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ON VARIATION IN THE SHELL OF THE DOG-WHELK, *NUCELLA LAPILLUS* (L.)

I. PEMBROKESHIRE

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Introduction

The Common Dog-Whelk, *Nucella lapillus* (L.), is unusual amongst marine animals in having no planktonic phase in its life cycle. This, coupled with its sluggish habits, means that the effective breeding populations (the panmictic units) are small, and it also makes feasible breeding experiments on the shore and in the laboratory. The species thus lends itself to a study of variation. Unfortunately, most papers on this topic consist of qualitative assessments from one restricted area. Frequently the conclusions of one author conflict with those of another and, in the absence of numerical data, it is difficult to know the meaning of "squat", "elongated" and so on. The only safe conclusion from the literature is that populations of *Nucella* vary one from another, and that patterns of variation found in one area will not necessarily appear in others.

In an attempt to clarify the situation I propose to describe variation in numerical terms wherever possible, and to relate my observations to the patterns seen in a type locality. This preliminary paper is an account of some 60 samples collected from my type locality: Pembrokeshire, West Wales.

Terminology

"The term 'population', like so may familiar terms, seems to present no difficulty until we have to define it more closely." (Briggs and Walters, 1969.) In previous papers I have used this term to denote the group of dog-whelks in a given site, assuming each isolated area of rocky shore to support a discrete breeding unit. Nothing, however, is known about the size of the panmictic unit in *Nucella* and, as an interim measure, I propose to use the *-deme* terminology to describe variation within and between "populations".

This terminology was originally suggested by Gilmour and Gregor (1939) and has been recommended more recently by Briggs and Walters (1969) from whence the definitions below are taken. The suffix *-deme* simply means "a group of individuals" and the terms are constructed by the addition of an appropriate prefix as follows:

Topodeme:	a group of individuals occurring in a specified geographical area.
Ecodeme:	a group of individuals occurring in a specified type of habitat.
Cytodeme:	a group of individuals differing cytologically from other groups (usually in chromosome number).
Gamodeme:	a group of individuals which are so situated spatially and temporally that, within the limits of their breeding system, all can interbreed.

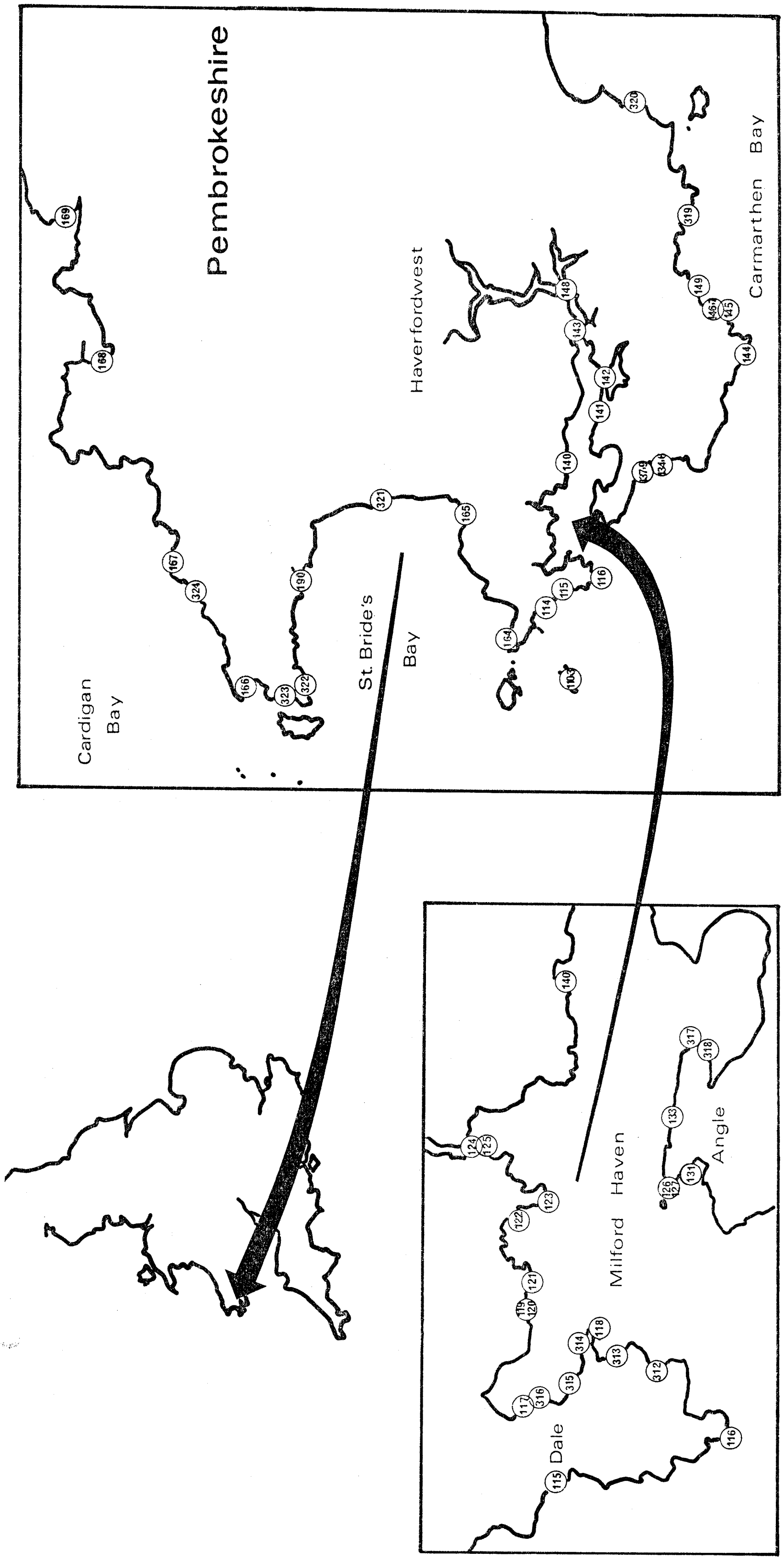

FIG. 1.
The sampling sites around the Pembrokeshire coast. The numerals can be identified from the Tables.

Caenogamodeme: a unit composed of all the gamodemes that are considered capable of exchanging genes to some extent, but not with freedom.

The advantages of such terms include the absence of the overtones which cloud the meaning of "race" and "population" in use in ordinary speech. They are not exclusive: two individuals of the same topodeme could belong to different cytodemes.

The Biology of Nucella lapillus

The Common Dog-Whelk is a marine snail found between the tide marks on rocky sea shores. In Pembrokeshire it usually feeds on three species of acorn barnacles: *Balanus balanoides* Bruguière, *Chthamalus stellatus* Poli, and *Elminius modestus* Darwin. The feeding process, described by Fretter and Graham (1962), takes hours if not days so that the whelk must remain on its prey over the period of low tide—in contrast to most shore predators which forage at high tide or at night and hide away at low tide and by day. Mussels, *Mytilus edulis* L., are usually eaten if available and may be preferred to barnacles. Mussel-feeding *Nucella* were included in my samples from Little Haven, Marloes Sands and Tenby. If the usual food is scarce, dog-whelks attack other barnacles and molluscs. On sheltered shores Flat Winkles, *Littorina littoralis* (L.) and Purple Topshells, *Gibbula umbilicalis* (da Costa) are the most frequent alternative. Some topodemes feed on limpets, although I have not found any that do so in Pembrokeshire, and occasionally on cockles *Cardium* (*Cerastoderma*) *edule* L. (Morgan, 1972). In Spain I have found holes drilled in the stalked barnacle *Pollicipes cornucopia* (Gmelin). In general the food of each topodeme is related to the available food supply.

The species may be cannibalistic, but whilst many shells show signs of boring few are drilled right through (Moore, 1938). If the attack is made too close to the shell lip the victim may be able to withdraw into its shell behind the threatened spot. I have seen this happen in an aquarium and the inner end of the hole was sealed over within a few days. Subsequent growth causes the repaired hole to move round the body whorl to sites where an attack would have been fatal.

