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STUDENT INVESTIGATIONS ON THE POPULATION STRUCTURE OF THE COMMON TOPSHELL, *MONODONTA LINEATA*, ON THE GORE, SOMERSET.

J. H. CROTHERS
Field Studies Council at Nettlecombe Court, Williton, Taunton. Somerset TA4 4HT

ABSTRACT

Groups of students attending Ecology courses at Nettlecombe Court have aged and measured large samples of *Monodonta lineata* on the Gore, a boulder shore west of Porlock Weir on the Somerset coast. This paper analyses the data collected between February and April (before growth commences in May) every year from 1988 to 1994. From the marked reduction in growth rate, maturity is deduced to occur at a shell height of 16mm, as the animal approaches its third birthday. Mortality amongst the adult population averages 46% per annum, rising above 50% in individuals of 7 years and older. Maximum size (26mm) and age (12 years) are less than those seen further south and west in Britain.

When the study began, the Gore was considered to be the effective eastern limit of *M. lineata* in the Bristol Channel and it was hoped that information might be obtained that could explain that limit. However, all the available evidence suggests that *M. lineata* has extended its range eastwards along the Somerset coast by 20, or more, kilometres in the past 50 years and may be still advancing.

INTRODUCTION

Monodonta lineata

The common or toothed topshell, *Monodonta lineata* (da Costa, 1778),* is widely distributed along the Eastern Atlantic seaboard from Portugal northwards to southwest Britain (Poppe & Gotto, 1991). For general biology see Fretter & Graham (1962, 1976 and 1994), Williams (1965), for breeding cycle see Garwood & Kendal (1985) and for growth Williamson & Kendall (1981), Kendall (1987).

Within the British Isles, the most northerly populations are found in Ireland (Southward & Crisp, 1954) but, in mainland Britain, the northern limit is on Anglesey, whilst the eastern limits are in South Glamorgan and Somerset (Bristol Channel) and Dorset (English Channel) (Boyden, Crothers, Little & Mettam, 1977, Crisp & Southward, 1958, Hawthorne, 1965, Seaward, 1982), Fig. 1.

In north Spain (Bode, Lombas & Anadon, 1986), *M. lineata* grows throughout the year, although more slowly between December and March. There is a protracted

* Cesari (1986) regards the genus *Monodonta* (sensu lato) better described as the sub-family Monodontinae Cossmann, 1916 which he regards as composed of four genera: *Monodonta* (sensu stricto) Lamarck, 1799, from Papua New Guinea and Australia ; *Diloma* Philippi, 1845, from Japan and New Zealand ; *Austrocochlea* Fischer, 1855, from Australia ; and *Osilinus* Philippi 1847 from the Eastern Atlantic and the Mediterranean. He would call the species mentioned in this paper *Osilinus*. Vaught (1989), and most other authorities, consider all these 'genera' to be sub-genera of *Monodonta*. That is the view followed in this paper.

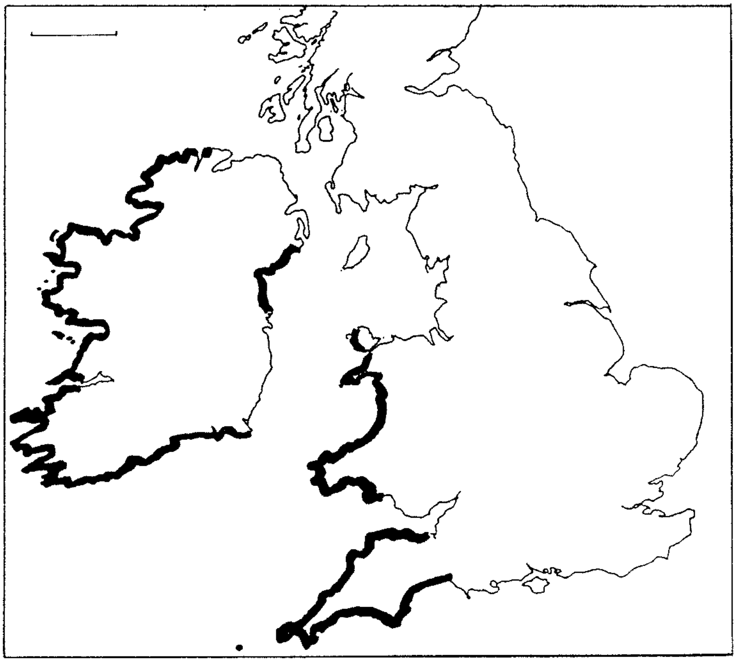


FIG 1
The distribution of *Monodonta lineata* around the British Isles. The scale line represents 100km. Based on a map in Lewis (1964)

breeding season from June to November; growth of juveniles is rapid and maturity is achieved by the time the snails reach 10mm. Length frequency plots show three distinct peaks and it would seem that few animals live more than four years.

Daguzan (1991), working in southern Brittany, wrote that winter growth was of little importance and that it was greatest in spring. There were two breeding seasons each year, the first from April to June and the second in September and October. Sexual maturity was reached after about one year when the 'big diameter' of the shell was 14.6mm. He concluded that the maximum life span was two and a half years.

In Britain, the growing season is greatly restricted and breeding is compressed into mid-summer (Lewis, 1986). At Aberaeron, mid-Wales, Garwood & Kendall (1985) reported spawning in late July and early August and found juvenile snails on the beach in mid September. Enclaves commonly include individual snails of 10-12 years old and exceptionally of 15-17 (Lewis, Bowman, Kendall & Williamson, 1982).

