

## Growth and recruitment of the deep-sea urchin *Echinus affinis*

J. D. Gage<sup>1</sup> and P. A. Tyler<sup>2</sup>

<sup>1</sup> Dunstaffnage Marine Research Laboratory, Scottish Marine Biological Association; P.O. Box 3, Oban PA34 4AD, Argyll, Scotland

<sup>2</sup> Department of Oceanography, University College; Singleton Park, Swansea SA2 8PP, South Wales, UK

### Abstract

Large samples of the sea urchin *Echinus affinis* Mortensen were obtained from a time-series of Agassiz trawlings from a 2 200 m-deep permanent station (Station "M"), and at neighbouring positions, in the Rockall Trough (North-east Atlantic Ocean) over a period of 7 yr (1978 to 1985). Counts of growth zones visible in the skeletal elements of the test were used to age individuals. Various growth functions were fitted to counts from a full range of the sizes available. Functions giving a sigmoidal growth curve fit the early phase of growth better than the von Bertalanffy model, although the latter provided better fit amongst larger sizes. The fit of a robust and flexible model recently developed by Preece and Baines to describe the human growth curve overcame this limitation. Skeletal banding is thought to result from seasonally varying growth as a result of annually pulsed fallout of phyto-detrital food to the deep-sea floor. Early stages were found in only a few of a time series of samples obtained with a fine-meshed epibenthic sledge, suggesting that recruitment to the population from its annual breeding may only occasionally be successful. Postlarval growth was estimated from samples taken soon after presumed settlement and later in the year. The fitted growth curve showed good agreement to that obtained from annual banding, and corroborates an initially exponentially increasing growth rate. Postlarval survivorship was estimated, by means of computer simulation, from a sample that included postlarvae along with a range in juvenile sizes, to be about 10% amongst postlarvae after settlement and thereafter about 90% yr<sup>-1</sup>. Adults are inferred to be up to about 28 yr old. A markedly uneven representation of ages in a large subsample of aged adults of even frequency in size is interpreted by means of simulations as probably reflecting multi-year cycles in recruitment success. The possible causes of a varying size structure amongst large samples of adults, which showed some spatial segregation in relation to the track of the trawl on the bottom at Station "M", are discussed.

### Introduction

Although our knowledge of the composition and distribution of the fauna of the deep sea has greatly expanded during the past two decades, data on the growth rates and survivorship of deep-sea species are practically non-existent.

The present paper investigates the growth and other population parameters of the sea urchin *Echinus affinis* Mortensen. This species is a conspicuous element of the megabenthic fauna of the deep North Atlantic Ocean (Rowe and Menzies, 1969; Grassle *et al.*, 1975; Haedrich *et al.*, 1975, 1980). Considerable numbers of *E. affinis* have been trawled from the Rockall Trough (North-east Atlantic) in the course of regular monitoring of a station (Station "M") at 2 200 m depth (Gage and Tyler, 1982), and from opportunistic trawling at other positions in the same general area (Gage *et al.*, in press). Tyler and Gage (1984) have already reported on the gametogenic cycle of *E. affinis* from examination of a time series of samples from Station "M". The results show that this regular sea urchin resembles its shallow-water relatives in having a clearly defined annual periodicity in reproduction with probably planktotrophic early development.

Although unexpected in the deep sea, recent data from the North-west and North-east Atlantic indicate that annual breeding occurs in various species of echinoderms and other taxa (Schoener, 1968; Lightfoot *et al.*, 1979; Tyler and Gage, 1980; Gage and Tyler, 1981; Tyler *et al.*, 1982; Van-Praet and Duchateau, 1984). In studies of shallow-water fauna, it is often possible to utilise such pulsed recruitment in tracking the growth of cohorts in a time series of size-frequency distributions. The occurrence of postlarval stages in the hauls obtained with a fine-meshed deep-sea epibenthic sledge has prompted this approach to be applied to measurements of body size of a time series of large samples of the population of *Echinus affinis* at Station "M". Furthermore, the possibility of an independent aging of individuals was investigated by fitting growth functions to counts of growth zones present in the skeletal

plates in large samples of the urchin. These have long been observed in the skeletal elements of sea urchins (M'Clelland, 1840; Agassiz, 1904; Deutler, 1926), and their ring-like pattern in the test plates has been utilised in several studies of shallow-water species that have assumed they represent annual banding similar to that found in the trunk of a tree (Moore, 1935; Zoeke, 1952; Durham, 1955; Gamble, 1967; Jensen, 1969 a, b; Raup, 1969; Pearse *et al.*, 1970; Birkeland and Chia, 1971; Miller and Mann, 1973; Sumich and McCauley, 1973; Kawamura, 1974; Crapp and Willis, 1975; Allain, 1978; Sime, 1982; Duineveld and Jenness, 1984; Nichols *et al.*, 1985).

The interpretation and significance of skeletal growth banding in the deep sea is discussed in the context of evidence for pulsed input of organic detritus from the surface. We finally attempt to relate hypotheses of the recruitment, growth and mortality of the population to the variable size structure observed.

### Materials and methods

The location of the main area of sampling within the Rockall Trough is shown in Fig. 1. Sampling was undertaken on Station "M" using both a 3-m-wide Agassiz trawl with square meshes 10 mm wide, and a Woods Hole-pattern, epibenthic sledge (Hessler and Sanders, 1967) (AT and ES stations, respectively, listed in Table 1). The mesh size of the epibenthic sledge was 1 mm in the main bag and 0.5 mm in the cod-end extension. The probable tracks of the trawls on the bottom at Station "M", where most of the samples were obtained, are shown in Fig. 2. Other samples

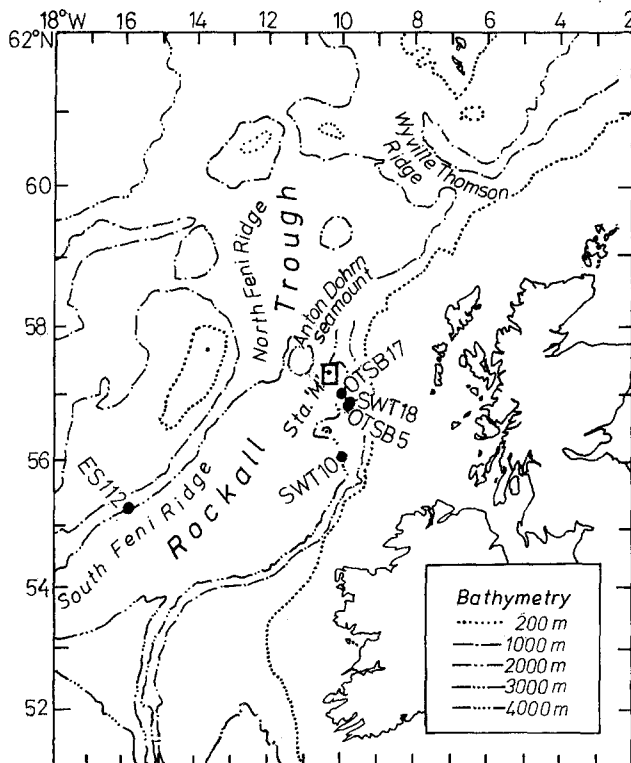


Fig. 1. Chart of Rockall Trough showing Station "M" and other sampling areas. Details of hauls (●) are given in Table 1

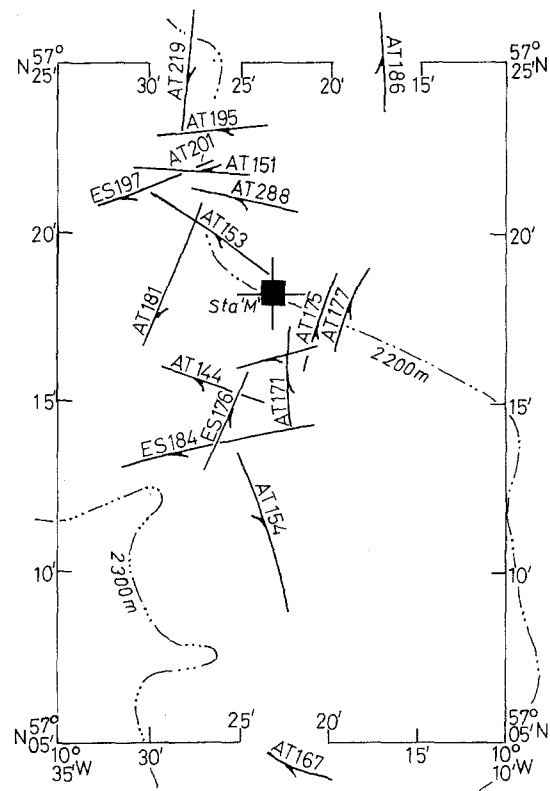


Fig. 2. Chart of sub-area delineated by "box" around Station "M" in Fig. 1, showing track and direction of each trawl haul on the bottom

Table 1. Details of benthic hauls from which *Echinus affinis* were examined. AT: Agassiz trawl; ES: epibenthic sledge; SWT: single-warp trawl; OTSB: semi-balloon otter trawl

