AN ECOLOGICAL GENETIC ANALYSIS OF THE SETTLING BEHAVIOUR OF A MARINE POLYCHAETE:

I. PROBABILITY OF SETTLEMENT AND GREGARIOUS BEHAVIOUR

TRUDY F. C. MACKAY* and ROGER W. DOYLE

Biology Department, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1

Received 4.xii.75

SUMMARY

The settling behaviour of larvae of *Spirorbis borealis* from several ecologically contrasting environments was analysed in terms of means and genetic variances (the latter expressed as heritability) of two components—the probability of settling when presented with a particular substrate, and the gregarious behaviour of the larvae. Larval behaviour differed markedly according to the population from which they came: animals from a sheltered tidepool prefer *Ascophyllum*, and are distinctly gregarious, while those from a semi-exposed embayment settle much more readily on *Fucus* and are not as gregarious. Animals collected from an environmental cline ranging in conditions from tidepool-like to embayment-like exhibit a corresponding range in behaviour. This interpopulation variation in character means is interpretable in terms of adaptation to differential selection pressures known to be acting on the populations; consideration of intra-population genetic variances gives an indication of the mechanism of the adaptation.

1. INTRODUCTION

THERE are basically two approaches to the characterisation of the genetic architecture of natural populations; the first involves consideration of characters controlled by one or a few genes, and the second, quantitative or metric characters. Genetic differentiation in the first type of study can be demonstrated by differences in gene frequency among populations, and correlation of the character with habitat type, an approach which has been followed in many of the earlier ecological genetic studies (Ford, 1965). The biochemical technique of electrophoresis has vastly extended the number of characters which may be analysed in this manner, however, this approach is restricted in scope in that few evolutionarily important traits are under control of a single major gene. Only in a few cases (*e.g.* Koehn and Rasmussen, 1967; Schopf and Gooch, 1971) have electrophoretic variants been found to be correlated with an environmental variable.

Investigation of the genetics of quantitative characters, on the other hand, affords a method by which we may directly study the components of fitness. Biometrical techniques developed in the context of plant and animal breeding enable one, through the knowledge of genetic correlations among relatives, to partition the observed phenotypic variance into genetic and non-genetic components. Depending on the complexity of the experimental design employed, the genetic variance may be further partitioned

* Present address: Department of Genetics, University of Edinburgh EH9 3JN.

into additive and non-additive (dominance, epistatic) components. These techniques have been successfully applied in many cases to the assessment of the degree and nature of the quantitative variation in a wide variety of natural populations: the poppy has been extensively investigated in this manner (*e.g.* Lawrence, 1965; Gale *et al.*, 1976), as have several fungi (Simchen, 1967; Butcher *et al.*, 1972), and, of course, *Drosophila* (Kearsey and Kojima, 1967; Barnes and Kearsey, 1970). However, rarely have these studies been conducted in conjunction with an analysis of the ecological situation in relation to the character of interest (but see Doyle, 1974; Chapman, 1974; Newkirk and Doyle, 1975). Consequently, the object of this work is to investigate, using the tools of biometrical genetics, and within the framework of ecological genetics, the settling behaviour of the serpulid polychaete, *Spirorbis borealis*.

Spirorbis is common along the coast of Nova Scotia; the sessile adults are found epiphytic upon various substrata, particularly members of the genera *Fucus* and *Ascophyllum*. The pelagic trochophore larvae settle upon one of the available substrates within 24 hours after release from the adult. The choice of substrate is thus the critical "decision" the animal makes and traits associated with this behaviour are therefore of particular interest. Previous studies have indicated that there is a substrate preference of *S. borealis* under experimental conditions for algae of the genus *Fucus* (*F. edentatus*, *F. vesiculosus*, and *F. serratus*) over other substrates, including *Ascophyllum* and clean petri plates (Knight-Jones, 1953; deSilva, 1962). We have observed that the strength of this preference, when tested in the laboratory, differs according to the ecological conditions experienced by the animals, as does the distribution of the animals on the algal substrates in the field (Doyle, 1975). Knight-Jones *et al.* (1971) have also observed interpopulation differences in substrate preference of *S. spirorbis*, which were maintained under laboratory conditions, suggestive of a genetic component of this behaviour.

