Vol. 37: 171–180, 1987 | MARINE ECOLOGY – PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published May 6

Reproduction and rapid growth in a deep-sea aplacophoran mollusc, *Prochaetoderma yongei*

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ABSTRACT: *Prochaetoderma yongei*, an aplacophoran mollusc with a wide geographic distribution between 450 and 2200 m depth and high densities in the North American Basin, grows to adult size within 2 mo and sexual maturity within 1 yr. Gametogenesis was asynchronous within individuals from a single sled-trawl sample. Periods of increased recruitment and numbers of ripe individuals occur; whether these recurrent periods are irregular or cyclic at regular intervals is not known. Males usually outnumber females in all size classes. The peak class in length-frequency distributions contains individuals less than 1 yr old. Repopulation of a disturbed area by this species may require about a decade. The rapid growth to maturity by *P. yongei* and its ability to colonize are attributes adapted to transient or disturbed environments, but its low egg numbers and lack of synchrony in egg development are not.

INTRODUCTION

Prochaetoderma yongei Scheltema has a wide geographic range, from the North American Basin in the northwestern Atlantic to the West European Basin and southward to the Namibia Basin in the eastern Atlantic. It ranges in vertical depth from 450 to about 2200 m (Scheltema 1985a, b). In the western Atlantic it occurs at densities up to 400 m^{-2}, and in recent replicate samples taken over 6 seasons at 1500, 1600, and 2000 m depth off Delaware Bay (USA), it ranked 4th in numerical dominance among all stations (Maciolek et al. 1986). The confamilial species *Spathoderma clenchi* Scheltema ranked 5th, and these 2 aplacophorans formed 3.7 and 3.3 %, respectively, of the total fauna. The next most numerous mollusc was a bivalve, which ranked 25th. In the eastern Pacific another member of the family, *Chevroderma whitlatchi* Scheltema, occurs at densities of 178 m^{-2} in the Panama Basin and 124 m^{-2} in the Aleutian Trench; in the latter, it ranks second in abundance. The question quite naturally arises, why are these particular molluscs so successful in the deep sea?

With much of the globe covered by deep oceanic sediments, it is perhaps not too surprising to find that the burrowing, worm-shaped aplacophoran molluscs are common and well adapted to both an infaunal and epifaunal existence. However, only among the Prochaetodermatidae are such high densities attained. This abundance may in part be due to their ability to feed on a wide range of sizes of organic particles (Scheltema 1981). It is the purpose of this paper to examine what part growth and reproduction may play in accounting for their abundance.

MATERIALS AND METHODS

The Prochaetodermatidae are a deep-sea molluscan group in which it is relatively easy to examine reproduction because the single gonad lies dorsally as a discrete sac and can be readily dissected free of the digestive gland (Fig. 1; Scheltema 1985a, Fig. 2A). In addition, most specimens of *Prochaetoderma yongei* are translucent and presence or absence of the gonad and sex of mature individuals can be determined without dissection.

The numbers and lengths of males, females, and juveniles were determined for 7 samples taken at different depths in the North American Basin and in 5 summer or early fall and 2 winter months of different years using various types of gear (Table 1). Lengths of individuals were measured with dividers or a digitizer; accuracy of length measurements is discussed in Scheltema (1985a). For a summer and a winter sample taken at 2000 m by epibenthic sled (Stns 115, 210),

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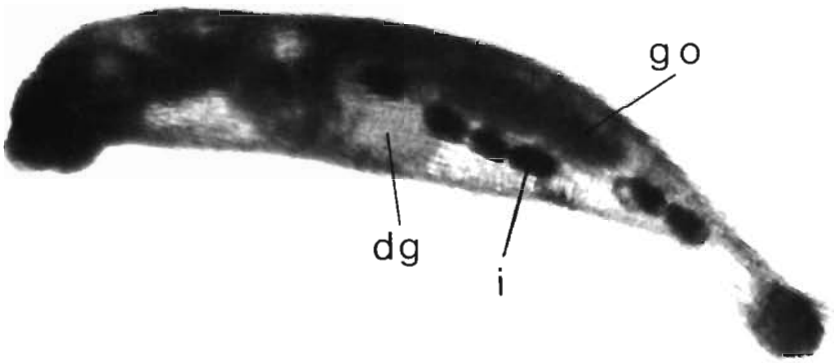

Fig. 1. *Prochaetoderma yongei* adult male. dg: digestive gland; go: gonad; i: intestine. Length of specimen = 2.6 mm

Table 1. Samples from which lengths of males, females, and juveniles of *Prochaetoderma yongei* were measured (listed in order of month)

