

# Reproduction and growth of the deep-sea brittlestar *Ophiura ljunghmani* (Lyman)

Oocytes  
Fecundity  
Population structure  
Recruitment  
Survivorship  
  
Ovocytes  
Fécondité  
Structure de la répartition  
des classes de tailles  
Recrutement  
Capacité de survie

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## ABSTRACT

Reproductive biology and population dynamics of *Ophiura ljunghmani* were studied by measuring disk diameters and by examining oocyte size-frequencies and fecundity from a sequential seasonal series of large samples from a 2900 m deep Permanent Station in the Rockall Trough (Northeast Atlantic). Egg size (max. 90  $\mu\text{m}$ ) and fecundity (up to 57000 eggs per individual) suggests indirect planktotrophic development, while a clear annual cycle in gametogenesis, with probably synchronous spawning in January-February, confirms a marked seasonality that is also seen as an annual, summertime set of postlarvae on to the bottom. Analysis of size structure of the population indicates annually discrete year classes with a maximum longevity of around 10 years. Individuals show fastest growth and lowest survivorship as postlarvae with a higher survivorship and lower growth rate of about 1 mm.yr<sup>-1</sup> among sizes > 1.5 mm. Reproductive maturity is reached in the third year at 3.5-4.0 mm with individuals thereafter probably reproducing annually. Possible factors controlling the annual cycle in the supposedly seasonless deep sea are discussed in relation to the possible significance of a likely seasonal pattern in downward flux of organic particles derived from surface production.

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## RÉSUMÉ

### Reproduction et croissance de l'ophiure benthique, *Ophiura ljunghmani* (Lyman)

Les événements survenus au cours de la vie de *Ophiura ljunghmani* ont été étudiés par la mesure du diamètre du disque, par l'examen de la fréquence des classes de tailles des ovocytes et l'estimation de la fécondité, à partir d'échantillons de grand volume prélevés en 3 ans à 2900 m à une station située dans le bassin de Rockall, dans le nord-est de l'océan Atlantique. La taille des œufs (maximum : 90  $\mu\text{m}$ ) et la fécondité (maximum : 57000 œufs par individu) suggèrent un développement planctonique indirect. Au contraire, un cycle annuel de la gamétogenèse avec, probablement, une ponte synchrone en janvier et février, confirme le caractère saisonnier marqué, qui est en outre corroboré par une limite saisonnière de la dominance des postlarves dans les échantillons d'été. L'analyse de la structure de la répartition des classes de tailles suggère une discrète répartition en classes annuelles, avec une longévité maximale de 10 ans. Les individus de cette espèce ont à la fois une croissance maximale et une survie minimale, en tant que postlarves, et une capacité de survie maximale avec un taux de croissance minimal de 1 mm par an, chez les individus de taille supérieure à 1,5 mm. La maturité sexuelle est atteinte après la troisième année, à la taille de 3,5-4 mm, avec une reproduction probablement annuelle. Le rôle de facteurs contrôlant le cycle annuel de cette espèce dans un environnement sans saison est discuté en relation avec la signification possible des rythmes apparemment saisonniers de la chute de particules organiques depuis la surface.

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## INTRODUCTION

Although information on life-history tactics of deep-sea ophiuroids is scant, data on egg size, fecundity and viviparity have allowed speculation on modes of reproduction (Mortensen, 1933; Schoener, 1972; Hendler, 1975), however, we still lack direct evidence of larval development. Of the deep-sea ophiuroids of the North Atlantic it has been proposed that *Ophiomusium lymani* Wyville Thomson has an abbreviated larval development (Hendler, 1975), whereas *Ophiura ljunghmani* (Lyman) may have an abbreviated development (Hendler, 1975) or indirect development with a pelagic larva (Schoener, 1972; Tyler, Gage, 1979) as is found in most shallow water ophiuroids (Thorson, 1946). Abbreviated development has been found in a limited number of shallow water ophiuroids (Fenaux, 1969; Stancyk, 1973; Hendler, 1977), and Hendler (1975) has proposed that this reproductive strategy may be common amongst deep-sea ophiuroids.

A marked seasonal reproductive periodicity based on the gametogenic cycle has been demonstrated in continental shelf populations of ophiuroids, and suggestions made on the environmental factors initiating and controlling these cycles (Fenaux, 1968; Singletary, 1970; Hendler, 1973; Tyler, 1977). In an apparently seasonless deep sea, such annual patterns of reproduction would not be expected (Orton, 1920). However, Schoener (1968) presented evidence for a seasonal reproduction in the deep-sea brittlestars *Ophiura ljunghmani* and *Ophiomusium lymani* from the Gay Head-Bermuda Transect in the Northwest Atlantic (Sanders *et al.*, 1965). Schoener's (1968) conclusion was based mainly on her interpretation of differences in population structure in summer and winter samples of these two species. Subsequently, Rokop (1974) suggested that populations of *Ophiomusium lymani*, *Ophiacantha normani* Lyman, together with seven out of nine other benthic invertebrate species studied in a seasonal sequence of samples from 1 200 m in the San Diego Trough, were reproductively active throughout the year.