Adults rarely grow between November and May but the edge of the shell is frequently abraded and otherwise damaged, which means that a conspicuous line is left on the surface when growth resumes (Fig. 2). Although Fretter & Graham (1976) thought to the contrary, these conspicuous growth checks were demonstrated by Williamson & Kendall (1981) to be annual. Between May/June and December, a count of these checks indicates the number of winters the animal has survived: in spring, before the current year's growth has begun, the shell lip must be included in the count. As growth continues throughout life (Fretter & Graham, 1962, 1994), it is possible to

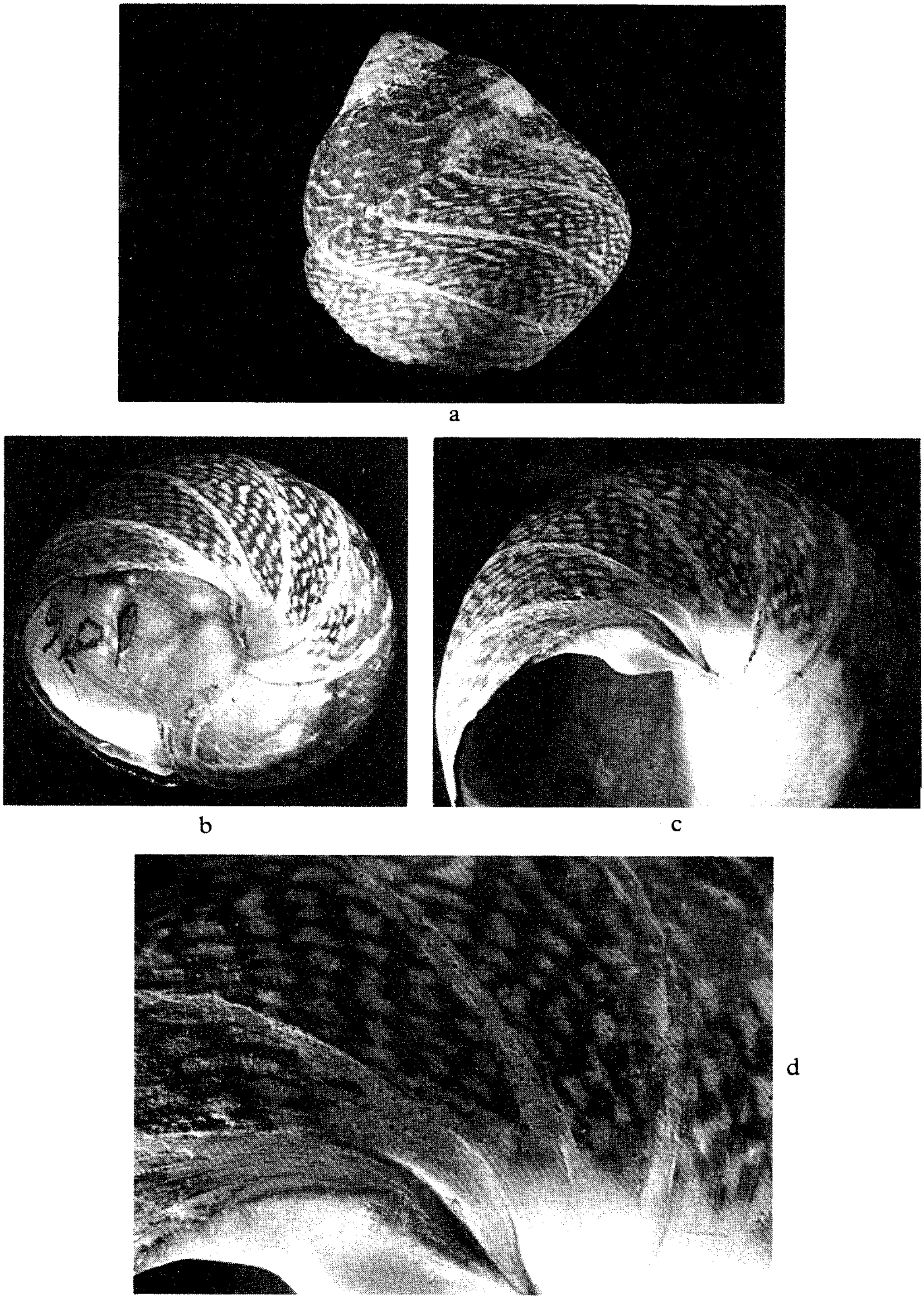


FIG. 2
Shells of *Monodonta lineata* showing growth checks. (c) and (d) are photographs of the same shell at different magnifications. From Little *et al.,* (1976).
The photographs were originally provided by Dr. M. A. Kendall

relate size to age in this species, which permits investigation of population structure, growth rates, mortality rates and longevity.

Limital Populations

In the presence of otherwise suitable habitats, the northern limit to a species' geographical distribution is primarily determined by abiotic factors directly or indirectly related to latitudinal gradients of temperature and light (Lewis *et al.*, 1982). Eastern ones are presumably due to temperature or to salinity, pollution or some other local factor.

Moving north, summer temperatures are generally lower and/or remain above any given value for a shorter period of time while winter temperatures become lower and/or remain below any given value for a longer period of time. Any of these features, acting alone or in consort, could prove to be the limiting factor. Moreover, different aspects may be limiting in different years.

If it is the survival of winter cold by adults which determines the distributional limit (in other words, if the species can breed successfully wherever it can live), a particularly severe winter will curtail the range whilst more benign ones will allow re-colonisation of the empty sites and further extension of the range. Outpost enclaves will be dominated by the younger age classes (Lewis *et al.,* 1982).

On the other hand, if it is some feature of the breeding system which limits the species range, outpost enclaves will probably have irregular age structures, missing age classes or a bias towards old individuals (Lewis *et al.,* 1982). Constraint to reproduction could be due to inadequate warmth for breeding in summer, or a disproportionate sensitivity of the juveniles to winter cold ; the effect would be the same.

