THE ABUNDANCE AND DISTRIBUTION OF BRITISH TELLINIDAE

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DECLARATION.

"Dispersion of Tellina tenuis da Costa from Kames Bay, Millport, Scotland" has been published in Marine Biology, 37, 371-376 (1976).[1]

"The distribution of two closely related species of Tellina, T. tenuis da Costa and T. fabula Gmelin" is in press in the Report of the Underwater Association 2 (N.S.) 1976.

"A scanning electron microscope study of the shell ornamentation of Tellina fabula Gmelin" is shortly to be submitted for publication.

"A comparison of the effects of increased temperatures on Tellina tenuis da Costa and Tellina fabula Gmelin" is shortly to be submitted for publication.

These have been included verbatim under the appropriate chapter heading.

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SUMMARY.

Tellina tenuis da Costa and Tellina fabula Gmelin (Bivalvia: Tellinacea) appear to be closely related and display considerable internal and external similarity. They are found together on many sandy shores in Britain and Europe; a typical situation exists in Kames Bay, Millport, where T. tenuis is littoral, T. fabula is sublittoral, and their ranges overlap little. There is extensive published information to suggest that the situation in the Bay has hardly changed over the past 50 years.

The factors which govern their distributions were investigated for two reasons. Firstly, to find the environmental influence on the two species' ranges, and secondly, to apply the findings to palaeoecological interpretation of fossil mollusc assemblages in which these Tellinids occur.

Distribution, lethal tolerances, rhythms, sediment analysis, burrowing and morphology were the factors investigated.

The distribution experiments proved that T. tenuis and T. fabula were largely randomly dispersed with a slight tendency toward aggregation, particularly in the laboratory. Mark and recapture experiments with T. tenuis showed that adult movement was limited to a few cm from their burrowing start position - due, perhaps, to the angle of burrowing. Attempts to monitor the spatfall met with little success; coring experiments suggested that the 1+ year groups were firmly established in their respective habitats.

T. fabula was around 5°C less tolerant than T. tenuis

to any increased temperature regime. T. fabula was also more susceptible to changes in salinity or to desiccation, and it appeared that T. tenuis would be more resistant than T. fabula to any environmental stress.

Neither species displayed pronounced rhythms, but there were slight traces of a circadian rhythm, the length of which, in T. fabula only, was inversely correlated with day length. The level of activity in both species was correlated with maximum predicted tidal range during the experiment, but not with tidal range on the day of collection. This suggested some endogenous component in largely exogenous rhythms.

Sediment analysis showed that there was little difference in grain size composition of beach and sublittoral sand. Sublittoral sand was, however, significantly less penetrable, less permeable, and less porous than littoral sand.

No distinction could be made in the burrowing behaviour (speed, digging cycles) provided that the animals were the same size, but T. tenuis burrowed significantly deeper than T. fabula. Burrowing of T. tenuis was affected by a change from littoral to sublittoral sand, but T. fabula was not affected by the reciprocal change. Size and burrowing depth were correlated only in field populations of T. tenuis.

T. fabula may be distinguished from T. tenuis by the presence of diagonal striae on the right valve; what purpose they serve is unclear. The shell of T. fabula was significantly thicker than that of similar-sized T. tenuis but it was impossible to identify medium sized animals on length/width, length/height, or length/weight ratios alone.

The results suggested that T. tenuis was considerably better suited to living under adverse environmental conditions, since it was bigger, burrowed deeper and was physically more tolerant than T. fabula. T. tenuis may be penalised for its adaptability by reduced efficiency, compared with T. fabula, under optimum conditions (i.e. in the sublittoral zone). However, the unknown effect of larval settlement patterns and larval tolerances must be considered before drawing firm conclusions regarding the control of the species' distributions.

INTRODUCTION.

The factors governing the abundance and distribution of a species are, at best, poorly understood. While it may be known why, for example, a rock epifaunal species cannot survive on soft mud, there are few studies of the factors which separate the distributions of very similar species living close together (e.g. Nørgaard, 1951). Two such species are Tellina tenuis and Tellina fabula, which are morphologically very similar (Yonge, 1949) and are usually found in close proximity to one another as, for example, in Kames Bay, Millport (Stephen, 1928; Watkin, 1942; Clark and Milne, 1955). This thesis is an investigation of various aspects of their life-style in an attempt to find out what factors govern and separate their respective distributions.

After consultation with Dr. A.D. Ansell and Dr. P.R.O. Barnett (Dunstaffnage Marine Research Laboratory, Oban), it was decided that the larvae would be too difficult to rear, so experiments were confined to adult animals. Fortunately, adults of both species could be gathered easily and in large numbers from Kames Bay but, since T. tenuis was more plentiful and more easily collected than T. fabula, experimental techniques were worked out first with T. tenuis.

In Kames Bay T. tenuis is found, at densities of up to 7,500 per square metre, from about 3.0 M above Chart Datum to about 0.01 M C.D. T. fabula, much less abundant than T. tenuis, is found from 0.01 M C.D. to around the 10 M contour, so that the two species' ranges overlap only slightly (Stephen, 1928, 1932; Watkin, 1942; Clark and Milne, 1955). The geographical distribution of both species ranges from Norway to Morocco (Forbes and Hanley, 1853; Jeffreys, 1863; Ockelmann, 1958; Tebble, 1966).

T. fabula is found in the early Pleistocene deposits such as the English Red Crag, along with other Tellinids such as Macoma obliqua, Macoma praetenuis, and Macoma calcarea, as well as, in later deposits, (Weybourne Crag) Macoma balthica (Norton and Spaink, 1974). T. tenuis may have arisen later still, in the Holsteinian or Eemian ~~deposits~~. Older identifications of these Tellinids are open to considerable doubt (Norton and Spaink, 1974). All have been interpreted as littoral infaunal forms (West and Norton, 1974), but M. obliqua and M. praetenuis are extinct today, while M. calcarea is restricted to the Arctic. The factors determining the relative niches of these species are therefore of great interest in an understanding of the paleoecological as well as ecological relationships.

The aspects investigated have been grouped under six headings, lethal tolerances, distribution, rhythms, sediment analysis, burrowing, and morphological characteristics, each of which has been allocated a separate chapter.

Chapter 1. Lethal Tolerances.

The lethal tolerances investigated were the tolerance to increased temperature, to increased and decreased salinity, and to desiccation. The first two factors were thought to be important because littoral species are subject to considerable fluctuations in temperature (e.g. Davies, 1970), thus restricting the distribution of some species (e.g. Connell, 1961), and it has already been found that the reduction in salinity in some parts of Kames Bay exerts great influence on the distribution of the polychaete <u>Nereis diversicolor</u> (Smith, 1955). On the other hand it is reasonable to assume that the infauna of a sandy beach would not be subject to desiccation stress, due to the presence of interstitial water. The results of this latter investigation would, it was hoped, show whether one species was, in general, more resistant than the other, or whether tolerance was limited to factors actually encountered on the beach.

Chapter 2. Distribution.

The distribution of <u>T. tenuis</u> and <u>T. fabula</u> in Kames Bay has been so thoroughly investigated over the years (Stephen, 1928, 1932; Watkin, 1942; Clark and Milne, 1955) that it was felt unnecessary to repeat the work by carrying out a large-scale sampling programme. Many sedentary invertebrates, including <u>T. tenuis</u> and <u>T. fabula</u>, have planktonic larvae (Thorson, 1950; Rasmussen, 1973) whose settlement preferences may largely control the eventual distribution of the adult animals (Wilson, 1950; Meadows and Campbell, 1972 a, b). However, adult <u>Tellina</u> can move through the sand, and it has been suggested (Holme, 1961) that they have adopted a horizontal position when burrowed to facilitate migration through the sediment. This suggestion was supported by previous work by Holme (1950) who found that a population of *T. tenuis* in the Exe estuary was overdispersed due to the animals moving away from each other to maintain feeding territories. Accordingly, it was decided to investigate the distribution of *T. tenuis* and *T. fabula* in Kames Bay from three angles - larval settlement, adult movement, and adult dispersion patterns.

Chapter 3. Rhythms.

Morton (1973) suggested that littoral bivalves display circatidal rhythms, while sublittoral (and, incidentally, freshwater) bivalves display circadian rhythms, but recently (Earll, 1975 b) doubts have been case not only on the existence of such clear-cut rhythms but also on the methods used to detect them. The best method of monitoring the activity is to record the adductor muscle rhythms (Morton, 1973), and so the valve rhythms of *T. tenuis* and *T. fabula*, in a steady-state system, were recorded to see if either species displayed noticeable circatidal or circadian rhythms. Some *T. tenuis* were left at the *T. fabula* sampling site, and vice versa, in a transplant experiment to ascertain whether the rhythms could be changed, that is, if the rhythms were exogenously or endogenously controlled, e.g. Morton (1956). The strength of the rhythms, as well as the periodicity, was also investigated with reference to the environmental variables of tidal rise and fall, and sunrise and sunset.

Chapter 4. Sediment Analysis.

As has been mentioned, certain sediments are attractive to settling larvae, and they may also be attractive to adult animals as well (Meadows and Campbell, 1972 a, b). The physical characteristics of sand from various sites in Kames Bay were therefore investigated to find out not only if there were any measurable differences, but also whether these differences could be related to the distribution of the animals. For instance, the distribution of the polycheate *Arenicola marina* has been correlated with the hardness of the sediment (Newell and Chapman, 1948). The physical characteristics investigated were grain size composition, porosity, permeability, and penetrability.

Chapter 5. Burrowing.

The hardness of the sediment controls the distribution of *A. marina* (see above) by affecting the speed and the ease of burrowing (Chapman, 1949). It would appear obvious that littoral infauna should be able to burrow again as quickly as possible if, for example, they had been washed out of the beach by severe wave action. Depth of burrowing may also be important with respect to predation by wading birds (Hughes, 1970). The speed and the depth of burrowing, with respect to size, of *T. tenuis* and *T. fabula* were monitored not only in their natural sediments but also in the other species' sediment.

Chapter 6. Morphology.

The internal morphology of *T. tenuis* and *T. fabula* has been extensively studied by Atkins (1937 a, b), and by Yonge (1949), who concluded that there were no significant differences between the two species. The shell morphology, however, differs considerably (Forbes and Hanley, 1853; Jeffreys, 1863; Tebble, 1966). An analysis of the external morphology of T. tenuis and T. fabula was therefore designed to try to relate the various characters to their respective life-styles (after Kauffman, 1969; Stanley, 1970).

Chapter 1

Lethal Tolerances.

Introduction.

The factors governing a species distribution can be divided into two categories - biological factors and physical factors. Amongst the most important physical factors for littoral species are their resistance to temperature, salinity, and desiccation. Of these factors, temperature is probably the most influential, and will be dealt with separately.

The effects of solar irradiation leading to increased salinity and desiccation, and of rainfall or freshwater inflow leading to decreased salinity, are less extreme on a sandy beach than on the rocks. This buffering action is due to the interstitial water, which is drawn up from the residual water table by capillary action (Bruce, 1928; Reid, 1930).

The variations in the salinity of the interstitial water depend largely on the influx of freshwater either from rainfall or from a stream flowing over the beach. Evaporation by solar irradiation, in temperate latitudes at least, results in at most a 1 ‰ rise in the salinity of the interstitial water (Southward, 1953). The salinity of the surface channel water in the Clyde estuary around Millport varies from 31.26 ‰ in January to 32.98 ‰ in June (Barnes, 1955, 1961) and in Kames Bay itself there is a considerable influx of freshwater from two streams on the western edge of the beach. Although Watkin (1942) suggested little variation, in places the salinity of the interstitial water is as low as 9 ‰ (at a depth of 6 inches at HWN)and lowered salinity persists even below the SW at high tide.

The vertical distribution of T. tenuis and T. fabula is well documented (Stephen, 1928; Watkin, 1942; Clark and Milne, 1955), but nothing has been published on their horizontal distribution across the Bay. However, Dr. P.R.O. Barnett (Dunstaffnage Marine Research Laboratory personal communication) has found that both populations are denser on the eastern side of the Bay.

There have been few studies of resistance to desiccation in bivalves, and these have been concerned only with epifaunal species (Morton et al, 1957; Kensler, 1967). Since the presence of the interstitial water in the sand should prevent any desiccation stress, it was felt that it would be interesting to compare a littoral infaunal species (T. tenuis) with a sublittoral infaunal species (T. fabula) to find out if the littoral species has a greater tolerance to desiccation.

Materials and Methods.

In the salinity experiments, the experimental chambers were 2 litre beakers, and in the desiccation experiments they were petri dishes with a piece of filter paper across the bottom. The required salinity was obtained by either diluting the laboratory seawater (salinity about 31 ‰) with copper-free freshwater or by adding "Instant Ocean" (Shirley Aquatics Ltd., Solihull). In this way salinities from 0% SW to 200% SW were obtained. The water in the beakers was aerated with an airstone which was regulated to give as little air as possible, in order to obviate the possibility of the salinity being changed by evaporation. All experiments were performed in a 10°C constant temperature room. An experiment was also conducted to find out whether T. tenuis were osmoregulators or osmoconformers by weighing the animals before and after they had been exposed to concentrations of 50%, 150% and 200% SW. The criterion for death was, as for the temperature experiments, that the valves should be gaping, and that they did not move when touched.

In the desiccation experiments, uniform conditions at the start of the experiment were obtained by soaking the filter paper in each dish. The dishes, with the animals on top of the soaked filter paper, were then put into 5°C, 10°C or 15°C constant temperature rooms. It was found that the criterion for death was not particularly applicable to the desiccation experiments. Some animals did gape, but others remained shut until completely dried out. To overcome this problem, subsamples were taken during the course of the experiment of those animals which were not gaping. These subsamples were returned to seawater at the appropriate temperature. The number of animals which recovered was noted, and the mortality was expressed as a percentage of the subsample, plus the number gaping.

The significance of the results was tested with the Sign Test (Siegel, 1956) and the Spearman Rank Correlation Coefficient (Moroney, 1951)

Results.

The results of the salinity experiments are shown in Fig. 1a. T. tenuis survived concentrations of 0% to 200% SW for around 24 hours by keeping its valves firmly closed, but there was considerable mortality in T. fabula in the first 24 hours.

The T. tenuis which were exposed to 50% SW were significantly heavier at the end of the experiment ($N = 19$, $x = 1$, $P > 0.01$ (Siegel, 1956)), but there was no significant change in the weight of the animals exposed to 200% SW or 150% SW ($N = 11$, $x = 4$, $P = 0.27$ and $N = 23$, $x = 10$, $P = 0.34$ (Siegel, 1956)).

In the desiccation experiments, T. tenuis was more resistant than T. fabula under all regimes ($N = 13$, $x = 1$, $P = 0.002$ (Siegel, 1956)), and, as might have been expected, the mortality rate was proportional to the air temperature ($F = 15.43$, $f_1 = 1.7$, $f_2 = 10.2$, $P > 0.001$ (Moroney, 1951)) (Table 1a).

Discussion.

There appears to be a consistent difference in tolerance between T. tenuis and T. fabula, not only to factors which they might expect to face, such as variations in temperature and salinity, but also to unlikely factors such as desiccation.

The results also support the theory that the tidal height of an animal, i.e. the extent of the tidal range over which it is distributed, is correlated with its tolerance to salinity (Arnold, 1957, 1972; Morton et al, 1957; Simpson, 1976) or to desiccation (Morton et al, 1957; Kensler, 1967; Simpson, 1976). It may be, however, that the difference in tolerance to salinity or desiccation is due to the fact that T. fabula is unable to close its valves completely. T. tenuis, like many other bivalves, can completely exclude certain adverse conditions for a short time at least (Freeman and Rigler, 1957; Morton et al , 1957; Pierce and Greenberg, 1973).

Nevertheless, both T. tenuis and T. fabula appear to be stenohaline when compared with other marine bivalves. Castagna and Chanley (1973) tested 29 species of which 25 survived at a salinity of 12.5‰ (about 35% SW), while Mya arenaria has a tolerance limit of 4‰ (Matthiessen, 1960).

The bivalve Lasaea rubra shows 100% survival after 12 hours in dry air at 30°C (Morton et al, 1957) and, while both T. tenuis and T. fabula were able to survive for 12 hours out of water, the maximum temperature was only 15°C. However, the combination of 12 hours out of water and a temperature of 15°C is probably the most adverse set of conditions the littoral infauna are likely to experience in Kames Bay (Watkin, 1942; Barnes, 1955) and so it seems unlikely that desiccation could be a factor influencing their distribution.

The lowering of the salinity of the interstitial water on the other hand may alone exclude T. fabula from the littoral zone. Certainly, when all the factors - temperature, salinity and desiccation - are taken into consideration, it seems reasonable to advance the argument that the relative tolerances in general of _T. tenuis_ and _T. fabula_ may be the answer as to why _T. fabula_ is confined to the sublittoral zone.

Table 1a. Percentage mortality of T. tenuis and T. fabula when left out of water in 5°C, 10°C, and 15°C constant temperature rooms.

Animal	Temp. °C	Time (hours)							
		12	24	36	48	60	72	84	96
T.tenuis	5	0	0	0	20	30	55	70	100
	10	5	10	15	30	45	70	100	-
	15	0	20	57.5	90	100	-	-	-
T.fabula	5	0	0	20	30	60	100	-	-
	10	0	10	30	70	100	-	-	-
	15	0	70	100	-	-	-	-	-

Fig. 1a. LD_{50} in days plotted against concentration of seawater (SW)

▲ T. tenuis;

■ T. fabula;

□ estimated (due to extreme rapidity of mortality) LD_{50} for T. fabula in 0% SW.

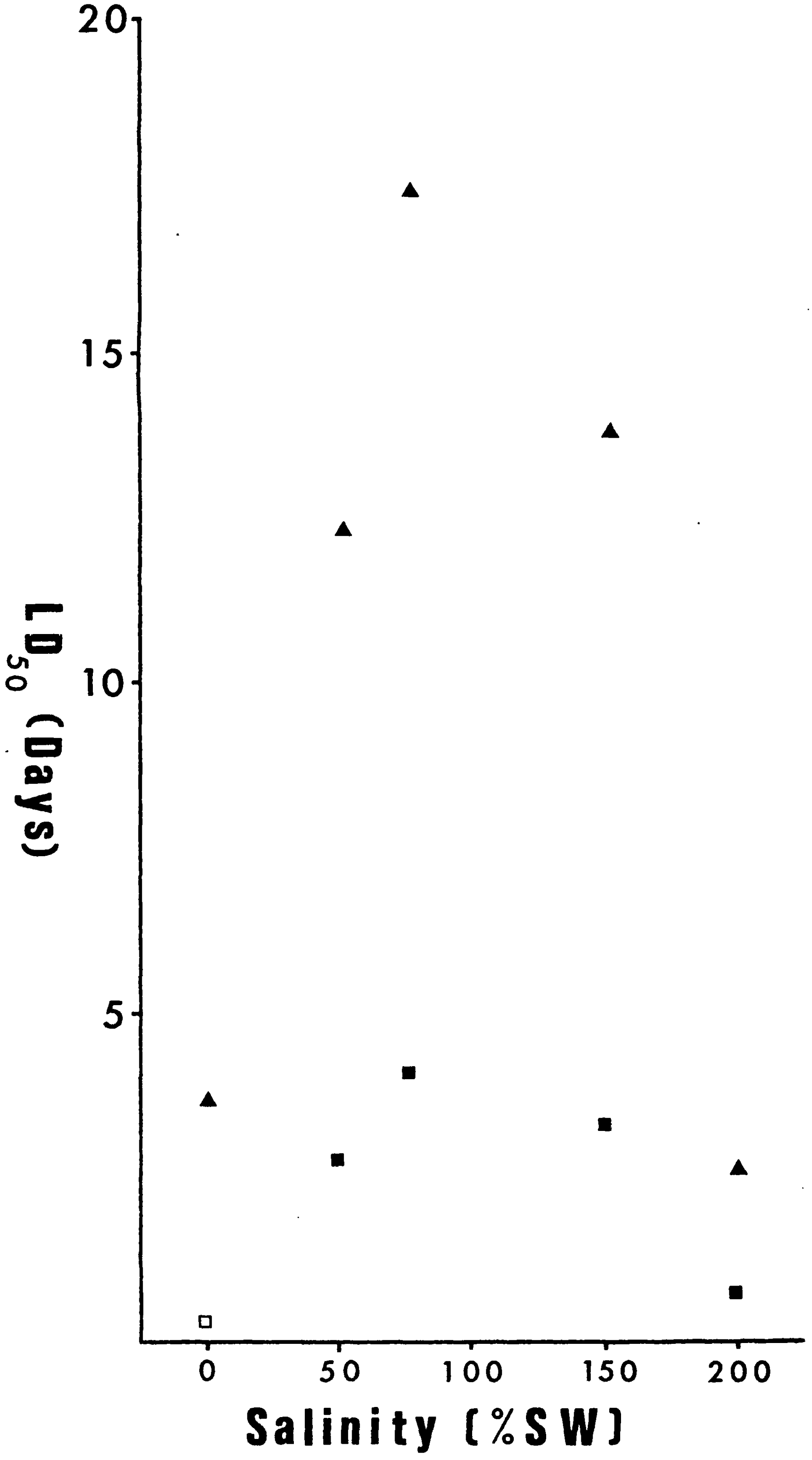


Fig.1a

Introduction.

Temperature is one of the most important abiotic factors in an animal's environment, and the tolerance of a species to temperature will be reflected in the past and present distribution (Hutchins, 1947; Gunter, 1957; Kinne,1963).

At Kames Bay, Millport, Tellina tenuis is found from HWN to just below LWS, while Tellina fabula is found from LWS to the 10 m contour (Stephen, 1928; Watkin, 1942; Clark and Milne, 1955).

The temperature range when the animals are exposed is proportional to their distance up the beach (Johnson, 1965; Perkins, 1974), due partly to the amount of interstitial water (Jansson, 1967a), and also to the depth at which they live (Bruce, 1928; Southward, 1953; Johnson, 1965; Fenchel and Jansson, 1966; Jansson, 1966; Hughes, 1971). When covered by the sea the temperature is that of the surrounding water (Perkins, 1974). The range of surface channel water temperatures to which they are exposed in Kames Bay varies from a maximum of around 15.5°C in September to a minimum of around 4°C in February (Mill, 1892-4; Barnes, 1955).

However, both T. tenuis and T. fabula have a geographical distribution from Norway to Morocco (Forbes and Hanley, 1853; Tebble, 1966), so both species must be able to withstand temperature extremes outwith those which they encounter in Kames Bay. Their present thermal niche may therefore be only part of their theoretical or potential temperature tolerance range.

Extensive investigations have been made of the temperature tolerances of molluscs, at all stages from larvae to adults. Andronikov (1975) has reviewed the heat resistance of the gametes and embryos, and a great deal of work has been carried out on the lethal tolerances of the larvae (Loosanoff et al, 1951; Kinne, 1963, 1964; Calabrese and Davis, 1970; Cain, 1973; Diaz, 1973; Kennedy et al, 1974). Much has also been done on the tolerances of adult molluscs (Orton, 1920; Henderson, 1929; Evans, 1948; Gunter, 1957; Dickie, 1958; Southward, 1958; Fraenkel, 1961, 1968; Read, 1964, 1967; Davies, 1965, 1969; Read and Cumming, 1967; Kennedy and Mihursky, 1971; Waugh and Garside, 1971; Boyden, 1972; Gabbot and Bayne, 1973; Widdows, 1973; Wallis, 1975), while Bayne et al (1975) observed that stress in the adults led to diminished viability in the larvae.

This paper deals with the tolerances of adult T. tenuis and T. fabula to increased temperatures, and attempts to relate the results to their distribution.

Materials and Methods.

The animals were collected from Kames Bay, Millport - T. tenuis from a site 1.5 m above Chart Datum, and T. fabula from a site 5.0 m below C.D. They were adjudged dead if the valves were gaping, that is, if they would not close when stimulated, and if there was no discernible movement. The location of the collecting sites was kept constant (Wallis, 1975) to avoid the possibility of differential environmental acclimatization (Davies, 1965, 1967). The terms "acclimation", "acclimatization", and "adaptation" are used throughout as defined by Fry (1958, 1967).

The apparatus, depicted diagrammatically in Fig. 1, was used for all regimes except those requiring a constant 5°C or 10°C temperature. These were carried out in constant temperature aquaria.

For the first experiments, the animals were put directly into the experimental chambers (after Precht, 1973)), and both short-term and long-term mortality was noted (Fry et al, 1946). In the short-term experiments, the mortality was noted after 24 hours exposure to the experimental temperature. In the long-term experiments, the experiments were allowed to run to their conclusion, that is, until all the animals were dead. When percentage mortality was plotted against time, the characteristic temperature-time curves (Orr, 1955) were obtained. These were straightened and subsequent analysis facilitated by plotting the mortality in probits, from the tables of Bliss (1935), against the log of the time (Bliss, 1935; Finney, 1947; Speakman and Krenkel, 1972; Stora, 1974).

In order to avoid the possibility of a mixed lethal effect due to temperature shock (Hutchison, 1961), and to investigate the effect of rate of temperature change (Cocking, 1959a,b; Speakman and Krenkel, 1972), experiments were set up in which the temperature was raised by 2°C every 1, 2 or 4 days. Again, the mortality in probits was plotted against log time (Bliss, 1935; Finney, 1947; Speakman and Krenkel, 1972; Stora, 1974).

It has been suggested by several authors (Brett, 1944, 1970; Fry, 1947, 1958, 1967; Hutchison, 1961; Newell, 1970) that the zone of thermal tolerance of a species is best obtained from acclimation experiments. Accordingly, a series of experiments was set up in which the animals were acclimated to different temperatures for two weeks before they were introduced to the experimental temperatures. Since T. tenuis was found to be more resistant than T. fabula, the acclimation temperatures were 5°C, 10°C, 15°C, 20°C and 25°C, and 5°C, 10°C, 15°C and 20°C respectively. Similarly the experimental temperatures for the acclimated T. tenuis were 5°C higher than for acclimated T. fabula, 5°C, 10°C, 15°C, 20°C, 25°C and 30°C as opposed to 5°C, 10°C, 15°C, 20°C, and 25°C. The area of the zone of upper temperature tolerance was determined from tolerance triangles (McErlean et al, 1969).

T. tenuis was collected on various dates from January to June, and tested at 10°C and at 25°C as in the long-term experiments to determine whether there was a seasonal variation in the mortality rate, that is, whether the animals were capable of seasonal acclimatization. This experiment was set up with T. tenuis alone, since it is exposed to the greater seasonal temperature range. T. tenuis was also used in an experiment to ascertain whether the size of the animals affected the mortality rate.

Results.

The results of the short-term (24 hour) tolerance experiments are shown in Fig. 2. The lethal dose for 50% mortality (LD_{50}) is 31.25°C for T. tenuis and 26.5°C for T. fabula.

In the long-term experiments, it was again found that T. tenuis was more tolerant, not only of high temperatures, but also of low temperatures (Table 1). The zone of resistance obtained by plotting the LD_{50} against the temperature (Fig. 3) of T. tenuis was almost three times as large as that of T. fabula (811.91 degree days and 264.97 degree days respectively). It was not possible to fit single straight lines to the plots of mortality in probits versus log time (Figs. 4, 5), so two regression lines were calculated for each temperature (Table 2). From these it is possible to estimate the effect on either species of a given temperature for a given length of time in the laboratory. There was no apparent mathematical relationship between the slopes of the regression lines at different temperatures in Fig. 4 and Fig. 5, although obviously the higher the temperature the steeper the mortality gradient.

From Fig. 4 and Fig. 5 it can be seen that when taken directly from the field, the animals could resist the effects of the higher temperatures before they began to die. However, when the temperature was raised gradually by 2°C every 1, 2 or 4 days, the mortality curve, in probits versus log time, can be represented by a single straight line (Figs. 6, 7). The equation for each line is given in Table 3, and it is apparent that the regression lines of the mortality under all regimes had approximately the same gradients (Table 4). The LD_{50} in °C was plotted against LD_{50} in days (Fig. 8) and the areas of the tolerance triangles of T. tenuis and T. fabula were calculated as 952.9 degree days and 498.0 degree days respectively.

It was found that acclimation to a higher temperature enhanced the animals' ability to withstand higher experimental temperatures; for example, the LD_{50} at 30°C for 5°C acclimated *T. tenuis* was 1.70 days, while for 25°C acclimated *T. tenuis* it was 2.86 days. The upper acclimation limit for *T. tenuis* and *T. fabula* appeared to be just below 25°C and 20°C respectively, although the regression line for *T. fabula* in Fig. 9 indicates that the acclimation limit is above 30°C. This is due to a low $LT_{50} - T_a$ value for a T_a of 5°C, perhaps because a low temperature also stresses the animals. Upper temperature tolerance triangles (McErlean et al, 1969) were constructed (Fig. 9), and the respective tolerance areas were calculated. The tolerance area of *T. tenuis* was 427.32 degrees^2 and of *T. fabula* was 232.9 degrees^2.

The results from the experiment on seasonal variation in mortality rate are shown in Fig. 10. The extreme variability of the results renders interpretation difficult, but there seems to be no correlation between the tolerance of the animals and the time of collection. The mortality rates (Fig. 11) of the two groups of *T. tenuis* of different sizes ($t = 14.29$, $P \quad 0.01$ (Bailey, 1959)) tested at 30°C were not significantly different ($t = 0.04$, $P = 0.96$ (Bailey, 1959)). It appears, therefore, that mortality was independent of the size or age of the animals.

The results suggest that *T. tenuis* in particular was capable of withstanding temperatures in excess of its normal environmental range. *T. fabula* was considerably more susceptible, its tolerance zone area generally about one-half, and its upper limits about 5°C less under any regime, when compared with *T. tenuis*.

Discussion.

The 5°C difference in temperature tolerance observed between T. tenuis and T. fabula in the 24 hour experiments persists in the long-term experiments, in that the 20°C and 25°C mortality curves for T. tenuis resemble the 15°C and 20°C curves respectively for T. fabula. The lag period and the resultant change in the mortality gradient in the long-term experiments, the mixed lethal effect (Hutchison, 1961) may be attributable to some factor related to temperature, e.g. starvation (Newell and Bayne, 1973) rather than to temperature itself. Whatever the cause, T. tenuis was much more temperature tolerant than T. fabula.

Most species can acclimate to temperature above or below the mean temperature of their environment, and the acclimated animals show a marked change in their tolerance. The higher the temperature to which an animal has been acclimated, the higher its lethal tolerance, until a limit is reached beyond which it is incapable of further acclimation (Prosser, 1958; Kinne, 1963). In the gradually increasing temperature experiments, the similarity of the mortality gradients and the fact that a faster increase led to a higher LD_{50} temperature, suggested that differential acclimation, proportional to the rate of temperature increase did not occur (Cocking, 1959 b). On the other hand, there was acclimation when the animals, especially T. fabula, were exposed to a steady increased temperature for two weeks, and, in general, the degree of acclimation was proportional to the increase in the acclimation temperature.

Studies by Ansell and Trevallion (1967), Trevallion (1971), and Trevallion et al (1973) have shown that the biochemical composition of the tissues and the oxygen consumption of T. tenuis vary throughout the year, so one might expect that the resistance to temperature changes would also vary. However, the tolerance of T. tenuis did not appear to be correlated with the season, and there was no evidence of seasonal acclimatization. Seasonal independence in temperature tolerance has also been shown to exist in some invertebrates (Southward, 1958; Crisp and Ritz, 1967; Fraenkel,1968; Foster, 1969) but not in fishes (Brett, 1944) or algae (Parker, 1960).

The persistent difference in tolerance between T. tenuis and T. fabula supports the theory that there is a difference in tolerance between littoral and sublittoral species (Henderson, 1929; Gunter, 1957; Southward, 1958; Connell, 1961; Davies, 1965; Fraenkel, 1968; Friedrich, 1969; Newell, 1970; Kennedy and Mihursky, 1971). There is, however, some doubt whether the temperature tolerance of animals of the same species varies with their position relative to tidal height. Various authors have found that the temperature sensitivity of a species was a function of the tidal height (Segal et al, 1953; Parker, 1960; Davies, 1965, 1967), while Simpson (1976) found that this was not the case with Patinigera macquariensis (Finlay). The temperature tolerance of sublittoral T. tenuis has been reported as being the same as littoral T. tenuis (A.D. Ansell, Dunstaffnage Marine Research Laboratory, personal communication).

In any species, the thermal tolerance, or indeed the tolerance to any environmental factor varies with the stage in the life cycle. Diaz (1973) noted that the mortality of Crassostrea virginica increased with the age of the larvae, but Loveland et al (1972) found the converse with the larvae of Mulinia lateralis. Other workers (Kennedy et al, 1974) have obtained results similar to Loveland et al (1972) and the more widely held view is that the early stages of mollusc development are more susceptible to temperature extremes (Loosanoff et al, 1951; Kinne, 1963, 1964; Loosanoff and Davis, 1963; Goodwin, 1970). The limiting factor for a species distribution is therefore a temperature which, throughout the year, exceeds the range for the development of the embryos (Andronikov, 1975) and, in general, the reproductive range is less than the total range (Hutchins, 1947; Kinne, 1970).

Once adult, the temperature tolerance of all age groups of T. tenuis was constant, although this does not hold for all bivalves (Kennedy and Mihursky, 1971; Wallis, 1975). Nevertheless, sublethal temperatures during adult life may affect the burrowing or mobility of an animal (Dickie, 1958; Southward, 1958; Fry, 1967) or reduce the feeding rate such that the energy balance between food uptake and energy expenditure becomes negative (de Wilde, 1975). The stress may also reduce fecudity and subsequent larval survival (Bayne et al, 1975).

Fluctuations in other environmental factors such as salinity will combine to lower the animal's resistance to temperature changes, and tolerance will be at a maximum only when the other environmental factors are at an optimum (Costlow et al, 1960; Kinne, 1964; Calabrese, 1969; Calabrese and Davis, 1970; Biggs and McDermott, 1973). The result of these interactions is that in nature thermal death itself is uncommon, and the degree of heat tolerance of a species is proportional, but not equal, to the environmental range (Evans, 1948; Newell, 1970; Simpson, 1976).

The thermal tolerance of _T. tenuis_ was greater than that of _T. fabula_ under any regime, yet both species have the same geographical range (Forbes and Hanley, 1853; Tebble, 1966), when one might expect the species with the wider tolerance to have the wider range (Newell, 1970). For example, the different geographical and intertidal distributions of _Balanus balanoides_ and _Chthamalus stellatus_ are correlated with their respective temperature tolerances (Connell, 1961). It may be, therefore, that temperature is not a limiting factor in the geographical distribution, or that there exists different thermal races of the same species (Fry, 1957; Vernberg, 1969), or that there are stages in the life cycle of _T. tenuis_ and _T. fabula_ which are equally vulnerable to extremes of temperature. In Kames Bay, however, the tolerance of the adults is reflected in their respective littoral and sublittoral distributions, and the species displaying the greater tolerance, _T. tenuis_, is found on the shore, while _T. fabula_ is confined to below low water.

Table 1. Length of time (days) to 50% mortality of *T. tenuis* and *T. fabula* at constant temperatures.

Temperature °C	*T. tenuis*	*T. fabula*
5	-	17.50
10	-	-
15	-	9.00
20	19.80	6.44
25	5.75	1.57
30	1.94	0.71

Table 2. Regression lines for mortality rates of *T. tenuis* and *T. fabula* at fixed temperatures:

y = Percentage dead in probits

x = Log time (days) (Bailey, 1959)

a) - first part of line

b) - second part.

Animal	Temperature	Equations
T. tenuis	20°C	a) $y = 3.3 + 1.1\,x$ b) $y = -0.9 + 4.7\,x$
T. tenuis	25°C	a) $y = 3.4 + 1.9\,x$ b) $y = -2.6 + 9.4x$
T. fabula	15°C	a) $y = 2.8 + 2.2\,x$ b) $y = 1.3 + 4.1\,x$
T. fabula	20°C	a) $y = 3.3 + 1.6\,x$ b) $y = 0.2 + 6.0\,x$

Table 3. Regression lines for mortality rates of *T. tenuis* and *T. fabula* at gradually increasing temperatures; notation as Table 2.

Expt. No.	Animal	Rate	Starting temp.	Equation
1	*T.tenuis*	2°C/1 day	20°C	$y = -2.1 + 9.4\ x$
2	"	2°C/2 days	"	$y = -4.4 + 9.9\ x$
3	"	2°C/4 days	"	$y = -4.6 + 8.7\ x$
4	*T.fabula*	2°C/1 day	10°C	$y = -2.9 + 8.9\ x$
5	"	2°C/2 days	"	$y = -7.6 + 12.3\ x$
6	"	2°C/4 days	"	$y = -8.2 + 11.4\ x$

Table 4. Slope comparisons of the regression lines of the mortality rates of <u>T. tenuis</u> and <u>T. fabula</u> at gradually increasing temperatures under the null hypothesis that the gradients are equal.

Experiment Number

1	1					
2	0.77	2				
3	0.70	0.12	3			
4	0.83	0.49	0.90	4		
5	0.17	0.10	0.02	0.08	5	
6	0.29	0.14	0.01	0.13	0.52	6

Fig. 1. Experimental set-up.

AS - airstone

CC - cooling coil

HC - heating coil

SP - specimens

SW - seawater

WB - waterbath

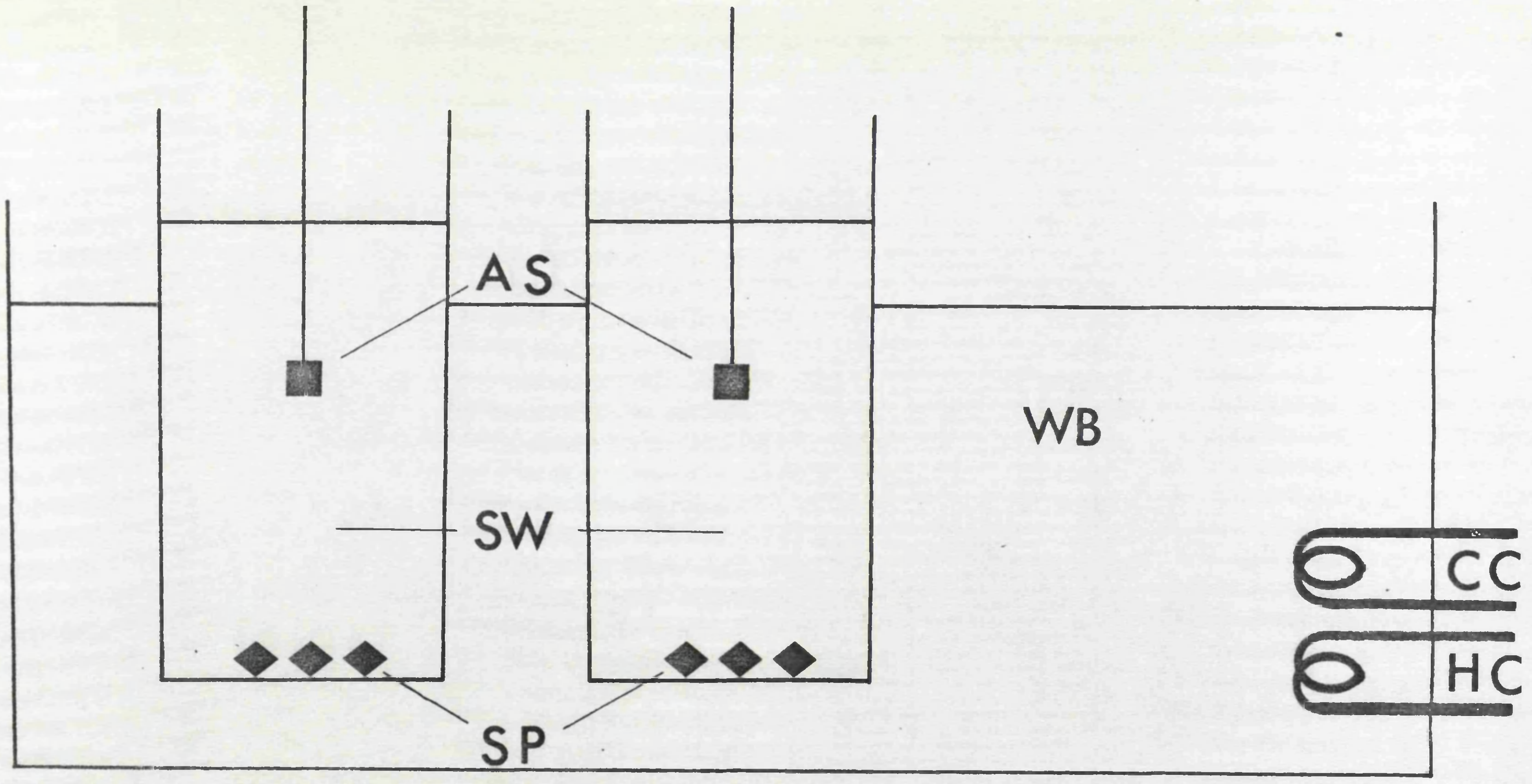


Fig.1

Fig. 2. Twenty-four hour experiments;
percentage mortality versus temperature.

▲——▲ T. fabula

○——○ T. tenuis

Dotted lines indicate respective LD_{50}.

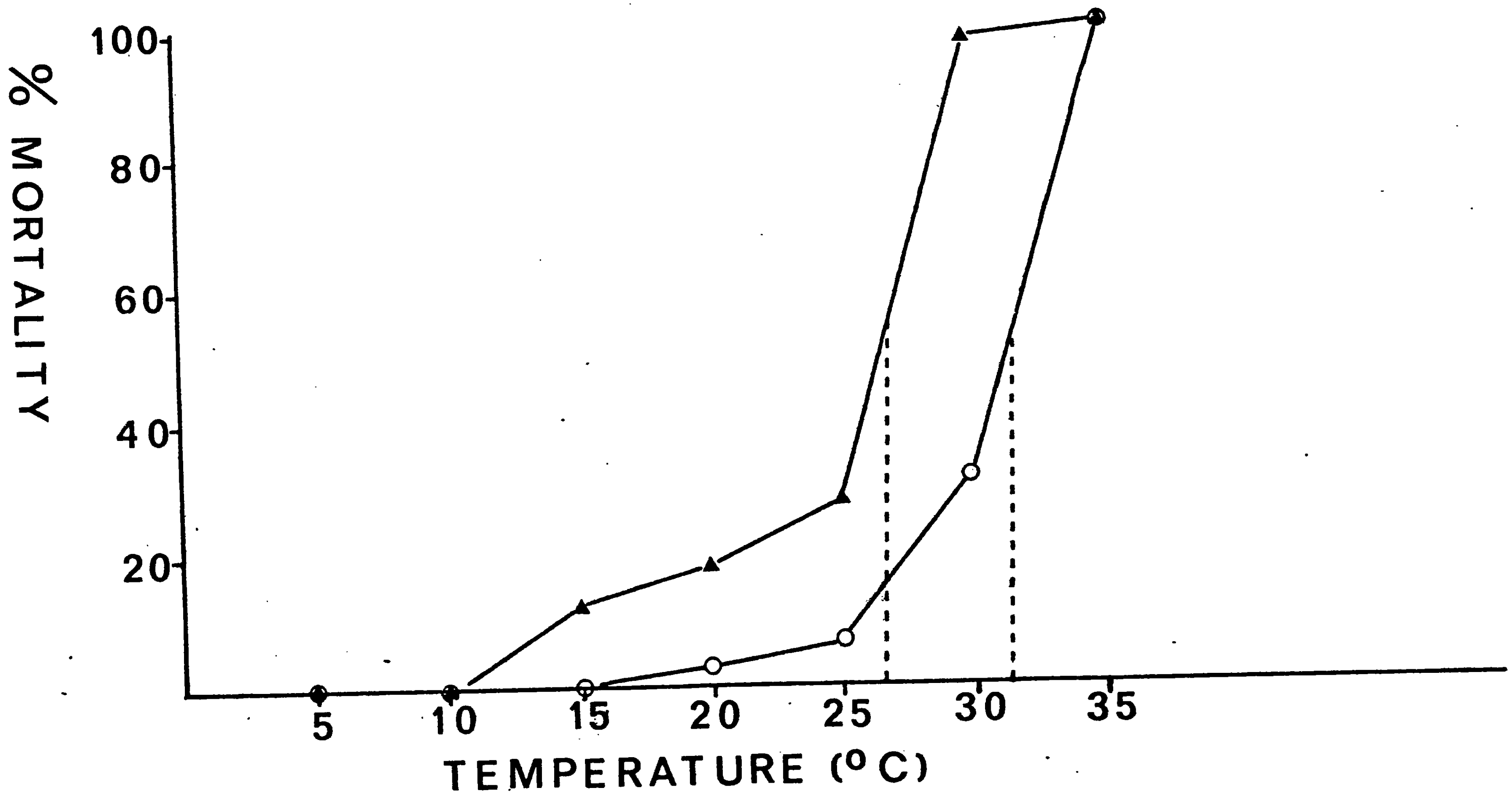


Fig. 2

Fig. 3. Least square regression lines (Bailey, 1959) and tolerance triangles of long-term experiments; LD_{50} in days is plotted against temperature (°C).