Newly-hatched individuals feed on the tube worm *Spirorbis* (Moore, 1936,1938)—and many certainly do so in Pembrokeshire, where worm tubes showing pin-prick sized drill marks can be found. They are not, however, restricted to this diet (Largen, 1967b) and I have reared *Nucella* to at least one-year-old on a diet of barnacles (*Elminius*).

Adults congregate on the lower shore to breed. Largen (1967a) found that egg capsules may be laid whenever the sea temperature rises above 7 °C. and, as the water in Milford Haven rarely drops below this figure (Nelson-Smith, 1967) Pembrokeshire *Nucella* may breed at almost any time of the year—in contrast to Yorkshire topodemes (Feare, 1970)—but I believe most capsules are laid in February and March. In my aquaria the capsules hatch after two or three months to release between ten and twelve snails. There is no planktonic or other dispersal phase in the life cycle, the veliger stage taking place within the egg capsule, so that the young animals must live on the same stretch of shore as their parents. The species is rarely found beneath the tide marks and does not voluntarily crawl across sand or mud, with the result that *Nucella* is distributed around the coastline of Europe in innumerable discrete gamodemes. This is particularly noticeable along the deeply-indented coastline of Pembrokeshire.

The young snails increase in size for about three years until they reach sexual maturity (Moore, 1936; Feare, 1970) when shell growth stops. Low temperatures inhibit feeding (Largen, 1967a) and topodemes in the North Sea probably feed only in summer, spending the winter in clefts where they may form massive aggregations (Feare, 1970, 1971). In Pembrokeshire *Nucella* is found on the open rock surface throughout the year and apparently aggregates only to breed. The life-span is unknown in Pembrokeshire but Feare estimates 5–6 years at his site in Yorkshire.

Nothing is known of the formal genetics of shell variation in *Nucella* but it is likely that intrinsic (genetic) and extrinsic (environmental) factors combine to produce variation in size, shape, colour, thickness and shell ornament. If this is the case, an individual may carry genes for white colour and yet appear purple through the growth of algae or lichens on the exterior. Similarly it may be worn smooth by abrasion even though it carries the genes for ridged suface; and the genes controlling shell shape will not find normal expression if the cells of the mantle, the site of shell secretion, are damaged. Damaged shells are repaired but the later secretion is never identical to the original and invisible damage to the animal, such as a period of starvation, may induce considerable changes in shell deposition which persist after the immediate cause has disappeared.

The shell records the history of that individual from the first-formed protoconch, which is carried on emergence from the egg capsule and retained at the tip of the spire, to the most recently formed part around the aperture.

MATERIAL AND METHODS

Pembrokeshire was chosen as type locality for my study of shell variation in *Nucella lapillus* because:

a. The animal is widespread and abundant.
b. Shores of widely differing exposure to wave action occur within a small geographical area.
c. The biological effects of differential wave action on rocky shores have been described by several authors, especially around the Dale peninsula where Ballantine (1961) devised his exposure scale.
d. I already had collections of shells from the County.
e. I know the area well.

The observations which form the basis of this paper are derived from an examination of some 10,000 shells in 60 samples taken from sites on the Pembrokeshire coast between 1966 and 1972 (Table 1). They fall into three groups:

1. Those collected during 1966/1967 in collaboration with Dr. R. J. Berry for work on stabilizing selection published in 1968 (see p. 47). These samples vary in size but most exceed 200 shells. A determined effort was made to include individuals of all ages.
2. Those collected during 1969/1970 in collaboration with Mr. E. B. Cowell for work on "teeth" published in 1970 and 1971. Each sample contains a minimum of 200 shells, collected as far as possible without bias toward size, shape or colour. In practice the smaller shells were under sampled.
3. Those collected subsequently to augment information in certain critical areas. Each comprises 100 shells, specifically taken for analysis of shell shape. They, too, are probably biased towards larger individuals.

The varied origin and purpose of these samples would preclude some analyses but all are thought to be representative of the full-sized component of the topodeme concerned; and most of the work described here is concentrated on these individuals.

The animals were killed very shortly after collection and extracted from their shells, which were cleaned in a liquid household bleach and stored dry. Most of the samples were dried in an oven and as, unfortunately, shell colour is altered by heat the collection can only be used for analyses of shell colour in a very general way.

The Investigations

The Dale Fort Marine Fauna (Bassindale and Barrett, 1957; Crothers, 1966) contains the observation that "as exposure increases so the shell (of *Nucella*) thickens, the ornamentation and the overall length decrease, and the proportion of the shell occupied by the aperture increases". This observation appeared to be generally true elsewhere in Pembrokeshire but has not previously been described in numerical terms.

Where possible 100 shells from each of my samples were measured (to the nearest 0·1 mm.) for length (L), aperture length (Ap) and thickness (T). The mean with its standard deviation, were obtained for each sample in respect of L, L/Ap and T.

The Assessment of Wave Action

Direct measurement of wave action on sea shores is not yet possible but a useful assessment of its biological effects may be made using Ballantine's (1961) scale in which the whole complex of factors that we loosely refer to as "exposure" is estimated through the integrated effect on the distribution of selected indicator organisms. It ranges from the extremely exposed grade 1 to the extremely sheltered grade 8. It was originally devised in relation to the Pembrokeshire coast, so here at least there can be no doubt as to its applicability. In later papers, when I plan to compare variation in other areas with the data presented here, it will be necessary to examine to what extent this scale may be relied on because the distribution and abundance of Ballantine's indicator species are influenced by many factors in addition to wave action.

Tables 1–3 list the mean values of L, L/Ap, and T for each sample. The samples are grouped by exposure but no attempt was made to list the sites in order of exposure within a grade. The same data are displayed graphically (Figs. 2, 4 and 5) in a way which makes no assumptions about the intercepts between the grades on Ballantine's exposure scale. This is important for, whilst the grades are undoubtedly sequential—that is, exposure 4 is certainly more exposed than exposure 5 and less exposed than exposure 3—they are not necessarily equally spaced along the exposure continuum. My own guess is that few errors are incurred by assuming the scale to be linear, and I have done so in some earlier papers (Cowell and Crothers, 1970; Crothers, 1971, 1973) but it is obviously better to avoid making such assumptions where possible.

Results

Length

Length (or height in strict conchological nomenclature) is the easiest character to measure on a dog-whelk shell. I have taken the maximum reading from apex to siphonal notch (Fig. 3). Damaged specimens and all obvious immatures were

Table 1. *Variation in the mean length (L) of* Nucella lapillus *shells collected in Pembrokeshire. Samples have been grouped by exposure grade, but are listed within each grade merely in numerical order of the sample number. The values for the mean and standard deviation of L were calculated from n shells*

