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Life History and Productivity of *Pectinaria koreni* Malmgren (Polychaeta)

A. Nicolaidou[a]
Marine Science Laboratories, Menai Bridge, Anglesey, Gwynedd, U.K.

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Growth, survivorship, reproduction and productivity of a *Pectinaria (Lagis) koreni* population was studied in Colwyn Bay, from July 1975 to August 1976. The cephalic disc diameter of the worms was chosen as an index of size, after the relations between linear and weight measurements of the body were established. Settlement of *Pectinaria* was estimated to have occured at the beginning of June, and the whole population had disappeared by April. Growth was initially fast but it ceased completely during the winter, probably due to low temperatures and disturbance by storms. Bundles of gametes first appeared in the coelomic fluid in November, but maturation was not completed before May. Mature ova, 60–65 μ in diameter, were released individually: sperms, a few microns in diameter, were released in bundles. The highest standing crop, 47·5 g m^{-2} was present in September and the total production of the cohort during its lifetime was 138·8 g m^{-2}. The ratio between total production and mean biomass was given by P/B: 7·3.

Introduction

Pectinaria (Lagis) koreni is a dominant species of the boreal offshore muddy sand community of Jones (1950) or the *Syndosmya (Abra) alba* community of Petersen (1914). As such it must be an important source of food for demersal fish and indeed Macer (1967) found *Pectinaria* to comprise an important constituent of the diet of the dab, *Limanda limanda* in Liverpool Bay. Both Eagle (1973; 1975) and Rees *et al.* (1976) described dramatic changes in *Pectinaria* dominated communities in Liverpool Bay, which they attributed to the sediment reworking activity of the deposit feeding *Pectinaria* and *Abra*. Their results, however, were based on surveys carried out over large areas and at long time intervals of, normally, six months. Thus it is hoped, that a closer examination of a single population of *Pectinaria* at shorter time intervals, as in the present study, may contribute to a better understanding of such population changes in the benthos.

Methods

Sampling of the *Pectinaria* dominated community off Colwyn Bay (Lat. 53°18′N, Long. 03°40′W, depth 5 m) was carried out at regular monthly intervals between July 1975 and

[a]Present address: Zoological Laboratory and Museum, University of Athens, Panepistimioupolis, Ilisia, Athens, Greece.

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August 1976. Twelve samples were collected each month with a vanVeen grab sampling 0·1 m^2 of the bottom. Sieving of the samples was done onboard the ship. The animals used in biometry were brought back alive, while those used in population studies were preserved in 4% formalin in sea water.

As the *Pectinaria* population in Colwyn Bay had disappeared by April, some additional observations on the reproductive cycle were made on animals collected from the nearby area of Beaumaris Bay. The settlement of *Pectinaria* there had occurred at the same time as in Colwyn Bay, but the population had survived longer probably due to reduced wave action in the area (Nicolaidou, 1977).

To study the growth rate of *Pectinaria* it was necessary to find the most suitable way of measuring the worms. The relations between the following measurements were first established:

(1) cephalic disc diameter, i.e. the diameter of the body along the bases of the paleae,
(2) body length,
(3) wet weight,
(4) dry weight.

Before measuring, the worms were starved for a week to empty their guts of ingested sand. As *Pectinaria koreni* are capable of reingesting their faeces they were placed in running sea water on a 2 mm mesh sieve through which the faeces were able to pass. The weight was obtained after removing the worms from their tubes and blotting them carefully with absorbent paper. The worms were then anaesthetized with 0·1% Nembutal in sea water for 2–5 minutes. The cephalic disc was measured under a microscope fitted with a graticule. Body length was measured with a ruler. Dry weight was obtained by drying in an oven at 80° C for 24 hours, after which time the weight remained constant.

Results

Biometry

Figure 1 shows the data obtained from the linear and weight measurements plotted against each other. The best fitting line was drawn using the least squares regression analysis. The regression equations are shown in Table 1. All the correlations were significant at the 0·001 level. The fact that in cases 1, 2, 4 and 5 the points fit a straight line indicates (see Crisp, 1971) that both cephalic disc diameter and body length provide a suitable index for calculating weight. However, body length may vary considerably depending upon the state of relaxation of the animal.