Sample	Date	Position <sup>a</sup>	Depth <sup>a</sup> (m)
ES4	5 June 1973	56°52'N; 10°01'W	1 993
ES15	22 Sep. 1973	56°44'N; 09°28'W	1 632
ES112	25 Oct. 1976	55°12'N; 15°50'W	1 900
SWT10	5 Aug. 1977	56°02'N; 10°00'W	2 015
SWT18	22 Oct. 1977	56°48'N; 09°41'W	1 815
AT144	19 April 1978	57°13'N; 10°20'W	2 240
AT151	6 June 1978	57°21'N; 10°22'W	2 175
AT153	15 Jan. 1979	57°20'N; 10°27'W	2 200
AT154	21 May 1979	57°08'N; 10°22'W	2 264
AT167	13 Aug. 1979	57°04'N; 10°23'W	2 300
AT171	3 March 1980	57°16'N; 10°17'W	2 225
AT175	28 May 1980	57°19'N; 10°16'W	2 210
ES176	28 May 1980	57°15'N; 10°26'W	2 245
AT177	29 May 1980	57°18'N; 10°16'W	2 200
AT181	16 Sep. 1980	57°19'N; 10°28'W	2 220
ES184	17 Sep. 1980	57°14'N; 10°24'W	2 260
AT186	12 April 1981	57°22'N; 10°19'W	2 170
AT195	18 Aug. 1981	57°23'N; 10°27'W	2 190
ES197	19 Aug. 1981	57°21'N; 10°29'W	2 200
AT201	9 May 1982	57°22'N; 10°30'W	2 180
AT219	3 Aug. 1982	57°25'N; 10°28'W	1 991
OTSB5 (13/83)	21 Sep. 1983	56°41'N; 09°47'W	1 805
AT288	4 April 1985	57°21'N; 10°25'W	2 215
OTSB17 (3/85)	21 April 1985	56°53'N; 09°57'W	1 975

<sup>a</sup> At midpoint of haul

were taken on the nearby continental slope using single-warp fish trawls (SWT and OTSB stations listed in Table 1) with stretched cod-end mesh dimensions of roughly 16 and 12 mm, respectively, and on the Feni Ridge using the epibenthic sledge. Positions of these trawlings are shown in Fig. 1, while positional coordinates and depths, along with all other trawlings considered, are given in Table 1.

Measurements of the test height and diameter were made on many hundreds of specimens of *Echinus affinis*. For postlarvae, measurements were made using a microscope with camera lucida focussed onto a graphics tablet coupled to a microcomputer. The height and diameter of the test of larger *E. affinis* initially were measured using vernier calipers. Later, a caliper system employing a linear potentiometer coupled to the microcomputer via an A/D interface was employed. Both computer-linked methods enabled measurements to be stored and quickly plotted as frequency histograms using either the graphics display on the computer or an x-y plotter.

Several techniques were tried in order to visualise the growth zones present in the skeletal elements of *Echinus affinis*. The charring technique of Jensen (1969 b) as modified by Duineveld and Jenness (1984) was found to be most reliable. In order to avoid error in estimating age from the number of growth zones as a result of the addition of new plates during the growth of the urchin (Fig. 9 A), the apical plates (Fig. 9 B) were employed in aging individuals. The plates of the apical system are formed at the stage of metamorphosis from the echinopluteus and, as such, would be expected to contain a complete record of growth through the lifetime of the urchin.

After measuring, the test was halved by cutting with scissors along the ambitus. The gonads were removed from the dorsal half and weighed after blotting. The remaining tissue was then removed using fine forceps and brush or by soaking in a 50% solution of domestic bleach (sodium hypochlorite). The preparation was further reduced in size to include only the uppermost parts of the columns of ambulacral and interambulacral plates along with those of the apical system. The plates were heated evenly in a bed of 1 mm glass beads on an electric hot plate until they turned from white to a brownish colour. They were then mounted on glass slides using an epoxy resin. The surface of each of the four non-madreporic genital plates was carefully ground smooth, removing the spines and spine bosses. The surface of the plate was carefully further ground with a very fine grade of waterproof silicon-carbide abrasive paper under a binocular microscope using reflected light. By frequently monitoring the progressive appearance of the earlier, innermost concentric growth zones revealed by flooding the preparation with xylene, it was possible to see all the growth zones present within the plate (Fig. 9 C, D). Often it was found that the growth zones appeared clearer on some plates than on others. When growth zones were clear on two or more of the genital plates, an average of the number of growth zones was taken for that specimen. However, quite often the earlier growth zones might be more clearly expressed on one plate than on another, and it

often was possible to relate the count of earlier zones, lying near the centre of the plate, to those laid down later, lying nearer the periphery, that were more easily seen on another plate. Specimens less than about 10 mm in diameter could be examined whole and it was found that the growth zones present could be seen clearly without the need to grind down the surface of the plates.

## Results

### Population structure of urchins from Station "M" and nearby positions

The relationship of test height to test diameter from the measurements on 205 individuals of *Echinus affinis* from station "M" is shown in Fig. 3. The regression agrees well with the result of a similar regression ( $r^2 = 0.97$ ,  $y = -0.72 + 0.56x$ ) of measurements given by Mortensen (1943), of 17 specimens of *E. affinis* from various localities in the North Atlantic.

The plotted relationship between gonad weight and the size of the urchin is shown in Fig. 4. Gonads were present (but insignificant in size) from a test diameter of about 4 mm, but were not well-developed until a size of about 20 mm. Hence, it is likely that full maturity is not attained until the urchins reach this size, although the histology of the gonads was not investigated in relation to test size.

Frequency distributions of the measurements of test diameter of all Agassiz-trawl samples from Station "M" are presented in Fig. 5. The absence of frequencies of sizes (< 20 mm) would seem to result from loss through the stretched meshes of the trawl (max. dimension 20 mm). The histograms show clearly that the size structure in the samples is variable from haul to haul, some showing a uni-

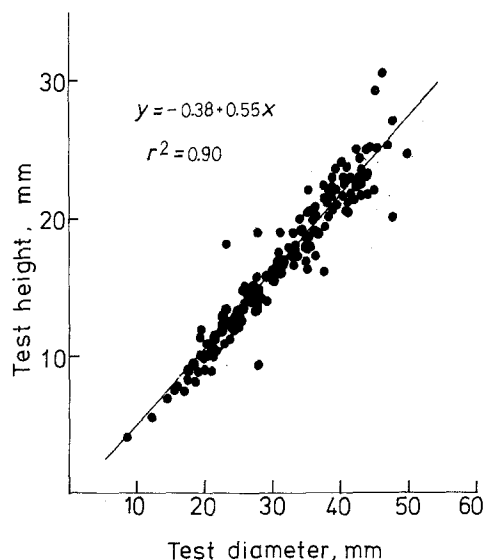


Fig. 3. *Echinus affinis*. Relationship of height to diameter of the test, with fitted regression

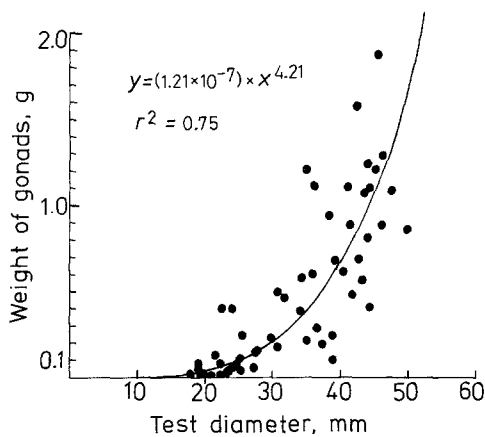


Fig. 4. *Echinus affinis*. Relationship of wet weight of gonads to test diameter, with fitted power curve calculated from linear regression of log-transformed data

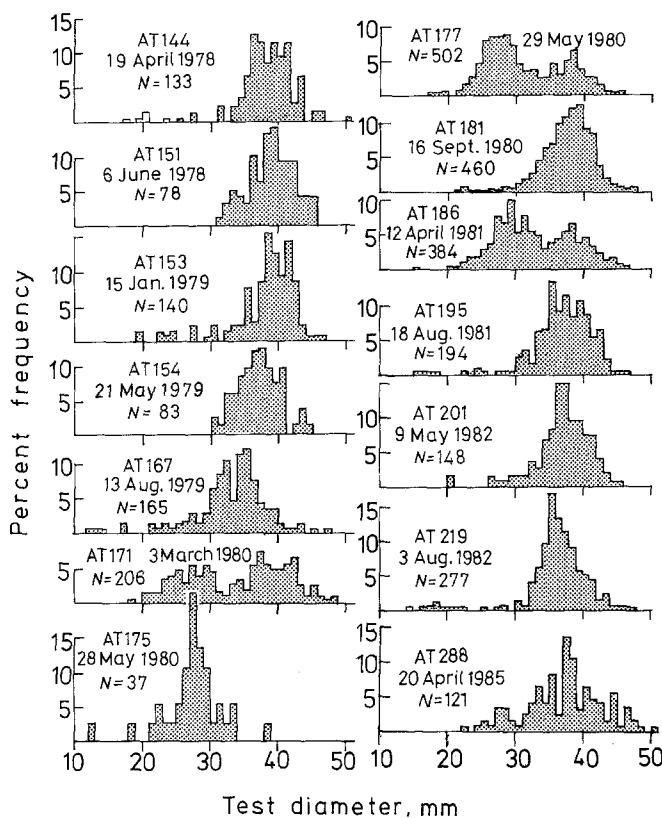


Fig. 5. *Echinus affinis*. Frequency histograms of test diameter from all Agassiz trawl samples examined from Station "M"

modal distribution while others are bimodal. The position of the modes shows some consistency from sample to sample, the position along the size axis of the right-hand mode falling between 30 and 40 mm. Reference to Fig. 2 suggests some relation of the variations in adult size structure to the position of the haul within the sampling area, which covered about 200 square (nautical) miles (687 km<sup>2</sup>). In general, the closer the track of the trawl the more similar the pattern in frequency distribution tended to be. The

large sample-cluster, lying in depths slightly exceeding 2 200 m, to the north-west and west of the position of Station "M", shows a unimodal distribution peaking between 35 and 40 mm, while those hauls (AT171, AT177 and AT186) in depths slightly less than 2 200 m to the south-east show a bimodal distribution. The bimodal distribution from Haul AT186 was taken from a more isolated position to the north-east. However, this haul, like the other bimodal distributions, was taken from a depth slightly less than 2 200 m. Haul AT167 was taken both farthest to the south and from the other hauls, and shows a single mode peaking at a slightly smaller size class than any other unimodal distribution, except for the small sample from Haul AT175. The track of the latter haul was close to that of AT177, which yielded a larger, bimodal distribution. Moreover, Sample AT175 was recovered from a badly torn trawl, so that some size-selective bias may well have operated during the haul.