▲——▲ *T. tenuis*;

△- - - -△ *T. fabula*;

for areas of triangles, see text.

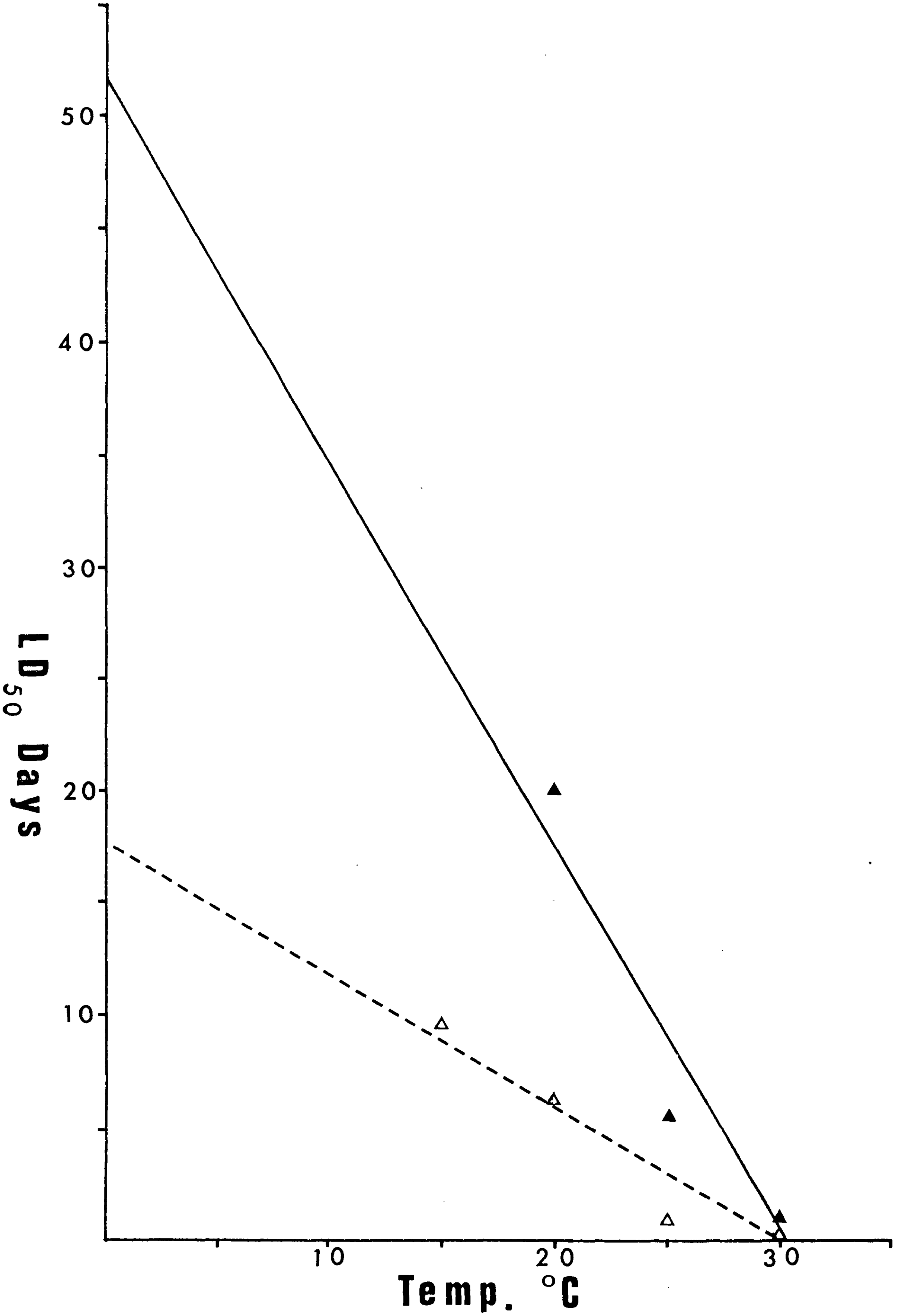


Fig. 3

Fig. 4. <u>T. tenuis</u> long-term experiments:

mortality in probits versus log time in days.

■ - 20°C

□ - 25°C

○ - 30°C

See Table 2 for equations of regression lines.

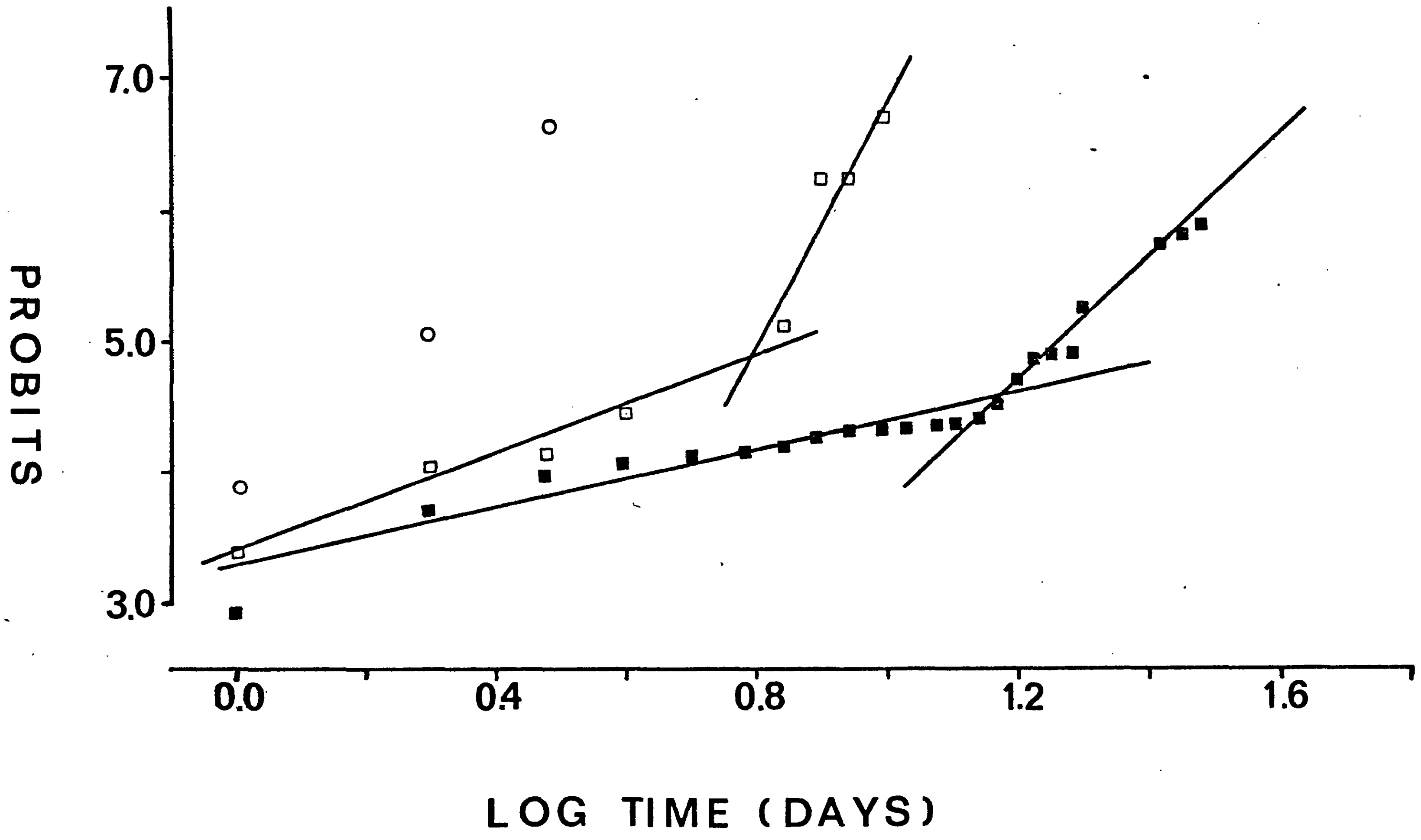


Fig. 4

Fig. 5. T. fabula. Long-term experiments;
mortality in probits versus log time in days

■ - 15°C

□ - 20°C

○ - 25°C

See Table 2 for equations of regression lines.

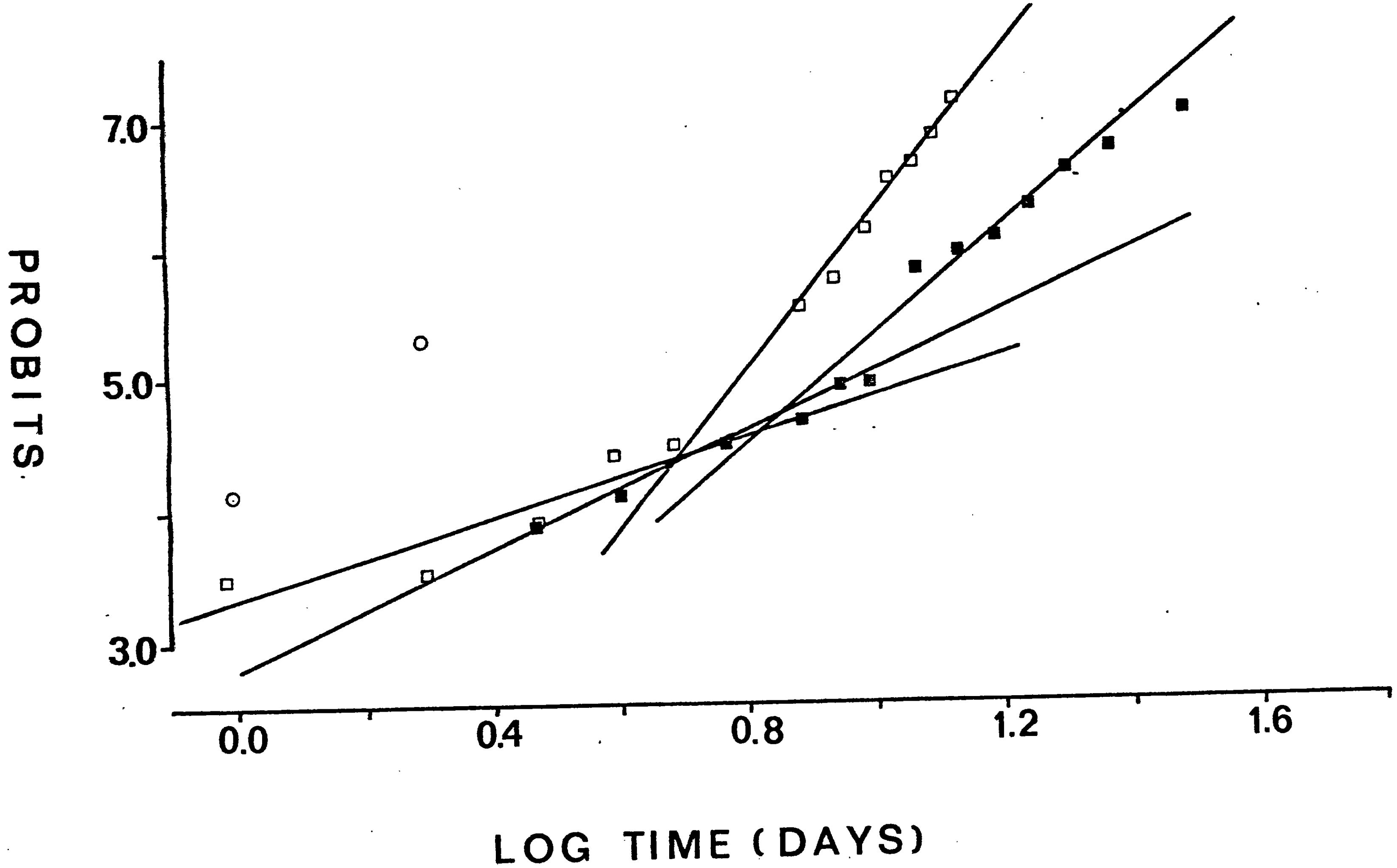


Fig. 5

Fig. 6. *T. tenuis*. Gradual increase temperature experiments; mortality in probits versus log time in days.

○ - EXPT. 1,
■ - EXPT. 2,
□ - EXPT. 3.

See Table 3 for rate of increase and equations of regression lines.

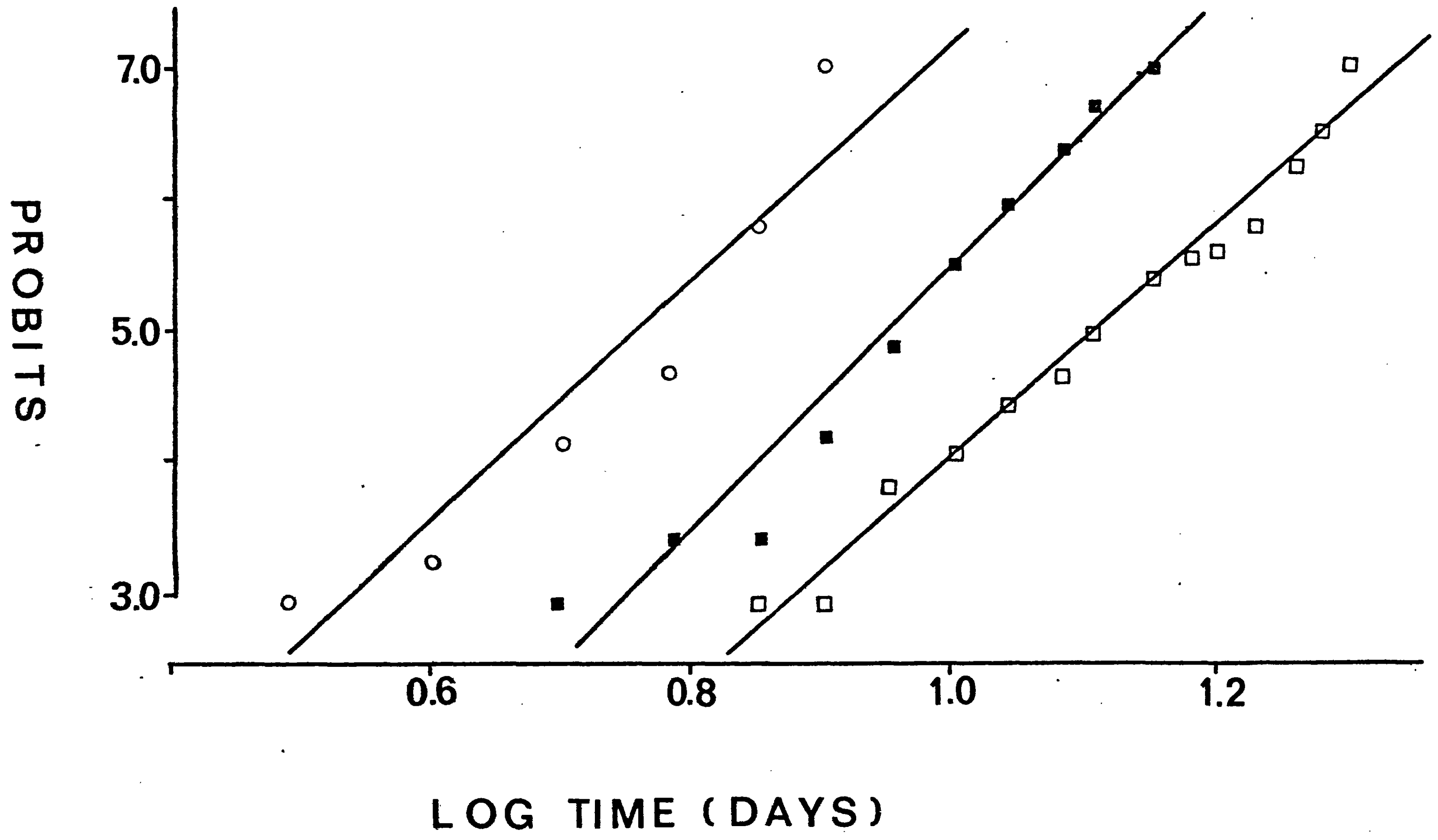


Fig.6

Fig. 7. T. fabula. Gradual increase temperature experiments; mortality in probits versus log time in days.

○ - EXPT. 4,
■ - EXPT. 5,
□ - EXPT 6.

See Table 3 for rate of increase and equations of regression lines.

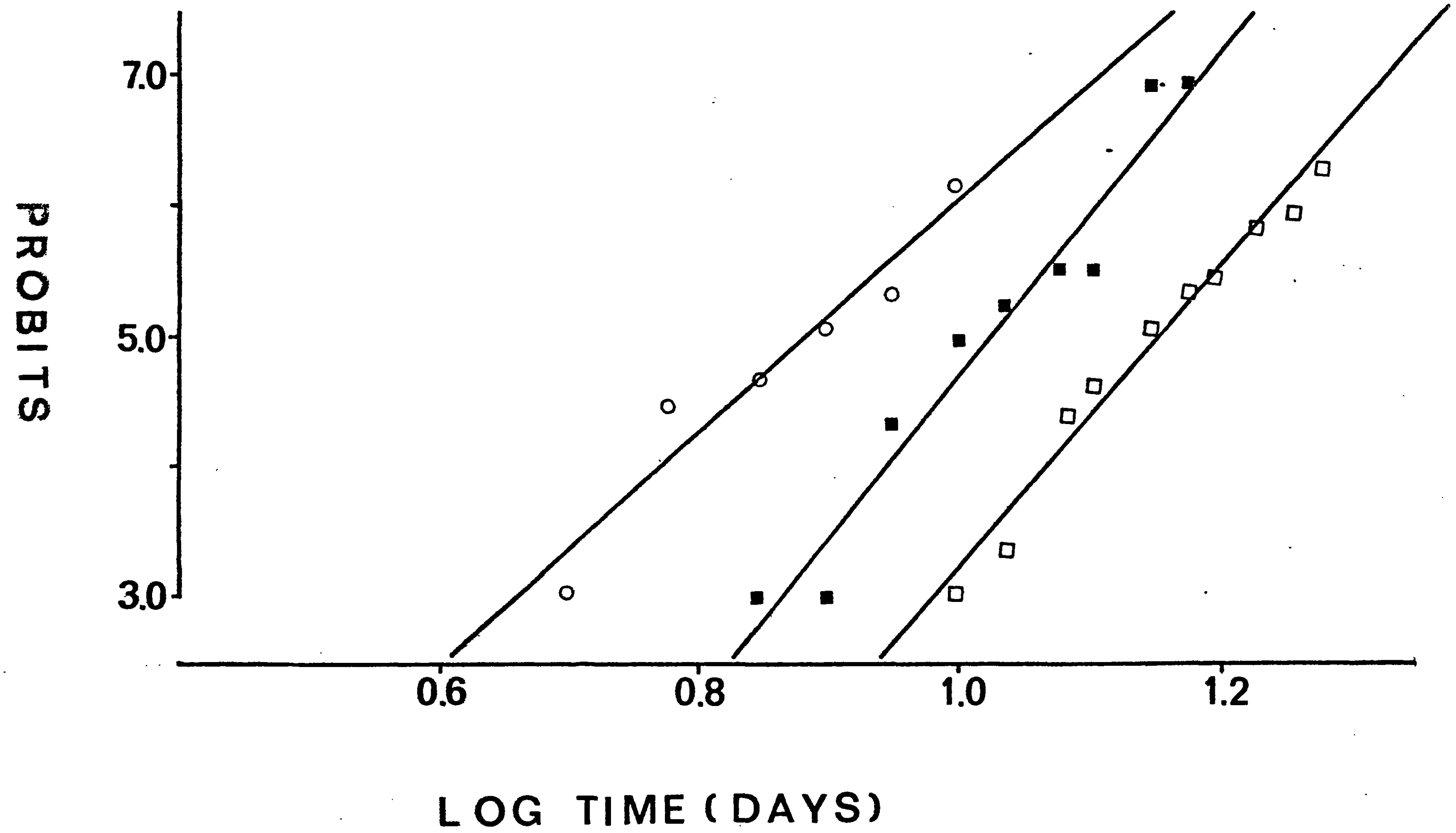


Fig. 7

Fig. 8. Least squares regression lines (Bailey, 1959) and tolerance triangles of gradual increase experiments;

LD_{50} (°C) is plotted against LD_{50} (days).

▲——▲ *T. tenuis*;

△- - -△ *T. fabula*;

for areas of triangles, see text.

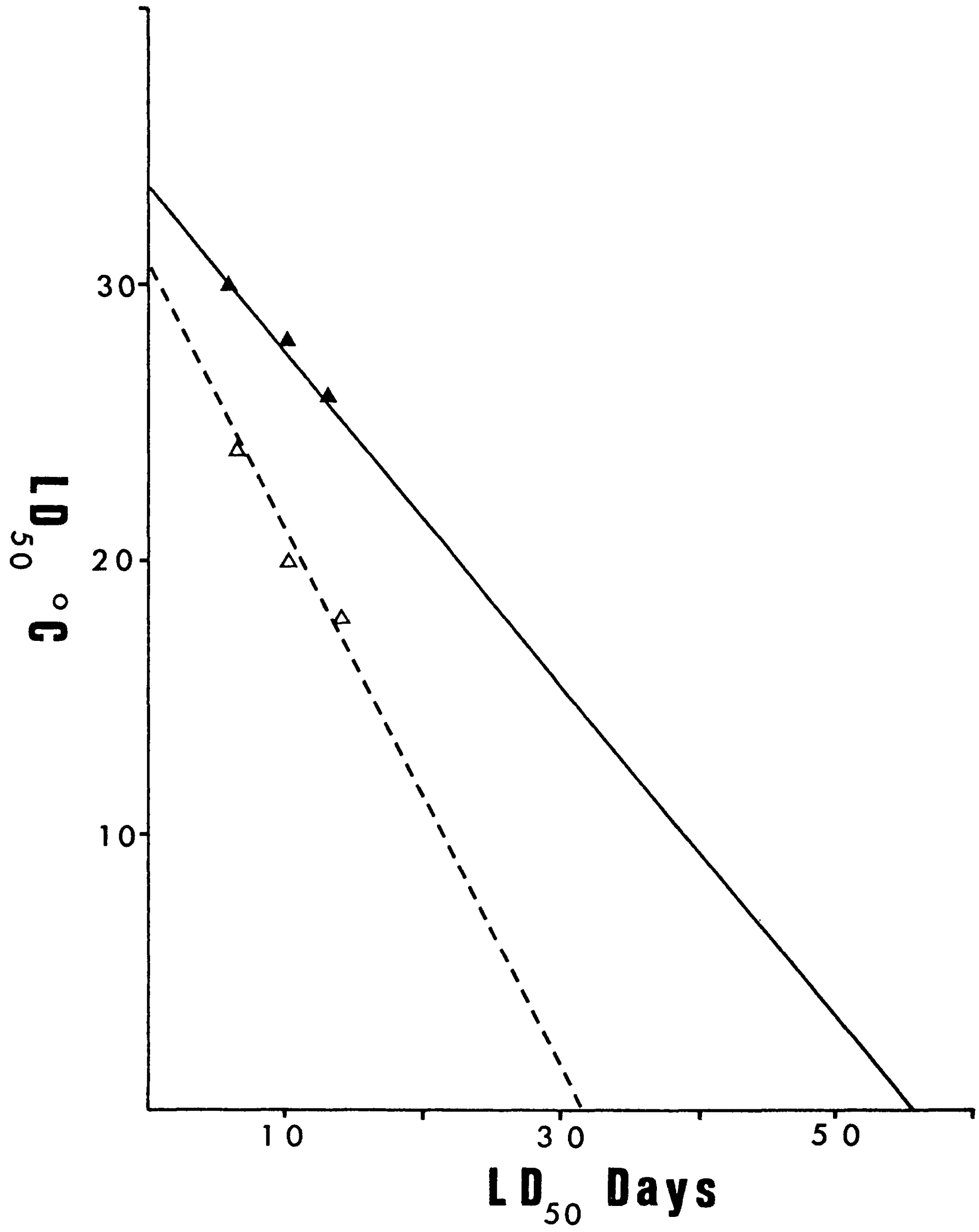


Fig.8

Fig. 9. Least squares regression lines (Bailey, 1959) and upper temperature tolerance triangles (McErlean et al, 1969), of acclimation experiments.

T_a : temperature of acclimation

$LD_{50} - T_a$: difference in °C between LD_{50} (°C) and temperature of acclimation.

▲——▲ *T. tenuis*

△– – –△ *T. fabula*;

for areas of triangles, see text.

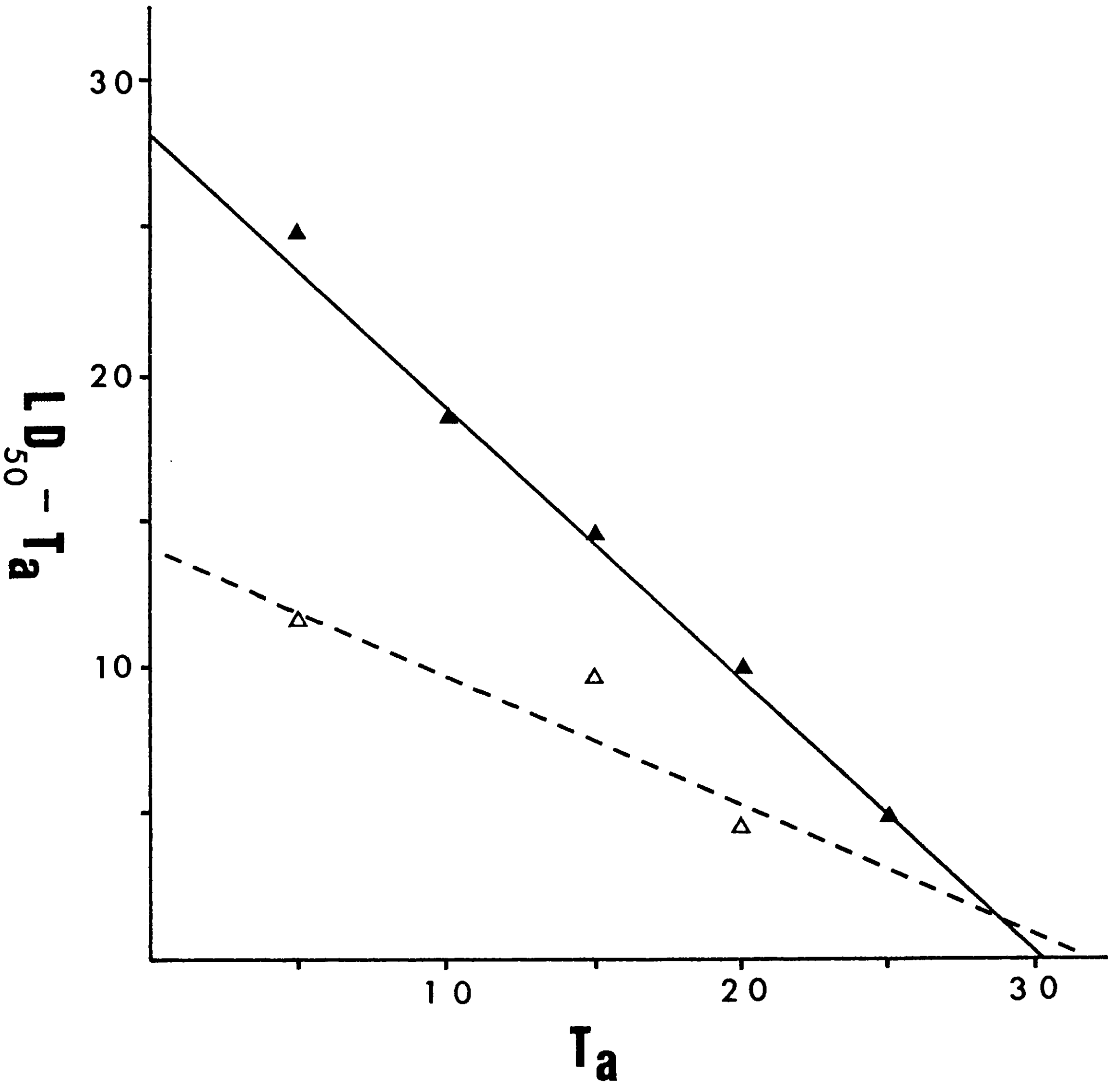


Fig. 9

Fig. 10. T. tenuis. Long-term seasonal variation experiments; starting date of the experiment versus its LD_{50} in days ($10^{\circ}C$) or hours ($25^{\circ}C$).

▲ - $10^{\circ}C$,

■ - $25^{\circ}C$.

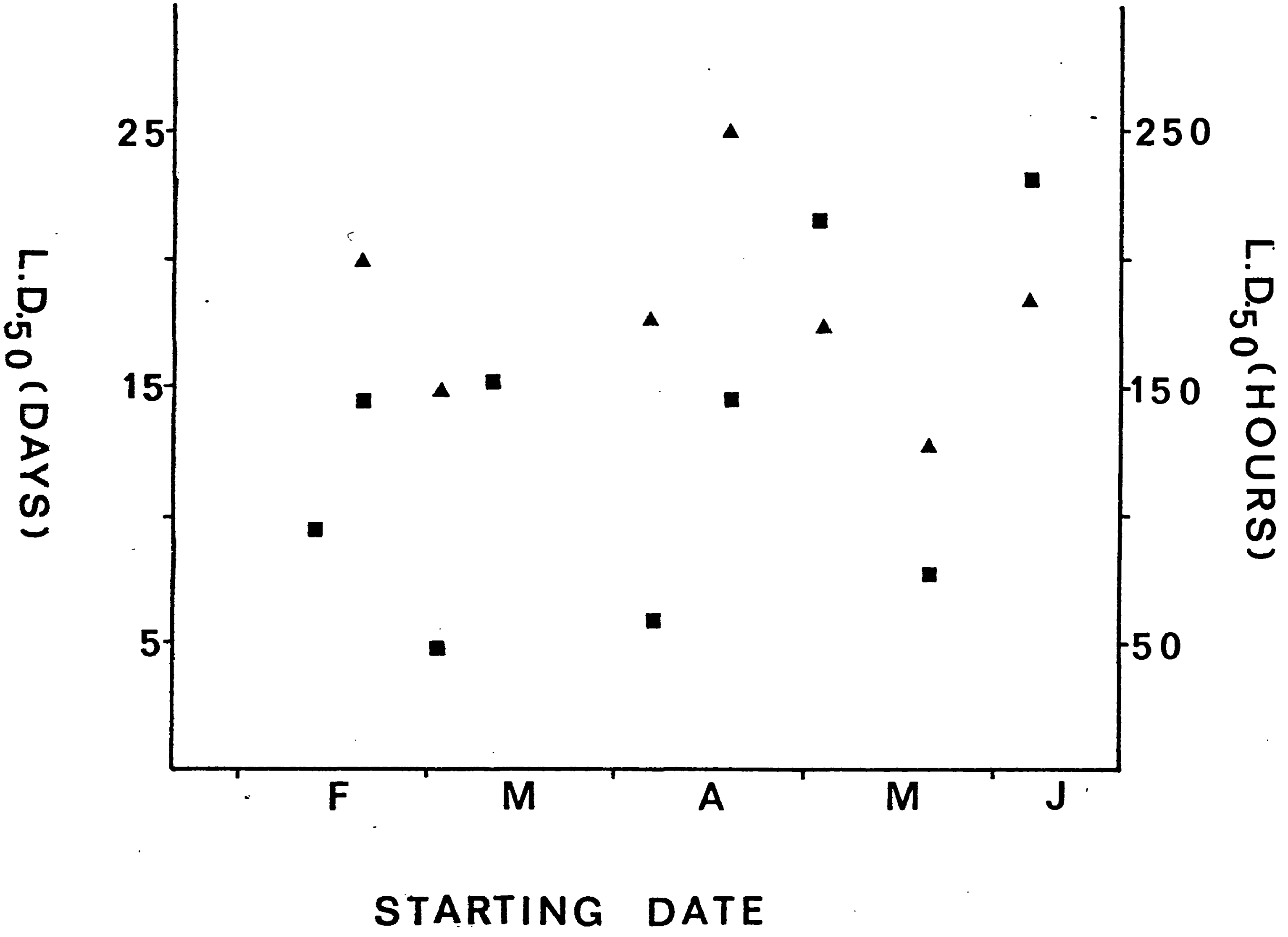


Fig.10

Fig. 11. T. tenuis Lethal tolerance of two groups of T. tenuis at 30°C; mortality in probits versus log time in hours.

Group A ($>$ 1.5 cm long),

Group B ($<$ 1.2 cm long)

The equations for the regression lines are

□- - - -□ (Group A) $y = 0.50 + 3.12\ x$

■———■ (Group B) $y = 0.33 + 3.17\ x$

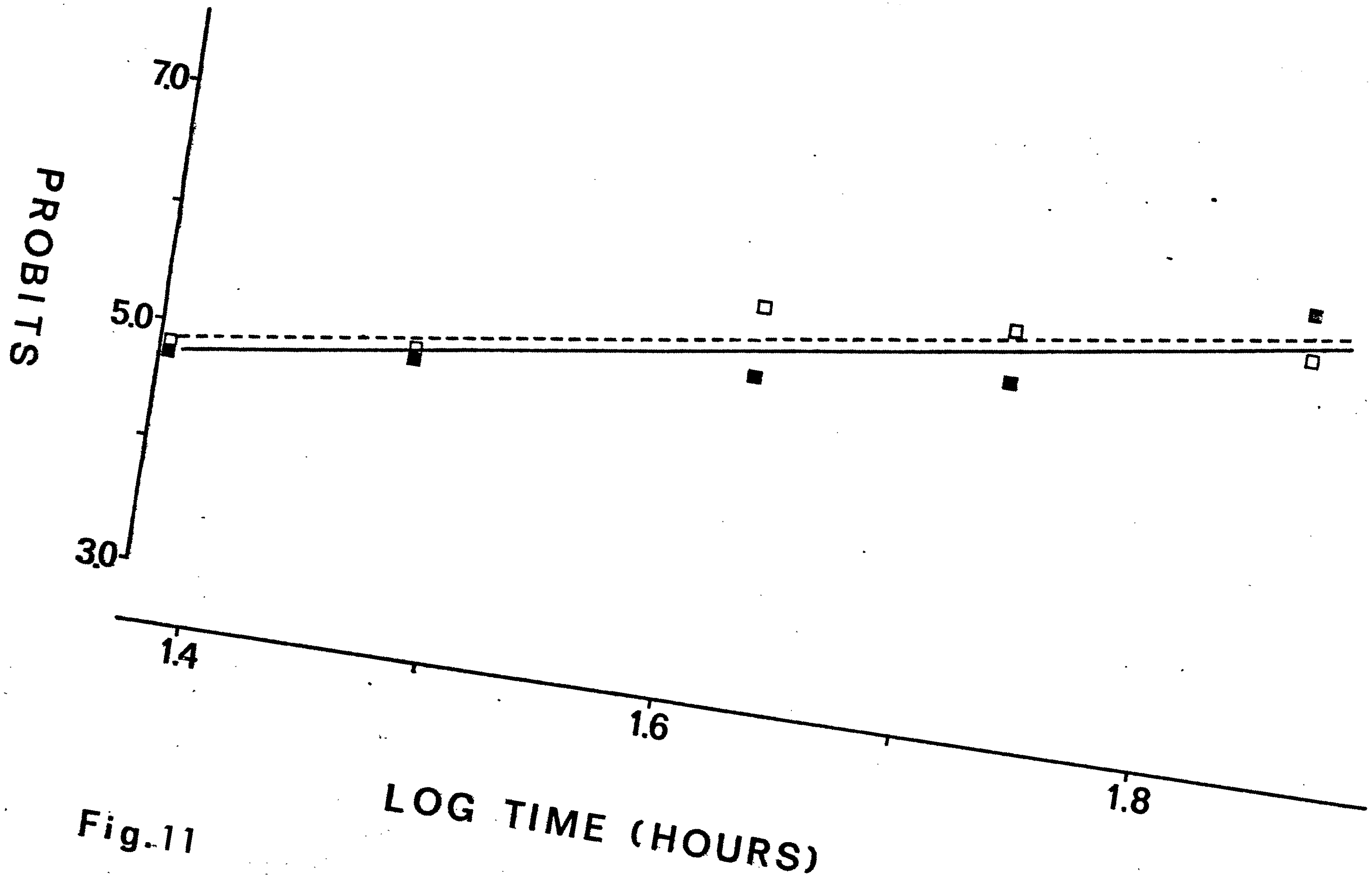


Fig. 11

Chapter 2

Distribution.

Introduction.

T. tenuis and T. fabula have been found in many places around Britain, mainly in clean sand on fairly exposed coasts (Ford, 1923; Stephen, 1933; Bassindale, 1940; Holme, 1949; Southward, 1953; Perkins and Williams, 1966; McIntyre, 1970; Perkins, 1972; Probert, 1975) and their geographical distribution ranges from Norway to Morocco (Forbes and Hanley, 1853; Tebble, 1966; Rasmussen, 1973).

The distribution of T. tenuis and T. fabula in Kames Bay, Millport, has been the subject of extensive investigation, particularly in the late 1920's and early 1930's by Stephen (1928, 1929, 1930, 1931, 1932). Later studies (Watkin, 1942; Clark and Milne, 1955) confirmed these earlier results, and it appears that populations of both species are well established in the bay.

In Kames Bay, the distribution of the two species with regard to tidal height is quite distinct; T. tenuis is littoral, T. fabula is sublittoral, and there is only a slight overlap occurring just below LWS (Stephen, 1928; Watkin, 1942, Clark and Milne, 1955).

It was decided to investigate both intraspecific and interspecific small-scale distribution (i.e. the dispersion patterns) of both species, in order to compare the patterns and to find out whether one species affected the distribution of the other. This investigation, which comprises the bulk of the chapter, forms the subject matter of two papers "The dispersion of Tellina tenuis da Costa from Kames Bay, Millport", Marine Biology, (1976) 37, 371-376 and "The distribution of two closely related species of Tellina (T. tenuis da Costa and T. fabula Gmelin)", Underwater Association Annual Symposium N.S.2 1976 (in press) (see end of Chapter).

Attempts were also made to find the settlement patterns of the larvae of the two species. For many years marine biologists had assumed that the settlement of planktonic larvae followed a random pattern, but experiments, particularly those of Wilson and Day (1934), Wilson (1937, 1948, 1952, 1953 a, b, 1968) and Knight-Jones (1951), have since shown that many larvae are capable to some extent of selecting a site for settlement and subsequent metamorphosis.

It has been suggested (Holme, 1961) that adult T. tenuis can, by virtue of their orientation within the sediment, undertake considerable horizontal migrations. In this way, although larval settlement might have been random, the adults could move to their preferred littoral or sublittoral situation. To investigate this suggestion, the movements of marked populations of T. tenuis were followed over a maximum period of fifteen months.

Materials and Methods.

Two methods were employed to sample the settling larvae. The first method employed enamel dissection trays 25 cm x 20 cm x 5 cm deep filled with different types of sediment. These were left for one month at various sites - on the beach 1.5 m above C.D.; in sand 5.0 m below C.D.; and on rock 8.0 m below C.D. To assist the finding of the trays, five, each joined with 2 m of string to its neighbour, were left at each site. The trays were collected underwater and put into polythene bags which were sealed and taken back to the laboratory. The contents of each tray were then examined under a binocular microscope for larvae or newly settled spat.

The second method involved hand cores, taken underwater, at three levels in Kames Bay. The levels chosen were, on the beach, at 1.0 m above C.D.; just below low tide, at 1.5 m below C.D.; and sublittorally near the main T. fabula collecting site, at 5.0 m below C.D. Two cores, each sampling an area of 50 cm^2 to a depth of 25 cm were taken at each site. The corers were then sealed and the contents examined as before in the laboratory. T. tenuis (size range 0.6 cm - 2.0 cm) for the mark and recapture experiments were sieved out of the sand, dried on paper towels, and marked with a fibre-tip magic marker (Artline 70, Shachihata, Japan). The marked animals, 200 in the first experiment and 400 in the second, were replaced inside a marked metre square 1.5 m above C.D. on the same day as they had been dug out. Black Perspex, 3 mm thick, was cut into rectangles 1.0 cm x 0.5 cm and buried with the animals in the second experiment to ascertain whether any animal movement observed was due to sediment transport alone. To record the movements of the marked animals, cores were taken at various time intervals with a corer 12.0 cm in diameter. In the first experiment, cores were taken from the marked metre square itself, but in the second experiment they were taken at distances of 1.0 m, 2.0 m, and 4.0 m each orientated N, S, E and W from the centre of the core and occasionally at the centre itself. The reason for this was not only to record the rate of spread (if any) of the animals, but also to minimise disturbance of the population within the marked metre square.

For explanation of the Clark and Evans' (1954) nearest neighbour test used in the dispersion pattern experiments (end of chapter), see statistical appendix.

Results.

None of the settlement trays which had been put down on the sand, either on the beach or sublittorally in Kames Bay were recovered, and it was presumed that they had been moved or lost during a period of bad weather. The trays which were recovered, from a rocky site 8.0 m below C.D. on the islands in the middle of the bay, yielded no trace of larvae or spat.

The results of the core samples for settling larvae and spat are shown in Table 1. It can be seen that the two uppermost sites, +1.0 m and -1.5 m, were dominated by T. tenuis, while the lowest site, -5.0 m, was dominated by T. fabula. The difference in numbers of T. tenuis between the top two sites was due principally to the large numbers of small (2.0 mm - 5.0 mm) animals (Fig. 1 and Table 2). The T. fabula shell lengths ranged from 0.8 mm to 12.7 mm.

Mark and recapture experiment 1 ran for only 5 days before the marker on the beach was lost; experiment 2 ran for nearly 15 months. The results of experiments 1 and 2 are shown in Table 3 and Table 4 respectively. In experiment 1 (Table 3) cores taken inside the marked metre square showed a significant change in the numbers of marked and unmarked animals recovered (X^2 = 13.31, d.f. = 5, p = 0.02 (Bailey, 1959). This change, however, appeared to have been due to loss of animals rather than to migration outwards, since the marked animals lost were not found outside the marked metre square. Cores taken on day 5 showed that there was a significant difference when the numbers of marked and unmarked animals inside the metre square were compared with the numbers outside (X^2 = 13.79; d.f. = 1, p = 0.0002 (Bailey, 1959)).