Exposure	Site	Grid Ref.	Collected	n	L	Grade mean L
1	110 Skokholm : Long Nose	SM 727047	April 1967	100	2·08±0·16	
1	111 Skokholm : Long Nose	SM 727047	Sept. 1969	100	2·00±0·25	2·01±0·10
1	192 Grassholm : South Gut	SM 598092	July 1965	25	1·81±0·19	
1	402 Grassholm : South Gut	SM 598092	July 1972	50	2·15±0·16	
2	112 Skokholm : Easter Rock		April 1967	100	2·61±0·41	
2	116 St. Ann's Head	SM 805028	June 1966	100	2·10±0·18	2·35±0·17
2	319 Manorbier Point	SS 059971	Sept. 1971	100	2·35±0·15	
2–3	149 Greenala Point	SS 008966	Aug. 1969	100	2·07±0·22	
3	114 Marloes Sands	SM 785074	June 1967	100	2·65±0·31	
3	118 Dale Point	SM 825052	Feb. 1970	100	2·55±0·25	
3	123 Great Castle Head	SM 847059	Feb. 1970	100	2·57±0·23	
3	127 Thorn Point	SM 848037	July 1969	100	2·68±0·20	2·63±0·07
3	144 St. Govan's Chapel	SR 968928	Aug. 1969	100	2·70±0·35	
3	167 Porth Gain	SM 814327	Oct. 1970	100	2·50±0·23	
3	324 Abereiddy	SM 795315	Sept. 1971	100	2·75±0·22	
3–4	115 West Dale	SM 797057	Sept. 1969	100	2·56±0·23	
3–4	121 Soldiers' Rock	SM 833063	Oct. 1966	100	2·75±0·22	2·68±0·08
3–4	137 Freshwater West	SM 876007	Aug. 1969	100	2·74±0·36	
4	119 Monk Haven	SM 827063	July 1966	100	2·53±0·22	
4	120 Monk Haven	SM 827063	Feb. 1970	100	2·37±0·15	
4	122 Lindsway Bay	SM 845065	Sept. 1969	100	2·65±0·16	
4	138 Freshwater West	SM 876007	July 1969	100	2·84±0·20	
4	139 Freshwater West	SM 876007	Sept. 1969	100	2·70±0·25	
4	145 Barafundle Bay	SR 993948	Aug. 1969	100	2·68±0·23	2·76±0·18
4	165 Little Haven	SM 855131	June 1966	100	2·75±0·35	
4	169 Newport Sands	SN 054408	Oct. 1970	100	2·90±0·24	
4	320 Tenby (North Beach)	SN 130001	Sept. 1971	100	2·90±0·24	
4	321 Nolton Haven	SM 857185	Sept. 1971	100	3·21±0·24	
4	283 Barrafundle: upper	SR 993948	Aug. 1969	100	2·90±0·31	
4	284 Barafundle: lower	SR 993948	Aug. 1969	100	2·68±0·30	
4–5	164 Martin's Haven	SM 760093	Mar. 1967	100	2·60±0·27	
4–5	166 Whitesands Bay	SM 732273	Oct. 1970	100	2·93±0·38	
4–5	322 Porth Clais	SM 743238	Sept. 1971	100	3·05±0·24	2·86±0·17
5	126 West Angle Bay	SM 850037	July 1969	100	2·72±0·25	
5	134 Furznip	SR 886995	July 1969	100	2·62±0·27	
5	135 Furznip	SR 886995	July 1969	100	3·10±0·27	2·79±0·16
5	136 Furznip	SR 886995	Aug. 1969	100	2·70±0·20	
5–6	131 West Angle Bay	SM 850035	Sept. 1969	100	2·75±0·27	
5–6	312 Watwick Bay	SM 817040	Sept. 1971	100	2·96±0·17	2·86±0·10
6	133 Chapel Bay	SM 863037	July 1969	100	2·65±0·15	
6	146 Stackpole Quay	SR 993958	Aug. 1969	100	2·93±0·28	
6	147 Stackpole Quay	SR 993958	Aug. 1969	100	3·00±0·27	
6	313 Gunkle (Dale)	SM 819047	Sept. 1971	100	2·85±0·20	
6	314 Slip Pier (Dale)	SM 823054	Sept. 1971	100	2·77±0·20	2·88±0·12
6	315 Point Wood (Dale)	SM 813036	Sept. 1971	100	2·98±0·22	
6	316 Black Rock (Dale)	SM 813061	Sept. 1971	100	3·08±0·22	
6	317 Angle Point	SM 875034	Sept. 1971	100	2·77±0·27	
6–7	140 Gelliswick	SM 885055	Mar. 1967	100	2·90±0·42	
6–7	142 Pennar	SM 943030	Sept. 1969	100	3·05±0·30	
6–7	143 Neyland	SM 965047	Mar. 1967	100	2·96±0·26	
6–7	190 Solva	SM 802241	Oct. 1970	31	3·17±0·31	2·98±0·11

Table 1—*continued*

Exposure	Site	Grid Ref.	Collected	n	L	Grade mean L
6–7	323 St. Justinian's	SM 723253	Sept. 1971	100	2·81±0·25	
7	117 Cliff Cottages (Dale)	SM 813063	June 1966	100	2·68±0·26	
7	124 Sandy Haven	SM 856070	June 1966	100	2·63±0·33	
7	125 Sandy Haven	SM 856070	Feb. 1970	100	2·86±0·30	
7	141 Martinshaven	SM 924034	Oct. 1969	100	2·72±0·24	
7	168 Goodwick	SM 960380	Oct. 1970	100	3·05±0·32	2·82±0·15
7	318 Angle Bay	SM 874032	Sept. 1971	80	3·00±0·25	
8	148 Lawrenny	SN 018065	Oct. 1969	100	3·33±0·25	
8	371 Mill Bay (Cosheston)	SN 000040	June 1972	100	3·00±0·25	3·17±0·17

NOTES: Samples 110–112 (Skokholm) were collected by Dr. R. J. Berry; nos. 115, 122, 371 and 402 by Mr. D. C. Emerson; nos. 126–139, 141–142, 145–149, and 283–284 by Mr. E. B. Cowell; and the remainder by myself.

The sample numbers are included for reference: they were devised for Crothers (1971)—in which they emphasized the location—and subsequent samples were simply allocated the next available number.

omitted, but it is not easy to identify adults in Pembrokeshire samples. The extended breeding season, coupled with the widely differing growth rates of individuals from the same brood, make it very difficult to recognize definite age classes. "Teeth" can no longer be used as a definition of adulthood (Cowell and Crothers, 1970) although it remains true that an animal having a thin sharp lip to its shell and no "teeth" is (in Pembrokeshire) almost certainly immature. The samples measured were thus a mixture of adults and nearly fullgrown immatures.

The mean length of topodemes from exposed shores is appreciably less than that of those inhabiting sheltered shores; the mean length of dog-whelk shells increases with increasing shelter from wave action.

Shape: as indicated by L/Ap

A variety of measurements have been used to describe the shape of dog-whelk shells but those involving maximum breadth, maximum distance across the body whorl or internal measurements of the aperture are all, to some extent, subjective. Measurement of the operculum is often the best indication of aperture shape but this is only really suitable for use on fresh, dead material—and some topodemes from the south-east of the County contain a high proportion of individuals in which the operculum is reduced or absent (e.g. Amroth and Lydstep Haven—see Cooke, 1917).

I have taken length (L) divided by aperture length (Ap) as defined in Fig. 3 as being the most convenient and objective assessment of shell shape in this species which can be made over the whole range of forms encountered.

The values of L/Ap increase with increasing shelter, indicating the occurrence of a short squat form on exposed sites which gradually gives way to a more elongated variety in shelter. A more detailed analysis of this data (Crothers, 1973) indicates continuous variation within and between topodemes.

Thickness

When growth stops, on cessation of feeding or at maturity, the shell lip of *Nucella* is thickened and a row of white dentiform tubercles (commonly referred to as "teeth") are laid down along the inner margin. Should growth subsequently