Station or Dive No.[a]	Date	Latitude (N)	Longitude (W)	Depth (m)	Gear[b]	Sample N
OC-10 Stn 367	Jul 76	39°45.5′	70°37.2′	1764	SBC #1	46
OC-10 Stn 370	Jul 76	39°44.9′	70°35′	1815	SBC #2	20
AII-12 Stn 73	Aug 64	39°46.5′	70°43.3′	1470	ES	133
AII-24 Stn 115	Aug 66	39°39.2′	70°24.5′	2030	ES	100[c]
AL 459, 460	Sep 72	39°46′	70°40′	1760	SC	18
AII-30 Stn 128	Dec 66	39°46.5′	70°45.2′	1254	ES	44
CH-88 Stn 210	Feb 69	39°43′	70°46′	2024	ES	72[c]

[a] AL: DSRV *Alvin;* OC: R/V *Oceanus;* AII: R/V *Atlantis II;* CH: R/V *Chain*
[b] SBC: spade box core 0.25 m^2 (#1, 25 subcores sampled; #2, inner 9 cores only sampled); ES: epibenthic sled; SC : tube corer manipulated from submarine, ten 35 cm^2 cores lumped
[c] All eggs measured in each female

gonads were dissected from females into a drop of glycerine and all eggs 20 µm in diameter or greater were measured by taking the mean of the longest dimension and the length perpendicular to it. The entire winter sample (Stn 210, N = 72) was examined; a subsample of 100 individuals was randomly selected from the summer sample (Stn 115, N = 175) by swirling the entire sample into a pile and physically dividing it in two. That N = 100 exactly is coincidence; the remaining 75 individuals have the same proportion of juveniles. Stn 73 (N = 133) is likewise a subsample.

RESULTS

Even though samples are neither replicates nor sequential, certain inferences can be made about the structure and dynamics of the populations they represent.

Ratio of males to females

In epibenthic-sled samples, there were 1.3 to 2.0 times more males than females (Table 2). In cores, males either equaled females (sample N = 46) or were fewer than females (sample N = 20 or less). In one large box core sample, data exist for each of 25 subcores (Stn 367); a test of goodness-of-fit to Poisson distribution for males, females, and juveniles showed males to be non-randomly distributed and females and juveniles to be randomly distributed. Thus, small core samples may not capture males evenly, resulting in ratios of 1.0 or less.

In all but one sample (Stn 115) there was no significant difference between mean lengths of males and females. Sex is already fixed in immature specimens with either spermatocytes or oocytes present in gonads in very early stages of development. Thus, males and females probably grow at about the same rate. The

Table 2. *Prochaetoderma yongei*. Ratio of males to females in 7 samples

Station or Dive*	Gear*	Male N	Male $\bar{X}$ length mm ± $S_{\bar{x}}$	Female N	Female $\bar{X}$ length mm ± $S_{\bar{x}}$	Ratio M/F
367	SBC	19	1.7 ± 0.1	19	1.7 ± 0.1	1.0
370	SBC	6	2.2 ± 0.2	8	2.0 ± 0.1	0.8
73	ES	68	2.1 ± 0.1	47	2.1 ± 0.1	1.4
115	ES	44	2.2 ± 0.07	35	2.0 ± .05	1.3
459, 460	SC	2	1.9 ± 0.1	4	1.7 ± 0.6	0.5
128	ES	27	1.9 ± 0.1	16	1.9 ± 0.1	1.7
210	ES	45	2.0 ± 0.09	22	2.0 ± 0.5	2.0

* See Table 1

preponderance of males is curious in the absence of obvious evidence for protandry.

Length distribution of males and females

Specimens were considered as male or female if spermatocytes or oocytes about 20 µm or larger could be detected.

Males and females are distributed rather evenly by length along a normal curve, which is steeper for males when they are more numerous (Fig. 2). It is not known whether age and length are correlated beyond 2 mm; it can only be said that all size classes with individuals in which sex can be determined fall into a normal curve, with the modal class for males and females the same or within one class of each other.

The above generalizations seem to hold whether samples are taken by epibenthic sled (Fig. 2) or by quantitative gear large enough to ensure a sample number of at least 40, although in the latter instance the rarer large specimens may not occur (Fig. 3). The 2 samples reported here with 20 or fewer individuals were collected from a surface area of only 350 cm^2 and 900 cm^2 (AL 459, 460 and OC-10 Stn 370, respectively), and the length frequencies did not produce recognizable curves.

Proportion of juveniles

Specimens were considered to be juveniles if the gonad could not be detected or appeared as a thin line.

The percentage of juveniles ranged from 2.3 to 66.7 %, with lowest values occurring in the 2 winter samples and the highest in the 5 summer and early fall samples (Table 3). A comparison of distributions by length of juveniles, males, and females in a summer and a winter sled trawl sample from 2000 m shows a bimodal distribution in the summer sample that is not present in the winter sample (Fig. 2). The 2 samples