In the second mark and recapture experiment, no marked animals nor any Perspex rectangles were recovered from the sampling sites 2.0 m and 4.0 m away from the centre of the marked metre square. These results have therefore been omitted from Table 4. Table 4 shows that there was no significant change in the number of unmarked _T. tenuis_ recovered 1.0 m from the centre of the marked metre square (X^2 = 19.07, d.f. = 27, p = 0.87 (Bailey, 1959)). Table 4 further shows that there were very few marked animals recovered from outside the marked square; in addition, no Perspex rectangles were recovered outside the marked metre square at all. As a check on these results, the centre of the marked metre square was also sampled (Table 5). It was found that there was no significant change in the numbers of marked animals to the numbers of Perspex rectangles either overall (X^2 = 2.07, d.f. = 4, p = 0.72 (Bailey, 1959)) or comparing the first sample (7.5.75) with the last sample (5.8.76) (p = 0.37, Fisher's Exact Probability Test (Siegel, 1956)). Likewise, there was no significant change in the numbers of unmarked animals, marked animals, and

Perspex rectangles ($X^2 = 7.46$, d.f. = 8, $p = 0.49$(Bailey, 1959)).

Discussion.

T. tenuis spawns around June (Ansell and Trevallion, 1967, Trevallion and Ansell, 1967), and according to Stephen (1928) the spatfall of *T. tenuis* is deposited over a period of 2 to 3 months during the summer. In more northerly latitudes the *T. tenuis* larvae all but disappear from the plankton by the end of July (Rasmussen, 1973).

No such information is available for the spawning and spatfall of *T. fabula* in British waters although Stephen (1932) suggested it was the same as *T. tenuis*. However, Muus (1973) has found that, in the Oresund, the main spatfall occurred in August, but there were still a few newly settled specimens in February.

The settlement trays were recovered towards the end of July, and so one would expect that they should have collected some of the spatfall of *T. tenuis* or *T. fabula*. The loss of the control trays, however, precludes drawing any firm conclusions from this experiment.

The results from the coring experiments suggest that *T. tenuis* settles exclusively from about 2.0 m below C.D. upward, and *T. fabula* settles exclusively in the deeper parts of the bay. These conclusions agree with those of Stephen (1928, 1932). Recently, Muus (1973) has cast doubt upon Stephen's (1928, 1932) method of ageing *T. tenuis* and *T. fabula*. Muus has suggested that the 0+ year groups described by Stephen

(1928, 1932), which were around 2.0 mm long, were in fact the 1+ year group, and that the newly-settled larvae were less than 1.0 mm long. If this is the case, my results largely reflect the distribution of _T. tenuis_ and _T. fabula_ after one year's exposure to the environmental factors, and the lack of newly-settled spat may have been due to natural fluctuation in brood production (Stephen, 1938).

Adult _T. tenuis_ do not move far from their original positions in the sand. It has been suggested by Holme (1961) that the Tellinidae undertook horizontal migrations within the sediment, although earlier he had noted that some artificially enlarged populations showed little spread (Holme, 1950).

Other littoral bivalves undertake horizontal migrations on top of the sediment (Brafield and Newell, 1961), while _Donax_ migrates up and down the beach with the surf (Trueman, 1971). Such migrations may enable the animals to take advantage of new feeding grounds (Brafield and Newell, 1961), and certainly _T. tenuis_ can move within the sediment (see Chapter 5). However, the animals in Kames Bay do not appear to move, and horizontal migration within the sediment may, if it occurs at all, be only of the order of a few centimetres.

Table 1. Date, site height with respect to Chart Datum, and faunal composition of cores, taken in Kames Bay.

Date	Site Height (m)	Number of molluscs		
		T.tenuis	T.fabula	Others
	+ 1.0	4	0	0
23rd July	- 1.5	26	0	0
	- 5.0	1	7	3
	+ 1.0	11	0	0
5th Aug.	- 1.5	54	0	0
	- 5.0	0	9	1
	+ 1.0	8	0	0
18th Aug.	- 1.5	37	0	0
	- 5.0	1	10	4

Table 2. Comparison (Fisher's Exact Probability Test (Siegel, 1956) and X^2 (Bailey, 1959)) of the sizes of T. tenuis sampled 1.0 m above C.D. and 1.5 m below C.D.

Collection date	Site	Size		P
		≤5.0 mm	>5.0 mm	
23rd July	+ 1.0 m	4	0	0.30
	- 1.5 m	20	8	
5th Aug.	+ 1.0 m	5	6	<0.001
	- 1.5 m	44	9	
18th Aug.	+ 1.0 m	3	5	<0.001
	- 1.5 m	23	14	
All	+ 1.0 m	12	11	<0.001
	- 1.5 m	87	31	

Table 3. Mark and recapture experiment No. 1;

200 marked *T. tenuis* placed inside a marked metre square 6.9.74.

Number of marked (B) and unmarked (W) *T. tenuis* recovered from (a) inside the marked metre square and (b) 1.0 m outside the marked metre square.

Time elapsed in days.

Time (Days)	(a) inside		(b) outside	
	B	W	B	W
0	12	74	0	110
1	30	87	-	-
2	16	44	-	-
3	17	54	0	128
4	12	57	1	130
5	17	128	1	132

Table 4. Mark and recapture experiment No. 2; 400 marked <u>T. tenuis</u> placed inside a marked metre square 6.5.75. Date of sampling and numbers of unmarked <u>T. tenuis</u> with (in brackets) numbers of marked <u>T. tenuis</u> (when found) recovered at a a distance of 1.0 m N, S, E and W of the centre of a marked metre square.

Date	Bearing			
	N	S	E	W
7.5.75	19	21	13	18
11.5.75	21	20	22	18(2)
15.5.75	23	13	24	22(2)
29.5.75	21	19	20	18(1)
13.6.75	21	20	22	20(1)
2.7.75	18(1)	14	12	21
5.8.75	24	18	21	15
11.11.75	17	28	17	19
18.4.76	18	13	14	19
5.8.76	21	20	16	12

Table 5. Mark and recapture experiment No. 2; 400 marked T. tenuis and 120 black Perspex rectangles placed inside a marked metre square 6.5.75. Date of sampling and number of unmarked T. tenuis (W), marked T. tenuis (B) and Perspex rectangles (P) recovered from the centre of a marked metre square.

Date	Category		
	W	B	P
7.5.75	17	13	7
10.5.75	24	16	10
11.11.75	16	10	3
18.4.75	9	6	1
5.8.76	17	4	2

Fig. 1. Shell length (mm) and number of specimens sampled at 1.0 m above C.D. (▧) and 1.5 m below C.D. (▨) .

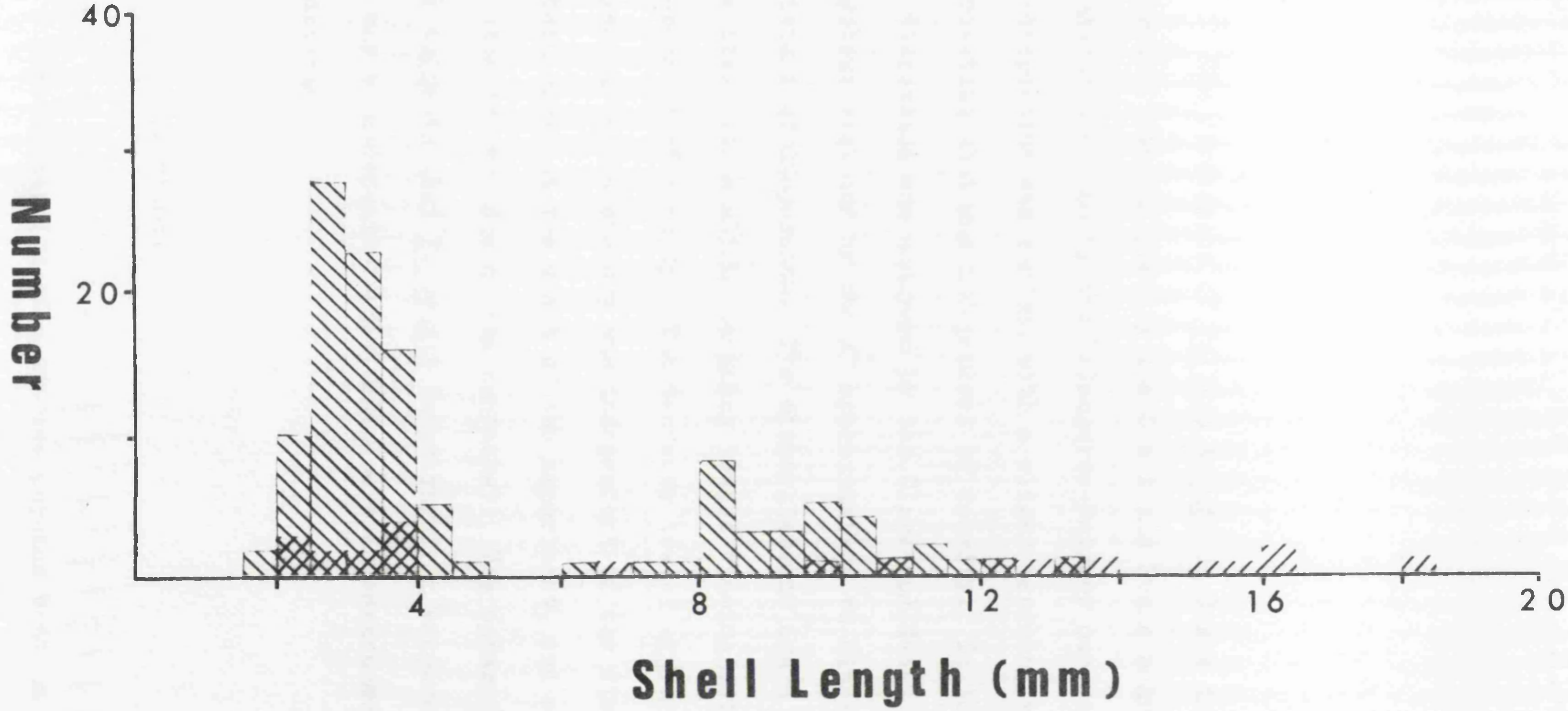


Fig.1

DISPERSION OF TELLINA TENUIS FROM KAMES BAY, MILLPORT, SCOTLAND.

Abstract.

The dispersion of Tellina tenuis da Costa in the laboratory was analysed by the Clark and Evans nearest-neighbour test and by the Kolmogorov-Smirnov one-sample test. The dispersion was random, with a slight tendency toward aggregation that was independent of density. In the field, the dispersion was analysed by the Clark and Evans nearest-neighbour test and by the X^2 approximation to Fisher's coefficient of dispersion. The dispersion was again random, this time with a slight tendency toward spacing out that was independent of density. The tendency toward aggregation displayed in the laboratory was independent of the dispersion pattern shown at the start of the experiment, and also unaffected by the edge of the container. The apparent randomness suggests that T. tenuis is primarily a suspension feeder, but may be a deposit feeder under certain environmental conditions.

Introduction.

The dispersion of a species depends both on the nature of its environment and its behaviour. If the species is rare, or if the environment is strongly heterogenous, the dispersion will tend toward aggregation, since its optimum habitat will occur patchily (Hairston, 1959; Levinton, 1972). Aggregation may also result from the gregarious behaviour of the species as larvae (Meadows and Campbell, 1972) or as adults (Campbell and Meadows, 1974). On the other hand, a negative interaction, such as territorial behaviour, might result in an even or uniform dispersion (Holme, 1950; Johnson, 1959; Crisp, 1961; Connell, 1963). Random dispersion would be expected in the absence of such behavioural patterns in a homogenous environment.

The dispersion of Tellina tenuis was studied by Holme (1950) both from sample counts and by plotting the positions of the bivalves within quadrats located on the shore. He found that dispersion was uniform at moderate densities, but became random if the density increased above $460/m^2$. He suggested that the characteristic spacing at moderate densities was correlated with the foraging activities of the inhalent siphon on the soil surface, and that at higher densities the spacing broke down owing to the confusion resulting from a number of siphons meeting one another on the surface. Other workers claim to have detected random or aggregated dispersions of T. tenuis from benthic sampling investigations (Clark and Milne, 1955; Eisma, 1966). A series of experiments was therefore designed to ascertain whether the dispersion of T. tenuis was aggregated, random or uniform, under laboratory conditions.

Materials and Methods.

Tellina tenuis da Costa is found at Kames Bay, Millport, from 3.0 m above chart datum (high-water neap) to 0.01 m chart datum (just below low-water spring) at densities of up to 8,000/m^2 (Stephen, 1928; Watkin, 1942; Clark and Milne, 1955). Bivalves and sand were gathered from an area 1.5 m above chart datum, roughly corresponding to Station 30 of Watkin (1942).

In the field, the top half of a dustbin, 33 cm in diameter, was pushed into the sand to a depth of 25 cm. The sand around was dug away and the entire core, with the dustbin around it, was lifted onto a polythene sheet. Cores were taken at various heights above chart datum to provide results for different densities of Tellina tenuis. The lifting caused little or no disturbance of the sand or of the bivalves, which were found as described by Holme (1950), i.e. lying quiescent with neither their foot nor their siphons protruding. The sand was then carefully excavated with a teaspoon. When a bivalve was encountered, its position was plotted on a piece of Perspex placed over the bin and the bivalve was then removed. Distances between bivalves were measured horizontally from the centre of the bivalve, and the Clark and Evans(1954) nearest-neighbour analysis was used to ascertain whether the observed distances were significantly different from random. The animals are aggregated if the statistic R, the measure of the degree of departure from randomness, is significantly less than 1, or spaced if R is significantly greater than 1, at $P = 0.05$.

Two cores, each covering 50 cm^2, were also taken from each one-metre-square in an 8 x 8 m grid, located 1.5 m above chart datum. The counts per metre square were tested by the X^2 approximation to Fisher's coefficient of dispersion (Blackman, 1942; Holme, 1950; Clark and Milne, 1955) for quadrat size 1 x 1 m, 2 x 2 m, 4 x 4 m, 8 x 1 m and 1 x 8 m. The coefficient tends to unity when the dispersion is random, is less than 1 when it is spaced out, and greater than 1 when it is aggregated. The significance of the departure from unity can be tested by the "index of dispersion". The index is equal to (n -1) times the coefficient of dispersion when n is the number of units in the sample, and is approximately distributed as X^2 with (n -1) degrees of freedom (Clark and Milne, 1955).

In the laboratory, circular troughs 33.5 cm in diameter by 15.25 cm deep were filled with the sand to a depth of around 10 cm and then topped up with sea water. Up to 350 Tellina tenuis per bowl were scattered over the surface of the sand on the same day that they had been collected. The experimental troughs were left at 10°C on a 12 h day:12 h night light regime, and were continuously aerated with an airstone. The slight current which was generated in the overlying water did not cause any discernable movement or sorting of the sand grains. After 1 week the sand was removed and the positions of the bivalves plotted on Perspex as in the field. The distances of the bivalves from the side of the dish were measured and analysed by a Kolmogorov-Smirnov one-sample test (Siegel, 1956). This test compares the observed cumulative frequency distribution of the distances with the cumulative frequency of a theoretical even distribution.

Results.

The *Tellina tenuis* in all the dustbin cores were randomly dispersed. There was some tendency toward spacing out, as all except two of the R values were greater than 1, but no value was significantly different from 1 (Table 1). There was no suggestion of spacing out at low densities, and the randomness of the dispersion was independent of the density ($r = 0.25$, $t = 0.74$, $P > 0.05$) (Bailey, 1959).

Similar results were obtained from the 8 x 8 m grid (Fig. 1). The bivalves in the 1 x 1 m quadrat were spaced out ($P = 1.7 \times 10^{-4}$), but those in the 2 x 2 m, 4 x 4 m, 1 x 8 m and 8 x 1 m quadrats were randomly dispersed ($P = 0.55$, 0.054, 0.46 and 0.18, respectively). Stephen (1928, 1929, 1930) himself made no statement on the dispersion of *Tellina tenuis* beyond emphasizing the variability in populations at any one place; however, Holme (1950) examined Stephen's results and came to the conclusion that the data showed no evidence of uniform populations. Clark and Milne (1955) found both random and aggregated populations, and stated that the disagreement of their conclusions with those of Holme (1950) was probably explained by different sample sizes.

My results indicated, however, that the population of

Tellina tenuis in Kames Bay was largely randomly dispersed and that the randomness was independent of density.

There was no evidence of spacing out in the laboratory; on the contrary the bivalves showed a tendency toward aggregation. All except two of the R values were less than 1, six of them significantly so (Table 2). Again there was no correlation between the degree of aggregation and the density ($r = 0.11$, $t = 0.47$, $P > 0.05$) (Bailey, 1959).

To ensure that the bivalves were moving during the experiment, and that the dispersion pattern observed was not due to the way they had been introduced into the dishes, the following experiment was set up. In 2 dishes the bivalves were scattered on the sand surface at random as usual, in 2 dishes they were aggregated, and in 2 further dishes they were evenly spaced. At the conclusion of the experiment it was found that the bivalves had aggregated in only 1 dish, into which they had been scattered at random; in all other dishes they were randomly dispersed (Table 3). Individuals had moved between 3 and 16 cm from their original positions at the start of the experiment.

Another experiment, in which 16 bivalves were put into each of 2 dishes, was left in the laboratory for 1 month with a subsand filter to keep the water clean. When the bivalves were removed and the results analysed, the dispersion in both dishes was found to be random ($R_1 = 0.89$, $C_1 = 0.80$; $R_2 = 0.78$, $C_2 = 1.70$); it was therefore concluded that the bivalves had remained randomly dispersed over this time span.

The tendency toward aggregation in the laboratory might have been caused by a reaction to the sides of the chamber, as has been found with hermit crabs (Meadows and Mitchell, 1973; Mitchell, 1975). When the Kolmogorov-Smirnov one-sample test was applied to the measurements obtained for the bivalves' distances from the edge, the results showed that there was no significant correlation between the aggregation of the bivalves and their reaction to the sides of the dish ($P = 0.082$) (Table 4). We can therefore conclude that their confinement in a closed container did not significantly affect their dispersion.

Discussion.

The results indicate that Tellina tenuis was randomly dispersed, with a tendency toward aggregation in the laboratory and towards spacing out in the field. It has been suggested by several authors (Holme, 1950; Connell, 1955, 1963; Johnson, 1959; Levinton, 1972) that the method of feeding of an animal influences its dispersion. T. tenuis is usually classified as a deposit feeder (Blegvad, 1915; Atkins, 1937; Yonge, 1949; Pohlo, 1969), and Holme (1950) advanced the hypothesis that the searching of the inhalent siphon is used to maintain feeding territories.

Personal observations of actively feeding Tellina tenuis suggest that, while the siphons are waving about, they do not scour or draw in the sediment itself. The mode of feeding of T. tenuis has been described by Yonge (1949), who observed that the inhalent siphon draws in material lying just above the sand, but does not actively pull in bottom material. Again this description suggests that T. tenuis is a suspension feeder, and not a deposit feeder such as the related *Macoma balthica* which has been observed actively stirring up the sediment with its inhalent siphon, leaving star-shaped feeding tracks on the surface (Hulscher, 1973). Indeed, Trevallion (1971) noted that *T. tenuis* can feed on particles in suspension as well as on deposits, and that it is found in an environment more favourable to filter feeding.

The uniform dispersion observed in many of the Bivalvia may be explained by competition for food (Heip, 1975), but if there is abundant food in suspension, then they have no necessity to maintain a feeding territory. Consequently, one would expect suspension feeders in a homogenous environment to be randomly dispersed.

Both random and aggregated dispersions of suspension-feeding bivalves have been observed by Connell (1955) in *Mya arenaria* and *Petricola pholadiformis* and by Jackson (1968) in *Mulinia lateralis*, while other workers have observed such dispersions within the Tellinidae. Gilbert (1968) found that juvenile *Tellina agilis* were aggregated owing to the spatfall being concentrated along mean low water, but that adults were randomly dispersed. Random and aggregated dispersions of *T. fabula* have been reported by Clark and Milne (1955) from Kames Bay, by Eisma (1966) from the Dutch coast and by Probert (1973) from Mevagissey Bay.

On the other hand, Holme (1950) found that *Tellina tenuis* showed a tendency toward an even dispersion as a consequence of siphonal activity during feeding, becoming random only at higher densities. An analogous situation was observed by Johnson (1959) in *Phoronopsis viridis*, which was spaced out owing to the lophophore searching the rock. Levinton (1972), however, found that the deposit feeder Nacula proxima, which works the sediment with its palps, was randomly dispersed.

The above examples show that, while it is difficult to relate the dispersion of a species to its mode of feeding, some correlation does exist. It may be that Tellina tenuis can adopt either deposit or suspension feeding depending on environmental conditions, and thus its dispersion may vary from place to place.

In Kames Bay, Tellina tenuis was found at much higher densities than those observed by Holme (1950). It may be that, as found by Rosenberg (1974), high densities of a species are positively correlated with aggregation. Rosenberg's data, however, was analysed with the variance:mean ratio, which is subject to the serious disadvantage that it approaches unity as density decreases (Pielou, 1969; Heip, 1975). Nevertheless, it is unlikely that the aggregation effect would be constant at all densities in the laboratory, nor was aggregation detected in the field.

The random dispersion of Tellina tenuis in Kames Bay indicates environmental homogeneity and lack of interactions between the bivalves as adults. The possible effect of larval behaviour, however, on the dispersion of the adult population remains unknown.

Table 1. Tellina tenuis. Nearest-neighbour analysis of dispersion in the field. R : measure of departure from random; c : standard variate of the normal curve.

Expt	No. of animals	R	c	Distribution
1	101	0.98	0.34	Random
2	92	1.05	0.84	"
3	85	1.11	1.89	"
4	77	1.02	0.50	"
5	30	1.06	0.63	"
6	28	1.01	0.09	"
7	27	1.03	0.25	"
8	21	0.98	0.20	"
9	18	1.07	0.54	"
10	17	0.93	0.54	"

Table 2. *Tellina tenuis*. Nearest-neighbour analysis of dispersion in the laboratory. Lettering as in Table 1.

Expt	No. of animals	R	c	Distribution
1	332	0.98	0.57	Random
2	341	0.96	1.30	"
3	183	0.96	1.13	"
4	181	0.955	1.15	"
5	100	0.98	0.43	"
6	99	0.92	1.60	"
7	95	0.91	1.65	"
8	94	0.89	2.03	Aggregated
9	90	0.79	3.80	"
10	95	0.81	3.48	"
11	52	1.06	0.81	Random
12	55	0.97	0.37	"
13	51	0.77	3.08	Aggregated
14	51	0.74	3.50	"
15	33	0.97	0.30	Random
16	33	0.92	0.92	"
17	16	0.73	2.05	Aggregated
18	16	0.97	0.21	Random
19	8	0.72	1.51	"
20	8	1.33	1.80	"

Table 3. *Tellina tenuis.* Nearest neighbour analysis of distribution in the laboratory when placed in bowls aggregated, random or spaced. orig : as put in; obs : as taken out. Other lettering as in Table 1.

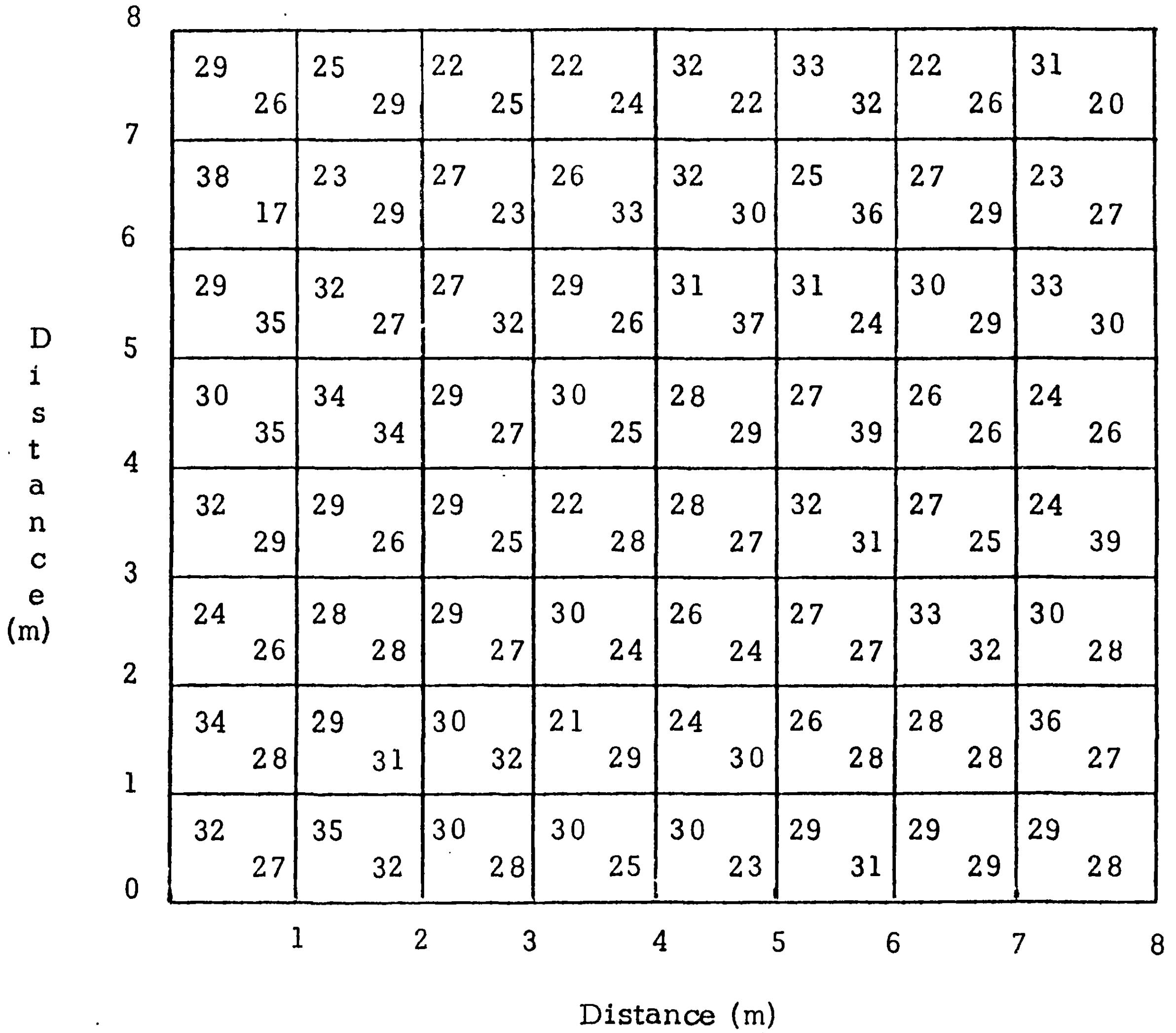
Expt		No. of animals	R orig	c orig	Orig distribution	R obs	c obs	Obs distribution
I	a	16	0.82	1.36	Random	0.73	2.10	Aggregated
	b	16	0.86	1.07	Random	0.92	0.61	Random
II	a	16	0.33	5.14	Aggregated	0.85	1.13	Random
	b	16	0.33	5.14	Aggregated	0.85	1.13	Random
III	a	16	1.31	2.36	Spaced	0.88	0.90	Random
	b	16	1.31	2.36	Spaced	1.00	0.01	Random

Table 4. Tellina tenuis. Dispersion; nearest neighbour compared to Kolmogorov-Smirnov one sample test. D = maximum deviation of observed values from expected values; S = significance of D at P = 0.05

Expt	Nearest-Neighbour distribution	D	Kolmogorov-Smirnov S
1	Random	0.04	No
2	"	0.05	"
3	"	0.06	"
4	"	0.10	"
5	"	0.13	"
6	"	0.16	Yes
7	"	0.20	"
8	Aggregated	0.10	No
9	"	0.18	Yes
10	"	0.23	"
11	Random	0.13	No
12	"	0.15	"
13	Aggregated	0.15	"
14	"	0.36	Yes
15	Random	0.51	"
16	"	0.14	No
17	Aggregated	0.45	Yes
18	Random	0.40	No
19	"	0.26	"
20	"	0.11	"

<u>Fig. 1</u>

Distribution of T. tenuis within an 8 x 8 quadrat.



29 26	25 29	22 25	22 24	32 22	33 32	22 26	31 20
38 17	23 29	27 23	26 33	32 30	25 36	27 29	23 27
29 35	32 27	27 32	29 26	31 37	31 24	30 29	33 30
30 35	34 34	29 27	30 25	28 29	27 39	26 26	24 26
32 29	29 26	29 25	22 28	28 27	32 31	27 25	24 39
24 26	28 28	29 27	30 24	26 24	27 27	33 32	30 28
34 28	29 31	30 32	21 29	24 30	26 28	28 28	36 27
32 27	35 32	30 28	30 25	30 23	29 31	29 29	29 28

Fig.1

THE DISTRIBUTION OF TWO CLOSELY RELATED SPECIES OF *TELLINA* (*T. tenuis* da Costa and *T. fabula* Gmelin).

Abstract.

The dispersion patterns of *T. tenuis* and *T. fabula* were studied in the field and in the laboratory. The patterns were found to be largely random with a slight tendency toward aggregation in the laboratory. The hypothesis that both *T. tenuis* and *T. fabula* are suspension feeders is discussed, along with the factors governing the separation of the two populations in Kames Bay.

Introduction.

I have been investigating the factors which govern the distribution of *T. tenuis* and *T. fabula*, and one of the factors I have considered is the effect that animals of one species have on the dispersion pattern of their own and of the other species.

Although Holme (1950) had concluded that *T. tenuis* in the Exe Estuary were largely uniformly dispersed, both aggregation and randomness were reported from field samples by Clark and Milne (1955) in Kames Bay, and by Eisma (1966) off the Dutch coast. There have been no intensive studies of the dispersion pattern of *T. fabula*, but Clark and Milne (1955), Eisma (1966), and Probert (1975) all reported aggregation and randomness.

Morphologically, T. tenuis and T. fabula are almost identical (Yonge, 1949), but they can be distinguished by the characteristic diagonal striations on the right valve of T. fabula, and, with practice, by the fact that T. tenuis is slightly bigger and less elongate.

However, the field distributions of both species are quite distinct. T. tenuis is the dominant animal from HWN to around MLW, while T. fabula is dominant from LWS down to the 10m mark.

The sampling sites at Kames Bay, Millport, were marked in such a way as to be inconspicuous to the general public, yet easily located by me. On the beach I selected two large boulders, about 30m apart, at 1.5m above Chart Datum, and buried a wooden stake just below the sand mid-way between them. This was my main shore site, and, since I sampled a grid here, it will be referred to as "grid level".

My main underwater site, referred to as "Donaljean" was at the end of a line leading out from the rocks fringing the bay. These rocks were covered even at low tide. I also sampled mid-way between "grid-level" and "Donaljean" at the children's paddling pool.

Methods.

To record the dispersion pattern of T. tenuis on the shore, the top half of a dustbin was pushed into the sand to a depth of 25 cm when the tide was out. The sand around was dug away and the entire core, with the dustbin around it, was lifted onto a polythene sheet. When the lifting was done carefully there was little or no disturbance of the sand, which could then be spooned out, and the position of the animals plotted on a piece of Perspex placed over the top of the bin. Distances were measured horizontally from the centre of the animal, and the results analysed with the Clark and Evans (1954) Nearest Neighbour Test to ascertain whether the observed distances were significantly different from random. The animals are aggregated if the statistic R, the measure of the departure from randomness, is significantly less than 1, or spaced if R is significantly greater than 1, at $P = 0.05$. Cores were taken at different heights above C.D. to obtain results for different densities of T. tenuis.

On a larger scale, T. tenuis was field sampled at 1.5m above C.D., again when the tide was out, by taking 2 cores/m^2 with a corer of diameter 15 cm over an 8 x 8 grid. The results were tested using the X^2 approximation to Fisher's Coefficient of Dispersion for the quadrat size 1 x 1m, 2 x 2m, 4 x 4m, 8 x 1m and 1 x 8m. The Coefficient tends to unity when the population is random, is less than 1 when the population is spaced out, and is greater than 1 when the population is aggregated. The significance of the departure from unity may be tested by the "Index of Dispersion" (Blackman, 1942; Clark and Milne, 1955). The Index is equal to (n-1) times the Coefficient of Dispersion, where n is the number of units in the sample, and is approximately distributed as X^2 with (n-1) degrees of freedom.

The sublittoral sampling was carried out with a corer

8 cm in diameter which was pushed 25 cm, or as deep as possible, into the sand. The cores were sieved through a 1 mm sieve underwater, and the animals identified and counted. Forty-five cores were taken at the T. fabula sampling site ("Donaljean"), 45 at the T. tenuis site ("grid level") when it was submerged, and 45 at a site where both species were found ("paddling pool").

In the laboratory, circular troughs 33.5 cm in diameter by 15.25 cm deep were filled with sand to a depth of approximately 10 cm and topped up with sea water. Then, T. tenuis or T. fabula, or both, at densities of up to 350/bowl were counted out and sprinkled on the surface of the sand. The sand for all the laboratory experiments was taken from "grid level". The experiment was set up on the same day that the animals had been collected, and then left for one week at 10°C on a 12-hr day/12-hr night light regime. The sand was then carefully excavated and the dispersion pattern of the animals calculated as in the field experiments.

To ensure that the animals were moving during the experiments, and that any pattern observed was not due to the pattern they had started with, the following experiment was set up. In two dishes the T. tenuis were put in at random, in two dishes aggregated, and in two dishes spaced out. Another experiment was left for one month to find out if the dispersion pattern changed with time.

In the analysis of his experiments, Holme (1950) ignored the nearest neighbour distances of those animals whose position was within one inch of the side of the quadrat. A more precise method is to measure the distance of each animal from the edge to ascertain whether they were uniformly distributed with respect to the edge. The test chosen was the Kolmogorov-Smirnov One Sample Test (Siegel, 1956), which compared the cumulative frequency distribution of the observed distances with the cumulative frequency distribution of a theoretical even distribution.

The final series of experiments tested the dispersion of T. tenuis and T. fabula when mixed together, and Fisher's Exact Probability Test (Siegel, 1956) was used to ascertain whether the dispersion pattern of either species had changed with the introduction of the other.

Results.

At "grid level" T. tenuis occurred in numbers in excess of $1500/m^2$, but at the "paddling pool" the density was around $250/m^2$. T. fabula was never as abundant as T. tenuis; the density at "Donaljean" was about $400/m^2$ and dropped to $280/m^2$ at the intermediate "paddling pool" site.

The dispersion pattern of T. tenuis in the field was largely random, with a tendency toward spacing out (Table 1 and Table 2). There was no correlation between the degree of spacing out, as measured by the Clark and Evans (1954) Nearest Neighbour Test, and the density ($r = 0.25$, $t = 0.74$, $P > 0.05$) (Bailey, 1959). The cores taken when the site was covered by the incoming tide confirmed the randomness of the dispersion (Coefficient of Dispersion = 1.14, $P > 0.05$).

In contrast, T. tenuis in the laboratory had a tendency toward aggregation (Table 3). The dispersion pattern was independent of the way the animals had been put in (Table 4) and of their reaction to the sides of the dish (Table 5). The experiments which had been left for a month also displayed randomness with a tendency toward aggregation ($R_1 = 0.89$, $C_1 = 0.80$; $R_2 = 0.78$, $C_2 = 1.70$). There was no correlation between the degree of aggregation and the density ($r = 0.11$, $t = 0.47$, $P > 0.05$) (Bailey, 1959).

The dispersion pattern of T. fabula was largely random. The analysis of the cores at the "Donaljean" site gave a Coefficient of Dispersion of 1.32 and although this does indicate a tendency toward aggregation, it was not significant ($P > 0.05$). In the laboratory, T. fabula was largely randomly dispersed (Table 6), and, as with T. tenuis, there was no correlation between the degree of aggregation and the density ($r = 0.55$, $t = 1.86$, $P > 0.05$) (Bailey, 1959).

From the cores taken at the "paddling pool" the Coefficient of Dispersion for both species together was 1.39 ($P = 0.05$), for T. tenuis alone was 1.52 ($P = 0.015$) and for T. fabula alone was 1.22 ($P = 0.15$). These coefficients indicate a strong tendency towards aggregation.

When the two species were mixed in the laboratory and the dispersion pattern of all Tellina within the dish (Table 7) compared with the sum of the dispersion patterns of the individual T. tenuis and T. fabula experiments, there was no change in the pattern ($P = 0.60$).

When each species was considered separately there was no difference in the dispersion of either species whether the distances were measured interspecifically (Table 8; P (T.tenuis = 0.37,P(T. fabula) = 0.11) or intraspecifically (Table 9; P (T. tenuis) = 0.17, P (T. fabula) = 0.11).

The results suggest that both species are randomly dispersed, possibly with a tendency toward aggregation. The pattern of the dispersion is independent of the density, nor does the presence of one species affect the distribution of the other.

Discussion.

The dispersion of a species within its environment depends on the nature of the environment and on the behaviour of the animals themselves.

If the environment is strongly heterogenous, the most favourable habitat for any one species will occur patchily, and the animals are aggregated around these patches (Hairston, 1959; Levinton, 1972). There is also a tendency toward aggregation with the increasing rarity of a species within the environment, especially if the reproductive behaviour involves copulation (Hairston, 1959; Heip, 1975).

In a homogenous environment the dispersion of a species depends on the behaviour of the animals themselves either as adults or as larvae. Aggregation in a homogenous environment will only result from strong positive interactions, such as may occur during the breeding season (Heip, 1975) or during larval settling (Crisp, 1961; Wilson, 1968). After settling, the metamorphosed larvae may display negative interactions toward each other, resulting in a spacing out (Crisp, 1961). Any species which requires a territory, e.g. for feeding, will display negative interactions and so the individuals of that species will be spaced out (Holme, 1950; Johnson, 1959; Connell, 1963).

The dispersion of a species will be random only in a homogenous environment and in the absence of interactions between individuals.

Several authors have suggested that the pattern of dispersion of a species may be influenced by its method of feeding (Holme, 1950; Connell, 1955, 1963; Johnson, 1959; Levinton, 1972; Heip, 1975). Both T. tenuis and T. fabula are usually classified as deposit feeders (Blegvad, 1915; Atkins, 1937; Yonge, 1949; Pohlo, 1969), and Holme (1950) advanced the hypothesis that the foraging of the inhalent siphon of T. tenuis was used to maintain feeding territories.

However, Yonge (1949) has described the mode of feeding of T. tenuis in the following terms "the inhalent siphon ...... draws in material lying upon or just above the surface of the sand, but it does not actively pull in bottom material .... It acts as a purely passive agent for the intake of fragments lying on or just above the bottom." Indeed, Trevallion (1971) noted that Tellina had the ability to feed on particles in suspension as well as on the deposit, and that they were found in an environment more favourable to filter feeding.

Personal observations confirm this for T. fabula as well as for T. tenuis.

The descriptions of feeding in *Tellina* can be compared with a description of the feeding habits of *Macoma balthica*, whose inhalent siphon "moves about while actively drawing in material lying on the surface of the mud" (Yonge, 1949) and "leaves a star-shaped feeding track on the substrate"(Hulscher, 1973).

T. tenuis, *T. fabula* and *M. balthica* have all been classified as deposit feeders, but Pohlo (1969) suggested that deposit feeding was not universal in the Tellinacea and that one type of feeding may intergrade with the next. It seems reasonable, therefore, to suggest that *T. tenuis* and *T. fabula*, from Kames Bay at least, may be primarily filter feeders.

According to Heip (1975), the uniform dispersions observed in many bivalve species may be explained by competition for food, but if there was abundant food in suspension, the animals would have no need to maintain feeding teritories. Consequently, one might expect suspension feeders in a homogenous environment to be randomly dispersed.

Both randomness and aggregation have been observed in suspension feeding bivalves such as *Mya arenaria* (Connell, 1955; Gaucher, 1965), *Petricola pholadiformis* (Connell, 1955), *Mulinia lateralis* (Jackson, 1968) and *Mysella planulata* (Franz, 1973). Other workers have reported aggregated and random dispersions within the Tellinidae. In America, Gilbert (1968) found that the juveniles of *Tellina agilis* were aggregated because they were concentrated around MLW by the spatfall, but the adults were randomly dispersed.

On the other hand, Holme (1950) found that *T. tenuis* showed a tendency toward spacing out because of the action of the inhalent siphons while deposit feeding and became random only at high densities. An analgous situation was observed by Johnson (1959) who found that Phoronopsis viridis was spaced out due to the action of the lophophore searching the rock. However, the deposit feeders Scrobicularia plana (Hughes, 1970) and Nucula proxima (Levinton, 1972) have random dispersions, so not all deposit feeders space out.

The above examples demonstrate that while there is no absolute agreement between feeding type and dispersion, there is nevertheless some correlation. It may be that T. tenuis and T. fabula can either deposit or suspension feed according to conditions, and so we are left with the problem that the dispersion pattern may vary according to the habitat from which the animals were taken!

With regard to the large scale distribution on the beach, both species would seem to be competing for the same environmental niche in the immediate sublittoral. One might expect that one species would be dominant and that, when mixed, it would crowd out or otherwise affect the dispersion of the other species, as happens with certain hermit crabs. The dispersion of Pagurus longicarpus is affected in the presence of Clibanarius vittatus, and P. longicarpus is partially excluded from the favoured areas of the experimental tanks (Mitchell, 1975). But it seems that siphonal contact does not affect the intraspecific or interspecific dispersion patterns of either T. tenuis or T. fabula, so perhaps some external factor governs their distribution.

If we examine the physical tolerances of T. tenuis and T. fabula, we find that T. tenuis can tolerate a much wider variation in temperature or salinity or pH etc. The range of these factors in the Kames Bay littoral zone is largely within the absolute lethal tolerance of T. fabula, but it may affect its ability to compete with T. tenuis. De Wilde (1975) has demonstrated that, with M. balthica, the energy balance between food uptake and energy expenditure becomes negative at higher, though not immediately lethal, temperatures. So T. tenuis would be expected to outcompete T. fabula in the littoral zone, but there seems no a priori reason why it should not occupy the sublittoral as well.

Stephen (1932) found that the spatfall of T. tenuis is deposited below LW during the summer, but by the autumn it is also to be found in large numbers up to halftide level, and in noticeably diminished numbers above this. Unfortunately, we do not know how far below LW T. tenuis spat settle, nor do we know if T. fabula spat settle above LW.

It is unlikely that those T. tenuis spat which settle below low water migrate toward the littoral zone, and certainly the adults do not move much after burrowing. Holme (1950) noted that many of the Tellina in his artificially increased populations had not spread out, and I have found that over a period of a year or so there was little movement of the animals outside the square metre into which they were introduced.

The decline in the T. tenuis population below LW may therefore be due to the fact that T. fabula can outcompete T. tenuis in this habitat. Certainly, Stephen (1932) found that the rate of growth of T. tenuis below LW was less than that of T. tenuis above LW. In fact, he found that they grew best at the landward part of their range provided that the beach remained uniform in nature, but he could advance no explanation for this phenomenon.

Preliminary experiments suggest that T. tenuis can survive when transplanted to "Donaljean", although the sublittoral does contain a greater percentage of fine sand. However, it would be strange if a supposed deposit feeder was excluded by a fine sand fraction comprising only 5% of the total dry weight of the substrate.

In conclusion, the randomness of the dispersions of T. tenuis and T. fabula indicates not only environmental homogeneity but also a lack of interactions between animals. Evidence has been presented to suggest that both species are primarily filter feeders. The large scale distribution of T. tenuis and T. fabula thus seems to be a consequence of two main influences - the settling behaviour of the larvae, and the physical tolerances of the adults.

Table 1. Nearest Neighbour analysis of the distribution of *T. tenuis* in the field. R = the measure of the degree to which the observed distribution departs from random; c = standard variate of the normal curve.