The phenomenon of gregariousness of the larvae has also been observed (Knight-Jones, 1951; Wiseby, 1960). Knight-Jones (1951) found that 77 per cent of freshly liberated larvae chose to settle on *Fucus serratus* with previously settled adults rather than bare *Fucus*. Mackay (1974) found that the strength of this property (as measured by change in probability of settlement with increasing density of larvae) varied as habitat.

The larval characters chosen for study were therefore "probability of settlement within 24 hours on a given substrate" and "gregarious settling behaviour"; for each the components of variation were partitioned among and within populations, and heritabilities were computed for each population.

2. METHODS

(i) *Ecological comparison of collection sites*

Three populations of *Spirorbis* were chosen as representing contrasting ecological situations. The first was a large sheltered middle-shore tidepool (the "Hulda" tidepool of Doyle, 1975) near Peggy's Cove, Nova Scotia; the second, a semi-exposed embayment at Terence Bay, N.S.; and the third population (the "Fjord") an inlet approximately 200 m long near Polly

Cove, N.S. *Spirorbis* chooses as substrate *Fucus* species (including *F. edentatus* and *F. vesiculosus*) at Terence Bay, although *Ascophyllum* is present in equal abundance and is readily accessible. They settle primarily on *Ascophyllum* at the Peggy's Cove location, in the absence of any other suitable fucoid. The distribution of animals on the algal substrates is somewhat more complex in the Fjord—animals are found both on *Fucus* and *Ascophyllum* all along the inlet—but the proportion of the population settling on *Ascophyllum* changes as one moves toward the mouth of the inlet. Whereas in the "Inner" Fjord (farthest from the open sea) there are from 10-100 animals found on *Fucus* for every one on *Ascophyllum*, the distribution in the "Outer" Fjord (closer to the mouth of the inlet) more nearly approximates a ratio of 1000+ *Fucus* settled animals for every one on *Ascophyllum*. The proportion of *Fucus* to *Ascophyllum* plants also changes in that there are fewer *Fucus* than *Ascophyllum* plants in the Inner Fjord, but they are in equal abundance in the Outer Fjord. The Fjord was thus chosen to represent a cline in conditions from "Peggy's Cove-like" (Inner Fjord) to "Terence Bay-like" (Outer Fjord).

(ii) *Experimental technique*

Algae bearing *Spirorbis* from each of these populations (Terence Bay; Peggy's Cove; Outer Fjord, *Fucus*; Outer Fjord, *Ascophyllum*; Inner Fjord, *Fucus*; and Inner Fjord, *Ascophyllum*) were maintained in the laboratory in tanks of running sea-water at ambient temperatures. Animals were fed regularly with a suspension of phytoplankton (*Platymonas*, *Phaeodactylum*, and/or *Thalassiosira*).

Spirorbis is hermaphroditic; oögonia which develop in the female segments are fertilised by uptake of sperm into the shell cavity. Embryos are enclosed in a transparent envelope-like structure to form a discrete embryo chain which is incubated within the shell of the animal. Cross-fertilised larvae were obtained by opening the calcareous shell of animals fertilised in the field and dissecting out the embryo chain; if the chain was at the most advanced stage of development larvae "spontaneously" released within a 20-minute period and were used in the experiment. DeSilva (1958) has demonstrated that even artificially liberated larvae by breaking the transparent covering does not significantly alter larval behaviour with respect to capability of metamorphosis and choice of substrate when compared to naturally liberated larvae.

The actual experiment consisted simply of introducing groups of 10 larvae into petri dishes containing sea-water plus either five 1-cm square pieces of *Fucus* or five 3-cm long *Ascophyllum* fronds, none of which had previously borne *Spirorbis*. The dishes were incubated for 24 hours at 14°C, after which the total number of larvae settled on each frond was counted. (It should be noted here that animals which remain unsettled after this period are not necessarily dead but may still be actively swimming or have not yet completed metamorphosis.) Each dish constitutes one replicate; there were up to four replicates per family, with approximately 30 families analysed for each population.