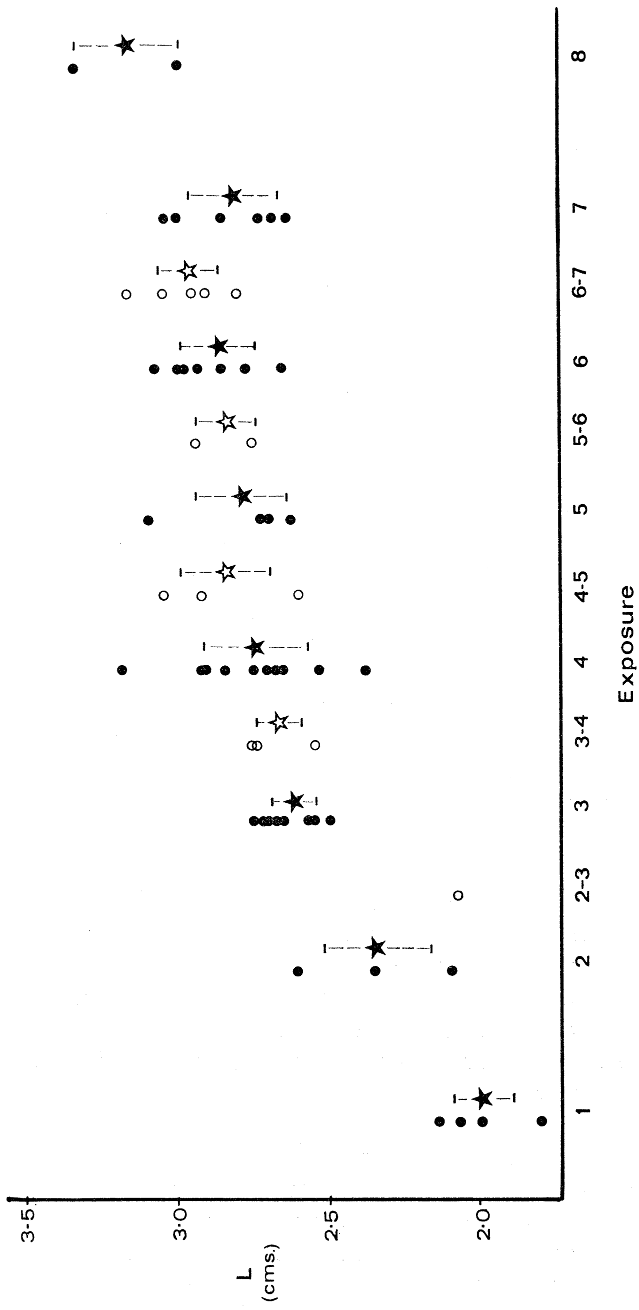

FIG. 2.
The relationship between shell length (L) and exposure for Pembrokeshire samples of *Nucella lapillus*. Samples from exposure grades and intergrades are represented by closed and open symbols respectively and the stars indicate the mean value for the samples of that exposure. It should be remembered that the intercepts between the exposure grades are not necessarily equal. Data from Table 1.

continue the thickened, "toothed", area remains and fresh shell of normal thickness is deposited around the lip. The process repeats itself whenever growth is seriously checked and exceptional shells have six or more rows of these "teeth". In these individuals it is impossible to determine the true thickness of the shell but fortunately few Pembrokeshire *Nucella* show more than two rows. Even so the thickened lip prevents the use of normal callipers. Dr. K. Bignell of Imperial College designed and

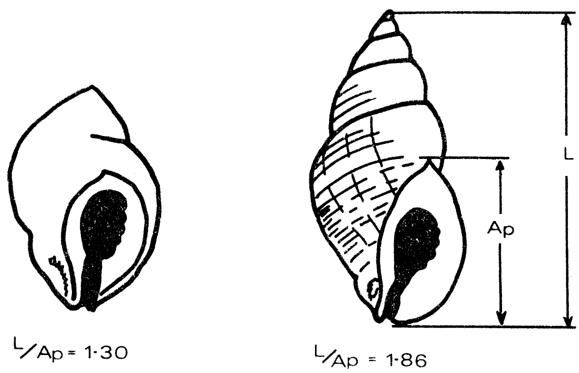

FIG. 3.
Shells of *Nucella lapillus* to indicate the measurements of L and Ap; and the use of L/Ap to indicate the shape of the shell.

made an ingenious spring calliper which measures thickness inside the body whorl and data obtained with this instrument are preferred to estimates based on weight and size such as have been used in the past.

Obviously damaged shells, and those bored by the worm *Polydora* or badly corroded by lichen and algal attack were not used. As mentioned above it is not always possible to recognize adults but as there seems to be little change in thickness, apart from the lip, on reaching maturity perhaps this does not matter.

The thickest shells were found on shores of intermediate exposure with the thinnest on the most exposed and most sheltered shores.

DISCUSSION

The results confirm that "as exposure increases so . . . the overall length decreases and the proportion occupied by the aperture increases". A short squat form occurs on exposed shores, which grades completely into a longer, thinner variant found in shelter. There is continuous variation between the very well marked extremes.

The data as presented do not, however, establish whether the correlations are with wave action itself or with some other associated factor. Fortunately there are two further sets of observations which help to clarify the situation.

Stabilizing Selection

A decrease in variability with age (that is, where the shells of adults are less variable than those of juveniles in the same topodeme) may indicate the operation of natural selection, presumably eliminating those shell types least fitted for survival in that locality. The phenomenon of "linkage" makes it difficult to determine just how the selection operates but the fact that it occurs is relatively easy to demonstrate. To investigate this phenomenon some parameter must be chosen which does not itself vary with age or size, and Berry and Crothers (1968, 1970) used length divided by the cube root of the dry weight. This, at first sight, unlikely choice is justified because length and dry weight are the least inaccurate measurements of small shells and a graph of these two parameters plotted against each other showed that length plotted against the cube root of the weight would be a straight line. In other words,

Table 2. *Variation in the shape of* Nucella lapillus *shells collected in Pembrokeshire. The mean and its standard deviation are given for the parameter L/Ap—length of the shell divided by maximum length of the aperture. From Crothers (1973)*

Exposure	Sample	n	L/Ap	Grade mean L/Ap
1	110 Skokholm : Long Nose	100	1·24±0·05	
1	111 Skokholm : Long Nose	100	1·22±0·04	1·24±0·01
1	192 Grassholm : South Gut	25	1·25±0·05	
1	374 Grassholm : North Gut	4	1·26	
1	402 Grassholm : South Gut	50	1·24±0·035	
2	112 Skokholm : Easter Rock	100	1·30±0·07	
2	116 St. Ann's Head	100	1·22±0·04	1·27±0·04
2	319 Manorbier	100	1·30±0·05	
2–3	149 Greenala Point	100	1·27±0·045	
3	114 Marloes Sands	100	1·36±0·05	
3	118 Dale Point	100	1·30±0·06	
3	123 Great Castle Head	100	1·38±0·05	
3	127 Thorn Point	100	1·37±0·06	1·34±0·03
3	144 St. Govan's Chapel	100	1·31±0·07	
3	167 Porth Gain	100	1·29±0·06	
3	324 Abereiddy	100	1·355±0·06	
3–4	115 West Dale	100	1·27±0·06	
3–4	121 Soldiers' Rock	100	1·365±0·055	1·32±0·035
3–4	137 Freshwater West	100	1·33±0·08	
4	119 Monk Haven	100	1·42±0·06	
4	120 Monk Haven	100	1·26±0·04	
4	122 Lindsway Bay	100	1·35±0·05	
4	138 Freshwater West	100	1·38±0·05	
4	139 Freshwater West	100	1·385±0·05	
4	145 Barafundle Bay	100	1·34±0·04	
4	165 Little Haven	100	1·40±0·04	1·37±0·033
4	169 Newport Sands	100	1·35±0·06	
4	320 Tenby	100	1·40±0·05	
4	321 Nolton Haven	100	1·43±0·06	
4	283 Barafundle—upper shore	100	1·345±0·065	
4	284 Barafundle—lower shore	100	1·35±0·06	
4–5	164 Martin's Haven	100	1·35±0·05	
4–5	166 Whitesands Bay	100	1·355±0·055	1·37±0·02
4–5	322 Porth Clais	100	1·40±0·05	
5	126 West Angle Bay	100	1·395±0·055	
5	134 Furznip	100	1·39±0·055	1·395±0·005
5	135 Furznip	100	1·40±0·055	
5	136 Furznip	100	1·395±0·05	
5–6	131 West Angle Bay	100	1·395±0·06	1·40±0·005
5–6	312 Watwick Bay	100	1·40±0·055	
6	133 Chapel Bay	100	1·42±0·06	
6	146 Stackpole Quay	100	1·395±0·07	
6	147 Stackpole Quay	100	1·38±0·06	
6	313 Gunkle	100	1·44±0·06	1·42±0·03
6	314 Slip Pier	100	1·39±0·06	
6	315 Point Wood	100	1·45±0·05	
6	316 Black Rock	100	1·46±0·07	
6	317 Angle Point	100	1·46±0·07	
6–7	140 Gelliswick	100	1·47±0·08	
6–7	142 Pennar	100	1·45±0·06	
6–7	143 Neyland	100	1·51±0·07	1·46±0·02
6–7	190 Solva	31	1·46±0·07	
6–7	323 St. Justinian's	100	1·42±0·06	