Reviewing these alternatives, Lewis (1986) concluded that northern geographical limits are set, primarily, by repopulation failure and that northern populations are characterised by short, mid-summer breeding periods. However, no evidence has been found for inadequate gonadial development in northern *M. lineata* and it is assumed that, in this species, the period of settlement and early shore life is critical. Kendal (1987) mentions that adult *M. lineata* were successfully transplanted to the North Yorkshire coast, survived the 1978-1979 winter and spawned successfully the following summer.

The eastern limits of M. lineata *in Mainland Britain*

The cold winter of 1962-1963 eliminated various enclaves of *M. lineata* in south Wales, including all those east of the Gower (Crisp, 1964) but, although that area has still (1994) not been recolonised, it does not follow that winter cold is the only limiting factor. A similar situation occurred in the English Channel. Prior to that cold winter, Hawthorne (1965) had found scattered individuals or occasional year classes in Weymouth Bay and east to St. Alban's Head—and he quotes various authors who had described similar patterns in the past. By the autumn of 1963, the populations at Lyme Regis and eastward were extinct or reduced below a sustainable level. Lyme Regis had been recolonised by 1986 (Kendall, 1987) but no more of its former range has been recovered (D. R. Seaward, *personal communication,* May 1994).

On the Somerset coast of the Bristol Channel (Fig. 3), however, the situation is different. The easternmost site at which the species is truly common is the Gore, west of

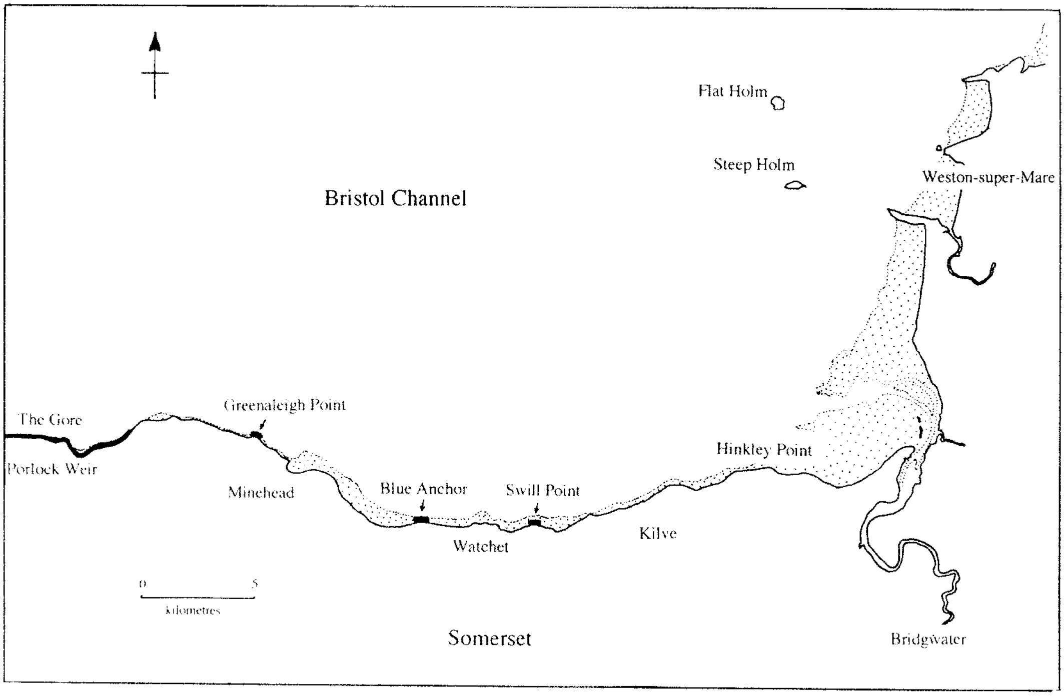


FIG 3
The distribution of *Monodonta lineata* in Somerset

Porlock Weir (British National Grid Reference SS 860486) although it spreads across Porlock Bay at a lower density. Porlock Weir was the only site at which Bassindale (1940, 1941, 1943) recorded the species (as *Osilinus lineatus*). Boyden *et al.*, (1977) noted isolated enclaves east of Porlock Bay on Greenaleigh Point (SS 955485), at Blue Anchor (ST 040438) [not noted here by Bassindale, 1940] and Watchet (ST 078436). The latter are probably of Porlock Weir origin, returned here by staff and students from Nettlecombe Court (for whom it is the nearest shore). No very young ones have ever been found at this site.

In 1990, an outlying enclave was discovered on Swill Point, Doniford (ST 095436), 2km east of Watchet. I have not found the species further up the Channel, although Bamber & Coughlan (1987), but not Martin (1994), list it from Hinkley Point (ST 2146).

The present paper

When this study began, in 1988, the Gore was considered to be at the effective eastern limit of *M. lineata* in the Bristol Channel. Although the population structure of enclaves close to the species' northern limit in Gwynedd and at its eastern limit in Dorset had been studied (Kendall, 1987), no information has been published about enclaves in the Bristol Channel. The nearest sites for which information was available are in Milford Haven (Little, Dicks & Crothers, 1986).

Most of the data presented here were collected by students attending ecology courses at The Leonard Wills Field Centre. The students, who were all on GCE A-level, first degree or university diploma courses, were (initially) inexperienced in finding, identifying, ageing and measuring topshells so that, undoubtedly, errors will have been made. To use the current jargon, these are 'noisy' data. However, I have demonstrated elsewhere (Crothers, 1991) that student data can, nevertheless, prove very useful for demonstrating unexpected patterns. Their saving grace lies in quantity; a great deal of information can be collected in a comparatively short time, and collections can be repeated through the seasons and the years. It is the normal practice to measure around 1,000 shells on each visit to the shore whereas Kendall (1987), for example, collected between 100 and 200.