Size frequencies of *Echinus affinis* from trawlings taken on the lower part of the Hebridean Slope are shown in Fig. 6. In general, these resemble the size structure of the Agassiz trawlings from Station "M". The two OTSB samples were the only ones with significant numbers of urchins < 25 mm in test diameter. However, it is unknown to what extent fishing bias may have operated to produce both the size structure observed and the greater similarity apparent between samples obtained with the same gear.

#### Description of growth zones in skeletal plates

Each skeletal plate of the test could be seen under the light microscope to be composed of a mesh-like stereom, organised in a pattern similar to that in other echinoids (Pearse and Pearse, 1975; Smith, 1980). Removal, by grinding, of the surface layer carrying the spine bosses and spines, exposes a middle layer of galleried stereom. A series of low ridges on the inner surface of the bleached plate running parallel to the edge could be seen to correspond, after charring, to concentric growth zones in the middle layer. The banding is most evident in reflected light and consists of translucent and opaque areas. The translucent

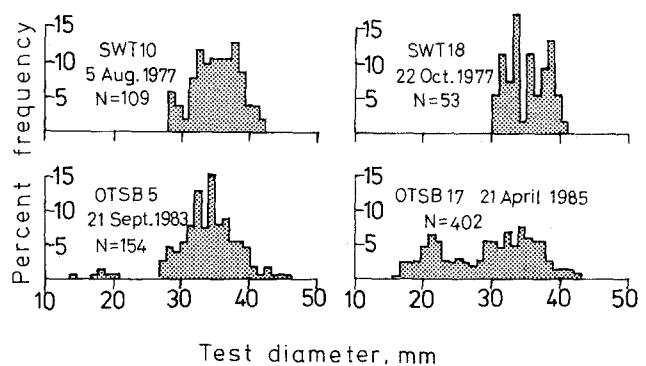
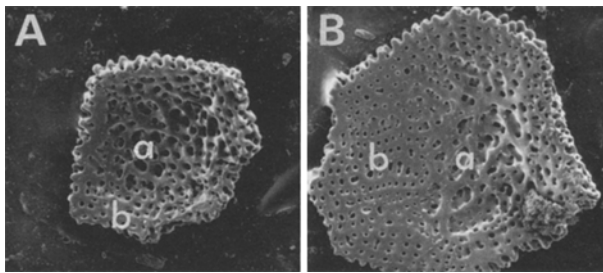
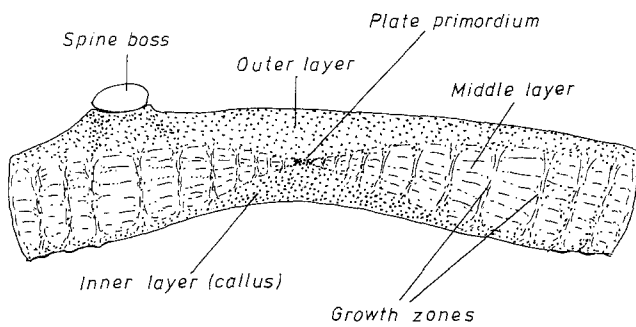


Fig. 6. *Echinus affinis*. Size-frequencies of samples taken on the continental slope adjacent to Station "M"



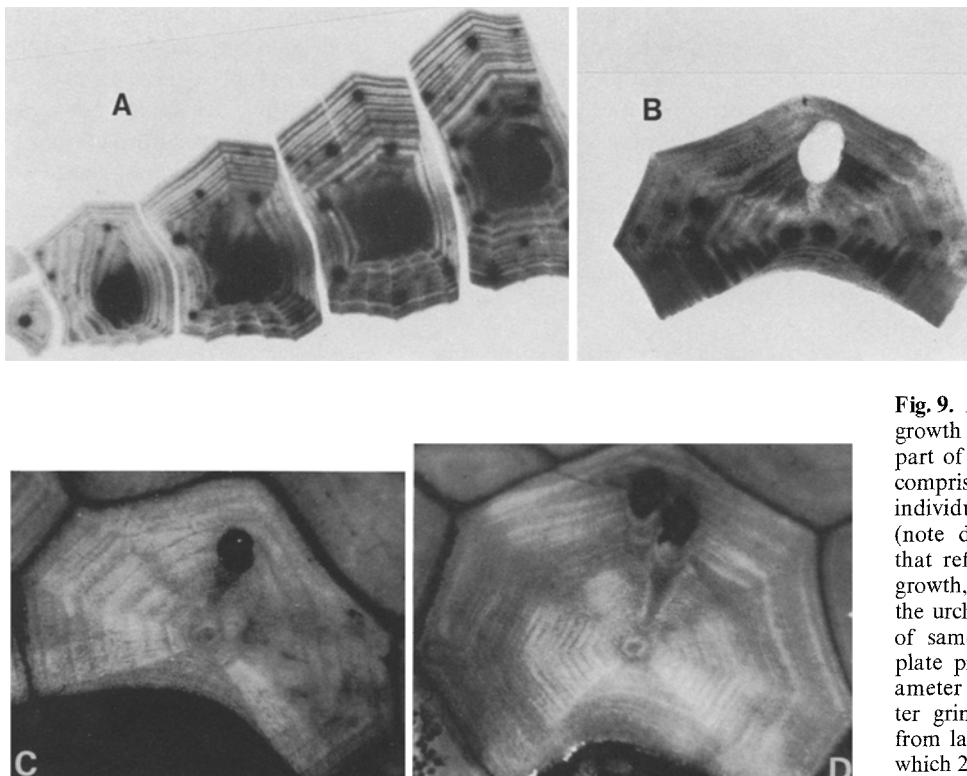
**Fig. 7.** *Echinus affinis*. Scanning electron micrographs of inner side of test plates of postlarvae from Sample ES112, that are shown entire in Fig. 10. (A) Early postlarva showing labyrinthine stereom (a) of plate primordium surrounded by narrow area of galleried stereom of postlarval plate growth (b); (B) later postlarva showing wider zone of postlarval growth (lettering as for A)



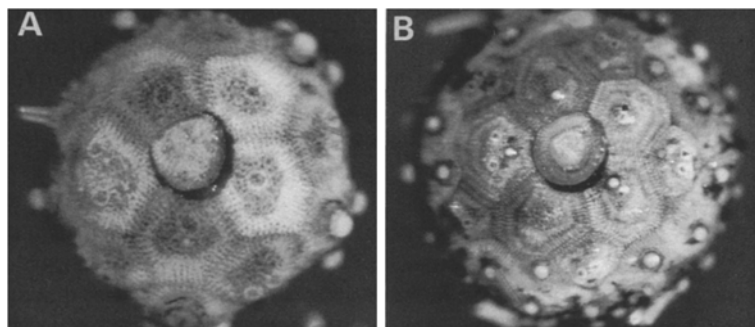
**Fig. 8.** *Echinus affinis*. Diagram of section through centre of genital plate of an adult

areas, since they reflect less light, appeared dark while the opaque areas, since they reflect most light, appeared white. As in other echinoids these zones correspond to differences in stereom density (Pearse and Pearse, 1975; Smith, 1980). The calcite trabeculae composing the stereom of the, usually narrow, dark bands are larger and thicker, with less space between them, than those of the translucent areas. The latter possess a more open stereom with larger intertrabecular spaces. These possess the radially orientated pattern typical of galleried stereom (Smith, 1980). The central part of each genital plate is distinctive in being composed of rather coarse-meshed, labyrinthine stereom where the trabeculae are randomly intertwining (Fig. 7). This represents the plate primordium, being laid down at metamorphosis from the echinopluteus (Gordon, 1926). The structure visible in the genital plates of adults is shown diagrammatically in Fig. 8 and in photomicrographs of preparations of the apical plates in Fig. 9.