(iii) *Heritabilities of probability of settlement*

The character "probability of settlement given a particular substrate" is phenotypically discontinuous in expression, but the behaviour within self-fertilised families does not seem to follow simple Mendelian rules of segregation; we may therefore consider the nature of inheritance to be polygenic and analyse it as a threshold character. Analysis of all-or-none traits has been examined by Wright (1933, 1934), Lush *et al.* (1948), Robertson and Lerner (1949), and Dempster and Lerner (1950), who assumed an underlying continuity with a threshold imposing discontinuity upon the phenotypic expression of the trait. Heritability is calculated from the percentage data (h_p^2) either by analysis of variance for binomial data—the procedure adopted here—(Lush *et al.*, 1948), in which case h_p^2 is r times the intraclass correlation coefficient, or from a $2 \times N$ chi-square analysis (Robertson and Lerner, 1949), in which case h_p^2 is a function of the heterogeneity chi-squared in the $2 \times N$ table. However, because on a percentage scale variances differ according to the mean, probit transformation is advised as it makes the genetic variance independent of the threshold value in the population: The genetic variance on the underlying scale

$$= \sigma_x^2 = [h_p^2 \cdot \bar{p}(1 - \bar{p})]/\bar{z}^2$$

where $\bar{p}$ is the mean incidence in the population, and $\bar{z}$ is the height of the ordinate of the standard normal curve corresponding to the abscissa value which cuts off a tail of area $\bar{p}$. Heritability on the probit scale is $h_x^2 = \sigma_x^2/(1 + \sigma_x^2)$, which may be compared to additive heritability on the percentage scale by the relationship $h_{pa}^2 = (\bar{z}^2 \cdot h_x^2)/(\bar{p}(1 - \bar{p}))$.

It is relevant at this point to mention an additional source of covariance which may serve to inflate the between family component of variance to an unknown but possible significant extent: this is the common environment, or maternal, effect caused by the incubation of embryo chains within the shell of the female parent. A more sophisticated design than that employed here is necessary to remove and estimate this source of covariance.

(iv) *Measurement of gregarious behaviour*

The degree of gregarious behaviour is quantified in terms of Lloyd's Index of Patchiness (Pielou, 1974), a modified variance to mean ratio, corrected for mean density. It is analogous to the classical variance to mean ratio in that the expectation given a random distribution is 1, values greater than 1 indicating aggregation and less than 1 overdispersion. The variance of the index is defined, enabling comparison of estimates from different populations.

Lloyd's Index of Patchiness for populations may be computed by considering each algal frond used in the experiment described above as a sampling unit, and the number of worms settled on each recorded irrespective of genetic sub-groups. To check whether the measure thus obtained was inflated by uncontrolled variance among the fronds, a separate experiment, in which animals settled on the surface of petri dishes evenly coated with bacterial film, was performed. Each dish was divided into 64 1 cm² quadrats, and the patchiness index computed. The genetic component of

variability within each population was determined by computing patchiness indices for each replicate (for which three or greater larvae had settled) and partitioning the variance among and within families as usual.

3. GENETIC INFERENCES FROM THE BREEDING STRUCTURE OF *SPIRORBIS* POPULATIONS

To compute heritability one needs to know exactly the degree of relationship among members of a family— r —which varies from 0.25 for half-sib families to 0.5 for full-sib families. With *Spirorbis* one is forced to draw inferences from the natural breeding scheme. The first assumption is that fertilisation is by a random sample of sperm from the whole population—this seems eminently reasonable in view of the mass release of motile male gametes into the sea. Not so reasonable is the assumption that members of an embryo chain are related as half-sibs, each egg being fertilised by a different male parent, or as full-sibs produced by either self-fertilisation or by sperm from a single individual. The degree of relationship is in all probability more close to that of half-sibs than full-sibs, in view of the above-mentioned method of spawning and the large population sizes involved; at any rate this is the alternative adopted. This procedure maximises heritability estimates.