TABLE 1. Regression equations with correlation coefficients for the various body measurements of *Pectinaria koreni*. Equation: $y=ax^b$; level of significance $P=0{\cdot}001$

	Constant a	Exponent b	Correlation coefficient r	Degrees of freedom
1 Disc diameter/wet weight	1·7923	3·1032	0·8436	322
2 Disc diameter/dry weight	0·3554	2·6588	0·8854	122
3 Disc diameter/body length	6·1625	0·7753	0·7101	122
4 Body length/wet weight	0·2026	2·1561	0·8440	122
5 Body length/dry weight	0·0166	2·2922	0·8159	122
6 Wet weight/dry weight	0·1408	0·9606	0·8993	122

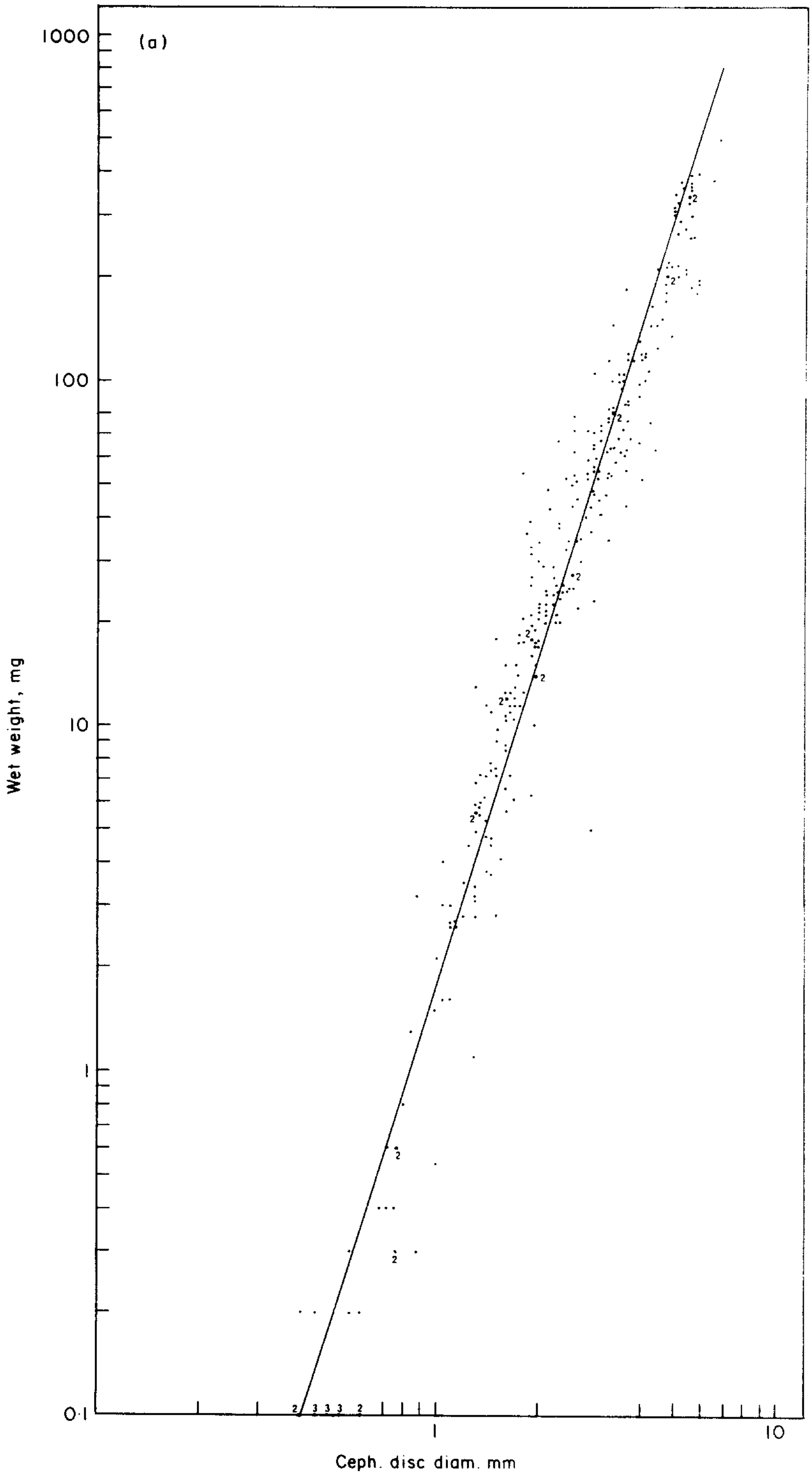
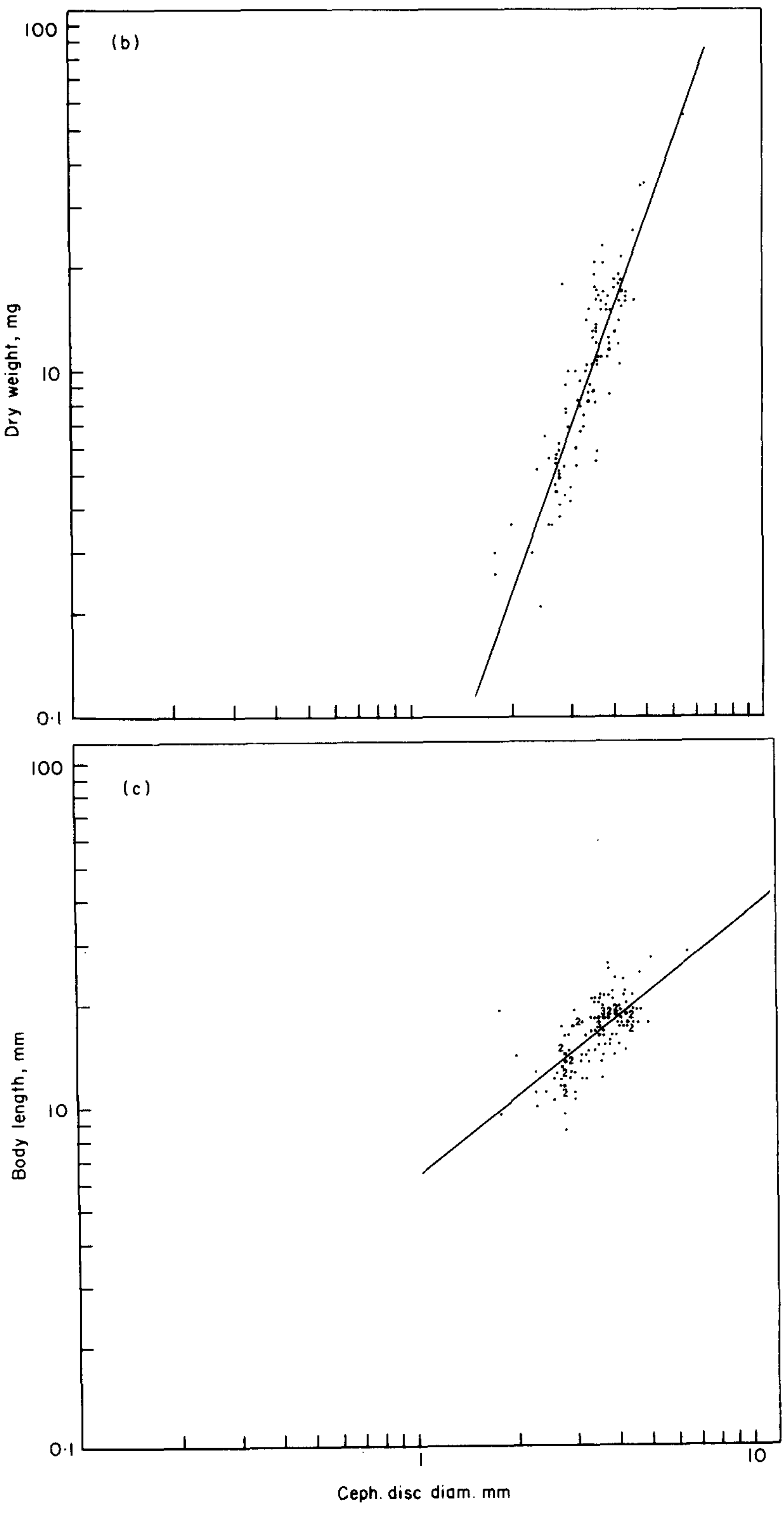
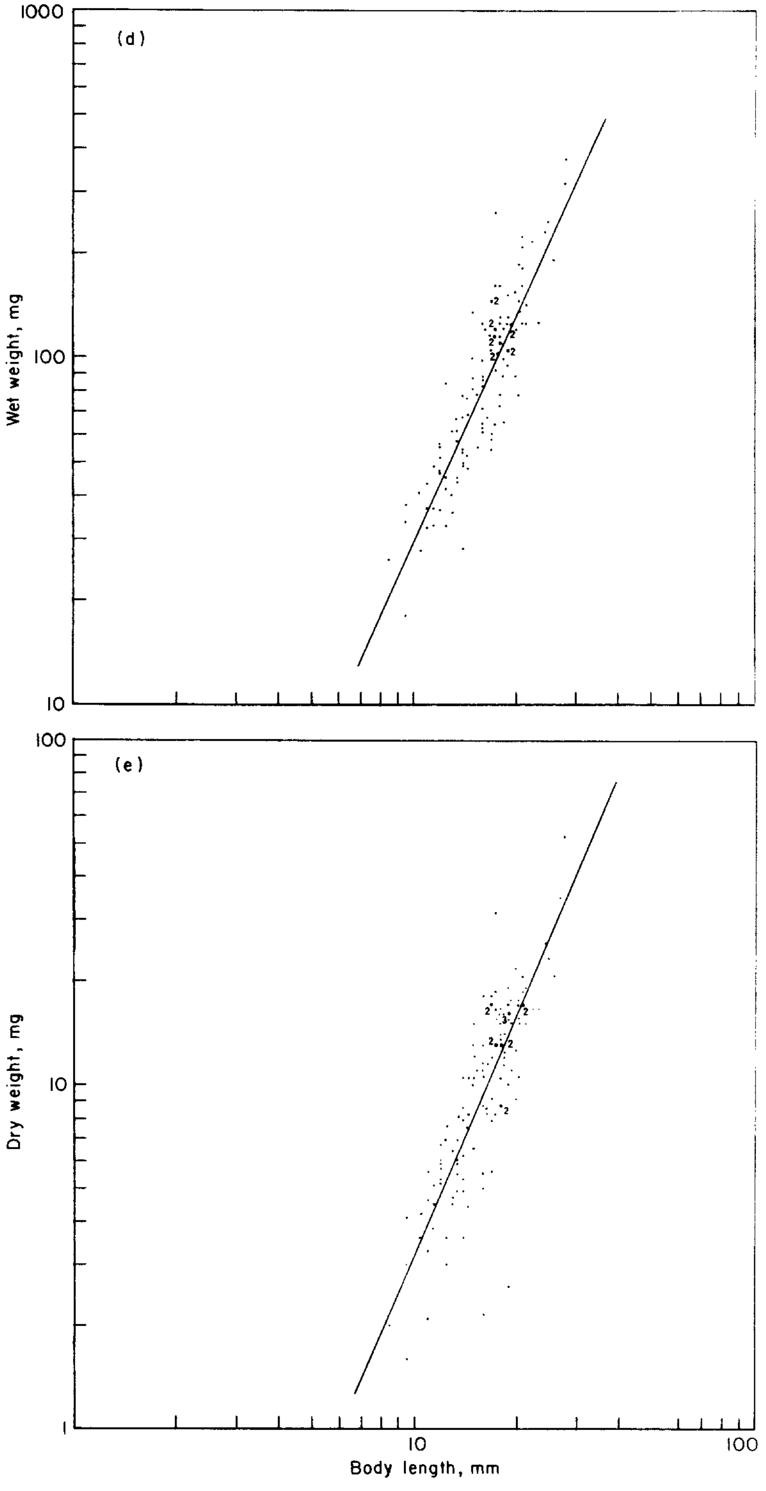
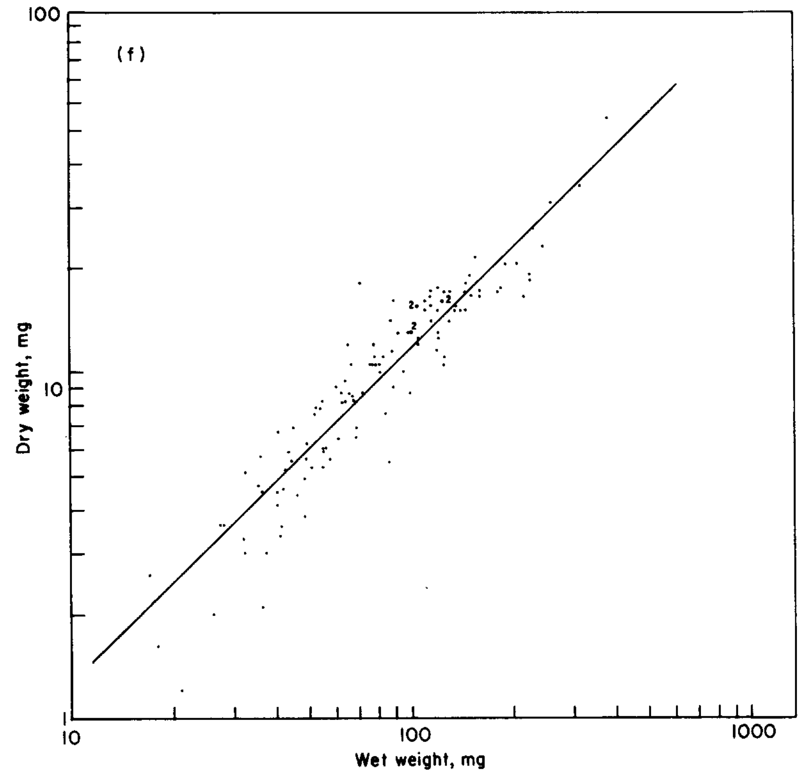


