A BIOMETRICAL STUDY OF NATURAL SELECTION IN *CARDIUM EDULE*

by

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Résumé

J'ai dénombré les stries de 607 *Cardium edule* de Saint-Efflam et de 73 de Roscoff. Le nombre de stries varie entre 23 et 30. La moyenne de la population de Roscoff est sans doute supérieure à celle de Saint-Efflam. Par des mesures linéaires simples, on peut séparer les animaux vivants âgés d'un an seulement de ceux qui sont plus âgés. Le nombre moyen des stries dans la population de Saint-Efflam augmente un peu avec l'âge, ce qui pourrait être un effet de sélection naturelle. En revanche, la variance ne diminue pas avec l'âge. La sélection centripétale, c'est-à-dire l'élimination des formes extrêmes, est donc beaucoup moins accusée chez *Cardium edule* que chez la plupart des espèces étudiées. Je souligne le grand avantage du *Cardium* pour des études biométriques sur les différences raciales ou sur la sélection naturelle.

INTRODUCTION

The study of natural selection in natural populations is far from simple. In principle it would be desirable to measure or count a character on a large juvenile population, and then to do so in the fraction of this population which survives to a later date. If the distributions differ significantly we have evidence for natural selection based on selective mortality. So far as I know this has only been done by Bumpus (1898) who compared the survivors and non-survivors among sparrows picked up after a storm, though Rendel (1943) made analogous observations on eggs of domestic ducks, and Karn and Penrose (1951) on human babies. It has been more usual to compare distributions in old and young members of a single population of the same species, collected simultaneously, so that the old could not have been survivors of the particular group of young studied.

Over 60 years ago Weldon (1901) saw that molluscs are particularly suitable for work on this latter type. He compared the number of turns per centimetre in living juvenile gastropods and in larger members of the same population in which the juvenile whorls could be examined. This however demanded careful preparation and accurate measurements. It is clear that similar work could be done in much less time and with much simpler technique on lamellibranchs which form shells with radial ridges

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starting from very near the umbo, and whose number appears to be constant during the life of an individual. *Pecten* and *Chlamys* would be well suited for this purpose if juveniles could be obtained in large numbers. But this is not so at Roscoff. However, large populations of *Cardium edule* are available throughout most of their life cycle.

If we compare an old with a young population in this way we may find significant changes in the mean or variance of a quantitative character. A difference in the mean implies what Simpson (1953) calls linear selection. It is this kind of selection which may cause evolutionary changes. However, in view of the extreme slowness of evolution such changes must very rarely be of a kind leading to changes in gene frequencies. Most, though not all, populations studied have shown a diminution in variance with age, that is to say a higher survival of individuals with values near to the mean. Simpson calls this centripetal selection. It must be emphasised that what is measured in this way is only selection during a part of the life cycle, and it is phenotypic, not genotypic selection. Thus a lesser survival of large individuals might be balanced by their higher fertility. Above all, selection for phenotypes may not give rise to genotypic change. The phenotypic differences may be wholly caused by the environment, and if they are genetically determined, may merely serve to stabilise gene frequencies.

RESULTS

680 specimens of *Cardium edule* were studied, 607 from St. Efflam and 73 from Roscoff. Of these 536 were dug out of the sand alive, and 144 were dead shells lying on the surface, usually fairly recently dead specimens with the valves still attached. All these shells were collected in August, 1961.

TABLE I

		No. of ridges on left valve						Total
		24	25	26	27	28	29	
No. of	24	1	0	0	0	0	0	1
ridges	25	2	4	1	0	0	0	2
on	26	0	9	7	0	0	0	16
right	27	0	0	2	8	2	0	12
valve	28	0	0	0	7	2	0	9
	29	0	0	0	0	3	0	3
Total		3	13	10	15	7	0	48

TABLE Ia

Right minus left		
+1	0	—1
23	22	3

A preliminary count showed that the number of ridges on the right and left valves were nearly equal. Tables I and Ia show the results on 48 pairs of valves. It will be seen that the numbers of ridges on the two valves never differred by more than unity. If they did so the valves could not interlock satisfactorily. In 23 pairs of valves the right valve had one more ridge than the left, while in 3 pairs, the left valve had one more ridge. This difference is highly significant ($P=8.8\times10^{-5}$). The correlation between the number of ridges on the two valves is +0.8674 so in a study of variation little information is lost by counting the ridges on one valve only. Right valves only were studied in the main samples.