Table 2—*continued*

Exposure	Sample	n	L/Ap	Grade mean L/Ap
7	117 Cliff Cottages	100	$1\cdot46\pm0\cdot07$	
7	124 Sandy Haven	100	$1\cdot47\pm0\cdot07$	
7	125 Sandy Haven	100	$1\cdot48\pm0\cdot06$	$1\cdot47\pm0\cdot01$
7	141 Martinshaven	100	$1\cdot48\pm0\cdot06$	
7	168 Goodwick	100	$1\cdot44\pm0\cdot06$	
7	318 Angle Bay	80	$1\cdot47\pm0\cdot05$	
8	148 Lawrenny	100	$1\cdot495\pm0\cdot07$	$1\cdot47\pm0\cdot03$
8	371 Mill Bay	50	$1\cdot43\pm0\cdot07$	
8	Lawrenny: live sample Sept. 1971	100	1·49	

length divided by the cube root of the dry weight does not show any trend with increasing shell size.

Shells were grouped into five sequential "age" classes on the basis of Moore's (1936, 1938) accounts of the life cycle, and the variance of the mean $L/\sqrt[3]{wt}$ obtained for each class in each sample. At the time of this investigation (1966/1967) the presence of "teeth" was generally considered to indicate maturity (see below) and we used this character to define our oldest age class. This we now know to be unreliable but the main conclusions of the work are not affected by this error for selection was found to operate primarily on younger individuals.

We found evidence of considerable variance-reduction (presumed selection) in samples from exposed sites but no obvious pattern could be seen in those from shelter (Fig. 6). We concluded that selection was acting to maintain the preponderance of short squat individuals on exposed sites and consider it an example of stabilizing selection maintaining the characteristic ecodeme under these conditions.

This clearly is only part of the story for it does not explain the situation on sheltered shores where the exposed-shore form is progressively replaced by the longer thinner variant.

"*Teeth*"

For some 30 years following Moore's work on dog-whelks nobody questioned his assumption that "teeth" were produced at the onset of maturity and at no other time. Then, in the late 1960s, three people, working entirely independently, noticed that they are also formed when growth is temporarily interrupted. Bryan (1969) recorded "tooth" formation in immature *Nucella* at Porthleven (Cornwall) and attributed it to starvation following the *Torrey Canyon* incident; Feare (1970) showed "tooth" development on the Yorkshire coast to be associated with winter cessation of feeding; whilst I noticed that shells with two or more rows of "teeth" are particularly common in Somerset.

The formation of these "teeth" simply indicate a prolonged interruption of growth. All mature individuals can be expected to show a row near the lip because they will permanently have finished growing and additional rows inside the body whorl corresponding to the number of periods of starvation they suffered as juveniles. In some places near the northern and southern limits of the species' range the shells of *Nucella lapillus* are very thin and "teeth" are not usually detectable, but this thin-shelled form does not occur in Pembrokeshire.

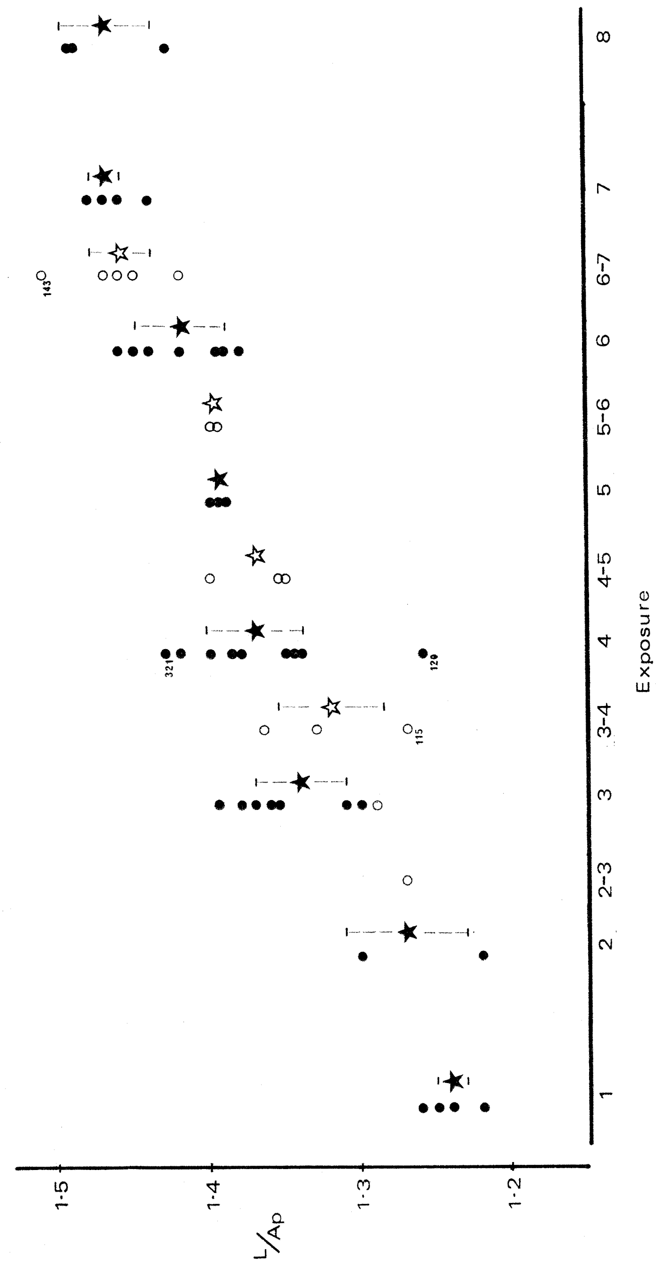

FIG. 4.

The relationship between shell shape (L/Ap) and exposure for Pembrokeshire samples of *Nucella lapillus*. Samples from exposure grades and intergrades are represented by closed and opens symbol respectively and the stars indicate the mean value for samples of that exposure. It should be remembered that the intercepts between exposure grades are not necessarily equal. Data from Table 2.

Mr. E. B. Cowell, then Warden of Orielton Field Centre (South Pembrokeshire) noted a relationship between the incidence of juvenile starvation (as revealed by "tooth" formation) and exposure. He and I (Cowell and Crothers, 1970) were able to demonstrate that some 42 per cent of toothed shells on very exposed shores can be expected to show signs of starvation, a proportion which decreases progressively to 7 per cent in extreme shelter. We consider that this relationship is produced directly by the effect of wave action and suggest that individuals on exposed shores

Table 3. *Variation in the mean thickness (T) of* Nucella lapillus *shells collected in Pembrokeshire*