Figure 1. Regression lines between different body measurements of *Pectinaria koreni* (a) cephalic disc diameter and wet weight, (b) cephalic disc diameter and dry weight, (c) cephalic disc diameter and body length, (d) body length and wet weight, (e) body length and dry weight, and (f) wet weight and dry weight.


(b)
Dry weight, mg
100
10
0·1
(c)
Body length, mm
100
10
0·1
1
10
Ceph. disc diam. mm


1000
(d)
100
10
Wet weight, mg
100
(e)
10
1
Dry weight, mg
10
100
Body length, mm
2
3



Wet weight appears to be as reliable an estimate of production as dry weight. From the regression line shown in Figure 1 (f) dry weight was found to be 12% of the wet weight. However, this relationship may not be constant but may vary with, for instance, the state of maturity of the worms. Thorson (1957), for example, citing results of Petersen & Boysen-Jensen (1911) and Durchon & Lafon (1951) estimated the dry to wet weight ratio to be 16·0–18·5%. However, calculation of the original showed that it ranged between 3·3% and 17·2%.

Thus, cephalic disc diameter was adopted as the most reliable index of size because, firstly it does not vary a lot with the state of relaxation of the animal and secondly it does not change with preservation. In addition, cephalic discs are less likely to be damaged during the collection of the samples. The same dimension has also been used by Estcourt (1971; 1974) and Nichols (1975; 1977) in measuring growth rates of *Pectinaria.*

Growth and survivorship

Figure 2 shows the size frequency histograms of *Pectinaria* at monthly intervals. Size class intervals of cephalic disc diameter of 0·5 mm are used.

When the Colwyn Bay area was first sampled, at the end of July, the bulk of the animals had a cephalic disc diameter of between 1·5–3·0 mm, the peak occurring at 1·5–2·0 mm. By December they had grown so that the peak was at 5·0–5·5 mm. After this there were no further shifts of the peak until March. The appearance of single small individuals in the months of October to January may represent sporadic spawning of a small part of the population during the winter months as reported by Nichols (1977).

