Growth and reproduction of the deep-sea brittlestar *Ophiomusium lymani* Wyville Thomson

J. D. Gage[a], P. A. Tyler[b]

[a] Dunstaffnage Marine Research Laboratory, Scottish Marine Biological Association, P.O. Box 3, Oban, Argyll PA34 4AD, UK.

[b] Department of Oceanography, University College of Swansea, Swansea SA2 8PP, UK.

ABSTRACT

Disk-size frequencies of the brittlestar were measured from large samples obtained from a 3-year time series of Agassiz-trawl hauls from a fixed location in the Rockall Trough (Northeast Atlantic). Parameters of Gaussian mixtures fitted to these data are interpreted to show a pattern of annual recruitment and von Bertalanffy growth. Juveniles are thought to grow to about 11-12 mm in disk diameter in their first year. Thereafter growth slows to about 7-8 mm in their second year, and to about 5 mm or less in their third when they attain reproductive maturity and breed. The year classes thereafter merge into a numerically dominant mode of slow growing adults. Mortality amongst postlarvae is sufficiently high to result in only a tiny proportion surviving to attain asymptotic size, L_∞. Egg-size (max. 460 μm), fecundity (up to 12 000 eggs per individual) and lack of brooding indicate a lecithotrophic larval development. Contingency table analysis of oocyte-size frequencies supports the absence of annual periodicity, as found in previous investigations. The gonad apparently remains reproductively active throughout the year with a mean female fecundity of 9 500 eggs. The authors reconcile this with the inferred pattern of annual recruitment by postulating a seasonal cycle in survival of postlarvae. This is thought to occur as a response to annual fluctuation in downward flux of food particles from the surface, reflecting the seasonal cycle of primary production. A marked increase observed in the proportion of postlarvae in late summer supports this hypothesis.

Oceanol. Acta, 1982, **5**, 1, 73-83.

RÉSUMÉ

Croissance et reproduction de l'Ophiure
Ophiomusium lymani Wyville Thomson

La fréquence des classes de taille du disque de l'ophiure a été mesurée à partir de nombreux échantillons prélevés pendant 3 ans à une station fixe, située dans le bassin de Rockall, au nord-est de l'océan Atlantique. Les paramètres de mélange de normalité de ces données mettent en évidence l'existence d'un recrutement annuel et une croissance de type von Bertalanffy. Durant la première année, le diamètre du disque des juvéniles croît de 11 à 12 mm. Cette croissance se réduit ensuite à environ 7-8 mm durant leur seconde année, puis à environ 5 mm lors de la troisième, lorsque ces Ophiures atteignent leur maturité sexuelle et se reproduisent. Les classes d'âge se fondent ensuite en un mode quantitativement dominant des adultes. La mortalité des postlarves est suffisamment élevée pour que la taille de ceux-ci n'atteigne pas l'asymptote L_∞.
La taille des œufs (maximum : 460 μm), la fécondité (maximum : 12 000 œufs par individu) et l'analyse par table de contingence des fréquences de taille des oocytes confirment l'absence de cycle annuel démontrée lors d'études antérieures. La gonade reste

apparemment active tout au long de l'année pour la reproduction. Les auteurs concilient ceci avec l'apparent cycle de recrutement annuel, déduit de l'étude des échantillons, en émettant l'hypothèse d'un cycle saisonnier de survie des postlarves. Cette survie dépend probablement des fluctuations annuelles dans la chute des particules alimentaires depuis la surface, reflétant le cycle saisonnier de la production primaire. L'augmentation marquée de la proportion de postlarves recueillies en été confirme cette hypothèse.

INTRODUCTION

Evidence from bottom trawlings (Rowe, 1971; Haedrich *et al.*, 1975) and from both seabed photographs and submersible observations (Barham *et al.*, 1967; Wigley, Emery, 1967; Grassle *et al.*, 1975) suggests that the brittlestar *Ophiomusium lymani* may constitute one of the most predictable and abundant elements of megafaunal biomass within the 700-4 000 m depth range along the continental margin of the NW Atlantic and NE Pacific. Although its vertical range at any one locality may be rather narrow (Grassle *et al.*, 1975), *O. lymani* probably has a continuous, ribbon-like distribution on the slope around the continents of the world ocean (Menzies *et al.*, 1973). Its worldwide distribution in the Atlantic and Indo-Pacific places it in a restricted group of deep-sea species of cosmopolitan range (Mortensen, 1927; Madsen, 1951; Cherbonnier, Sibuet, 1972).

There are few published data on the breeding of *Ophiomusium lymani*. The large size of ripe oocytes in specimens from the N Atlantic led Mortensen (1933) to speculate that this ophiuroid species has a direct development of its young without an ophiopluteus stage. Schoener (1968) found differentiated gonads in samples taken in both May and December in a limited seasonal spread of samples taken at a range of depths between the years 1964 and 1966 in the NW Atlantic. Ahlfeld (1977) suggests a definite reproductive periodicity based on comparison of samples taken in December, 1971 and in August of the following year in the NW Atlantic. However, in a seasonally spaced sampling programme over one year in the San Diego Trough (NW Pacific), Rokop (1974; 1975) postulates a year-round reproductive cycle with relatively low fecundity.

On the basis of data on postlarval development and on egg number and size (Schoener, 1967; 1972), *O. lymani* is thought to have a free-living, though possibly abbreviated, development (Mileikovsky, 1971; Schoener, 1972; Hendler, 1975).

Even less is known of the size structure and growth of populations of *Ophiomusium lymani*. Grieg (1921) inferred a population structure of one or more discrete year classes from the sometimes polymodal distribution of disk-size frequency in samples of this species collected by the "Michael Sars" N Atlantic deep-sea expedition of 1910. Presumably on the basis of these data, Mortensen (1927) asserted that it seemed certain that *O. lymani* took three or four years to reach reproductive maturity. Schoener (1968) suggested, from differences in the size distribution of summer compared to winter samples, that a seasonal recruitment occurs in July and August. At other times of the year individuals increase in size but decrease in abundance, although adults were not present in all of her samples.

Rokop (1975) considered that the pattern of disk-size frequencies reflected an essentially bimodal population size structure, the large sizes representing reproductively mature animals that are present year-round.

Results from a study (Tyler, Gage, 1979) of gametogenesis of *O. lymani* in a seasonal spread of samples from the Rockall Trough (NE Atlantic) confirm the absence of an annually synchronous reproductive periodicity. These authors also postulate an abbreviated, possibly demersal, free-living development.

We now extend the latter study by analysis of measurements of disk diameters and oocyte size frequencies of specimens, mainly from a series of large samples taken in a time series spanning three years at a single fixed position in the northern Rockall Trough. By this means we attempt to reconcile the apparently contradictory findings of previous studies. A hypothesis is developed of annual recruitment controlled not by a gametogenic cycle but by probable seasonal periodicity in downward flux of sedimented food particles which directly regulates larval survival.

STUDY AREA

The fixed sampling area of the present investigation is located in the northern Rockall Trough between the Anton Dohrn Seamount and the continental slope lying to the west of Scotland (Fig. 1). Sampling was centred on a station (station « M ») at 57°18'N, 10°11'W in soundings of about 2 200 m that comprises one of a series in a hydrographic section under current study by the Scottish Marine Biological Association (Ellett, 1978).