Exposure	Site	n	T (mm.)	Grade mean T
1	110 Skokholm: Long Nose	100	1·7 ±0·5	
1	111 Skokholm: Long Nose	100	1·3 ±0·6	1·4±0·2
1	192 Grassholm	25	1·25±0·25	
2	112 Skokholm: Easter Rock	100	2·1 ±0·8	
2	116 St. Ann's Head	100	2·15±0·5	2·2±0·1
2	319 Manorbier	100	2·3 ±0·3	
2–3	149 Greenala	100	1·85±0·4	
3	114 Marloes Sands	100	1·5 ±0·45	
3	118 Dale Point	100	2·1 ±0·3	
3	123 Great Castle Head	100	2·1 ±0·4	
3	127 Thorn Point	100	2·5 ±0·5	2·5±0·45
3	144 St. Govan's Chapel	100	2·7 ±0·4	
3	167 Porth Gain	100	3·3 ±0·5	
3	324 Abereiddy	100	3·15±0·55	
3–4	115 West Dale	100	2·25±0·6	
3–4	121 Soldiers' Rock	100	2·7 ±0·35	2·5±0·2
3–4	137 Freshwater West	100	2·6 ±0·5	
4	119 Monk Haven	100	2·0 ±0·4	
4	120 Monk Haven	100	2·25±0·4	
4	122 Lindsway Bay	100	1·8 ±0·45	
4	138 Freshwater West	100	2·5 ±1·5	
4	139 Freshwater West	100	2·2 ±0·4	
4	145 Barafundle	100	1·8 ±0·4	2·3±0·3
4	165 Little Haven	100	2·5 ±0·5	
4	169 Newport Sands	100	2·2 ±0·4	
4	320 Tenby	100	2·2 ±0·4	
4	321 Nolton Haven	100	3·0 ±0·5	
4–5	164 Martin's Haven	100	2·7 ±0·5	
4–5	166 Whitesands Bay	100	3·4 ±0·55	2·9±0·3
4–5	322 Porth Clais	100	2·8 ±0·5	
5	126 West Angle Bay	100	1·8 ±0·4	
5	134 Furznip	100	2·4 ±0·5	2·2±0·3
5	135 Furznip	100	2·4 ±0·5	
5–6	131 West Angle Bay	100	2·25±0·5	2·5±0·3
5–6	312 Watwick Bay	100	2·80±0·25	
6	133 Chapel Bay	100	2·5 ±0·5	
6	146 Stackpole Quay	100	2·6 ±0·55	
6	147 Stackpole Quay	100	2·6 ±0·5	
6	313 Gunkle	100	2·4 ±0·5	2·2±0·35
6	314 Slip Pier	100	1·85±0·5	
6	315 Point Wood	100	1·7 ±0·4	
6	316 Black Rock	100	1·9 ±0·45	
6	317 Angle Point	100	1·85±0·4	
6–7	140 Gelliswick	100	1·9 ±0·4	
6–7	142 Pennar	100	1·9 ±0·5	
6–7	143 Neyland	100	1·9 ±0·45	2·1±0·2
6–7	190 Solva	31	2·3 ±0·45	
6–7	323 St. Justinian's	100	2·4 ±0·6	
7	117 Cliff Cottages	100	1·4 ±0·3	
7	124 Sandy Haven	100	1·3 ±0·3	
7	125 Sandy Haven	100	1·25±0·3	1·5±0·2
7	168 Goodwick	100	2·1 ±0·5	
7	318 Angle Bay	80	1·35±0·4	
8	148 Lawrenny	100	1·6 ±0·4	

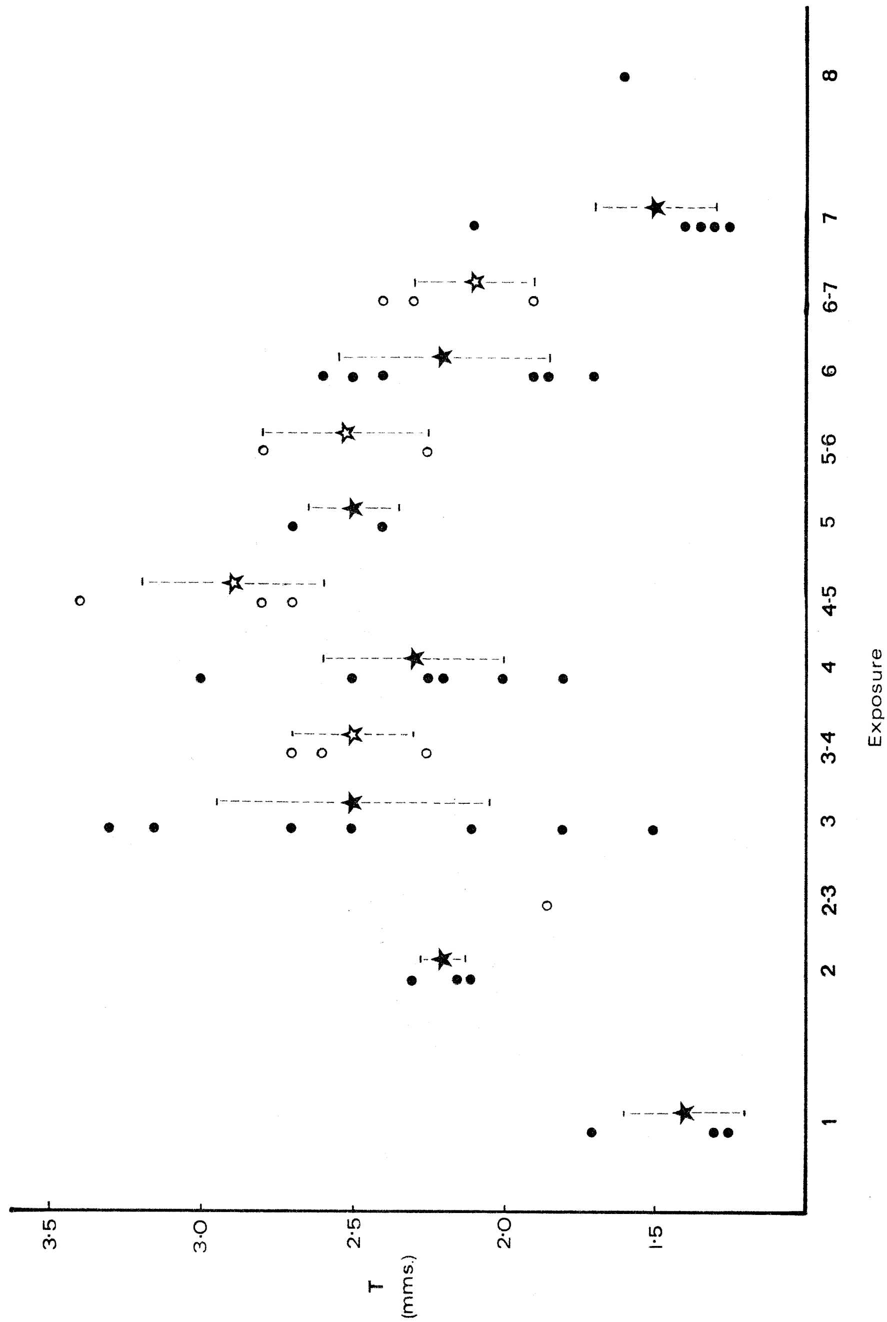

FIG. 5.

The relationship between shell thickness (T) and exposure for Pembrokeshire samples of *Nucella lapillus*. Samples from exposure grades and intergrades are represented by closed and open symbols respectively and the stars indicate the mean value for samples of that exposure. It should be remembered that the intercepts between exposure grades are not necessarily equal. Data from Table 3.

are that much more likely to be dislodged by the waves (and thus swept away from their food supply) than those in shelter. The pattern cannot be explained simply by availability of food for both mussels and barnacles are most abundant on exposed shores.

Starvation can be caused by other factors as well so that unexpectedly high

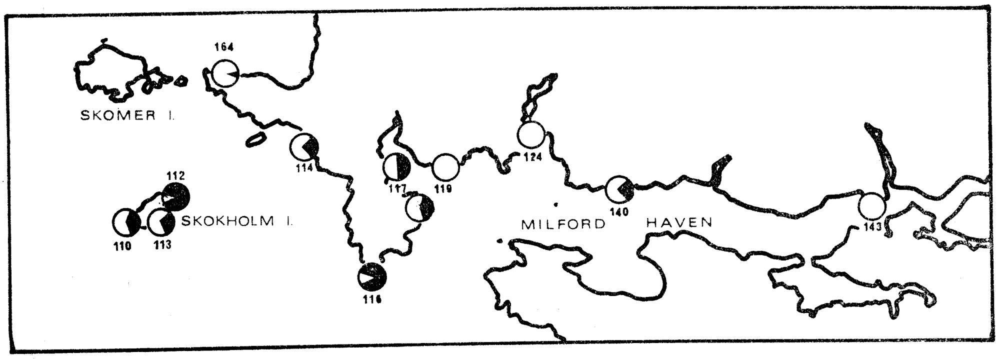

FIG. 6.
The intensity of stabilizing selection by wave action on *Nucella lapillus* near Dale: Pembrokeshire. The black portion of each circle represents the decrease of variance with age (and hence the intensity of selection) of a convenient shell character. The small figures identify the samples. (After Berry (1971) on data from Berry and Crothers (1968).)

numbers of shells show additional rows of "teeth" in some areas. One such factor is low winter temperature which can prevent feeding (Largen, 1967a; Feare, 1970a, 1971) and this may explain the data from the North Sea (Crothers, 1971) but locally pollution can be more important as may be the case at Polkerris (Cornwall).