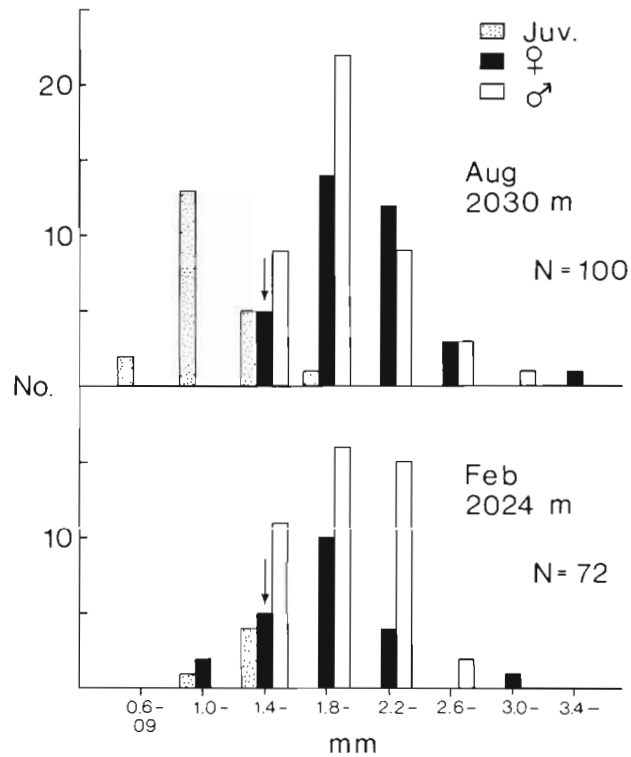

Fig. 2. *Prochaetoderma yongei*. Length-frequency distributions of juveniles, females, and males in two 2000 m samples from approximately the same location taken with an epibenthic sled trawl in Aug and 2½ yr later in Feb. Arrows over bars for females denote smallest size class with mature eggs. (Aug sample: Stn 115, Feb sample: Stn 210; see Table 1)

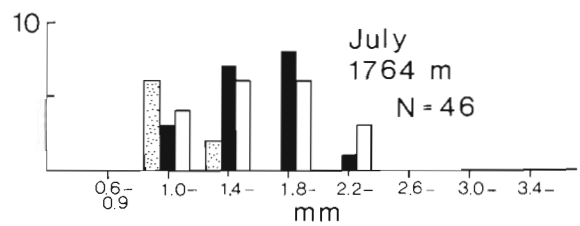

Fig. 3. *Prochaetoderma yongei*. Length-frequency distributions of juveniles, females, and males in a 0.25 m^2 spade box core taken at 1764 m in Jul (Stn 367; see Table 1). Bar conventions as in Fig. 2

Table 3. *Prochaetoderma yongei*. Percentage of juveniles ranked by month

Month/ year	Stn/ Dive*	Gear*	Depth	Total sample (N)	% Juveniles
Jul 76	367	SBC	1764	46	17.4
Jul 76	370	SBC	1815	20	30.0
Aug 64	73	ES	1470	133	13.5
Aug 66	115	ES	2030	100	21.0
Sep 72	459, 460	SC	1760	18	66.7
Dec 66	128	ES	1254	44	2.3
Feb 69	210	ES	2024	72	6.9

* See Table 1

were taken 2½ yr apart. Another winter sample examined, also a sled trawl but from about 1200 m (Stn 128, Table 1), had only a single juvenile, while a summer trawl sample from about 1400 m (Stn 73) had the same bimodal frequency-distribution for juveniles and males/females as the August 2000 m station. This bimodality in length-frequency is seen only if juveniles are plotted separately from the adults; owing to their rapid growth, juveniles overlap mature adults in length (see below). A single curve will result if juvenile and adult length frequencies are combined. The graphs of summer and winter size distributions show that recruitment does not occur at a constant rate, but the samples are too few to be certain that the differences reflect seasonal periodicity.

The clear bimodality of summer populations collected from 1400 and 2000 m by epibenthic sled appears dampened in a large box-core summer sample from 1764 m (Fig. 3). In this sample there is a larger proportion of small males and females than in the epibenthic-sled summer samples, a situation which may reflect either a difference in mean lengths among the populations, a patchy distribution in age classes, or collecting bias by the different types of gear.

The high percentage (66.7 %) of juveniles in 10 tube cores (350 cm^2 total area) collected by submarine in September 1972 at 1760 m (Table 3) was not duplicated in 0.25 m box-core samples from the same locality 4 yr later in July 1976 or in a 169 cm^2 core taken by submarine in September 1978 which contained no juveniles at all. These differences in proportions of juveniles in core samples may be due to irregular, noncyclic recruitment into the population or to patchy settlement of juveniles at a spatial scale such that their presence was not detected.

Egg development and production

The total number of eggs larger than 20 µm in diameter ranges from 4 to 6 in immature individuals up to 39 in mature females; the average number per female was 21 in the August trawl sample (Stn 115) and 14 in the February trawl sample (Stn 210). Various stages of development and egg sizes are present in all individuals. Three egg stages were determined as follows (Fig. 4). Stage I eggs have 2 or several nucleoli, a distinct nuclear membrane, and semi-translucent yolk granules; diameters range from 20 to 96 µm. Stage II eggs have a single large nucleolus greater than 12 µm in diameter, a distinct nuclear membrane, and dense yolk granules; diameters range from 55 to 177 µm. Eggs are considered to be mature (Stage III) when the nuclear membrane disappears and the nucleolus is less than 10 µm or absent; diameters range from 90 to 226 µm. Mature eggs are free in the lumen of the gonad; there is a distinct clear area between the vitelline membrane and yolk. (The great range in size of so-called 'mature' eggs may reflect an inadequacy in definition.) The distinction among stages was unambiguous; the implication is that development from one stage to the next is rapid.