Expt	No. of animals	R	c	Distribution
1	101	0.98	0.34	Random
2	92	1.05	0.84	"
3	85	1.11	1.89	"
4	77	1.02	0.50	"
5	30	1.06	0.63	"
6	28	1.01	0.09	"
7	27	1.03	0.25	"
8	21	0.98	0.20	"
9	18	1.07	0.54	"
10	17	0.93	0.54	"

Table 2. X^2 Approximation analysis of the field distribution of *T. tenuis* within an 8 x 8 m grid. Probability values in brackets.

		Quadrat length (m)			
		1	2	4	8
Quadrat Breadth (m)	1	Spaced (0.01)			Random (0.46)
	2		Random (0.55)		
	4			Random ? (0.054)	
	8	Random (0.18)			

Table 3. Nearest Neighbour analysis of the distribution of *T. tenuis* in the laboratory. Symbols as Table 1.

Expt	No. of animals	R	c	Distribution
1	332	0.98	0.57	Random
2	341	0.96	1.30	"
3	183	0.96	1.13	"
4	181	0.955	1.15	"
5	100	0.98	0.43	"
6	99	0.92	1.60	"
7	95	0.91	1.65	"
8	94	0.89	2.03	Aggregated
9	90	0.79	3.80	"
10	95	0.81	3.48	"
11	52	1.06	0.81	Random
12	55	0.97	0.37	"
13	51	0.77	3.08	Aggregated
14	51	0.74	3.50	"
15	33	0.97	0.30	Random
16	33	0.92	0.92	"
17	16	0.73	2.05	Aggregated
18	16	0.97	0.21	Random
19	8	0.72	1.51	"
20	8	1.33	1.80	"

Table 4. Nearest Neighbour analysis of the distribution of T. tenuis in the laboratory when put in with different distributions. Symbols as Table 1; orig = as put in; obs = as taken out

	Expt	No. of animals	R orig	c orig	Orig distribution	R obs	c obs	Obs distribution
I	a	16	0.82	1.36	Random	0.73	2.10	Aggregated
	b	16	0.86	1.07	"	0.92	0.61	Random
II	a	16	0.33	5.14	Aggregated	0.85	1.13	Random
	b	16	0.33	5.14	"	0.85	1.13	"
III	a	16	1.31	2.36	Spaced	0.88	0.90	Random
	b	16	1.31	2.36	"	1.00	0.01	"

Table 5. Distribution of *T. tenuis* in the laboratory. Nearest Neighbour compared with the Kolmogorov-Smirnov One Sample test. D = maximum deviation of observed values from expected values; S = significance of D at P = 0.05

Expt	Nearest-Neighbour distribution	D	Kolmogorov-Smirnov S
1	Random	0.04	No
2	"	0.05	"
3	"	0.06	"
4	"	0.10	"
5	"	0.13	"
6	"	0.16	Yes
7	"	0.20	"
8	Aggregated	0.10	No
9	"	0.18	Yes
10	"	0.23	"
11	Random	0.13	No
12	"	0.15	"
13	Aggregated	0.15	"
14	"	0.36	Yes
15	Random	0.51	"
16	"	0.41	No
17	Aggregated	0.45	Yes
18	Random	0.40	No
19	"	0.26	"
20	"	0.11	"

Table 6. Nearest Neighbour analysis of the distribution of *T. fabula* in the laboratory. Symbols as Table 1.

Experiment No.	No. of Animals	R	c	Distribution
1	109	0.98	0.48	Random
2	104	0.98	0.38	"
3	50	0.96	0.54	"
4	50	1.03	0.10	"
5	40	0.91	1.14	"
6	34	0.90	1.13	"
7	28	0.80	2.00	Aggregated
8	28	0.96	0.38	Random
9	16	0.88	0.92	"
10	16	0.92	0.32	"

Table 7. Nearest Neighbour analysis of the distribution of T. tenuis and T. fabula when mixed in the laboratory. Symbols as Table 1

Expt No.	No. of animals	R	c	Distribution
1	48	1.05	0.62	Random
2	48	0.91	1.16	"
3	32	1.04	0.35	"
4	32	0.95	1.75	"
5	48	0.78	2.90	Aggregated
6	48	1.05	0.75	Random

Table 8. Nearest Neighbour analysis of the interspecific distances of the distribution of T. tenuis and T. fabula when mixed in the laboratory. Symbols as Table 1.

Experiment No.		No. of Animals	R	c	Distribution
1	T.tenuis	32	1.02	0.29	Random
	T.fabula	16	1.12	1.56	"
2	T.tenuis	32	0.98	0.33	"
	T.fabula	16	0.78	2.94	Aggregated
3	T.tenuis	16	1.39	4.18	Spaced
	T.fabula	16	0.69	3.31	Aggregated
4	T.tenuis	16	1.09	1.15	Random
	T.fabula	16	0.80	2.64	Aggregated
5	T.tenuis	16	0.89	1.52	Random
	T.fabula	32	0.87	1.75	"
6	T.tenuis	16	1.32	3.71	Spaced
	T.fabula	32	0.92	1.04	Random

Table 9. Nearest Neighbour analysis of the intraspecific distances of the distribution of *T. tenuis* and *T. fabula* when mixed in the laboratory. Symbols as Table 1

Expt No.		No. of animals	R	c	Distribution
1	*T. tenuis*	32	0.97	0.32	Random
	T. fabula	16	0.83	1.32	"
2	*T. tenuis*	32	1.02	0.20	"
	T. fabula	16	0.92	0.61	"
3	*T. tenuis*	16	1.18	1.38	"
	T. fabula	16	0.53	3.62	Aggregated
4	*T. tenuis*	16	0.85	1.15	Random
	T. fabula	16	0.71	2.19	Aggregated
5	*T. tenuis*	16	1.19	1.46	Random
	T. fabula	32	0.91	1.02	"
6	*T. tenuis*	16	0.97	0.24	"
	T. fabula	32	0.76	2.64	Aggregated

Chapter 3

Rhythms.

Introduction.

Many lamellibranchs possess activity rhythms of tidal or diurnal frequency (Morton, 1973, review), although the possession of such rhythms is by no means universal within the class (Salanki, 1966a; Hughes, 1969; Earll, 1975b). Nevertheless, in those species in which a rhythm has been found, Morton (1973) noted that littoral species displayed a tidal rhythm, while sublittoral and freshwater species displayed a diurnal rhythm.

At Kames Bay, Millport, T. tenuis is largely littoral, while T. fabula is largely sublittoral, and the ranges of the two species overlap only slightly (Stephen, 1928; Watkin, 1942; Clark and Milne, 1955). According to Morton's (1973) hypothesis T. tenuis should therefore display an endogenous tidal activity rhythm, and T. fabula an endogenous diurnal activity rhythm. If, however, the rhythms are exogenously controlled or initiated there will be little trace of a tidal rhythm, or the rhythm will decay in time, under constant conditions in the laboratory (Salanki, 1971).

Several parameters have been used to monitor the level of activity in a bivalve, including heart rate (Coleman, 1974), pumping rate (Rao,R.D.,1953), and valve movement (Morton, 1970). These parameters are all interrelated (Coleman, 1974) and both Salanki (1971) and Morton (1973) considered that the most informative method of monitoring the activity was to record the valve movements. Accordingly, experiments were carried out to record and compare the valve movements of T. tenuis and T. fabula under laboratory conditions and to establish, if possible, the nature and periodicity of their rhythms.

Materials and Methods.

Both species were collected from the middle of their respective ranges, T. tenuis from an area 1.5m above C.D., and T. fabula from an area 5m below C.D. For the transplant experiments, 12 T. tenuis were left at the T. fabula collecting site (and vice versa with T. fabula) before they were brought into the laboratory. The experiments were started on the same day that the animals were collected.

The experimental design, after Morton (1970), is depicted diagrammatically in Fig. 1. The left valve of the specimen (A) was glued to a watch glass with Epoxy Patch 608 quick-setting resin (Dexter Corporation, Olean, N.Y. 14760) and the right valve was glued to a length of thread. The thread was attached to an isometric force displacement transducer (T1, T2) type D1 (Scientific Instruments Centre Ltd.,Edinburgh) which in turn was connected to a pen recorder (PR) type 400 MD2 (George Washington Ltd., Sheerness, Kent). The experiment was maintained at a temperature of 10°C by a waterbath (WB).

The data was divided up into blocks of 41.5 minutes, since this was the length of time taken for one sheet of recording paper to pass through the machine at its slowest speed, 0.75 cm per minute. The number of adductions on one sheet was taken to constitute one block of data. The blocks of data were analysed for evidence of periodicity by periodogram analysis (Enright, 1965; Williams and Naylor, 1967) and by pattern analysis (Kershaw, 1960) (see also statistical appendix).

Correlation was sought between the measured activity, in adductions per sheet, and three environmental variables, calculated as the animal would have encountered them in the field. These variables were tidal rise and fall, day length, and tidal range.

Results.

The activity of 12 animals of each species was analysed (Table 1, Table 2). In the Tables, animals number 1 to number 10 were taken from their usual position on the beach; animals number 11 and number 12 were transplanted for the two weeks immediately prior to the experiment.

There was little evidence of a circatidal activity rhythm in the periodogram analysis of the activity of T. tenuis (Table 1); that is, C.V. peaks did not consistently occur at a periodicity of 12 hours 25 minutes. However, most animals displayed a circadian activity rhythm, although the C.V. peak varied from around 20 hours (animal number 8) to around 27 hours (animal number 6) (Table 1).

As with T. tenuis, the periodogram analysis of the activity of T. fabula showed little evidence of a circatidal rhythm (Table 2). The evidence (Table 2) for a circadian rhythm was not as strong as with T. tenuis, and only animal number 10 could be said to show a C.V. peak of the correct circadian periodicity.

No consistent rhythm of either circatidal or circadian frequency could be observed in the pattern analysis of the activity of either species (Table 4).

In view of the variability of the results of the analyses of the activity of the animals from the original positions in Kames Bay, it was felt that no meaningful comparison could be made between the rhythms of these animals and of the transplanted specimens. Therefore, although the results from the transplanted specimens have been included in the Tables and in Fig. 4, they have been omitted from the correlation calculations.

There was considerable variation in the level of activity, measured in adductions per sheet (41.5 minutes), not only between individual animals, but also in the sheet to sheet record of any one animal (Fig. 2, Fig. 3). Fig. 2 represents the activity record of T. tenuis animal number 2, and Fig. 3 represents the activity record of T. fabula animal number 9. Examination of Fig. 2 and Fig. 3 revealed that the level of activity, that is, the number of adductions per sheet, was not noticeably correlated either with the state of the tide or with the periods of light and darkness to which the animal would have been exposed in the field.

However, regression analysis (Bailey, 1959) of all the activity experiments showed that the mean activity in adductions per sheet of each experiment was correlated with the tidal range taken as the maximum predicted difference between high and low tide during the experiment (Table 5, Fig. 4). There was no significant difference between the slopes of the regression lines of T. tenuis and T. fabula ($t = 1.27$, $P = 0.23$), and the regression line drawn in Fig. 4 is for all experiments.

In spite of the fact that there was a correlation between the mean activity of the animals and the maximum predicted tidal range, there was no correlation between the mean activity and the tidal range on the day that they had been collected either in T. tenuis (r = 0.20, t = 0.58, P = 0.57) or in T. fabula (r = 0.30, t = 0.87, P = 0.41) (Bailey, 1959). One may therefore conclude that both species can predict the height of the tides, and can adjust their activity accordingly.

Although the tidal range affected the animals' activity level, it did not affect the strength of the rhythm, taken as the maximum value of the coefficient of variability (Williams and Naylor, 1967), and there was no correlation between tidal range and the strength of the rhythm either in T. tenuis (r = 0.34, t = 1.02, P = 0.34) or T. fabula (r = 0.36, t = 1.09, P = 0.30) (Bailey, 1959).

Despite the fact that there appeared to be a slight circadian rhythm in both T. tenuis and T. fabula (see page 97), there was no correlation between mean activity and day length (r = 0.19, t = 0.54, P = 0.60 and r = 0.06, t = 0.17, P = 0.86 respectively) nor between the strength of the rhythm and day length (r = 0.11, t = 0.30, P = 0.77 and r = 0.27, t = 0.79, P = 0.45 respectively) (Bailey, 1959).

An attempt was made to quantify the circadian rhythms of both species and to relate the periodicity of these rhythms, that is, the C.V. peak, to the length of the periods of darkness and daylight. It was found that the longer the period of daylight, the shorter the period of the circadian rhythm of T. fabula (r = 0.83, t = 3.31, P = 0.02) (Bailey, 1959) but the periodicity of the circadian rhythm of T. tenuis was independent of the number of hours of daylight ($r = 0.08$, $t = 0.20$, $P = 0.85$) (Bailey, 1959). However, it must be remembered that positive evidence for a circadian rhythm in either species was rather scanty (Table 1, Table 2) and the results of this last analysis should be viewed with caution.

The results suggest that neither species possessed an endogenous tidal rhythm, but there appeared to be evidence of a circadian rhythm, particularly in T. tenuis. The level of activity in both species was correlated with the predicted tidal range, but not with the day length which they would have encountered in the field. The strength of the rhythm was not correlated with either tidal range or day length. The results further suggest that the circadian rhythm of T. fabula may be connected to the hours of darkness, but that there was no such correlation in the activity rhythm of T. tenuis.

Discussion.

Although many bivalves possess endogenous activity rhythms (Morton, 1973, Palmer, 1974), instances have been found of non-rhythmic activity in some species (Salanki,1966 a; Hughes, 1969, Earll, 1975 a, b; Taylor, 1976). Endogenous tidal rhythms exist in many other littoral animals (Naylor, 1958; Enright, 1963; Jones and Naylor, 1970; Benson and Lewis, 1976) and these rhythms can be modified or altered by various factors in the environment (Naylor, 1960, 1963; Enright, 1965;

Salanki, 1966 b; Naylor et al, 1971; Atkinson, 1973).

The results suggest that there is no endogenous tidal rhythm of the adductor muscles in either T. tenuis or T. fabula although there may be other endogenous rhythms which were not monitored. No single method is sufficient to decide on the existence or otherwise of any endogenous rhythm (Earll, 1975 b) although in many species the activity rhythms of the various functions are interrelated (Coleman, 1974).

In many species the physiological rhythms are reflected morphologically by banding (Wells, 1963; Neville, 1967; House and Farrow, 1968; Bourget and Crisp, 1975 a; Crisp and Richardson, 1975; Stromgren, 1976). In pelecypod shells, Barker (1964) found five groups of layers, each with their own characteristic crystal formation, lying one within the other and reflecting the environmental periodicities. Others (Bourget and Crisp, 1975 b; Crisp and Richardson, 1975) have related such bands directly to one factor in the environment such as tidal immersion. Continuous immersion led to two ill-defined bands per day, so it appears that these physiological rhythms have only a weak endogenous component.

Banding exists on the shells of both T. tenuis and T. fabula and, although they lack distinct growth rings, the bands are clearly visible under low magnification. There are various factors which may influence the formation of such banding rhythms.

It has been shown that the level of the water table within the sand has a marked effect on both the adductor activity and the heart rate (Earll, 1975 a) but of course only T. tenuis is subject to the tidal cycle of immersion and emersion. Both T. tenuis and T. fabula are subject to cyclic oscillations of pressure and water flow with the tides, as well as the diurnal alternation between night and day. The effect of pressure on the rhythmic behaviour of inshore species has been reviewed by Naylor and Atkinson (1972), and Walne (1972) found that the rate of water flow affected both the filtration rate and the heart rate of the bivalves. Light is an important, if not the most important, factor in the entrainment of rhythms in many littoral species (Enright, 1965; Jones and Naylor, 1970; Naylor et al, 1971; Palmer, 1974; Benson and Lewis, 1976), but the valve rhythm of the sublittoral brachiopod Terebratulina septentrionalis could not be correlated with light factors (McCammon, 1971). Recently Stromgren (1976) has found that Mytilus edulis grew faster in darkness than during the daytime, and that this diurnal rhythm persisted even in continual darkness.

The fact that the maximum activity was correlated with the maximum tide during the experiment, but not with the tide at the start of the experiment, suggests that the animals are capable of predicting the tides. High levels of activity in the laboratory correlated with spring tides in the field have also been noted in other species (Heusner and Enright, 1966; Enright, 1972; Naylor and Atkinson, 1972; Benson and Lewis, 1976) resulting in a circalunar rhythm. Unfortunately, none of my series of experiments ran for long enough to ascertain whether a circalunar rhythm existed in either T. tenuis or T. fabula.

It has been suggested that tidal exposure involves little or no stress to littoral infauna (Earll, 1975 b), and that many species have the ability to feed at low tide in the ripples or surface pools, or even in the interstitial water (Hughes, 1969). A rhythm involving inactivity at low tide would clearly hamper such facultative feeding, and natural selection may favour such species as are able to take advantage of every feeding opportunity.

In conclusion, it appears that both T. tenuis and T. fabula have an endogenous circadian, but not tidal, rhythm of activity. The rhythm is independent of day length in T. tenuis, but a longer day length is correlated with a shorter circadian rhythm period in T. fabula. Day length has no effect on either the activity or the strength of the rhythm of either species, but the mean level of activity in both species was positively correlated with the maximum tidal range occurring during the experiment. It is therefore suggested that there may be long-term circalunar rhythms of activity, but some other method must be devised to record them.

Table 1. Coefficient of variability values (see statistical appendix) of the periodogram analysis (Enright, 1965; Williams and Naylor, 1967) of the rhythms of <u>T. tenuis</u>. For explanation of numbering see text. The periodicity is given in sheets and in hours and minutes (1 sheet = 41.5 minutes, see text).

Periodicity		Animal Number											
Sheets	Hours.Minutes	1	2	3	4	5	6	7	8	9	10	11	12
8	5.32	18.28	9.06	7.54	24.10	4.77	11.12	14.37	15.84	17.41	10.65	8.72	74.18
9	6.13½	21.18	14.43	10.64	21.31	8.91	9.34	15.76	20.00	13.30	8.70	6.63	100.00
10	6.55	20.77	13.10	8.00	24.07	13.21	9.44	14.88	16.24	15.34	11.48	11.12	116.53
11	7.36½	18.22	10.80	13.17	21.39	9.65	10.81	14.19	17.29	14.43	17.77	10.73	137.39
12	8.18	26.19	20.31	10.75	25.22	10.10	13.37	19.69	17.72	21.53	15.74	8.83	115.47
13	8.59½	27.09	13.96	14.37	21.01	11.42	14.89	9.91	14.61	17.72	23.27	26.41	112.42
14	9.41	21.93	19.40	11.66	25.67	18.17	16.15	15.69	14.90	19.03	24.21	13.35	93.67
15	10.22½	23.57	16.44	14.83	20.81	12.13	12.44	13.75	19.62	15.24	25.04	15.54	130.63
16	11.04	27.43	18.48	14.84	31.15	7.97	12.84	22.74	24.16	23.92	19.53	19.08	111.85
17	11.45½	24.73	15.75	17.12	21.62	18.12	18.25	21.56	26.23	22.17	15.52	15.53	122.55
18	12.27	31.57	18.73	15.60	28.28	17.28	17.63	20.20	27.32	22.61	25.40	11.83	123.67
19	13.08½	28.69	24.99	17.61	30.16	17.37	17.23	23.24	24.43	18.68	28.63	11.02	129.15
20	13.50	31.33	24.47	14.02	25.65	19.24	28.56	19.88	23.79	19.04	26.66	16.65	143.75
21	14.31½	30.96	21.48	15.63	26.15	24.53	23.13	21.35	21.55	25.47	25.95	17.00	129.31
22	15.13	30.80	16.33	17.90	28.28	17.27	16.89	20.37	26.75	22.20	22.30	17.93	175.45
23	15.54½	41.20	26.62	18.76	34.29	26.26	17.06	23.11	33.54	20.49	27.55	23.83	149.00
24	16.36	34.76	24.78	19.42	35.74	19.50	22.97	31.99	37.00	26.89	22.32	25.52	153.54
25	17.17½	28.11	22.34	16.57	30.30	18.04	22.79	31.88	32.08	26.12	26.35	20.03	167.82

Table 1. (contd.)

Periodicity		Animal Number											
Sheets	Hours.Minutes	1	2	3	4	5	6	7	8	9	10	11	12
26	17.59	36.05	23.79	17.42	30.10	18.85	25.92	26.07	25.21	29.66	34.18	32.55	151.60
27	18.40½	32.50	33.84	20.67	35.47	25.32	26.01	33.88	36.76	21.63	36.20	21.75	155.66
28	19.22	34.19	27.62	18.23	38.01	28.58	25.34	34.17	40.23	25.69	38.27	20.95	159.62
29	20.03½	42.27	28.93	19.06	31.03	22.56	22.84	29.69	42.08	28.12	45.91	22.02	169.05
30	20.45	45.79	21.66	20.30	32.59	19.33	19.84	30.08	40.68	30.80	40.68	18.06	188.76
31	21.26½	44.17	23.72	18.27	37.05	20.06	25.39	34.63	40.25	34.38	40.36	19.67	176.61
32	22.08	49.25	28.25	18.89	42.44	27.36	22.52	38.64	38.49	30.58	44.18	26.49	185.84
33	22.49½	48.12	33.55	22.32	45.33	35.78	25.84	36.66	32.93	39.57	38.72	21.87	224.96
34	23.31	53.76	34.55	23.15	37.26	41.67	31.41	36.84	39.09	54.25	30.02	22.33	198.57
35	24.12½	51.76	32.95	23.48	39.95	48.20	33.96	32.07	35.32	52.66	38.11	22.46	190.82
36	24.54	52.98	28.83	25.64	41.91	41.06	33.67	31.18	38.37	42.98	37.44	25.56	200.00
37	25.35½	51.63	30.93	26.06	40.11	37.37	27.99	29.33	37.79	28.56	39.28	24.07	203.38
38	26.17	42.76	34.84	26.96	39.92	33.60	32.80	30.26	36.01	27.98	34.79	23.12	206.71
39	26.58½	45.51	33.26	25.13	33.27	27.80	36.77	25.76	32.28	29.55	39.92	33.24	197.87
40	27.40	42.13	36.74	20.80	39.69	26.57	40.25	27.61	33.11	25.32	34.41	29.51	200.98
41	28.21½	45.69	30.48	24.55	42.08	26.97	36.59	28.67	34.93	33.27	40.73	28.47	204.04
42	29.03	43.39	30.26	21.03	43.74	28.98	31.90	28.28	29.04	36.81	44.09	29.31	207.06
43	29.44½	48.50	32.76	22.06	42.94	25.85	26.63	30.73	31.96	32.99	50.85	31.42	210.03
44	30.26	52.45	33.41	29.83	42.15	27.92	24.12	29.54	37.81	36.60	39.48	25.86	212.96
45	31.07½	50.20	30.68	29.48	45.15	26.34	22.03	30.89	44.18	28.33	40.58	31.90	215.85

Table 2. Coefficient of variability values (see statistical appendix) of the periodogram analysis (Enright, 1965; Williams and Naylor, 1967) of the rhythms of <u>T. fabula</u>. Symbols as Table 1.

Periodicity		Animal Number											
Sheets	Hours.Minutes	1	2	3	4	5	6	7	8	9	10	11	12
8	5.32	7.58	3.69	18.26	72.14	6.30	6.29	14.46	20.62	2.87	3.15	9.17	8.67
9	6.13½	10.59	6.86	19.20	69.01	9.23	6.80	16.78	12.68	3.15	4.47	11.00	7.65
10	6.55	11.85	8.91	11.47	57.36	7.71	7.11	20.20	22.97	3.13	3.25	14.09	10.91
11	7.36½	14.51	7.67	20.93	68.43	10.78	8.31	11.69	23.57	3.41	3.80	13.21	13.45
12	8.18	8.66	9.64	17.37	69.37	14.22	9.30	20.83	23.77	4.10	4.07	11.29	10.49
13	8.59½	7.37	11.08	17.09	80.09	13.01	10.41	20.43	23.27	3.12	3.73	18.86	21.38
14	9.41	8.73	7.05	29.26	74.46	20.22	10.78	15.78	36.26	3.96	3.93	23.57	16.52
15	10.22½	11.66	7.66	20.62	90.58	18.58	8.53	23.35	29.41	4.28	4.86	27.43	15.76
16	11.04	13.01	7.22	21.19	105.11	21.04	10.26	26.84	30.50	4.68	4.13	22.20	12.91
17	11.45½	14.58	10.70	18.59	96.69	25.28	10.50	25.95	29.37	4.58	7.47	13.68	15.54
18	12.27	16.78	11.32	22.95	100.17	27.33	11.29	25.01	26.36	5.41	10.22	14.53	13.79
19	13.08½	16.78	8.30	17.70	103.29	26.19	10.41	21.89	23.78	4.84	5.41	16.88	17.90
20	13.50	15.37	10.42	20.83	90.82	26.28	11.49	28.72	33.09	5.48	4.02	16.30	15.90
21	14.31½	20.43	6.02	29.65	84.06	30.60	15.03	19.62	36.47	5.32	6.23	15.25	16.21
22	15.13	29.46	10.08	29.11	85.66	28.13	12.28	20.04	37.48	4.57	5.79	17.64	20.30
23	15.54½	30.44	10.41	29.26	107.52	29.24	13.96	19.55	32.61	3.05	7.61	18.90	20.78
24	16.36	28.39	14.53	29.65	100.56	35.63	12.28	27.60	38.39	4.89	5.60	16.04	21.37
25	17.17½	24.53	18.85	28.74	104.64	37.30	13.83	31.20	35.54	5.65	6.12	17.66	26.98

Table 2. (contd.)

Periodicity		Animal Number											
Sheets	Hours.Minutes	1	2	3	4	5	6	7	8	9	10	11	12
26	17.59	22.59	19.60	31.39	117.11	37.56	13.06	32.99	42.21	5.19	5.70	22.04	27.34
27	18.40½	21.82	18.21	37.00	115.27	37.98	10.45	35.98	38.23	5.16	7.76	26.38	26.99
28	19.22	18.10	15.03	41.22	115.99	38.13	12.89	27.05	44.72	6.62	8.34	30.28	26.10
29	20.03½	20.28	15.82	35.25	113.39	36.59	13.95	28.52	35.59	8.38	9.62	32.99	23.82
30	20.45	18.47	13.66	29.54	119.91	35.56	15.14	31.94	40.62	8.33	10.09	35.60	23.02
31	21.26½	15.73	10.51	31.18	123.23	36.44	16.66	30.42	40.98	8.32	10.00	33.93	21.92
32	22.08	17.15	10.92	31.95	116.78	39.42	14.71	33.58	43.77	7.59	11.53	32.67	18.67
33	22.49½	20.69	13.44	30.31	135.71	41.87	12.80	31.44	41.24	6.60	13.75	30.89	20.46
34	23.31	20.09	14.48	33.37	122.90	41.58	16.34	33.80	40.96	7.01	13.65	27.57	18.88
35	24.12½	21.38	18.12	35.62	135.68	42.06	16.55	36.93	38.80	7.98	14.52	27.54	19.23
36	24.54	20.44	18.38	35.58	125.27	41.44	18.45	38.18	40.47	8.12	11.73	27.24	17.81
37	25.35½	21.01	18.52	32.74	128.06	41.00	18.28	38.71	41.01	7.64	8.23	27.44	24.02
38	26.17	25.03	19.44	29.35	130.80	40.46	19.65	39.13	40.65	7.27	8.46	28.35	26.67
39	26.58½	25.47	20.04	31.07	137.00	41.29	19.68	37.80	42.01	6.33	8.02	29.29	29.57
40	27.40	25.18	21.77	35.64	136.11	42.71	18.28	41.64	45.06	7.04	8.86	28.43	28.64
41	28.21½	25.02	21.04	39.54	145.71	45.59	17.54	38.10	46.34	6.86	9.06	29.58	29.93
42	29.03	28.80	19.90	41.57	141.21	48.23	21.74	33.99	50.98	7.37	8.80	30.07	28.10
43	29.44½	32.34	20.53	42.86	147.29	48.94	20.65	30.83	51.16	8.61	7.98	30.99	29.81
44	30.26	35.15	21.38	41.77	149.75	50.00	21.11	32.68	55.02	7.39	9.83	34.22	30.58
45	31.07½	35.91	21.64	42.50	148.53	51.77	23.53	33.49	60.59	6.25	9.16	33.79	30.75

Table 3. Pattern analysis (Kershaw, 1960) of the activity of <u>T. tenuis</u>. For explanation of numbering see text. For explanation of method and of parts "a" and "b" see statistical appendix. The periodicity is given in sheets and in hours and minutes (1 sheet = 41.5 minutes, see text).

Periodicity		Animal Number									
Sheets	Hours.Minutes	1a	1b	2a	2b	3a	3b	4a	4b	5	6
1	0.41½	69.1	32.9	43.9	43.5	122.2	85.2	10.5	5.5	23.2	43.6
2	1.23	42.3	88.3	52.9	67.5	261.4	211.3	14.1	9.1	42.5	57.8
4	2.46	95.5	54.2	39.9	45.5	201.0	177.1	22.3	7.9	38.5	48.9
8	5.32	328.2	40.7	87.0	93.5	253.8	446.9	13.0	18.4	93.7	184.9
16	11.04	39.5	531.6	96.6	196.0	1274.0	437.4	21.2	20.0	167.5	135.6
32	22.08	272.3	125.8	288.1	206.2	169.8	2280.6	7.7	14.2	1199.4	392.7
64	44.16	19.5	3.4	555.9	1148.4	3973.5	1947.8	166.5	130.0	2.8	2136.9
128	88.32	-	-	309.4	228.4	8016.8	8564.1	-	-	-	-

Sheets	Hours.Minutes	7a	7b	8a	8b	9a	9b	10	11a	11b	12
1	0.41½	23.1	12.1	24.0	47.3	6.3	55.6	13.1	19.5	31.8	0.1
2	1.23	30.6	15.8	30.8	53.8	4.8	60.3	12.7	23.8	99.8	0.4
4	2.46	59.2	14.2	59.5	47.7	9.5	106.1	21.2	45.2	99.5	0.5
8	5.32	113.6	45.8	113.3	207.8	31.9	104.2	26.0	64.8	41.9	0.8
16	11.04	163.8	14.6	160.3	337.2	94.5	162.2	73.8	118.2	533.0	0.3
32	22.08	14.4	2.8	16.0	507.5	59.0	165.5	20.8	199.0	322.3	1.8
64	44.16	1937.6	46.3	1968.8	670.7	74.8	395.1	182.8	82.8	2433.7	1.1
128	88.32	-	-	-	-	367.9	4050.0	202.5	612.5	1006.9	-

Table 4. Pattern analysis (Kershaw, 1960) of the activity of <u>T. fabula</u>. Symbols as Table 1.

Periodicity		Animal Number								
Sheets	Hours.Minutes	1a	1b	2a	2b	3	4a	4b	5a	5b
1	$0.41\frac{1}{2}$	1.5	2.2	20.8	24.6	1.8	0.1	0.3	12.2	4.3
2	1.23	2.3	4.8	28.2	24.1	2.5	0.1	0.1	28.4	4.3
4	2.46	9.1	8.4	117.8	88.0	11.7	0.4	0.6	165.8	5.9
8	5.32	27.2	52.5	155.9	121.4	4.8	0.2	0.1	102.6	5.6
16	11.04	34.1	1.0	416.2	1455.8	0.9	0.9	0.1	995.1	37.2
32	22.08	13.1	182.9	5243.5	1987.4	0.6	-	-	558.7	255.2
64	44.16	-	-	66.1	6626.9	-	-	-	1703.8	2520.5
128	88.32	-	-	-	-	-	-	-	-	-

Sheets	Hours.Minutes	6a	6b	7	8	9	10	11	12
1	$0.41\frac{1}{2}$	41.6	5.6	8.2	1.1	50.7	58.8	30.8	49.1
2	1.23	115.3	4.5	20.6	2.5	36.0	129.4	73.8	65.7
4	2.46	56.1	19.5	25.3	0.8	72.3	267.5	93.3	119.4
8	5.32	56.6	29.2	46.9	12.7	287.7	1309.5	346.7	336.7
16	11.04	84.1	645.3	59.4	24.9	909.1	981.3	1878.5	655.3
32	22.08	3514.1	1694.5	716.4	48.8	9428.1	883.6	6968.3	8269.9
64	44.16	1378.1	236.5	306.3	-	53739.1	21158.0	10.1	1914.3
128	88.32	-	-	-	-	4656.1	55945.0	-	-

Table 5. Equations and probabilities of the analysis of mean activity versus maximum predicted tidal range by least squares regression analysis (Bailey, 1959). Symbols as Bailey (1959), axes as Fig 4.

Animal	equation	r	t	P
T. tenuis	$y = -24.02 + 10.95x$	0.57	1.95	0.08
T. fabula	$y = -70.44 + 25.03x$	0.68	2.61	0.03
all	$y = -42.95 + 16.87x$	0.61	3.29	0.004

Fig. 1

Experimental design.

For explanation of symbols see text.

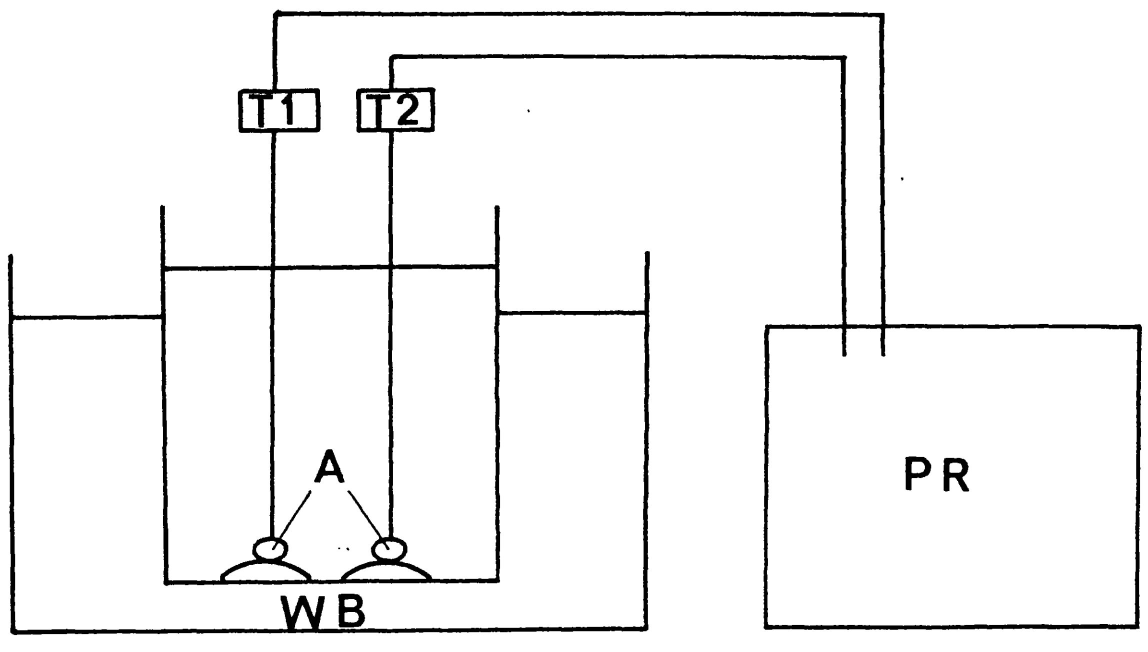


Fig.1

Fig. 2

Record of the activity of *T. tenuis*
(Animal No. 2)

The vertical lines indicate the number of adductions per sheet (41.5 minutes), the black bars the hours of darkness, and the predicted tidal height in metres is shown at the top.
Total experimental time - 7 days.

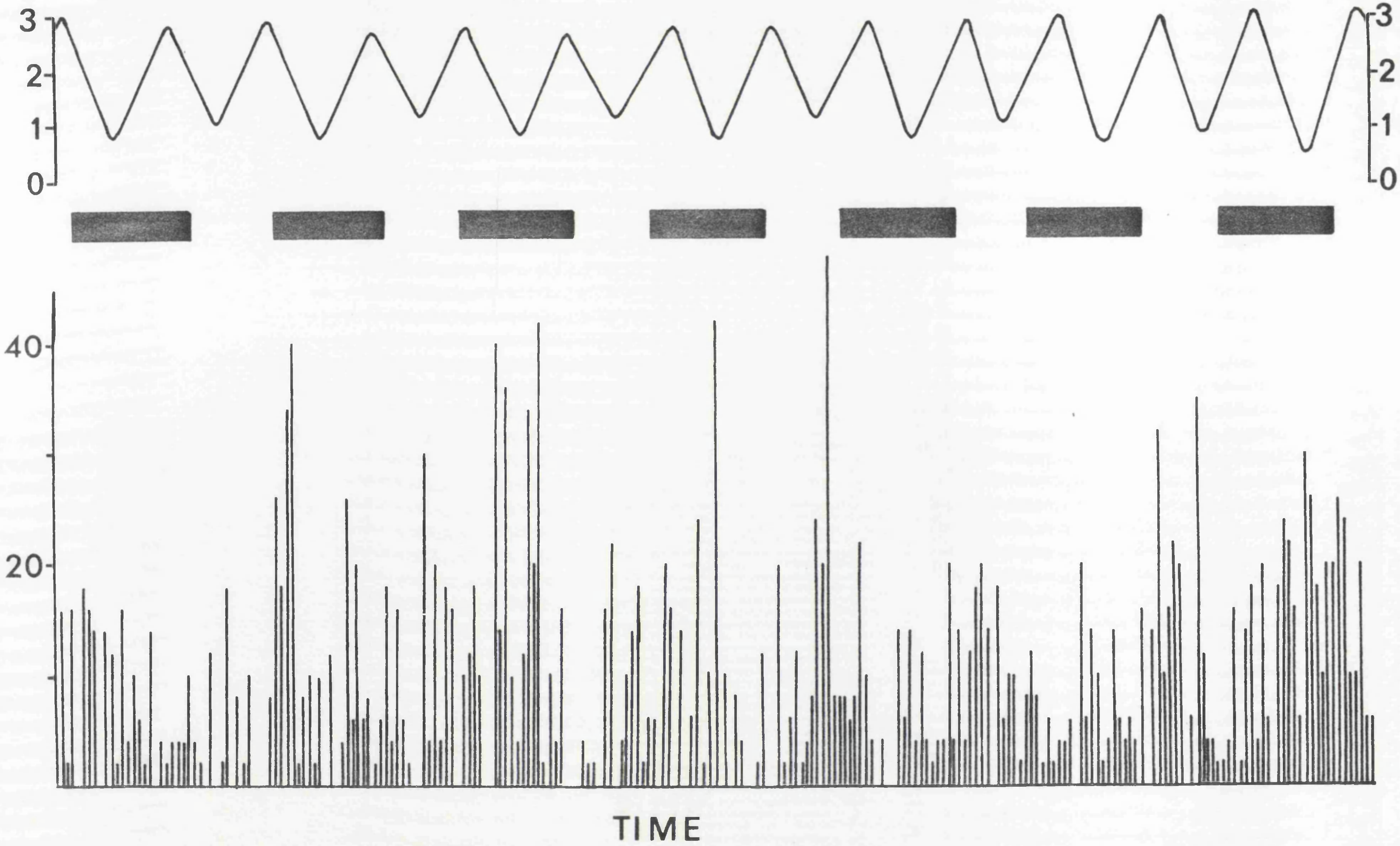


Fig.2

Fig. 3

Record of the activity of *T. fabula*
(Animal No. 9)

Symbols as Fig. 2.

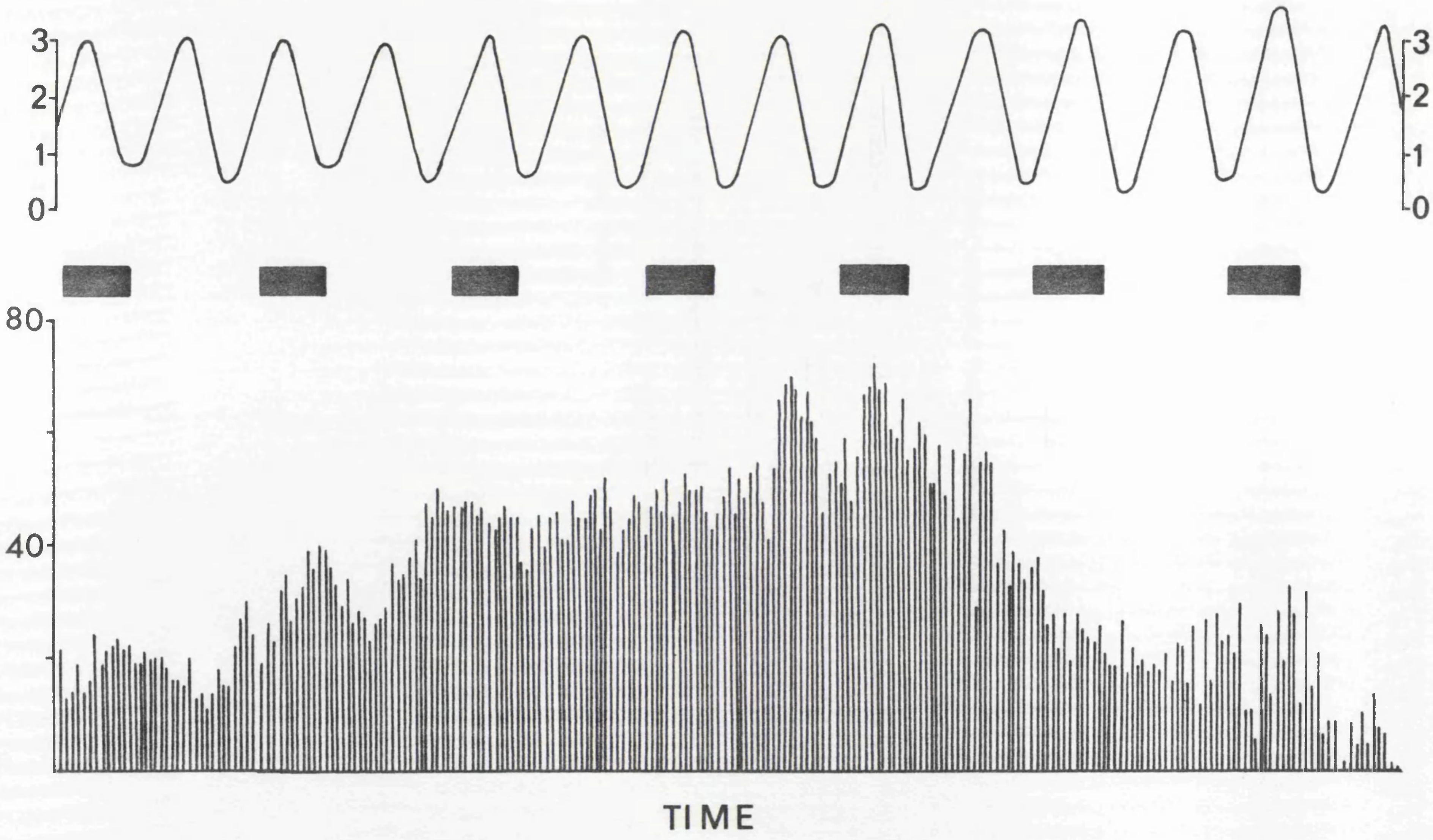


Fig.3

Fig. 4

Mean activity (adductions per sheet)

versus

maximum predicted tidal range during the experiment.

● T. tenuis; ○ T. tenuis transplant;

■ T. fabula; □ T. fabula transplant.

The regression equations are given in Table 5; for clarity only the regression line for all equations has been drawn.

