THE GROWTH AND DISTRIBUTION OF *MONODONTA LINEATA* (da Costa) ON A ROCKY SHORE IN WALES

By EDWARD E. WILLIAMS

*University College of Wales, Aberystwyth**

Monodonta lineata (da Costa) is a southern form and the north coast of Ireland represents the limit of its distribution in the British Isles.

McMillan (1944) describes the species as having a west and south-west range in the British Isles as a whole and Southward and Crisp (1964) in their investigations in Ireland found it predominantly on the south and west coasts. Jeffreys (1865) gives its extra European locality as West Africa. It occurs throughout Wales and is reported as abundant along the Gower coast (McMillan, 1944), at Dale in Pembrokeshire, (Moyse and Nelson-Smith, 1963), and is found as far north as Anglesey (Lewis, 1953). Its distribution in the Aberystwyth area of Cardigan Bay has been studied by Walton (1915), and more recently by Evans (1947). Both reported that its distribution in this region is local.

M. lineata prefers rather sheltered shores with large areas of rock, bound boulders and many gulleys, but with a minimum of sand and loose shingle. Preference for this kind of shore has been noted by Evans (1947), Southward (1954) and Moyse and Nelson-Smith (1963).

Since no worker so far has dealt with the dynamics of a *M. lineata* population, it was decided to select a suitable population and study the detailed structure and any variations, seasonal or otherwise, which may occur over a period of at least 12 months. At the same time the breeding cycle and zonation on the beach was to be investigated.

The site and sampling methods

The area selected for the survey is some two-thirds of a mile (1·1 km.) south of Borth and lies beneath the 200 ft. (66 m.) high rocky headland Craig-yr-Wylfa (Map Ref. SW (22) 600886). In addition to a population of *M. lineata*, the beach also supported populations of *Littorina littorea* (L)., *L. saxatilis* (Olivi), and *Gibbula umbilicalis* (da Costa).

The top part of the shore consists of an unstable steeply shelving region of loose shingle extending some 30–35 feet (10–11 m.) from the base of the cliffs down to M.T.L. (Mean Tide Level). *M. lineata* was invariably absent from this region which was therefore excluded from the survey. The remainder of the beach consists of gradually shelving flat slabs of solid rock running some 250–260 feet (82–85 m.) down to E.L.W.S. (Extreme Low Water Spring tides).

The beach as a whole faces south-west which is the direction of the prevailing

* Present address: Department of Zoology, The University, Sheffield.

wind and wave action. The extreme paucity of algal growth indicates at least a moderately high factor of exposure to wave action. *Fucus spiralis* is one of the most abundant species of fucoids and even this is limited to a few sparse tufts on the upper regions of the shore immediately below the unstable shingle beach.

Eleven 1 sq. m. stations were marked out from the top of the rocky zone, which was just below M.T.L., down to E.L.W.S. (Fig. 1). Each station was designed to be representative of the beach level on which it was located. Samples were taken at approximately monthly intervals on spring tides from May, 1961 to January, 1963. At each collection every specimen of *M. lineata* was taken from each of the 1 sq. m. stations. At all times of the year × 10 bench magnifiers were used on the beach to assist in the search for the young forms. In addition rock pools were drained and samples of rock removed to the laboratory in order that these small forms be located and adequately sampled.

During the period of the survey 4,574 specimens of *M. lineata* were taken on 22 collections, the average number per collection being 208.

TREATMENT OF SAMPLES

A linear measurement, shell width, was used as a growth indicator. Shells were measured using a sliding hand micrometer and allocated to 0·5 mm. size groups, e.g. shells whose width is given as 7 mm. include all those 6·75 mm. wide and over and less than 7·25 mm.

The data were analysed using arithmetical probability graph paper. This method enables the means of unequal and overlapping components of a population to be determined, Harding (1949) and Williams (1964).

ANALYSIS OF POPULATION STRUCTURE

Probability graphs showing population structure were constructed for each monthly sample. The population of *M. lineata* at Craig-yr-Wylfa had a polymodal frequency distribution and the component populations present in successive samples for the whole of the survey period are shown (Fig. 2).