Collections from Little Haven and further south in the County do in general conform to the expected pattern for south-west England (Fig. 7) but those from Nolton Haven and further north give substantially higher values. The discontinuity between these two sites in St. Bride's Bay compares with those others in Lynmouth Bay, Carmarthen Bay and Lyme Bay described by Crothers (1971) but as yet unexplained.

Despite these interesting anomalies, it is clear that young *Nucella* are much more likely to suffer starvation on exposed shores than in shelter and that there is considerable evidence that wave action itself is affecting the maintenance of the short squat shell form on the more exposed sites.

Shell Thickness

The pattern of variation shown for this character is more complicated than that of length or shape. If all the data are considered together the thickest samples are seen to occur on shores of intermediate exposure which agrees with the situation near Roscoff (Brittany) (Staiger, 1954; 1957 in English), where *Nucella lapillus* shows chromosomal polymorphism between n = 13 and n = 18. There is no difference in the amount of chromosomal material present so that the two forms are fully interfertile and individuals may be found with any of the possible diploid combinations between 26 and 36. The haploid set of form 13 contains 5 metacentric chromosomes, each of which corresponds to two non-homologous chromosomes in form 18, so that the two sets are really $n = 8 + 5$ in form 13 and $n = 8 + (5 \times 2)$ in form 18.

Near Roscoff the cytodeme homozygous n = 13 occupies exposed situations and cytodeme n = 18 sheltered ones. Intermediate sites are occupied by heterozygous cytodemes showing continuous variation (within and between topodemes) in chromosome number. The homozygous forms have thin light shells whilst the heterozygous shells are thick and heavy. (Staiger did not measure thickness directly but estimated it from a combination of weight and linear measurements.)

This particular situation may not be generally true. Staiger (1957) could find only the n = 13 form east of the Baie de Morlaix in Brittany, which is also the case in Norway (Hoxmark, 1970) and on the Atlantic coast of America (Mayr, 1963). Current research in this Country (Dr. C. R. Bantock, personal communication) has shown that the n = 13 form predominates in many areas, though in others both are present. No information is available for Pembrokeshire at present.

It may be misleading to lump all the thickness data together, for in some areas a different pattern is seen. In the north-west of the County thickness is related directly to exposure, which is as Staiger (1957) described when only the n = 13 form was present. But elsewhere the data conform to Staiger's description where both forms and the intermediates were found.

Chromosomal data for Pembrokeshire topodemes is urgently required and without it no further conclusions can be drawn. It should be noted also that whilst my data do fit closely with Staiger's in relation to thickness the two sets do not agree in respect of length. He found the longest shells at the extremes of exposure and the shortest ones in the middle.

Shell Ornament

Colton (1922) wrote that "The shell surface may be smooth or it may have 10 distinct ridges. In some cases alternate ridges become reduced or obliterated, giving the shell six distinct ridges. The most striking variation of all is one called *imbricata* in which the ten ridges become fluted. Experience seems to show that all these varieties grade one into another." Most Pembrokeshire *Nucella* are ridged but the six-ridged form has only been noted at Amroth and the 10 primary ridges may have secondary ridges between them giving a total between 10 and 16. The only smooth shells I have seen in the County had clearly been abraded or corroded by environmental conditions. The variety *imbricata* is widespread but not common. Usually shells which appear to have been imbricated when young have lost the fluting on later whorls. Largen (1971) is convinced that this is always due to abrasion of the body whorl.

Colour

Most Pembrokeshire *Nucella* are white or yellow but dark-coloured shells can be found at some localities. Non-white shells may be self-coloured—that is the colour is uniformly distributed—or there may be coloured bands on a white background. A wide banded form, usually with three darker bands, is easily recognized but is much less common than a narrow-banded one in which the ridges on the shell surface are white and the pigment confined to the hollows. In other parts of the country the banding may be superimposed on a (differently) coloured base colour but I have not noticed this in Pembrokeshire.

Some shells show a combination of wide and narrow bands so that the broad bands are represented by three or four narrow stripes. In a few shells the banding is seen only on the inside, the outside surface being white.

Moore (1936) related colours to food supply, showing that purple pigment comes from mussels. Animals feeding on mussels would be pigmented and those feeding on

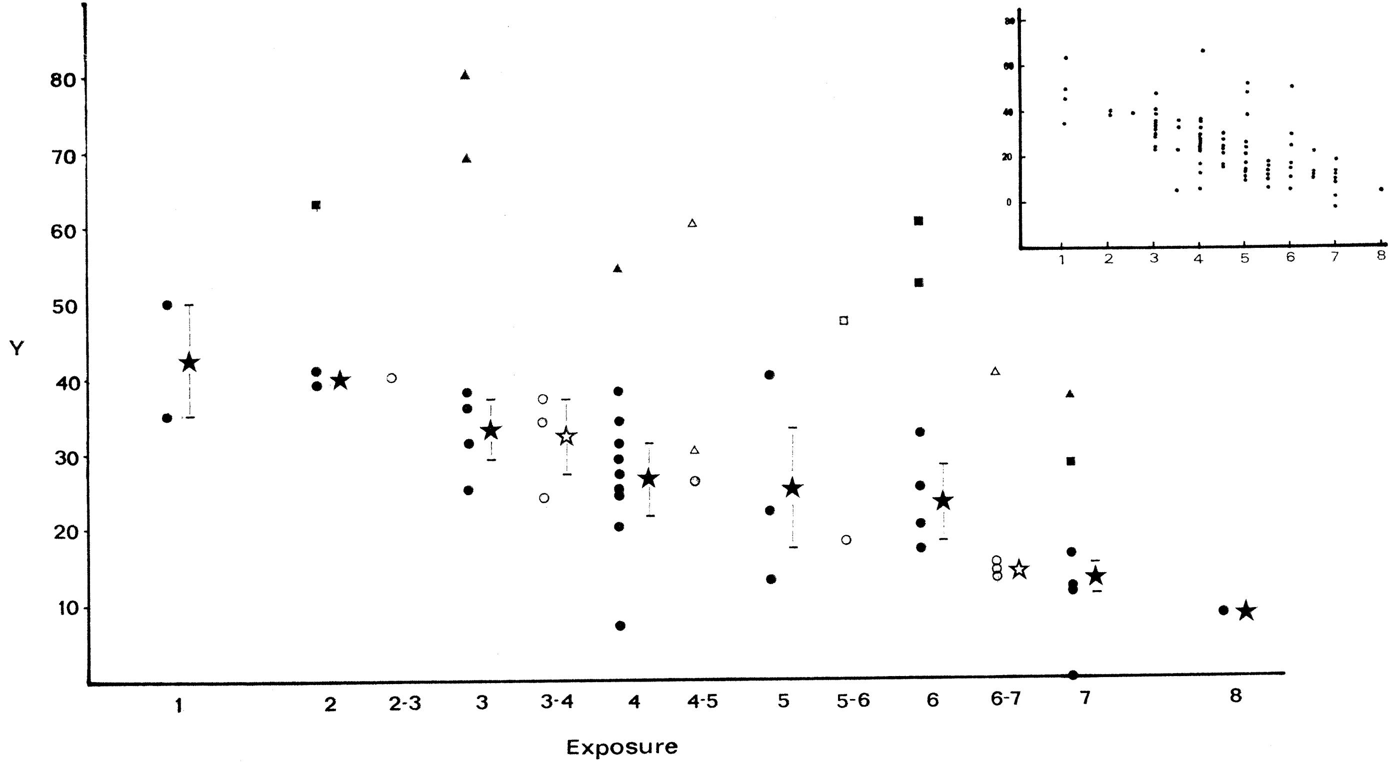

Fig. 7.