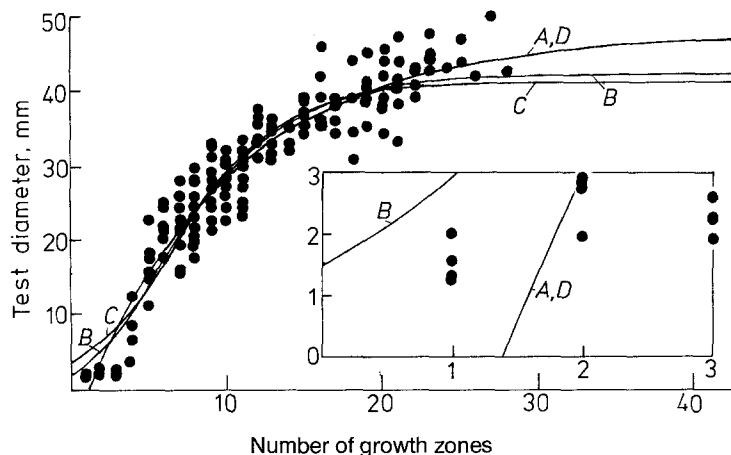
*Echinus affinis* is unusual amongst echinoids in appearing to lack test pigmentation, which in the plates of other echinoids may occur as clearly pigmented growth-banding (Deutler, 1926; Moore, 1935; Jensen, 1969 a, b; Sime, 1982; Nichols *et al.*, 1985). We assume that the translucent zones in *E. affinis* contain organic material incorporated within the trabeculae that is charred brown by heating (Pearse and Pearse, 1975). This was confirmed in the present material since, after charring, growth zones showed clearly after all organic tissue was bleached from the surface of the plates. Pearse and Pearse concluded that the opaque growth-zones are laid down during periods of fast plate-



**Fig. 9.** *Echinus affinis*. Photomicrographs of growth zones in skeletal plates. (A) Upper part of one side of the double row of plates comprising each interambulacrum, from an individual measuring 44 mm in test diameter (note decreasing number of growth zones that reflects the addition, as well as lateral growth, of plates in the course of growth of the urchin); (B) growth zones in genital plates of same individual as in (A); (C) genital plate preparation from a test 36 mm in diameter showing 13 growth zones revealed after grinding; (D) genital plate preparation from largest urchin measured (50 mm) from which 27 growth zones were counted



**Fig. 10.** *Echinus ?affinis*. Photomicrographs of apical plates of postlarvae from Sample ES112 after charring the plates to show up growth zones. (A) Early postlarva, showing radial pattern of galleried stereom of postlarval growth surrounding labyrinthic stereom of plate primordium (no growth zones are apparent at this size); (B) later stage that shows two narrow growth zones in the galleried stereom of postlarval plate growth



**Fig. 11.** *Echinus affinis*. Counts of growth zones in apical plates from all specimens examined, plotted with respect to test diameter, showing fitted growth curves. Inset: area near the origin showing the points from counts on postlarvae (*E. ?affinis*) from Sample ES112. A: von Bertalanffy; B: Gompertz; C: single logistic; D: Preece and Baines (1978) Model 1

growth, while translucent zones are formed during periods of slow growth.

#### Analysis of growth zones as age markers

A total of 205 apical-plate preparations, from specimens from Stations AT171, AT175, AT186 and AT219, were examined and on 188 of these the growth zones are clear enough for counts to be made. Early stages of *Echinus affinis* are rare in the fine-meshed epibenthic trawl samples from Station "M". Hence, the growth zones of juveniles were studied on material from an epibenthic sledge haul (ES112) from the southern Feni Ridge. This is the only one of many sledge hauls taken in the Rockall Trough to yield large numbers of juveniles. It is not possible to be certain at this size of their specific identity (see Gage *et al.*, in press), but it is likely that most, if not all, are *E. affinis*. This sample differed also from the Station "M" samples in lacking sizes above 30 mm in test diameter. The size-frequency distribution of this sample is given in Fig. 12. These specimens were examined whole, the spines and the surface layer overlying the growth-zones in the middle layer being sufficiently undeveloped to allow the rings to be seen clearly after charring (Fig. 10). A total of 16 counts were made on these individuals, most of which were less than 3 mm in diameter.

The number of growth zones counted on all specimens examined is plotted in relation to test in Fig. 11. The counts

of growth zones on the test of *Echinus affinis* range from 1 on post-larval specimens with test-diameters ranging from 1.2 to 2.0 mm to a count of 28 on a specimen of 42.5 mm. The means and standard deviations of test diameters with respect to these ring counts are given in Table 2. The plotted counts (Fig. 11), although showing increasing scatter amongst the larger test sizes, strongly suggest an asymptotic growth curve. Furthermore, the inclusion of the early stages from Station ES112 suggests the total growth curve to be sigmoidal, with an early, initially slow, but accelerating rate of growth amongst postlarvae and juveniles.

#### Growth-curve fit

Non-linear regression techniques have been found superior to traditional linear methods such as a Ford-Walford regression for fitting growth functions to size-at-age data (Gallucci and Quinn, 1979; Vaughan and Kanciruk, 1982). The methods require the user to provide both the function and its derivatives. In most cases, the search employs a step-wise procedure to minimise the residual sum of squares in order to achieve optimal estimates of the parameters. The optimisation software, written in BASIC by Schnute (1982) for implementation on a microcomputer, was employed in fitting a series of growth functions to the present data. The program employs the simplex algorithm of Nelder and Mead (1965) in an iterative search to locate optimal values for the parameters of the growth function

**Table 2.** *Echinus affinis*. Means and standard deviations of test diameters with respect to numbers of growth zones ( $N=197$ )

No. of growth zones	Test diameter	
	Mean	SD
2	1.6	0.3
3	2.4	0.4
4	2.3	0.3
5	7.7	3.6
6	16.1	4.0
8	20.8	4.4
9	23.1	3.5
10	26.9	2.9
11	27.7	3.0
12	28.3	3.3
13	34.2	2.4
14	33.4	1.6
15	36.8	1.6
16	36.2	1.6
17	37.1	1.8
18	37.1	5.6
19	40.2	2.4
20	40.0	3.7
21	40.7	4.5
22	41.3	1.8
23	44.6	1.9
24	43.0 <sup>a</sup>	—
25	44.6	1.9
26	42.0 <sup>a</sup>	—
27	49.8 <sup>a</sup>	—
28	42.5 <sup>a</sup>	—

<sup>a</sup> One observation only

**Table 3.** *Echinus affinis*. Von Bertalanffy parameters fitted to counts of growth zones from hauls considered separately

Station	$y_{\infty}$	$K$	$t_0$	Residual sum-of-squares
AT171	71.18	0.04	-2.89	498.5
AT186	44.99	0.11	0.19	349.5
AT219	50.43	0.08	1.06	598.5

specified, and does not require the user to specify derivatives.

Several growth functions described in the literature were tried. The familiar von Bertalanffy equation (see Table 4) provided a reasonable fit to adult sizes. Fair agreement was obtained in estimates of von Bertalanffy parameters when the counts from three Station “M” samples were considered separately (Table 3). The estimates of von Bertalanffy parameters for the total data set yield a value of 1.95 mm for size at zero age. This is more than could be expected as reasonable, and indicates that a sigmoidal function, such as the Richards, Gompertz and single logistic, growth equations (Ricker, 1979; Schnute, 1981), may be appropriate. These incorporate an increasing growth rate preceding the decaying rate embodied in the von Bertalanffy equation. The Richards function incorporates an added curve-shape parameter ( $p$ ) that provides flexibility

**Table 4.** *Echinus affinis*. Parameters of growth functions fitted to growth-zone counts from all urchins examined. Formulation of the functions follows Schnute (1981) where  $Y(t)$  = size at time  $t$ ,  $K$  = rate constant, and RSS = residual sum-of-squares (see “Results – Growth-curve fit” for further details)

Function	$Y_{\infty}$	$K$	$t_0$	$p$
Von Bertalanffy $Y(t) = y_{\infty} \{1 - e^{-K(t-t_0)}\}$	47.70	0.10	1.39	—
	RSS = 2 120.1			
Richards $Y(t) = y_{\infty} \left\{1 + \frac{1}{p} e^{-K(t-t_0)}\right\}^{-p}$	42.42	0.22	5.65	106.89
	RSS = 2 322.8			
Gompertz $Y(t) = y_{\infty} e^{-K(t-t_0)}$	42.42	0.22	5.65	—
	RSS = 2 319.3			
Single logistic (= Richards with $p = 1$ ) $Y(t) = y_{\infty} \{1 + e^{-K(t-t_0)}\}^{-1}$	41.10	0.31	7.29	—
	RSS = 2 693.2			
Preece and Baines (1978) Model 1	$y_{\infty}$	$K_0$	$K_1$	$y_{\theta}$ $\theta$
	47.30	0.12	0.09	3.54   9.54
	RSS = 2 120.0			

with respect to the position of the “inflection” point of the sigmoidal curve. Of the three, the single logistic model yields the slightly greater residual sum of squares (Table 4). The single logistic curve differs from the other two sigmoidal curves in being symmetrical on either side of the inflection point. This suggests that the early accelerating rate is not exactly the inverse of the decelerating rate of the decaying part of the curve covering the adult sizes.

The remaining two functions yield residual sums of squares (Table 4) indicating a fit to the observed data slightly inferior to that of the von Bertalanffy equation. However, the fitted curves for the Richards and Gompertz functions are virtually identical, indicating that the inflection point embodied by the Gompertz function is very close to that estimated by the Richards function in the present data. This indicates the additional shape parameter ( $p$ ) of the Richards function to be unnecessary in the present context. Both the formulation and parameter estimates obtained with these functions are given in Table 4.

Comparison of the fitted curves (Fig. 11) obtained from the Richards and Gompertz functions to that from the von Bertalanffy shows that the growth asymptote given by the flattening of the curve seems to occur somewhat lower than that suggested by the upward trend of the points – which the von Bertalanffy curve followed closely. This seems to result from a dependence of the upper part of such S-shaped curves on the shape of the lower limb. The resulting curve clearly represents a compromise between a fit to the two limbs of the “S”.

Because of this, the fit of the present data to the model developed by Preece and Baines (1978), in order to describe the human growth curve, was investigated. The fit of Model 1 of Preece and Baines, which incorporates two time-dependent rate parameters, is shown also in Fig. 11,

and the parameter values in Table 4. This model is defined by the differential equation:

$$\frac{dY}{dt} = kt(y_{\infty} - y_t),$$

where  $Y$  is size at time  $t$ ,  $y_{\infty}$  is final (asymptotic) size and  $kt$  is a function of time. The five parameters of the model take the form:

$$Y(t) = y_{\infty} - \frac{2(y_{\infty} - y_{\theta})}{e\{K_0(t - \theta)\} + e\{K_1(t - \theta)\}},$$

where  $K_0$  and  $K_1$  are rate constants,  $\theta$  is a time constant, and  $y_{\theta}$  is size at  $t = \theta$ . The residual sum of squares of the curve shown in Fig. 11 is marginally lower than that obtained from the von Bertalanffy equation and yields a virtually identical growth curve.