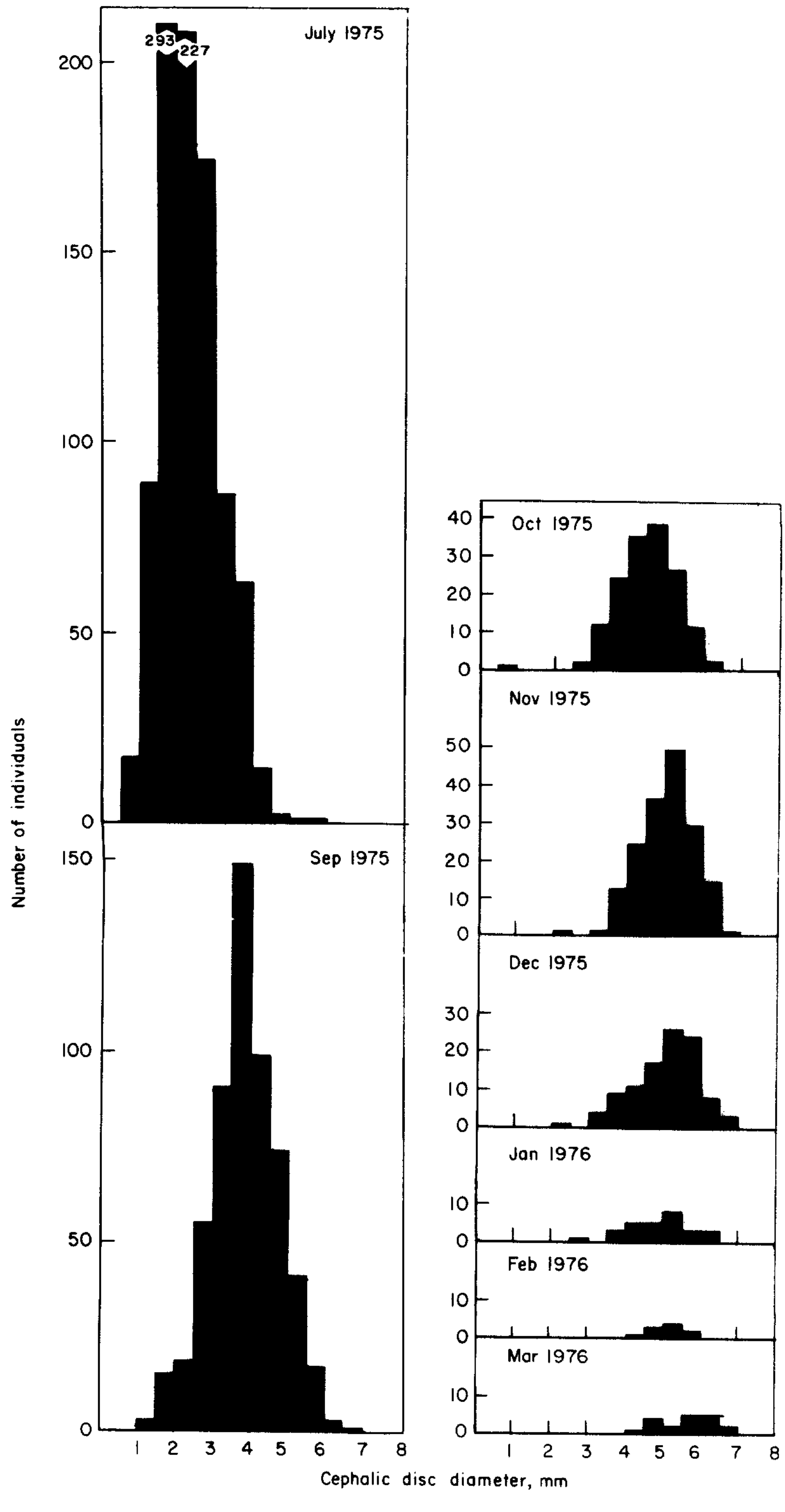


Figure 2. Size frequency histograms of *P. koreni* in Colwyn Bay.

The number of animals decreased rapidly, especially during the first four months, and the whole population had disappeared by April. Although sampling in the area was continued until August no more *Pectinaria* of the 1975 cohort were found.

Reproduction

Each month the coelomic fluid of several worms was examined for gametes, in order to follow the reproductive cycle from gametogenesis to spawning. The observations are summarized in the following.

November: Gametes first appear in coelomic fluid. Gametes in bundles only, diameter of bundles 30–35 μ. No distinction between males and females.

December–January: Same condition as above.

February: Gametes are numerous, visible externally after removal of worm from tube. Bundles of eggs 30–40 μ in diameter and free eggs 25–50 μ in diameter. Spermatozoa bundles 50–60 μ in diameter with flagella protruding.

March: Gametes fill coelom, eggs mostly isolated. When worms removed from tube, they vigorously shed the gametes. Gametes not fully matured: germinal vesicles of eggs remained intact and sperm did not leave bundles to become motile. Artificial fertilization failed.

April–May: Maturation completed. Disturbance of worms during sampling induced spawning. Orange reproductive material ejected by females, while male material was white. Diameter of mature free eggs 60–65 μ. Diameter of individual spermatozoa a few microns. Sperm released as bundles breaking free after 20 minutes in sea water. Artificial fertilization easily achieved.

Productivity

The standing crop of *Pectinaria*, its production and mortality were computed arithmetically by means of formulae given by Crisp (1971). The production was also calculated graphically by means of the method described by Allen (1951) for freshwater fish populations and applied by Nees & Dugdale (1959), Mann (1969) and Peer (1970) to calculate production of invertebrate populations. The production of *Pectinaria koreni* in Colwyn Bay was calculated for the period from June 1975, when the settlement was estimated to have occurred, until April 1976 when all the animals of the original recruitment had gone. Virtually all the animals in the samples belonged to the same year class. The few animals which appeared to belong to a different year class or cohort were excluded from the calculations.

As the settlement of *Pectinaria* in Colwyn Bay had already taken place before sampling started, it was necessary to back-calculate to determine the time of settlement and the mean weight at that time. Use was made of the method described by Peer (1970) which is based upon the relation existing between mean weight and age of the animals.

A series of arbitrary times were tested to find the one that correlated best with the weight at the known sampling intervals. Only the data for the first four months were used as the animals showed a fairly constant growth at this stage. The curve fitted to the data was given by

$$\bar{w} = at^b,$$

where $\bar{w}$ is the mean weight of an individual, t is the time from settlement in days, a is the weight at settlement and b is a constant. The highest correlation coefficients (r: 1·0000) were obtained for settlement times of 54 to 62 days prior to first sampling. The equation