As can be seen, two component populations were detected in the samples collected from May to July, 1961; population A with shell width means of 9–11 mm. and population B with means of 15·5–16·24 mm. In August, 1961 a third population, A^1, with a mean of 2·74 mm. representing the young brood, appeared. Instead of now having three populations, however, only two were apparent, the new one with a mean of 2·74 mm. and a second with a mean of 16 mm. representing the original two populations. As can be seen the merging of these was not a gradual process.

From a study of the growth of population A^1 (Fig. 2) population A is considered to represent the survivors of the 1960 settlement. Though the number of animals in population A is very low, owing probably to a relatively poor settlement in 1960, they represent a considerably percentage of the total population prior to the settlement of the 1961 brood. The latter, population A^1, was first collected on 11 August, 1961. This was a good settlement and the numbers were such that component A was difficult to detect if the entire population was analysed as a whole. The size of the animals in population A^1 is such, however, that they form an easily recognizable component which can

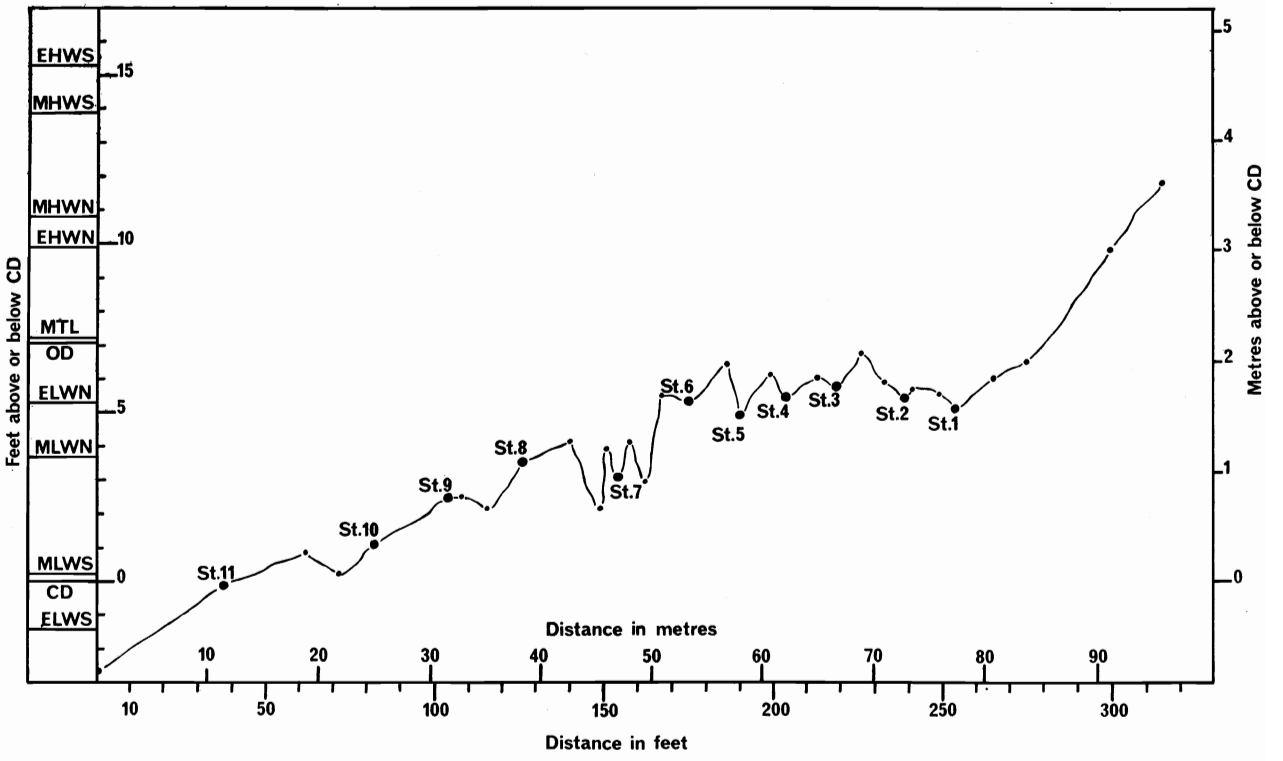

FIG. 1.

Section of shore at Craig-yr-Wylfa showing the 1 sq. m. stations from which *M. lineata* was collected from May, 1961 to January, 1963.