As a measure of size the valve was rolled along a millimetre scale. The length in millimetres from near the umbo to the end of the median ridge was measured. This is of course a curvilinear measure like some of those used in craniometry, and was used because it was a convenient measure of size for both living and dead animals. The number of ridges was then counted. With a little practice I obtained repeatable results; but about 20% of the large shells and somewhat fewer of the small ones were doubtful in the sense that another observer might have given a result differing by unity from my own. If this research is continued, it is very desirable that the same worker should do so during several consecutive years.

TABLE II

SIZE (mm)	ST. EFFLAM		ROSCOFF	
	Live	Dead	Live	Dead
4	1	1	—	—
5	7	4	—	—
6	10	2	—	—
7	28	—	—	—
8	27	2	—	—
9	23	3	—	—
10	34	5	—	—
11	40	2	—	—
12	44	4	—	—
13	55	3	—	1
14	56	1	—	—
15	37	1	1	—
16	9	—	—	—
17	2	2	—	—
18	1	—	—	—
19	1	1	—	1
20	—	1	—	—
21	—	2	—	—
22	1	2	—	1
23	—	2	—	1
24	1	1	—	1
25	—	1	—	1
26	—	—	—	1
27	1	1	—	—
28	1	—	—	—
29	4	—	1	—
30	3	1	1	—
31	8	1	—	2
32	12	1	1	5
33	7	5	—	—
34	4	2	1	5
35	2	3	1	4
36	5	3	5	3
37	12	—	1	6
38	7	3	—	4
39	14	4	2	5
40	15	4	2	3
41	12	6	2	1
42	11	8	4	2
43	4	4	—	—
44	9	2	—	—
45	—	3	1	—
46	1	2	1	1
47	2	—	1	—
48	—	2	—	—
Totals	511	95	25	48

The results of the measurements are given in Table II. Only the live cockles from St. Efflam represent an unbiassed sample. Large patches of sand were dug to a depth of about four inches and all animals found were collected. In the other samples there was probably a bias in favour of large shells. In this collection of live animals from St. Efflam it is clear that the distribution is multimodal. Only 2 out of 511 measurements occurred in the interval between 19 and 27 mm, and there is another statistically significant antimode at 35 mm. *Cardium edule* breeds in summer, and the group from 4 to 19 mm. doubtless consisted of individuals approximately one year old, while the antimode at 35 mm. may separate the classes of two and three years old. As the 22 mm. shell of the live sample showed a ring suggesting two years' growth it was assigned to the "large" group while the 19 mm. shell of the dead sample, which showed no such ring, was grouped with the juveniles. The dead shells show no clear antimodes in their distribution. This is quite intelligible. The "small" live group were about a year old, as they were collected during the breeding season. Six months later the animals which began life in 1960 probably had a mode at about 20 mm. The dead shells were made by animals which died throughout the year, and naturally did not fall into well defined groups. This is one good reason for working on live animals.

TABLE III

	ST. EFFLAM				ROSCOFF	
No. of ridges on right valve	Live small	Live Large	Dead small	Dead Large	Live	Dead
23	10	1	—	—	—	—
24	43	10	3	2	—	1
25	112	41	9	15	10	7
26	124	38	9	31	3	16
27	61	34	7	14	9	12
28	21	9	3	3	3	9
29	4	1	—	—	—	3
30	—	2	—	—	—	—
Totals	375	136	31	65	25	48
Means	25.699 $\pm$0.061	25.993 $\pm$0.105	25.935 $\pm$0.207	26.015 $\pm$0.109	26.480 $\pm$0.174	26.625 $\pm$0.173
Variances	1.39 $\pm$0.09	1.49 $\pm$0.15	1.33 $\pm$0.29	0.77 $\pm$0.15	0.76 $\pm$0.22	1.43 $\pm$0.24