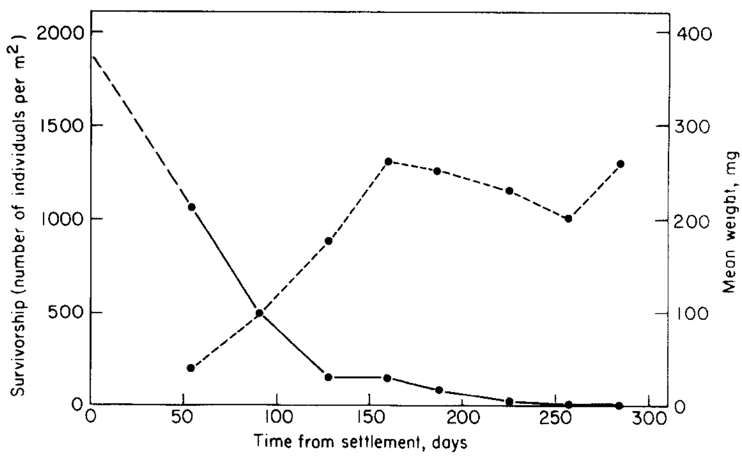


Figure 3. Growth (– – –) and survivorship (——) curves for *P. koreni* in Colwyn Bay.

$$\bar{w} = 0{\cdot}0420t^{1{\cdot}7184},$$

corresponding to a time interval of 54 days, was finally chosen as giving a more realistic value of '*a*'. Longer periods would give weights at settlement that are much too small. From the relation between wet weight and cephalic disc diameter in Figure 1(a) this weight is found to correspond to a cephalic disc diameter of 0·3 mm. This agrees with the results of Vovelle (1973) who found the 'superior diameter' of a worm at a young post-larval stage to be 300 μ. The time of settlement having been established, the corresponding number of animals was found by projecting the line between the first two points of the survivorship curve in Figure 3 back to time zero. This gave a density at settlement of 1920 individuals per m^2.

The total life of the population was between 285 and 330 days. Figure 3 shows that the mean weight increased rapidly during the first five months and then decreased in the winter, perhaps reflecting lower consumption of food. A possible explanation is that the feeding activity of the worms decreases or stops completely because of the low winter temperatures. Gordon (1966) found experimentally that the amount of sediment reworked by *Pectinaria gouldii* decreased with decreasing temperature between 19° and 13° C. Experiments on the rate of sediment reworking by *P koreni* at different temperatures (Nicolaidou, 1977) showed that the rate is significantly lower at 7° C than at 10° C and 15° C. Some worms had completely ceased their reworking activity at 7° C. In the present study *Pectinaria* in nature were subject to temperatures of 5·1° C to 17° C. Another explanation for the weight loss may be the disturbance of animals during winter storms. Either their feeding was inhibited or they were forced to utilize energy reserves in re-burrowing and re-establishing themselves.

The arithmetic calculations of production in Table 2 show that production was high originally, resulting in a rapid increase of biomass. The highest biomass or standing crop (47·5 g m^{-2}) was present in September, 90 days after settlement. Most of the total production was achieved by November. After that, the monthly production increments became negative, which means that during the winter the worms used energy reserves produced earlier in the year. The total production of the cohort during its lifetime was calculated to be 138·8 g m^{-2}, which is in good agreement with the figure of 136 g m^{-2} obtained by measuring the area under the Allen curve shown in Figure 4. This amount of organic matter

TABLE 2. Arithmetic calculations of standing crop, production and mortality for the 1975 settlement of *Pectinaria koreni*

Date	Time from recruitment in days	Mean individual weight $\bar{w}$ (mg)	Population density N (no. m^{-2})	Standing crop $N\bar{w}$ g m^{-2}	Average value N over period Δt $\frac{1}{2}(N_t+N_{t+\Delta t})$ (no.m^{-2})	Average mean weight over period $\frac{1}{2}(\bar{w}_t+\bar{w}_{t+\Delta t})$ (mg)	Decrease in population $-\Delta N$ (no. m^{-2})	Increase in weight $\Delta\bar{w}$ (mg)	Production increment $\Delta P=N\Delta\bar{w}$ (g m^{-2})	Mortality increment $\Delta M=\bar{w}\Delta N$ (g m^{-2})	$\sum_0^t \Delta P$ (g m^{-2})	$\sum_0^t \Delta M$ (g m^{-2})
Jun 5	1	0·04	1920·0	0·08	—	—	—	—	—	—	—	—
Jul 28	54	40·00	1062·0	42·48	1491·0	20·02	858·0	39·96	59·58	17·18	59·58	17·18
Sep 2	90	95·00	500·0	47·50	781·0	67·50	562·0	55·00	42·96	37·94	102·54	55·12
Oct 10	128	174·30	151·0	26·32	325·5	134·70	349·0	79·30	25·81	47·01	128·35	102·13
Nov 11	160	259·40	151·7	39·35	151·4	216·90	−0·7	85·10	12·88	−0·15	141·23	101·98
Dec 8	187	250·70	83·3	20·88	117·5	255·10	68·4	−8·70	−1·02	17·45	140·21	119·43
Jan 15	225	225·40	21·7	4·89	52·5	238·10	61·6	−25·30	−1·33	14·67	138·88	134·10
Feb 16	257	200·30	6·1	1·22	13·9	212·90	15·6	−25·10	0·35	3·32	139·23	137·42
Mar 15	285	257·90	5·8	1·50	6·0	229·10	0·3	57·6	0·35	0·07	139·58	137·49
Apr 29	330	—	0	0	2·9	129·0	5·8	−257·9	−0·75	0·75	138·82	138·24

