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REPRODUCTION AND DISPERSAL OF BOTTOM  
DWELLING DEEP-SEA INVERTEBRATES:  
A SPECULATIVE SUMMARY<sup>1</sup>

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The stability and physical monotony of the deep-sea presents a remarkable environment where bathyal and abyssal benthic organisms successfully live and reproduce. To elaborate here about the nature of this deep-sea environment is unnecessary (vide Bruun, 1957). Suffice to say it is one of great hydrostatic pressure where temperature is constant and uniformly cold (less than 4°C), where day and night are indistinguishable, and where as a consequence there are no obvious seasonal or diurnal cyclic phenomena. Moreover the amount of available food is very low relative to that found in shallow, inshore-waters. It is particularly interesting to know therefore how living creatures manage to maintain themselves in this seemingly unpromising habitat, presenting such unusual physiological demands. It is my purpose to review here what little is known about one basic biological process of the deep-sea benthos, namely reproduction.

There are three aspects of reproduction that I will consider briefly; (1) the reproductive potential or fecundity, (2) the periodicity of reproduction, and (3) the mode of development; that is, whether deep-sea species have direct development without a dispersal stage or, alternatively, if there is some sort of free-drifting larval form. I will try to point out in a very general way how these three aspects of reproduction are related to the dynamics of the deep-sea community.

### Reproductive Potential

The reproductive potential or fecundity of deep-sea benthic invertebrates is known in only a very general way. For example, among the isopod crustacea, in particular the *Asellotes*, a few relatively large eggs are carried by each female. On the other hand, some species of ophiuroids or brittle stars are believed to have large numbers of eggs because "...deep-sea samples usually have a large ratio of young specimens to adults, implying that few adults produce a great many young..." (Schoener, 1967, p. 646). Between these extremes lie many bivalves, and in particular the protobranchs.

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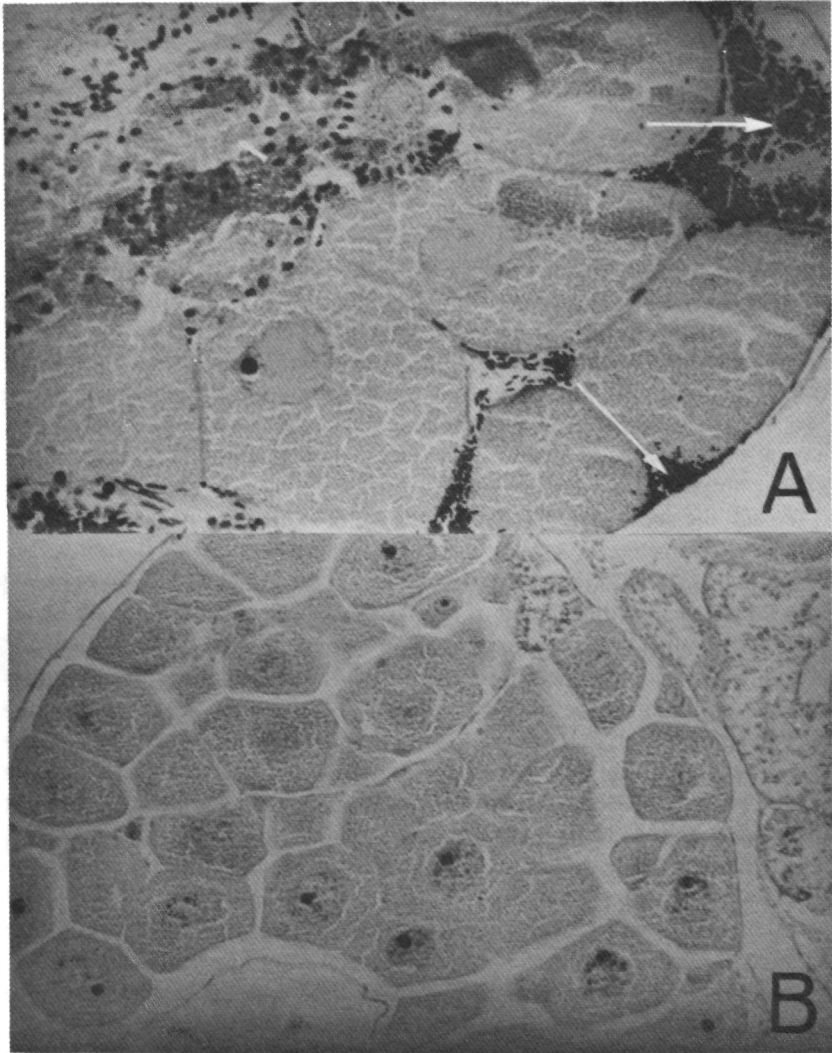
Perhaps the most useful way to understand the fecundity of deep-sea forms is to compare their reproductive potential with that found among species inhabiting the continental shelf. Recent preliminary data make such a comparison possible among various species within the bivalve genus *Nucula* found off the northeastern coast of the United States (Scheltema and Sanders, unpublished manuscript). All members of this genus insofar as known are infaunal deposit feeders; seven New England species occur from the shallow sub-tidal to the abyssal depths. Three, *Nucula proxima*, *Nucula annulata* (vide Hampson, 1971), and *Nucula delphinodonta*, are known only from the continental shelf (i.e., down to 200 m). Three other species, *Nucula subovata*, *Nucula granulosa* (= *corticaa*), and *Nucula cancellata*, are characteristically found on the slope from the edge of the shelf to 2000m. However, *Nucula subovata* is largely an upper slope species, while *Nucula cancellata* occasionally extends into the abyss. Finally, the single remaining species, *Nucula verrilli* is restricted entirely to abyssal depths.