Because of the absence of modal structure that could be related to age-marked cohorts, it is not possible to attempt to relate the values of growth parameters derived from the counts of growth zones to the movement of age-marked cohorts along the size axis in successive samples of the Agassiz-trawl time series from Station "M". However, the occurrence of numbers of postlarvae in an epibenthic sledge haul, ES176, taken in late May 1980, offers the possibility of tracking the growth of this settlement in subsequent sledge hauls. These postlarval frequencies are given as histograms in Fig. 12. The frequencies form a well-defined, sharp spike peaking in the 0.7 to 0.8 mm size-class. The only other specimens of *Echinus affinis* present in this haul were a single juvenile measuring 8.6 mm and seven adults in the 30 to 41 mm size-range. Owing to the absence in the sample of postlarvae larger than 0.9 mm, it is likely that they all result from the same settlement. This probably occurred a month or so previously (Tyler and Gage, 1984). A second epibenthic haul (ES184) was made on Station "M" in mid-September of the same year. This yielded smaller numbers of postlarvae, whose size frequencies peaked in the 0.9 to 1.0 mm interval. A further epibenthic sledge haul (ES197) was taken in mid-August of the following year (1981). In this sample, the sizes of the few postlarvae present were spread between 0.7 and 1.7 mm. In a further sledge haul on Station "M" taken in early February of 1982 only one postlarva, measuring 1.4 mm in diameter, was found. The spread of postlarval frequencies in the 1981 sample might be interpreted as incorporating both survivors of the previous year's settlement that had grown to more than 1.5 mm, and individuals from another settlement occurring earlier in 1981.

Early stages of *Echinus affinis* were not found in two epibenthic sledge samples taken subsequently from Station "M". However, further support for the supposition that the position of the peaks on the size axis in the 1980 samples reflect postlarval growth is available from measurements of postlarvae likely to belong to *E. affinis* in samples taken in 1973 from nearby positions (Fig. 12). In the sample (ES4) taken in early June from 1993 m depth on the lower Hebridean Slope near Station "M", the size frequencies

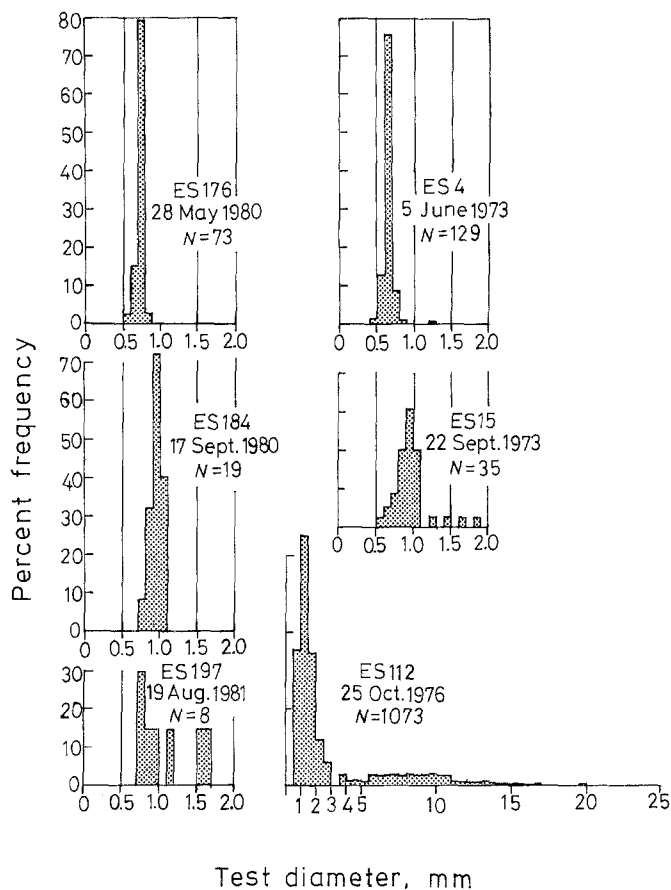


Fig. 12. *Echinus ?affinis*. Frequency histograms of test diameters of postlarvae and juveniles from epibenthic sledge hauls from Station "M" and the southern Feni Ridge (ES112)

show a spike-like mode, peaking in the 0.6 to 0.7 mm interval. Postlarvae that probably also are of *E. affinis* and peak in the 0.9 to 1.0 size-interval occurred in a further epibenthic sledge sample taken in late September nearby, at 1 632 m depth.

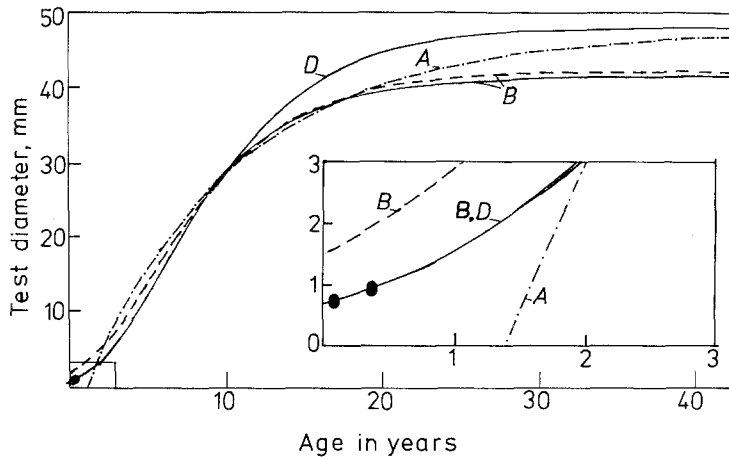
Growth functions fitted to the means of the clearly defined postlarval "spikes" from ES4, ES15, ES176 and ES184 yield growth curves (Fig. 13) quite close to those obtained from the growth-ring data. The parameters of the growth functions fitted are listed in Table 5.

## Discussion

### Interpretation of growth zones as annual banding

Studies on shallow-water urchins have clearly linked the occurrence of growth zones, reflecting periodic variation in stereom microstructure, with a seasonal variation in growth rate of the test (Moore, 1935; Jensen, 1969a; Kobayashi and Taki, 1969; Taki, 1971, 1972, 1978; Crapp and Willis, 1975; Pearse and Pearse, 1975). Although opinions on the causation of such growth fluctuations are sometimes contradictory, most workers agree that growth zones are laid down annually (Smith, 1980). In view of the close simi-





**Fig. 13.** *Echinus affinis*. Means of postlarval settlement from Samples ES4, ES15, ES176, and ES184 plotted at same scale as Fig. 11, with fitted growth curves (continuous lines). Pecked lines are growth curves shown in Fig. 11, fitted from counts of growth zones. Inset: area near the origin showing plotted points. A: von Bertalanffy; B: Gompertz; D: Preece and Baines (1978) Model 1

**Table 5.** *Echinus affinis*. Parameters of growth functions fitted to growth of postlarvae in Samples ES4, ES15, ES176, ES184

Growth function	Parameters					RSS
Gompertz	$y_{\infty}$	$K$	$t_0$			5.45
	41.84	0.21	6.77			
Preece and Baines (1978) Model 1	$y_{\infty}$	$K_0$	$K_1$	$y_{\theta}$	$\theta$	5.85
	48.30	0.21	-0.05	4.37	9.07	

larity of the microstructural pattern of banding in *Echinus affinis* to that seen in shallow-water sea urchins (Pearse and Pearse, 1975; Smith, 1980) the supposition that they represent annual banding is persuasive. Pearse and Pearse point out that both because growth zones are frequently difficult to resolve and because they may be altered by changes in food or other conditions, counts of growth zones may sometimes be unreliable in aging individuals. However, with *E. affinis*, both the clarity and regularity of banding in the test plates (Figs. 9, 10) suggest that the pattern reflects an annual cycle in rate of plate growth. It remains unclear what causes the seasonal variation in growth that may be inferred from the banding. *E. affinis* is known to show a sharply defined annual cycle in gametogenesis, with spawnout occurring in January/February (Tyler and Gage, 1984). There is other evidence that the transfer of organic particulates from the surface, on which urchins might be expected to feed, is both rapid and highly seasonal (Deuser and Ross, 1980; Honjo, 1980; Deuser *et al.*, 1981; Honjo *et al.*, 1982; Billett *et al.*, 1983). Surface-derived phytodetritus sometimes appears as large patches lying on the bottom in deep-water photographs taken in the nearby Porcupine Seabight (Billett *et al.*, 1983). It is interesting that Billett *et al.* noted that the photographs show *E. affinis* grazing directly on this material, suggesting that it constitutes an important food source for the urchin. Growth rate in sea urchins is known to be closely related to feeding (Swan, 1961; Fuji, 1967; Ebert, 1968; Jensen, 1969a; Taki, 1978), so that maximal test growth would be expected during the late spring and summer months when the amount of phytodetritus appears to be greatest on the bottom. It is

possible that this period is associated with the “opaque”, light-reflecting zones of rapid growth; the narrower dark-coloured “translucent” zones of slower growth coinciding both with the period when phytodetritus has disappeared and with gametogenic maturation in the adult urchins (Tyler and Gage, 1984). Fig. 10 shows that growth-banding is present also in pre-reproductive sizes. Hence, food availability may be more important than metabolic changes associated with the reproductive cycle in causing the seasonal pattern in growth that is inferred from banding. Although often difficult to resolve in adults, the zones nearest the plate primordium appeared closer together than those a little farther out. On the assumption that these closely-spaced growth lines are laid down annually before reproductive maturity is attained, and are otherwise similar to those formed later by urchins of breeding size, a sigmoidal growth curve is indicated. This conclusion is corroborated from growth curves fitted to the presumed growth of postlarvae observed in the two pairs of epibenthic sledge samples (Fig. 13). These samples were taken in late spring and late summer when fastest growth would be expected. The similarity of the postlarval curves to those obtained from banding suggests that the period of fast growth occupies most of the year, otherwise a greater disparity in growth parameter estimates might have been evident.