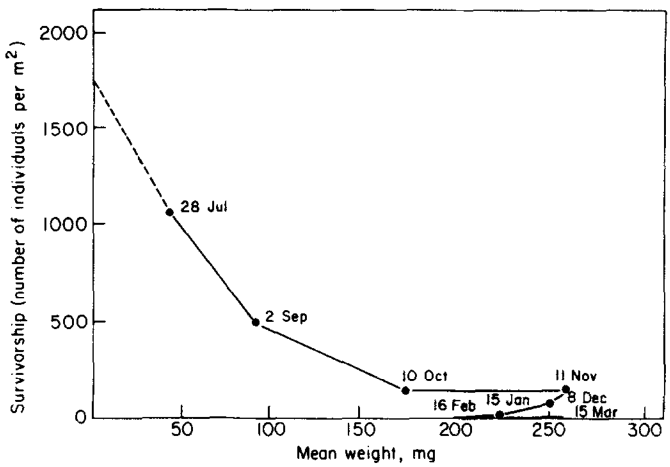


Figure 4. Allen curve for *P. koreni* in Colwyn Bay.

must have been transferred to the predators and to the environment in general as the cohort died. The mean biomass of the cohort for its whole lifetime was 19 g m^{-2}. The ratio between total production P and mean biomass $\bar{B}$, was estimated as $P/\bar{B}$: 7·3.

Discussion

The life cycle of *Pectinaria* in Colwyn Bay falls generally in the pattern described in the literature. There is a general agreement about the time of spawning of *Pectinaria koreni* between various authors as summarized in Table 3.

Estcourt (1971) working off the Northumberland coast found specimens of *P. koreni* with eggs in the coelom between February and May. Gametes were not seen earlier probably because the worms were only examined externally. In the present study examination of the coelomic fluid proved that immature gametes were present from November but only became externally visible in February.

TABLE 3. Time of spawning and early development of *P. koreni*, according to various authors

Author	Place	Time	Stage
Nielsen (1925) (in Thorson 1946)	Kristineberg	May, June, July	Spawning
Wilson (1936)	Plymouth	April	Mature gametes
Watson (1928)	Port Erin	July	Swimming larvae
Vovelle (1973)	Helsingor	July	Early post larvae and medium sized adults
Nichols (1977)	Kiel Bay	Early summer	First recruitment
		Late summer	Additional recruitment
		Throughout most of year	Sporadic recruitment
Estcourt (1971)	Off Northumberland coast	February-May	Gametes in Coelom
Nicolaidou (present study)	Colwyn Bay	June	Spawning

The longevity of *P. koreni* appears to be uncertain. Nielsen (1925, in Thorson, 1946) considers it an annual species and Estcourt (1971) found populations with only a one year life span. In the present case some animals lived in the laboratory for two and a half years. It may be possible that *Pectinaria* has the potential of living longer than one year but in nature longevity is restricted by environmental conditions, including predation. Storms play an important role since animals were still present in May in the slightly more sheltered Beaumaris Bay (Rees *et al.*, 1977). It is equally possible, however, that the laboratory population survived because it never reached maturity and spawning.

Waters, (1969), found that when the ratio between annual production and mean annual biomass ($P/\bar{B}$) of benthic invertebrates is calculated over a life cycle, it shows a fair degree of agreement between various authors. He produced a whole series of Allen curves for theoretical populations of different growth types. For a population with a concave Allen curve (produced by high mortality in the early stages), with an approximately logarithmic growth and with no final survivors, which closely resembles the *P. koreni* population sampled in Colwyn Bay, the theoretical $P/\bar{B}$ was 7·8. This is very close to the estimated ratio for Colwyn Bay *P. koreni* which was 7·3. This value also concurs with the values for short lived species of molluscs originally calculated by Zaika (1972) and later converted by Mann (1976) to give $P/\bar{B}$ ratios between 5 and 10. If the ratio $P/\bar{B}$ is indeed constant, it may be possible in the future, as Mann (1976) hoped, to estimate the production when the biomass and a few environmental factors are known.

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