Students attending ecology courses from The Leonard Wills Field Centre have regularly visited the Gore to investigate an apparently anomalous distribution of mussels (Wilson, Crothers & Oldham, 1983). It takes 30 or more minutes to set up that investigation, so some activity is required to occupy the class for that time. It is also necessary for the class to become proficient in finding and identifying the common shore snails at this site, and the collection of *M. lineata* provides a purpose for that activity. This remains a useful spin-off, and explains the reason for choosing the site, but the investigation of population structure in this topshell is now an integral component of the course. A summary of part of this work was given by Crothers (1993).

MATERIALS AND METHODS

The member of staff conducting the investigation demonstrates how to identify the animal and the size range to be expected. Then, the students spread out over the shore and each collects 50 living *M. lineata* without conscious bias for size. If the class numbers fewer than 20, the collecting target is increased to achieve the 1,000 target. In clement weather, the shells are aged and measured on site and the animals released immediately. On other occasions, measurement is carried out back at the Field Centre and the animals returned at low tide on the following day.

White plastic trays are laid out in a row and the students distribute their catches according to the number of 'conspicuous growth checks' they can see on the shell. Members of staff quickly check the trays, removing any winkles (*Littorina littorea*) and purple topshells (*Gibbula umbilicalis*) they see and suggesting a recount for any surprisingly large or small shells.

A group of students is allocated to each tray and they record the shell height (the maximum dimension of the shell including the apex), in mm, of every individual. A scribe in each group writes down the numbers from 1 to 27 (the size range applicable to this site) in a note book and ticks off each measurement as it is called out, using the '5-barred gate' notation. As the data usually adopt a normal distribution, anomalous shells are easily detected and their ages can be checked. Back in the laboratory, the class data are summarised on the blackboard and, later, entered into a computer.

It has been found that data recorded in this way are less 'noisy' than those obtained when the collecting groups age and measure their own shells. I have usually collected a small sample myself, whilst all this is going on, to establish in my own mind the current size/age relationship.

In practice, it is often very difficult to see the first growth check in all but the youngest animals and even then, if the previous winter was mild, growth may not have been interrupted for long enough to form one on all individuals. Students are, therefore, told to ignore any check near the apex of the shell and base their counts on the first 'conspicuous' check which marks the animal's second winter. The 'no growth check' category is, therefore, bimodal and data have been allocated to the two year classes concerned on a subjective assessment. After their second winter, every individual shows annual growth checks at this site—but they may show additional ones if their growth was further checked by predator attack, storm damage, or starvation during the growing season.

For an overview analysis, I grouped each year's student data by season. February-April is called spring; May-July, summer; and August-October, autumn. We have little or no data for the winter months. Inevitably, different numbers of topshells were measured in different seasons and in different years so all the data are here expressed as percentages. No serious attempt has been made to compare overall abundance from year to year but there is no reason to assume that it has changed.

Results

Shell height frequency analysis

It is immediately obvious that the spread of the data—both in shell height and in the number of growth checks—collected by classes of students (Table 2) is greater than that collected by one person (Table 1). This reflects not only the larger sample size but also the discrepancies inherent when many people are involved in measurement. However, the mean values so obtained may be much more reliable than those collected by any one individual because personal biases cancel out.

Students have collected similar data from the Gore on one or more occasions during the spring of every year from 1988 to 1994. Table 3 has been compiled to enable us to examine the fate of each successive year class or 'cohort'. Spring data are probably the best set to use for this comparison as it is presumed that none of the topshells are growing significantly during this season. Averaging data collected over a three-month span is, therefore, justifiable. Inevitably, more data were collected in some years than others and the results presented in Table 3 are expressed as percentages of the total measured in any particular year. No record of population density was kept although, as mentioned earlier, there is no reason to suppose that this has changed significantly. It would appear that another five years of data will be required before we can appreciate the first complete cycle of a cohort—that for 1988.

Coincidentally, 1988 is the year chosen for Table 4. A particularly rich set of data are available for that year. They have been grouped by season and scaled out of 5,000 (to avoid the decimal points that would have been essential had they been expressed as percentages).

Discussion

Population Structure

In both Tables 1 and 2, the 1993 cohort is poorly represented and that of 1991 the most significant. In a perfectly stable population, where recruitment, growth and mortality are constant, the youngest year class would be the most abundant because, whilst an animal may die at any age, it can only be born at age 0. Class discussion is initially centred on this point.

TABLE 1: *The relationship between shell height and age, as indicated by conspicuous growth checks, for* Monodonta lineata *collected on the Gore in early April 1994. Data collected by the author*

	Number of Growth Checks											
Shell Height (mm)	0	1	2	3	4	5	6	7	8	9	10	**Total**
1												
2												
3												
4	1											1
5	5											5
6	1											1
7	8											8
8	3											3
9	3	1										4
10		2										2
11		6										6
12		10										10
13		10										10
14		8	4									12
15		1	26									27
16			28	5								33
17			5	12	1							18
18				8	3							11
19				3	5	1						9
20					4	2	1					7
21						2						2
22							2	1			1	4
23								1	1		1	3
24												
25												
26												
27												
TOTALS	21	38	63	28	13	5	3	2	1	0	2	176
Apparent year of settlement	1993	1992	1991	1990	1989	1988	1987	1986	1985	1984	1983	

• Had the 1993 cohort been severely hit by some environmental catastrophe ? a severe storm, winter cold, summer heat, heavy rain etc. ? (Nobody can ever remember reading about a suitable event.).

• Were we simply inefficient at finding juveniles ? This is certainly a factor but I, aware of that possibility, concentrated my collection (Table 1) in an area where I knew juveniles could be found and still recorded fewer than would be expected from the model.

