (L.) *Mar. Biol. Lett., 4,* 151-161.

BEAUMONT, A. R. GOSLING, E. M., BEVERIDGE, C. M., BUDD, M. D. AND BURNELL, G. M. In press. Studies on heterozygosity and size in the scallop, *Pecten maximus* (L.). *Proc. 19th European Marine Biology Symposium.* Cambridge University Press, pp 443-455.

BOTTINI, E., GLORIA-BOTTINI, F., LUCARELLI, P., POZONETTI, A., SANTORO, F. AND VARVERI, A. 1979. Genetic polymorphisms and intrauterine development: evidence of decreased heterozygosity in light for dates human newborn babies. *Experientia, 35,* 1565-1567.

CHAKRABORTY, R. 1981. The distribution of the number of heterozygous loci in an individual in natural populations. *Genetics, 98,* 461-466.

COTHRAN, E. G., CHESSER, R. K., SMITH, M. H. AND JOHNS, P. E. 1983. Influences of genetic variability and maternal factors on fetal growth in white-tailed deer. *Evolution, 37,* 282-291.

CUSHING, D. H. 1969. The regularity of the spawning season of some fishes. *J. Cons. Int. Explor. Mer., 33,* 81-92.

DIEHL, W. J. AND KOEHN, R. K. 1985. Multiple-locus heterozygosity, mortality and growth in a cohort of *Mytilus edulis. Mar. Biol., 88,* 265-271.

FOLTZ, D. W. AND ZOUROS, E. 1984. Enzyme heterozygosity in the scallop *Placopecten magellanicus* (Gmelin) in relation to age and size. *Mar. Biol. Lett., 5,* 255-263.

GARTON, D. W., KOEHN, R. K. AND SCOTT, T. M. 1984. Multiple-locus heterozygosity and the physiological energetics of growth in the coot clam, *Mulinia lateralis,* from a natural population. *Genetics, 108,* 445-455.

GIBSON, R. N. 1973. The intertidal movements and distribution of young fish on a sandy beach with special reference to the plaice (*Pleuronectes platessa* L.) *J. Exp. Mar. Biol. Ecol., 12,* 79-102.

GORDON, R. R. 1977. Premature baby statistics. *Br. Med. J., i,* 1313-1315.

GRANT, M. C., MITTON, J. B. AND LINHART, Y. B. 1982. Ecological and evolutionary studies of forest trees in Colorado. In Halfpenny J. (ed.) *Ecological Studies in the Colorado Alpine: A Festschrift for John W. Marr. Univ. Colo. Occas. Pap. No. 37,* pp. 96-100.

GREEN, R. H., SINGH, S. M., HICKS, B. AND McCUIAG, J. 1983. An intertidal population of *Macoma balthica* (Mollusca, Pelecypoda): genotypic and phenotypic components of population structure. *Can. J. Fish. Aquat. Sci., 40,* 1360-1371.

KARN, M. N. AND PENROSE, L. S. 1951. Birthweight and gestation time in relation to maternal age, parity, and infant survival. *Ann. Eugen., 15,* 206-233.

KING, D. P. F. 1985. Enzyme heterozygosity associated with anatomical character variance and growth in the herring (*Clupea harengus* L.). *Heredity, 54,* 289-296.

KNOWLES, P. AND GRANT, M. C. 1981. Genetic patterns associated with growth variability in ponderosa pine. *Am. J. Bot. 68,* 942-946.

KNOWLES, P. AND MITTON, J. B. 1980. Genetic heterozygosity and radial growth variability in *Pinus contorta. Silvae Genet., 29,* 114-117.

KOEHN, R. K. AND GAFFNEY, P. M. 1984. Genetic heterozygosity and growth rate in *Mytilus edulis. Mar. Biol., 82,* 1-7.

LEDIG, F. T., GURIES, R. P. AND BONEFIELD, B. A. 1983. The relation of growth to heterozygosity in pitch pine. *Evolution, 37,* 1227-1238.

MACER, C. T. 1972. The movements of tagged adult plaice in the Irish Sea. *Fish. Investig., London, Ser. 2, 27(6),* 41pp.