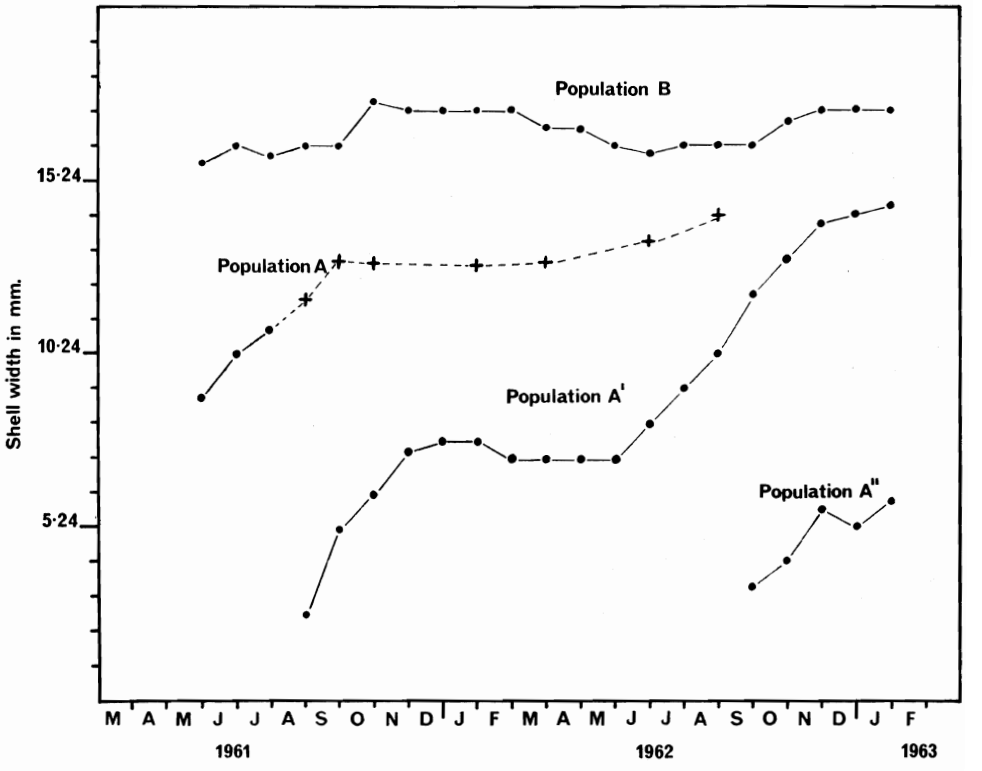

FIG. 2.

Growth curves showing component populations present in successive samples of the *M. lineata* population at Craig-yr-Wylfa, from May, 1961 to January, 1963. The method of analysis is described in the text.

be readily separated from the total population until August, 1962. Beyond this date the population, i.e. A^{I}, begins to overlap and merge with population A. Between August, 1961 and August, 1962 it is therefore possible to examine the growth of population A by removing population A^{I} from any sample and analysing the remainder in the usual way. The growth of this component is shown by the dotted line (Fig. 2). Although the relatively small population A was largely obscured by the settlement of A^{I} in August, 1961 this effect was not repeated in August, 1962. When at this time the total population was analysed, A^{I} could readily be detected even in the presence of the new settlement, i.e. population A^{II}.

As can be seen (Fig. 2), the growth of young forms (population A^{I}) is very rapid, increasing from 2·74 mm. on 11 August, 1961 to 7·54 mm. on 10 November, 1961, i.e. more than 4·5 mm. in three months. Initially growth must have

been even faster since no representatives of the young brood were taken intertidally in the sample obtained on 16 July, 1961, yet on 11 August, 1961 they are represented by a population with a mean shell width of 2·74 cm. No reference is made in the literature to the size of *M. lineata* immediately following settlement, however the smallest specimens found during the present survey had shell widths of only 1 mm.

As is shown (Fig. 2), growth in these small forms, population A, is halted during the winter months and the reason for this is thought to be reduced feeding activity due to low temperatures. The cessation of growth during the winter of 1961/62 cannot be correlated with an increase in sexual activity since during this period population A^1 is represented by animals with a mean shell width of 7–7·5 mm. only, and a breeding cycle survey indicated that animals smaller than 11–11·5 mm. do not mature at the appropriate time of the year. At the end of May growth recommenced and by August, 1962, at the end of their first year's growth, the animals comprising population A^1 had a mean of 10·24 mm.