• Did most of the juveniles occupy a different area of the shore? and were, therefore, over-looked by our collection. Little *et al.*, (1987) found one population for which there was a distinct nursery area low on the shore from which the high shore adult population

TABLE 2: *The relationship between shell height and age, as indicated by conspicuous growth checks, for* Monodonta lineata *collected on the Gore in Spring 1994. Data collected by students attending courses at the Leonard Wills Field Centre. As explained in the text, students were told to ignore the, almost indistinguishable, first winter check on all shells and the bimodal "0" category was divided subjectively*

	Number of Growth Checks											
Shell Height (mm)	0	0	1	2	3	4	5	6	7	8	9	**Total**
1												
2												
3												
4	4											4
5	7											7
6	9											9
7	15											15
8	7											7
9	6	18										24
10	3	68										71
11		94										94
12		139	2									141
13		72	32	2								106
14		74	142	5								221
15		31	358	43								432
16		14	365	136	14							529
17		1	147	173	43							364
18			34	144	72	28	6	1				285
19			3	49	66	31	5					154
20				9	62	40	9	4	1			125
21				3	37	18	7	4	2		1	72
22					16	7	8	6	1	1	1	40
23					1	2	6	2	1	3	1	16
24							2	1	1			4
25							1					1
26												
27												
TOTALS	51	511	1083	564	311	126	44	18	6	4	3	2721
Apparent year of settlement	1993	1992	1991	1990	1989	1988	1987	1986	1985	1984	1983	

was, presumably, 'recruited' *. We have been unable to locate a comparable nursery on the Gore, but the juveniles might still be occupying a different habitat, possibly utilising narrow crevices.

The first interpretation can be rapidly eliminated, for the same pattern is displayed in all years for which I have kept the data (Table 3). In each year of sampling, the best-

* Recruitment. Strictly speaking, recruitment to the *Monodonta* population, at any particular location, occurs when the young snails settle from the plankton. That cohort of animals is most abundant immediately after settlement is completed. Thereafter their numbers can only decline. However, I have used the term, in parentheses, to refer to the continued appearance of additional juveniles in the samples measured.

TABLE 3: *The springtime data, collected between 1988 and 1994, regarding the age-distribution of the* Monodonta lineata *population on The Gore. The total number of shells measured varied from year to year so the data are expressed as percentages (row by row)*

	Year of Settlement=Cohort																		
	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	Total
Year of Measurement																			
1988	0.1	0.1	0.6	2.3	4.0	8.8	16.6	26.0	22.8	17.3	1.5								100.0
1989	0.1	0.2	0.9	1.6	3.3	5.7	9.6	15.0	13.1	15.6	31.3	3.6							99.0
1990				0.4	1.5	2.4	4.8	9.8	9.4	17.9	19.1	30.0	4.9						100.0
1991		0.3	0.5	0.4	0.8	2.0	2.8	4.0	7.4	10.1	14.1	32.8	17.1	7.7					100.0
1992			0.2		0.3	0.5	1.5	3.0	5.5	6.3	13.5	21.6	27.6	19.0	0.9				100.0
1993				0.1		9.2	0.5	0.9	2.1	2.1	5.0	13.2	19.1	27.5	28.6	0.6			100.0
1994							0.1	0.1	0.2	0.7	1.6	4.6	11.4	20.7	39.8	18.8	1.9		100.0
Totals	0	1	2	5	10	20	36	59	61	70	86	106	80	75	69	19	2	0	

TABLE 4: *Student data for size and age of* Monodonta lineata *collected on The Gore in 1988. The data sets were divided into Spring (February—April), Summer (May—July) and Autumn (August-October) measurements. Spring and summer sets totalled nearly 5000 measurements, autumn a little over 3,000. Expressed as percentages, the largest number is 8 and much detail is lost, so all three seasons are expressed as though 5,000 had been measured. Spring totals are underlined for easy comparison with Table 3. Modal values for each cohort are in heavy type. Cohorts prior to 1981 are not shown.*

Shell Height (mm)	1988	1987 Cohort			1986 Cohort			1985 Cohort			1984 Cohort			1983 Cohort			1982 Cohort			1981 Cohort		
	Autumn	Spring	Summer	Autumn	Spring	Summer	Autumn	Spring	Summer	Autumn	Spring	Summer	Autumn	Spring	Summer	Autumn	Spring	Summer	Autumn	Spring	Summer	Autumn
1																						
2																						
3		1																				
4	4	5	6																			
5	4	7	36																			
6	7	17	63																			
7	4	15	88	18																		
8		14	113	22																		
9		10	78	62																		
10			28	187	15		7															
11			2	213	61	44	7															
12				363	117	113	11															
13				473	183	211	18															
14				337	220	237	59	41	47	29												
15				158	129	145	162	77	71	154	36		40									
16				11	71	113	190	253	306	154	176	135	77	44		29						
17				7	67	79	151	386	407	220	325	308	176	113	84	40	19		44			
18							18	246	306	103	351	335	238	180	199	139	50	57	26	10	27	11
19								64	95	26	229	255	150	197	217	238	72	65	70	30	31	22
20								43	27		104	97	18	133	107	99	131	68	81	41	40	18
21									6		58	28	15	89	45	15	69	55	55	55	34	44
22											9	8		40	11	4	53	19	22	35	27	11
23											10	1		23	1		28	10	11	19	8	7
24														11			17	3	4	11		4
25																		1				
26																						
Total	18	73	410	1851	863	942	624	1140	1265	685	1299	1167	715	830	664	565	438	279	312	201	166	117

represented year class is usually that in its second or third year but once, 1988, it was the fourth (read Table 3 from right to left for this purpose). The same is true for individual cohorts: the 1987 group was most significant in 1989 measurements, 1988 snails in 1991 measurements, 1989 in 1992, 1990 in 1993 and so on.