Although such "continuous" or asynchronous reproductive cycles may be common in the deep sea, more recent evidence suggests that annual periodicities in reproductive development may also occur (Mead *et al.*, 1964; Gordon, 1979; Lightfoot *et al.*, 1979).

In the present paper we seek to confirm and extend Schoener's (1968) hypothesis to a consideration of life-history tactics in *Ophiura ljunghmani*. Morphological details of the gametogenic cycle as further evidence for reproductive seasonality in this species are given by Tyler and Gage (1979). The present study is accomplished by examining oocyte size-frequency and fecundity, and by analysing population structure, recruitment, growth and survivorship from measurements of disk diameter.

## MATERIALS AND METHODS

Samples of *Ophiura ljunghmani* were collected in November 1973 and at approximately 2 to 6 months

intervals from November 1975 to June 1978 from benthic hauls at the Scottish Marine Biological Association's Permanent Station (54°40'N, 12°16'W) at 2900 m depth in the southern Rockall Trough. For details of physical conditions at this station, collecting methods and sample comparability, see Gage *et al.* (this issue).

Measurements of (and all subsequent references to) body size are made as the diameter of the disk on the aboral side measured from the base of one arm to the opposite interradius. Although not present, or conspicuous, in juveniles (see Fig. 1, Schoener, 1967), the development of a dorsal notch in specimens longer than about 1.5 mm complicated the selection of an easy reference point at the base of the arm. In practice, the distal margin of the first dorsal arm plate was taken as approximating the base of the arm, although in large specimens this might lie some way within the notch. Although the identification of juvenile brittlestars is not easy, it was possible to be reasonably certain of the identity of even the smallest specimens measured by reference to the sequential growth stages of *Ophiura ljunghmani* figured by Schoener (1967). Juveniles of only two other brittlestar species were present, *Ophiocten latens* Koehler and *Ophiomusium lymani*. However, these were few and, especially for *Ophiomusium*, easily distinguished from *Ophiura ljunghmani*.

*Ophiura ljunghmani* is dioecious (Schoener, 1968), and from each sample of the time series the gonads of at least 25 adults (Table 1) were dissected out, embedded in paraffin wax and sectioned at 5  $\mu$ m. The oocytes were measured as for other *Ophiura* species (Tyler, 1977). For determination of fecundity the number of gonads per interradius was multiplied by the average number of oocytes counted in serial sections of five gonads from that interradius in order to give the total number of oocytes per interradius. Total egg volume was calculated from each oocyte grouping of the oocyte size-frequency results (Table 2). "Reproductive potential", as a measure of relative biomass devoted to reproduction, was calculated in a manner analogous to Scheltema (1972) by dividing disk diameter by gonad volume.

Table 1

Numbers of males and females amongst *Ophiura ljunghmani* specimens dissected.

Sample date	Males	Females	Indeterminate
3 Nov. 1973	14	9	—
15 Nov. 1975	12	13	—
1 Mar. 1976	10	13	2
21 June 1976	12	13	—
22 Oct. 1976	8	17	—
29 Jan. 1977	22	3	—
7 Apr. 1977	8	14 <sup>a</sup>	1
7 Aug. 1977	15	14 <sup>a</sup>	2
22 Feb. 1978	7	17	1
14 Apr. 1978	13	12	—
2 June 1978	11	13	1
$\bar{x}$	12	12.64	
Student's $t = 0.38$ for 20 <i>df</i> .			

<sup>a</sup> excluding two diseased females.

## RESULTS

## Population structure

Frequencies of the size measurements of *Ophiura ljungmani* (Table 2) indicate a population dominated by small specimens (< 4 mm). This is most clear in samples taken during the summer months (June-August) which are overwhelmingly dominated by small (< 1.00 mm), probably freshly settled, juveniles. Through the summer months an increasing proportion of these juveniles were found lacking arms and dorsal integument, the body being reduced to the skeletal parts associated with the mouth. Comparisons of the proportion of presumably dead to living individuals recovered in the hauls taken at different times during summer from 1976-1978 (Table 2) suggest that this proportion increases during the summer. Only extremely rarely were specimens larger than 1 mm found in this condition. However, a very small proportion (e. g. four specimens measuring 1.4 to 2.1 mm from the June 1978 sample) were found showing evidence of regeneration of single arms.

Except for the marked peaks caused by the presumably newly settled brittlestars, the size frequencies show no obvious structure of consecutive year classes that might be expected to result from such an annual recruitment to the population. However, this seemed to be because the number of adults relative to juveniles was too small, and the modes in their frequency distribution possibly too overlapping, to yield a clear pattern. Hence, the data were plotted as cumulative percent frequencies and Cassie's (1954) modification of Harding's (1949) method of analysis of polymodal frequencies, using probability paper, then applied.