One further point to be considered is that it is possible the populations are somewhat inbred, caused by a degree of self-fertilisation, mating among individuals settled upon a single plant, seasonal variation in effective population size, or a combination of all three. Dr E. Zouros (personal communication) has conducted an electrophoretic survey of the populations concerned at the xanthine dehydrogenase (XDH) and aldehyde oxidase (AO) loci, and has computed Wright's inbreeding coefficient, F , for each. The estimates vary wildly (from small and negative to 0.451), with that from XDH consistently higher than AO, and a combined estimate from both loci is not available for each population, but the best estimates are presented below:

Population	F	Locus used to estimate F
Terence Bay	0.277	XDH + AO
Peggy's Cove	0.267	XDH
Fjord (Inner + Outer)	0.256	AO (Inner), XDH (Outer)

One must therefore modify the heritability estimate by multiplying the intra-class correlation by a factor $4/(1 + F)$ (Kempthorne, 1969), thus adopting the half-sib hypothesis and correcting for the observed degree of inbreeding.

4. RESULTS

(i) *Probability of settlement on Fucus and on Ascophyllum*

(a) *Population means*

The proportions of larvae which settled on *Fucus* and *Ascophyllum* are given for each population in table 1. Since the absolute magnitude of the response differs for each population, the difference between the proportion

settled on *Fucus* and on *Ascophyllum* was taken as a measure of the degree to which the animals "prefer" to settle on one or the other substrate—a negative measure means they settle more on *Ascophyllum*, the value zero indicates the animals settle equally frequently on either substrate, while a positive value indicates greater settlement on *Fucus*. (The word "prefers" is here used loosely, since no actual choice of substrate is involved.)

TABLE 1
Proportions ($\pm$ standard error) of larvae settled on *Fucus* and *Ascophyllum*

Population	Substrate		Difference
	<i>Fucus</i>	<i>Ascophyllum</i>	
Terence Bay	0.838 $\pm$ 0.011	0.471 $\pm$ 0.015	0.367
Peggy's Cove	0.374 $\pm$ 0.015	0.654 $\pm$ 0.015	-0.280
Outer Fjord, <i>Fucus</i>	0.919 $\pm$ 0.008	0.575 $\pm$ 0.015	0.344
Outer Fjord, <i>Ascophyllum</i>	0.526 $\pm$ 0.016	0.245 $\pm$ 0.015	0.281
Inner Fjord, <i>Fucus</i>	0.538 $\pm$ 0.014	0.267 $\pm$ 0.014	0.271
Inner Fjord, <i>Ascophyllum</i>	0.350 $\pm$ 0.014	0.293 $\pm$ 0.017	0.057

It can be seen that the Terence Bay animals settle much more frequently on *Fucus* than *Ascophyllum*, while the reverse is true of the animals from Peggy's Cove. The Fjord populations exhibit a gradient in settling frequencies corresponding to the geographical cline, from settling predominantly on *Fucus* (Outer Fjord, *Fucus*) to no difference in settlement on either substrate (Inner Fjord, *Ascophyllum*).

(b) *Within population variances*

The analyses of variance for larval settlement on each substrate are given in table 2. In every case there was significant added variation among families at the 5 per cent level, with the exception of the Outer Fjord, *Fucus* population (which had very little total phenotypic variation). Significant variation among replicates was also generally observed; since one would ordinarily expect the among and within replicate components to be of the same order, this is attributable to the phenomenon of gregarious settlement.