Hydrographic data relevant to the sampling area are given in the publication cited above and extend more general studies on regional circulation and geomorphology within the Rockall Trough area (Ellett, Martin, 1973; Roberts, 1975; Lonsdale, Hollister, 1979). Direct measurements of currents at about 435 m from the bottom at station « M » show a variable direction in residual flow superimposed on a pronounced rotating oscillation with a maximum amplitude of 18 cm.sec.$^{-1}$ and max. total flow of 21 cm.sec.$^{-1}$ (Edelsten, 1980).

Analysis of sediment samples from a single box core (sample no. SBC 166) taken on this station on 12 August 1979 indicates a carbonate ooze with organic content [0.39 % determined by the wet oxidation method of Gaudette *et al.* (1974)] similar to that measured at the
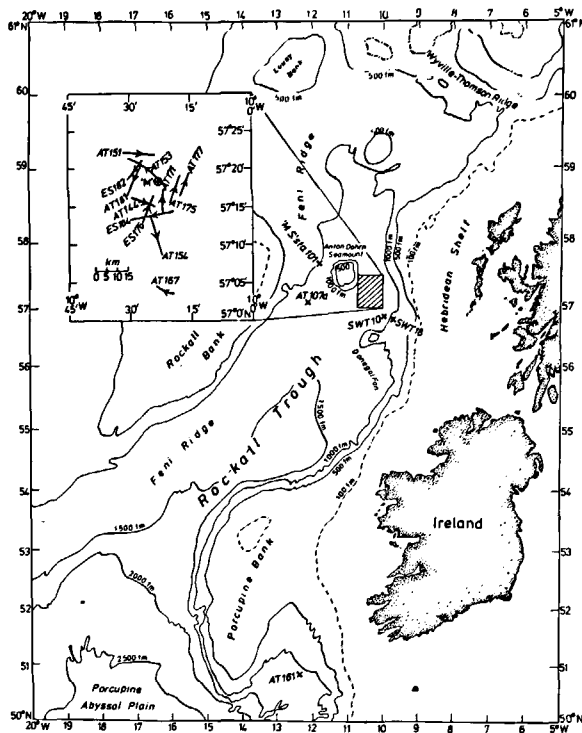
Figure 1

Chart showing station "M" sampling area (hatched square) and the positions of other stations given in Table 2. Inset chartlet shows the direction and probable track on the bottom of the bottom hauls comprising the station "M" time series, plotted from satellite and Decca Navigator fixes and calculated towing warp profile. Bathymetry in fathoms (fm) where 1 fm = 1 829 m (chart modified from Roberts, 1975).

SMBA Permanent Station lying 320 km further south in deeper water (Gage *et al.*, 1980). However, carbonate content measured, by loss on combustion, at 48 % was somewhat lower while granulometric analysis (Table 1) indicated proportionately more sand (33.2 % by weight) and less silt/clay (43.1 %) than at the Permanent Station (27.4 % sand, 57.9 % silt clay).

METHODS

A time series of bottom trawlings using a 3-metre wide Agassiz trawl taken at varying intervals on station « M » from April 1978 up to September 1980 has provided the main source of material for the present study. *Ophiomusium lymani* is one of the most conspicuous and certainly the numerically dominant element of megafauna in these samples.

The hauls (Table 2) were standardised to an approximately 1-hour period on the bottom. Because of weather constraints on the direction of ship's steaming and strong surface flow, a uniform towing direction could not be adopted (Fig. 1). Details of two additional hauls taken with the Woods Hole pattern epibenthic sled (Hessler, Sanders, 1967) and processed as described in Gage *et al.* (1980) are also included.

Samples of *O. lymani* were also studied from bottom hauls made elsewhere in Rockall Trough (Table 2).

Table 1

Granulometry of superficial sediment at station M.

	Coarse to medium sand				Fine to very fine sand				Silt						Clay	
Phi Unit	+0.5	+1.0	+1.5	+2.0	+2.5	+3.0	+3.1	+4.0	+4.5	+5.0	+5.5	+6.0	+7.0	+8.0	+9.0	+10.0
μm	1000-710	710-500	500-351	351-250	250-177	177-125	125-88	88-62	62-44	44-31	31-22	22-16	17-7.8	7.8-3.9	3.9-1.9	1.9-1.0
Percent by weight	0.1	0.4	0.9	3.8	8.0	9.3	8.0	2.7	3.7	2.6	3.0	2.7	7.0	9.0	7.8	6.9
	(wet sieving)								(pipette analysis)							

Table 2

Details of bottom hauls considered in the present investigation.

Station No.	107 a	114	SWT 10	SWT 18	138	139	144	151	153
Date	11 Jul. 1976	28 Sept. 1976	5 Aug. 1977	22 Oct. 1976	23 Feb. 1978	24 Feb. 1978	19 Apr. 1978	6 June 1978	15 Jan. 1979
Gear	Agassiz trawl (AT)	AT	Semi-balloon otter trawl		AT	AT	AT	AT	AT
Mean depth (m)	1 600	2 400	2 019	1 809	2 450	2 450	2 240	2 175	2 200
Position (*)	57°07'N 12°06'W	56°48'N 10°54'W	56°51'N 09°58'W	56°45'N 09°41'W	55°31'N 10°24'W	55°35'N 10°25'W			

Station N:	154	161	167	171	175	176	177	181	184
Date	21 May 1979	8 Aug. 1979	13 Aug. 1979	3 Mar. 1980	28 May 1980	28 May 1980	29 May 1980	16 Sept. 1980	17 Sept. 1980
Gear	AT	AT	AT	AT	AT	Epibenthic sled (ES)	AT	AT	ES
Mean depth (m)	2 264	2 055	2 300	2 225	2 210	2 245	2 200	2 220	2 260
Position (*)		50°52'N 12°21'W							

(*) where not on station "M" (see Fig. 1).

Trawl hauls were sorted on deck. Although the aim was to remove and measure all *O. lymani* in the samples collected in 1979 and 1980, this was not the case in 1978 where only about half of the total catch was retained for study. In the 1978 samples the number of juvenile *O. lymani* was proportionally higher since a deliberate search was made for them on deck amongst the unwanted material. Material usually was fixed in seawater formalin and transferred after about one week to 70 % ethanol after washing. In a few cases the brittlestars were air dried directly after washing in order to facilitate disk measurement. In other samples, disks were measured after blotting damp-dry from the alcohol. Because of the heavily calcified and rigid plate structure of *O. lymani*, the validity of the measurements probably was not affected by these differing treatments; test measurements of specimens measured before and after drying showing no significant change when measured over the same radius-interradius.

Disk diameters were measured to the nearest millimetre from a reference on the dorsal base of the arm midway between the outer edges of the two radial shields (Fig. 2). In small specimens (see Grieg 1921, Plate V, Fig. 8-10), where the radial-shields were not differentiated, the measurement was taken from the outer edge of the two contiguous disk plates.
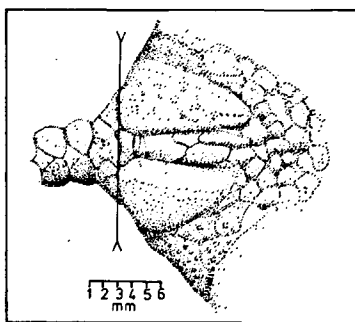

Figure 2

Part of dorsal disk of Ophiomusium lymani *showing the reference point for disk measurements to the opposite interradius.*

For measurements of oocyte size frequencies, the gonad from females in subsamples of 25 large specimens was dissected out, embedded in paraffin wax and sectioned at 5 µm. The diameters of at least 100 oocytes from each female specimen were measured in each sample using 40-µm increments from 20 to 420 µm.