The relationship between juvenile starvation, as indicated by the formation of "teeth" by immature *Nucella lapillus*, and exposure for Pembrokeshire samples compared with (inset) the pattern for south-western Britain as a whole (Crothers, 1971). Starvation (Y) is assessed by the percentage of "toothed" individuals which show obvious signs of "tooth" formation as juveniles

Samples from exposure grades and intergrades are represented by closed and open circles respectively. Shells from North Pembrokeshire are more likely to show signs of starvation than others collected from the southern part of the County (Crothers, 1971) and are shown by triangles. They have not been used to obtain the mean values for the various exposure grades (indicated by stars) and nor have the surprisingly high figures relating to some Milford Haven samples (indicated by squares) collected in 1971.

It should be remembered that the intercepts between exposure grades are not necessarily equal.

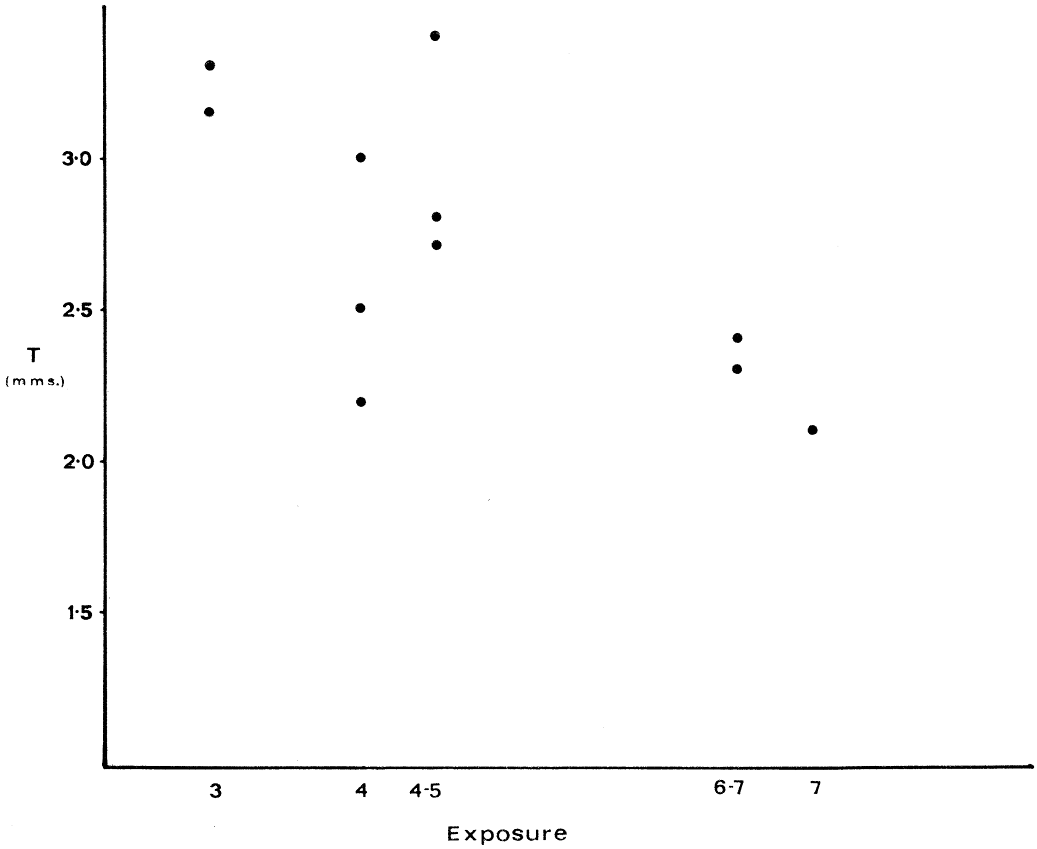

Fig. 8.

The relationship between shell thickness (T) and exposure in samples of *Nucella lapillus* from St. Brides Bay and Cardigan Bay. It should be remembered that the intercepts between the exposure grades are not necessarily equal.

barnacles white. (Yellow coloration is not apparently related to food.) This explanation appears to fit field observations in Cornwall (where Moore collected many of his samples) and in some other places but in much of Britain coloured shells are scarce even in topodemes that regularly feed on mussels. This might be accounted for if it is assumed that the expression of purple pigment in the shell is controlled by three groups of genes. One set would control the uptake of the pigment and its deposition in the shell; another would control the intensity, and hence the colour observed; whilst a third would control any banding. Clearly the first set would be critical, for unless the animal is able to take up and deposit pigment in its shell the other two cannot find expression. We may postulate that this critical set is widespread in the Cornish caenogamodeme(s) but very scarce in Pembrokeshire. *Mytilus* is generally distributed but abundant at only a few sites (Crothers, 1966) so that the incidence of individuals which carry the requisite set of genes feeding regularly on mussels (and hence the incidence of purple coloured *Nucella*) is low. Most coloured shells are banded, so perhaps the genes for this character are widespread.

Even this explanation cannot be the whole story for I have raised the progeny of coloured parents from egg capsules laid in the laboratory on a diet of only barnacles, and many were coloured. But before Moore's explanation is entirely discredited it must be emphasized that coloured *Nucella* shells are only common in areas of mussels.

The occurrence of coloured individuals in the field is affected by extrinsic factors in addition to the presumed genetic ones. Not only does the human observer notice conspicuous individuals more than others but birds probably do so too. Selection for protective patterns (crypsis) is thus expected but has not yet been demonstrated for this species. The extreme crypsis of certain colour patterns amongst dense mussel patches is very striking. However, there is little evidence that avian predation is critical in Pembrokeshire and all topodemes sampled contain numbers of very conspicuous shells.

Berry and Crothers (1974) review colour variation in *Nucella* throughout the British Isles.

Summary

1. *Nucella lapillus* exists in innumerable distinct topodemes around the shores of Pembrokeshire. The very limited dispersion of individuals suggests that each topodeme may be a discrete breeding unit and should properly be considered a gamodeme.
2. Pembrokeshire gamodemes show continuous variation in the length (height) of full-sized shells correlated with the exposure of the site to wave action so that the mean length of 100 shells decreases with increasing exposure.
3. Pembrokeshire gamodemes show a related variation in shape. A short squat form is typical of exposed situations and a more elongated variety in shelter.
4. This variation in shell size and shape is, in part, maintained by the selective effect of wave action on exposed shores where the short squat type is less likely to be dislodged. The incidence of juvenile starvation, as indicated by the occurrence of "teeth", accords with this view.
5. There is little variation between Pembrokeshire gamodemes in colour or ornament and all are thought to be genetically similar in this respect. The apparent differences arise from the abrasion of the ornamentation on exposed shores and/or the colonization of the shell surface by various algae and lichens.
6. Individual gamodemes can exhibit characters not seen in others; for example, the occurrence of reduced or absent opercula at Amroth and Lydstep Haven.
7. Pembrokeshire gamodemes do not show a simple pattern of variation in shell thickness. Area effects occur. Shell thickness is thought to be influenced by chromosomal polymorphism in this species and a comparison is mooted between the situation in Pembrokeshire and that in Brittany where the chromosomal pattern is known.
8. The Pembrokeshire gamodemes could either be considered as forming several caenogamodemes on the basis of shell thickness (each containing a closely similar genetic constitution with respect to size, shape, colour and ornament) or as one caenogamodeme encompassing a considerable range of variation in thickness. I favour the latter explanation.

9. The observed variation in *Nucella lapillus* is a complex of genotypic and phenotypic factors. Some of the more easily studied patterns of variation seen around the Pembrokeshire coast are described in a manner to facilitate comparison with the situation encountered in other parts of Europe, a first step in the identification of caenogamodemes.

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