Table 3 summarises the various heritability estimates which may be calculated from the observed intra-class correlations. It is most interesting that for several populations the heritability estimates seem to differ according to the substrate presented. The Terence Bay, Outer Fjord, *Fucus*, and Inner Fjord, *Fucus* populations all have higher point estimates of heritability of settlement on *Ascophyllum* than *Fucus*, while the Peggy's Cove population has a higher heritability of settlement on *Fucus* than *Ascophyllum*. Although these estimates are not statistically different from one another (indeed, with heritabilities of the magnitude observed the size of experiment necessary to attain the requisite precision for statistical significance is practically prohibitive), the qualitative trend is that the rarer response is possessed of a greater degree of genetic variability. It should be borne in mind that the effect of common environment mentioned above may have increased the magnitude of these estimates, but there is no reason to suppose the pattern observed should be likewise affected.

TABLE 2
Analyses of variance of settlement probabilities

Source of variation	Population											
	Terence Bay		Peggy's Cove		Outer Fjord, <i>Fucus</i>		Outer Fjord, <i>Ascophyllum</i>		Inner Fjord, <i>Fucus</i>		Inner Fjord, <i>Ascophyllum</i>	
	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.
Settlement on <i>Fucus</i>												
Among families	31	1.056*	25	2.874*	29	0.262	29	1.173*	30	1.023*	29	1.245*
Among replicates, within families	83	0.217*	76	0.443	89	0.185*	70	0.419*	89	0.503*	87	0.314*
Within replicates	1035	0.102	9	0.145	1071	0.060	900	0.207	1080	0.206	1053	0.193
Total	1149		1019		1189		999		1199		1169	
Settlement on <i>Ascophyllum</i>												
Among families	29	4.412*	25	1.095*	27	2.468*	20	1.789*	26	1.528*	20	0.994*
Among replicates, within families	82	0.307*	71	0.516*	82	0.450*	63	0.424*	74	0.301*	52	0.455*
Within replicates	1008	0.125	873	0.178	990	0.163	756	0.123	909	0.149	657	0.164
Total	1119		969		1099		839		1009		729	

* Significant at $\alpha = 0.05$, tested using the method for unbalanced designs (Sokal and Rohlf, 1969).

TABLE 3

Heritability estimates ($\pm$ standard error) of "settlement in 24 hours" on *Fucus* (F) and *Ascophyllum* (A)

Population	Substrate	Heritability estimates			
		h_p^2	h_p^2 , F	h_{pa}^2	h_{pa}^2 , F
Terence Bay	F	0.672	0.526	0.269 ± 0.091	0.242 ± 0.075
	A	1.740	1.363	0.465 ± 0.134	0.433 ± 0.114
Peggy's Cove	F	1.048	0.827	0.388 ± 0.127	0.353 ± 0.104
	A	0.280	0.222	0.191 ± 0.083	0.162 ± 0.068
Outer Fjord, <i>Fucus</i>	F	0.108	0.086	0.080 ± 0.048	0.067 ± 0.040
	A	0.840	0.669	0.360 ± 0.113	0.324 ± 0.098
Outer Fjord, <i>Ascophyllum</i>	F	0.368	0.293	0.233 ± 0.088	0.200 ± 0.072
	A	0.728	0.580	0.308 ± 0.121	0.278 ± 0.102
Inner Fjord, <i>Fucus</i>	F	0.208	0.166	0.157 ± 0.066	0.132 ± 0.054
	A	0.672	0.535	0.303 ± 0.111	0.272 ± 0.095
Inner Fjord, <i>Ascophyllum</i>	F	0.420	0.334	0.247 ± 0.088	0.215 ± 0.074
	A	0.308	0.245	0.200 ± 0.092	0.171 ± 0.076

(ii) Gregarious behaviour

(a) Population means

Lloyd's Indices of Patchiness for settlement of larvae on *Fucus* and *Ascophyllum* are given in table 4. It can readily be seen that animals from all populations are gregarious, although to varying degrees; the measurement of gregariousness for Terence Bay animals is very much less than in other populations, while animals from the Peggy's Cove and Inner Fjord, *Ascophyllum* populations are highly gregarious. It is noteworthy that everywhere, with the exception of the Peggy's Cove animals, gregarious behaviour is more marked on *Ascophyllum* than *Fucus*, this is partially explicable because gregarious behaviour is decreased with high settlement densities (correlation between these factors: -0.63).