On the basis of inflexions in the cumulative curve, and a process of trial and error, a sequential series of component curves (Fig. 1) were extracted each of which provided the best fit obtainable to the normal distribution. In most samples the numbers of large individuals was insufficient to permit analysis. The analyses must therefore, be considered incomplete with respect to the total number of component modes.

The present size frequency distributions are numerically heavily skewed in favour of the smallest sizes whose modes, therefore, were resolved with least equivocation. Hence, the possible effect of cumulative errors in resolving modes amongst larger sizes is much reduced.

## Age classes

Three apparently likely assumptions are made in further analysis of these data. The first is that the summer-time juvenile peak represents an annual recruitment of a discrete year class to the population. Secondly, we assume that the hauls in the seasonal series sampled the same population of *Ophiura ljungmani*. The third assumption we must make is that any possible effect on population growth of negative growth of individuals, such as the decrease in disk size experimentally shown

Table 2  
Percentage size frequencies of *Ophiura ljungmani* in the samples. Numbers in parentheses give the percentage considered dead on capture.

Date	Size group (mm)																	N	
	0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0	3.0-3.5	3.5-4.0	4.0-4.5	4.5-5.0	5.0-5.5	5.5-6.0	6.0-6.5	6.5-7.0	7.0-7.5	7.5-8.0	8.0-8.5	8.5-9.0		9.0-9.5
3 Nov. 1973	21.1	13.7	10.3	13.1	5.1	5.7	6.9	1.7	3.4	4.0	2.8	1.7	0.6	0.6	1.1	2.3	0.6	1.1	175
17 Nov. 1975	73.8	7.5	4.6	4.7	2.9	2.3	1.8	1.1	0.4	0.4	0.2	—	—	0.1	—	—	—	—	822
1 Mar. 1976	36.2	15.9	4.0	11.4	8.9	7.6	5.3	3.3	2.0	1.8	0.8	0.3	0.5	0.3	—	—	—	—	395
21 June 1976	(1.3)	(0.5)	94.3	2.1	0.6	1.0	0.9	0.2	< 0.1	—	< 0.1	< 0.1	< 0.1	< 0.1	—	—	—	—	2329
(44.4)	27.2	6.7	12.8	8.9	( $< 0.1$ )	9.4	3.9	2.2	1.1	—	—	—	—	—	—	—	—	—	180
22 Oct. 1976	27.8	27.2	6.7	12.8	8.9	9.4	3.9	2.2	1.1	—	—	—	—	—	—	—	—	—	200
28 Jan. 1977	43.5	37.5	5.5	4.0	1.0	2.5	1.5	1.5	2.0	—	—	—	0.5	0.5	—	—	—	—	491
7 April 1977	(0.4)	(0.4)	27.9	6.3	3.0	2.6	0.6	1.6	1.0	—	—	—	0.2	—	—	—	—	—	2397
7 Aug. 1977	94.6	3.1	0.9	0.4	0.3	0.2	0.1	0.2	0.1	0.1	—	—	—	—	—	—	—	—	627
(57.0)	31.1	24.1	20.9	13.6	2.8	2.6	2.1	1.1	0.6	0.3	0.2	0.2	0.2	0.2	—	—	—	—	1056
22 Feb. 1978	11.3	33.1	25.0	9.1	8.7	6.1	4.6	0.9	0.8	—	—	< 0.1	< 0.1	—	—	—	—	—	11124
13 April 1978	(0.4)	(0.4)	96.0	1.9	1.2	0.1	< 0.1	< 0.1	< 0.1	—	—	—	—	—	—	—	—	—	—
2 June 1978	(29.5)	( $< 0.1$ )	96.0	1.9	1.2	0.1	< 0.1	< 0.1	< 0.1	—	—	—	—	—	—	—	—	—	—