RESULTS

Size structure of the population and sampler bias

Frequencies of the disk measurements from the Agassiz and epibenthic sled samples at station « M » are given in Table 3 and shown as percent frequencies in Figure 3.

In every sample, the right-hand frequencies are numerically dominated by large individuals with a mode at 26-27 mm. Smaller individuals from the Agassiz samples are less numerous and spread over a wide range of frequencies from about 2-3 mm (corresponding to Grieg, 1921, Plate V, Fig. 8, and Schoener, 1967, Fig. 3 E) up to around 20 mm when the animals become reproductively mature (see below). The coarse meshes of
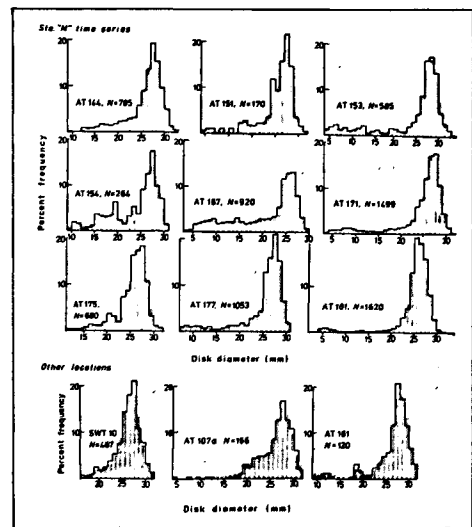

Figure 3

Percent size frequencies histograms of frequency data listed in Table 3 (except for samples ES 176 and ES 184) showing fitted Gaussian mixtures (stippled).

the Agassiz trawl net (mesh aperture ca. 10 mm when fishing) made it unlikely that the smallest postlarvae (Fig. A-D in Schoener, 1967) would be caught, since their overall diameter including arms would not exceed 10 mm.

Winnowing of the material within the open-mouthed sampler when it was being winched back to the ship must also have resulted in a selective loss of the smaller, lighter bodied juveniles.

A mouth-closing gate and a long extension to the fine-meshed (0.5-mm meshes) cod end (for further details see Gage *et al.*, 1980) minimized sample winnowing, and hence selective loss of small, light-bodied juvenile stages, from the epibenthic sled hauls.

Size frequencies from the two sled hauls (Fig. 4) reflect this in the presence of large numbers of such postlarval stages in the distribution. On the assumption that there was no bias in the sled hauls operating against capture of the large individuals, the sled samples are taken as reasonably unbiased samples of the total parent population.

Although the resulting size distributions appear markedly bimodal, the postlarval and adult modes are well separated by a range of low frequencies of juvenile and young adult stages with no really obvious peaks.
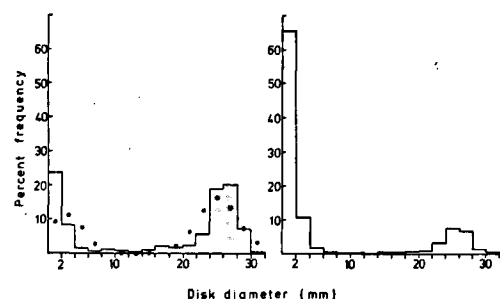

Figure 4

Expected frequencies of bimodal (filled circles) and polymodal (stippled) mixtures fitted to the two epibenthic sled samples (ES 176 and ES 184) taken on station "M". Probably because the first (postlarval) mode was very skewed, it was found difficult to fit a normal distribution; and it was not possible to fit a polymodal mixture with frequencies < 8 mm included.

Table 3

Disk-size frequencies of Ophiomusium lymani *from Station "M" and elsewhere.*

| | Size group (mm) | | | | | | | | | | | | | | | | | |
Sample	0-0.9	1.0-1.9	2.0-2.9	3.0-3.9	4.0-4.9	5.0-5.9	6.0-6.9	7.0-7.9	8.0-8.9	9.0-9.9	10.0-10.9	11.0-11.9	12.0-12.9	13.0-13.9	14.0-14.9	15.0-15.9	16.0-16.9	17.0-17.9
AT 107a	–	–	–	–	1	–	–	1	–	1	–	–	1	1	–	–	1	1
AT 101	–	–	–	–	–	–	–	–	–	1	1	2	2	–	–	–	–	1
SWT 10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1
Station "M"																		
AT 144	–	–	–	–	–	–	–	–	2	1	–	–	7	6	7	8	13	12
AT 151	–	–	–	–	2	1	1	–	–	1	2	2	–	2	–	2	–	4
AT 153	–	–	–	–	7	11	14	7	10	6	7	10	13	2	6	8	4	3
AT 154	–	–	1		4	4	5	4	1	1	5	4	1	2	3	10	9	8
AT 167	–	–	–	2	4	15	18	22	23	27	18	19	21	19	29	22	17	19
AT 171	–	–	–	1	10	12	14	19	19	16	11	11	8	10	7	12	12	18
AT 175	–	–	–	–	–	–	–	–	–	–	–	3	3	2	5	10	10	8
ES 176	33	63	22	11	1	6	1	3	5	1	2	2	2	1	3	2	3	7
AT 177	–	–	–	2	7	17	18	9	13	10	12	11	6	11	3	5	8	12
AT 181	–	–	1	2	14	16	11	8	5	2	3	5	6	8	3	3	6	7
ES 184	448	320	90	36	11	9	4	1	2	0	1	1	0	0	2	1	2	2

Sample	18.0-18.9	19.0-19.9	20.0-20.9	21.0-21.9	22.0-22.9	23.0-23.9	24.0-24.9	25.0-25.9	26.0-26.9	27.0-27.9	28.0-18.9	29.0-29.9	30.0-30.9	31.0-31.9	32.0-32.9	33.0-33.9	36.0-36.9
AT 107a	3	5	4	7	8	8	9	14	21	28	21	18	10	3	–	–	–
AT 101	4	2	–	1	3	4	6	7	14	25	21	14	8	4	–	–	–
SWT 10	3	11	7	11	17	24	35	67	84	98	50	36	15	6	–	–	–
Station "M"																	
AT 144	11	14	18	19	23	24	45	70	106	151	120	75	40	11	4	1	–
AT 151	5	3	3	4	4	6	17	16	27	37	25	6	3	1	–	–	1
AT 153	10	9	6	5	13	18	28	52	97	102	81	30	16	8	2	–	–
AT 154	9	17	6	4	9	14	10	24	33	46	26	19	4	–	–	–	–
AT 167	22	26	26	27	32	51	108	119	122	74	30	8	–	–	–	–	–
AT 171	17	21	24	32	47	93	116	187	259	268	162	69	23	6	–	–	–
AT 175	7	13	24	21	13	49	58	111	118	125	72	23	8	4	–	–	–
ES 176	4	4	5	6	4	20	29	48	40	42	27	3	2	–	–	–	–
AT 177	14	14	20	14	31	36	47	136	169	222	161	70	19	–	–	–	–
AT 181	8	9	17	26	54	87	214	335	308	263	137	49	10	2	0	1	–
ES 184	1	7	7	4	14	23	29	61	55	26	10	4	3	–	–	–	–

Periodicities in size structure

Visual comparison of histograms of the intermediate disk-size frequencies in the series of Agassiz trawl samples, however, suggested an underlying polymodality, but one which was by no means clearly evident in all the samples.

This seemed possibly the consequence of the varying sample size, the largest samples showing most clear evidence of polymodality. Taking one of the largest samples, AT 171 (where $N = 1\,499$), as illustrative of this underlying polymodality, the frequency histogram suggests a juvenile peak of a wide dispersion and a mode at about 8 mm (Fig. 3). Another widely dispersed peak is indicated at about 18 mm, with a third, possibly less dispersed, at about 24 mm that bulges the left hand tail of the conspicuous mode of large-sized adults.