TABLE 4

Lloyd's Indices of Patchiness ($\pm$ standard error) of larvae settled on *Fucus* and *Ascophyllum*

Population	Substrate	
	<i>Fucus</i>	<i>Ascophyllum</i>
Terence Bay	1.629 ± 0.040	2.133 ± 0.049
Peggy's Cove	2.728 ± 0.081	2.508 ± 0.140
Outer Fjord, <i>Fucus</i>	2.186 ± 0.121	4.232 ± 0.516
Outer Fjord, <i>Ascophyllum</i>	1.943 ± 0.046	8.356 ± 0.491
Inner Fjord, <i>Fucus</i>	1.837 ± 0.034	5.051 ± 0.088
Inner Fjord, <i>Ascophyllum</i>	2.786 ± 0.073	9.768 ± 0.656

It is possible the estimates of gregariousness were enhanced by differences in suitability of substrates within each petri dish, so that on the average only one or a few fronds per dish were really adequate for settlement. The results of settlement on bacterial film evenly distributed over the surface of petri dishes show this not to be true, at least for Terence Bay and Peggy's Cove populations. A highly significant difference ($F_{1, 88} = 15.758$) was

observed between the two groups; Peggy's Cove animals (mean index of dispersion—6.1) being more gregarious than those from Terence Bay (mean index of dispersion—2.8).

(b) *Within population variances*

Analyses of variance of Lloyd's Indices of Patchiness on each substrate are presented in table 5. Not all the experiments could be analysed in this manner as where the overall settling frequencies were low there were insufficient families available with over three animals settled per replicate. Of the 10 experiments thus analysed, however, significant variation among families was detected in only two, and heritabilities detected from these intra-class correlations were not significantly different from zero due to large standard errors. We must therefore conclude, on the basis of the available information, no additive genetic variation in gregarious behaviour.

5. DISCUSSION

It is possible to interpret changes of mean values of characters within and between populations in terms of response to variations in selective forces known to be acting on the populations. The primary selective agent determining the probability of settlement once presented with an algal substrate must be the suitability of that alga as a substrate. It is known that *Ascophyllum* is inferior to *Fucus* as substrate for *Spirorbis* in that the animals do not adhere as strongly to its surface, and that this difference is particularly important in exposed or turbulent conditions, where removal from the inferior substrate is a major source of mortality (Doyle, 1975). Therefore animals from Terence Bay have substantially reduced fitness should they choose to settle on *Ascophyllum* rather than *Fucus*, and the probability of *Ascophyllum* settlement is only half that of *Fucus* settlement. Conversely, Peggy's Cove animals are selected to settle on *Ascophyllum*, since no other fucoid alga is available to them, and here observed settlement on *Ascophyllum* is twice that on *Fucus*. Analogously, the Fjord exhibits a clinal pattern in substrate preference (from *Fucus* more attractive than *Ascophyllum*, to both equally suitable), as one moves away from the mouth of the inlet.

Directional selection for settling strategy accounts for the interpopulation variability observed in gregarious behaviour. It is known that animals from Peggy's Cove settle more quickly than those from Terence Bay (Mackay, 1974), possibly as the result of selection in the latter habitat for a settling strategy which minimises the error made by choosing an inferior substrate and thus reducing fitness, and risking loss of fitness by prolonging planktonic existence. Then the tidepool environment is homogeneous with respect to fucoid substrate for *Spirorbis*, and selection would favour those individuals which settle quickly since this minimises loss of fitness due to predation and no gain in fitness is incurred by searching for a more suitable substrate. At Terence Bay, however, settlement on *Fucus* is of selective advantage and a longer period in the plankton increases the probability of encountering a *Fucus* plant. Since the gregarious response is a stimulus to settle, it is not surprising that animals selected to settle quickly (Peggy's Cove) have enhanced gregarious behaviour over those selected for longer planktonic life (Terence Bay). Although time to settlement has not been measured in the Fjord populations, one may assume similar selection pressures, as the