An early slow, but accelerating, phase of growth is known in seastars from shallow water (Yamaguchi, 1975). A sigmoidal growth curve is thought also to occur in populations of the coastal congeneric echinoid *Echinus esculentus* (Nichols *et al.*, 1985).

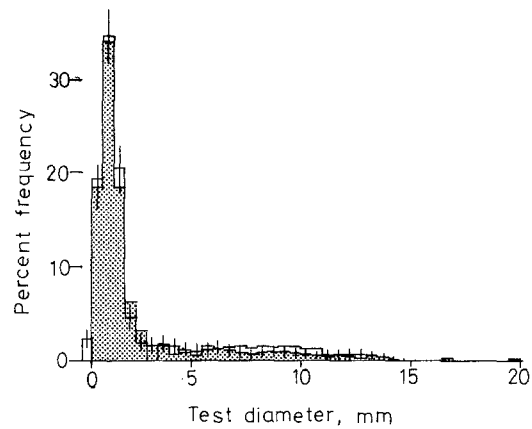
#### Processes underlying observed size structure

An understanding of the age structure of the population of *Echinus affinis* requires information on recruitment and survivorship as well as growth rate. The admittedly negative evidence from the absence of early forms of this urchin in samples taken using a fine-meshed epibenthic sledge once a year from Station “M” from 1982 to 1985 indicates that successful settlement may not take place every year. This may also explain the absence of larger sizes in the

single sample from the Feni Ridge (ES112), which consisted only of postlarval and later juvenile stages. However, it must be said that the large specimens so conspicuous in the Agassiz trawl hauls were rather rare in the epibenthic-sledge samples from Station "M", so that few would have been expected anyway.

It seems likely from the size-frequency distributions of postlarvae and juveniles (Fig. 12) that survivorship operates at at least two rates during the life-time of the urchin. It seems likely that a high mortality must have occurred after the 1980 settlement at Station "M" because few were found in hauls taken in the following year. Furthermore, the size of most of the postlarvae in the 1981 haul suggests that most of them may have settled during that year. The sample from the Feni Ridge (ES112) that included postlarval and juvenile frequencies, could be simulated using a procedure described by Gage (in press). This applies a specified growth and mortality rate to normally distributed annual recruitment waves, resulting in a normal-distribution mixture of frequencies where each component represents a discrete year-class. In the present case, it was possible to stop further recruitment taking place once the size-frequency distribution generated by the model approached that of the observed sample. This resulted in the simulation shown in Fig. 14. The parameters of the simulated year-class structure are given in Table 6. These results indicate that, after an initially high mortality of postlarvae, an improved survivorship amongst juveniles with an annual loss of the order of 10%, would result in a size structure similar to that observed.

The size structure of adult urchins observed at trawlings from Station "M", and from the adjacent continental slope, is more difficult to understand. It seems possible that the unimodal distributions revealed in many of the samples illustrated in Fig. 5 result from a low rate of mortality amongst adults, with a "stacking" of age classes as they approach the growth asymptote. The bimodal distribution shown by others is more puzzling. One explanation may be that it results from varying recruitment; a series of unsuccessful recruitments to the population being in turn followed by another set of successful years. Such variation in recruitment success is well-known amongst shallow-water benthic fauna, including echinoderms, and is particularly evident amongst species with pelagic larvae (Thorson, 1950; Buchanan, 1967; Ebert, 1983). It is relevant to note that Ebert (1975) commented that the size-frequency distributions given by Sumich and McCauley (1973) for a population of the echinoid *Allocentrotus fragilis* from 200 m depth off Oregon (USA) also indicated highly unpredictable recruitment. A long time-series of observations by Ebert (1983) on the size structure of a population of the in-shore echinoid *Strongylocentrotus purpuratus* allows some interesting comparisons with *Echinus affinis* in Rockall. Ebert's population showed only one period of good recruitment to an existing stock that occurred the year prior to the start of 15 years of observations. This resulted in an initially bimodal distribution in size-frequencies that eventually became merged into a single peak at about the

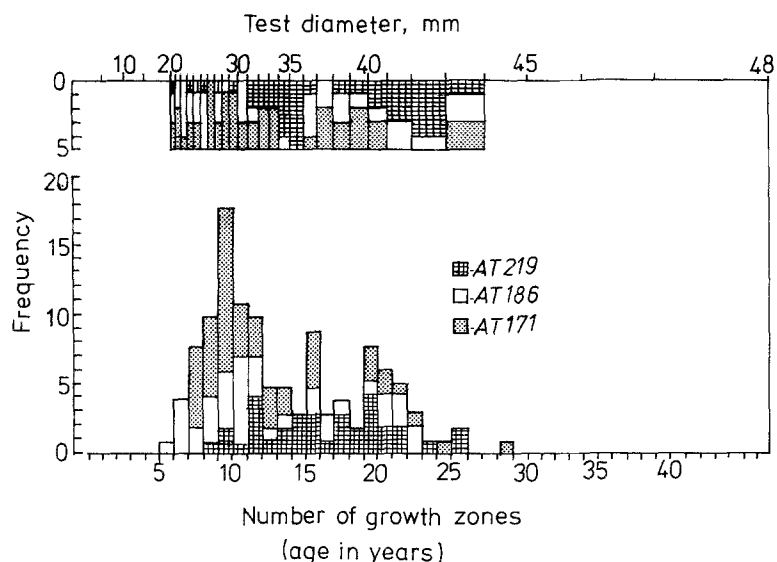


**Fig. 14.** *Echinus ?affinis*. Simulation (stippled) of observed size-frequency structure of young specimens in Sample ES112, employing growth parameters of Preece and Baines's Model 1 fitted to the growth-zone counts (see Table 4). Vertical bars indicate 95% confidence limits of simulated frequencies calculated by means of a binomial approximation (see Gage, in press)

**Table 6.** *Echinus affinis*. Parameters of simulation (shown in Fig. 14) of year-class structure in ES112, using parameters of Preece and Baines' Model 1 given in Table 4

Age (yr)	Mean test diameter (mm)	SD (mm)	No. of individuals	Cumulative no. of individuals
0.5	1.50	0.40	760	760
1.5	2.19	0.60	76	836
2.5	3.98	0.78	68	904
3.5	6.37	0.94	62	966
4.5	9.29	1.09	55	1 021
5.5	12.61	1.23	50	1 071

same position as that of the adults when the initial large recruitment occurred. In the Rockall population, the results from aging indicate that each of the two modes was composed of a considerable, but only slightly overlapping, range in age. Fig. 15 shows that the frequencies in numbers of growth zones present in the adult specimens examined from a subsample, made up so that there was an exactly even number in each size-class, do not conform to the von Bertalanffy expectation of an increasing number of individuals within each class with increasing age. The distribution instead shows a peak at a presumed age of 10 yr, with smaller, less clear peaks at about 17 and 21 yr. Reference to both the fitted growth curves and the size distributions of these hauls indicates that the peak at 10 yr corresponds to the left peak of the bimodal distributions (AT171 and AT186). The right-hand of the two remaining peaks in the growth-zone frequencies corresponds to those making up the right peak in size-frequencies of these two hauls, while the unimodal peak of AT219 corresponds in position to the less clearly defined peak lying between the other two. Hence, it is possible that the modal pattern evident in the inferred age structure of this subsample results from cyclic variations in recruitment. Simulations were undertaken incorporating a varying, rather than constant,



**Fig. 15.** *Echinus affinis*. Age structure (lower distribution inferred from counts of growth zones in a sub-sample, from three Agassiz hauls, of the total from Station "M", made up of an exactly even representation of size-frequencies (upper distribution). The test-size scale is shown related to an age scale based on von Bertalanffy parameters given in Table 4

rate of recruitment that corresponded to the representation of age structure (standardised to zero mortality) shown for each of the three hauls in Fig. 15. These yielded size-distributions similar to those observed, those for AT171 and AT186 being bimodal while that for AT219 was unimodal.

The spread of points plotted in Fig. 11 indicates a considerable dispersion in test diameters corresponding to each year-class. The scatter must also incorporate error from counting growth bands in estimating age. The likely dispersion of each age-class was therefore difficult to estimate accurately for the simulation. The results, nevertheless, demonstrated that because most individuals were well short of asymptotic age, there is only modest "stacking" in age-class composition amongst frequencies on the right-hand side of the distribution. The corollary is that the frequencies corresponding to smaller sizes would, even in large samples, be subject to considerable stochastic variability from sample to sample.

Although it is possible to see how such a bimodal distribution in the population may arise, it is more difficult to explain how differences in recruitment by means of pelagic larvae might occur at sites that are as relatively close together as indicated by the tracks of the hauls from Station "M". Possibly mesoscale variations, such as fronts and eddies, in hydrographic conditions associated with differing surface water masses, have played a part. Certainly, indications from satellite-tracked drogues have shown that the nearby Anton Dohrn seamount may have an important effect on surface water-mass properties (D. A. Booth, Scottish Marine Biological Association, unpublished report).