If we make the assumption that the parent distribution is a mixture of Gaussian (normal) size-frequency distributions, the components of the sample become identifiable in terms of their means and standard deviations, and the mixture in terms both of these values and in the proportion of these components. It then becomes possible to analyse the data using a variety of graphical and statistical procedures in order to arrive at the best fitting model distribution.

The alternative, or null, hypothesis would be that no such periodicities are present and that hence intermediate frequencies represent either the overlapping tails of a postlarval and an adult peak, or a continuous distribution with no central value between postlarval and adult modes.

In proceeding with the analysis, the choice between the two hypotheses was based on not only goodness-of-fit but also that the models fitted are consistent with each other and make biological sense. For example, we should reject as implausible a result identifying components which could not easily be identified in consecutive samples, or if identifiable implied negative rather than positive growth of a component.

Mixture analysis of disk-size frequencies

Numerical methods of analysis of grouped data consisting of distribution mixtures has become feasible with the development of fast computer search methods employing efficient function minimization algorithms (Hasselblad, 1966; Macdonald, 1969; 1975).

The method applied in the present investigation employed the interactive computer program described by Macdonald and Pitcher (1979) for age grouping of

fisheries data. The statistical basis of the method is fully described in their paper. By alternating between a Nelder-Mead constrained direct search for optimal estimates of means and standard deviations and fast iterative calculations, a model distribution mixture is fitted and progressively refined until parameter estimates and goodness-of-fit stabilize, and the precision of the parameter estimates is acceptable. The user specifies constraints on parameters based on other information or a particular hypothesis.

By including the postlarval frequencies, the two epibenthic sled samples (ES 176 and ES 184) represent the least biased samples of the total population available. The observed frequencies hence allow test of the null hypothesis that the intermediate frequencies represent no more than the overlapping tails of the postlarval and adult modes. The results of such a bimodal fit (Fig. 4) clearly lead us to reject the null hypothesis in favour of a polymodal fit with four or five normal components.

We then proceeded on the assumption that the largest sample by visual inspection probably would give us the best guess of the actual number of possible components, and their parameter values, assuming the underlying distribution to be Gaussian.

Starting values were estimated visually, from a histogram of the size frequencies for AT 171. These values were then refined to those listed in Table 4. It will be noted that the best fit was obtained for a heteroscedastic mixture where the intermediate proportions were each roughly one tenth of the total.

A further approach towards biological and statistical plausibility was made by analysing the three replicate samples (AT 175, ES 176 and AT 177) obtained on 28-29 May 1980 nearly three months after AT 171. Sample AT 175 was recovered with ripped net, hence diminishing the representation of the smaller lighter-bodied individuals through winnowing. However, there was good agreement in terms of values of fitted normal parameters between ES 176 and AT 177, and the larger disk-size components of AT 175; the widely dispersed components in the smaller sizes showing most variation.

When these component estimates are compared to those fitted to AT 171, a pattern of increased means is evident in all except the largest adult mode. However, a smaller increment is evident amongst the larger disk sizes; this being associated also with a decrease in standard deviation. This might be interpreted as a slowing of growth with increased disk size; growth at reproductive maturity being sufficiently slow to result in the merging of successively recruited year classes into a single, numerically dominant, adult mode.

A growth in component means could not be obtained when alternative polymodal distributions with one fewer component were fitted, although goodness-of-fit often compared well with those including the additional component. We therefore adopted constraints in computer analysis of the remaining Agassiz samples that were based on the previous hypothesis. This assumed three or four components with means showing a pattern of decreasing growth increments with age and a corresponding contraction in component dispersion, but with no significant decrease in the proportional size of year classes as they become absorbed into the large adult peak. The results of these fits are given in Table 4 while Figure 3 shows the expected frequencies of the fitted Gaussian mixtures plotted on the observed data.

Growth of age classes

The apparent slowing of brittlestar disk growth with age suggests the possibility of describing population growth in terms of the von Bertalanffy growth equation:

$$l_t = L_\infty - (L_\infty - L_0) e^{-Kt},$$

Table 4

Parameter estimates of Gaussian mixtures fitted to disk-size frequencies of the samples of Ophiomusium lymani *shown in Figure 3. Station "M" samples are identified by italics.*

Sample	Proportions (as fractions)				Means (mm)				Standard deviations (mm)			
	π_1	π_2	π_3	π_4	μ_1	μ_2	μ_3	μ_4	δ_1	δ_2	δ_3	δ_4
AT 107a	0.09	0.16	0.75	–	18.00	21.97	27.63	–	4.00	1.57	1.91	–
SWT 10	0.11	0.89	–	–	21.09	26.93	–	–	2.07	1.86	–	–
AT144	0.10	0.11	0.79	– ;	16.88	22.23	27.59	–	2.82	1.87	1.76	–
AT151	0.04	0.10	0.11	0.74	11.59	18.67	23.47	27.10	1.70	1.67	1.50	1.51
AT153	0.14	0.10	0.08	0.67	8.72	18.27	24.22	27.49	3.12	3.62	1.68	1.60
AT154	0.05	0.25	0.12	0.58	11.20	18.09	23.66	27.43	1.48	2.16	1.19	1.37
AT161	0.05	0.06	0.10	0.79	11.21	18.96	23.72	28.10	2.00	1.00	1.06	1.64
AT167	0.16	0.14	0.13	0.57	8.59	15.00	20.49	25.73	2.27	2.22	1.72	1.56
AT171	0.08	0.09	0.15	0.68	8.21	18.19	23.58	27.02	2.34	3.05	1.60	1.53
AT175	0.07	0.11	0.30	0.52	16.64	21.41	25.17	27.38	2.91	1.60	1.25	1.36
ES176	0.05	0.15	0.33	0.46	9.23	18.89	25.16	26.92	1.91	3.18	1.47	1.48
AT177	0.07	0.08	0.06	0.78	10.75	19.57	23.00	27.21	2.76	2.17	1.00	1.47
AT181	0.04	0.02	0.11	0.83	5.94	12.55	22.90	26.23	1.43	1.63	3.47	1.61
ES184	0.04	0.09	0.87	–	13.09	20.32	25.75	–	3.00 (*)	1.50 (*)	1.50 (*)	–

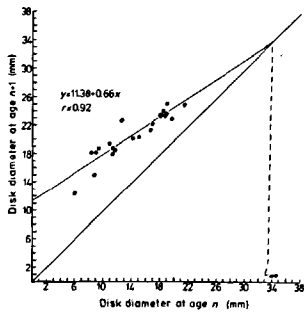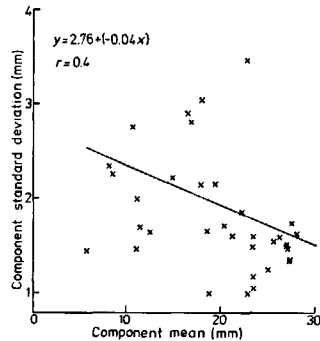(*) Not estimated, starting values available only

Figure 5
"Ford-Walford" plot of year-class-means estimated from the fitted normal mixtures.