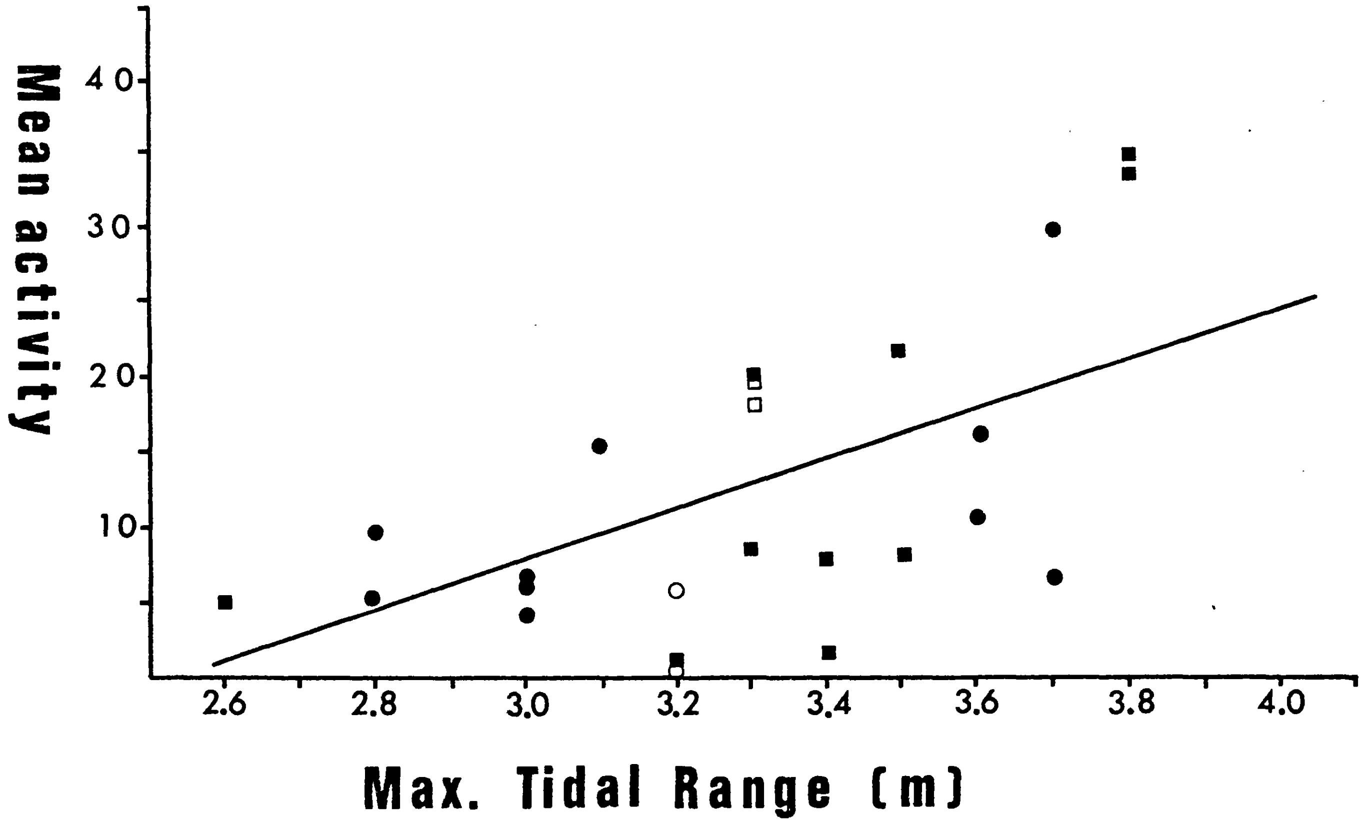

Mean activity
40
30
20
10
2.6
2.8
3.0
3.2
3.4
3.6
3.8
4.0
Max. Tidal Range (m)

Fig.4

Chapter 4

Sediment Analysis.

Introduction.

Different substrates are inhabited by different fauna and it has long been recognised that the nature of the sediment exerts great influence on the composition of the benthos. There exist differences in faunal composition not only between rocky bottoms and soft bottoms, but also amongst the various grades of soft bottom. These differences are consistent, and one faunal community is usually associated with one particular type of sediment (Davis, 1925; Thorson, 1957).

Various features of soft bottoms have received attention as being of special importance in influencing animal distribution. Perhaps the most widely investigated are the physical parameters of grain size, porosity, permeability and resistance of the sediment to penetration (Morgans, 1956).

The size of the sand grains in a sediment not only affects the behaviour and the distribution of adult animals (Wieser, 1956, 1959; Webb, 1958; Webb and Hill, 1958; Williams, 1958; Meadows, 1964; Gray, 1966, 1967b; Tenore et al, 1968; Morgan, 1970, Gale, 1971) but also is an important factor in the settling and metamorphosis of larvae (Wilson and Day, 1934; Wilson, 1948, 1952; Gray, 1967a). The distribution of some species depends on both the size and the arrangement of the sand grains (Bacescu, 1971), and the limiting factors of other species' distributions are sediment porosity and permeability (Webb, 1958; Jansson, 1967b) or the resistance of the sediment to penetration (Newell and Chapman, 1948; Chapman, 1949).

Although Crisp and Williams (1971) have demonstrated that there is no clear correlation between particle size and porosity, grain size is the most important parameter on which the others depend (Fraser, 1935; Webb, 1958, 1969; Jansson, 1967b). Certainly grain size is the most easily investigated factor since, unlike the other factors mentioned, it does not change with consolidation (Webb, 1969). However, no one factor can be viewed independently (Bacescu, 1971, Gray, 1974) and the field distribution will be the result of the interaction of all environmental factors (LaRow, 1970; Gale, 1971; Meadows and Campbell, 1972a).

Materials and Methods.

The sand was collected from Kames Bay, Millport, either with a spade from the beach when the tide was out, or with hand corers while SCUBA diving.

Four samples were taken from the beach, at LWS, LWN, MTL and HWS. The analysis of these samples was confined to grain size composition only. Three samples were also taken from my main collecting and experimental sites, "GL" (1.5 m above C.D.), "PP" (1.5 m below C.D.), and "DJ" (6 m below C.D.). These samples were analysed for grain size composition, porosity, permeability, and penetrability.

The grain size composition of the sediments was obtained in the following manner. The sands were dried for one week at 80°C before being placed in a nest of sieves, manufactured to BSS 410, on a mechanical shaker. After shaking for 24 hours, the amount retained by each sieve was weighed. For an explanation of the analysis of the grain size composition see Table 1.

The porosity of the samples is defined as the volume of space per 100 ml of sediment (Perkins, 1974), although Webb (1969) has defined porosity as the volume of space per 100 ml particles (the "void space" of Perkins (1974)).

The dried sand, in a measuring cylinder, was first consolidated in an ultrasonic generator to obtain uniform consolidation in all experiments (Webb, 1969). The volume of the space between the grains was then obtained by gradually adding seawater until the first traces of overlying water appeared. The sand was then considered to be completely saturated, and the height of the sand column was checked against the height of the column at the start of the experiment to ensure that no further consolidation had occurred.

The permeability apparatus, in essence a glass tube 3.14 cm internal diameter with gauze mesh aperture 70 µm over one end was modified from Webb (1958). Permeability was defined as the length of time taken for a column of seawater to pass through a column of sand 25 cm deep at a temperature of 22°C. The coefficient of permeability "p" was obtained from the equation

$$p = (al/AT)\log_e (h_1/h_2)\text{cm/sec} \text{ - - - - - - - - - - } (1)$$

where a and A are the cross sectional areas of the water and of the sand columns respectively, l is the length of the sand column, and h_1, h_2 are the heights of the water at the start, and after time T respectively (Perkins, 1974, p. 108). In my apparatus, a and A were the same, $l = 25$ cm and $h_1 = 25$ cm, $h_2 = 5$ cm. Equation (1) therefore becomes

$$p = 40.24/T \text{ - - - - - - - - - - - - - - - - } (2)$$

The penetrability of the samples was measured by the fall cone test for the shear strength of sediments (Caldenius and Lundstrom, 1956; Hansbro, 1957). In this test a weighted cone is dropped on to the sediment surface, and the depth of penetration by the cone can be converted into the shear strength by the formula

$$T_f = KQ/h^2$$

where T_f = undrained shear strength, K = empirical coefficient proportional to the cone angle, Q = weight of the cone, and h = depth of penetration (Hansbro, 1957, p.19). Ten fall cone tests were carried out for each combination of sand and water content. Each water content was obtained from subsamples taken from the dish immediately prior to the experiment. The subsamples were weighed, dried for 24 hours at 80°C, and then reweighed.

Results.

The sand from LWS, LWN, MTL and HWS was largely composed of grains 1.75 ϕ to 2.25 ϕ (300 µm to 200 µm) in size, and there seemed little difference in the grain size composition of the samples (Fig. 1, Table 2). The σ_I of around 0.35 indicates that the grains were well sorted (Folk and Ward, 1957). The Sk_I of around -0.3 shows that there was a tail of coarse grains ($-2 \leq \phi < 2$), and that the smaller particles were better sorted than the larger (Morgans, 1956). The particles were better sorted in the centre than at the extremes, and the curve, with a K_G of $>$ 1.11, is leptokurtic (excessively peaked)(Folk and Ward, 1957).

Similar results were obtained from the analysis of the three other samples, GL, PP and DJ (Fig. 2, Table 3). The main differences in these samples was that the particles from the DJ site (6 m below C.D.) were slightly finer (Md_ϕ = 2.51 (175 μm)), less well sorted, and more leptokurtic than the particles from GL or PP, while the particles from PP (1.5 m below C.D.) had a tail of fine grains.

In spite of these differences among the samples, the results (Figs. 1, 2; Tables 2, 3) suggest that there is little variation in the grain size composition of Kames Bay from HWS to 6 m below C.D.

The porosity of GL and PP sand (38.25% and 38.04% respectively) was considerably higher than that of the DJ sand (31.07%), as was the permeability (Table 4). The drainage time of the DJ sand was around 10 times slower, and consequently the permeability 25 times less, than that of the GL or PP sand. The "correction factor" (Webb, 1969, p.363-4) was 1.6 seconds for the total 20 cm fall in water level. It was decided that the correction factor could not be adequately measured for 5 cm intervals, so it has been omitted from Table 4. Since the height of sand column remained unchanged throughout the experiment, it was concluded that no further consolidation of the column had occurred.

The results of the penetrability experiments (Table 5) show that the penetrability of all three sands, GL, PP and DJ, decreased with decreasing water content. The DJ sand was less penetrable than GL or DJ sand when saturated (Table 6) but the distinction was lost when the sands were allowed to dry out.

Discussion.

While the sand composition and character remained fairly constant from the top of the beach down to just below low water, there was a slight change in composition accompanied by a radical change in character at the DJ site. This conclusion emphasises the importance of investigating other parameters than grain size, since the change in sand character could not have been wholly predicted by particle size analysis alone.

However, as expected (Bruce, 1928), porosity was correlated with the degree of sorting, and the least well-sorted sand from DJ ($\sigma_I = 0.626$) had the least pore space.

The permeability of a sediment, in general, is proportional to the grade of the sand, but it is only related to the porosity when all other factors, especially grain size, are constant (Webb, 1969; Perkins, 1974). It has been noted (Zeigler, 1964; Steele et al, 1970; Webb and Theodor, 1972) that decreased permeability, along with greater depth, may result in decreased interstitial water circulation. The conditions of decreased permeability and greatest depth existed at the DJ site suggesting, along with the presence of an anaerobic sulphide layer, that there was a decreased interstitial water circulation at this site, when compared with the GL or PP sites.

Both porosity and permeability are related to the thixotropy or dilatancy of the sand (Perkins, 1974) which may influence the faunal composition by helping or hindering burrowing (Newell and Chapman, 1948; Perkins, 1974). For example, the burrowing time of Arenicola depends on the degree of thixotropy of the sediment (Chapman and Newell, 1947; Chapman, 1949) such that on some beaches their density is inversely related to the hardness of the sand (Perkins, 1974). All the Kames Bay sands were dilatant, that is, they offered increased resistance to penetration with an increased rate of shear and the slight difference in penetrability between GL and DJ sands does affect the depth to which Tellina, particularly T. tenuis, will burrow. (see Chapter 5).

There is some discussion (see Chapter 2) as to the relative importance of deposit and filter feeding in T. tenuis and T. fabula. Evidence for both species as filter feeders was gained from the fact that the optimum grain size for filter feeders is 180 µm (Bloom et al, 1972). The median grain size in Kames Bay ranges from a minimum of 175 µm at DJ to 260 µm at PP. The relative coarseness of the grains may also preclude the modification of the sediment by deposit feeding inhabitants (Rhoads, 1974).

With regard to the beach itself, the results of the grain size analysis agree closely with those of Watkin (1942) so the composition seems to be fairly stable over a considerable period of time.

One may conclude that, in general, the physical parameters of the beach sands (GL, PP) and of the DJ sand do differ in some respects, notably in porosity, permeability and penetrability. These differences may contribute toward the separation of the distributions of *T. tenuis* and *T. fabula*.

Table 1. Descriptive measures of sediments adapted from Inman (1952), Folk and Ward (1957).

Measure	Nomenclature	Symbol	Definition
Central Tendency	Phi Median Diameter	Md_ϕ	$= \phi_{50}$
	Phi Mean Diameter	$M\phi$	$= \frac{1}{2} (\phi_{16} + \phi_{84})$
Sorting(Dispersion)	Inclusive Graphic Standard Deviation	σ_I	$= \frac{(\phi_{84} - \phi_{16})}{4} + \frac{(\phi_{95} - \phi_5)}{6.6}$
Skewness	Skewness Index	Sk_I	$= \frac{\phi_{16} + \phi_{84} - 2\phi_{50}}{2(\phi_{84} - \phi_{16})} + \frac{\phi_5 + \phi_{95} - 2\phi_{50}}{2(\phi_{95} - \phi_5)}$
Kurtosis (Peakedness)	Graphic Kurtosis	K_G	$= \frac{\phi_{95} - \phi_5}{2.44 (\phi_{75} - \phi_{25})}$
	5th Percentile Diameter	ϕ_5	
Diameter in Phi Units corresponding to a given percentage.	16th " "	ϕ_{16}	
	50th " "	ϕ_{50}	
	84th " "	ϕ_{84}	
	95th " "	ϕ_{95}	

Table 2. Analysis of Beach Sand.

For explanation of symbols, see Table 1.

Symbol	Position on Beach			
	LWS	LWN	MTL	HWS
Md_{ϕ}	2.18	2.22	2.18	2.18
M_{ϕ}	2.175	2.15	2.135	2.165
σ_I	0.344	0.429	0.360	0.282
Sk_I	-0.269	-0.386	-0.276	-0.118
K_G	2.09	2.06	1.64	1.23
ϕ_5	1.02	0.82	1.20	1.58
ϕ_{16}	1.95	1.84	1.84	1.91
ϕ_{50}	2.18	2.22	2.18	2.18
ϕ_{84}	2.40	2.46	2.43	2.42
ϕ_{95}	2.55	2.63	2.60	2.60

Table 3. Analysis of Beach and Sublittoral Sand.

For explanation of symbols, see Table 1.

Symbol	Position in Bay		
	GL	PP	DJ
Md_{ϕ}	2.18	1.95	2.51
M_{ϕ}	2.145	1.985	2.315
σ_I	0.377	0.318	0.626
Sk_I	-0.203	+0.126	-0.467
K_G	1.23	1.01	2.62
ϕ_5	1.40	1.50	0.62
ϕ_{16}	1.80	1.67	1.80
ϕ_{50}	2.18	1.95	2.51
ϕ_{84}	2.49	2.30	2.83
ϕ_{95}	2.75	2.56	3.05

Table 4. Permeability of Kames Bay sands.

Mean drainage time (minutes. seconds) taken for water column level to fall, and coefficient of permeability, p.

Height (cm) of water column above sand.	GL	PP	DJ
25 → 20	1.11	1.16	10.06
20 → 15	1.21	1.27	12.29
15 → 10	1.35	1.40	17.42
p (cm/sec)	1.12×10^{-1}	1.06×10^{-1}	4.17×10^{-3}

Table 5. Penetrability and water content of Kames Bay sands

T_f = shear strength in g/cm^2 (penetrability);

water content expressed as % by weight.

A - sand saturated plus overlying water film;

B - sand saturated, no overlying water;

C - sand left to dry for one hour.

For explanation of symbols GL, PP and DJ see text;

$\bar{x}$, s are the mean and standard deviation (Bailey, 1959) respectively of ten trials.

		GL		PP		DJ	
		$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
A	T_f	8.77	0.46	9.03	0.86	9.86	0.71
	Water Content	33.8		30.40		31.85	
B	T_f	27.03	10.5	25.53	6.7	44.10	15.0
	Water Content	29.44		27.75		29.62	
C	T_f	416.0	148.4	392.0	94.7	412.0	127.4
	Water Content	21.29		20.98		22.35	

Table 6. Probability values (P) for the comparison by t - test (Bailey, 1959) of the penetrability of GL, PP and DJ sands.

For explanation of symbols see Table 5.

Comparison	A		B		C	
	t	P	t	P	t	P
GL & PP	0.84	0.41	0.38	0.71	0.43	0.67
GL & DJ	4.09	<0.001	2.95	0.01	0.07	0.95
PP & DJ	2.35	0.03	3.58	0.003	0.40	0.69

Fig. 1 Grain size composition of beach sands.

■——■ - LWS

▲- - - -▲ - LWN

●-·-·-● - MTL

×······× - HWS

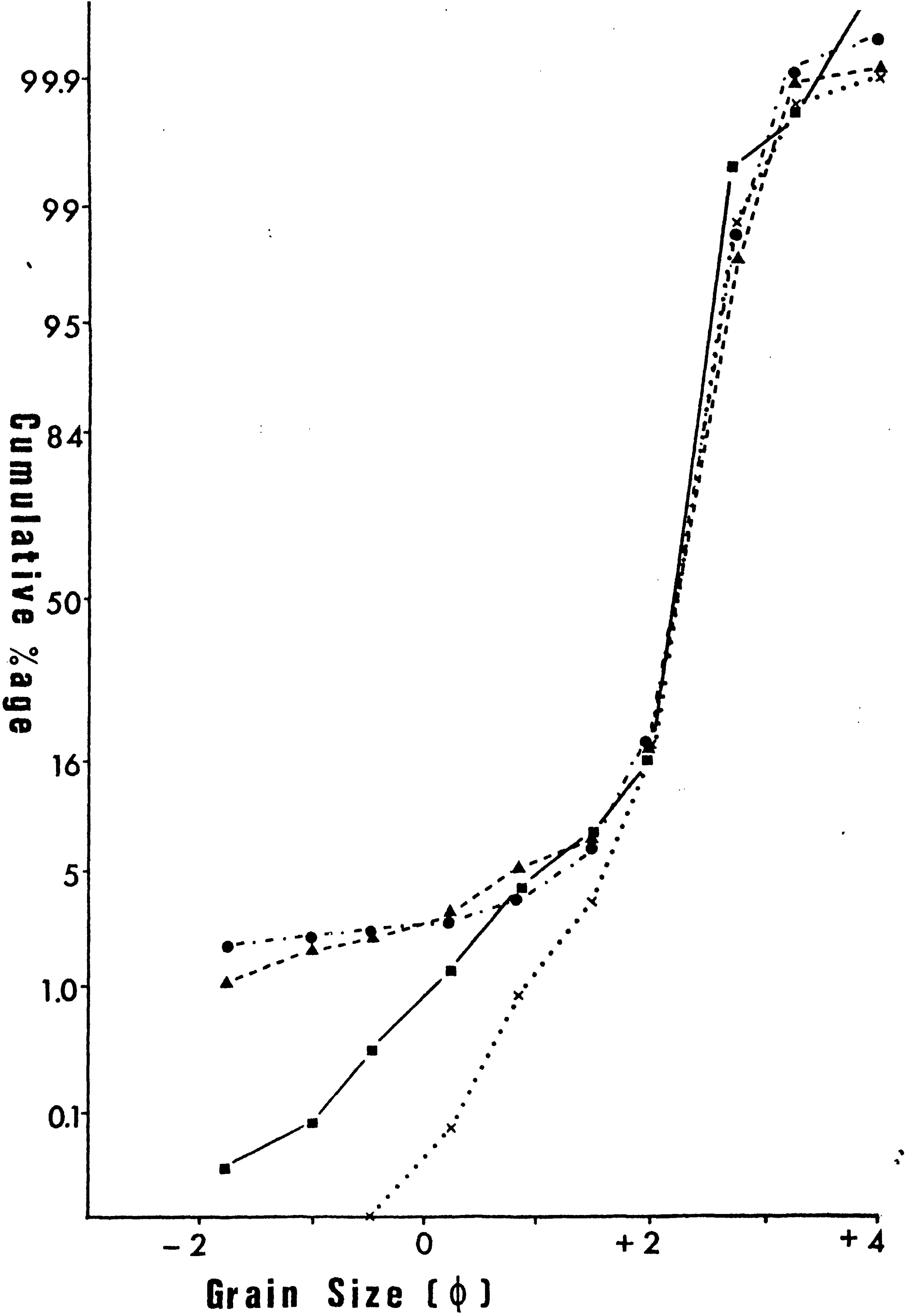


Fig. 1

Fig. 2 Grain size composition of beach and sublittoral sands.

×——× – GL

▲- - - -▲ – PP

■······■ – DJ

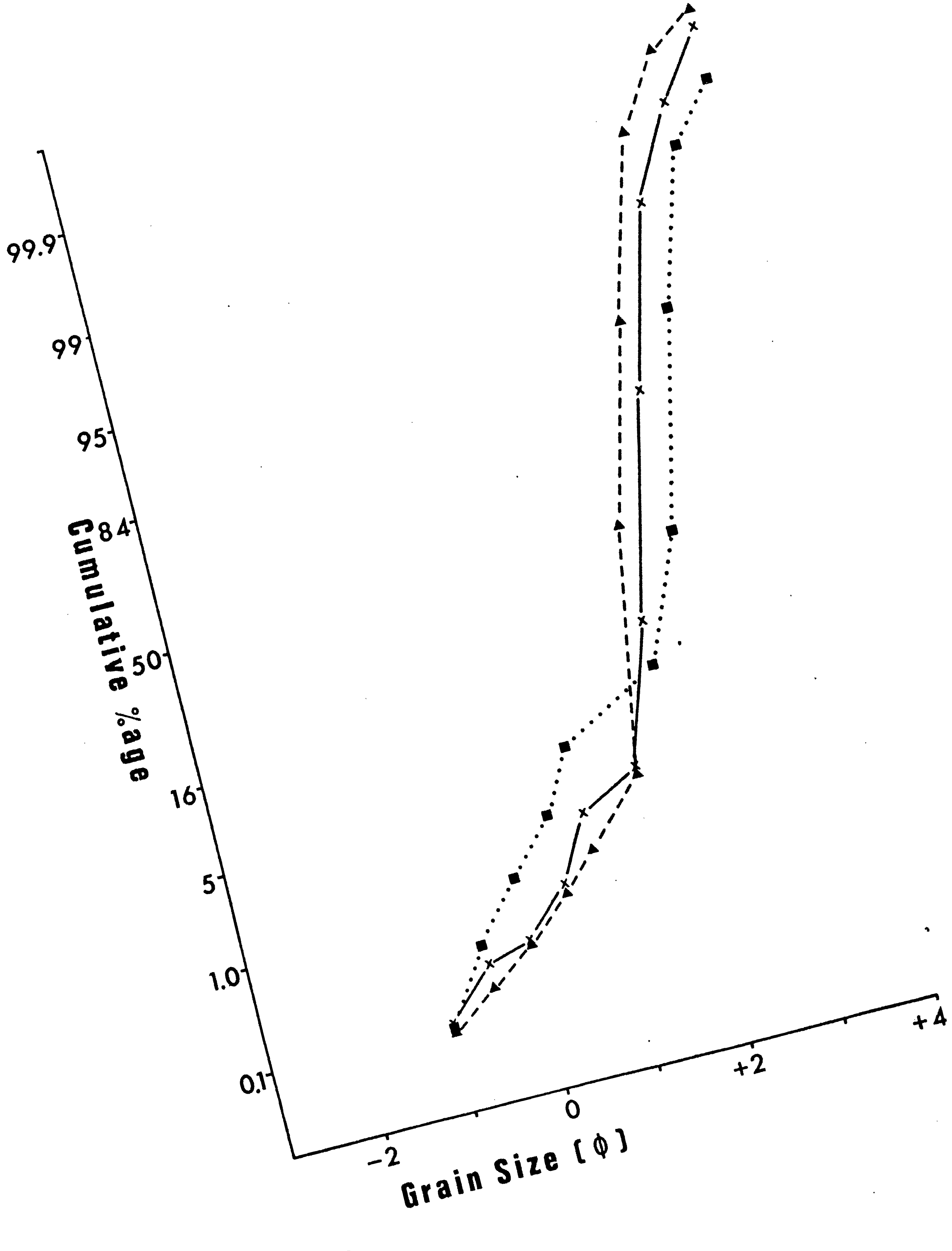


Fig. 2

Chapter 5

Burrowing.

Introduction.

The Bivalvia have evolved into many varied infaunal and epifaunal types, but they are probably best known for the variety of species inhabiting soft substrates. Bivalves, such as T. tenuis have filled this evolutionary niche with such success that they are the dominant animal on many beaches (Stephen, 1928; McIntyre, 1970), and they are absent only on beaches exposed to extremes of wave action (McIntyre, 1970). Part of this success is due to the bivalves' ability to penetrate and to live within the sediment, thus escaping to some extent both predators and adverse environmental conditions.

The process of burrowing has been studied in many species, including members of the Solenacea (Fraenkel, 1927; Pohlo, 1963), the Lucinacea (Allen, 1958), the Veneracea (Quayle, 1949; Ansell, 1962; Nair and Ansell, 1968), the Mactracea (Trueman, 1968a), the Cyprinacea (Saleuddin, 1964; Taylor, 1976), the Arcacea (Ansell and Trueman, 1967), the Cardiacea (Trueman et al, 1966 a, b), and the Tellinacea (Trueman et al 1966 a, b; Nair and Ansell, 1968; Trueman, 1968 b).

The digging cycle of Tellina, or indeed almost any bivalve, can be divided into 6 main stages (after Trueman et al, 1966 b)

(i) foot probing followed by pedal dilation;
(ii) siphons close;
(iii) rapid adduction of the valves along with maximum pedal dilation and the ejection of water from the ventral mantle margin;
(iv) contraction of retractor muscles, the anterior slightly

before the posterior, resulting in a "slicing" motion;

(v) relaxation of adductor muscles, siphons re-open, valve gape increases and pedal dilation is reduced;

(vi) static period, often marked by small probing movements of the foot, until the next cycle begins at stage (i).

Both T. tenuis and T. fabula exhibit a preference for burrowing on their left sides and, although this preference is not as marked as in some other Tellinidae (Holme, 1961), they are usually found lying in the sand on the left valve (Holme, 1950, 1961).

The two species are morphologically very similar (Yonge, 1949; Holme, 1961) yet they have quite separate distributions in Kames Bay (Stephen, 1933; Watkin, 1942; Clark and Milne, 1955). T. tenuis is a littoral species, T. fabula is a sublittoral species, and there is little overlap of the ranges.

There are some passing references (Yonge, 1949; Holme, 1950; Trevallion, 1971) to the depth to which T. tenuis will burrow, but there are none at all for T. fabula.

It was therefore decided to investigate the depth distributions of T. tenuis and T. fabula, and also various aspects of their burrowing behaviour, in both littoral and sublittoral sediments.

Materials and Methods.

For the laboratory experiments, T. tenuis and littoral sand were gathered from a site 1.5 m above C.D. (hereafter referred to as GL) and T. fabula and sublittoral sand from a site 6.0 m below C.D. (hereafter referred to as DJ). These were also the principal sites for the field experiments.

The burrowing behaviour of T. tenuis and T. fabula was studied in the following way. The animals were dug out of the sand, their shell length was noted, and they were allowed to burrow again as soon as possible. Animals on the beach were placed in a pool deep enough to cover the erect shell. Three observations were made of each animal burrowing. These were the time taken from the animal being placed on the sand to the start of the initial probing movements of the foot (Time to start); the time taken from initial probing to the animal's disappearance from sight (Time started); and the number of digging cycles the animal required to disappear beneath the sand (No. cycles). Those animals which had not burrowed within 1 hour of the experiment starting were discarded.

The depth distribution in the field was measured using hand corers. The cores were cut into 5 cm lengths, and the number and shell lengths of the animals in each 5 cm length was noted down. More accurate measurement of the depth distribution was not attempted since the cores, especially those taken underwater, were subject to considerable disturbance before they could be examined.

In the laboratory, the depth of each individual animal was measured. The experimental chambers (2 l beakers) were filled with sand to a depth of 15 cm, and topped up with seawater. 20 animals were sprinkled into each beaker and the experiment was left for 1 week. The sand was then spooned out, and the burrowing depth and shell length of each animal was noted. An experiment, using T. tenuis, was also set up to investigate the effect of keeping the sand or the animals in the laboratory.

Attempts were also made to monitor the depth and the movements of the animals in situ using natural sand and x-radiography or cryolite (Josephson and Flessa, 1972) crushed to between 125 µm and 350 µm in diameter and a time lapse cine camera. The experimental chambers, 15 cm high by 15 cm across, for these experiments were made of transparent Perspex.

Results.

The depth at which T. tenuis and T. fabula were found in the field are shown in Table 1. There was no significant difference in the depth distribution of T. tenuis with the state of the tide,(Table 1, row 1 and 2, $X^2 = 1.03$, d.f. = 2, $P = 0.32$).

There was, however, a significant difference between the depth distributions of T. tenuis (Table 1, rows 1 and 2 combined) and T. fabula (Table 1, row 3) ($X^2 = 20,30$, d.f. = 2, $P < 0.001$).

The shell length of the animals was correlated with the depth at which they were found in T. tenuis, where the bigger animals were found deeper, but not in T. fabula (Table 2).

In the laboratory, T. tenuis burrowed deeper than T. fabula in GL or in DJ sand (Table 3). The burrowing of T.tenuis in the DJ sand was significantly shallower than in the GL sand, but the burrowing of T. fabula was not affected by the change in sediment (Table 3). T. tenuis in GL sand burrowed significantly deeper than T. fabula in DJ sand ($t = 10.23$, $P < 0.001$).

It was found that three weeks storage of the sand or the animals significantly affected the burrowing of T. tenuis. Fresh animals in stored sand and stored animals in fresh sand burrowed significantly shallower ($t = 8.29$, $P < 0.001$ and $t = 6.39$, $P < 0.001$ respectively) (Bailey, 1959) when compared with the results of fresh T. tenuis in fresh GL sand.

In the laboratory there was no correlation, when tested by regression analysis (Bailey, 1959), between the depth of burrowing and shell length with T. tenuis in GL sand ($r = 0.15$, $t = 0.92$, $P = 0.36$) or T. fabula in DJ sand ($r = 0.15$, $t = 1.32$, $P = 0.19$).

The burrowing behaviour observations in the field showed that smaller animals burrowed faster and with fewer digging cycles than larger animals in both T. tenuis (Fig. 1, Table 4) and T. fabula (Fig 2, Table 5). There was also a significant correlation between the log of the burrowing time and the number of digging cycles in both species in both GL and DJ sands (Fig. 3, Table 6).

The change from GL sand to DJ sand had little effect on the burrowing behaviour of T. tenuis. Neither time started nor No. cycles was significantly changed, although both were raised slightly (Table 4). However, there was a significant rise in the log time started plotted against No. cycles (Table 6) suggesting that there was a longer pause between each of the digging cycles.

The change from DJ sand to GL sand affected the burrowing of T. fabula in that, in the GL sand, there was no correlation between shell length and time started or No. cycles (Table 5). As with T. tenuis, the log time started versus No. cycles was less in the GL sand, although not significantly so (Table 6).

There was no indication in either species that time to start varied with the size of the animal (Table 4, Table 5). However, it must be remembered that only about $^2/_3$ of all animals starting the experiment burrowed within the 1 hour time limit, and so only $^2/_3$ of the sample were used in the experiment.

The height up the beach at which the T. tenuis were found did not affect the time they took to burrow (Table 7). For this experiment the time limit was twenty minutes (the period of exposure at the lowest position on the beach).

Although neither the x-radiography nor the time-lapse experiments were very successful, some photographs were obtained of Tellina burrowing and in life position. Plates 1, 2, and 3 are a sequence from a time-lapse film, total length about 24 hours, of the animals in natural sand. Plate 4 is from an x-radiograph. For explanation of plates, see legends.

Discussion.

The burrowing behaviour of T. tenuis has already been described by several authors (Yonge, 1949; Holme, 1961; Trueman et al, 1966 a), and it seems, from my observations, that T. fabula and T. tenuis perform a similar series of movements.

The depth to which T. tenuis will burrow appears to be fairly constant at all localities. Depths down to 12 cm in

Kames Bay (Yonge, 1949), 2-4 inches (5-10 cm) in the Exe estuary (Holme, 1951) and down to 10 cm, depending on the water table in Loch Ewe (Trevallion, 1971), fall well within the range described here. Unfortunately, no such information is available for the burrowing of T. fabula, but the magnitude of the difference between the depth distributions of T.tenuis and T. fabula in either GL or DJ sand suggests that T. tenuis will always burrow deeper than T. fabula. It is worth noting, however, that no diminution of burrowing depth with distance down the shore, as described by Trevallion (1971) in Loch Ewe, was observed in the T. tenuis population in Kames Bay.

The difference in the depth distributions of T. tenuis and T. fabula may have been due to the difference in the size of the adult animals as happens with Mactra corallina and Mactra glauca (Trueman, 1968 a). Certainly, in the field, large T. tenuis burrow deeper than small, and although this was not found to be the case with T. fabula, other workers have described similar situations in Scrobicularia plana (Hughes, 1970), Macoma inconspicua and Mya arenaria (Vassallo, 1971). The correlation between shell length and depth of burrowing may, however, apply only to a limited range of shell lengths (Hughes, 1970) or burrowing depths (Vassallo, 1971) while an inverse relationship between shell length and depth of burrowing has been reported in Macoma balthica (Hulscher, 1973).

The cessation of burrowing, and hence the depth of burrowing, was at one time considered to be under the control of a factor such as fatigue (Fraenkel, 1927), but this suggestion has since been discounted (Quayle, 1949; Ansell, 1962).

In the Lucinacea, burrowing depth is allied to the length of the foot (Allen, 1958), but it has been suggested that, in less aberrant species, burrowing depth may be controlled by the degree of siphon extension (Nair and Ansell, 1968; Trueman, 1968 a, 1971). Under this hypothesis, one would expect that burrowing depth would be related to size, and that the siphon tips would remain in contact with the surface (e.g. plate 2, photographs 5, 6). However, the siphons of Tellina were not always in contact with the surface (plate 1, photographs 2, 3), but they could be forced back up through the sand into a fresh position (plate 3, photograph 8). In this way, Tellina may be able to migrate horizontally through the sand (Holme, 1961) and to keep their depth constant by checking the degree of extension of their siphons at each fresh position. Deeper burrowing may be possible by the animals using interstitial water for respiration (Ansell and Trueman, 1967), such that burrowing depth is then controlled by the porosity and permeability of the sediment, or by respiring anaerobically, as does Arctica islandica (Taylor, 1976).

It has been suggested that (Trueman et al, 1966 a) the resistance of a sediment to penetration increases with depth, and that burrowing ceases when the penetration per unit effort falls below a minimum value (Nair and Ansell, 1968). This mechanism may play a part in the control of burrowing depth of Tellina, since T. tenuis burrowed significantly deeper in GL sand which is more penetrable than DJ sand (see Chapter 4). However, it must be remembered that T. fabula did not burrow deeper in GL sand, and that shell length and burrowing depth were correlated in field samples of T. tenuis. The control of burrowing depth in Tellina may therefore result from a combination of siphon extension and sediment penetrability and permeability.

Although the burrowing depth of T. fabula was not altered by the change in sediment, the burrowing behaviour was affected. Both time started and No. cycles ceased to be correlated with shell length. This may have been due to the small range of animal sizes obtained for the experiment (0.9 cm to 1.2 cm) and no such loss of correlation was noted in T. tenuis. The time per digging cycle of T. tenuis, however, was significantly slower in DJ sand, suggesting that the static period, which incorporates the exploratory probing, had lengthened due to the decreased penetrability of the sediment (Trueman, 1968 b).

In conclusion, the results show that T. tenuis burrowed deeper, but not faster, than T. fabula of similar size. The burrowing depth of T. tenuis alone was restricted by the less penetrable DJ sand, and the time per digging cycle was increased.

Table 1. Depth distribution of _T. tenuis_ and _T. fabula_ in the field.

Numbers per 5 cm length of core.

	Depth (cm)			
	0–5	5–10	10–15	15–20
T.tenuis (tide out)	12	58	11	3
T.tenuis (tide in)	7	48	15	0
T.fabula	18	26	2	0

Table 2. Comparison by t-test (Bailey, 1959) of the mean shell lengths (cm) of *T. tenuis* and *T. fabula* in 5 cm lengths of core.

		Depth (cm)		
		0-5	5-10	10-15
shell length (cm) mean ± standard deviation	*T. tenuis*	0.70 ± 0.07	1.18 ± 0.32	1.40 ± 0.20
	P		< 0.001	< 0.001
shell length (cm) mean ± standard deviation	*T. fabula*	0.79 ± 0.22	0.84 ± 0.21	-
	P		0.43	

Table 3. Comparison by t-test (Bailey, 1959) of the depth distribution of *T. tenuis* and *T. fabula* in different sediments in the laboratory (both animals and sand fresh).

		Sediment type			
		GL	DJ	t	P
Mean depth (cm) ± standard deviation	*T.tenuis*	6.72 ± 3.18	5.59 ± 2.24	2.53	0.01
	T.fabula	2.96 ± 1.45	3.17 ± 1.16	0.72	0.48
	t	10.40	6.02		
	P	< 0.001	< 0.001		

Table 4. Regression analysis (Bailey, 1959) of the burrowing behaviour of <u>T. tenuis</u>. Length (cm) versus (a) number of cycles; (b) time started (minutes); and (c) time to start (minutes). Axes as Fig. 1.

	Sediment	r	P	Equation	Slope Comparison
(a)	GL	0.60	<0.001	$y = 15.3 + 5.0\,x$	P = 0.43
	DJ	0.59	<0.001	$y = 12.6 + 5.69\,x$	
(b)	GL	0.38	0.015	$y = -0.33 + 1.0\,x$	P = 0.28
	DJ	0.70	<0.001	$y = -0.73 + 1.61\,x$	
(c)	GL	0.26	0.10	-	-
	DJ	0.32	0.16	-	

Table 5. Regression analysis (Bailey, 1959) of the burrowing behaviour of *T. fabula*.

Length (cm) versus (a) number of cycles;

(b) time started; and

(c) time to start (minutes).

Axes as Fig. 2.

Sediment		r	P	Equation	Slope Comparison
(a)	GL	0.11	0.62	-	-
	DJ	0.42	0.01	$y = 17.97 + 8.06\,x$	
(b)	GL	0.04	0.86	-	-
	DJ	0.36	0.03	$y = -0.5 + 1.95\,x$	
(c)	GL	0.13	0.59	-	-
	DJ	0.08	0.64	-	

Table 6. Regression analysis (Bailey, 1959) of log time started versus No. cycles in *T. tenuis* and *T. fabula*. Axes as Fig.3.

Animal	Sediment	r	P	Equation	Slope Comparison
T.tenuis	GL	0.62	< 0.001	$y = 1.2 + 0.026\,x$	P = 0.07
	DJ	0.78	< 0.001	$y = 0.88 + 0.045\,x$	
T.fabula	GL	0.40	0.07	$y = 1.15 + 0.023\,x$	P = 0.53
	DJ	0.57	< 0.001	$y = 0.94 + 0.032\,x$	

Table 7. Burrowing time of *T. tenuis* from various positions on the beach (Bailey, 1959).

Height above C.D. (m)	Mean Time (minutes)	t		P	
2.7	5.69				
		0.16		0.87	
2.0	5.57		0.63		0.53
		0.97		0.34	
0.5	6.21				

Fig. 1a. Number of digging cycles versus shell length in a field population of T. tenuis.

■ - in GL sand

x - in DJ sand.

Fig. 1b. Burrowing time once started versus shell length in a field population of T. tenuis.

■ - in GL sand

x - in DJ sand.

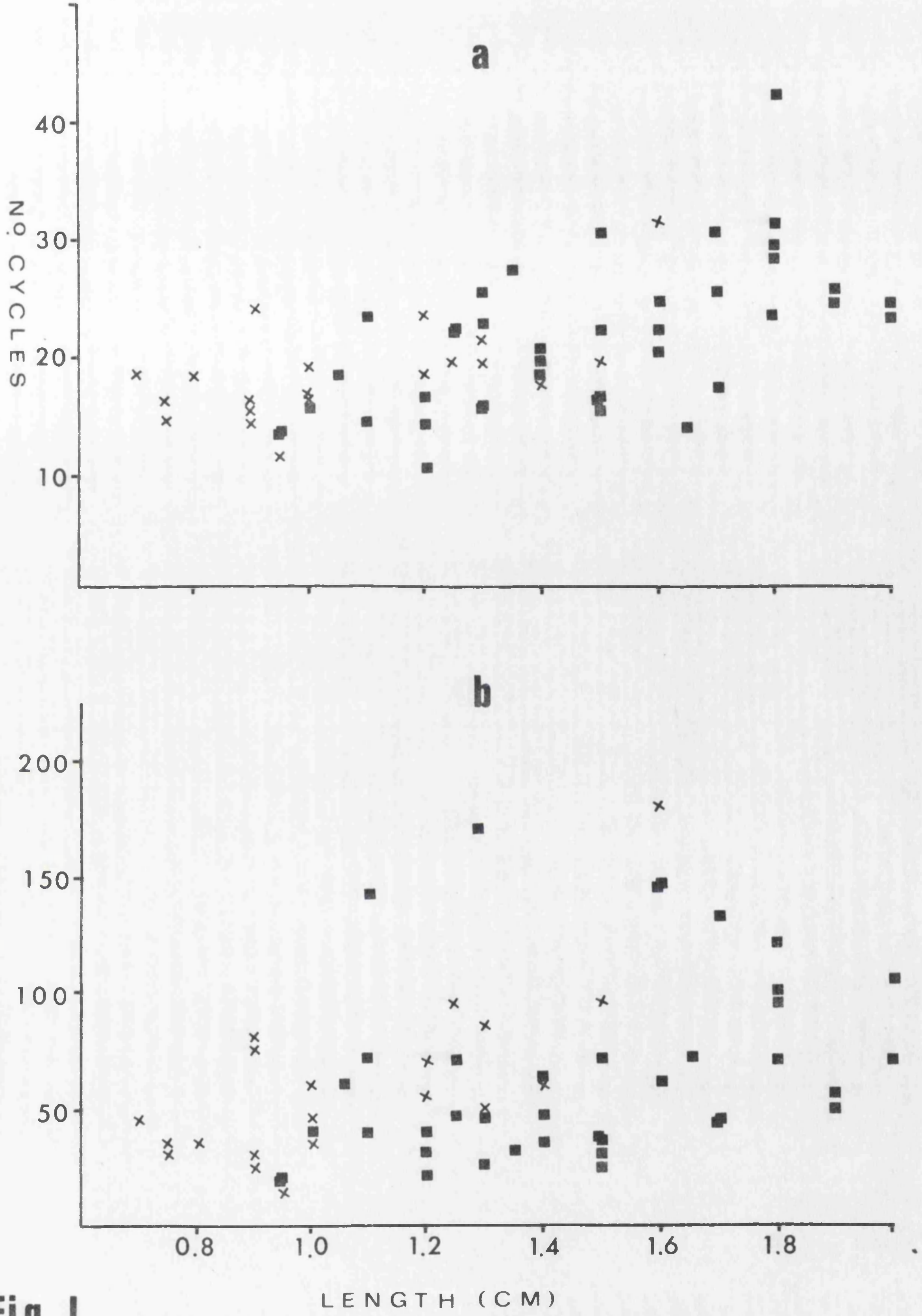

a
Nº CYCLES
40
30
20
10
b
TIME STARTED (SEC)
200
150
100
50
0.8
1.0
1.2
1.4
1.6
1.8
LENGTH (CM)

Fig. I

Fig. 2a. Number of digging cycles versus shell length in a field population of *T. fabula*.