#### Growth rates in the deep sea

There are few data on the growth of deep-sea organisms. However, the deep sea has often been described as an environment with low rates of biological activity (e.g. Sanders, 1979), although this is based mainly on sparse data

from *in situ* studies of sediment, microbial and fish respiration, and sediment recolonisation (Jannasch and Wirsen, 1977; Smith and Teal, 1973; Smith, 1974, 1978; Smith and Hessler, 1974; Grassle, 1977; Smith *et al.*, 1979). Other *in situ* recolonisation observations indicate that certain species may settle and grow to maturity within a year or two (Turner, 1973, 1977; Desbruyères *et al.*, 1980). Estimates of age and growth rate of individual species are few, frequently based on sparse data, and present no clear pattern (Turekian *et al.*, 1975; Zezina, 1975; Rannou, 1976; Roux, 1979). These varied results suggest a variability in absolute rates of biological processes that, in turn, indicate a lack of any dependence on physical parameters, such as high pressure and low temperature, that characterise the deep-sea environment.

Although it has been possible to infer population parameters of *Echinus affinis* from the present study, these are necessarily based on indirect data. Clearly, direct data from marked individuals monitored *in situ* are required in order to test our conclusions. However, the present results suggest that the population of *Echinus affinis* in Rockall is both slow-growing and long-lived compared to other sea urchins for which data are available (Swan, 1966; Jensen, 1969a; Crapp and Willis, 1975; Ebert, 1975, 1982; Duineveld and Jenness, 1984; Nichols *et al.*, 1985), few of which would appear to survive longer than 10 to 15 yr. But *E. affinis* resembles other benthic animals closely in its pattern of low survivorship amongst early benthic stages, followed by a much higher survivorship amongst later juvenile stages and adults (Thorson, 1966; Mileikovsky, 1971).

The evidence from the size of the gonad suggests that *Echinus affinis* are able to reproduce by the age of 5 yr. Since gonads were present, although small, in much smaller specimens, it is possible that breeding may take place at a considerably earlier age. Ebert (1975, 1983) presents evidence that longevity in sea urchins is related to the predictability of survival of pre-reproductive individuals; longer life-spans are associated with greater unpredictability

bility in postlarval survival that, in turn, is associated with a planktotrophic mode of early development, as in other benthic fauna (Thorson, 1950; Mileikovskiy, 1971). Although direct evidence from capture of pelagic larvae of *E. affinis* is lacking, investigation of gametogenesis and maximum egg size by Tyler and Gage (1984) strongly suggests an early development as a feeding larva in the plankton. If development occurs in the photic zone near the surface, then wastage in larvae will undoubtedly occur in the course of vertical transport of the tiny eggs and larvae through the water column. Further loss may result from transport to areas where depth or bottom conditions are unsuitable. If such constraints operate during the life history in causing low recruitment predictability, then it seems reasonable to conclude that these factors play an important part in determining the slow growth and longevity of the urchin. Moreover, such factors may be more important than either the presumed low availability of nutrient energy or the physically demanding regime of the deep sea in determining the demographic characteristics of the population of *E. affinis* in the Rockall Trough.

**Acknowledgements.** We are grateful to J. Schnute of the Pacific Biological Station, Nanaimo, British Columbia, Canada for kindly making available a copy of his powerful computer software. We also thank S. Pain for help at Swansea in measuring urchins, and at Dunstaffnage, J. Graham for constructing the digitising caliper, R. Summers for photographic assistance, J. Gordon for providing additional material from fishing cruises, and C. Comely for advice and help with equipment. We also thank L. Tetley of the electron microscope unit and P. Meadows of the Department of Zoology at Glasgow University for kindly providing scanning electron micrographs of urchin plates. Helpful comments on earlier drafts of the paper were made by M. Jensen (Copenhagen) and two anonymous referees. The Scottish Marine Biological Association is grant-aided through the U.K. Natural Environment Research Council.

## Literature cited

- Agassiz, A.: The Panamic deep-sea echini. Mem. Mus. comp. Zool. Harv. 31, X+246 pp (1904)
- Allain, J.-Y.: Age et croissance de *Paracentrotus lividus* (Lamarck) et de *Psammechinus miliaris* (Gmelin) des cotes nord de Bretagne (Echinoidea). Cah. Biol. mar. 19, 11–21 (1978)
- Billet, D. S. M., R. S. Lampitt, A. L. Rice and R. F. C. Mantoura: Seasonal sedimentation of phytoplankton to the deep-sea benthos. Nature, Lond. 302, 520–522 (1983)
- Birkeland, C. and F.-S. Chia. Recruitment risk, growth, age and predation in two populations of sand dollars, *Dendraster excentricus* (Eschscholtz), J. exp. mar. Biol. Ecol. 6, 265–278 (1971)
- Buchanan, J. M.: Dispersion and demography of some infaunal echinoderm populations. Symp. zool. Soc. Lond. 20, 1–11 (1967)
- Crapp, G. B. and M. E. Willis: Age determination in the sea urchin *Paracentrotus lividus* (Lamarck), with notes on the reproductive cycle. J. exp. mar. Biol. Ecol. 20, 157–178 (1975)
- Desbruyères, D., J. Y. Bervas et A. Khripounoff: Un cas de colonisation rapide d'un sediment profond. Oceanol. Acta 3, 285–291 (1980)
- Deuser, W. G. and E. H. Ross: Seasonal change in the flux of organic carbon to the deep Sargasso Sea. Nature, Lond. 283, 364–365 (1980)
- Deuser, W. G., E. H. Ross and R. F. Anderson: Seasonality in the supply of sediment to the deep Sargasso Sea and its implications for the rapid transfer of matter to the deep ocean. Deep-Sea Res. 28, 495–505 (1981)
- Deutler, F.: Über das Wachstum des Seeigelskeletts. Zool. Jb. (Abt. Anat. Ont. Tiere) 48, 119–200 (1929)
- Duineveld, G. C. A. and M. I. Jenness: Differences in growth rates of the sea urchin *Echinocardium cordatum* as estimated by the parameter of the von Bertalanffy equation applied to skeletal rings. Mar. Ecol. Prog. Ser. 19, 65–72 (1984)
- Durham, J. W.: Classification of clypeasteroid echinoids. Univ. Calif. Publs. geol. Sci. 31, 73–198 (1955)
- Ebert, T.: Growth rates of the sea urchin *Strongylocentrotus purpuratus* related to food availability and spine abrasion. Ecology 49, 1075–1091 (1968)
- Ebert, T.: Growth and mortality of post-larval echinoids. Am. Zool. 15, 755–775 (1975)
- Ebert, T.: Longevity, life history, and relative body wall size in sea urchins. Ecol. Monogr. 52, 353–394 (1982)
- Ebert, T.: Recruitment in echinoderms. Echinoderm Stud. (Bal-kema, Rotterdam) 1, 169–203 (1983)
- Fuji, A.: Ecological studies on the growth and food consumption of Japanese common littoral sea urchins, *Strongylocentrotus intermedius* (A. Agassiz). Mem. Fac. Fish. Hokkaido Univ. 15, 83–160 (1967)
- Gage, J. D.: The analysis of population dynamics in deep-sea benthos. Proc. 19th Eur. mar. Biol. Symp. (In press) (Cambridge: University Press)
- Gage, J. D., D. S. M. Billet, M. Jensen and P. A. Tyler: Echinoderms of the Rockall Trough. 2. Echinoidea and Holothuri-idea. Bull. Br. Mus. nat. Hist. (D. Zool.) (In press)
- Gage, J. D. and P. A. Tyler: Non-viable seasonal settlement of larvae of the upper bathyal brittle star *Ophiocten gracilis* in the Rockall Trough abyssal. Mar. Biol. 64, 153–161 (1981)
- Gage, J. D. and P. A. Tyler: Growth and reproduction of the deep-sea brittlestar *Ophiomusium lymani* Wyville Thomson. Oceanol. Acta 5, 73–83 (1982)
- Gallucci, V. F. and T. J. Quinn: Reparameterizing, fitting, and testing a simple growth model. Trans. Am. Fish. Soc. 108, 14–25 (1979)
- Gamble, J. C.: Ecological studies on *Paracentrotus lividus* (Lmk.). Underwat. Ass. Rep., Malta 1966–67, 85–88 (1967)
- Gordon, I.: The development of the calcareous test of *Echinus miliaris*. Phil. Trans. R. Soc. (Ser. B) 214, 259–312 (1926)
- Grassle, J. F.: Slow recolonisation of deep-sea sediment. Nature, Lond. 265, 618–619 (1977)
- Grassle, J. F., H. L. Sanders, R. R. Hessler, G. T. Rowe and T. McClellan: Pattern and zonation: a study of the bathyal megafauna using the research submersible *Alvin*. Deep-Sea Res. 22, 457–481 (1975)
- Haedrich, R. L., G. T. Rowe and P. T. Polloni: Zonation and faunal composition of epibenthic populations on the continental slope south of New England. J. mar. Res. 33, 191–212 (1975)
- Haedrich, R. L., G. T. Rowe and P. T. Polloni: The megabenthic fauna in the deep sea south of New England, USA. Mar. Biol. 57, 165–179 (1980)
- Hessler, R. R. and H. L. Sanders: Faunal diversity in the deep sea. Deep-Sea Res. 14, 65–78 (1967)
- Honjo, S.: Material flux and modes of sedimentation in the mesopelagic and bathypelagic zones. J. mar. Res. 38, 53–97 (1980)
- Honjo, S., S. J. Manganini and J. J. Cole: Sedimentation of biogenic matter in the deep ocean. Deep-Sea Res. 29, 609–625 (1982)
- Jannasch, H. W. and C. O. Wirsen: Microbial life in the deep sea. Scient. Am. 236, 42–52 (1977)
- Jensen, M.: Breeding and growth of *Psammechinus miliaris* (Gmelin), Ophelia 7, 65–78 (1969 a)