In general, Stage I eggs are less than 60 µm; most eggs from 100 to 120 µm are Stage II eggs; and 'mature' eggs are usually greater than 140 µm. Eggs about to be spawned elongate as they move down the narrow gonopericardial duct and account for egg measurements 190 µm and larger (Fig. 4D).

The size frequency of mean diameters for each stage was plotted for each female from the August and February sled trawls from 2000 m (Fig. 5). The larger size and number of Stage III eggs in the August sample than in the February sample perhaps indicate a potentially higher spawning rate; they co-occur with the greater number of small juveniles in the August sample. The percentage of females with mature eggs in August was 82 %, more than 1½ times the percentage (48 %) in February (Table 4). All 3 oocyte stages are present in 77 % of the August females, but only 33 % of February females have all stages. The mean of means of egg diameters for all females and number of eggs per female for each stage also indicate greater potential reproductive activity in the August population than in the February population (Table 4); however, there is no significant difference in size of Stage I and II eggs in the 2 samples.

Data on growth and reproduction from experimental boxes

Two sets of data are available for *Prochaetoderma yongei* from experimental boxes of azoic mud placed by submarine at 1760 m (Table 5); 2 more sets of data are available from free-vehicle boxes of azoic mud deployed at 2020 m, the same depth but not location as

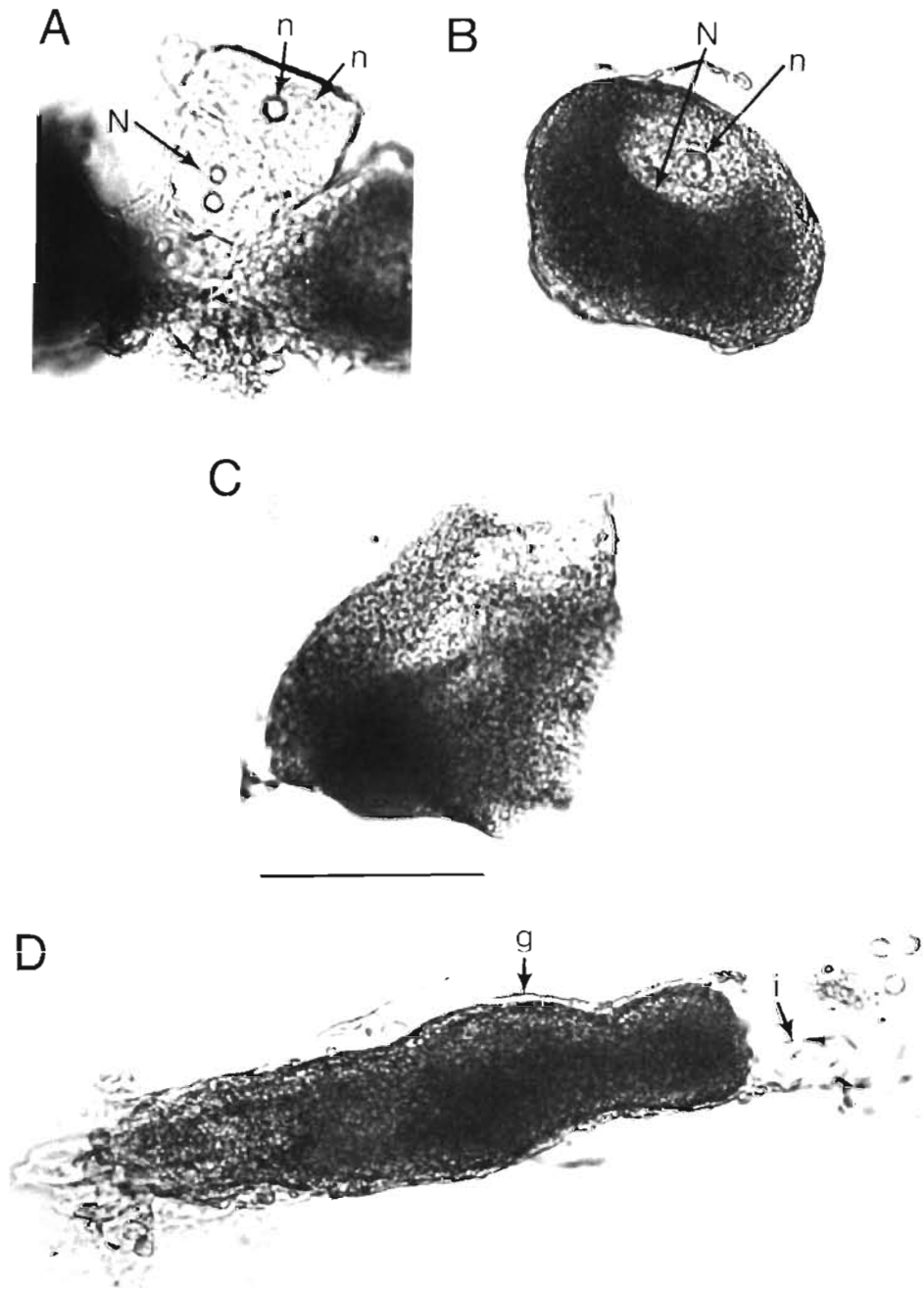

Fig. 4. *Prochaetoderma yongei*. Egg developmental stages. (A) Stage I with transparent yolk, nuclear membrane, and 2 large, or one large and several small, nucleoli. (B) Stage II with dense yolk granules, large nucleolus and nuclear membrane. (C) Stage III, a mature egg with no nuclear membrane or nucleolus. (D) Mature egg within gonopericardial duct. n: nucleolus; N: nuclear membrane; g: wall of gonopericardial duct; i: intestine. Scale = 100 µm

the August and February trawl samples described above (Stn 115, 210). From recruitment of *P. yongei* into these experimental boxes, estimates can be made of the minimum growth rate and maximum time to reach reproductive maturity.