Population A^1 continued to grow throughout 1962, albeit at a much reduced rate, and by December had a mean shell width of 14·5 mm. Thereafter very little growth took place. This trend could not be properly evaluated, however, because the entire population of *M. lineata* at Craig-yr-Wylfa was wiped out by the extremely cold winter of 1962-63. Consider, however, the growth of population A (Fig. 2), detectable only when population A^1 was excluded from the samples. By August, 1962 this had a calculated mean shell width of 14·24 mm., and it is thought likely that at Craig-yr-Wylfa *M. lineata* attains a shell width of 14–14·5 mm. at the end of the second year. Above this size it is very difficult to detect year groups owing to the relatively small numbers of animals in the larger size groups. However, population B (Fig. 2) is considered to represent individuals at least three years old.

Desai (1959), working at Criccieth in North Wales, describes size/age groups for *M. lineata*. He does not, however, describe the method of analysis used to establish them and as a result his findings cannot be compared with those of the present survey.

Whether the picture of the composition of the *M. lineata* population at Craig-yr-Wylfa is a true one is not certain in view of the relatively small number of specimens taken in the collections. For reasons given the 1960 brood was considered a bad year; even in 1961 the numbers of small forms taken intertidally were relatively small and can only be considered barely sufficient to maintain the adult population. *M. lineata* is a southern form and even in the Aberystwyth area is close to its northernmost limit. A more detailed and accurate survey requires that a population much farther south, nearer the centre of the geographical distribution of the species, e.g. west coast of France, should be studied.

Breeding cycle

In a survey involving the estimation of the state of maturity of an animal it is essential that as many relevant factors as possible be considered in order to minimize error.

As a member of the Trochidae *M. lineata* shows no development of such specialized copulatory and accessary sexual structures as are found for example

in the Littorinidae, in which they can be used for the recognition of developmental stages (Williams, 1964a). The sexing of immature or partially mature specimens of *M. lineata* is often difficult; in order to do so the right kidney opening, lying in the mantle cavity, must be examined. In the female this opening is surrounded by large swollen lips but in the males the lips are much smaller and non-swollen (Randles, 1905; Fretter and Graham, 1962). When the animals are fully mature sexing presents no problem since the females contain large well developed oocytes.

Desai (1959) described a gonad index for *M. lineata* broadly based on one described by Orton *et al.* (1956) for *Patella vulgata* L. In both males and females Desai recognized five developmental and three spawning stages. A modification of this index was used in the present survey. The various developmental and spawning stages are described elsewhere (Williams, 1964b).

Preliminary investigations revealed that in the *M. lineata* population at Craig-yr-Wylfa animals smaller than 11–11·5 mm. do not mature at the appropriate time of the year, i.e. the animals do not mature until their second year. The present survey was based on a consideration of animals with a shell width of at least 11 mm. from all levels of the beach. To avoid unnecessary depletion of the population, samples of animals taken in the main collections were utilized. Animals were removed from their shells, examined in water under a binocular microscope and assigned to one of the developmental or spawning stages. During the survey, which lasted from 9 January, 1962 to 28 January, 1963, a total of 834 animals was examined. As can be seen (Table 1) the cycle in males and females is very similar.

In both sexes development started at the end of October (developmental stage 2), but it was some 10 months later, in the following August, that the first animals were considered capable of spawning, i.e. spawning stage 1. Spawning, though gradual, occupied a much shorter period of time, and both sexes were fully spent, spawning stage 3, by the beginning of October. The gonad remained inactive (developmental stage 1) for only a very short period of time. Only in October were all specimens considered to be at this stage, for by the beginning of the following November the animals had started to mature again. These results are comparable to those of Desai (1959) and correspond very closely with the breeding cycle in *G. umbilicalis* (Williams, 1964b). Because the gonad in *M. lineata* is active for most of the year, it seems probable that maturation has little effect on growth rate.