- Jensen, M.: Age determination of echinoids. *Sarsia* 37, 41–44 (1969b)
- Kawamura, K.: On the age determining character and growth of a sea-urchin. *Rep. Jap. Soc. scient. Fish.* 6, 56–61 (1974)
- Kobayashi, S. and J. Taki: Calcification in sea urchins. I. A tetracycline investigation of growth of the mature test in *Strongylocentrotus intermedius*. *Calif. Tissue Res.* 4, 210–223 (1969)
- Lightfoot, R. H., P. A. Tyler and J. D. Gage: Seasonal reproduction in deep-sea bivalves and brittlestars. *Deep-Sea Res.* 26A, 967–973 (1979)
- M'Clelland, J.: On *Cyrtoma*, a new genus of fossil Echinida. *Calcutta J. nat. Hist.* 1, 153–187 (1840)
- Mileikovsky, S. A.: Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. *Mar. Biol.* 10, 193–213 (1971)
- Miller, R. J. and K. H. Mann: Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. III. Energy transformations by sea urchins. *Mar. Biol.* 18, 99–114 (1973)
- Moore, H. B.: A comparison of the biology of *Echinus esculentus* in different habitats. Part II. *J. mar. biol. Ass. U.K.* 20, 109–128 (1935)
- Mortensen, T.: A monograph of the Echinoidea. Vol. 3, Pt. 3. Camarodonta II, Echinidae, Strongylocentrotidae, Parasalenidae and Echinometridae, 446 pp. Copenhagen: C. A. Reitzel Co. 1943
- Nelder, J. A. and R. Mead: A simplex method for function minimisation. *Comput. J.* 7, 308–313 (1965)
- Nichols, D., A. A. T. Sime and G. M. Bishop: Growth in populations of the sea-urchin, *Echinus esculentus* L. (Echinodermata: Echinoidea) from the English Channel and Firth of Clyde. *J. exp. mar. Biol. Ecol.* 86, 219–228 (1985)
- Pearce, J. S., M. E. Clark, D. L. Leighton, C. T. Mitchell and W. J. North: Marine waste disposal and sea urchin ecology. A Rep. W. M. Keck Lab. envrl Hlth Engng Calif. Inst. Technol. Appendix to Kelp Habitat Improvement Project 1969–1970, 1–93 (1970)
- Pearse, J. A. and V. B. Pearse: Growth zones in the echinoid skeleton. *Am. Zool.* 15, 731–753 (1975)
- Preece, M. A. and M. J. Baines: A new family of mathematical models describing the human growth curve. *Ann. hum. Biol.* 5, 1–24 (1978)
- Rannou, M. R.: Age et croissance d'un poisson bathyl: *Nezumia sclerorhynchus* (Macrouridae: Gadiforme) de la Mer d'Alboran. *Cah. Biol. mar.* 17, 413–421 (1976)
- Raup, D. M.: Theoretical morphology of echinoid growth. *J. Paleont.* 42 (Suppl. to No. 5), 50–63 (1969)
- Ricker, W. E.: Growth rates and models. *In: Fish physiology*, Vol. 8, pp 677–743. Ed. by W. S. Hoar, D. J. Randall and J. R. Brett. New York: Academic Press 1979
- Rowe, G. T. and R. J. Menzies: Zonation of large benthic invertebrates in the deep-sea off the Carolinas. *Deep-Sea Res.* 16, 531–681 (1969)
- Roux, M.: Aspects de la variabilité, et de la croissance au sein d'une population de la Pentacrine actuelle: *Annacrinus wyville thomsoni* Jeffreys (Crinoidea). *Thalassia jugosl.* 12, 307–320 (1979)
- Sanders, H. L.: Evolutionary ecology and life-history patterns in the deep sea. *Sarsia* 64, 1–7 (1979)
- Schnute, J.: A versatile growth model with statistically stable parameters. *Can. J. Fish. aquat. Sciences* 38, 1128–1140 (1981)
- Schnute, J.: A manual for easy nonlinear parameter estimation in fishery research with interactive microcomputer programs. *Tech. Rep. Fish. aquat. Sciences Can.* 1140, xvi+116 pp (1982). (Internal publication)
- Schoener, A.: Evidence for reproductive periodicity in the deep sea. *Ecology* 49, 81–87 (1968)
- Sime, A. A. T.: Growth ring analysis in regular echinoids. *Prog. Underwat. Sci.* 7, 7–14 (1982)
- Smith, A. B.: Stereom microstructure of the echinoid test. *Spec. Pap. Palaeont.* 25, 1–81 (1980)
- Smith, K. L.: Oxygen demand of San Diego Trough sediments: an *in situ* study. *Limnol. Oceanogr.* 19, 939–944 (1974)
- Smith, K. L.: Metabolism of the abyssopelagic rattail *Coryphaenoides armatus* measured *in situ*. *Nature, Lond.* 274, 362–364 (1978)
- Smith, K. L. and R. R. Hessler: Respiration of benthopelagic fishes: *in situ* measurements in 1230 meters. *Science, N.Y.* 184, 72–73 (1974)
- Smith, K. L. and J. M. Teal: Temperature and pressure effects on respiration of the tectosomatous pteropods. *Deep-Sea Res.* 20, 853–858 (1973)
- Smith, K. L., G. A. White and M. B. Laver: Oxygen uptake and nutrient exchange of sediments measured *in situ* using a free vehicle grab respirometer. *Deep-Sea Res.* 26A, 337–346 (1979)
- Swan, E. F.: Some observations on the growth rate of sea urchins in the genus *Strongylocentrotus*. *Biol. Bull. mar. biol. Lab., Woods Hole* 120, 420–427 (1961)
- Swan, E. F.: Growth, autotomy, and regeneration *In: Physiology of Echinodermata*, pp 397–434. Ed. by R. A. Booloottian. New York: Interscience Publishers 1966
- Sumich, J. L. and J. E. McCauley: Growth of a sea urchin, *Allorcentrotus fragilis*, off the Oregon coast. *Pacif. Sci.* 27, 156–167 (1973)
- Taki, J.: Tetracycline labelling of test plates in *Strongylocentrotus intermedius*. *Scient. Rep. Hokkaido Fish. expl Stn* 13, 19–29 (1971)
- Taki, J.: A tetracycline labelling observation on growth zones in the test plate of *Strongylocentrotus intermedius*. *Bull. Jap. Soc. Scient. Fish.* 38, 117–125 (1972)
- Taki, J.: Formation of growth lines in test plates of the sea-urchin *Strongylocentrotus intermedius*, reared with different algae. *Bull. Jap. Soc. scient. Fish.* 44, 955–960 (1978)
- Thorson, G.: Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.* 25, 1–45 (1950)
- Thorson, G.: Some factors influencing the recruitment and establishment of marine benthic communities. *Neth. J. Sea Res.* 3, 267–293 (1966)
- Turekian, K. K., J. K. Cochran, D. P. Kharkar, R. Cerrato, J. Vaisnys, H. L. Sanders, J. F. Grassle and J. A. Allen: Slow growth rate of a deep-sea clam determined by 228Ra chronology. *Proc. natn. Acad. Sci. U.S.A.* 72, 2829–2832 (1975)
- Turner, R. D.: Wood-boring bivalves, opportunistic species in the deep sea. *Science, N.Y.* 180, 1377–1379 (1973)
- Turner, R. D.: Wood, mollusks, and deep-sea food chains. *Bull. Am. malac. Union* 1977, 13–19 (1977)
- Tyler, P. A. and J. D. Gage: Reproduction and growth in the deep-sea brittlestar *Ophiura ljungmani* (Lyman). *Oceanol. Acta* 3, 177–185 (1980)
- Tyler, P. A. and J. D. Gage: Seasonal reproduction of *Echinus affinis* (Echinodermata: Echinoidea) in the Rockall Trough, north-east Atlantic Ocean. *Deep-Sea Res.* 31, 387–402 (1984)
- Tyler, P. A., A. Grant, S. L. Pain and J. D. Gage: Is annual reproduction in deep-sea echinoderms a response to variability in their environment? *Nature, Lond.* 300, 747–750 (1982)
- Van-Praet, M. et G. Duchateau: Mise en évidence chez une Actinie abyssale (*Paracalliactis stephensoni*) d'un cycle saisonnier de reproduction. *C.r. hebd. Séanc. Acad. Sci., Paris* 299, 687–690 (1984)
- Vaughan, D. S. and P. Kanciruk: An empirical comparison of estimation procedures for the von Bertalanffy growth equation. *J. Cons. int. Explor. Mer* 40, 211–219 (1982)
- Yamaguchi, M.: Estimating growth parameters from growth rate data. Problems with marine sedentary invertebrates. *Oecologia (Berl.)* 20, 321–322 (1975)
- Zeina, O. N.: On some deep-sea brachiopods from the Gay Head-Bermuda transect. *Deep-Sea Res.* 22, 903–912 (1975)
- Zoeke, M. E.: Sur la croissance du squelette des *Clypeaster fossiles*. *C.r. hebd. Séanc. Acad. Sci., Paris* 234, 1999–2002 (1952)

Date of final manuscript acceptance: July 19, 1985.

Communicated by J. Mauchline, Oban