□ - in DJ sand

● - in GL sand.

Fig. 2b. Burrowing time once started versus shell length in a field population of *T. fabula*.

□ - in DJ sand

● - in GL sand.

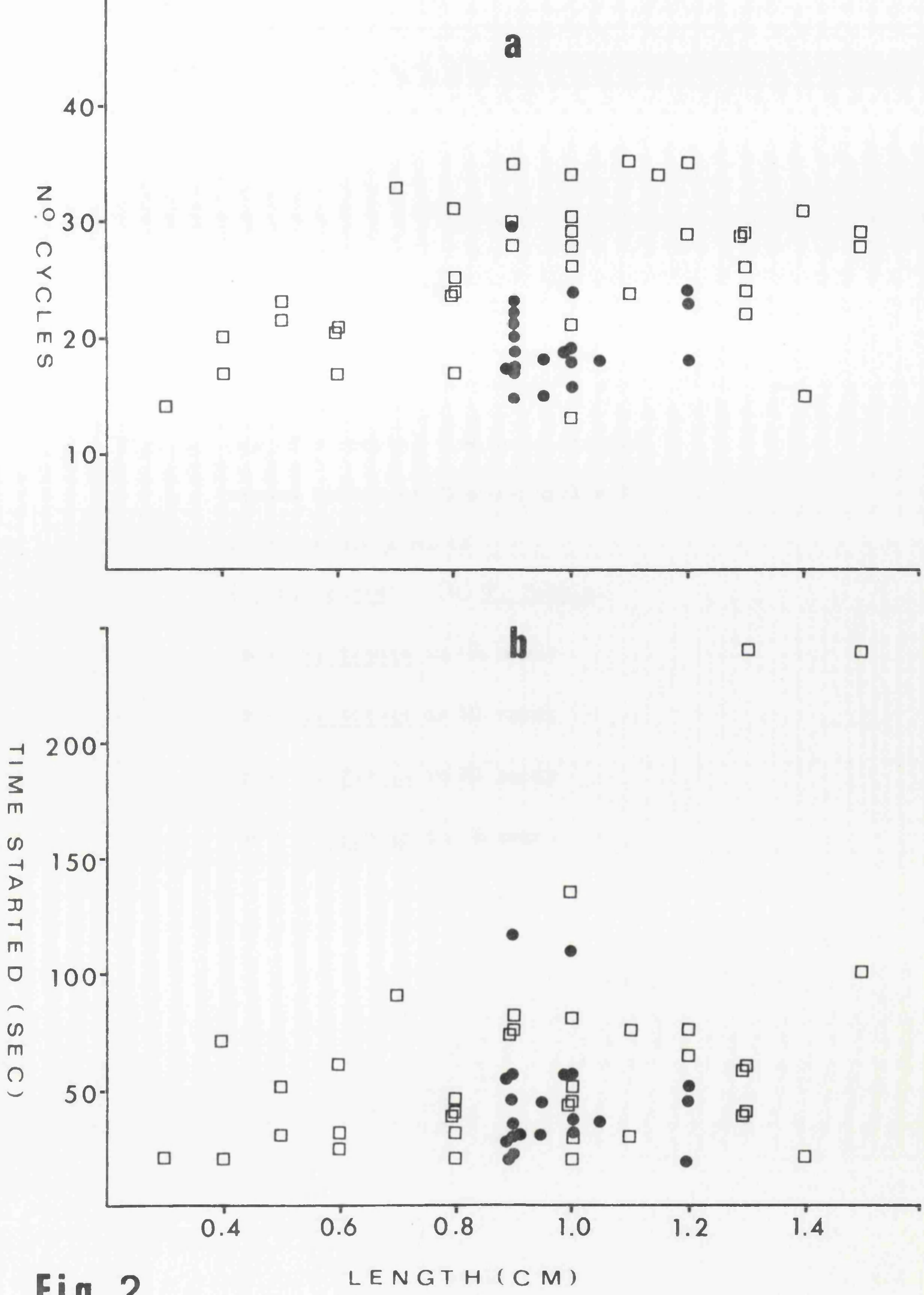

a
N° CYCLES
40
30
20
10
b
TIME STARTED (SEC)
200
150
100
50
0.4
0.6
0.8
1.0
1.2
1.4
LENGTH (CM)

Fig.2

Fig. 3. Log of burrowing time once started versus number of digging cycles in field populations of (a) _T. tenuis_; (b) _T. fabula_.

■ - _T. tenuis_ in GL sand;

x - _T. tenuis_ in DJ sand;

□ - _T. fabula_ in DJ sand;

● - _T. fabula_ in GL sand.

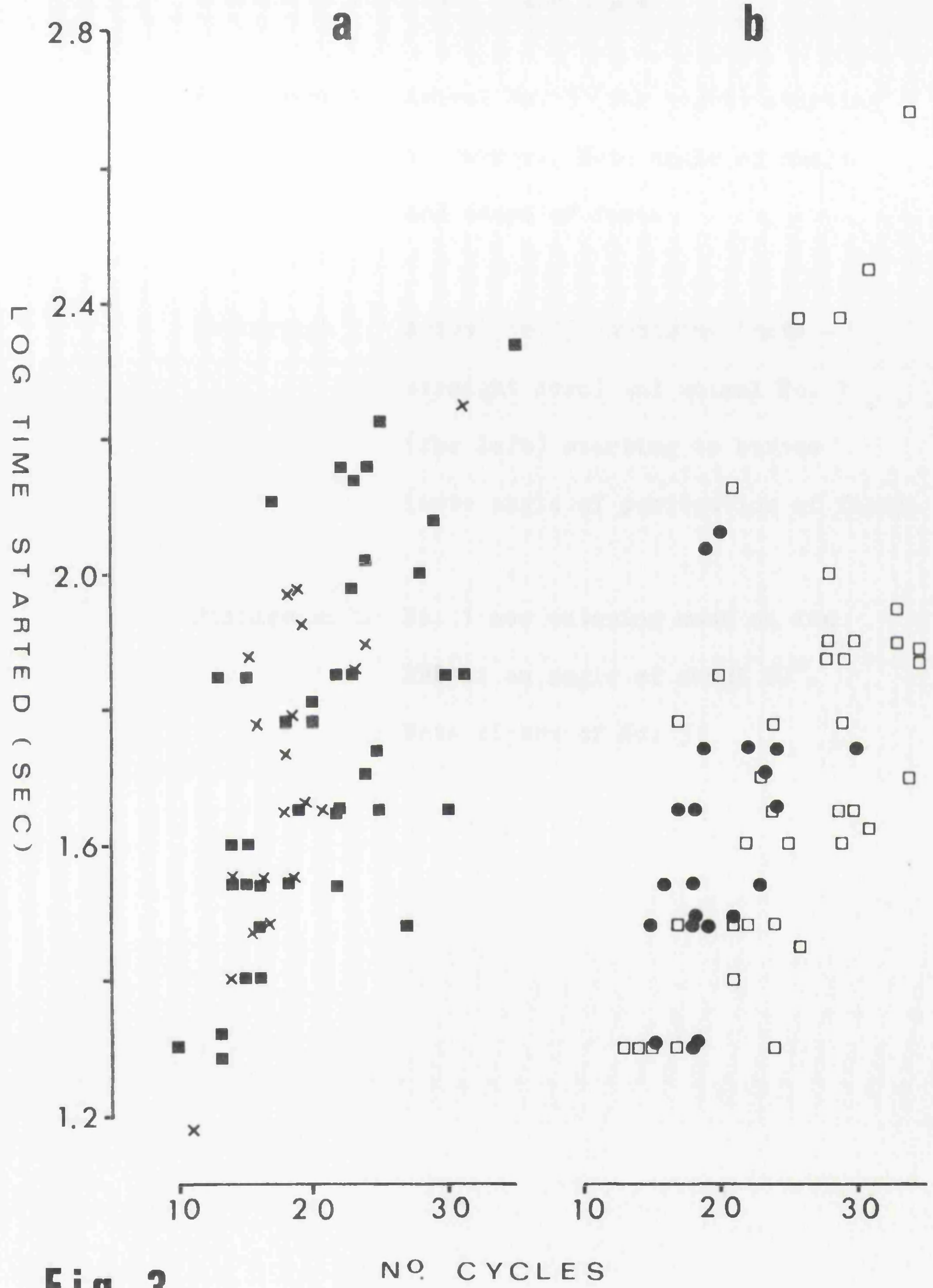


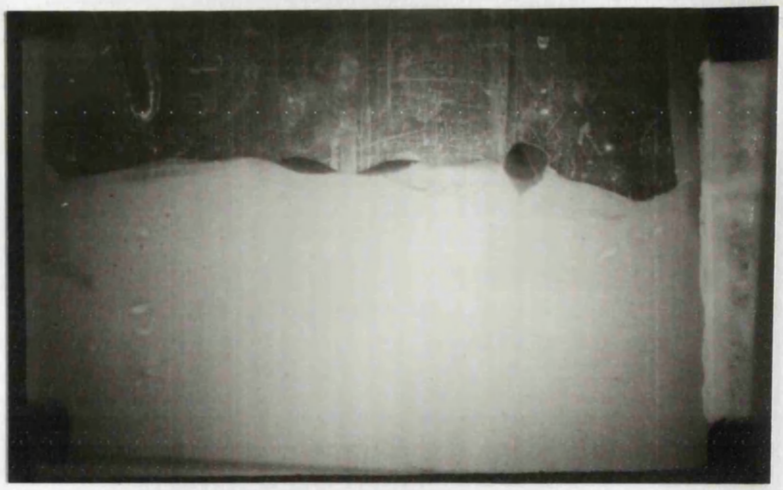
Fig. 3

Plate 1. Animals in Cryolite; time lapse.

Photograph 1. Animal No. 3 (far right) starting to burrow. Note angle of shell and shape of foot.

Photograph 2. Animal No. 3 burrowing (note - straight down) and animal No. 1 (far left) starting to burrow (note angle of penetration of foot).

Photograph 3. No. 1 now entering sand on its RHS at an angle of about 60°. Note siphon of No. 3.



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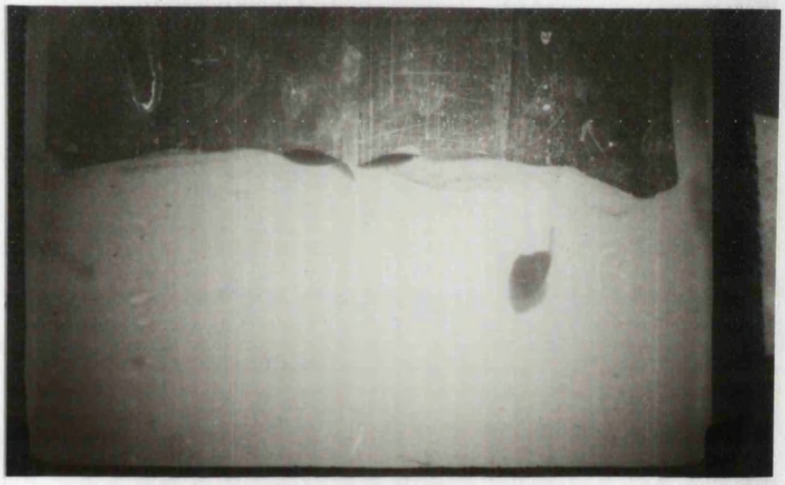


2

3

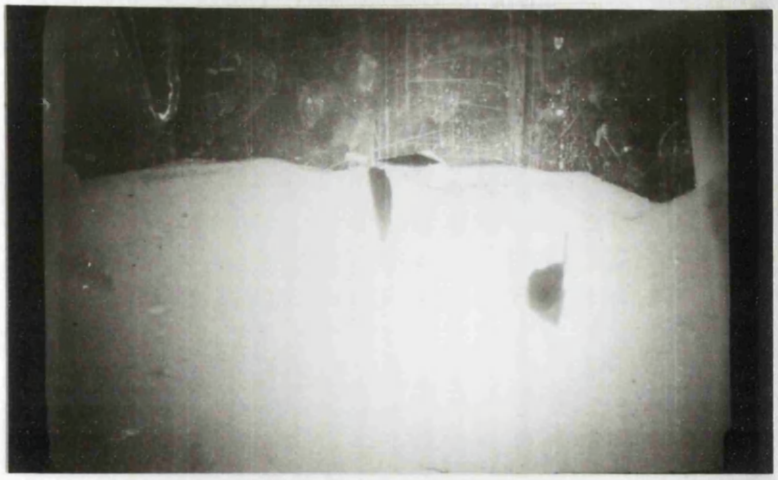
Plate 1

<u>Plate 2</u>. Animals in Cryolite; time lapse (Contd.)

Photograph 4. No. 1 now burrowing vertically; note siphon.

Photograph 5. No. 1 now turning onto LHS, siphon still in contact with surface. No. 3 siphon completely withdrawn.

Photograph 6. No. 1 at an angle of 45° on LHS, still burrowing - note length of siphon! Animal No. 2 (centre) starting to burrow. No. 3 - siphon just protruding.



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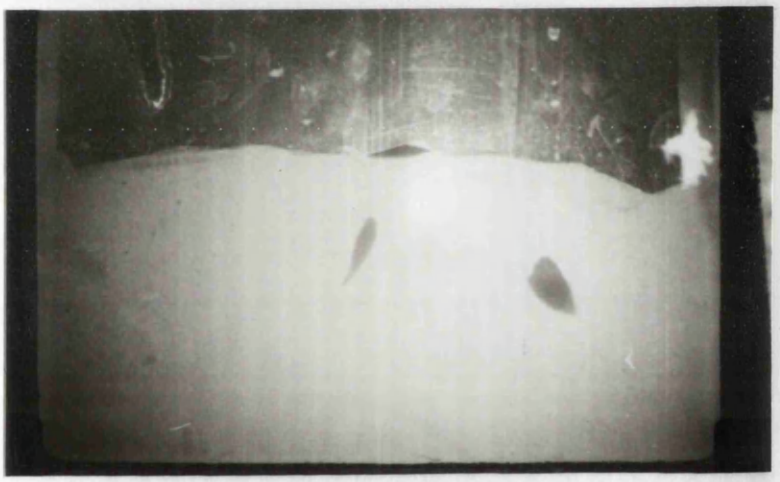

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6

Plate 2

Plate 3. Animals in Cryolite; time lapse (Contd.)

Photograph 7. No. 1 and No. 3 quiescent (no foot protruding); exhalent siphon of No. 1 just visible alongside inhalent siphon. No. 2 (upper left) still burrowing.

Photograph 8. Tank has leaked and all three animals are quiescent. Note final position of siphons in No. 3 (now in centre).

7

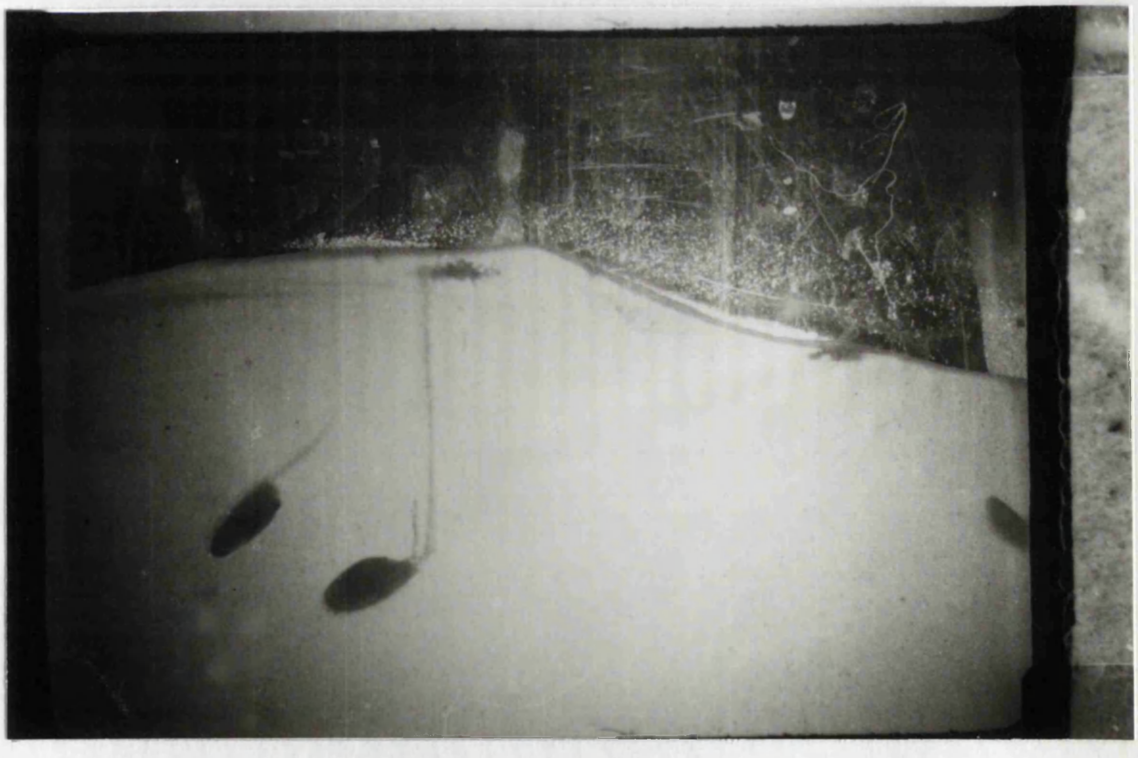

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Plate 3

Plate 4. Animals in sand; x-radiographs.

Photograph 9. Note position of siphons of animal on right; outline of foot just visible in both animals. The black blobs are air bubbles within the sediment.

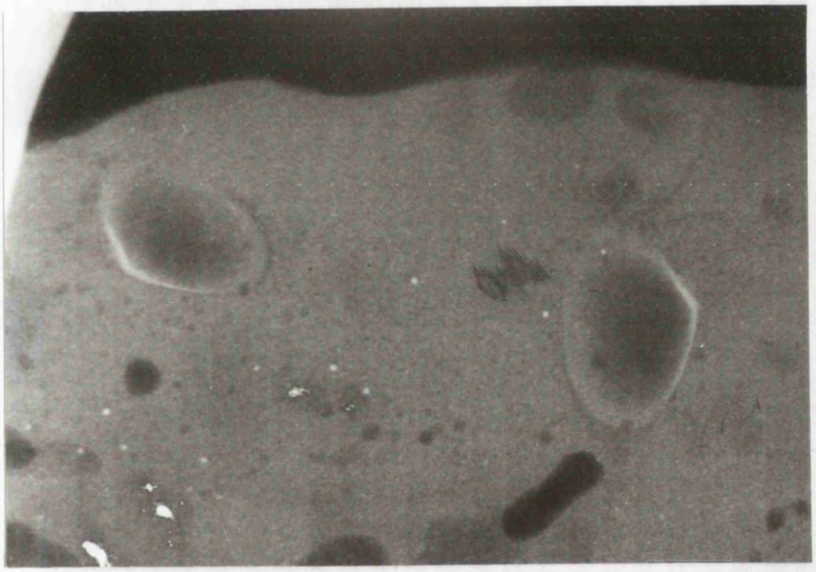


Plate 4

Chapter 6

Morphology.

Introduction.

At first sight, T. tenuis and T. fabula, according to Stephen (1933) "display considerable external similarity". As regards their internal structure, Yonge (1949) concluded that examination of the two species revealed no significant differences, although Forbes and Hanley (1853) suggested that the siphons of T. fabula were slightly longer, and Atkins (1937 a, b) noted some differences in gill and palp structure.

With practice, however, T. fabula may be distinguished from T. tenuis by the fact that it is slightly more elongate, and by the possession of ridges running diagonally across the right valve (Tebble, 1966). The paper entitled "A Scanning Electron Microscope study of the shell ornamentation of Tellina fabula Gmelin"(to be submitted for publication) on the form and possible function of these striations, has been included at the end of this chapter.

According to Stanley (1970), the most important features in relation to functional morphology and life habits are those of gross shell shape, shell thickness and shell ornamentation. This study is a comparative investigation of these features in T. tenuis and T. fabula.

Materials and Methods.

The various physical features of the animals were defined as follows (after Stanley, 1970); length (L) was taken as the maximum shell dimension parallel to the anterior/posterior axis; height (H) as the maximum shell dimension perpendicular to length; width (W) as the maximum shell dimension perpendicular to the plane of commissure of the valves; and thickness index (T.I.) as the ratio between the volume of shell material and the volume of the entire animal. Total weight was obtained by weighing the intact animal, including shell, after the outside had been thoroughly dried on a paper towel, while the shell weight was obtained from the dried shells after they had been boiled in NaOH to remove all scraps of flesh.

The linear dimensions of the animals were measured with a vernier calliper capable of measuring to 0.01 cm, the intact animals were weighed on a Mettler P120 balance, and the dry shells were weighed on an EMB 1 Microbalance (Beckmann/RIIC).

Shell length was taken as the standard parameter against which height, width, $\log_{10}$ total weight and $\log_{10}$ shell weight were plotted.

Results.

The plots of height and width versus length (Fig. 2), show that it would be impossible to distinguish the two species on L/H or L/W ratios in the middle of their size ranges. However, in the larger sizes ($L > 1.0$ cm) T. fabula was considerably more elongate, and there was a significant difference in the slopes of the L/H and L/W regression lines (Table 2).

There was no significant difference in the slopes of the regression lines for $\log_{10}$ total weight versus length (Fig. 3,

Table 2), but the shell alone of T. fabula was heavier than that of T. tenuis of the same length (Fig. 3, Table 2). This latter result is supported by the fact that the thickness index of T. fabula was almost one and a half times that of T. tenuis (T.I. = 0.50 and 0.355 respectively.)

Discussion.

It was surprising that the total weight of both species was the same (if anything T. fabula was lighter) considering that the shell of T. fabula was significantly heavier yet, in the middle of the range at least, the width and the height were the same. This apparent discrepancy may be explained by the fact that neither T. tenuis nor T. fabula are regular geometric figures! The increase in thickness of the T. fabula shell may render it less vulnerable to predatory gastropods (Carriker, 1951 b). This theory is supported by Ansell (1960) who reported that the maximum sizes of T. tenuis and T. fabula valves found with Natica holes were 1.43 cm and 0.94 cm respectively. However, it must be remembered that, on average, T. tenuis is larger than T. fabula, and there is a greater probability of Natica finding a larger T. tenuis than vice versa, and in Ansell's (1960) experiments there was no evidence of species selection. In fact, one might expect that Natica would be able to attack all sizes of T. fabula by inserting its radula into the slight siphonal gape, and it has been suggested by K.P. Rao (1953) that shell thickness is merely a function of tidal height.

When measured by Stanley's (1970) criteria, both T. tenuis and T. fabula are categorised as rapid burrowers in shifting sand, although his conclusion that shell thickening was adopted at the expense of burrowing speed does not hold for these two species (see Chapter 5).

In conclusion, therefore, it is doubtful whether the slight differences in their external morphology contribute toward the regulation of the respective field distributions of adult T. tenuis and T. fabula. The exception to this is the presence of the siphonal gape in T. fabula which may prevent the animal from temporarily isolating itself from adverse conditions (see e.g. Chapter 1) and so T. fabula may only really become competitive with T. tenuis in the more stable conditions of the sublittoral environment.

Table 2. Least squares regression lines and slope comparisons (Bailey, 1959) for the plots of

(a) height (cm) versus length (cm);

(b) width (cm) versus length (cm);

(c) $\log_{10}$ total (animal plus shell) weight (mg) versus length (cm); and

(d) $\log_{10}$ dry shell weight (mg) versus length (cm),

for *T. tenuis* and *T. fabula*

Plot	Animal	r	t	P	equation	Comparison	
						t	P
a	*T. tenuis*	0.99	39.1	0.001	$y = -0.10 + 0.75\,x$	4.50	0.001
	T. fabula	0.89	9.20	"	$y = 0.13 + 0.50\,x$		
b	*T. tenuis*	0.96	24.0	"	$y = -0.12 + 0.27\,x$	2.50	0.02
	T. fabula	0.85	7.70	"	$y = -0.03 + 0.20\,x$		
c	*T. tenuis*	0.98	27.4	"	$y = 1.02 + 0.96\,x$	1.03	0.31
	T. fabula	0.88	8.70	"	$y = 0.78 + 1.10\,x$		
d	*T. tenuis*	0.99	33.07	"	$y = 0.15 + 1.19\,x$	3.09	0.004
	T. fabula	0.96	17.18	"	$y = -0.03 + 1.48\,x$		

Fig. 2. Height (cm) and width (cm) versus length (cm) for T. tenuis (▲———▲) and T. fabula (△------△).

For equations of regression lines see Table 2, plots a) and b) respectively.

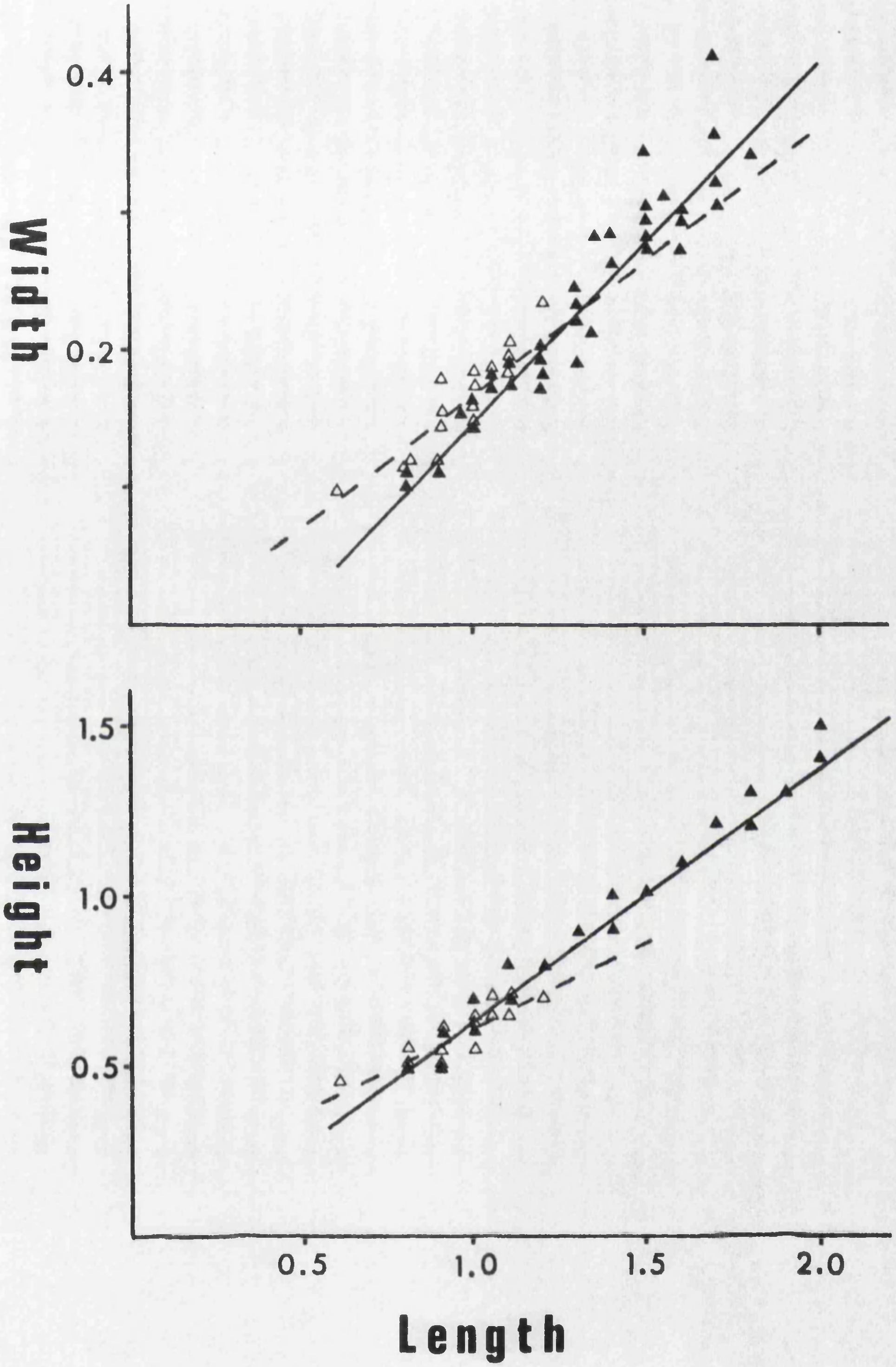


Fig. 2

Fig. 3. Log$_{10}$ total (animal plus shell) weight (mg) and log$_{10}$ dry shell weight (mg) versus length (cm) for T. tenuis (▲———▲) and T. fabula (△------△).

For equations of regression lines see Table 2, plots c) and d) respectively.
For clarity the regression lines for plot c) have been omitted since there was no significant difference between T. tenuis and T. fabula.

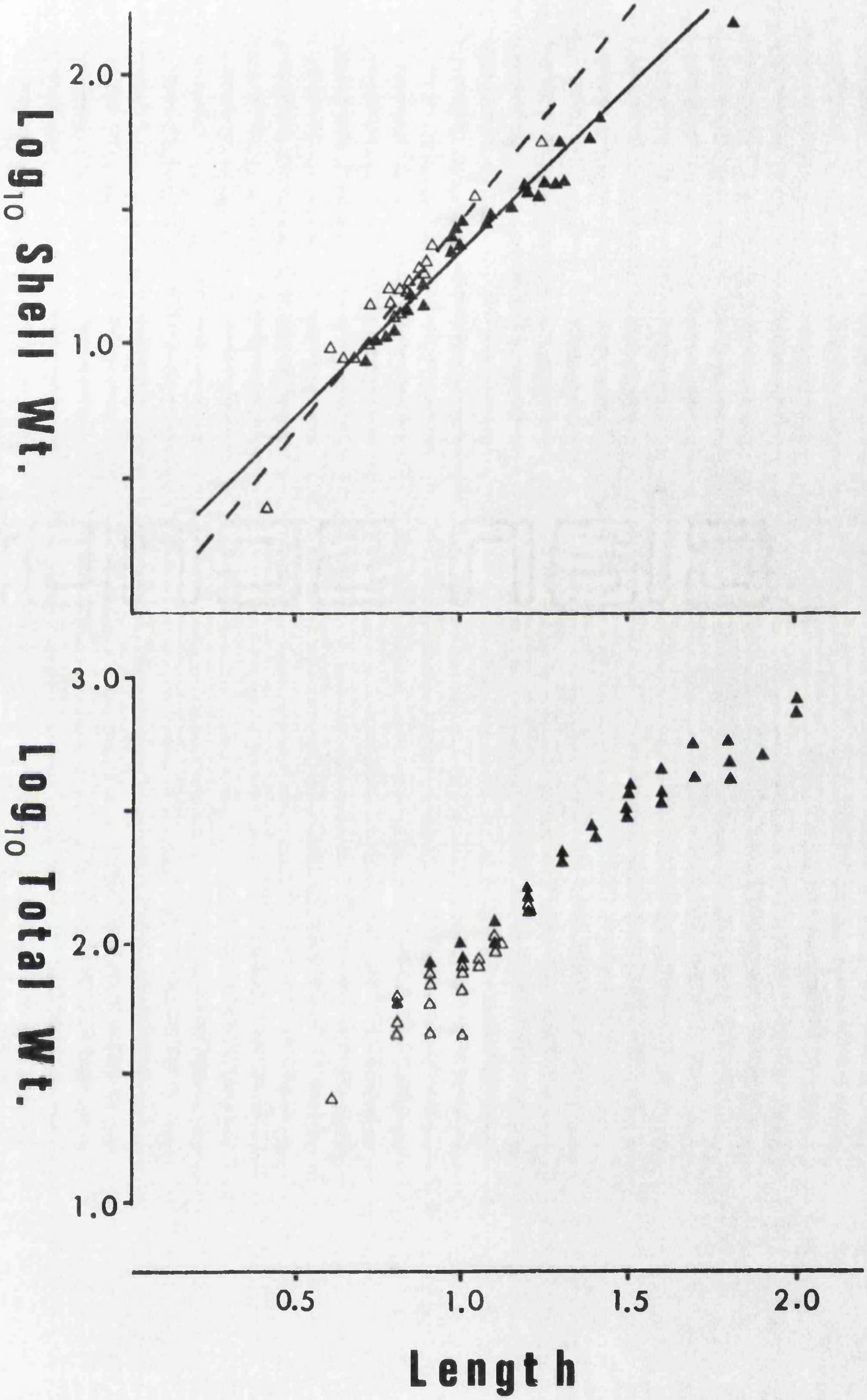


Fig.3

A Scanning Electron Microscope Study of the Shell Ornamentation of *Tellina fabula* Gmelin.

To be submitted for publication.

T. fabula is unique amongst the Tellinacea in having the oblique striae present on one valve only. In Tellina similis, both valves are striated, but in T. fabula it is always the right valve, and the right valve only, which bears the striae. What purpose this ornamentation serves in T. fabula is unclear. The present study investigated the morphology of the striae by means of the scanning electron microscope (SEM).

The SEM has been used to investigate the formation of pearls and mother-of-pearl in the Pacific oyster fisheries (Watabe, 1954; Wada, 1957 a, b, 1960; Watabe, Sharp and Wilbur, 1958; Tsujii, Sharp and Wilbur, 1958; Watabe and Wilbur, 1961).

More recently SEM studies have been made of gastropod-radulas (Runham and Thornton, 1967; Thompson and Hinton, 1968; Runham, 1969; Solem, 1973 a, b; Thompson and Bebbington, 1973), and Té and Mardinly (1975) declared many previous studies obsolete, since the smaller cusps on the radula were not visible by light microscopy.

The excellent resolution of the SEM has also been utilised in studies of the shell sculpture and micro-ornamentation (Solem, 1970; Fretter and Pilkington, 1971; Hoefs and Sarnthein, 1971; Robertson, 1971; Bé et al, 1972; Giusti, 1973; Boltovsky, 1974; Burch, 1975; Paul, 1975).

Of these later studies, only Runham and Thornton (1967) used the SEM to investigate functional morphology, although Boltovsky (1974) did comment on the function of the ornamentation on some of the shells. It was hoped that this study, by an examination of the morphology of the striae would show whether they are endogenously or exogenously regulated (e.g. Neville, 1967) and would find out if a relationship existed between form and function.

Materials and Methods.

The specimens were obtained from a site 6.0 m below Chart Datum in Kames Bay, Millport.

The animals were killed, and the flesh removed from the valves by boiling in a NaOH solution. The clean shells were then washed in distilled water and dried. The valves were then mounted individually on a stub, using silver paint as an adhesive, and the complete assembly was shadowed with gold.

The right and left valves of other specimens were weighed on a microbalance (Beckman, RIIC).

Correlation was sought, using regression analysis (Bailey, 1959), between valve length and number of striae; valve length and average distance between the striae; and number of striae and average distance between striae.

Results.

Photograph 1 shows the left valve of <u>T. fabula</u>. Photograph 2 et seq. shows the right valve. The characteristic diagonal striations on the right valve can be clearly seen.

Fig. 1 demonstrates that there was a significant correlation between the length of the valve and the number of striae ($r = 0.63$, $t = 2.42$, $P = 0.04$). The equation for the regression line is

$$y = 18.37 + 2.24\ x$$

where y = number of striae and x = length of valve in mm(Bailey,1959).

There was no significant correlation between the average distance between the striae and the length of the valve ($r = 0.26$, $t = 0.80$, $P = 0.55$), nor was there correlation between the number of striae and the average distance between the striae ($r = 0.27$, $t = 0.84$, $P = 0.58$). The variation in ornamentation of valves of the same length is illustrated in photographs 3 and 4. The specimen in photograph 3 has 33 striae with an average distance of 98 um between them, while the specimen in photograph 4 has 20 striae with an average distance of 173 um between them, yet both specimens were 6.4 mm long.

The striae are not present on the early stages of the valve, the prodissoconch II (Werner, 1939). They become prominent only after the first growth ring and appear to originate from the concentric rings (photograph 5). Occasionally, they originate spontaneously and with no apparent origin (photograph 6) or disappear at a growth ring (photograph 7).

The angle of the approach of the striae to the edge of the valve is altered not only at the edge itself (photographs 2, 3, 4) but also at the growth rings (photograph 8), although they subsequently resume their normal angle. They are also much distorted around areas of damage (photograph 9).

In close-up (photograph 10), the striae appear as flat ridges, overlapping from anterior to posterior. They have a fairly constant height, and greatly resemble the overlapping calcite crystals pictured in Watabe and Wilbur (1961) and Wilbur (1964), although they are, of course, many times larger.

The valves of 25 <u>T. fabula</u> were weighed individually on a microbalance (Table 1). The right valve was heavier in 10 specimens, the left valve heavier in 11 specimens, and in 4 specimens both valves weighed the same.

Discussion.

Eisma (1965) claimed that the number of ribs on Cardium was dependent on the salinity, but Russel (1972) refuted this claim, and added that the number of ribs has little or no physiological significance. The situations are not truly analagous, however, as the number of ribs of Cardium is not correlated with size, while the number of striae of T. fabula increases with age. As to the function of the striae, they may serve to strengthen the valve, or to assist the burrowing, or both.

The radiating ribs in Pecten may strengthen the valve (Stanley, 1970) and it has been suggested that the ribs on pteropod shells provide strength with economy of material (Boltovsky, 1974). However, the striae run obliquely across part of one valve only and would therefore add strength only to a diagonal stress. It also seems unlikely that stress would be greater on one valve, and always the right, than on the other. If the striae are a compensation for the asymmetry of the valves, it is strange that nothing similar has been reported in other asymmetric Tellinacea.

Lever (1958) postulated, from the evidence of differential sorting of the right and left valves on the beach, that the striae made the right valve more solid than the left, and that the valves differed in weight. However, my results indicate that this is not so, and the differential sorting must be due to the effect the striae have on the movement of the valve in a current.

The ridges of the striae have their edges aligned roughly at an angle of 45° to the anterior/posterior axis and are consequently parallel to the angle at which the animal burrows (Trueman et al, 1966 b), resulting in a "ratchet" profile being presented to the sand. The oblique ornamentation of Tellina similis, in which ridges of a similar shape to those of T. fabula are present on both valves, alternately grips and slides past the sediment, and aids the animal's burrowing (Stanley, 1970). In theory then, the right valve of T. fabula should go down faster than the left, until the animal lies in the sand with the left valve uppermost. However, I find that T. fabula burrows at an angle into the sand, with the right valve uppermost, and eventually comes to rest in the sand in a near horizontal position on its left valve. In fact, they will rarely attempt to burrow with the left valve uppermost but they will turn over to be on their preferred side.

This preference for burrowing at an angle may result in an unequal stress on the valves so that the striae are required to strengthen the right valve against the pull of the foot. Tellina tenuis has been observed to burrow in a similar manner (Holme, 1950, 1961; Trevallion, 1971), yet no such ornamentation exists on its right valve. The shell of T. tenuis is, however, thicker than that of T. fabula so reinforcement may not be necessary.

The absence of the striae from the early stages of the shell does not mean that they are not present in the young _T. fabula_. The umbonal region of all the specimens was considerably worn and so any striae or other ornamentation may have been rubbed off (House and Farrow, 1968). Fretter and Pilkington (1971) observed that the fine detail on the larval shells was almost invariably lost in the adult. Nevertheless, Rees (1950) made no mention of striae on the larval _T. fabula_ shell, and A.D. Ansell (Dunstaffnage Marine Research Laboratory, Oban, personal communication) observed that the ornamentation on _Donax_ shells often does not develop until fairly late in the animal's life. Similarly, van Benthem Jutting (1943) noticed that the first traces of the ribs on _Cardium_ do not appear until the animal is 14mm long.

Occasionally the striae originate between two existing striae, or disappear without trace, so perhaps the animal can regulate the number of striae on its shell! However, such fine control is unlikely in view of the large variation in the numbers of striae in animals of similar size, and in view of the relative infrequency of such happenings.

It is noticeable that the striae alter shape at the growth rings, that is, under conditions of slow or nil growth, and that they are considerably distorted around previously damaged areas. Many animals and plants exhibit circular growth rings of tidal or daily or longer periodicity (Wells, 1963; Berry and Barker, 1968; House and Farrow, 1968; Bourget and Crisp, 1975 a, b; Crisp and Richardson, 1975). These rings are modified by environmental factors such as temperature, tides or storms, and it seems reasonable to suppose that the striae of T. fabula will be likewise affected.

In conclusion, we can say that the striae are a series of oblique ridges running toward the posterior end of the animal. Their numbers increase roughly with the size of the animal, but they do not appear to be present in the early prodissoconch stages of the valve. The function of the striae may be to strengthen the valve while burrowing.

Summary.

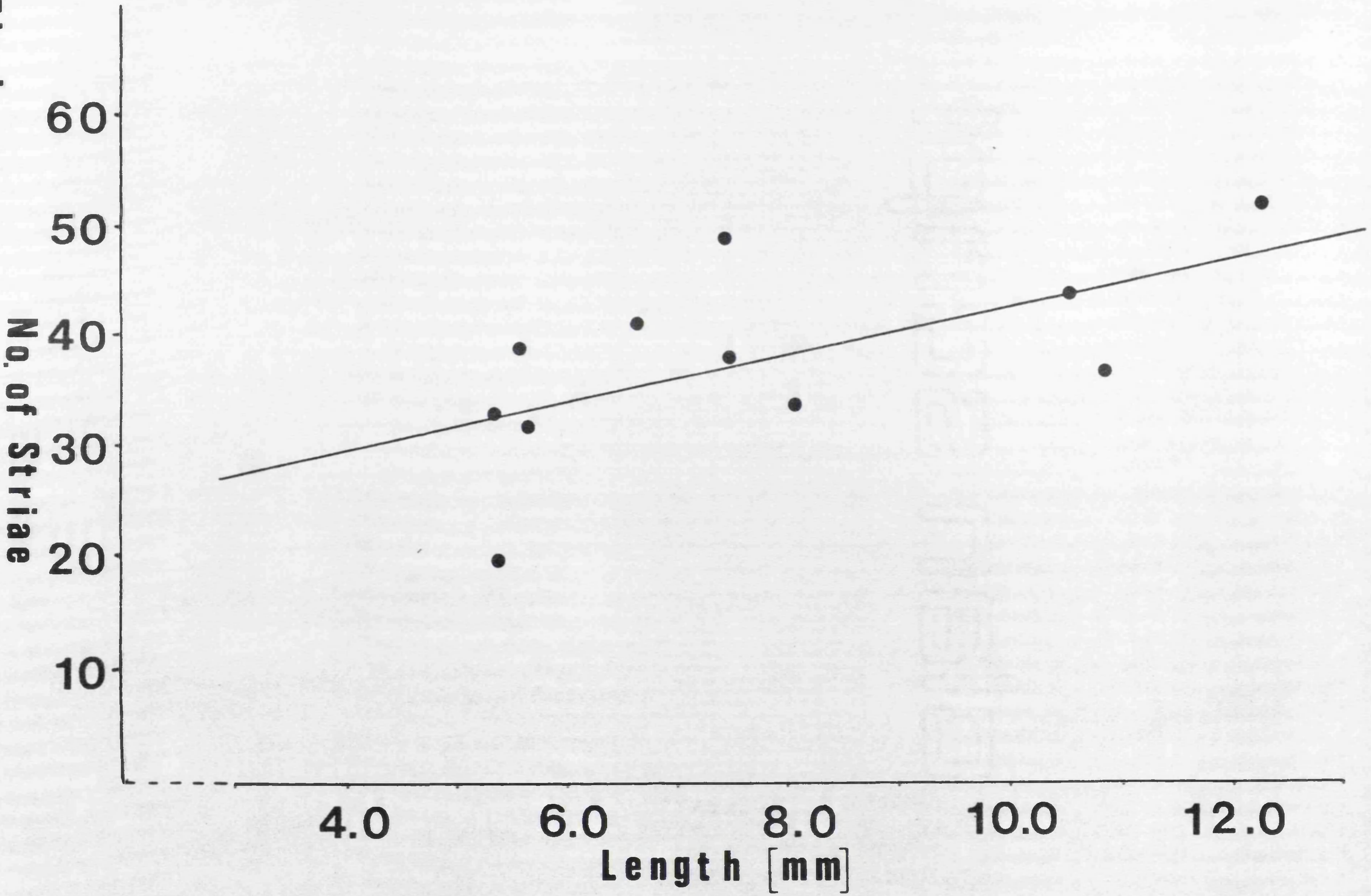
Scanning electron micrographs were taken of the right valve of T. fabula. The number of striae was found to increase with the size of the shell, but there was no correlation between size and inter-strial distance and between number of striae and inter-strial distance. The function of the striae may be to strengthen the valve.