A particularly large set of data was taken in 1988. In both spring and summer, of that year, nearly 5000 shells were measured and so the data in Table 4 are presented as though 5000 had been measured in each season. Had they been expressed as percentages, the detail would have been lost amidst a plethora of decimals. In spring, the 1987 cohort (modal height 6mm) represented less than 2% of the seasonal total. During the summer, the modal height increased to 8mm and more individuals were measured—7.5% of the seasonal total. Autumn courses gave 13mm and 31% respectively. The data thus demonstrate the 'recruitment' of juveniles into the measured population. Doubtless, they became increasingly conspicuous—but whether this was due mainly to sampling 'error' earlier in the year or to a change in the animals' distribution or behaviour as the season progressed, remains to be discovered.

It *is,* however, clear from Table 4 that young animals grow much more rapidly than do their elders. This observation forms the second point for class discussion. The 1988 cohort had reached a modal shell height of 6mm by the autumn of that year (the data include November measurements). The 1987 cohort gave modal values of 6mm in spring, 8mm in summer and 13mm in autumn. That of 1986 gave values of 14mm, 14mm and 17mm and all subsequent years showed increases of 1mm or less. In other words, the new settlers reached 6mm by their first autumn, and their predecessors grew from 6mm to 14mm in their second summer. After that, growth was significantly curtailed with third-year snails only growing 3mm and all subsequent year classes increasing by 1mm or less.

- Why does the growth rate decrease so abruptly in the third year ?

Because the animals reach sexual maturity at that time. This agrees with the data of Garwood & Kendall (1985) who found that all animals breeding for the first time showed two growth checks—i.e., they had survived two winters. Molluscs in general can only grow when (if) they can devote most of their energy to shell production (Vermeij, 1993). A juvenile animal may commit all its excess energy, not required for simply staying alive, to growth, whereas an adult expends most of this energy on reproduction and will only commence growth once it has recuperated from spawning. Close to their northern limit, adult *M. lineata* have little time for growth before the onset of winter cold.

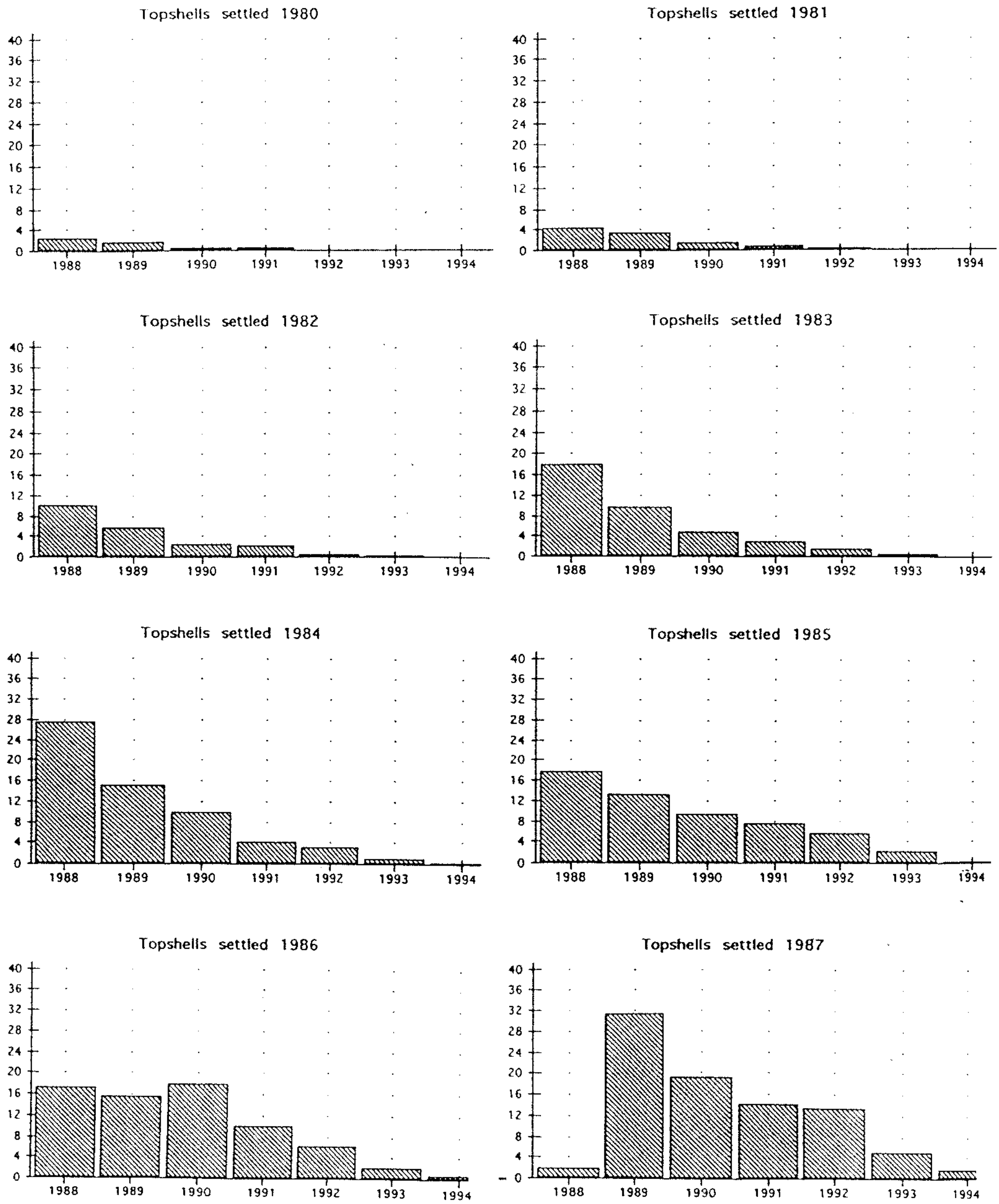
- What is the life expectancy of an adult *M. lineata* ?