Recruitment into experimental boxes is considered to be by larvae. Although the embryology is not known for any chaetodermomorph, there is no indication for direct development or brooding in Prochaetodermatidae. In the other group of aplacophorans, the footed Neomeniomorpha, 3 species are known to release zygotes and have free-swimming larvae; egg sizes range from 120 to 260 µm (Hadfield 1979, Table 2). Mean mature egg sizes of *Prochaetoderma yongei* from February and August samples are 141 and 165 µm, respectively (Table 4), and fall within the sizes expected for aplacophorans with larvae.

Because *Prochaetoderma yongei* burrows, it is not likely that it has crept up the sides of an experimental box, nor can recruitment have occurred by lateral transport. The most likely explanation for the existence of *P. yongei* in experimental boxes is by larval settle-

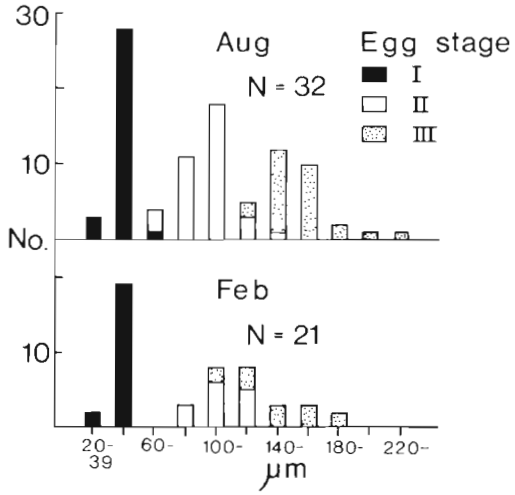

Fig. 5. *Prochaetoderma yongei.* Frequency distribution of egg developmental stages in females from the 2000 m Aug and Feb samples shown in Fig. 2. Mean diameter is plotted for each stage in each female. Discrepancies in numbers of females (N) between this figure and Table 2 reflect incomplete gonad dissections

ment, and growth is assumed to have taken place there.

The following data, which are pertinent in interpreting results from experimental boxes, are from all specimens of *Prochaetoderma yongei* listed in Table 1:

Largest egg measured	diameter 226 μm
Smallest juvenile measured	length 0.3 mm
Largest juvenile measured	length 1.8 mm
Smallest female with mature eggs	length 1.7 mm
Smallest specimen determined to be male	length 1.0 mm
Smallest specimen determined to be female	length 1.3 mm

A juvenile specimen of *Prochaetoderma yongei* measuring 1.4 mm in length was recovered from a 2 mo box (Table 5, *Alvin* 597). This is the size at which developing gonads have first been seen; it is nearly 5 times larger than the smallest recorded juvenile.

A single male occurred in a 6 mo box from 2020 m (MID-6, Stn 2). It was 2.6 mm in length, longer than the mean lengths recorded for males from the 2000 m epibenthic-sled samples (Stn 115, 2.2 mm; Stn 210, 2.0 mm; Table 2) and longer than the largest known juvenile (1.8 mm).

Ten specimens were recovered from three 8 mo boxes: 2 juveniles, 5 males, and 3 females (*Alvin* 834). Two of the females were less than 1.7 mm, the size individual in which mature eggs have first been seen. The largest female (2.1 mm), although large enough to be sexually mature, had only immature eggs smaller than 75 μm. Lengths of males varied between 1.7 and 2.3 mm, from less than the largest juvenile to greater than the average for any of the stations (Table 2). Like most other populations sampled by trawl or cores, there were more males than females (1.7 times).