ZONATION

The vertical distribution of *M. lineata* has been described by several workers. Fleure and Gettings (1907) described it as occurring at "high tide level" in Cardigan Bay; Colman (1933), working at Wembury, found that it occupied a very narrow vertical range, from just below E.H.W.N. (Extreme High Water Neap tides) to just below M.H.W.N. (Mean High Water Neap tides), a range of some 2 feet (0·6 m.). Moore (1940), however, also working at Wembury, found the species over a much wider range, M.L.W.N.–M.H.W.N., a range of some 7 feet (2 m.).

Evans (1947), working at Aberystwyth, regarded it as being common at M.H.W.N. and occasionally as high as M.H.W.S. (Mean High Water Spring

tides), in localities where there is a lot of weed cover. Evans stated that the species is common down to M.T.L. (Mean Tide Level), and the furthest down the shore he collected specimens was 18 inches (0·5 m.) below M.L.W.N. At other localities in the area, however, E.L.W.N. (Extreme Low Water Neap tides) appeared to be the lower limit, and Evans concluded that the lower limit of *M. lineata* is generally variable. Southward and Crisp (1954), working in Ireland, record the "preferred tidal level" as M.T.L.–H.W.N., and Moyse and Nelson-Smith (1963), at Dale, give the vertical distribution as M.L.W.S. to just above M.H.W.N.

Owing to the presence of the unstable shingle beach just above station 1 (E.L.W.N.), which acts as a physical barrier, the *M. lineata* population at Craig-yr-Wylfa can be considered to be a mid or lower littoral one. The zonation of the population for the period of the survey is shown (Fig. 3). As can be seen the animals remain on the upper regions during the summer months moving down the beach as temperatures begin to fall in October and November. The coldest months of the year are spent on the lower regions where the animals are exposed for the shortest possible time. Desai (1959) records a similar seasonal vertical migration in a *M. lineata* population at Criccieth in North Wales.

As well as postulating that the migration is governed by temperature Desai also suggests that the movement up the shore is connected with spawning, animals moving up the beach to spawn. It is true that in the present survey movement up the beach coincides almost exactly with the spawning of the fully mature section of the population (Table 1). However, animals below 11–11·5 mm., i.e. immature, also migrate up the beach in the summer. It is thought likely, therefore, bearing in mind that *M. lineata* is a southern form, that the migration, both up and down the beach, is largely temperature-controlled. Moreover, this seasonal migration possibly explains the somewhat different vertical zones ascribed to the species by various authors.

SUMMARY

1. Monthly samples of *M. lineata* were collected from May, 1961 to January, 1963, from eleven 1 sq. m. stations along a transect line at Craig-yr-Wylfa, just south of Borth. In all 4,574 individuals were collected and measured.

2. Data obtained each month was analysed using arithmetical probability graph paper. The population was found to have a polymodal frequency distribution, the overall structure being dynamically maintained.

3. The various component populations had different growth rates resulting in shell widths of 10–10·5 mm. at one year, 14–14·5 mm. at two years, and over 14·5 mm. at three or more years.

4. Growth is reduced by low temperatures but appears to be little affected by maturation.

5. The animals showed a marked seasonal migration: down the beach in the winter and up again in the summer.

6. Animals mature for the first time at 11–11·5 mm. shell width.

7. In both sexes development of the gonad begins in late October and

Table 1. *The breeding cycle of* M. lineata *at Craig-yr-Wylfa based on analysis of specimens larger than 11 mm. shell width from all levels on the beach.* The number of animals in each stage is expressed as a percentage.

Developmental stages, 1 = inactive, 2 = beginning of maturation, 3 to 4 = progressive increase in gonadial tissue, 5 = fully mature. Spawning stages, 1 = fully mature and spawning, 2 = partially spent, 3 = fully spent (corresponding approximately to development stage 1).