MEDDIS, R. 1984. *Statistics using Ranks: a Unified Approach.* Blackwell, Oxford.

McANDREW, B. J., WARD, R. D. AND BEARDMORE, J. A. 1982. Lack of relationship between morphological variance and enzyme heterozygosity in the plaice, *Pleuronectes platessa. Heredity, 48,* 117-125.

MITTON, J. B. 1983. Conifers. In Tanksley, S. and Orton, T. (eds.) *Isozymes in Plant Genetics and Breeding, Part B.* Elsevier, Amsterdam, pp. 443-472.

MITTON, J. B. AND GRANT, M. C. 1980. Observations on the ecology and evolution of quaking aspen, *Populus tremuloides,* in the Colorado Front Range. *Am. J. Bot. 67,* 202-209.

MITTON, J. B. AND GRANT, M. C. 1984. Associations among protein heterozygosity, growth rate, and developmental homeostasis. *Ann. Rev. Ecol. Syst., 15,* 479-499.

MITTON, J. B. AND PIERCE, B. A. 1980. The distribution of individual heterozygosity in natural populations. *Genetics, 95,* 1043-1054.

MITTON, J. B., KNOWLES, P., STURGEON, K. B., LINHART, Y. B. AND DAVIS, M. 1981. Associations between heterozygosity and growth rate variables in three western forest trees. In Conkle, M. T. (ed.) *Proc. Symp. Isozymes North Am. For. Trees and For. Insects, US Dep. Agric. Gen. Tech. Rep. PSW-48,* U.S.G.P.O., Washington, D.C., pp. 27-34.

NIE, N. H., HULL, C. H., JENKINS, J. G., STEINBRENNER, K. AND BENT, D. H. 1975. *Statistical Package for the Social Sciences,* 2nd ed., McGraw Hill, New York.

PIERCE, B. A. AND MITTON, J. B. 1982. Allozyme heterozygosity and growth in the tiger salamander, *Ambystoma tigrinum. J. Hered., 73,* 250-253.

ROBSON, E. B. 1978. The genetics of birth weight. In Falkner, F. and Tanner, J. M. (eds.) *Human Growth, Vol. 1: Principles and prenatal growth.* Bailliere, Tindall, London, pp. 249-297.

SIMPSON, A. C. 1959. The spawning of plaice (*Pleuronectes platessa*) in the Irish Sea. *Fish. Investig., London, Ser. 2, 22(8),* 30pp.

SINGH, S. M. AND ZOUROS, E. 1978. Genetic variation associated with growth rate in the American oyster (*Crassostrea virginica*). *Evolution, 32,* 342-353.

STEELE, J. H. AND EDWARDS, R. R. C. 1970. The ecology of O-group plaice and common dab in Loch Ewe. IV. The dynamics of plaice populations. *J. Exp. Mar. biol. Ecol., 4,* 174-187.

WARD, R. D. AND BEARDMORE, J. A. 1977. Protein variation in the plaice, *Pleuronectes platessa* L. *Genet. Res., 30,* 45-62.

WARD, R. D. AND McANDREW, B. J. 1985. A search for gametic disequilibrium in the plaice, *Pleuronectes platessa. Heredity, 55,* 105-110.

WARD, R. D., SARFARAZI, M., AZIMI-GARAKANI, C. AND BEARDMORE, J. A. 1985. Population genetics of polymorphisms in Cardiff newborn: relationship between blood group and allozyme heterozygosity and birth weight. *Hum. Hered., 35,* 171-177.

ZOUROS, E., SINGH, S. M. AND MILES, H. E. 1980. Growth rate in oysters: an overdominant phenotype and its possible explanations. *Evolution, 34,* 856-867.

APPENDIX

Mean lengths of fish with heterozygosity scores of 0 to 5 in each of the samples.