A female 2.1 mm in length was found in a 12 mo box at 2020 m recovered in May (MID-4 Stn 2). This individual had 4 Stage III ('mature') eggs having a mean diameter of 152 μm; egg number totaled 15. Table 6 compares this specimen with females from an August 2000 m trawl sample for which eggs were measured (Stn 115, Tables 1 & 4). There is no significant difference between the female from the experimental box and the summer trawl sample females in length or in mean diameters of egg Stages I, II, and III; thus this individual is considered to be mature.

Recruits into the experimental boxes indicate that both growth and development to maturity are rapid in *Prochaetoderma yongei,* as fast as or faster than many common subtidal molluscs of the temperate zone. A recruit can grow within 2 mo to a minimum size at

Table 4. *Prochaetoderma yongei.* Egg number per female and egg diameter mean of means for developmental Stage I, II, and III in Feb 1969 and Aug 1966

Stage	Feb[a]				Aug[b]				
	Mean no. eggs female^{-1} (range)	$\bar{\bar{X}}$[c] egg diameter (μm)	S^2	% females with eggs	Mean no. eggs female^{-1} (range)	$\bar{\bar{X}}$[c] egg diameter (μm)	S^2	% females with eggs	t-test $\bar{\bar{X}}$
I	11.6 (4–25)	46	28.29	100.0	12.7 (5–29)	47	28.393	100.0	ns
II	1.6 (0–4)	114	456.84	71.4	4.3 (0–11)	106	272.94	97.0	ns
III	0.6 (0–2)	141	504.93	47.6	2.6 (0–13)	165	443.31	81.8	$p < 0.01$

[a] 39°43.0'N, 70°46.0'W, 2024 m; CH-88 Stn 210
[b] 39°39.2'N, 70°24.5'W, 2030 m; AII-24 Stn 115
[c] $\bar{\bar{X}} = \frac{\Sigma \bar{X}}{N}$ where $\bar{X}$ is mean egg diameter for each female and N is total number of females. Individuals without Stage II and III eggs are not included in the computation for that stage

Table 5. *Prochaetoderma yongei*. Colonization data for specimens from experimental boxes

Station	Date recovered	Total mo (d) of experiment	Length mm Juvenile	Male	Female	Largest egg diameter (μm)
1760 m; 39°46′N, 70°40′W						
Alvin Dive 597	30 Aug 75	2 (60)	1.4	0	0	–
Alvin Dive 834	18 Sep 78	8 (248)				
Box A			0	1.7	1.4	< 75
(with screen cover)				1.7	1.4	75
Box C			1.7	1.7	2.1	< 75
(with screen cover)				2.3		
Box D				2.0		
(without screen cover)			1.0	0	0	–
2020 m; 38°35.78′N, 72°53.65′W						
*MID-4 Stn 2						
Free Vehicle C	20 May 85	12 (359)	0	0	2.1	162
Tray 2						
*MID-6 Stn 2						
Free Vehicle H	12 Dec 85	6 (179)	0	2.6	0	–
Tray 6						

*See Maciolek et al. (1986)

Table 6. *Prochaetoderma yongei*. Comparison of a female from a 1 yr experimental box with females from an Aug trawl sample at 2000 m: body length; and egg number per female and mean egg diameter by developmental stage

	Aug trawl sample[a]	1 yr exp. box[b]	t-test
Total N females	35	1	
Mean length mm ± SD	2.2 ± 0.07	2.1	ns
Stage I eggs: $\bar{\bar{X}}$ diam. (μm) ± $S_{\bar{x}}$	47 ± 0.8[c]	44	ns
No. female^{-1}	12.0	10	
Stage II eggs: $\bar{\bar{X}}$ diam. (μm) ± $S_{\bar{x}}$	106 ± 3.0[c]	101	ns
No. female^{-1}	3.9	1	
Stage III eggs: $\bar{\bar{X}}$ diam. (μm) ± $S_{\bar{x}}$	165 ± 4.1[c]	152	ns
No. female^{-1}	2.3	4	

[a] 39°39.2′N, 70°24.5′W, 2030 m; AII 24 Stn 115
[b] 38°35.78′N, 72°53.65′W, 2020 m; MID-4 Stn 2
[c] $\bar{\bar{X}} = \frac{\Sigma \bar{X}_i}{N}$ See Table 4 for variances and footnote

which gonad maturation may proceed and reach sexual maturity within a year. These are maximum estimates, since the actual time of recruitment into the boxes is unknown. It may be only fortuitous that in the 8 mo experiments, development of female specimens fell between the 2 and 12 mo experiments.

Correlation of growth data from experimental boxes and length-frequency histograms

When length frequencies of juveniles are separated from those for males and females, the pulse of recruitment which occurred in summer samples has a peak size class of 1.0 to 1.3 mm (Fig. 2 & 3). Recruits into experimental boxes show that a length of 1.4 mm can be attained within 2 mo, and 2 mm or greater within 6 mo (Table 5). Therefore, evidence from length frequencies for a pulse in recruitment would probably disappear after 2 mo.