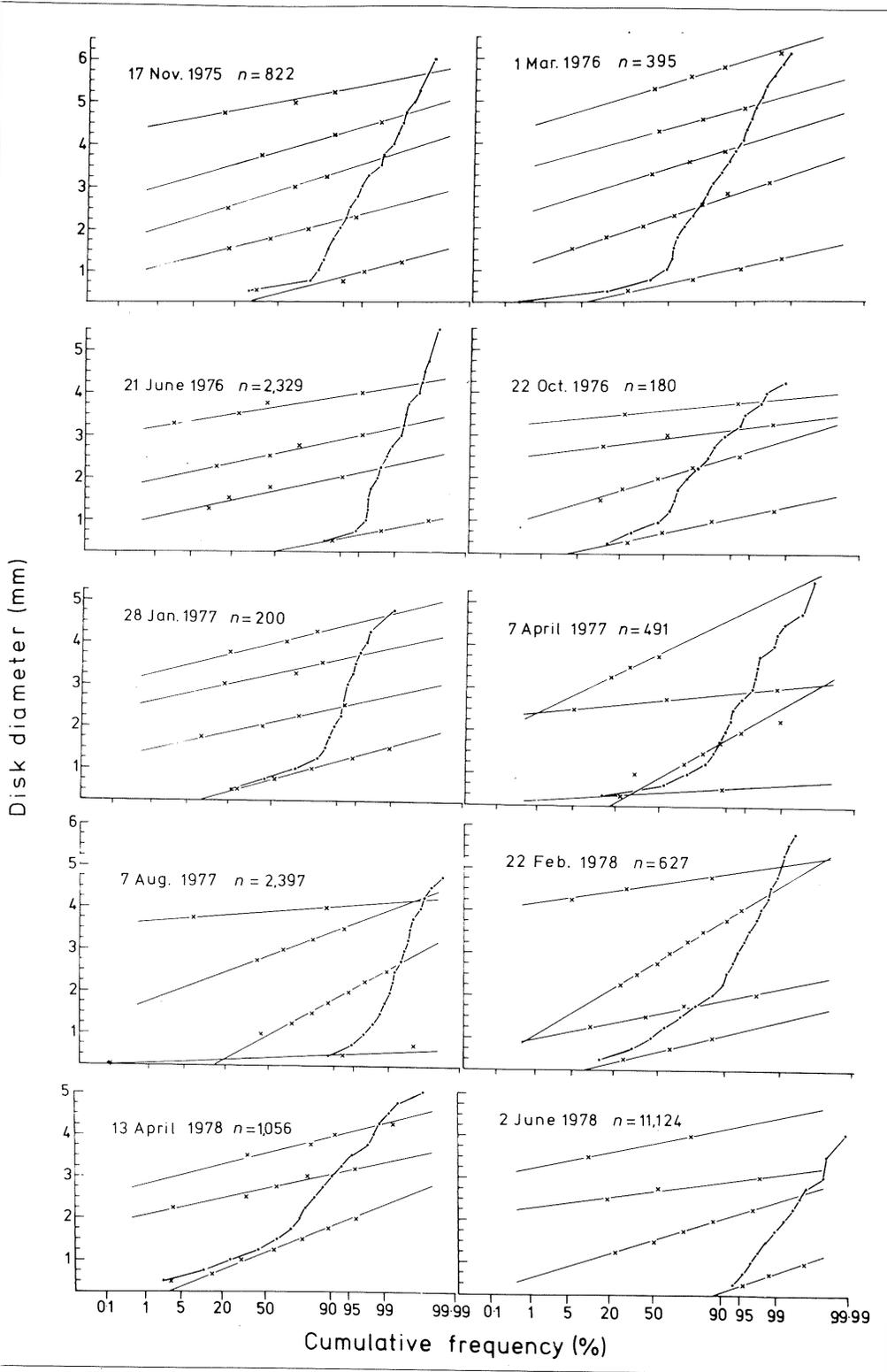
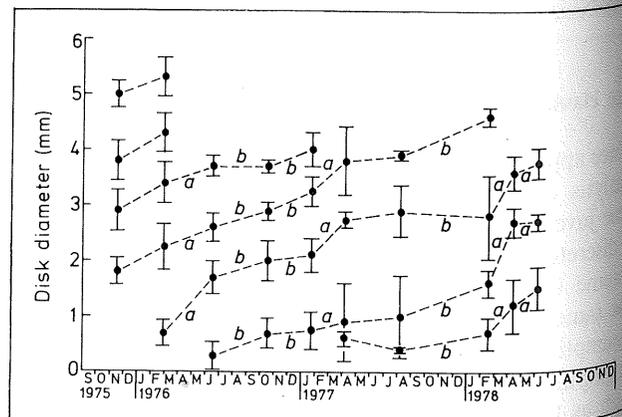


Figure 1  
Probability paper analysis of size frequencies in *Ophiura ljunghmani* samples. Solid circles and heavy lines, cumulative percent disk-size frequencies; straight lines, normal curves fitted to the size class points (crosses) extracted using the Harding-Cassie method.

Figure 2  
Recruitment and year-class growth of *Ophiura ljunghmani* from November 1975 to June 1978, showing the mean (solid circles) and  $\pm 1$  standard deviation (vertical bars) of disk size of the putative year classes. Lines joining consecutive year classes are identified a if taken as reflecting growth in the first half, and b for those showing growth in the second half of the year (see text for explanation).

in *Amphiura filiformis* after regeneration of all five arms (Salzwedel, 1974), is insignificant in the population. Estimates of the mean and standard deviation of the size of the putative year-classes were made graphically from the fitted normal curves (Fig. 2). Examination of the size/frequency distribution yielding the largest number of normal components indicates at least five year-classes present in the sampled population. The size of the largest of these was about 5 mm. However, specimens of *Ophiura ljunghmani* measuring up to 12 mm are recorded (Mortensen, 1933) whilst specimens measuring up to 10 mm were obtained in the present study.