		Multi-locus heterozygosity class									
	Site	N^0	$\bar{x}$	N^1	$\bar{x}$	N^2	$\bar{x}$	N^3	$\bar{x}$	N^4	$\bar{x}$
1	Pendine	19	76·74	41	77·20	34	72·85	14	71·00	1	64·00
2	Pendine	31	85·87	70	78·76	63	78·75	17	79·88	5	99·40
3	Pendine	20	45·35	43	45·56	24	47·25	6	44·17	2	49·00
4	Pendine	8	65·75	21	62·14	16	61·44	8	57·63		—
5	Pendine	2	29·50	15	29·13	8	30·88	5	29·80		—
6	Pendine	13	36·16	27	39·04	32	39·50	9	34·44	2	37·00
7	Pendine	7	57·29	11	58·00	5	53·20	6	59·17		—
8	Pendine	13	65·92	34	62·62	23	63·96	7	64·86		—
9	Pendine	14	81·50	42	74·07	25	70·52	13	70·23	2	80·50
10	Pendine	28	74·93	46	71·54	45	73·04	14	71·07	4	64·25
11	Pendine	18	63·67	34	71·85	31	71·09	18	65·17	1	57·00
12	Pendine	8	72·38	17	65·59	19	73·32	13	69·00		—
13	Pendine	14	68·43	29	69·62	23	67·70	14	68·29	3	76·67
14	Pendine	3	78·67	14	78·71	10	71·00	2	88·00	3	69·33
15	Pendine	6	77·33	7	80·86	12	78·66	5	74·60	1	78·00
16	Pendine	7	82·71	10	86·20	8	96·75	3	93·33		—
17	Pendine	1	104·00	8	104·88	4	112·00	3	103·33		—
18	Pendine	2	26·00	13	25·00	13	25·92	5	22·80		—
19	Pendine	30	35·63	115	36·94	70	36·07	30	35·53	3	34·33
20	Pendine	105	40·02	273	39·47	213	39·71	75	40·33	21	40·29
21	Pendine	20	59·20	55	63·00	46	61·65	21	61·81	7	71·57
22	Pendine	7	67·57	20	68·25	10	61·10	5	60·80		—
23	Pendine	22	71·73	64	70·81	58	71·35	20	67·90	7	78·29
24	Pendine	21	72·05	37	65·87	21	66·76	10	69·50	2	71·50
25	Pendine	14	69·93	55	65·80	44	68·00	16	62·00	3	63·67
26	Pendine	30	73·00	58	69·10	44	72·05	27	73·30	3	62·67
27	Pendine	21	68·71	41	68·56	37	71·62	19	65·68	2	77·00
28	Pendine	4	72·25	15	76·53	9	73·67	2	65·50	1	86·00
29	Pendine	4	81·25	14	84·57	16	90·87	2	87·50	1	98·00
30	Swansea	13	41·23	32	45·25	38	42·79	10	40·90	3	39·33
31	Swansea	12	54·67	35	50·43	18	47·83	6	49·33		—
32	Swansea	8	58·50	15	61·13	8	56·88	3	57·33		—
33	Swansea	6	57·00	7	54·71	5	60·60	3	58·00	1	65·00
34	Swansea	4	72·50	9	59·44	12	65·33	4	63·00		—
35	Swansea	4	76·00	12	82·42	9	82·66	4	85·25		—
36	Swansea	11	76·91	36	74·44	29	79·10	8	80·63	3	79·00
37	Swansea	2	83·00	11	83·46	7	90·86	6	74·83	1	65·00
38	Swansea	4	92·25	10	78·90	9	84·44	3	96·33		—
39	Oxwich	19	74·32	23	77·52	23	77·52	5	85·00	3	74·00
40	Oxwich	15	86·13	25	89·52	28	88·93	8	79·75	1	65·00
41	Oxwich	8	58·88	30	63·43	15	61·80	8	62·75	3	60·67
42	Oxwich	6	66·17	11	69·18	11	65·09	4	59·50		—
43	Oxwich	3	62·33	7	69·43	10	70·50	3	66·33		—
44	Oxwich	5	68·00	12	68·17	9	68·56	1	65·00		—
45	Oxwich	7	93·86	28	73·25	12	72·42	8	88·63	1	69·00
46	Oxwich	6	91·17	14	93·14	11	98·73	8	87·38	1	80·00

Three samples had fish with 5 heterozygous loci:
sample 20, $N = 2$, $\bar{x} = 39{\cdot}00$;
sample 40, $N = 1$, $x = 109$;
sample 41, $N = 1$, $x = 75$,