Table 1. The weight in mg of right valves (RV) and left valves (LV) of *T. fabula*.

RV	LV	RV	LV	RV	LV	RV	LV
27.5	28.1	8.52	8.79	7.92	8.04	4.95	5.00
17.6	16.9	8.92	8.92	6.43	6.43	7.78	8.33
9.30	9.30	7.97	8.12	10.80	10.80	4.51	4.69
7.22	7.17	8.12	7.87	6.94	7.07	4.64	5.14
7.03	6.82	1.18	1.17	11.71	11.52	8.08	8.05
6.97	7.08	8.11	8.22	8.40	7.95	6.82	6.72
4.62	4.52						

Fig. 1. Regression analysis of the number of striae versus shell length.

Fig. I

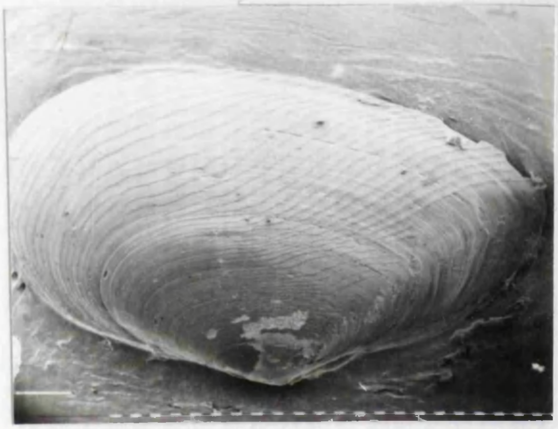


Explanation of Plate 1

Photograph 1	Left valve of *T. fabula* x 24
2	Right valve x 24
3 and 4	Right valves showing variation in the number of striae x 24 (Photograph 4 - specimen broke in mounting, but was included as the best specimen to show the variation).
5	Origin of striae (arrowed) x 96

1

2



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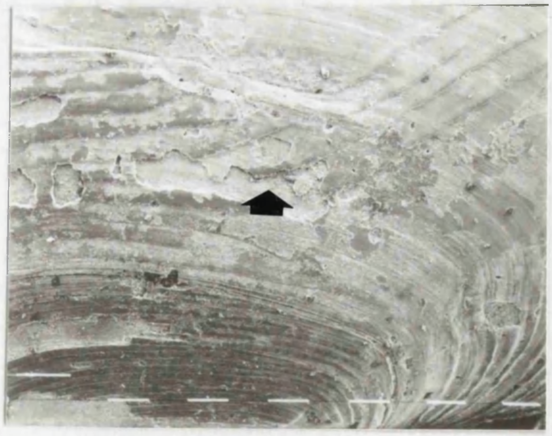


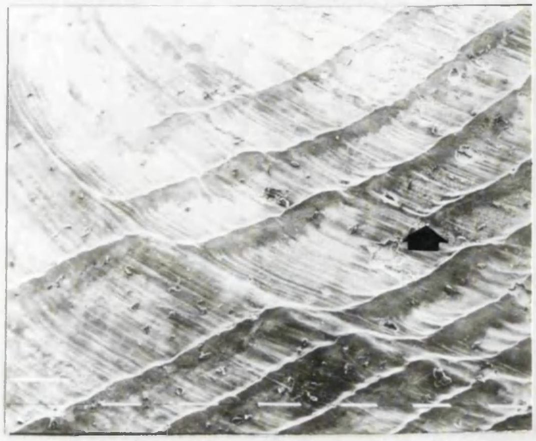
5

Plate 1

Explanation of Plate 2

Photograph	6	Spontaneous origin (arrowed) of a stria x 192
	7	Interruption and disappearance of a stria (arrowed) at a growth ring x 96
	8	Distortion of striae at a growth ring x 192
	9	Distortion of striae around an area of damage x 48
	10	Close-up, showing shape of striae x 768.

6



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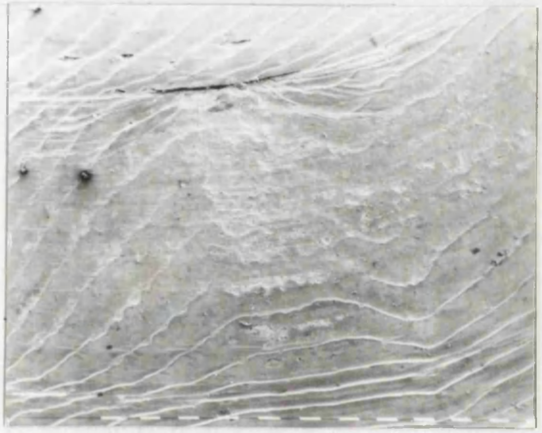
8



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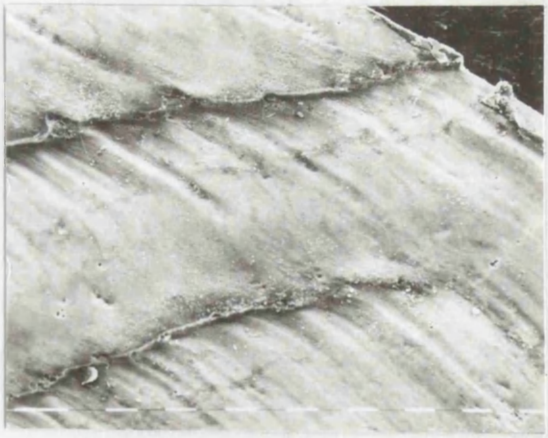


10

Plate 2

CONCLUSIONS.

Chapter 1.

The tolerance of T. tenuis was greater than that of T. fabula in all the tolerance experiments.

The temperature tolerance of T. tenuis was consistently higher, by about 5°C, than that of T. fabula, and this difference is reflected in their respective littoral and sublittoral distributions, but not in their respective geographical distributions. The zoographical range may therefore be limited by the tolerance limits and survival rate of the larvae (Thorson, 1946, 1950, 1966; Kinne, 1970; Andronikov, 1975). However, Barnett (1971, 1972) has suggested that T. tenuis larvae can pass unharmed through a power station cooling system, and that the heated water discharged had not affected the nearby T. tenuis population. Unfortunately, no such data is available for the survival of T. fabula larvae.

In their tolerance to salinity and desiccation, T. fabula was again more susceptible, but the situation is complicated by the fact that the valves of T. fabula have a siphonal gape. T. tenuis, on the other hand, can shut its valves completely, so the difference in tolerance may be due to this difference in morphology. The reduction in salinity along the western side of Kames Bay (Smith, 1955) may affect the populations of T. tenuis and T. fabula, since both are more abundant on the eastern side of the Bay. The interaction of all factors (e.g. van Winkle et al, 1976) may, however, result in the exclusion of T. fabula from the more stressful zone, that is, from the shore.

Chapter 2.

The attempts to monitor the larval settlement patterns would seem to indicate that either the larvae do select their habitat or the environment selects for the "suitable" species in the first year or so of life. Many other invertebrate larvae exhibit settlement preferences (Wilson and Day, 1934; Wilson, 1937, 1948, 1952, 1953 a,b, 1968; Knight-Jones and Stevenson, 1950; Knight-Jones, 1951; Carriker, 1961; Crisp, 1961; Bayne, 1969; Stebbing, 1972) and can delay metamorphosis to increase their chance of finding the preferred substrate (Wilson and Day, 1934; Bayne, 1965). The larvae may also utilise the movement of different strata in the water column to increase their chance of arriving at a favourable site (Carriker, 1951 a, 1961; Hardy and Bainbridge, 1951; Haskin, 1964; Knight-Jones and Morgan, 1966; Lough and Gonor, 1971; Wood and Hargis, 1971; Cragg and Gruffydd, 1975), although some authors (Korringa, 1952, Verwey, 1966) have expressed doubts about this mechanism of active transport. Selection may also occur due to hydrographic concentration (Turner, 1961), in which the young post-metamorphosis bivalves are sorted, along with sand grains of a particular size, by the waves or currents until they are large enough to burrow into the sediment and so escape the water movements (Kreger, 1940; Baggerman, 1953; Carriker, 1961; Knight-Jones and Moyse, 1961; Turner, 1961). If one accepts that the slight difference in grain size between littoral and sublittoral Kames Bay sands was due to wave or current sorting, then it is possible that waves or currents may also be able to sort out the slight differences in size or shape of the juvenile *T. tenuis* and *T. fabula*.

With regard to the movement of adult *Tellina*, it appears that the movement away from an artificial positioning was due largely to the angle at which the animals burrowed. Once within the sand, they moved little, if at all. This result, and the results of the dispersion pattern experiments were largely contrary to those of Holme (1950, 1961), but it may be that his population had adopted a different life style, based on deposit rather than filter feeding, from the population in Kames Bay. The randomness of the distribution suggests that there are neither intraspecific nor interspecific interactions in *T. tenuis* and *T. fabula*, and neither species can be said to exclude the other from the habitat by its presence alone.

Chapter 3.

There was little trace of a consistent rhythm in either *T. tenuis* or *T. fabula*. If anything, it was the littoral *T. tenuis* which had the circadian rhythm predicted (Morton, 1973) for the sublittoral species. The control of the short-term rhythms in both species must therefore be almost totally endogenous, and neither species would be restricted to or excluded from a habitat because of an "unsuitable" endogenous rhythm. The lack of a marked circatidal rhythm may also indicate that, like Scrobicularia plana (Earll, 1975 a), T. tenuis and T. fabula can both suspension feed or deposit feed according to environmental conditions.

Chapter 4.

The sand of Kames Bay changes little from EHWS to just below LWS, but those sands are significantly different from the deeper sublittoral (5.0 m below C.D.) sand. There was a greater percentage of silt in the deeper sublittoral sand, but it seems unlikely that T. tenuis, supposedly a deposit feeder (Blegvad, 1915; Atkins, 1937 a, b; Yonge, 1949; Pohlo, 1969), would be excluded by such a small fraction (less than 5% of total dry weight). However, T. fabula may be able to utilise the sublittoral conditions more successfully than T. tenuis, since Atkins (1937 a, b) considered that the gills of T. fabula were better adapted for deposit feeding, and Stephen (1932) found that T. tenuis grew best at the landward part of their range.

Chapter 5.

The burrowing movements of T. tenuis and T. fabula in their respective sediments are identical, and there was no difference between the species in the number of digging cycles needed or the speed of burrowing. T. tenuis, however, burrowed almost twice as deep as T. fabula. A burrowing depth of around 5 cm might, if T. fabula was found on the beach, render it vulnerable to predation by oystercatchers at low tide (Hughes, 1970). When T. tenuis was allowed to burrow in the sublittoral sand, which was less penetrable, more initial foot probing was needed, and the burrowing depth was shallower than in the littoral sand while the burrowing of T. fabula seemed unaffected by a change from sublittoral to littoral sand. This effect on the burrowing of T. tenuis may contribute towards its exclusion from the sublittoral zone. The fact that burrowing depth was correlated with size in field populations of T. tenuis suggested that, as found by Nair and Ansell (1968) in the Veneridae, burrowing depth may be correlated with siphon length. It is interesting to consider this suggestion in the light of the observation of Forbes and Hanley (1853) that the siphons of T. fabula might be longer than those of T. tenuis, yet T. fabula consistently burrowed shallower than T. tenuis. This, and the fact that T. tenuis burrowed shallower in less penetrable sand, indicates that the major control of burrowing depth was more probably the amount of penetration per unit effort (Nair and Ansell, 1968).

Chapter 6.

The major morphological difference between T. tenuis and T. fabula, the striations on the right valve of T. fabula, seem to have no effect on the burrowing. While the striae may strengthen the shell (Kauffman, 1969; Stanley, 1970), it is not known why they should be needed on one valve only. The shell of T. fabula was heavier and more solid than that of T. tenuis in any case, and may afford it more protection against predatory gastropods such as Natica alderi or Philine aperta (Ansell, 1960).

T. tenuis would therefore appear to be, on average, bigger, more tolerant, and capable of burrowing deeper than T. fabula, and hence one might expect that T. tenuis would exclude T. fabula where the two species are in direct competition. This happens only in the littoral zone, and it is difficult to understand how T. fabula excludes T. tenuis from the littoral zone.

However, it must be remembered that such provinces exist in time as well as space (Hedgepeth, 1957) so that the present-day distribution may not be the same as that existing 2M years ago and may be completely different again from that existing 2M years hence. The fossil record of T. tenuis (from Heering, 1950) implies that the species has moved north from Portugal since the Pliocene, but Heering's (1950) catalogue is open to considerable criticism (e.g. Spaink and Norton, 1967). Forbes and Hanley (1853) and Jeffreys (1863) both place the origin of T. tenuis in the late Pleistocene, while West (1968) states that the species is recognised as first appearing in the Ipswichian faunas. Brøgger (1901) considered that T. tenuis was a boreal species which has moved west into Kristiania fjord (South Norway) since the postglacial period, and that T. fabula was a lusitanian species which has become extinct in Kristiania fjord since postglacial times. The origins of T. fabula appear to have been in the early Pleistocene (Wood, 1848-82; Forbes and Hanley, 1853; Jeffreys, 1863), although Moore (1970) dates it as far back as the Miocene. It is possible, therefore, that T. tenuis is slowly displacing T. fabula from all habitats. There are, in addition, numerous records of other fossil

Tellinidae which are thought to be from a habitat not unlike that of Kames Bay (Norton, 1967; West and Norton, 1974) and which may in turn have occupied a similar niche to that now occupied by T. tenuis and T. fabula.

At present, however, the distribution of T. tenuis and T. fabula would appear to be largely due to the interaction of the physical environmental parameters such as temperature or salinity etc. and of sediment characteristics. The physical parameters may act on both adults and larvae, but the sediment, while it may influence adult feeding or burrowing, is probably more important with regard to larval settlement. The tolerances and behaviour of the larvae remain among the most important, if not the most important, unknown factors governing the species' distributions.

STATISTICAL APPENDIX.

i) Clark and Evans (1954) Nearest Neighbour Test.

The distance from one individual to another, its nearest neighbour, provides a measure of the spacing which obviates the use of quadrats and so eliminates the effect of quadrat size.

For explanation of symbols, see Table 1.

To apply the test, a series of nearest neighbour distances (r) is measured, using all the individuals or a random sample of the population, and the value of the mean nearest neighbour distance ($\bar{r}_A$) is calculated. The mean nearest neighbour distance that would be expected in a random population ($\bar{r}_E$) of the same density (p) is also calculated. The ratio of the observed to the expected mean distance (R) indicates the measure of the departure from randomness. The significance of R can be tested by the normal curve using the formula

$$c = \frac{\bar{r}_A - \bar{r}_E}{\sigma_{\bar{r}_E}}$$

where c is the standard variate of the normal curve and $\sigma_{\bar{r}_E}$ is the standard error of the mean nearest neighbour distance in a random population of density p.

Example.

From Chapter 2, pages 68 and 85, Table 1, experiment number 1.

Area sampled by dustbin = $855.6\ \text{cm}^2$

Number of animals(measurements)N = 101

$$\text{Density } p = \frac{101}{855.6} = 0.118$$

Sum of measurements Σr = 144.1 cm

$$\bar{r}_A = \frac{\Sigma r}{N} = 1.43\ \text{cm}$$

$$\bar{r}_E = \frac{1}{2\sqrt{p}} = 1.456\ \text{cm}$$

$$R = \frac{\bar{r}_A}{\bar{r}_E} = 0.98$$

$$\sigma_{\bar{r}_E} = \frac{0.26136}{\sqrt{Np}} = 0.0758$$

$$c = \frac{\bar{r}_A - \bar{r}_E}{\sigma_{\bar{r}_E}} = 0.34$$

An R value of less than 1.0 indicates that the observed nearest neighbour distances were less than those expected, i.e. the dispersion pattern was aggregated. However, a c value of 0.34 means that the result was not significantly different from unity, and so the dispersion pattern may be said to be random.

Table 1. Symbols and definitions for nearest neighbour analysis (Clark and Evans, 1954)

N - number of nearest neighbour distances measured.

r - distance in units between nearest neighbours.

p - density in indiduals per unit area.

$\bar{r}_A = \frac{\Sigma r}{N}$ - mean of observed nearest neighbour distances.

$\bar{r}_E = \frac{1}{2\sqrt{p}}$ - " " expected " " "

$R = \frac{\bar{r}_A}{\bar{r}_E}$ - measure of the degree of departure from randomness of observed from expected nearest neighbour distances.

$c = \frac{\bar{r}_A - \bar{r}_E}{\sigma_{\bar{r}_E}}$ - standard variate of normal curve.

$\sigma_{\bar{r}_E} = \frac{0.26136}{\sqrt{Np}}$ - standard error of mean nearest neighbour distance in a random population of density p.

2) Periodogram analysis (Williams and Naylor, 1967).

Periodogram analysis may be used in the analysis of time series of values for any measure of the activity of an animal to detect the existence and frequency of a rhythm.

The measure of the activity may be divided into blocks of data (x) for any predetermined frequency (f). The blocks of data for my experiments were 41.5 minutes long, and consequently the frequencies scanned for rhythms occurred in multiples of 41.5 minutes. The frequencies scanned were from 8 blocks (5 hours 32 minutes) to 45 blocks (31 hours 7.5 minutes).

The blocks of data (x_1, x_2, x_3 - - - x_n) are divided into f columns, and the values in each column are added thus:-

$$\begin{array}{cccc}
x_1 & x_2 & ---- & x_f \\
x_{f+1} & x_{f+2} & ---- & x_{2f} \\
x_{2f+1} & x_{2f+2} & ---- & x_{3f} \\
x_{n-f+1} & x_{n-f+2} & ---- & x_n \\
\hline
y_1 & y_2 & ---- & y_f
\end{array}$$

and a mean value obtained

Lack of rhythmicity is indicated when the total values y_1, y_2 etc. approximately equal the overall mean activity. Rhythmicity is indicated when y_1, y_2 etc. are distributed about a sine curve, that is, they show extensive deviation from the mean activity value.

The standard deviations (s) of the means of each of the frequencies are obtained from the formula

$$s^2 = \frac{1}{f - 1} \left(\Sigma y^2 - \frac{1}{f} (\Sigma y)^2 \right)$$

These values may be plotted on a periodogram to obtain the frequency of the rhythm. It is better to calculate the coefficient of variability (c.v.) which expresses s as a percentage of overall mean activity, thus permitting easier comparison of the results of different experiments. The computer programme and flow diagram are shown in Fig. 1 and Fig. 2 respectively.

Example.

From Chapter 3, Table 2, page 106, T. tenuis animal number 2 (see also Fig. 2, page 112).

Row number 1, f = 8

mean values = 5.27, 5.82, 5.93, 6.10, 6.35, 4.71, 5.74, 6.04

Σ means = $\underline{45.96}$ $\Sigma(\text{means})^2 = \underline{265.92}$

standard deviation

$$s = \sqrt{\frac{1}{7}\left(265.92 - \frac{1}{8}(45.96)^2\right)}$$

$$= \underline{0.52}$$

mean activity $= \underline{5.75}$

$$\text{c.v.} = 0.52/5.75 \times 100$$

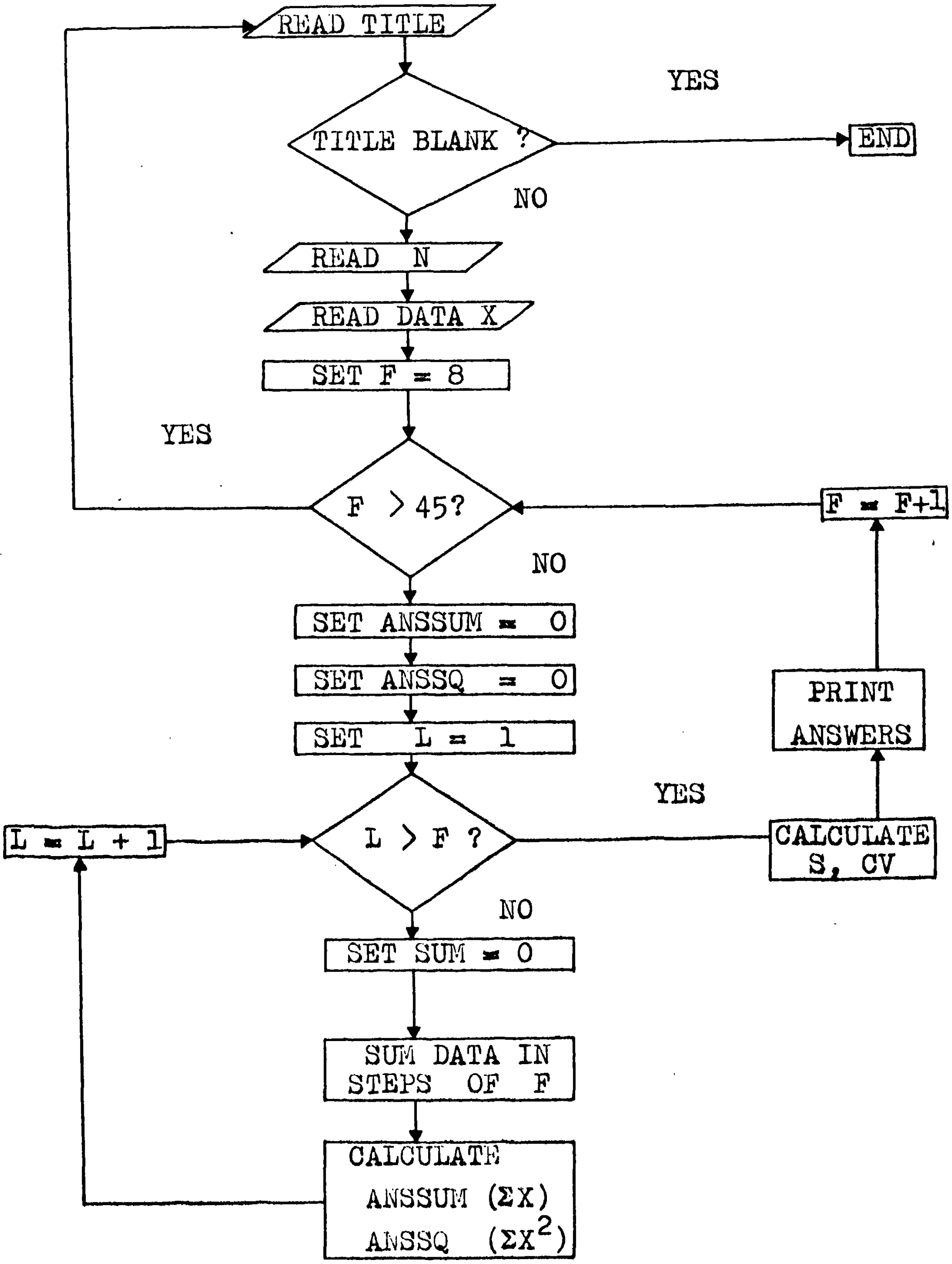
$$= \underline{9.06}$$

Fig. 1. Computer programme for periodogram analysis (Williams and Naylor, 1967).

```
C   M.D.BURNS  ZOOLOGY GLASGOW   GBZA01J2
C
C       PROGRAMME FOR RHYTHM ANALYSIS
C       WILLIAMS AND NAYLOR
C
        DIMENSION TITLE (20)
1       FORMAT (I3)
  2     FORMAT (40I2)
  8     FORMAT  (20A4)
  9     FORMAT  ('1',20A4)
C
C       PROGRAMME STOP CARD
        DATA BL/4H    /
C
        INTEGER F,X(500),SUM
  99    READ (5,8) TITLE
C
C       PROGRAMME STOP CARD
        IF  (TITLE(1).EQ.BL)  CALL EXIT
C
        WRITE (6,9) TITLE
        READ (5,1) N
        READ (5,2) (X(J),J=1,N)
        WRITE (6,3)
        DO100 F=8,45
        ANSSUM =0
        ANSSQ=0
        DO 40 L=1,F
        SUM-0
        DO20 J=L,N,F
  20    SUM=SUM+X(J)
C
C       OBTAIN SUM  DIVIDE BY N/F FOR AVERAGE
C
        IF(F-8)66,56,66
  56    WRITE(6,16)SUM
  66    CONTINUE
C
C       MAKE F,SUM,N REAL FOR CALCULATION
C
        RF=F
        RSUM=SUM
        RN=N
C
        ANSSUM=ANSSUM+RSUM*RF/RN
  40    ANSSQ=ANSSQ+(RSUM*RF/RN)**2
        V=(ABS(ANSSQ-ANSSUM**2./RF))/(RF-1)
        S=SQRT(V)
        CV=S*100.*RF/ANSSUM
        WRITE(6,4)F,ANSSUM,ANSSQ,S,CV
  100   CONTINUE
        GO TO 99
   16   FORMAT (15)
   3    FORMAT ('0',T4,'F',T13,'ANSSUM',T39,
       1'ANSSQ',T53,'S',T62,'CV',//)
    4   FORMAT (I5,F15.5,F25.5,F10.4,F10.2)
```

Fig. 1

Fig. 2. Flow diagram for periodogram analysis (Williams and Naylor, 1967).



READ TITLE
TITLE BLANK ?
YES
END
NO
READ N
READ DATA X
SET F = 8
YES
F > 45?
NO
F = F+1
SET ANSSUM = 0
SET ANSSQ = 0
SET L = 1
PRINT ANSWERS
L = L + 1
L > F ?
YES
CALCULATE S, CV
NO
SET SUM = 0
SUM DATA IN STEPS OF F
CALCULATE ANSSUM (ΣX) ANSSQ (ΣX²)

Fig. 2

3) Pattern analysis (Kershaw, 1960).

The pattern analysis is derived from Grieg-Smith's (1952) technique of analysis of variance for detection of pattern, in which the graph of mean square versus block size rises to a peak at the block size corresponding to the dimensions (spatial or temporal) of a "clump" or "mosaic" unit. (See also Kershaw, 1964; Pielou, 1969, page 104; for discussion and criticisms.)

To apply the analysis, the scores for each unit within the block are added together, and the total values are then squared and summed. The sum of the squares is then divided by the block size. The resultant block square is subtracted from the block square for the next block size, and divided by the corresponding degrees of freedom to obtain the mean square (see equation 1). The number of the degrees of freedom is equal to the number of observations, minus 1, minus the number of degrees of freedom already accounted for.

$$\text{Mean square} = \frac{\Sigma x^2_a/a - \Sigma x^2_{2a}/2a}{\text{d.f.}} \quad \text{- - - - - - - - - - - - -} \; 1$$

The block sizes increase in a geometrical series 1, 2, 4, 8, etc., and to facilitate analysis a limit of a block size of 256 was set on the computer programme. If the dimensions of the data were considerably different from the largest block size the data was divided into two parts, a and b, e.g. a recording 90 sheets long would be divided into part a, sheets 1 - 64, and part b, sheets 37 - 90; a recording

400 sheets long would be divided into part a, sheets 1 - 256, and part b, sheets 145 - 400.

The computer programme and flow diagram are shown in Fig. 3 and Fig. 4 respectively.

Example.

From Chapter 3, Table 2, page 106, _T. tenuis_ animal number 2 (see also Fig. 2, page 112).

Number of sheets = 337

Part a sheets 1 - 256; Part b sheets 82 - 337

Block size = 4

	a	b
Σx^2 of block size 4 =	88,226	96,362
Σx^2 of block size 8 =	166,250	181,086

d.f. (a and b same) $= 64 - 1 - 3\cancel{2}^{1} = 32$

$$\text{M.S. (a)} = \frac{\frac{88,226}{4} - \frac{166,250}{8}}{32} = \underline{39.85}$$

$$\text{M.S. (b)} = \frac{\frac{96,362}{4} - \frac{181,086}{8}}{32} = \underline{45.46}$$

Fig. 3. Computer programme for
pattern analysis (Kershaw, 1960).

```
C ..M.D.BURNS  ZOOLOGY GLASGOW  GBZA01JW
C
C   PROGRAM FOR RHYTHM ANALYSIS
C
 1      FORMAT  (40I2)
 2      FORMAT  (' ',I10,10X,2F20.4)
 3      FORMAT  (20A4)
 4      FORMAT  ('1',20A4,//' ',5X,'BLOCK SIZE',15X
       1'MEAN SQUARE',10X,'ANSWER',//)
  96    FORMAT (F10.5,F12.6)
C
        DIMENSION I(256), TITLE (20)
        DATA FIN / 4H      /
C
C   READ TITLE
 10     READ (5,3)  TITLE
        IF  (TITLE (1).EQ.FIN)  CALL EXIT
        WRITE (6,4)  TITLE
C   READ DATA
        READ  (5,1)  I
C   DO CALCULATIONS
        DO  100  M=1,9
        Y2=0
        JJ=2**(M-1)
        L=256/JJ
C   ADD NUMBERS IN GROUP
        DO 40 J=1,L
        K2=J*JJ
        K1=K2-JJ+1
        Y=0
        DO 20 K=K1,K2
 20     Y=Y+1(K)
C
C       PRINT INDIVIDUAL SUMS AND SQUARES
        WRITE(6,96)Y,Y2
C
C  FIND MEAN SQUARE
 40     Y2=Y2+Y**2
        SQMN=Y2/JJ
        IF (M.GT.1)  GO TO 60
        WRITE (6,2) JJ,SQMN
        GO TO 100
 60     ANS=(SQ1-SQMN)*2/L
        WRITE (6,2)  JJ,SQMN,ANS
 100    SQ1=SQMN
        GO TO 10
        END
```

Fig. 3

Fig. 4. Flow diagram for pattern analysis
(Kershaw, 1960).

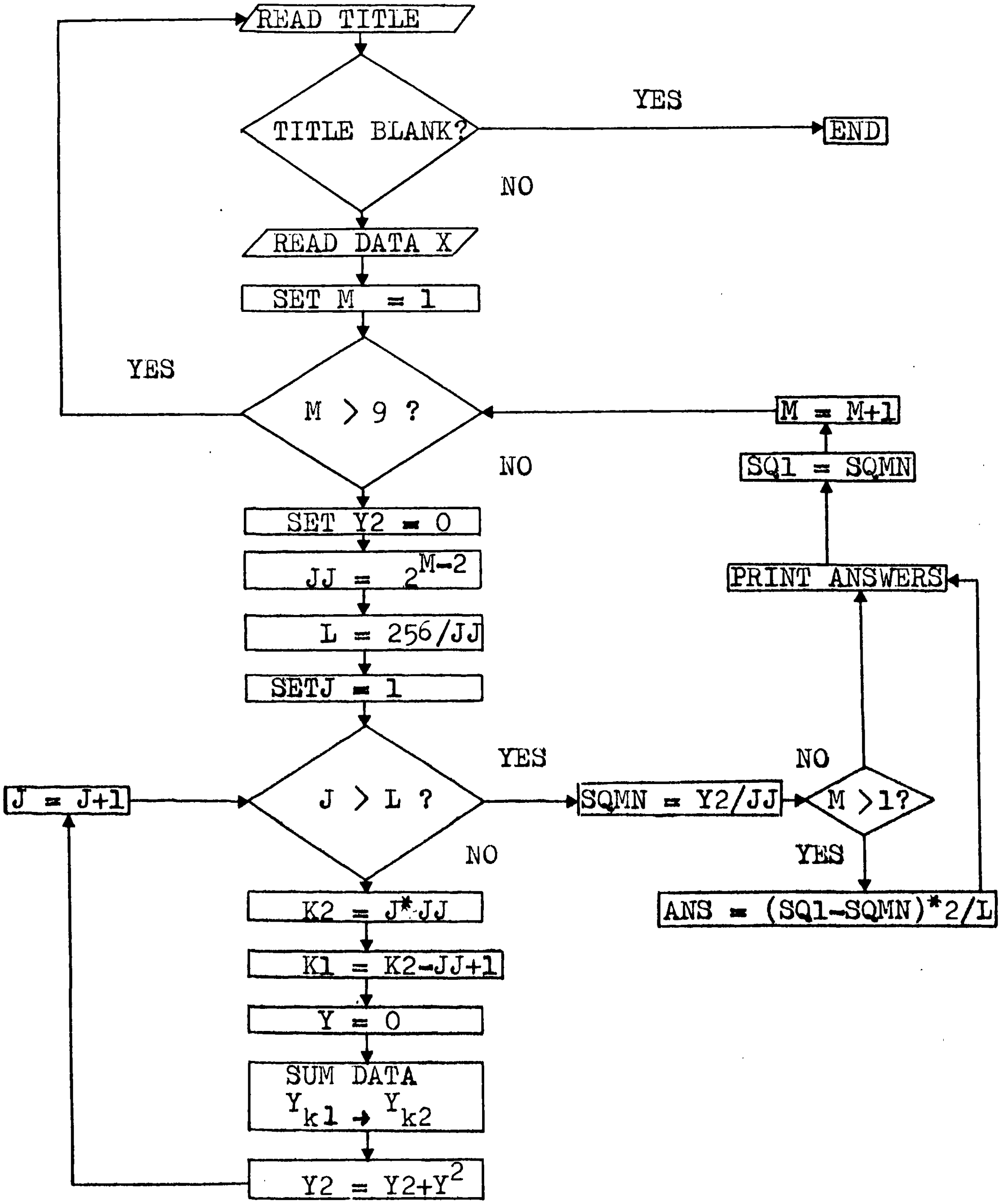

READ TITLE
TITLE BLANK?
YES
END
NO
READ DATA X
SET M = 1
YES
M > 9 ?
NO
M = M+1
SQ1 = SQMN
SET Y2 = 0
JJ = 2^{M-2}
PRINT ANSWERS
L = 256/JJ
SETJ = 1
YES
NO
J = J+1
J > L ?
SQMN = Y2/JJ
M >1?
NO
YES
K2 = J*JJ
ANS = (SQ1-SQMN)*2/L
K1 = K2-JJ+1
Y = 0
SUM DATA
Yk1 → Yk2
Y2 = Y2+Y^2

Fig. 4

References

Allen, J.A. (1958). The basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia). Philosophical Transactions of the Royal Society (Series B), 241, 421-481.

Andronikov, V.B. (1975). Heat resistance of gametes of marine invertebrates in relation to temperature conditions under which the species exist. Marine Biology, 30, 1-13.

Ansell, A.D. (1960). Observations on predation of Venus striatula (da Costa) by Natica alderi (Forbes). Proceedings of the Malacological Society of London, 34, 157-164.

Ansell, A.D. (1962). Observations on burrowing in the Veneridae (Eulamellibranchia). Biological Bulletin. Marine Biological Laboratory, Woods Hole, Mass., 123, 521-530.

Ansell, A.D. and Trevallion, A. (1967). Studies on Tellina tenuis da Costa. 1. Seasonal growth and biochemical cycle. Journal of Experimental Marine Biology and Ecology, 1, 220-235.

Ansell, A.D. and Trueman, E.R. (1967). Observations on burrowing in Glycimeris glycimeris (L) (Bivalvia, Arcacea). Journal of Experimental Marine Biology and Ecology, 1, 65-75.

Arnold, D.C. (1957). The response of the limpet Patella vulgata L. to waters of different salinities. Journal of the Marine Biological Association of the United Kingdom, 36, 121-128.

Arnold, D.C. (1972). Salinity tolerances of some common Prosobranchs. Journal of the Marine Biological Association of the United Kingdom, 52, 475-486.

Atkins, D. (1937a). On the ciliary mechanisms and interrelationships of lamellibranchs. Part II. Sorting devices on the gills. Quarterly Journal of Microscopical Science, 79, 339-373.

Atkins, D. (1937b). On the ciliary mechanisms and interrelationships of lamellibranchs. Part III. Types of lamellibranch gills and their food currents. Quarterly Journal of Microscopical Science, 79, 375-445.

Atkinson, R.J.A. (1973). Seasonal patterns of migration and locomotor rhythmicity in populations of Carcinus. Netherlands Journal of Sea Research, 7, 81-93.

Bacescu, M.C. (1971). Substratum : Animals. In Marine Ecology, Volume 1, Part 3, Ed. Kinne, O. London, New York: Wiley - Interscience, 1291-1322.

Baggerman, B. (1953). Spatfall and transport of Cardium edule. Archives Neerlandaises de Zoologie, 10, 315-342.

Bailey, N.T.J. (1959). Statistical methods in Biology. London : The English Universities Press Ltd.

Barker, M. (1964). Microtextural variation in pelecypod shells. Malacologia, 2, 69-86.

Barnes, H. (1955). Climatological and salinity data for Millport, Scotland. Glasgow Naturalist, 17, 193-204.

Barnes, H. (1961). The general hydrography of the Clyde Sea Area, Scotland. Part 1. Description of the area ; drift bottle and surface salinity data. Bulletin of Marine Ecology, 5, 112-150.

Barnett, P.R.O. (1971). Some changes in intertidal sand communities due to thermal pollution. Proceedings of the Royal Society (Series B), 177, 353-364.

Barnett, P.R.O. (1972). Effects of warm water effluents from power stations on marine life. Proceedings of the Royal Society (Series B), 180, 497-509.

Bassindale, R. (1940). The invertebrate fauna of the southern shores of the Bristol Channel and Severn Estuary. Proceedings of the Bristol Channel Naturalists Society, *9*, 143-201.

Bayne, B.L. (1965). Growth and the delay of metamorphosis of the larvae of *Mytilus edulis* (L.). Ophelia, *2*, 1-47.

Bayne, B.L. (1969). The gregarious behaviour of the larvae of *Ostrea edulis* at settlement. Journal of the Marine Biological Association of the United Kingdom, *49*, 327-356.

Bayne, B.L., Gabbott, P.A. and Widdows, J. (1975). Some effects of stress in the adult on the eggs and larvae of *Mytilus edulis* (L.). Journal of the Marine Biological Association of the United Kingdom, *55*, 675-689.

Be, A.W.H., MacClintock, C. and Currie, D.C. (1972). Helical shell structure and growth of the pteropod *Cuvierina columnella* (Rang). Biomineralization Research Reports, *4*, 47-49.

Benson, J.A. and Lewis R.D. (1976). An analysis of the activity rhythm of the sand beach amphipod *Talorchestia quoyana*. Journal of Comparative Physiology, *105*, 339-352.

Benthem Jutting, W.S.S. van (1943). Lamellibranchia. Fauna van Nederland, *12*, Mollusca (1) C.

Berry, W.B.N. and Barker, R.M. (1968). Fossil bivalve shells indicate longer month and year in Cretaceous than Present. Nature, London, *217*, 938.

Biggs, D.C. and McDermott, J.J. (1973). Variation in the temperature-salinity tolerance between two estuarine populations of *Pagurus longicarpus* Say (Crustacea : Anomura). Biological Bulletin. Marine Biological Laboratory, Woods Hole, Mass., *145*, 91-102.

Blackman, G.E. (1962). Statistical and ecological studies on the distribution of species in plant communities. Annals of Botany, N.S. *6*, 351-370.

Blegvad, H. (1915). Food and conditions of nourishment among the communities of invertebrate animals found on or in the sea bottom in Danish Waters. Report of the Danish Biological Station to the Board of Agriculture, 22, 41-78.

Bliss, C.I. (1935). The calculation of the dosage mortality curve. Annals of Applied Biology, 22, 134-167.

Bloom, S.A., Simon, J.L. and Hunter, V.D. (1972). Animal-sediment relationships and community analysis of a Florida Estuary. Marine Biology, 13, 43-56.

Boltovsky, D. (1974). Study of surface-shell features in Thecosomata (Pteropoda : Mollusca) by means of a scanning electron microscope. Marine Biology, 27, 165-180.

Bourget, E. and Crisp, D.J. (1975a). Factors affecting deposition of the shell in Balanus balanoides (L.). Journal of the Marine Biological Association of the United Kingdom, 55, 231-249.

Bourget, E. and Crisp, D.J. (1975b). An analysis of the growth bands and ridges of barnacle shell plates. Journal of the Marine Biological Association of the United Kingdom, 55, 439-461.

Boyden, C.R. (1972). Aerial respiration of the cockle Cerastoderma edule in relation to temperature. Comparative Biochemistry and Physiology, 43A, 697-712.

Brafield, A.E. and Newell, G.E. (1961). The behaviour of Macoma balthica (L.). Journal of the Marine Biological Association of the United Kingdom, 41, 81-87.

Brett, J.R. (1944). Some lethal temperature relations of Algonquin Park fishes. University of Toronto Studies. Biological Series, 52, 1-49.

Brett, J.R. (1970). Temperature : Animals : Fishes. In Marine Ecology Volume 1, Part 1, Ed. Kinne, O., London, New York : Wiley - Interscience, 513-560.

Brøgger, W.C. (1901). Om de senglaciale og postglaciale nivaforandringer i Kristianiafelted (Molluskfaunen). Norges geologiske undersogelse, 31, 1-731.

Bruce, J.R. (1928). Physical factors on the sandy beach. Journal of the Marine Biological Association of the United Kingdom, 15, 535-565.

Burch, J.B. (1975). SEM studies of the shell apices of freshwater limpets. Malacological Review, 8, 119-120.

Cain, T.D. (1973). The combined effects of temperature and salinity on embryos and larvae of the clam Rangia. Marine Biology, 21, 1-7.

Calabrese, A. (1969). Individual and combined effects of salinity and temperature on embryos and larvae of the coot clam, Mulinia lateralis (Say). Biological Bulletin, Marine Biological Laboratory, Woods Hole, Mass., 137, 417-428.

Calabrese, A. and Davis, H.C. (1970). Tolerances and requirements of embryos and larvae of bivalve molluscs. Helgolander Wissenschaftliche Meersuntersuchungen, 20, 553-564.

Caldenius, C. and Lundström, R. (1956). The landslide at Surte on the River Gota, Alv. Sveriges Geologiska Undersokning. Afhandlinger och Uppsatser, 27, Stockholm.

Campbell, J.I.C. and Meadows, P.S. (1974). Gregarious behaviour in a benthic marine amphipod (Corophium volutator). Experientia,, 30, 1396-1397.

Carriker, M.R. (1951a). Ecological observations on the distribution of oyster larvae in New Jersey estuaries. Ecological Monographs, 21, 19-38.

Carriker, M.R. (1951b). Observations on the penetration of tightly closed bivalves by Busycon and other predators. Ecology, 32, 73-83.

Carriker, M.R. (1961). Interrelation of functional morphology, behaviour, and autecology in early stages of the bivalve Mercenaria mercenaria. Journal of the Elisha Mitchell Scientific Society, 77, 168-241.

Castagna, M. and Chanley, P. (1973). Salinity tolerance of some marine bivalves from inshore and estuarine environments in Virginia waters on the western Midatlantic coast. Malacologia, 12, 49-76.