Perusal of the spring 1994 data (Table 2) shows that 1083 of the individuals measured probably settled from the plankton in 1991, whilst there were only 564 remaining of those that settled in 1990. Assuming a stable population size (unfortunately, no detailed records have been kept of the abundance of *M. lineata* from year to year on the Gore but, subjectively, this has not noticeably changed), these figures suggest a 48% mortality of the 1990 cohort between 1993 and 1994. Similar assessment of older year classes suggest, sequentially, 45%, 59%, 65%, 59%, and 67% year-on-year mortality for the cohorts with a reasonable number of measurements, which average out

FIG. 4
Mortality of adult *M. lineata* on the Gore.

TABLE 5: *The data from Table 3 re-tabulated to compare each spring's measurements by age for calculation of mortality rates.*

Year of Measurement	Age Class 0+	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	11+	12+
1988	1.5	17.3	22.8	26.0	16.6	8.8	4.0	2.3	0.6	0.1	0.1	0.0	0.0
1989	3.6	31.3	15.6	13.1	15.0	9.6	5.7	3.3	1.6	0.9	0.2	0.1	0.0
1990	4.9	30.0	19.1	17.9	9.4	9.8	4.8	2.4	1.5	0.4	0.0	0.0	0.0
1991	7.7	17.1	32.8	14.1	10.1	7.4	4.0	2.8	2.0	0.8	0.4	0.5	0.3
1992	0.9	19.0	27.6	21.6	13.5	6.3	5.5	3.0	1.5	0.5	0.3	0.0	0.1
1993	0.6	28.6	27.5	19.1	13.2	5.0	2.1	2.1	0.9	0.5	0.2	0.0	0.1
1994	1.9	18.8	39.8	20.7	11.4	4.6	1.6	0.7	0.2	0.1	0.1	0.0	0.0
Mean	3.0	23.2	26.5	18.9	12.7	7.4	4.0	2.4	1.2	0.5	0.2	0.1	0.1
Age class on age class reduction				7.5	6.2	5.4	3.4	1.6	1.2	0.7	0.3	0.1	0.0
Percentage Mortality				28.5	32.7	42.3	46.2	40.1	50.0	60.2	60.6	53.8	0
Mean percentage mortality (2+ to 11+ classes) =								46.0					


Topshells settled 1980
Topshells settled 1981
Topshells settled 1982
Topshells settled 1983
Topshells settled 1984
Topshells settled 1985
Topshells settled 1986
Topshells settled 1987
0 4 8 12 16 20 24 28 32 36 40
1988 1989 1990 1991 1992 1993 1994

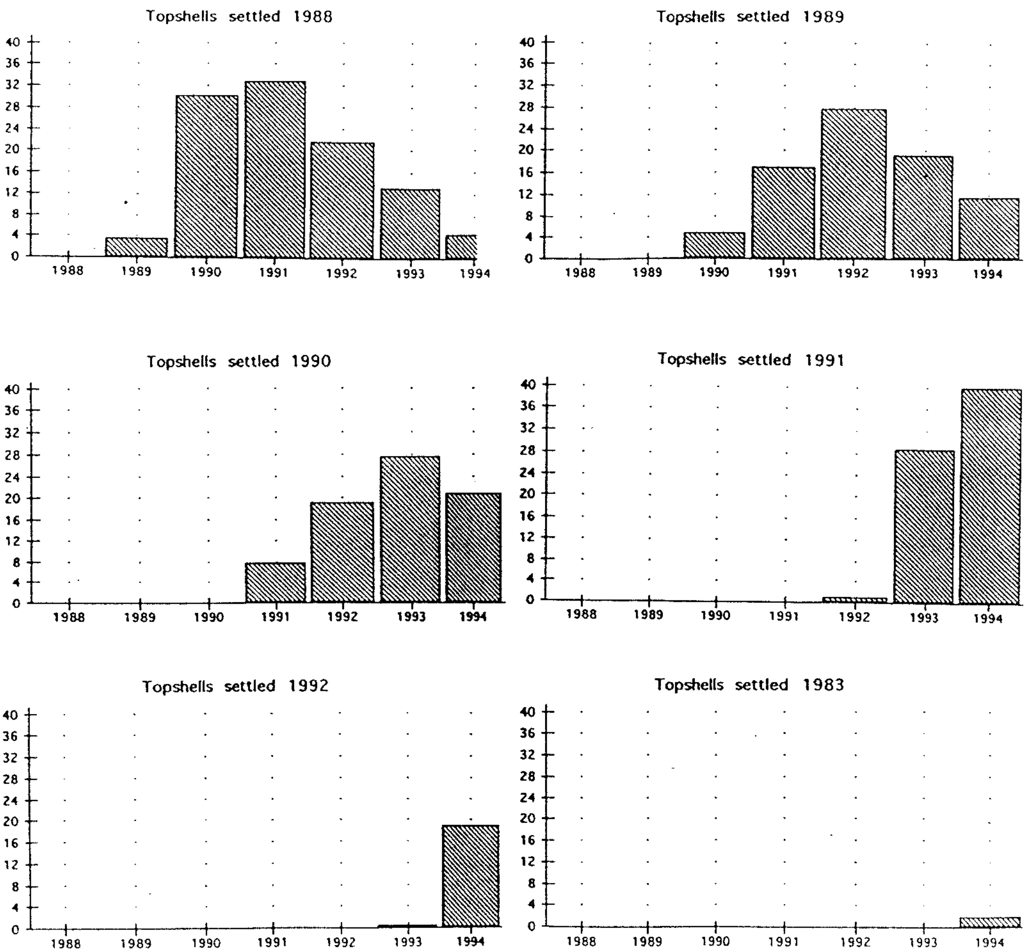


FIG 5

The data from Table 3 plotted out, column by column. Separate graphs are shown for each cohort. The x-axes indicate the years in which the samples were measured: the y-axes show the percentage frequency of the cohort in the year they were measured at 57%. That is to say, 57% of adults alive in one spring will probably die before the next.