The distribution of ridge numbers in the six groups are shown in Table III. Among the St. Efflam specimens the small live shells have a mean value significantly smaller than that of the remainder ($P=.002$). The difference between the means of the small live specimens and the large live specimens only is also significant ($P=.016$). These differences could be due to selection, to faulty counting, or to different effects on growth of the environment in different years. If it were due to selection we should except the dead small shells to have fewer ridges than the live ones. They do not. As for error, I consider that I was more likely to miss a ridge on a larger shell, than on a small one. The small ones were examined with a binocular microscope and some of the large shells were somewhat worn. The most striking difference is between the populations of Roscoff ($m=26.5755\pm0.128$) and St. Efflam ($m=25.8155 \pm0.047$). The difference is 0.76 which is 5.58 times its standard error of 0.1363 and very highly significant ($P=1.9\times10^{-8}$). The distribution of ridge numbers of the small specimens from St. Efflam does not differ significantly from normality ($g_1=+0.135\pm0.126$, $g_2=+0.408 \pm0.252$).

The variance of the larger shells is slightly but not significantly greater than that of the younger. There is no evidence in favour of centripetal selection, and no serious evidence for centrifugal selection, though the low variance of the large dead group favours the latter hypothesis. On the other hand the Roscoff sample, with less variance among the living than the dead, suggests centripetal selection. The variance ratio is $F=1.88$ ($P=0.05$) which is not highly significant.

A study of the size distribution of shells from St. Efflam brings out the following. Of the living animals 375 (or 73.4%) were in their first year, while of the empty shells 31 (or 32.3%) were in their first year, the difference being highly significant. It is a measure of the bias earlier mentioned and perhaps of the drifting of empty shells by waves and currents. However, the live and dead specimens in their first year may be compared. The mean linear measurement of the living was 11.453 ± 0.148 mm, of the dead, 10.323 ± 0.707 mm. They do not differ significantly. On the other hand the variance of the live specimens was 8.1625, of the dead 15.161. $F=1.86$ which is significant at the 1% level. It can be explained by the greater variance of ages in the dead. Among the living $k_3=+7.715$, so $g_1=+0.33\pm0.13$, that is to say, the distribution was significantly skew positively. This may reflect the distribution of spawning times during a season. The coefficient of variation for the live shells was 25%. It would doubtless have been less had they all been of exactly the same age.

DISCUSSION

The number of ridges is about as variable as the characters of unworn mammalian teeth, the coefficient of variation in the whole population being 5.4%, those for Roscoff and St. Efflam being 5.2% and 4.4%. These values are quite comparable with those found by Davenport and Hubbard (1904) for *Chlamys* (*Pecten*) *opercularis*.

There can be no doubt that the populations of St. Efflam and Roscoff differ significantly. This difference may be determined genetically, environmentally, or more probably in both ways. It would be of interest to compare the populations on a number of beaches and to see whether their mean ridge number can be correlated with the physical properties of the sand, or any other measurable features of the environment. About 120 specimens would be needed to reduce the standard error of the mean to 0.01.

The cause of the difference between the means of the old and young populations from St. Efflam could probably be determined by studies spread over several years. It is of course entirely possible that other characters, such as the ratio of length to breadth, would yield more valuable information than the number of ridges. But their investigation would take a good deal longer.

The evidence as regards variance suggest centrifugal rather than centripetal selection. But a sample of several thousand would be needed to establish this, if it is true. We can only say that if there is centripetal selection it is far from intense. Centripetal selection occurs with very high probability in the following species.

Passer domesticus (Bumpus, 1898), *Clausilia laminata* (Weldon, 1901), *Anas platyrhynchos* (Rendel, 1943), *Homo sapiens* (Karn and Penrose, 1951). It probably occurs or occurred, but on the basis of smaller samples, in *Ursus spelaeus* (Kurtén, 1953, 1955). It was not found in a population of *Clausilia itala* from the citadel of Brescia (Weldon, 1904), and in a few small samples of mammalian teeth studied by Kurtén (1953). It appears, however, to be usual.