Figure 6
Regression of standard deviations of components of fitted mixtures plotted against their means.

where l_t = disk size at time where $t = n$, an integral number of years; and L_0 and L_∞ are constants, respectively, representing size at zero age and maximum possible size (Crisp, 1971; Ricker, 1975). The "Ford-Walford" plot (Walford, 1946; Crisp, 1971) shown in Figure 5. indicates that juvenile (disk diameter < ca. 20 mm) growth may be acceptably modelled by a growth increment described by the slope of the regression of l_{n+1} on l_n (where slope = e^{-K}) using the means of the fitted normal components as estimates of l_n. The expected contraction in dispersion of age classes implied by von Bertalanffy growth is demonstrated in Figure 6. The scatter of these estimates probably results from non-normality and overlapping of components; the estimates of means probably being less affected by these factors (McNew, Summerfelt, 1978). The estimates of L_∞ agrees well with the maximum size of individuals observed in the samples (Fig. 3). Von Bertalanffy growth curves estimated from the juvenile year-class means as described previously show best fit to a plot of the estimated component parameters with time when recruitment (L_0) occurs in the middle of the year (Fig. 7).
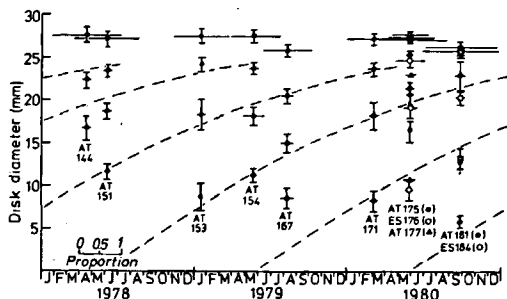

Figure 7
Parameter estimates of fitted 4-component mixtures from station "M" time series shown with fitted von Bertalanffy growth curves derived from Ford-Walford plots.

Estimates of year-class survivorship from the estimated component proportions given in Table 4 are difficult owing to the error associated with the scatter in component dispersions referred to above. However, a low or zero mortality is suggested from the constancy apparent in proportions of consecutive juvenile components. Assuming the fitted von Bertalanffy growth parameters apply also to adults, this would result in a negatively skewed peak near L_∞ representing the merging of adult year classes approaching asymptotic growth. Clearly such a model does not fit in with observed size structure where a roughly normally distributed peak of adult frequencies occurs with a mean at about 27 mm. Even if a considerably higher mortality than that operating on juveniles applies to adults, a reduced growth rate at the onset of reproductive maturity is necessitated in order to account for the position and size of the observed adult mode. Otherwise the observed frequencies would far exceed those expected on the basis of merging of year classes. Although such slowed adult growth is biologically reasonable as a result of the metabolic "cost" of reproduction, a difficulty remains in that the markedly reduced growth increment necessitated by this hypothesis would reduce L_∞ to a value far short of that observed. Possibly adults surviving after reproduction grow faster again. However, there is a possible interaction of age specific growth and mortality schedules that models the observed adult size structure but it will not be further pursued here.

Size at reproductive maturity

No gonads were found in specimens measuring less than 14 mm in disk diameter. In individuals of 14-20 mm, gonads were not easily visible to the naked eye but histological examination demonstrated the presence of small, newly developed gonads with a maximum oocyte size of 200 μm. In specimens > 20 mm, gonadal development proceeded through to previtellogenesis followed by a limited number of oocytes entering vitellogenesis (Tyler, Gage, 1979). For the determination of reproductive periodicity specimens with a disk diameter > 20 mm were used.

Sex ratio and hermaphroditism

Only females were used in determination of reproductive maturity in the present investigation. However, of the 25 individuals examined from each sample, there were slightly more females than males, this difference from the expectation of equality probably being significant ($t = 2.89$ for 12 df $p < 0.02$, two tailed). A low percentage (2 — 3 %) of the individuals examined showed evidence of hermaphroditism. These hermaphrodites, however, were confined to five samples (see Table 6). The hermaphroditism varied from intragonadal to intergonadal. The incidence of hermaphroditism showed no correlation to either time of year or, when samples other than those from Station M were included, to sample depth.

Egg size, fecundity and reproductive potential

The maximum egg size observed in *Ophiomusium lymani* was 460 μm. However, only 15% of all oocytes counted were larger than 300 μm, suggesting that only a limited number of oocytes undergo vitellogenesis at any time. Calculation of potential fecundity from clutch size suggests that a maximum of 12000 eggs could be produced by a single individual, although only approximately 1800 eggs per individual were >300 μm. As there appears to be no obvious seasonal periodicity in oogenesis (see below), measurement of relative biomass devoted to reproduction, or "reproductive potential" (*sensu* Scheltema, 1972) does not present the seasonal problem encountered with the species *Ophiura ljungmani* (Tyler, Gage, 1980).

Measurement of oocyte number and volume (Table 5) and a mean fecundity of 9500 give a total egg volume of 24.48 mm³ and a reproductive potential (=disk diameter divided by gonad volume) of 0.96, slightly greater than that for *O. ljungmani*.

Periodicity in gametogenesis

A total of 300 specimens (180 females) were examined from different samples (Fig. 8). The oocyte-size frequencies observed for each specimen in a sample were compared with the chi squared expectation in k by r contingency tables. The values of total chi squared for each sample were in every case in excess of the 0.001% level for $(k-1)(r-1)$ degrees of freedom in Table 8 of Pearson and Hartley (1966), indicating significant differences between oocyte size frequencies of individuals within each sample. If the individual sets of frequencies
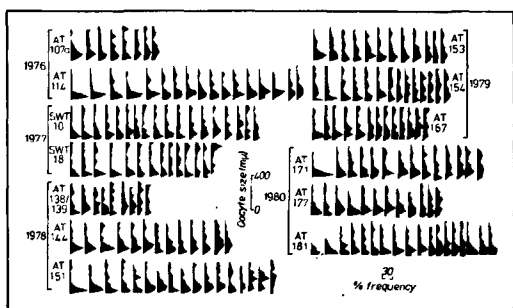
Figure 8

Oocyte size frequencies of all Ophiomusium lymani *examined.*
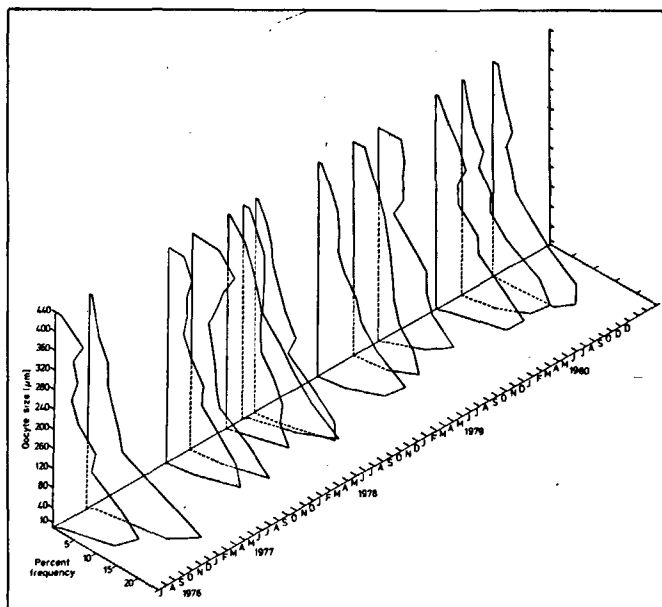
Figure 9

Oocyte size frequencies, averaged for each sample, plotted against time.

are then averaged for each sample (Fig. 9) the samples may be compared in a similar contingency table (Table 6). A total chi squared of 121.55 with 121 df suggests neither total synchrony nor total asynchrony of oocyte development ($Q=0.5\%$).