That was from just one sample. Table 3 shows the age-distribution of the population according to measurements taken in the spring of each year from 1988 to 1994 expressed as percentages, row by row. The same information is tabulated again (Table 5) to facilitate comparison of the various age-classes year by year. As the sampled population 'recruits' juveniles for their first two or three years, no mortality amongst these classes is apparent from the data—although it undoubtedly occurs. Once 'recruitment' is completed and maturity has been attained, mortality is high.

Thus, in Table 5, the 0+ and 1+ age classes, composed of snails approaching their first and second birthdays respectively, are still 'recruiting'. Thereafter, each subsequent age class is less important to the population than its predecessor. The mean mortality (from the 2+ to the 11+ age class) is seen to be 46%, rising with age and becoming total after 12+ (Fig. 4).

Although one cannot compare the actual abundance of any one cohort (year on year) in Table 3, reading down a given column does reveal the general trend—which may be easier to visualise from Fig. 5. Starting with the data for the topshells presumed to have settled in 1980, a series of histograms are plotted for each column in the Table.

The first six graphs, 1980 to 1985, all reveal the same pattern—that of an ageing cohort steadily decreasing in importance within the population. After 1986, which is inconclusive, the patterns are influenced by the three (or four) year 'recruitment' period of young animals joining the adult group. In the most recent year classes, 'recruitment' dominates the pattern.

Limital Distribution

Although at the easternmost site in the Bristol Channel where common topshells can be truly called 'common', *Monodonta lineata* on the Gore shows few characteristics of a population limited by reproductive capability. There are plenty of immature animals now and no signs of uneven recruitment in the past. Hence, there is no suggestion that climatic variables have significantly influenced reproductive success from year to year. Adult mortality, however, is high and few individuals attain old age or a large size. The largest shell measured in the data sets used for this paper was 26mm high—and students can be relied upon to find the biggest individuals available! There is a 34mm shell in the Natural History Museum collection, from Pembrokeshire, and an individual on Skokholm was recaptured regularly for 15 years (Stanbury, 1974). Thus, Porlock individuals fall considerably below the maxima for *M. lineata,* suggesting that a size-limiting factor is operating on adults. The, equally abundant, populations of both the edible winkle, *Littorina littorea* (L.) (Crothers, 1992) and the purple topshell, *Gibbula umbilicalis* (da Costa) appear to be similarly stunted on the Gore, attaining a much smaller maximum size there than elsewhere in Somerset. The extent to which grazers compete for food is not clear but there is considerable evidence that microbial film resources may be limiting (Hawkins *et al.,* 1989).

Kendall (1987) found a strong negative correlation between maximum size and abundance in *M. lineata* (individuals in dense populations do not attain as large a maximum size as those in sparse ones) but no such relationship was apparent between abundance and maximum age. It seems likely, therefore, that the restrictions to adult

TABLE 6: *Population structure of a small population of* Monodonta lineata *on Swill Point, Doniford, Somerset. Autumn 1994*

Number of Growth Checks	0	0	1	2	3	4	5	6	7	
Length (mm)										Total
1										
2										
3										
4	1									1
5	1									1
6	2									2
7										
8										
9										
10		4								4
11		1								1
12		7								7
13		7								7
14		9								9
15		6								6
16		17	1							18
17		27	8	1						36
18		6	7							13
19			10	3						13
20			4	1						5
21				1						1
22				1		1				2
23				1						1
24										
25										
26										
27										
28										
29										
TOTALS	4	84	30	8	0	1	0	0	0	127
	1994	1993	1992	1991	1990	1989	1988	1987	1986	

growth shown by this population are more to do with overcrowding and competition for food than to any discernible 'eastern' factor.

The 1962-1963 cold winter had little long-term effect on *M. lineata* in Somerset. Unlike the situation on the south-facing shores of Glamorgan and Dorset, where the species has yet to recover its former range, all the available evidence suggests that common topshells have spread some 20km east along this north-facing shoreline during the last 50 years—and maybe more if the Hinkley Point record was not an isolated individual. Unlike at the species' absolute northern and eastern limits in mainland Britain (Kendal, 1987) there was no geomorphological barrier to expansion. Apparently-suitable habitats existed further east and the animal appears to be extending its range. It may be noted, in passing, that *Gibbula umbilicalis* (another topshell with a predominately southern and western distribution in Britain, although less restricted than that of *M. lineata*) has also spread east along this coastline during the same period.

Bassindale (1941, 1943) did not record it east of Blue Anchor. By 1974 (Crothers, 1976), it had reached Watchet, West Beach, but did not figure on the transect of Helwell Bay, where it is now common. Boyden *et al.,* (1977) recorded it east to Kilve with a single record from Hinkley Point in 1972. Bamber & Coughlan (1987) recorded it as reaching a density of 2 m^{-2} locally at the latter site whilst, by 1993,. Martin (1994) found it to average 4 m^{-2} over a much larger area.

The small population of *M. lineata* on Swill Point, Doniford, was investigated by students for the first time in September 1994. By comparison with the population on the Gore, it will be seen that there are no old individuals but the main difference lies in their much faster growth rates (Table 6). These animals show all the signs of a recently-established population exploiting a hitherto untapped food supply. They deserve monitoring in future.

Until the current eastward spread of *M. lineata* along the Somerset coast has been halted it will not be possible to determine what is the limiting factor. It seems likely that the most dangerous phase in this animal's life cycle is in the transition from planktonic larva to young snail and through the first winter. It may be that conditions for this have been easier in recent years, allowing an extension of the range. When the new limit is established, it may be that estuarine- rather than eastern- factors are involved.

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