Chapman, G. (1949). The thixotrophy and dilutancy of a marine soil. Journal of the Marine Biological Association of the United Kingdom, 28, 123-140.

Chapman, G. and Newell, G.E. (1947). The role of the body fluid in relation to movement in soft bodied invertebrates. 1. The burrowing of Arenicola. Proceedings of the Royal Society (Series B), 134, 431-455.

Clark, P.J. and Evans, F.C. (1954). Distance to nearest neighbour as a measure of spatial relationships in populations. Ecology, 35, 445-453.

Clark R.B. and Milne, A. (1955). The sublittoral fauna of two sandy bays on the Isle of Cumbrae, Firth of Clyde. Journal of the Marine Biological Association of the United Kingdom, 34, 161-180.

Cocking, A.W. (1959a). The effects of high temperatures on roach (Rutilus rutilus) I. The effects of constant high temperatures. Journal of Experimental Biology, 36, 203-216.

Cocking, A.W. (1959b). The effects of high temperatures on roach (Rutilus rutilus) II. The effects of temperature increasing at a known constant rate. Journal of Experimental Biology, 36, 217-226.

Coleman, N. (1974). The heart rate and activity of bivalve molluscs in their natural habitats. Oceanography and Marine Biology. An Annual Review, 12, 301-314.

Connell, J.H. (1955). Spatial distribution of two species of clams *Mya arenaria* and *Petricola pholadiformis* in an intertidal area. Report of Investigations of Shell-fisheries of Massachusetts, *8*, 15-25.

Connell, J.H. (1961). The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology, *42*, 710-723.

Connell, J.H. (1963). Territorial behaviour and dispersion in some marine invertebrates. Research into Population Ecology, *2*, 87-101.

Costlow, J.D., Bookhout, C.G. and Monroe, R. (1960). The effect of salinity and temperature on larval development of *Sesarma cinereum* (Bosc) reared in the laboratory. Biological Bulletin, Marine Biological Laboratory, Woods Hole, Mass., *118*, 183-202.

Cragg, S.M. and Gruffydd, L.D. (1975). The swimming response and the pressure response of the veliconcha larvae of *Ostrea edulis*. In Proceedings of the Ninth European Marine Biology Symposium. Ed. Barnes, H., 43-57.

Crisp, D.J. (1961). Territorial behaviour in barnacle settlement. Journal of Experimental Biology, *38*, 429-446.

Crisp, D.J. and Richardson, C.A. (1975). Tidally produced internal bands in the shell of *Elminius modestus*. Marine Biology, *33*, 155-160.

Crisp, D.J. and Ritz, D.A. (1967). Changes in temperature tolerance of *Balanus balanoides* during its life cycle. Helgolander Wissenschaftliche Meersuntersuchungen, *15*, 98-115.

Crisp, D.J. and Williams, R. (1971). Direct measurement of pore-size distribution on artificial and natural deposits and prediction of pore space accessible to interstitial organisms. Marine Biology, 10, 214-226.

Davies, P.S. (1965). Environmental acclimation in the limpet *Patella vulgata* (L.). Nature, London, 205, 294.

Davies, P.S. (1967). Physiological ecology of *Patella*. II. The effect of environmental acclimation on the metabolic rate. Journal of the Marine Biological Association of the United Kingdom, 47, 61-74.

Davies, P.S. (1969). Effect of environment on metabolic activity and morphology of Mediterranean and British species of *Patella*. Pubblicazioni della Stazione zoologica di Napoli, 37, 641-656.

Davies, P.S. (1970). Physiological ecology of *Patella*. IV. Environmental and limpet body temperatures. Journal of the Marine Biological Association of the United Kingdom, 50, 1069-1077.

Davis, H.M. (1925). Quantitative studies on the fauna of the sea bottom No. 2. Southern North Sea. Great Britain Fisheries Investigations, Series 11, Volume 8, Number 4, 1-50.

De Wilde, P.A.W.J. (1975). Influence of temperature on behaviour, energy metabolism and growth of *Macoma balthica*. In Proceedings of the Ninth European Marine Biology Symposium, ed. Barnes, H., 239-257.

Diaz, R.J. (1973). Effects of brief temperature increases on larvae of the American oyster (*Crassostrea virginica*). Journal of the Fisheries Research Board of Canada, 30, 991-993.

Dickie, L.M. (1958). Effects of high temperature on survival of the giant scallop. Journal of the Fisheries Research Board of Canada, 15, 1189-1211.

Earll, R. (1975a). Temporal variation in the heart activity of *Scrobicularia plana* (da Costa) in constant and tidal conditions. Journal of Experimental Marine Biology and Ecology, 19, 257-274.

Earll, R. (1975b). Some aspects of heart rate and activity in bivalve molluscs in the laboratory and the natural environment. Ph.D. Thesis, University of Manchester.

Eisma, D. (1965). Shell characteristics of Cardium edule L. as indicators of salinity. Netherlands Journal of Sea Research, 2, 493-540.

Eisma, D. (1966). The distribution of benthic marine molluscs off the main Dutch coast. Netherlands Journal of Sea Research, 3, 107-163.

Enright, J.T. (1963). The tidal rhythm of activity of a sand beach amphipod. Zeitschrift für Vergleichende Physiologie, 46, 276-313.

Enright, J.T. (1965). The search for rhythmicity in a biological time-series. Journal of Theoretical Biology, 8, 426-468.

Enright, J.T. (1972). A virtuoso amphipod. Circa-lunar rhythms and their tidal fine structure. Journal of Comparative Physiology, 77, 141-162.

Evans, R.G. (1948). The lethal temperatures of some common British littoral molluscs. Journal of Animal Ecology, 17, 165-173.

Fenchel, T. and Jansson, B.O. (1966). On the vertical distribution of the microfauna in the sediments of a brackish-water beach. Ophelia, 3, 161-177.

Finney, D.J. (1947). Probit Analysis, Cambridge : Cambridge University Press.

Folk, R.L. and Ward, W.C. (1957). Brazos River Bar : a study on the significance of grain size parameters. Journal of Sedimentary Petrology, 27, 3-26.

Forbes, E. and Hanley, S. (1853). A history of British Mollusca and their shells. London : John van Voorst.

Ford, E. (1923). Animal communities of the level sea bottom in the waters adjacent to Plymouth. Journal of the Marine Biological Association of the United Kingdom, 13, 164-224.

Foster B.A. (1969). Tolerance of high temperatures by some intertidal barnacles. Marine Biology, 4, 326-332.

Fraenkel, G. (1961). Resistance to high temperatures in a Mediterranean snail, Littorina neritoides. Ecology, 42, 604-606.

Fraenkel, G. (1968). The heat resistance of intertidal snails at Bimini, Bahamas; Ocean Springs, Mississippi; and Woods Hole, Massachusetts. Physiological Zoology, 41, 1-13.

Fraenkel, G.V. (1927). Die Grabbewegung der Soleniden. Zeitschrifte für Vergleichende Physiologie, 6, 167-220.

Franz, D.R. (1973). The ecology and reproduction of a marine bivalve Mysella planulata (Erycinacea). Biological Bulletin. Marine Biological Laboratory, Woods Hole Mass., 144, 93-107.

Fraser, H.J. (1935). Experimental study of the porosity and permeability of clastic sediments. Journal of Geology, 43, 910-1010.

Freeman, R.F.H. and Rigler, F.H. (1957). The responses of Scrobicularia plana (da Costa) to osmotic pressure changes. Journal of the Marine Biological Association of the United Kingdom, 36, 553-567.

Fretter, V. amd Pilkington, M.C. (1971). The larval shell of some Prosobranch gastropods. Journal of the Marine Biological Association of the United Kingdom, 51, 49-62.

Friedrich, H. (1969). Marine Biology. London : Sidgwick and Jackson.

Fry, F.E.J. (1947). Effects of the environment on animal activity. University of Toronto Studies. Biological Series, 55, 5-62.

Fry, F.E.J. (1957). The lethal temperature as a tool in taxonomy. Annee Biologique, 33, 205-219.

Fry, F.E.J. (1958). Temperature compensation. Annual Review of Physiology, 20, 207-224.

Fry, F.E.J. (1968). Responses of vertebrate poikilotherms to temperature. In Thermobiology, Ed. Rose, A.H. London, New York : Academic Press, 375-409.

Fry, F.E.J., Hart, J.S. and Walker, K.F. (1946). Lethal temperature relationships for a sample of young speckled trout Salvelinus fontalis. University of Tononto Studies. Biological Series, 54, 9-35.

Gabbott, P.A. and Bayne, B.L. (1973). Biochemical effects of temperature and nutritive stress on Mytilus edulis L. Journal of the Marine Biological Association of the United Kingdom, 53, 269-286.

Gale, W.F. (1971). An experiment to demonstrate the substrate preference of the fingernail clam Sphaerium transversum (Say). Ecology, 52, 367-370.

Gaucher, T.A. (1965). Dispersion in a subtidal Mya arenaria (L.) population. Proceedings. National Shellfisheries Association, 56, 3-4.

Gilbert, W.H. (1968). Distribution and dispersion patterns of the dwarf Tellin clam, T.agilis. Biological Bulletin. Marine Biological Laboratory, Woods Hole, Mass., 135, 419-420.

Giusti, F. (1973). The minute shell structure of the glochidium of some species of the genera Unio, Potomida, and Anodonta (Bivalvia, Unionacea). Malacologia, 14, 291-301.

Goodwin, C.L. (1970). Some observations on the laboratory spawning of the geoduck Panope generosa, and the culture of its larvae. Proceedings. National Shellfisheries Association, 60, 13-14.

Gray, J.S. (1966). Selection of sands by Protodrilus symbioticus Giard. Veroffentlichungen des Instituts fur Meeresforschung in Bremerhaven, 2, 105-116.

Gray, J.S. (1967a). Substrate selection by the Archiannelid Protodrilus rubropharyngeus Jagersten. Helgolander wissentschaftliche Meeresuntersuchungen, 15, 255-269.

Gray, J.S. (1967b). Substrate selection by the Archiannelid Protodrilus hypoleucus Armenante. Journal of Experimental Marine Biology and Ecology, 1, 47-54.

Gray, J.S. (1974). Animal-Sediment relationships. Oceanography and Marine Biology. An Annual Review, 12, 223-261.

Grieg-Smith, P. (1952). The use of random and contiguous quadrats in the study of the structure of plant communities. Annals of Botany, 16, 293-316.

Gunter, G. (1957). Temperature. In Treatise on Marine Ecology and Palaeoecology (Ecology). Ed. Hedgepeth, J.W. Memoirs. Geological Society of America, 67, 159-184.

Hairston, N.G. (1959). Species abundance and community organisation. Ecology, 40, 404-416.

Hansbro, S. (1957). A new approach to the determination of the shear strength of clay by the fall-cone test. Proceedings. Royal Swedish Geotechnical Institute, 14, 1-43.

Hardy, A.C. and Bainbridge, R. (1951). Effects of pressure on the behaviour of decapod larvae (Crustacea). Nature, London, 167, 354-355.

Haskin, H.H. (1964). The distribution of oyster larvae. Symposium on Experimental Marine Ecology. Occasional Publications, 2, 76-80.

Hedgepeth, J.W. (1957). Marine Biogeography. In Treatise on Marine Ecology and Palaeoecology (Ecology). Ed. Hedgepeth, J.W. Memoirs, Geological Society of America, 67, 359-383.

Heering, J. (1950). Pelecypoda (and Scaphopoda) of the Pliocene and older Pleistocene deposits of the Netherlands. Mededlingen van de Geologische stichting, Serie C IV-1, 9, 1-225.

Heip, C. (1975). On the significance of aggregation in some benthic marine invertebrates. In Proceedings of the Ninth European Marine Biology Symposium. Ed. Barnes, H., 527-538.

Henderson, J.T. (1929). Lethal temperatures of lamellibranchs. Contributions to Canadian Biology and Fisheries, N.S. 4, 399-411.

Heusner, A.A. and Enright, J.T. (1966). Long term activity recording in small aquatic crustaceans. Science, 154, 532-533.

Hoefs, J. and Sarnthein, M. (1971). $^{18}O/^{16}$ ratios and related temperatures of recent pteropod shells (Cavolina longirostris Lesueur) from the Persian Gulf. Marine Geology, 10, 11-16.

Holme, N.A. (1949). The fauna of sand and mud banks near the mouth of the Exe estuary. Journal of the Marine Biological Association of the United Kingdom, 28, 189-237.

Holme, N.A. (1950). Population dispersion in Tellina temuis da Costa. Journal of the Marine Biological Association of the United Kingdom, 29, 267-280.

Holme, N.A. (1961). Notes on the mode of life of the Tellinidae (Lamellibranchia). Journal of the Marine Biological Association of the United Kingdom. 41, 699-703.

House, M.R. and Farrow, G.E. (1968). Daily growth banding on the shell of the cockle. Nature, London, 219, 1384-1386.

Hughes R.N.(1969). A study of feeding in Scrobicularia plana. Journal of the Marine Biological Association of the United Kingdom, 49, 805-823.

Hughes, R.N. (1970). Population dynamics of the bivalve Scrobicularia plana (da Costa) on an intertidal mud flat in North Wales. Journal of Animal Ecology, 39, 333-356.

Hughes, R.N. (1971). Reproduction of Scrobicularia plana da Costa. Veliger, 14, 77-81.

Hulscher, J.B. (1973). Burrowing depth and Trematode infection in Macoma balthica. Netherlands Journal of Sea Research, 6, 141-156.

Hutchins, L.W. (1947). The bases for temperature zonation in geographical distribution. Ecological Monographs, 17, 325-335.

Hutchinson, J.H. (1961). Critical thermal maxima in salamanders. Physiological Zoology, 34, 92-125.

Inman, D.L. (1952). Measures for describing the size distribution of sediments. Journal of Sedimentary Petrology, 22, 125-145.

Jackson, J.B. (1968). Bivalves : Spatial and size-frequency distributions of two intertidal species. Science, N.Y., 161, 479-480.

Jansson, B.-O. (1966). Microdistribution of factors and fauna in marine sandy beaches. Veroffenlichungen des Instituts fur Meeresforschung in Bremerhaven, 2, 77-86.

Jansson, B.-O. (1967a). Diurnal and annual variations of temperature and salinity of interstitial water in sandy beaches. Ophelia, 4, 173-201.

Jansson, B.-O. (1967b). The significance of grain size and pore water content for the interstitial fauna of sandy beaches. Oikos, 18, 311-322.

Jeffreys, J.G. (1863). Btitish Conchology. London : John van Voorst.

Johnson, R.G. (1959). Spatial distribution of Phoronopsis viridis Science, N.Y., 129, 1221.

Johnson, R.G.(1965). Temperature variation in the infaunal environment of a sand flat. Limnology and Oceanography, 10, 114-120.

Jones, D.A. and Naylor, E. (1970). The swimming rhythm of the sand beach isopod Eurydice pulchra. Journal of Experimental Marine Biology and Esology, 4, 188-199.

Josephson, R.K. and Flessa, K.W. (1972). Cryolite : a medium for the study of burrowing aquatic organisms. Limnology and Oceanography, 17, 134-135.

Kauffman, E.G. (1969). Form, function and evolution. In Treatise on Invertebrate Palaeontology. Ed. Moore, R.C. Mollusca 6. Lawrence, Kansas : Geological Society of America and the University of Kansas Press, 130-205.

Kennedy, V.S. and Mihursky, T.A. (1971). Upper temperature tolerances of some estuarine bivalves. Chesapeake Science, 12, 193-204.

Kennedy, V.S., Roosenburg, W.H., Zion, H.H. and Castagna, M. (1974). Temperature-time relationships for survival of embryos and larvae of Mulinia lateralis (Mollusca : Bivalvia). Marine Biology, 24, 137-147.

Kensler, C.B. (1967). Desiccation resistance of intertidal crevice species as a factor in their zonation. Journal of Animal Ecology, 36, 391-406.

Kershaw, K. (1960). The detection of pattern and association. Journal of Ecology, 48, 233-242.

Kershaw, K. (1964). Quantitative and dynamic ecology. London : William Clowes and Sons Ltd.

Kinne, O. (1963). The effects of temperature and salinity on Marine and brackish water animals. I. Temperature. Oceanography and Marine Biology. An Annual Review, 1, 301-340.

Kinne, O. (1964). The effects of temperature and salinity on marine and brackish water animals. II. Salinity and temperature-salinity combinations. Oceanography and Marine Biology. An Annual Review, 2, 281-341.

Kinne, O. (1970). Temperature : Invertebrates. In Marine Ecology, Volume 1, Part 1, Ed. Kinne O. London, New York : Wiley - Interscience, 407-514.

Knight-Jones, E.W. (1951). Gregariousness and some other aspects of the settling behaviour of Spirorbis. Journal of the Marine Biological Association of the United Kingdom, 30, 201-222.

Knight-Jones, E.W. and Morgan, E. (1966). Responses of marine animals to changes in hydrostatic pressure. Oceanography and Marine Biology. An Annual Review, 4, 267-299.

Knight-Jones, E.W. and Moyse, J. (1961). Intraspecific competition in sedentary marine animals. Symposia of the Society for Experimental Biology, 15, 72-95.

Knight-Jones, E.W. and Stevenson, J.P. (1950). Gregariousness during settlement in the barnacle Elminius modestus Darwin. Journal of the Marine Biological Association of the United Kingdom, 29, 281-297.

Korringa, P. (1952). Recent advances in oyster biology. Quarterly Review of Biology, 27, 274-308, 339-365.

Kreger, D. (1940). On the ecology of Cardium edule L. Archives Neerlandaises de Zoologie, 4, 157-200.

LaRow, E.J. (1970). The effect of oxygen tension on the vertical migration of Chaoborus larvae. Limnology and Oceanography, 15, 357-362.

Lever, J. (1958). Quantitative beach research. I. The "left-right" phenomenon : sorting of lamellibranch valves on sandy beaches. Basteria, 22, 21-51.

Levinton, J. (1972). Spatial distribution of Nucula proxima : an experimental approach. Biological Bulletin. Marine Biological Laboratory, Woods Hole, Mass., 143, 175-183.

Loosanoff, V.L. and Davis, H.C. (1963). Rearing of bivalve mollusks. Avances in Marine Biology, 1, 1-136.

Loosanoff, V.L., Miller, W.S. and Smith, P.B. (1951). Growth and settling of larvae of Venus mercenaria in relation to temperature. Journal of Marine Research, 10, 59-81.

Lough, R.G. and Gonor, J.J. (1971). Early embryonic stages of Adula californiensis (Mytilidae) and the effect of temperature and salinity on developmental rate. Marine Biology, 8, 118-125.

Loveland, B.E., Moul, E.T., Busch, D.A., Sandine, P.H. Shafto, S.A. and McCarty, J. (1972). The qualitative and quantitative analysis of the benthic flora and fauna of Barnegat Bay before and after the onset of thermal pollution. Report No.8 to New Jersey Public Health Utilities Commission, 37-42. Department of Zoology, Rutgers University, New Brunswick, New Jersey.

McCammon, H.M. (1971). Behaviour in the Brachiopod Terebratulina septentrionalis. Journal of Experimental Marine Biology and Ecology, 6, 35-45.

McErlean, A.J., Mihursky, J.A. and Brinkley, H.J. (1969). Determination of upper temperature triangles for aquatic organisms. Chesapeake Science, 10, 293-296.

McIntyre, A.D. (1970). The range of biomass in intertidal sand with special reference to the bivalve Tellina tenuis. Journal of the Marine Biological Association of the United Kingdom, 50, 561-575.

Matthiesen, G.C. (1960). Observations on the ecology of the soft clam Mya arenaria in a salt pond. Limnology and Oceanography, 5, 291-300.

Meadows, P.S. (1964). Substrate selection by Corophium species : the particle size of substrate. Journal of Animal Ecology, 33, 387-394.

Meadows, P.S. and Campbell, J.I.C. (1972a). Habitat selection by aquatic invertebrates. Advances in Marine Biology, 10, 271-382.

Meadows, P.S. and Campbell, J.I.C. (1972b). Habitat selection and animal distribution in the sea : the evolution of a concept. Proceedings of the Royal Society of Edinburgh, Section B (Biology), 73, 145-157.

Meadows., P.S. and Mitchell, K.A. (1973). An analysis of inter- and intraspecific aggregations in two sympatric species of hermit crab (Decapoda, Anomura, Paguridae). Marine Behaviour and Physiology, 2, 187-196.

Mill, H.R. (1892-4). The Clyde Sea Area. Transactions of the Royal Society of Edinburgh, 36, 641-729; 38, 1-161.

Mitchell, K.A. (1975). Habitat selection by hermit crabs. Ph.D. Thesis, University of Glasgow.

Moore, R.C. (1970). Treatise on Invertebrate Paleontology. Lawrence, Kansas : Geological Society of America and the University of Kansas Press.

Morgan, E. (1970). The effect of environmental factors on the distribution of the amphipod Pectenogammarus planicrurus with particular reference to grain size. Journal of the Marine Biological Association of the United Kingdom, 50, 769-785.

Morgans, J.F.C. (1956). Notes on the analysis of shallow water soft substrates. Journal of Animal Ecology, 25, 367-387.

Moroney, M.J. (1951). Facts from figures. London : Penguin Books Ltd.

Morton, B.S. (1970). The tidal rhythm of feeding and digestion in Cardium edule. Journal of the Marine Biological Association of the United Kingdom, 50, 499-512.

Morton, B.S. (1973). A new theory of feeding and digestion in the filter feeding Lamellibranchia. Malacologia, 14, 63-79.

Morton, J.E. (1956). The tidal rhythm and action of the digestive system of the lamellibranch Lasaea rubra. Journal of the Marine Biological Association of the United Kingdom, 35, 563-586.

Morton, J.E., Boney, A.D. and Corner, E.D.S. (1957). The adaptations of Lasäea rubra (Montagu), a small intertidal bivalve. Journal of the Marine Biological Association of the United Kingdom, 36, 383-405.

Muus, K. (1973). Settling, growth and mortality of young bivalves in the Øresund. Ophelia, 12, 79-117.

Nair, N.B. and Ansell, A.D. (1968). Characteristics of penetration of the substrate by some marine bivalve molluscs. Proceedings of the Malacological Society of London, 38, 179-197.

Naylor, E.(1958). Tidal and diurnal rhythms of locomotor activity in Carcinus maenas (L.). Journal of Experimental Biology, 35, 602-610.

Naylor, E.(1960). Locomotor rhythms in Carcinus maenas(L.) from non-tidal conditions. Journal of Experimental Biology, 37, 481-488.

Naylor, E. (1963). Temperature relationships of the locomotor rhythm of Carcinus. Journal of Experimental Biology, 40, 669-679.

Naylor, E. and Atkinson, R.J.A. (1972). Pressure and the rhythmic behaviour of inshore marine animals. Symposia of the Society for Experimental Biology, 26, 395-415.

Naylor, E., Atkinson, R.J.A. and Williams, B.G. (1971). External factors influencing the tidal rhythm of shore crabs. Journal of Interdisciplinary Cycle Research, 2, 173-180.

Neville, A.A. (1967). Daily growth layers in animals and plants. Biological Reviews, 42, 421-441.

Newell, G.E. and Chapman, G. (1948). Distribution of lugworms. Nature, London, 162, 75.

Newell, R.C. (1970). The biology of intertidal animals. London : Logos Press Ltd.

Newell, R.C. and Bayne, B.L. (1973). A review on temperature and metabolic acclimation in intertidal marine invertebrates. Netherlands Journal of Sea Research, 7, 421-433.

Nørgaard, E.(1951). On the ecology of two lycosid spiders (Pirata piraticus and Lycosa pullata) from a Danish sphagnum bog. Oikos, 3, 1-21.

Norton, P.E.P. (1967). Marine molluscan assemblages in the early Pleistocene of Sidestrand, Bramerton, and the Royal Society borehole at Ludham, Norfolk. Philosophical Transactions of the Royal Society, Series B, 253, 161-200.

Norton, P.E.P. and Spaink, G. (1973). The earliest occurrence of Macoma balthica (L.) as a fossil in the North Sea deposits. Malacologia, 14, 33-37.

Ockelmann, W.K. (1958). The zoology of East Greenland. Marine Lamellibranchiata. Meddelelser om Grønland, 122.4, 1-256.

Orr, P.R. (1955). Heat death. 1. Time temperature relationships in marine animals. Physiological Zoology, 28, 290-293.

Orton, J.H. (1920). Sea temperature, breeding and distribution in marine animals. Journal of the Marine Biological Association of the United Kingdom, 12, 339-366.

Palmer, J.D. (1974). Biological clocks in marine organisms. New York, London : John Wiley and Sons.

Parker, J. (1960). Seasonal changes in cold-hardiness of Fucus vesiculosus. Biological Bulletin. Marine Biological Laboratory, Woods Hole, Mass., 119, 474-478.

Paul, C.R.C. (1975). Columella in the British Isles. Journal of Conchology, 28, 371-383.

Perkins, E.J. (1972). Spectrum. British Science News, 97, 12-13.

Perkins, E.J. (1974). The biology of estuaries and coastal waters. London : Academic Press.

Perkins, E.J. and Williams, B.R.H. (1966). Biology of the Solway Firth in relation to the movement and accumulation of radioactive materials. II. The distribution of sediments and benthos. H.M.S.O., United Kingdom Atomic Energy Authority, Report 587 (C.C.).

Pielou, E.C. (1969). An introduction to mathematical ecology. New York, London : Wiley-Interscience.

Pierce, S.K. (1973). The initiation and control of free amino acid regulation of cell volume in salinity stressed marine bivalves. Journal of Experimental Biology, 59, 435-440.

Probert, P.K. (1973). The bottom fauna of china clay waste deposits in Mevagissey Bay. Ph.D. Thesis, University of London.

Probert, P.K. (1975). The bottom fauna of china clay waste deposits in Mevagissey Bay. Journal of the Marine Biological Association of the United Kingdom, 55, 19-44.

Pohlo, R.H. (1963). Morphology and mode of burrowing in Siliqua patula and Solen rosaceus. Veliger, 6, 98-104.

Pohlo, R.H. (1969). Confusion concerning deposit feeding in the Tellinacea. Proceedings of the Malacological Society of London, 38, 361-364.

Precht, H. (1973). Limiting temperatures of life functions. In Temperature and Life, Ed. Precht, H., Christophersen, J., Hensel, H. and Larcher, W. Berlin : Springer Verlag, 400-440.

Prosser, C.L. (1958). Physiological adaptation. Washington : American Physiological Society.

Quayle, D.B. (1949). Movements in Venerupis (= Paphia) pullastra (Montagu). Proceedings of the Malacological Society of London, 28, 31-37.

Rao, K.P. (1953). Shell weight as a function of intertidal height in a littoral population of pelecypods. Experientia, 9, 465-466.

Rao, R.D. (1953). Rate of water propulsion in Mytilus californianus as a function of latitude. Biological Bulletin. Marine Biological Laboratory, Woods Hole, Mass., 104, 171-181.

Rasmussen, E. (1973). Systematics and ecology of the Isefjörd marine fauna. Ophelia, 11, 1-495.

Read, K.R.H. (1964). Ecology and environmental physiology of some Puerto Rican bivalve molluscs and a comparison with boreal forms. Caribbean Journal of Science, 4, 459-465.

Read, K.R.H. (1967). Thermal tolerance of the bivalve mollusc Lima scabra Born, in relation to environmental temperature. Proceedings of the Malacological Society of London, 37, 233-241.

Read, K.R.H. and Cumming, K.B. (1967). Thermal tolerance of the bivalve molluscs Modiolus modiolus L., Mytilus edulis L., and Brachidontes demissus Dillwyn. Comparative Biochemistry and Physiology, 22, 149-155.

Rees, C.B. (1950). The identification and classification of bivalve larvae. Hull Bulletins of Marine Ecology, 3, 73-104.

Reid, D.M. (1930). Salinity interchange between seawater in sand and overflowing fresh water at low tide. Journal of the Marine Biological Association of the United Kingdom, 16, 609-614.

Rhoads, D.C. (1974). Organism-sediment relationships on the muddy sea floor. Oceanography and Marine Biology. An Annual Review, 12, 263-300.

Robertson, R. (1971). Scanning electron microscopy of planktonic larval marine shells. Veliger, 14, 1-12.

Rosenberg, R. (1974). Spatial dispersion of an estuarine benthic faunal community. Journal of Experimental Marine Biology and Ecology, 15, 69-80.

Runham, N.W. (1969). The use of the scanning electron microscope in the study of the gastropod radula : the radulae of Agriolomax reticulatus and Nucella lapillus. Malacologia, 9, 179-187.

Runham, N.W. and Thornton, P.R. (1967). Mechanical wear of the gastropod radula : a scanning electron microscopy study. Journal of Zoology, 153, 445-452.

Russel, P.J.C. (1972). A significance in the number of ribs on the shells of two closely related *Cardium* species. Journal of Conchology, 27, 402-411.

Salanki, J.A. (1966a). Comparative studies on the regulation of the periodic activity in marine lamellibranchs. Comparative Biochemistry and Physiology, 18, 829-843.

Salanki, J.A. (1966b). Daily activity rhythm of two Mediterranean lamellibranchiata *Pecten jacobeus* and *Lithophaga lithophaga*, regulated by light-dark period. Annales Instituti biologici, Tihany, Hungaricae academiae scientiarum.

Salanki, J.A. (1971). Control of periodicity by non-oscillating external factors in *Pelecypoda*. Journal of Interdisciplinary Cycle Research, 2, 181-186.

Saleuddin, A.S.M. (1964). Observations on the habit and functional morphology of *Cyprina islandica* (L.). Proceedings of the Malacological Society of London, 36, 149-162.

Segal, E., Rao, K.P. and James, T.W. (1953). Rate of activity as a function of intertidal height within populations of some littoral molluscs. Nature, London, 172, 1108-1109.

Siegel, S. (1956). Non-parametric statistics for the behavioural sciences. Tokyo : McGraw-Hill Kogakusha Ltd.

Simpson, R.D. (1976). Physical and biotic factors limiting the distribution and abundance of littoral molluscs on Macquarie Island (Sub-Antartica). Journal of Experimental Marine Biology and Ecology, 21, 11-49.

Smith, R.I. (1955). Salinity variation in interstitial water of sand at Kames Bay, Millport, with reference to the distribution of *Nereis diversicolor*. Journal of the Marine Biological Association of the United Kingdom, 34, 33-46.

Solem, A. (1970). Malacological applications of scanning electron microscopy. 1. Introduction and shell surface features. Veliger, 12, 394-400.

Solem, A. (1973a). Convergent evolution in pulmonate radulae. Malacologia, 14, 144-146.

Solem, A. (1973b). Convergence in pulmonate radulae. Veliger, 15, 165-171.

Southward, A.J. (1953). The fauna of some sandy and muddy shores in the south of the Isle of Man. Proceedings and Transactions of the Liverpool Biological Society, 59, 51-71.

Southward, A.J. (1958). Notes on the temperature tolerances of some intertidal animals in relation to environmental temperatures and geographical distribution. Journal of the Marine Biological Association of the United Kingdom, 37, 49-66.

Spaink, G. and Norton, P.E.P. (1967). The stratigraphical range of Macoma balthica (L.) (Bivalvia : Tellinacea) in the Pleistocene of the Netherlands and Eastern England. Mededelingen van de Geologische Stichting, Nieuwe Serie, 18, 39-44.

Speakman, J.N. and Krenkel, P.A. (1972). Quantification of the effects of rate of temperature change on aquatic biota. Water Research, 6, 1283-1290.

Stanley, S.M. (1970). Relation of shell form to life habits of the Bivalvia (Mollusca). Memoirs. Geological Society of America, 125, 1-296.

Stebbing, A.R.D. (1972). Preferential settlement of Bryozoan and Serpulid larvae on the younger parts of Laminaria fronds. Journal of the Marine Biological Association of the United Kingdom, 52, 765-772.

Steele, J.H., Munro, A.L.S. and Giese, G.S. (1970). Environmental factors controlling the epipsamnic flora on beach and sublittoral sands. Journal of the Marine Biological Association of the United Kingdom, 50, 907-918.

Stephen, A.C. (1928). Notes on the biology of Tellina tenuis da Costa. Journal of the Marine Biological Association of the United Kingdom, 15, 683-702.

Stephen, A.C. (1929). Studies on the Scottish marine fauna : the fauna of the sandy and muddy areas of the tidal zone. Transactions of the Royal Society of Edinburgh, 56, 291-306.

Stephen, A.C. (1930). Studies on the Scottish marine fauna : additional observations on the fauna of the sandy and muddy areas of the tidal zone. Transactions of the Royal Society of Edinburgh, 56, 521-535.

Stephen, A.C. (1931). Notes on the biology of certain lamellibranchs on the Scottish coast. Journal of the Marine Biological Association of the United Kingdom, 17, 277-300.

Stephen, A.C. (1932). Notes on the biology of some lamellibranchs in the Clyde area, Journal of the Marine Biological Association of the United Kingdom, 18, 51-68.

Stephen, A.C. (1933). Studies on the Scottish marine fauna : the natural faunistic divisions of the North Sea as shown by the quantitative distributions of the Molluscs. Transactions of the Royal Society of Edinburgh, 57, 601-616.

Stephen, A.C. (1938). Production of large broods in certain marine lamellibranchs with a possible relation to weather conditions. Journal of Animal Ecology, 7, 130-143.

Stora, G. (1974). Computation of lethal concentrations. Marine Pollution Bulletin, 5, 69-71.

Stromgren, T. (1976). Growth patterns of *Mytilus edulis* in relation to individual variation, light conditions, feeding and starvation. Sarsia, *60*, 25-40.

Taylor, A.C. (1976). Burrowing behaviour and anaerobiosis in the bivalve *Arctica islandica*. Journal of the Marine Biological Association of the United Kingdom, *56*, 95-109.

Te, G.A. and Mardinly, A. J. (1975). Scanning electron microscope study of radular teeth of *Physa gyrina hildrethiana* (Basommatophora : Physidae). Malacological Review, *8*, 117-118.

Tebble, N. (1966). British Bivalve Seashells. London : Trustees of the British Museum (Natural History).

Tenore, K.R., Horton, D.B. and Duke, T.W. (1968). Effects of bottom substrate on the brackish water bivalve *Rangia cuneata*. Chesapeake Science, *9*, 238-248.

Thomson, T.E. and Bebbington, A. (1973). Scanning electron microscope studies of gastropod radulae. Malacologia, *14*, 147-165.

Thomson, T.E. and Hinton, H.E. (1968). Steroscan electron microscope observations on opisthobranch radulae and shell structure. Bijdragen tot de Dierkunde, *38*, 91-96.

Thorson, G. (1946). Reproduction and larval development of Danish marine bottom invertebrates. Meddelelser fra Kommissionen for Danmarks Fiskeri og Havundersøgelser, *4*, 1-523.

Thorson, G. (1950). Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews, *25*, 1-45.

Thorson, G. (1957). Bottom communities (sublittoral or shallow shelf). In Treatise on Marine Ecology and Palaeoecology (Ecology) Ed. Hedgepeth, J.W. Memoirs, Geological Society of America, *67*, 461-534.

Thorson, G. (1966). Some factors influencing the recruitment and establishment of Marine Benthic communities. Netherlands Journal of Sea Research, 3, 267-293.

Trevallion, A. (1971). Studies on Tellina tenuis da Costa III. Aspects of general biology and energy flow. Journal of Experimental Marine Biology and Ecology, 7, 95-122.

Trevallion, A., Johnston, R., Finlayson, D.M. and Nicoll, N.T. (1973). Studies on the bivalve Tellina tenuis da Costa IV. Further experiments in enriched seawater. Journal of Experimental Marine Biology and Ecology, 11, 189-206.

Trueman, E.R. (1968a). A comparative account of the burrowing process of species of Mactra and of other bivalves. Proceedings of the Malacological Society of London, 38, 139-153.

Trueman, E.R. (1968b). The burrowing activities of bivalves. Symposia of the Zoological Society of London, 22, 167-186.

Trueman, E.R. (1971). The control of burrowing and the migratory behaviour of Donax denticulatus (Bivalvia : Tellinacea). Journal of Zoology, 165, 453-469.

Trueman, E.R., Brand, A.R. and Davis, P. (1966a). The dynamics of burrowing of some common littoral bivalves. Journal of Experimental Biology, 44, 469-492.

Trueman, E.R., Brand, A.R. and Davis, P. (1966b). The effect of substrate and shell shape on the burrowing of some common bivalves. Proceedings of the Malacological Society of London, 37, 93-109.

Tsujii, T, Sharp, D.G. and Wilbur, K.M. (1958). Studies on shell formation VII. The submicroscopic structure of the shell of the oyster Crassostrea virginica. Journal of Biophysical and Biochemical Cytology, 4, 275-279.

Turner, H.J. (1961). Problems involved in the development of clam farms. Oceanus, 7, 465-472.

Van Winkle, W., Feng, S.Y. and Haskin, H.H. (1976). Effect of temperature and salinity on extension of siphons by Mercenaria mercenaria. Journal of the Fisheries Research Board of Canada, 33, 1540-1546.

Vassallo, M.T. (1971). The ecology of Macoma inconspicua in Central San Francisco Bay. Part 11. Stratification of the Macoma community within the substrate, Veliger, 13, 279-284.

Vernberg, F.J. (1969). Acclimation of intertidal crabs. American Zoologist, 9, 333-341.

Verwey, J. (1966). The role of some external factors in the vertical migration of marine animals. Netherlands Journal of Sea Research, 3, 245-266.

Wada, K. (1957a). Electron microscope observations on the shell structure of pearl oyster (Pinctada martensii) II. Observations on the aragonite crystals on the surface of the nacreous layers. Bulletin of the National Pearl Research Laboratory, 2, 74-85.

Wada, K. (1957b). Electron microscope observations on the shell structure of pearl oyster (Pinctada martensii) III. On the laminary structure of the shell. Bulletin of the National Pearl Research Laboratory, 2, 86-93.

Wada, K. (1960). Crystal growth on the inner shell surface of Pinctada martensii. Journal of Electron Microscopy, 9, 21-23.

Wallis, R.L. (1975). Thermal tolerance of Mytilus edulis of Eastern Australia. Marine Biology, 30, 183-191.

Walne, P.R. (1972). The influence of current speed, body size and water temperature on the filtration rate of five species of bivalves. Journal of the Marine Biological Association of the United Kingdom, 52, 345-372.

Watabe, N. (1954). Electron microscope observations on the aragonite crystals on the surface of cultured pearls. Report of the Faculty of Fisheries, Prefectural University of Mie, 1, 449-454.

Watabe, N, Sharp, D.G. and Wilbur, K.M. (1958). Studies on shell formation VIII. Electron microscope observations of crystal growth of the nacreous layer of the oyster, Crassostrea virginica. Journal of Biophysical and Biochemical Cytology, 4, 281-286.

Watabe, N. and Wilbur, K.M. (1961). Studies on shell formation IX. An electron microscope study of crystal layer formation in the oyster. Journal of Biophysical and Biochemical Cytology, 9, 761-772.

Watkin, E.E. (1942). The macrofauna of the intertidal sand of Kames Bay, Millport, Buteshire. Transactions of the Royal Society of Edinburgh, 60, 543-561.

Waugh, D.L. and Garside, E.T. (1971). Upper lethal temperatures in relation to osmotic stress in the ribbed mussel, Modiolus demissus. Journal of the Fisheries Research Board of Canada, 28, 527-532.

Webb, J.E. (1958). The ecology of Lagos Lagoon V. Some physical properties of lagoon deposits. Philosophical Transactions of the Royal Society, Series B, 241, 393-419.

Webb, J.E. (1969). Biologically significant properties of submerged marine sands, Proceedings of the Royal Society, Series B, 174, 335-402.

Webb, J.E. and Hill, M.B. (1958). The ecology of Lagos Lagoon IV. On the reactions of Branchiostoma nigeriense Webb to its environment. Philosophical Transactions of the Royal Society, Series B, 241, 355-391.

Webb, J.E. and Theodor, J.L. (1972). Wave induced circulation in submerged sands. Journal of the Marine Biological Association of the United Kingdom, *52*, 903-914.

Wells, J.W. (1963). Coral growth and geochronometry. Nature, London, *197*, 948.

Werner, B. (1939). Uber die entwickling unt artunterschiedung von muschellarven des Nordseeplanktons, unter besonder berucksichtigung der schalenentwicklung. Zoologische Jahrbücher, *66*, 1-54.

West, R.G. (1968). Pleistocene geology and biology with special reference to the British Isles. London : Longmans.

West, R.G. and Norton, P.E.P. (1974). The Icenian Crag of southeast Suffolk. Philosophical Transactions of the Royal Society, *269*, 1-28.

Widdows, J. (1973). Effect of temperature and food on heart beat, ventilation rate and oxygen uptake of *Mytilus edulis*. Marine Biology, *20*, 269-276.

Wieser, W. (1956). Factors influencing the choice of substratum in *Cumella vulgaris* Hart (Crustacea : Cumacea). Limnology and Oceanography, *1*, 274-284.

Wieser, W. (1959). The effect of grain size on the distribution of small invertebrates inhabiting the beaches of Puget Sound. Limnology and Oceanography, *4*, 181-194.

Wilbur, K.M. (1964). Shell formation and regeneration. In Physiology of Mollusca Ed. Wilbur, K.M. and Yonge, C.M. New York, London : Academic Press, Volume 1, 243-277.

Williams, A.B. (1958). Substrates as a factor in shrimp distribution. Limnology and Oceanography, *3*, 283-290.

Williams, B.G. and Naylor, E. (1967). Spontaneously induced rhythm of tidal periodicity in laboratory-reared *Carcinus*. Journal of Experimental Biology, *47*, 229-234.

Wilson, D.P. (1937). The influence of the substratum on the metamorphosis of Notomastus larvae. Journal of the Marine Biological Association of the United Kingdom, 22, 227-243.

Wilson, D.P. (1948). The relation of the substratum to the metamorphosis of Ophelia larvae. Journal of the Marine Biological Association of the United Kingdom, 27, 723-760.

Wilson, D.P. (1950). Larval metamorphosis and the substratum. Annee Biologique, 27, 491-501.

Wilson, D.P. (1952). The influence of the nature of the substratum on the metamorphosis of the larvae of marine animals, especially the larvae of Ophelia bicornis Savigny. Annales de l'Institut Oceanographique, 27, 49-156.

Wilson, D.P. (1953a). The settlement of Ophelia bicornis Savigny larvae. The 1951 experiments. Journal of the Marine Biological Association of the United Kingdom, 31, 413-438.

Wilson, D.P. (1953b). The settlement of Ophelia bicornis Savigny larvae. The 1952 experiments. Journal of the Marine Biological Association of the United Kingdom, 32, 209-33.

Wilson, D.P. (1968). The settlement behaviour of the larvae of Sabellaria alveolata (L.). Journal of the Marine Biological Association of the United Kingdom, 48, 387-435.

Wilson, D.P. and Day, J.H. (1934). On the relation of the substratum to the metamorphosis of Scolecolepis fuliginosa (Claparede). Journal of the Marine Biological Association of the United Kingdom, 19, 655-662.

Wood, L. and Hargis, W.J. (1971). Transport of bivalve larvae in a tidal estuary. In Proceedings of the Fourth European Marine Biology Symposium Ed. Crisp, D.J., 29-45.

Wood, S.V. (1848-82). A monograph of the Crag Mollusca. Paleontographical Society (Monographs), 4 volumes.

Yonge, C.M. (1949). On the structure and adaptations of the Tellinacea, deposit feeding Eulamellibranchia. Philosophical Transactions of the Royal Society, Series B, 234, 29-76.

Ziegler, J.M. (1964). Some modern approaches to beach studies. Oceanography and Marine Biology. An Annual Review, 2, 77-95.