We believe these data to suggest no obvious annual periodicity, but we cannot preclude the possibility of a longer (>1 year) periodicity in reproduction.

When the values of chi squared for each cell of the table are compared in terms of differences between oocyte size classes, it is evident that the greatest variation occurs amongst oocytes <20 μm and >380 μm in diameter. When these cell values are excluded, the null hypothesis of no difference between samples may be accepted. This suggests to us that there is a large "pool" of previtellogenic and early vitellogenic oocytes that are being continually augmented by developing oogonia, and are continually releasing oocytes to develop to maximum maturity before release.

In a single very large specimen (36 mm disk diam.) examined from AT 151, there were no obvious gonads present. Possibly those few individuals reaching this size enter a period of reproductive senility before death, as has been recorded in populations of the sea star *Asterias*

Table 5

Oocyte volume (mm³) per oocyte size group and "reproductive potential" in Ophiomusium lymani.

	Oocyte size-group (mm)											
	0-20	20-59	60-99	100-139	140-179	180-219	220-259	260-299	300-339	340-379	380-419	>420
Egg volume (mm³)	5.22 × 10⁻⁷	3.34 × 10⁻⁵	2.67 × 10⁻⁴	9.02 × 10⁻⁴	2.138 × 10⁻³	4.176 × 10⁻³	7.216 × 10⁻³	0.011	0.017	0.024	0.033	0.044
Total oocyte volume (mm³)	1.5 × 10⁻⁴	0.07	0.68	1.21	1.99	2.58	3.61	6.61	6.53	6.41	3.84	1.01

Table 6

Numbers and sexual status of specimens dissected and values of total chi squared from contingency-table analysis of oocyte-size frequencies within each sample.

Sample

	AT 107a	AT 114	SWT 10	SWT 18	AT 138/139	AT 144	AT 151	AT 153	AT 154	AT 167	AT 171	AT 177	AT 181
Females	8	17	18	14	9	13	17	13	14	13	14	12	18
Males	13	5	7	10	12	11	8	12	11	12	9	12	6
Immature	–	3	–	–	1	–	–	–	–	–	–	–	–
Hermaphrodite	4	–	–	–	–	1	–	–	–	–	2	1	1
χ^2	132.8	503.0	323.6	366.8	203.9	258.8	696.5	187.3	332.8	310.7	601.6	284.3	670.2
df	66	176	187	143	88	132	176	121	143	132	143	121	187
Q							<0.001						

rubens (Thorson, 1946) and the spatangoid urchin *Brissopsis lyrifera* (Mortensen, 1920; Brattström, 1946).

Life-history of Ophiomusium lymani

The pattern of intermediate modes revealed by the analysis of disk-size frequencies is strongly suggestive of a pattern of annual reproduction, with each intermediate component representing a single year class. Although a shorter periodicity than a year may be envisaged, such as one cued to tidal rhythms, the rate of growth increments necessary would far exceed those known for shallow water populations of species of coastal brittlestars (Taylor, 1958; Buchanan, 1964; 1967; Gorzula, 1977). We therefore regard the latter alternative as biologically less reasonable.

The relatively dispersed and overlapping intermediate modes, together with a tendency to an irregular, and perhaps even bimodal, outline within each of them (Fig. 3) would account for their sometimes rather poor and variable fit to the normal distribution (Table 4). This may result from an extended breeding season, possibly with two peaks in the rate of generation of larvae. However, consideration of the conspicuous absence of any seasonal periodicity in oocyte size frequencies forces us to unequivocally reject any hypothesis based on a seasonality in reproduction. The resulting paradox although embarrassing is not irreconcilable: we postulate an annual peak in recruitment based on seasonal changes in larval survival.

Support for such a notion comes from a comparison of the relative numbers of postlarvae present in the two epibenthic sled samples:

· 1980

	28 May (%)	17 September (%)
Proportion of total sample comprised of individuals <6 mm disk diameter (see also Fig. 4)	32.8	77.1

If in the food-poor deep sea the amount of detrital organic material, as the chief source of food available, varies seasonally, the survival of postlarvae metamorphosing from lecithotrophic larvae that are produced continuously should show a similar periodicity, with a lag determined by the fecundity of females and the duration of the larval stage.

Such a process may explain the somewhat irregular, or even slightly biomodal, outline of the histograms for each of the intermediate components seen in Figure 3: we propose these directly reflect the typical annual cycle in plankton production in the North Atlantic, where a sharp peak in spring is followed by a slow decline and sometimes a secondary peak in the autumn (Heindrich, 1962). However, other sources of seasonal forcing having a similar effect, such as seasonal periodicities in food-transporting bottom currents, cannot be precluded. Although the annual cycle of zooplankton biomass lags behind that of phytoplankton, it is similar in pattern; for example, that for the ubiquitous, and probably quantitatively dominant copepod, *Calanus finmarchicus*, showing significant variation only in the timing of its cycle throughout its range (Matthews, 1969).

Although the numerical method of analysis employed evidently was robust enough to allow fitting normal mixtures to these data, the difficulty experienced in estimating the widely dispersed intermediate components (reflected in the wide spread and larger standard errors of the estimates of juvenile compared to adult parameters given in Table 4) is not surprising. The normal model would best fit recruitment resulting from simultaneous reproduction triggered by optimization of a physical variable such as temperature. McNew and Summerfelt (1978) comment that such normality in age-class structure may even then be unexpected since it demands besides a short, uninterrupted breeding season and a normal distribution in frequency of spawning, that juveniles feed and hence grow at uniform rate.

Accelerated transfer of surface production to the deep sea by fast sinking of detrital aggregates such as copepod faecal pellets (McCave, 1975; Wiebe et al., 1976; Bishop et al., 1977; Honjo, 1978; Knauer et al., 1979) would be expected to result in a seasonal variation in both quantity and quality food available to the benthos. Deuser and Ross (1979) provide preliminary evidence for seasonal fluctuations in sedimentation in the deep Sargasso Sea.

Comparison of the two late summer samples with the remainder shows a drop in modal disk-size of the adult peak. It was not possible by finer size grouping to resolve the component, just recognizable in the preceding May, that had merged into the adult mode in the late summer samples of 1979 and 1980. However, we feel that the shift downwards in modal size may reflect a mortality mainly amongst the largest individuals.

We therefore postulate a seasonal recruitment of juveniles to the population as a direct response to seasonal sedimentation of organic aggregates enhancing the survival of larvae newly metamorphosed (and measuring around 0.6 mm disk diameter) from an abbreviated, lecithotrophic demersal phase. Fitted von Bertalanffy growth curves (Fig. 5, 7) suggest juveniles grow to about 11-12 mm in disk diameter in their first year. Thereafter incremental growth slows to about 7-8 mm in their second year and to 5 mm or less in their third, when they attain reproductive maturity and breed. A low rate of mortality in the juvenile year classes is suggested by the almost uniform proportions of the corresponding fitted components (Table 4). We have previously suggested that the observed adult size structure may result from interaction of slower growth and increased mortality amongst adults.

Possibly, the slightly smaller mean disk size of the adult peak that was observed in the late summer of two consecutive years reflects mortality amongst adults being intensified at this time. However, we can offer no explanation why survival of adults declines in summer, while that of juveniles is enhanced.