TABLE 5
Analyses of variance of Lloyd's Indices of Patchiness

	Population											
	Terence Bay		Peggy's Cove		Outer Fjord, <i>Fucus</i>		Outer Fjord, <i>Ascophyllum</i>		Inner Fjord, <i>Fucus</i>		Inner Fjord, <i>Ascophyllum</i>	
	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.
Source of variation												
Settlement on <i>Fucus</i>												
Among families	29	4.562	18	6.371	29	9.007*	26	4.185	29	4.849	26	6.712
Within families	78	2.884	43	3.967	87	5.421	56	4.880	72	3.837	53	5.903
Total	107		61		116		82		101		79	
Settlement on <i>Ascophyllum</i>												
Among families	22	4.552	25	7.024	26	10.594	19	11.194*	—	—	—	—
Within families	49	2.951	65	6.816	66	8.783	36	4.717	—	—	—	—
Total	71		90		92		55		—	—	—	—

* Significant at $\alpha = 0.05$.

Outer Fjord, *Fucus* animals are definitely less gregarious than those from Inner Fjord, *Ascophyllum*.

One can infer adaptation of populations to varying selection pressures from analysis of interpopulation differentiation of character means, but it is from study of the within population genetic variances that we have an indication of the mode of such adaptation. There are basically two mechanisms by which a population may adapt to a heterogeneous environment, either by increased individual homeostasis, or by genetic differentiation such that fitnesses of the genotypes vary in the alternative habitats. If the character studied is quantitative or metric, the two mechanisms can be distinguished on the basis of the genotype-environment interaction (a measure of the extent to which a given trait expressed under different environmental conditions is controlled by the same set of genes); one expects no interaction if the population is responding to environmental heterogeneity by the first mechanism, while if genetic differentiation is the mode of adaptation such interaction would be present.

A more elaborate experimental design than that employed here is necessary to estimate interactions, but the pattern of differences in heritability of settlement between substrates within each of several of the populations studied (in which the point estimate of heritability differs according to substrate) is certainly suggestive of an interaction of genotype with environment. We may therefore tentatively attribute differences in mean settlement on the two substrates within populations to actual genetic differentiation. It is not possible to deduce interaction by comparison of calculated heritabilities of gregarious behaviour, as they were not significantly different from zero nor from each other. Although there are few experimental studies of mechanisms of population adaptation to heterogeneous environments to which this work may be compared, the conclusion from this study and from the earlier work of Antonovics and his colleagues (*e.g.* Antonovics, 1971) must be that there is increasing evidence of adaptation to varying ecological conditions within populations due, at least in part, to precise genetic differentiation.

Acknowledgments.—We wish to thank Drs G. Newkirk and L. Haley for helpful and interesting discussions, and L. Richard and A. Finley for technical assistance at critical moments. T. F. M. was supported by National Research Council of Canada and Killam Postgraduate Scholarships.

6. REFERENCES

- ANTONOVICS, J. 1971. The effects of a heterogeneous environment on the genetics of natural populations. *Am. Sci.*, 59, 593-599.
- BARNES, B. W., AND KEARSEY, M. J. 1970. Variation for metrical characters in *Drosophila* populations. *Heredity*, 25, 1-10.
- BUTCHER, A. C., CROFT, J., AND GRINDLE, M. 1972. Use of genotype-environmental interaction analysis in the study of natural populations of *Aspergillus nidulans*. *Heredity*, 29, 263-283.
- CHAPMAN, A. R. O. 1974. The genetic basis of morphological differentiation in some *Laminaria* populations. *Mar. Biol.*, 24, 85-91.
- DEMPSTER, E. R., AND LERNER, I. M. 1950. Heritability of threshold characters. *Genetics*, 35, 212-236.
- DOYLE, R. W. 1974. Choosing between darkness and light: The ecological genetics of photic behaviour in the planktonic larvae of *Spirorbis borealis*. *Mar. Biol.*, 25, 311-317.
- DOYLE, R. W. 1975. Settlement of planktonic larvae: a theory of habitat selection in varying environments. *Amer. Natur.*, 109, 113-126.