## Growth rates

Taking the mean differences between consecutive points in Figure 2 as a measure of brittlestar growth rate, comparison between the value of  $1.0 \text{ mm} \cdot \text{yr}^{-1}$  yielded by brittlestars  $> 3.5\text{--}4.0 \text{ mm}$ , that have probably all reached reproductive maturity, with that of  $1.5 \text{ mm} \cdot \text{yr}^{-1}$  from prereproductive sizes  $< 3.5 \text{ mm}$  indicates slightly faster juvenile, compared to adult, growth. However, the error in these growth estimates, like that in fitting normal curves to polymodal size frequencies from which they are derived, will increase rapidly with decreasing numbers of available size measurements. There appears to be no slowing of growth amongst the largest individuals; although, again because of the rarity of such specimens, it was not possible to analyse age structure of individuals  $> 6 \text{ mm}$  in size.

Values of mean growth increment of classes between consecutive samples were grouped into those occurring in the first half and those in the second half of the year (Fig. 2). The means of these two sets of values ( $0.56 \text{ mm}$  for the first half, and  $0.28$  for the second half of the year) are significantly different at the 5% level on the null hypothesis that they are both drawn from samples of the same parent population ( $t = 2.12$  for  $23 \text{ df}$ ), despite there being a smaller time increment (mean, 65 days) between samples occurring in the first half of the year than between those occurring in the second half (mean, 106 days). This indicates a seasonally varying pattern, with accelerated growth in the early months compared to the later months of the year.

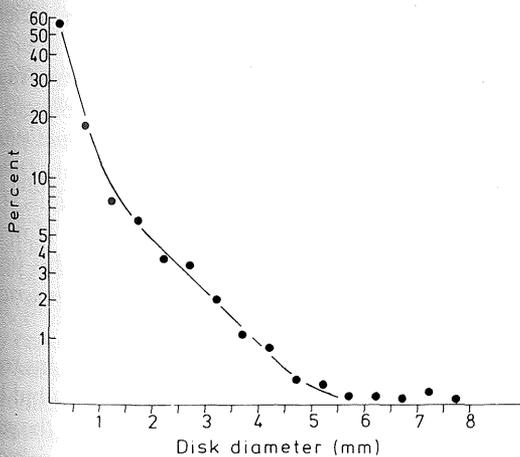


Figure 3

Survivorship curve of *Ophiura ljungmani* based on the percentage representation of size-frequency classes. Points are means of values extracted from each of the samples.

## Survivorship

On the assumption of a population at equilibrium, with no gross change in year-class survivorship from year to year, it is possible to derive a static survivorship curve (Fig. 3) based on the mean numerical representation of size classes in the samples. This shows a somewhat positively skewed curve that is typical of populations where mortality is greatest amongst juveniles. The fitted curve also indicates a constant rate of mortality from  $1.5\text{--}5 \text{ mm}$ . The survivorship curve also may suggest that this mortality decreases amongst specimens  $> 5 \text{ mm}$ , although the small number of such specimens measured must substantially increase the likely error in the estimate.

## Egg size, fecundity and reproductive potential

The maximum egg size achieved in a developing ovary of *Ophiura ljungmani* was  $90 \mu\text{m}$  (Fig. 4). Calculation of fecundity suggests that up to 57 000 eggs could be produced by a single specimen. This agrees with the result of Schoener (1972), and exceeds the fecundity of up to 35 000 (personal observations) for the shallow-water species *Ophiura albida* Forbes, which attains a roughly similar size to *Ophiura ljungmani*.

The calculation of reproductive potential will vary with the stage of oogenic growth within the adult. When based on a November sample with a mean oocyte size of  $40 \mu\text{m}$  and an average fecundity of 28 000 (Table 3), the gonad volume is  $2.003 \text{ mm}^3$ , giving a value of reproductive potential of 0.29. As the adults of this month are mostly in stage III (Tyler, Gage, 1979), this figure is an underestimate. Determination of reproductive potential on a small sample ( $n = 4$ ) from February, with a mean oocyte size of  $56 \mu\text{m}$  and a maximum fecundity of 55 000, gives a value of 0.65 (Table 3) for *Ophiura ljungmani*.

## Reproductive periodicity

The gametogenic cycle commences most probably in February/March of each of the years studied (Fig. 4). There is a slight variation in the time of initiation of gametogenesis. In March 1975 development of oocytes had started (mean diameter:  $-11.13 \mu\text{m}$ ) whereas in early April of 1976 all oocytes examined for this month were still in Stage I (mean diameter:  $-10 \mu\text{m}$ ) (Tyler, Gage, 1979). This variation in the time of initiation

Figure 4

Oocyte size-frequency distribution of *Ophiura ljungmani* in samples taken at different times of the year from 1973 to 1978. Solid circles indicates mean oocyte size. In January 1977 all gonads examined were spent.