CONCLUSION

By fitting alternative Gaussian mixtures to disk-size frequencies of samples of Ophiomusium lymani from localities in the Rockall Trough area (NE Atlantic), a polymodal, rather than bimodal, size structure clearly is more appropriate. Comparison of the parameters of the mixtures fitted to a 3-year time series of samples from a fixed station indicate a pattern of annual recruitment. Von Bertalanffy growth structure fitted to the estimated component means indicate juveniles probably grow to about 11-12 mm in disk diameter in their first year. In their second year growth slows to an increment of about 7-8 mm, and to about 5 mm or less in their third year, when they have attained reproductive maturity.

Thereafter, the year classes merge into a numerically dominant adult mode. Mortality amongst juveniles > 5 mm probably is low since each juvenile component was estimated as a roughly constant proportion (ca. 10%) of the total. Adult mortality may be relatively high, and may increase in summer. It is thought likely that only a tiny proportion of individuals comprising each juvenile year class survive to asymptotic growth.

Comparison of oocyte-size frequencies by contingency table analysis, both between individuals of a sample and between samples compared as averaged frequencies, however, shows no annual periodicity in oogenesis, the gonad apparently remaining active at low level throughout the year. We reconcile this to the inferred pattern of annual recruitment by postulating a seasonal cycle in survival of postlarvae: this may occur in response to annual fluctuation in flux of organic particles from the surface, which may constitute their prime source of food; this cycle reflecting the seasonal cycle of primary production.

The marked increase in proportion of postlarvae observed in a late summer sample taken with the epibenthic sled compared to that taken in spring supports this hypothesis.

Clear annual cycles in oceanic production are absent in the tropics, hence a bimodal rather than polymodal size structure may be expected there. Similar analysis applied to samples of this brittlestar from low latitudes therefore may provide a test of the validity of our hypothesis.

REFERENCES

Ahlfeld T. E., 1977. A disparate seasonal study of reproduction of eight deep-sea macroinvertebrate species from the Northwestern Atlantic Ocean, Ph. D. Thesis, Florida State Univ., 108 p.

Barham E. G., Ayer J. J., Boyce R. E., 1967. Macrobenthos of the San Diego Trough: photographic census and observations from bathyscaphe, Trieste, Deep-Sea Res., 14, 773-784.

Bishop J. K. F. B., Ketten D. R., Edmond J. M., 1977. The chemistry, biology and vertical flux of particulate matter from the upper 400 m of the Cape Basin in the southeast Atlantic Ocean, Deep-Sea Res., 25, 1121-1161.

Brattström H., 1946. Observations on Brissopsis lyrifer (Forbes) in the Gullmar Fjord, Ark. Zool., 37 A, 18, 27 p.

Buchanan J. B., 1964. A comparative study of some features of the biology of Amphiura filiformis and Amphiura chiajei (Ophiuroidea) considered in relation to their distribution, J. Mar. Biol. Assoc. UK, 44, 565-576.

Buchanan J. B., 1967. Dispersion and demography of some infaunal echinoderm populations, Symp. Zool. Soc. Lond., 20, 1-11.

Cassie R. M., 1954. Some uses of probability paper in the analysis of size frequency distributions, Aust. J. Mar. Freshwater Res., 5, 513-522.

Cherbonnier G., Sibuet M., 1972. Résultats scientifiques de la campagne Noratlante : astérides et ophiurides, Bull. Mus. Nat. Hist. Nat. Zool., 76, 102, 1333-1394.

Crisp D. J., 1971. Energy flow measurements, in: *Methods for the study of marine benthos*, edited by N. A. Holme and A. D. McIntyre, IBP Handbook, No. 16, Blackwell Scientific Publications, London, 197-279.

Deuser E. G., Ross E. H., 1979. Seasonal change in the flux of organic carbon to the Deep Sargasso Sea, *Nature*, 283, 364-365.

Edelsten D. J., 1980. *Current measurements in the Rockall Channel*, 1978, Scottish Marine Biological Association, Dunstaffnage Marine Research Laboratory, Internal Reports, Series 26.

Ellett D. J., 1978. *Sub-surface temperatures at the Scottish continental slope*, Scottish Marine Biological Association, Dunstaffnage Marine Research Laboratory, Internal Reports, Series 14.

Ellett D. J., Martin J. H. A., 1973. The physical and chemical oceanography of the Rockall Channel, *Deep-Sea Res.*, 20, 585-625.

Fell H. B., 1966. The ecology of ophiuroids, in: *Physiology of echinodermata*, edited by R. A. Boolootian, Interscience, New York, 129-143.

Gage J. D., Lightfoot R. H., Pearson M., Tyler P. A., 1980. An introduction to a sample time-series of abyssal macrobenthos: methods and principle sources of variability, *Oceanol. Acta*, 3, 2, 169-176.

Gaudette H. E., Flight W. R., Toner L., Folger D. W., 1974. An inexpensive titration method for the determination of organic carbon in recent sediments, *J. Sediment. Petrol.*, 44, 249-293.

Gorzula S. J., 1977. A study of growth in the brittle-star *Ophiocomina nigra*, *West. Naturalist*, 6, 13-33.

Grassle J. F., Sanders H. L., Hessler R. R., Rowe G. T., McLellan T., 1975. Pattern and zonation: a study of the bathyal megafauna using the research submersible *Alvin*, *Deep-Sea Res.*, 22, 457-481.

Grieg J. A., 1921. Echinodermata, *Rep. Sci. Results Michael Sars N Atlantic Deep Sea Exped.* 3, 1, 1-47.

Haedrich R. L., Rowe G. T., Polloni P., 1975. Zonation and faunal composition of epibenthic populations on the continental slope south of New England, *J. Mar. Res.*, 33, 191-212.

Harding J. P., 1949. The use of probability paper for the graphical analysis of polymodal distributions, *J. Mar. Biol. Assoc. UK*, 28, 141-153.

Hasselblad V., 1966. Estimation of parameters for a mixture of normal distributions, *Technometrics*, 8, 431-441.

Heindrich A. K., 1962. The life histories of plankton animals and seasonal cycles of plankton communities in the oceans, *J. Cons. Int. Explor. Mer.*, 27, 15-24.

Hendler G., 1975. Adaptational significance of the patterns of ophiuroid development, *Am. Zool.*, 15, 691-715.

Hessler R. R., Sanders H. L., 1967. Faunal diversity in the deep sea, *Deep-Sea Res.*, 14, 65-78.

Honjo S., 1978. Material fluxes and modes of sedimentation in the mesopelagic and bathypelagic zones, *J. Mar. Res.*, 38, 93-97.

Knauer G. A., Martin J. H., Bruland K. W., 1979. Fluxes of particulate carbon, nitrogen and phosphorus in the upper water column of the Northeast Pacific, *Deep-Sea Res.*, 26, 97-108.

Lonsdale P., Hollister C. D., 1979. A near bottom traverse of Rockall Trough: hydrographic and geologic interferences, *Oceanol. Acta*, 2, 1, 91-105.

Macdonald P. D. M., 1969. Fortran programme for statistical estimation of distribution mixtures: some techniques for statistical analysis of length-frequency data, *Fish. Res. Board Can. Tech. Rep.*, 129, 45 p.

Macdonald P. D. M., 1975. Estimation of finite distribution mixtures, in: *Applied statistics*, edited by R. P. Gupta, North-Holland, Amsterdam, 231-245.

Macdonald P. D. M., Pitcher T. J., 1979. Age-groups from size-frequency data: a versatile and efficient method of analyzing distribution mixtures, *J. Fish. Res. Board Can.*, 36, 987-1001.

Madsen F. J., 1951. Ophiuroidea, *Rep. Swedish Deep-Sea Exped.*, 2, 105-117.