Date	Females								Males							
	Breeding					Spawning			Breeding					Spawning		
	1	2	3	4	5	1	2	3	1	2	3	4	5	1	2	3
9 January, 1962 ..	2·2	62·2	—	—	—	—	—	—	4·4	31·1	—	—	—	—	—	—
8 February, 1962 ..	2·6	57·9	—	—	—	—	—	—	2·6	36·8	—	—	—	—	—	—
7 March, 1962 ..	—	65·8	—	—	—	—	—	—	13·1	21·0	—	—	—	—	—	—
6 April, 1962 ..	—	50·0	—	—	—	—	—	—	4·8	45·2	—	—	—	—	—	—
4 May 1962 ..	1·9	7·5	26·4	17·0	—	—	—	—	1·9	9·4	22·6	13·2	—	—	—	—
4 June, 1962 ..	—	—	1·7	18·6	42·4	—	—	—	—	—	—	5·1	30·0	—	1·7	—
1 July, 1962 ..	—	—	—	—	23·5	29·4	—	—	—	—	—	—	—	47·0	—	—
2 August, 1962 ..	—	—	—	—	—	6·2	14·6	27·1	—	—	—	—	—	12·5	31·2	8·3
30 August, 1962 ..	—	—	—	—	—	3·6	3·6	41·1	—	—	—	—	—	—	—	51·8
2 October, 1962 ..	51·72	—	—	—	—	—	—	—	48·3	—	—	—	—	—	—	—
30 October, 1962 ..	32·2	16·1	—	—	—	—	—	—	33·9	17·7	—	—	—	—	—	—
27 November, 1962	18·9	22·6	5·7	—	—	—	—	—	13·2	18·9	20·7	—	—	—	—	—
27 December, 1962	3·6	38·2	5·4	—	—	—	—	—	9·1	9·1	34·5	—	—	—	—	—
28 January, 1963 ..	—	38·7	16·1	—	—	—	—	—	3·2	12·9	12·9	12·9	—	—	—	—

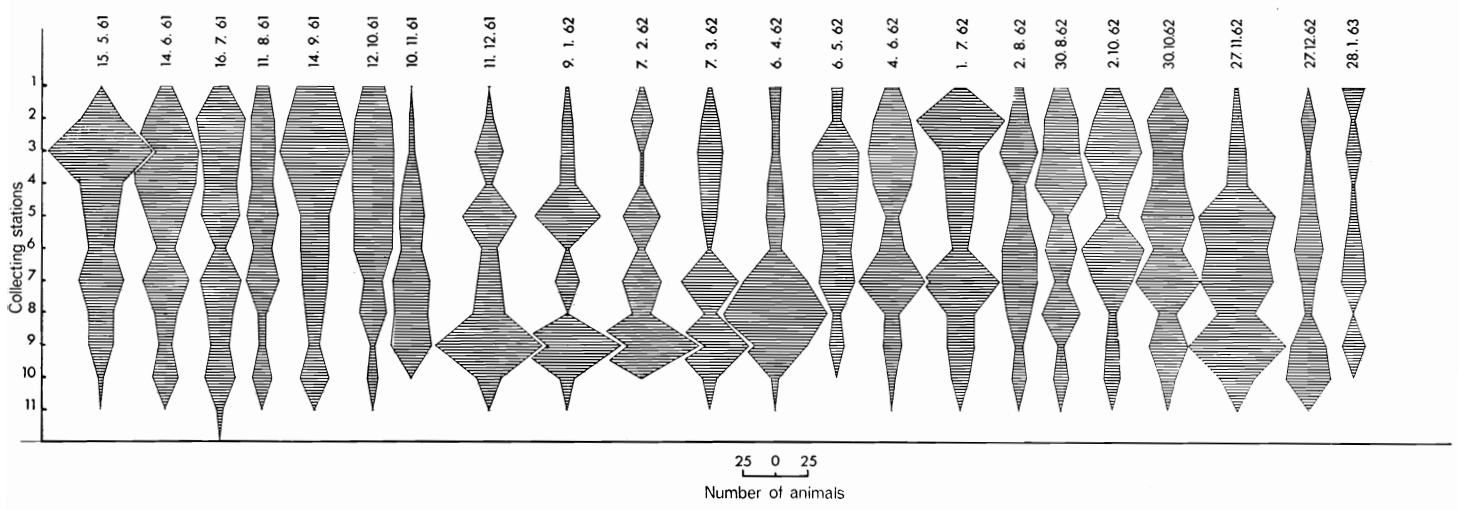

FIG. 3.

The overall zonational pattern of the *M. lineata* population at Craig-yr-Wylfa from May, 1961 to January, 1963.

proceeds gradually for some 10 months. Spawning begins in August and the animals are spent by early October, maturation beginning again in the following November.

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