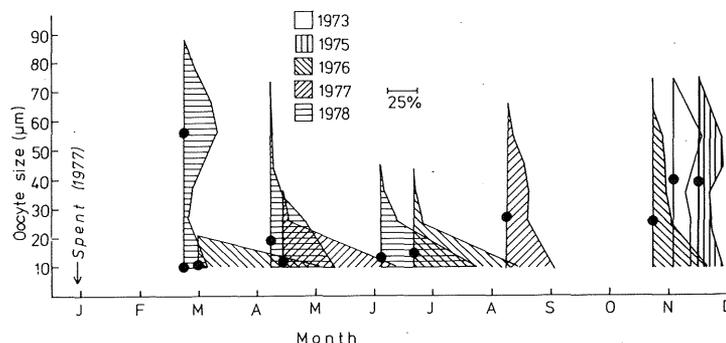


Table 3

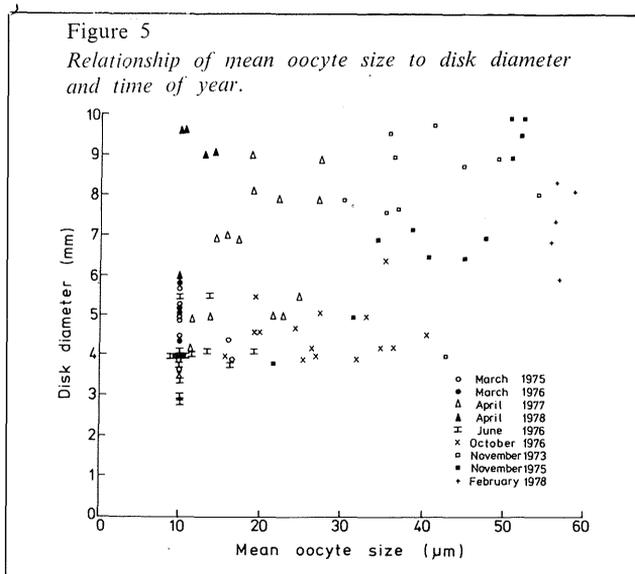
Oocyte volume ( $\text{mm}^3$ ) per oocyte size-group, and "reproductive potential" in *Ophiura ljungmani*.

	Oocyte size-group ( $\mu\text{m}$ )							Total oocyte volume ( $\text{mm}^3$ )	"Reproductive potential" (ratio disk diameter to gonad volume)
	0-20	20-30	30-40	40-50	50-60	60-70	70-80		
November	$3.91 \times 10^{-3}$	0.0358	0.088	0.389	0.72	0.62	0.15	2.003	0.29
February	$2.58 \times 10^{-4}$	$4.3 \times 10^{-3}$	0.044	0.27	1.089	1.68	0.14	3.263	0.65

of gametogenesis is reflected in the oocyte size-frequency distribution pattern for the April samples (Fig. 4). Oocyte growth through June and July would appear to be slow, suggesting previtellogenic growth. This is followed by rapid vitellogenic growth in autumn to give a mean oocyte size in November of  $40 \mu\text{m}$ .

By late January/early February, the ovaries are at maximum development (mean diameter  $56.86 \mu\text{m}$ ), or spent, suggesting a spawnout between mid-January and late February.

The mean oocyte size of *Ophiura ljungmani* shows a strong correlation with season but no correlation with disk diameter (Fig. 5). Oocytes larger than  $10 \mu\text{m}$  were not observed in specimens smaller than  $3.7 \text{ mm}$  disk diameter, although newly developing oocytes were present in even the largest adults (Fig. 5). This suggests that sequential breeding cycles occur once annually in any one individual.



## DISCUSSION

Although lacking the desirable corroboration from knowledge of the larvae, we may make certain suppositions on the life history of *Ophiura ljungmani* from egg size, fecundity, total egg volume, reproductive periodicity and from the size structure of the population.

The present data on egg size and fecundity agree with Schoener's (1972) data for samples of this species from the western North Atlantic. This suggests that *O. ljungmani* has an indirect, planktotrophic larval development. Comparison of the egg size and fecundity of *O. ljungmani* with the congeneric shallow-water species, *Ophiura*

*albida*, which has indirect, planktotrophic larval development (Mortensen, 1927), would support this view. However, egg volume ( $3.0 \text{ mm}^3$  per individual) would suggest direct, or abbreviated, larval development (*sensu* Hender, 1975) for *O. ljungmani*. As no evidence of viviparity has been found in any of the adults examined, or of any brooded larvae, we infer an indirect development.