- FORD, E. B. 1965. *Ecological Genetics*. Methuen and Co., Ltd. London.
- GALE, J. S., SOLOMON, R., THOMAS, W. T. B., AND ZUBERI, M. I. 1976. Variation in wild populations of *Papaver dubium*. XI. Further studies on direction of dominance. *Heredity*, 36, 417-422.
- KEARSEY, M. J., AND KOJIMA, K. I. 1967. The genetic architecture of body weight and egg hatchability in *Drosophila melanogaster*. *Genetics*, 56, 23-37.
- KEMPTHORNE, O. 1969. *An Introduction to Genetic Statistics*. Iowa State University Press.
- KNIGHT-JONES, E. W. 1951. Gregariousness and some other aspects of the settling behaviour of *Spirorbis*. *J. Mar. Biol. Assoc. U.K.*, 30, 201-222.
- KNIGHT-JONES, E. W. 1953. Decreased discrimination during settling after prolonged planktonic life in larvae of *Spirorbis borealis* (Serpulidae). *J. Mar. Biol. Assoc. U.K.*, 32, 337-345.
- KNIGHT-JONES, E. W., BAILEY, J. H., AND ISAAC, M. J. 1971. Choice of algae by larvae of *Spirorbis spirorbis*. Fourth European marine biology symposium. Cambridge University Press.
- KOEHN, R. K., AND RASMUSSEN, D. J. 1967. Polymorphic and monomorphic serum esterase heterogeneity in catostomid fish populations. *Biochem. Genet.*, 1, 131-144.
- LAWRENCE, M. J. 1965. Variation in wild populations of *Papaver dubium*. I. Variation within populations; diallel crosses. *Heredity*, 20, 183-204.
- LUSH, J. L., LAMOREUX, W. F., AND HAZEL, L. N. 1948. The heritability of resistance to death in the fowl. *Poult. Sci.*, 27, 375-388.
- MACKAY, T. F. C. 1974. Ecological genetics of some aspects of the settling behaviour of larvae of *Spirorbis borealis* (Daudin). Hons. Thesis, Dalhousie University, Halifax, N. S., Canada.
- NEWKIRK, G. F., AND DOYLE, R. W. 1975. Genetic analysis of shell shape variation in *Littorina saxatilis* on an environmental cline. *Mar. Biol.*, 30, 227-237.
- PIELOU, E. C. 1974. *Population and Community Ecology: Principals and Methods*. Gordon and Breach.
- ROBERTSON, A., AND LERNER, I. M. 1949. The heritability of all or none traits: viability of poultry. *Genetics*, 34, 394-411.
- SCHOPF, T. J. M., AND GOOCH, J. L. 1971. Gene frequencies in a marine ectoproc: a cline in natural populations related to sea temperature. *Evolution*, 25, 286-289.
- DESILVA, P. H. D. H. 1958. Use of artificially liberated larvae in experiments on the settling behaviour of *Spirorbis*. *Nature*, 182, 1751-1752.
- DESILVA, P. H. D. H. 1962. Experiments on choice of substrata by *Spirorbis* larvae (Serpulidae). *J. exp. Biol.*, 39, 483-490.
- SIMCHEN, G. 1967. Independent evolution of a polygenic system in isolated populations of the fungus *Schizophyllum commune*. *Evolution*, 21, 310-315.
- SOKAL, R. R., AND ROHLF, F. J. 1969. *Biometry: The Principles and Practise of Statistics in Biological Research*. W. H. Freeman and Company.
- WISEBY, B. 1960. Observations on the settling behaviour of larvae of the tubeworm *Spirorbis borealis* Daudin (Polychaeta). *Aust. J. Mar. Freshw. Res.*, 11, 55-72.
- WRIGHT, S. 1933. An analysis of variability in number of digits in an inbred strain of guinea pigs. *Genetics*, 19, 506-536.
- WRIGHT, S. 1934. The results of crosses between inbred strains of guinea pigs, differing in number of digits. *Genetics*, 19, 537-551.