Matthews J. B. L., 1969. Continuous plankton records: the geographical and seasonal distribution of *Calanus finmarchicus* s. l. in the North Atlantic, *Bull. Mar. Écol.*, 6, 251-273.

McCave I. V., 1975. Vertical flux particles in the ocean, *Deep-Sea Res.*, 22, 491-502.

McNew R. W., Summerfelt R. C., 1978. Evaluation of a maximum-likelihood estimator for analysis of length-frequency distributions, *Trans. Am. Fish Soc.*, 107, 730-736.

Menzies R. J., George R. Y., Rowe G. T., 1973. *Abyssal environment and ecology of the world oceans*, John Wiley and Sons, New York, 488 p.

Mileikovsky S. A., 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-valuation, *Mar. Biol.*, 10, 193-213.

Mortensen T., 1920. Notes on the development and larval forms of some Scandinavian echinoderms, *Vidensk. Medd. Dansk. Naturh. Foren. Kbh.*, 7, 133-160.

Mortensen T., 1927. *Handbook of the echinoderms of the British Isles*, Oxford University Press, 471 p.

Mortensen T., 1933. Ophiuroidea, *Danish Ingolf-Exped.*, 4, 121 p.

Pearson E. S., Hartley H. O., 1966. *Biometrika tables for statisticians*, 3rd ed., Cambridge University Press, 264 p.

Ricker W. E., 1975. Computation and interpretation of biological statistics of fish populations, *Fish. Res. Board Can. Bull.*, 191, 382 p.

Roberts D. G., 1975. Marine geology of the Rockall Plateau and Trough, *Philos. Trans. R. Soc. Lond.*, Ser. A, 278, 447-509.

Rokop F. J., 1974. Reproductive patterns in the deep-sea benthos, *Science*, 186, 743-745.

Rokop F. J., 1975. Breeding patterns in the deep sea, *Ph. D. Thesis*, Univ. California, San Diego, 174 p.

Rowe G. T., 1971. Observations on bottom currents and epibenthic populations in Hatteras Submarine Canyon, *Deep-Sea Res.*, 18, 569-581.

Scheltema R., 1972. Reproduction and dispersal of bottom dwelling deep-sea invertebrates: a speculative summary, in: *Barobiology and the experimental biology of the deep sea*, edited by R. W. Brauer, Univ. North Carolina, Chapel Hill, 177-186.

Schoener A., 1967. Post-larval development of five deep-sea ophiuroids, *Deep-Sea Res.*, 14, 645-660.

Schoener A., 1968. Evidence for reproductive periodicity in the deep sea, *Ecology*, 49, 81-87.

Schoener A., 1972. Fecundity and possible mode of development of some deep-sea ophiuroids, *Limnol. Oceanogr.*, 27, 193-199.

Sokolova M. N., 1957. The feeding of some carnivorous deep-sea benthic invertebrates of the eastern seas and the northwest Pacific Ocean (in Russian), *Trudy Inst. Oceanol. Akad. Nauk SSSR*, 20, 227-244 (English translation published by the American Institute of Biological Science, Washington, DC, 1959).

Taylor A. M., 1958. Studies on the biology of the offshore species of Manx Ophiuroidea, *M. Sci. Thesis*, Univ. Liverpool, 59 p.

Thorson G., 1946. Reproduction and larval development of Danish marine bottom invertebrates, *Medd-Kommn Dan. Fisk. Havunders.*, Ser. Plankton, 4, 1, 523 p.

Tyler P. A., Gage J. D., 1979. Reproductive ecology of deep-sea ophiuroids from the Rockall Trough, in: *Cyclic phenomena in marine plants and animals*, edited by E. Naylor and R. G. Hartnoll, Pergamon Press, Oxford, 1979, 215-222.

Tyler P. A., Gage J. D., 1980. Reproduction and growth of the deep-sea brittlestar *Ophiura ljungmani* (Lyman), *Oceanol. Acta*, 3, 2, 177-185.

Walford L. A., 1946. A new graphic method of describing the growth of animals, *Biol. Bull. Mar. Biol. Lab.*, Woods Hole, 90, 141-147.

Wiebe P. H., Boyd S. H., Winget C., 1976. Particulate matter sinking to the deep-sea floor at 2000 m in the Tongue of the Ocean, Bahamas, with a description of a new sedimentation trap, *J. Mar. Res.*, 34, 341-354.

Wigley R. L., Emery K. O., 1967. Benthic animals, particularly *Hyalinoecia* (Annelida) and *Ophiomusium* (Echinodermata), in sea-bottom photographs from the continental slope, in: *Deep-sea photography*, edited by J. B. Hersey, the John Hopkins Press, Baltimore, 235-249.

PUBLICATION ANNOUNCEMENT

Undergoing the last stages of printing is at present the *Atlas of the Zooplankton of the Southwestern Atlantic and methods in marine zooplankton research,* which will be available by the end of 1981.

The book, which comprises about 1000 pages+350 figures+60 plates, was edited by Demetrio Boltovskoy, and includes contributions prepared by A. Alvarino (USA), M. V. Angel (UK), T. Antezana (Chile), E. Balech (Argentina), J. R. Beers (USA), T. S. K. Bjôrnberg (Brazil), D. Boltovskoy (Argentina), E. Boltovskoy (Argentina),E. E. Boschi (Argentina), E. Brinton (USA), F. Campaner (Brazil), L. R. A. Capurro (UN, IOC), J. D. de Ciechomski (Argentina), G. B. Esnal (Argentina), S. Frontier (France), S. S. Jankilevich (Argentina), F. C. Ramirez (Argentina), H. F. Steedman (UK), S. Souto (USA), C. Støp-Bowitz (Norway), S. Van der Spoel (The Netherlands), M. O. Zamponi (Argentina).

Its contents is as follows (all texts are in Spanish):

Part I. — Methods in marine zooplankton research.

Collection of *in situ* information. Collection of plankton samples (nets; automatic, continuous and high-speed samplers; pump sampling; bottle sampling). Related problems (shape of sampler, the gauze, dodging, estimation of volume of water filtered, estimation of depth of towing, towing speed, sampling design). Further treatement of the samples (narcotization, relaxation and dying; fixation and preservation, biomass determination; subsampling; fractioning, sorting and picking; counting and data analysis). Marine zooplankton cultivation. General handling of data, literature and material.

Part II. — The Southwestern Atlantic.

Physical features of the SW Atlantic. Water masses of the SW Atlantic. Biological features of the SW Atlantic.

Part III. — Zooplankton of the SW Atlantic.

Radiolaria. Foraminifera. Tintinnina. Siphonophorae. Hydromedusae. Polychaeta. Pteropoda. Cladocera. Ostracoda. Copepoda. Euphausiacea. Decapoda larvae. Chaetognatha. Thaliacea: Salpidae. Appendicularia. Ichtyoplankton.

Each one of the chapters of Part III includes a brief account on the biology, reproduction, general distribution, importance and applications, trophic relationships and methods of research of the particular group. Detailed information is given on the distribution of the species in the Southwestern Atlantic (0 to 60°S and 70 to 25°W), including critical analysis of the previous records in the area under study. The last section of each chapter is devoted to the identification of the species known to occur in the Southwestern Atlantic, including descriptions, keys and illustrations of all the taxa.

The book is being published by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP, Argentina).

For further information contact the editor:

Dr.Demetrio Boltovskoy,
Departamento de Ciencias Biológicas,
Facultad de Ciencias Exactas y Naturales,
Universidad de Buenos Aires,
1428 Buenos Aires, Argentina.