Centripetal selection may have no effect at all. It may occur in a pure line or a clone, the individuals most affected by the environment being most inviable or infertile. If it is directed against homozygotes and in favour of heterozygotes it is called stabilising selection (Schmalhausen, 1949) and serves to stabilise an existing genetic polymorphism. If it is directed against genotypes which are most susceptible to the effects of environmental change it is called normalising selection (Waddington, 1953) and is likely to have some evolutionary effects. Haldane (1958) gives a further discussion.

The failure to find it in *Cardium edule* presumably means that individuals with different ridge numbers are equally fit. This suggests that the variation is mainly due to environmental differences, and not to a genetical system stabilised by heterosis. It is, I think, clear that many populations of many species must be investigated before generalisations can be made about natural selection; however, the fact that I was able, in two weeks, to obtain the results here published suggests that Lamellibranchs are very suitable material.

The fact that only 26% of the living specimens from St. Efflam were over one year old is of interest. The figure is probably fairly representative but it is more likely to be too large then too small, since a few small specimens may have been overlooked when searching sand; also, the small specimens are more fragile. It will of course be desirable to see how far this figure remains constant in subsequent years. It may depend on how good or bad the previous spawning season has been. If it is approximately constant, we could argue as follows. The animals which reach the age of one year are a small unknown fraction s_1 of the eggs fertilised in the previous year. A fraction, say s_2, of the one-year old animals survive to the age of two years, and of these a fraction s_3 survive to the age of three years. Therefore, of a sample collected one year, a fraction $(1+s_2+s_2s_3+s_2s_3s_4+....)^{-1}$ will be in their first year. If the survival rates s_1,s_2,s_3, etc. do not depend on the age of the animals, as in some birds, then the fraction of animals in their first year will be (1-s) where $s=s_1=s_2$, etc. However, assuming only constant death rates at a given age we have in the St. Efflam sample:

$$(1+s_2+s_2s_3+s_2s_3s_4+.....)^{-1}=0.74$$

and therefore

$$s_2\ (1+s_3+s_3s_4+.....)=0.35$$

s_2 is therefore less than 0.35 or the death rate in the second year exceeds 65%. 74% seems the best estimate.

The fact that 74% of live specimens but only 32% of dead specimens belonged to the youngest group is of some interest for the evaluation of palaeontological data. I could probably have collected a larger amount of small empty shells. But the small shells are more liable to be carried away by waves and currents than the large empty shells. And I was certainly less likely to overlook small specimens than a palaeontologist who rarely discovers every fossil in a volume of rock, but may extract any which may be seen on its surface. While, therefore, it is a remarkable achievement to have constructed life tables for fossil species as Kurtén (1953) has done, I believe that such life tables are likely to underestimate mortality, as is evident from the estimate of 32% that would have been obtained from the St. Efflam data on the basis of empty shells, whereas the true figure exceeds 65%.

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Summary

The number of ridges on the shell of *Cardium edule* has a modal value of 26 and a coefficient of variation of about 5%. Two populations differred significantly in their mean number. No evidence was found for centripetal selection, but some for selection in favour of high ridge number.

Zusammenfassung

Ich haben die Streifen von 607 Exemplaren von *Cardium edule* von Saint-Efflam und von Roscoff ausgezählt. Die Zahl der Streifen variiest zwischen 23 und 30. Der Mittelwert für die Population von Roscoff ist höher als derjenige für die Population von Saint-Efflam. Mittels einfacher linearer Messung kann man lebende Tiere die ein Jahr alt sind, von älteren Tieren unterscheiden. Die Anzahl der Streifen erhölt sich etwas mit dem Alter der Tiere in der Population von Saint-Efflam, was eine Folge der natürlichen Zuchtwahl sein könnte. Die Varianz dagegen nimmt nicht ab mit zunehmendem Alter. Die zentripetale Selektion, das heisst die Ausmerzung der extremen Formen, ist also bei *Cardium edule* weniger ausgemägt, als bei der Mehrzahl der untersuchten Arten. Ich möchte auf die besondere Eignung von *Cardium* für biometrische Studien über Rassenunterschiede und die natürliche Zuchtwahl hinweisen.

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