The present results confirm Schoener's (1968) assertion of annual reproduction in *Ophiura ljungmani* that was based on an apparent seasonal variation in recruitment to the population in the Northwest Atlantic. The *Ophiura ljungmani* population in the Rockall Trough possesses a marked seasonal reproductive cycle, with the initiation of gametogenesis in February/March, a period of slow previtellogenic growth until August, followed by a period of rapid vitellogenic growth in October-January. Spawning appears to be synchronous in late January/February.

Further evidence for a seasonal reproductive pattern in *Ophiura ljungmani* is provided by the massive seasonal recruitment of juveniles to the benthic population seen in the summer samples.

The evidence suggests a planktonic larval life of up to 4-5 months. Since the proportion of juveniles increased from early to late summer, settlement may occur over a prolonged period, possibly from April/May-August. We have no direct evidence of an ophiopluteus for *Ophiura ljungmani* in deep water, although *Ophiopluteus ramosus* (Mortensen, 1898) and postlarval *Ophiura ljungmani* were taken in oblique plankton hauls, from 2700 m to the surface, during this period. However, Semenova *et al.*, (1964) have proposed that this ophiopluteus is one of the larval forms of *Ophiocten sericeum gracilis* G. O. Sars.

The relative benefits for *Ophiura ljungmani* of this reproductive strategy may be apparent (Chia, 1974) but both the proximate and ultimate factors determining the gametogenic cycle and controlling spawning are more obscure. In shallow continental shelf areas the synchrony of gametogenesis and spawning in marine invertebrates, including ophiuroids, has been attributed to temperature (Orton, 1920; Fenaux, 1968), daylength (Giese, Pearse, 1974) or lunar periodicity (Korringa, 1947) whilst food supply exerts a selective pressure on the timing of breeding cycles (Giese, Pearse, 1974). In the physically seasonless deep sea, however, the ultimate controls of gametogenesis may include seasonal food availability (Schoener, 1968; Rex *et al.*, 1978) whilst internal tides may control reproductive synchrony (Rokop, 1974). At the Permanent Station site there appears to be almost

imperceptible variation in the deep-sea physical environment with the probable exception of a tidal cycle in bottom current (see Gage *et al.*, this issue).

Recent evidence (McCave, 1975; Wiebe *et al.*, 1976; Turner, 1977; Bishop *et al.*, 1978), has confirmed early conjecture (Moseley, 1880, p. 259) that surface production may be quite rapidly transferred to the deep-sea by the aggregation of the originally fine particles into large faecal pellets hence increasing their settling velocity. If this phenomenon occurred in the Rockall Trough, there would be a great enough increase in organic carbon at the sea bed in late summer, derived from a spring/summer-time peak in surface production (see e. g., Colebrook, Robinson, 1965) to provide the energy requirements of the *Ophiura* population to undergo vitellogenesis.

Although it is tempting to relate the apparent seasonally varying growth rate to metabolic diversion of resources from somatic to gonadal growth, this seems unlikely because growth of prereproductive individuals (< 3.5 mm) appeared to show similar seasonality (Fig. 2).

Although settlement of young brittlestars is accompanied by heavy mortality, as evidenced by the increasing proportion of presumably dead individuals found during summertime, the survivors appear to grow rapidly during the first 18 months of life. An apparent slow initial change during summer in the size of the O-year class (Fig. 2) may reflect its continuous augmentation by postlarvae during a prolonged settlement period. Individuals start to become reproductively mature in their third year at a size of about 3.5-5 mm, with a pattern of slower, but apparently steady growth beyond this size. Because the sexual stages of gametogenesis of *Ophiura ljungmani* are related to the time of year rather than disk diameter, we suggest that, in addition to the population exhibiting seasonal reproductive periodicity, individuals reproduce more than once, and possibly annually, during their lifetime.

The indication of size-dependent changes in survivorship may be explained by different causal factors predominating at different stages of growth. An initial high rate of postlarval mortality that is reflected in the high proportion probably dead on capture possibly may result from competition for limited food resources. The subsequent lower rate of mortality among pre-reproductive and reproductive adults may result from predation. There may also be selective cropping, or cannibalism, of arms (as is indicated by arm regeneration) that is known to occur among shallow-water brittlestars (Pagett, 1978).

There are few data available for comparison from analysis of populations of coastal brittlestars. However, similarities are evident on comparison with Ursin's (1960) results from congeneric populations of *Ophiura albida* and *O. texturata* Lamarck in the North Sea. These species are known to possess a pelagic larva. Annual recruitment to the *O. albida* population appears as a well-defined juvenile peak in size frequencies although the composition of older individuals that comprised a single adult peak could not easily be interpreted.

Measurements of *O. texturata*, on the other hand, showed three distinct year classes with probably annual recruitment.