Sexual maturity is experimentally known to be reached within 1 yr (Tables 5 & 6). As there are mature females in the 1.4 to 1.7 mm size class (Fig. 2), it can be assumed that that size class contains individuals whose ages span 2 mo to 1 yr. The peak size class in both summer and winter samples of Fig. 2 & 3 is 1.8 to 2.1 mm; included in this class are individuals of 6 mo in age or less, since the recruit into a 6 mo experimental box was 2.6 mm (Table 5). Thus growth during 1 yr is included in size classes from 0.6 to 2.6 mm and falls within the peak size class.

The age beyond 1 yr or mortality at any age cannot be inferred from the growth and recruitment data given here.

Data on recruitment rate from experimental boxes

The faunal contents of the 8 mo experimental boxes are directly comparable to box core samples taken from the same locality (Stn 367) or slightly deeper (Stn 370). All are 0.25 m^2 in area with twenty-five 10 cm^2 subsections; all can be considered summer populations, albeit the termination of the experimental box was 1 yr after the box cores were taken. The numbers of *Prochaetoderma yongei* per 10 cm^2 subcore in the 2 box cores were 1.8 and 2.2 (Stn 367 and 370, respectively), or an average of 2.0. In each screened experimental box (*Alvin* 834A and C, Table 5) the number of *P. yongei* per 10 cm^2 subsection was 0.2 specimens. Thus, if it takes 248 d to recruit 0.2 individuals per 10 cm^2, then it would take 2480 d or about 7 yr to recruit to numbers found in the natural population, all else being equal and ignoring predation, variation in rates of recruitment, and recruitment by lateral transport (but see Smith [1985] on the importance of disturbance and lateral transport). Predation may account for the absence of *P. yongei* in a 26 mo unscreened experimental box placed in the same area several years earlier (Grassle 1977) and the presence of only a single individual in the 8 mo unscreened experimental box (Table 5, *Alvin* 834D).

DISCUSSION

Reproduction of invertebrates in level bottom communities of the deep sea should reflect the effects of a stable environment of permanent darkness, low temperatures, and great pressure. Thus the questions of whether there is reproductive periodicity in such an environment and what the growth rates might be are of interest.

Certain terms are used in the following discussion of reproductive patterns. They are defined as follows: 'asynchrony' and 'synchrony' refer to both gametogenesis and spawning. Gametogenesis is considered asynchronous if several stages of oocyte development are present in each female in a population; it is assumed, but cannot be observed, that at least some females are spawning at any one time (period undefined) and that the population as a whole never stops reproducing. Gametogenesis is synchronous when all oocytes in all females are at the same stage in a population; synchronous spawning, or the release of all eggs, can be seen to have occurred by examination of the gonads. 'Recruitment' includes such considerations as type of development, presence or absence of a dispersal stage, conditions affecting settlement, and mortality of early postlarvae; here recruitment refers only to the presence of juveniles in a population as indicated by size frequencies of individuals. Three terms define time as it relates to reproductive events. 'Continuous' reproduction has a steady rate of mature oocyte production and recruitment into a population; it can only result from asynchrony of gametogenesis. 'Periodic' reproduction has regularly reoccurring cyclic gametogenesis and spawning that can only result from synchrony. Continuous reproduction overlayed by periods of increased intensity of reproduction is here called 'fluctuating'; it also results from asynchrony and may be either cyclic or irregular in occurrence. 'Fecundity', the total reproductive capacity of an individual over its lifetime, is not treated here.

The earliest measurements of reproduction in deep-sea level-bottom molluscs were based on histologic examination of gamete development and gonad volume in the bivalve genus *Nucula* (Scheltema 1972; preliminary findings quoted in Sanders & Hessler 1969). In at least one species some portion of a population had mature eggs year-round. Scheltema suggested that 'deep-sea species must either survive better, live longer, or reproduce more continuously than their counterparts on the shelf' in order to maintain a fecundity equal to sublittoral species but that little was known about periodicity of reproduction in the deep sea.

Later studies have addressed both recruitment and gametogenesis by comparing gamete development, oocyte size-frequencies, and length frequencies among individuals from single populations over time. These studies show that among species of deep-sea molluscs 3 patterns of reproduction can be discerned: continuous-asynchronous, periodic-synchronous, and fluctuating-asynchronous. In continuous-asynchronous reproduction no cyclic events are observed, juveniles are always present in the same proportion in a population, and some or all females have ripe eggs at all times (e.g. gastropods: *Benthonella tenella,* Rex et al. 1979 [although size-frequencies were erratic]; *Colus jeffreysianus,* Colman et al. 1986; bivalves: *Nucula darella, Tindaria cervola,* Rokop 1974, 1979). Periodic-synchronous reproduction results in cyclic spawn-out over an entire population followed by peaks in recruitment (e.g. bivalves: *Ledella messanensis* and *Yoldiella jeffreysi,* where the cycle is seasonal, Lightfoot et al. 1979, Gage 1985). Fluctuating-asynchronous reproduction occurs in species which have the capacity for continuous reproduction but which nevertheless have times of increased recruitment and production of

mature oocytes (e.g. bivalves: *Nucula cancellata*, Gage et al. 1986).

The rate of recruitment can vary within a pattern of reproduction. For instance, among certain deep-sea bivalves that reproduce continuously more than 25 % of all individuals within a population may be juveniles (Rokop 1979), whereas in the gastropod *Colus jeffreysianus*, also a continuously reproducing species, only a few juveniles occur in a population at one time (Colman et al. 1986).

Among the 3 patterns, *Prochaetoderma yongei* has a fluctuating-asynchronous reproduction. Females have more than one stage of oocyte development, a population has some ripe individuals at all times, and there are fluctuations in number of ripe individuals, size and proportion of mature oocytes, and proportion of juveniles. It is not certain from data presented here that the fluctuations are seasonal.

The time needed for juveniles to reach sexual maturity has been estimated in a few instances from length-frequency data and expressed in qualitative terms, e.g. Rokop (1979) described the rapid advent of sexual maturity in some bivalves. Graphs of length-frequency data from the deep sea have so far not been related to known time intervals, but age structure underlying length frequencies in 4 bivalve species collected over many seasons and years in the Rockall Trough has been modeled by Gage et al. (1986) after estimating age from shell growth-lines; maturity is apparently achieved in 2 to 3 yr. Turekian et al. (1975) estimated from radiometric measurement that the shell of an abyssal bivalve, *Tindaria callistiformis*, was 98 ± 76 yr old; by extrapolating from growth rates of shallow water species they further estimated that this specimen had reached maturity in 50 to 60 yr.

Direct measurements of time to maturation classically have depended on the ability to sample a cohort from recruitment through time, but in deep-sea populations there are difficulties in doing this: (1) the labor involved in sequential sampling (including ship time and sorting) is prohibitively expensive, and (2) the pattern of continuous and asynchronous reproduction in many deep-sea species makes time of recruitment, or release of a specific cohort, virtually unknowable. However, recruitment of juveniles and unambiguous maximum growth rates to maturity can be determined from colonization experiments for species with planktonic larval stages (see Grassle [1980] for a description of experiments). Besides the rates given here for *Prochaetoderma yongei*, 2 other experiments have yielded rapid growth rates for deep-sea molluscs; both are from about the same 1800 m area as the 2 and 8 mo experiments described above (Table 5). Mature-sized specimens of the bivalve *Nucula cancellata* were recovered from a 26 mo experimental box of azoic mud (Grassle 1977, 1978). Wood panels exposed for 3½ mo on the sea bottom were twice colonized by each of 2 species of wood-boring bivalves (Xylophagainae) (Turner 1973). Gonads were nearly ripe in the older individuals, although the specimens were small owing to crowding. Although most published results of recruitment experiments have addressed questions of faunal recolonization rates rather than growth rates of individual species (Grassle 1977, Desbruyères et al. 1980), one of Grassle's stated purposes (1978) for recruitment experiments is to establish growth rates, and the data presented here are based on his experimental boxes.

The question of precisely how growth and reproduction traits of *Prochaetoderma yongei* affect its numerical abundance in the North American Basin remains unanswered. The ability of *P. yongei* to recruit and grow quickly to maturity, combined with its small size, is characteristic of species adapted to transient environments (so-called opportunistic species). However, lack of synchrony in reproduction and low numbers of eggs are not the marks of a species adapted to rapid change and may be contrasted to the 30 000 eggs present in individuals of the deep-sea Xylophagainae (Turner 1973). Moreover, the numerical success of *P. yongei* in the northwestern Atlantic for some reason does not continue over the rest of its range in the eastern Atlantic, where the diversity of species among the Prochaetodermatidae is very much higher but densities of individuals in a species are much lower (Scheltema 1985a, b).

The stimuli that bring about times of increased reproduction – cyclic or fluctuating – in deep-sea species remain to be ascertained and the seeming constancy of the deep sea questioned. The data presented here and from earlier studies on molluscs indicate that growth and maturation times in many deep-sea species are on the same time scale as in shallow-water species. Certainly in these cases constant low temperatures, darkness, and high pressures have not resulted in slow growth.

Acknowledgements. I thank Steven Boyd and Armando Tamse for arranging the use of their digitizer and training me in its use. I have benefitted from Rudolf Scheltema's reference collection on reproduction in the deep sea and critical reading of the manuscript. Discussions with James Weinberg have helped clarify my thoughts. Howard Sanders and J. Frederick Grassle have been enthusiastic in encouraging research arising from samples collected by them. The following grants supported the collections, experiments and digitizer use reported here: National Science Foundation Grants GB 6027X, GA 31105, GA 36554, OCE78-19820, OCE81-17586, and OCE85-8350; Minerals Management Service Contract #14-12-0001-30064. Contribution No. 6357 from the Woods Hole Oceanographic Institution.

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This article was presented by Dr. J. D. Gage; it was accepted for printing on February 9, 1987