Although life-history and growth data for deep-sea benthos are still sparse, recent studies (e. g., Ockelmann, 1965; Knudsen, 1970; Hessler, 1970; Scheltema, 1972; Schoener, 1972; Grassle, Sanders, 1973; Gardiner, 1975; Turekian *et al.*, 1975; Rokop, 1974, 1977 *a, b*, 1978; Rex *et al.*, 1978) suggest typical "deep-sea" tactics of year-round reproduction, direct larval development, small brood size, an age structure not dominated by young stages, and concomitant slow adult growth rates.

The present results for *Ophiura ljungmani* show a pattern of annual synchronous reproduction, iteroparity, large brood size, probable larval planktotrophy, serial annual recruitment, an age structure dominated by young specimens that are subjected to high mortality at settlement, an adult age structure of overlapping, yet discrete, year classes, and an overall pattern of steady annual growth in body size superimposed upon an apparently seasonally fluctuating pattern. The present data also suggest a pattern of continuous depletion of adult stocks possibly through predation, while the few data available for other deep-sea species have been interpreted as reflecting rates of predation that are insufficient to control the size or structure of populations (Grassle, Sanders, 1973; Rex, 1978).

If this present interpretation of life-history tactics of *Ophiura ljungmani* is correct, then it is clear that, as was suggested by Grassle and Sanders (1973), this abundant and widespread bathyal-upper abyssal brittlestar is atypical of deep-sea benthic taxa studied to date. Yet the apparent success of this species, which is found in both the North and South Atlantic (Mortensen, 1933; Tomassi, 1970) and recorded from 370-4070 m (Cherbonnier, Sibuet, 1972), suggests that it is well adapted to life in the deep sea.

For a species with a planktotrophic larva an annual reproductive cycle attuned to a seasonal surface production would ensure maximal food resources are available to the pelagic young provided they are capable of migrating to the euphotic zone. Although we are lacking certain knowledge of the larva of *Ophiura ljungmani*, such a planktotrophic development seems likely. Vertical migration through 2-3 km of water seems, however, less probable, although larvae of the deep-sea gastropod *Benthonella tenella* (Jeffreys) have been found at the surface (Bouchet, 1976 *a*). It is also possible that deeper living, feeding larvae may benefit, as may benthic adults, from the likely seasonal pattern in sedimentation.

That reproductive periodicity has adaptive value in the deep sea is supported by the recent discovery of synchronous annual gametogenic cycles in two species of abyssal protobranch bivalve (Lightfoot *et al.*, 1979). However, size structure, fecundity and inferred mode of larval development suggest that in other respects they resemble other deep-sea bivalves (Ockelmann, 1965; Knudsen, 1970; Scheltema, 1972; Grassle, Sanders, 1973; Rokop, 1978). There appears as yet to be no reliable evidence for annual periodicity amongst deep-sea benthic

fauna with the exception of the bathyal populations of single species of brachiopod and scaphopod (Rokop, 1977*b*), both of which occur also in shallow water. Therefore, any explanation for the occurrence of such annual periodicity must also explain why such periodicity apparently is absent amongst other species (Rokop, 1974, 1977*a*, 1978; Rex *et al.*, 1978; Tyler, Gage, 1979) which one might expect to be equally well adapted to life in the deep sea.

We are able to offer no fully satisfactory answers, except to reiterate the concluding remarks of Rex *et al.* (1978): "that it may be no more meaningful to speak of a typical deep-sea reproductive strategy than it would be to typify a single shallow water or terrestrial strategy".

Moreover, if we extend the argument of Strathman (1978*a*) to the deep sea, could it be that the apparent rarity of larval planktotrophy in certain taxa has resulted from irreversible loss of such larval forms as the ophiopluteus in species spreading into the deep ocean from polar seas, where larval planktotrophy is rare (Thorson, 1950)? *Ophiura ljunghmani* may be a (possibly recent?) invader that is exploiting a vacated adaptive type (*sensu* Strathman, 1978*b*) resulting from inability of other taxa to reacquire a planktotrophic larva—that is nevertheless potentially well suited to existing conditions.

It also remains to explain how *Ophiura ljunghmani* is able in the food-poor deep sea to sustain life-history traits, such as larval planktotrophy, that would apparently require high energy consumption (Crisp, 1974; Chia, 1974). For the only other deep-sea species known to possess larval planktotrophy, *Benthonella tenella* [although larval planktotrophy is suspected amongst other deep-sea prosobranchs (Bouchet, 1976*b*)], typical "low-energy" life-history traits of continuous reproduction low recruitment and a population structure dominated by older and possibly slow-growing, long lived, individuals are indicated (Rex *et al.*, 1978).

Up to 29 postlarval and five larger *Ophiura ljunghmani* have been found in single 0.25 m<sup>2</sup> box cores (see Gage, 1977, 1979), taken in June and September near the Permanent Station. Could the high energy requirement of adult *Ophiura ljunghmani* be at least partially met by directly scavenging, or cannibalising, this massive spat fall and its associated mortality, as well as from sedimentation of other organic particulates?

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