Among these seven species of the genus *Nucula*, two differ from all the rest in having larger eggs, and these quite clearly have direct development (See Fig. 12); the other five forms appear to be lecithotrophic, presumably having non-feeding, drifting, larval stages of short duration (vide Chanley, 1968).

As will be seen later, this predominance of lecithotrophic development is a general characteristic among deep-sea bivalves.

If only the lecithotrophic species are considered, and if these are ordered in accordance with their depth range, it can be seen that the gonads of the shelf forms have a larger volume than the species found along the slope and abyss. Some account should be taken of difference in size of the various species, and this can be done by comparing the ratio of gonad volume and shell length (Table 1). This quotient gives a value for the volume of the gonad relative to the total size of the organism and can be used to compare various species of different dimensions. Its biological significance is that it gives some notion of the relative biomass devoted to reproduction. The shell length rather than body volume has been used because the former is much easier to measure.

Looking now at our specific examples of the genus *Nucula* (Table 1), the average "gonad volume to shell length ratio" for the two shelf species, *Nucula proxima* and *Nucula annulata*, was 0.28 whereas that for the slope and abyssal forms, *Nucula granulosa*, *Nucula cancellata*, and *Nucula verrilli*, was only 0.06. The proportion of biomass being devoted to reproduction by lecithotrophic shelf species at any one instant is larger, approximately three times greater, than that of slope and abyssal forms.



**Figure 12.** Histological sections of gonads from bivalves belonging to the genus *Nucula*. Both figures were photographed at the same magnification (160X).

a) *Nucula subovata*: section showing large eggs typical of direct development. Note also darkly staining sperm indicated by arrows. Shell length of specimen 1.9 mm.

b) *Nucula annulata*: sections showing eggs typical of species with lecithotrophic development. There is no evidence of hermaphroditism in this form. Shell length of specimen 2.2 mm.



Table 1

Comparison of Reproductive Potential Between Shoal and Deep-water Lecithotrophic Species of the Genus *Nucula* from off the Coast of the Northeastern United States

Species	Vertical distribution	Shell length mm	Gonad volume mm <sup>3</sup>	Gonad volume Shell length mm	Total number of eggs	Eggs Shell length mm
<i>Nucula proxima</i>	Shelf	6.6	2.06	0.31	4120	624
<i>Nucula annulata</i>	Shelf	3.3	0.80	0.37	1233	374
<i>Nucula granulosa</i>	Slope	2.2	0.11	0.07	217	99
<i>Nucula cancellata</i>	Slope	3.3	0.24	0.15	194	59
<i>Nucula verrilli</i>	Abyss	4.3	0.24	0.11	260	60

The number of eggs produced by lecithotrophic species of the continental shelf is also considerably more than slope and abyssal forms. If the number of eggs is expressed as "eggs per millimeter of shell length," then a seven fold difference is seen between shelf and abyssal species (Table 1).

The significance of these differences in *fecundity* between shoal-water and deep-sea species of *Nucula* becomes evident if one considers the reproductive requirements of any stable or steady-state benthic population. If a bottom population is to maintain itself, it is necessary on the average that each individual be replaced once during its lifetime. But species that produce small numbers of eggs must offset this low reproductive rate either by (1) better survival or (2) a longer period of reproduction during the course of its life.

If the former is true then deep-sea species of bivalves may be expected to have *survivorship curves* with a high initial survival expectancy (vide Deevey, 1947, p. 285, approaching type I curve), whereas shelf species will have a relatively lower initial expectancy of survival (approaching type III curve, Deevey, op. cit. ). Stated differently, the minimum average required survival for a shelf species to maintain itself will about 0.05 percent, whereas the average for slope and abyssal species will need to be 0.4 percent. The two groups thus tend toward different reproductive "strategies". It has been shown that frequently these differences in "strategies" are related to other characteristics of *species*, the so-called "K" selection or biologically controlled as contrasted with the "r" or physiologically selected species (vide MacArthur and Wilson, 1967; Sanders, 1968; Pianka, 1970).

If the latter or second possibility proves true, that is if deep-sea forms have a longer period of reproduction, it means either (a) that the species must live longer or (b) that they spawn more frequently or perhaps continuously, rather than periodically as is the case for most shoal-water boreal species. Considering the energy required for continuous spawning, the

latter alternative seems rather less likely in the relatively impoverished deep-sea environment.

### Periodicity and Reproduction

*Periodicity* in reproduction is advantageous to a species because all members of a population can then spawn synchronously. This doubtless enhances the likelihood of fertilization. Among shoal-water species having phytoplankton-trophic development, seasonal reproduction is required in order that larvae may take advantage of the high seasonal phytoplankton productivity. As scarcely any of the deep-sea species are thought to have feeding-larvae, the latter advantage evidently does not apply.

The work done thus far on this aspect of reproduction in the deep-sea has been somewhat controversial until now because the data are scanty and difficult to obtain. George and Menzies (1967, 1968) suggested that certain deep-sea isopods have a seasonal cyclic-reproduction, but the data are so meager that their conclusions must be regarded as largely speculative. The evidence used was the occurrence of gravid females.

Sanders and Hessler (1969) found no evidence for reproductive periodicity in an unidentified species of isopod from the genus *Ilyarchna*. Dredge samples taken in August had 24% of all specimens with eggs in their marsupium, and 27% were in a reproductive condition during December.

Schoener (1968) studied two species of brittle stars collected on a transect between Woods Hole and Bermuda and concluded that their reproduction was periodic and seasonal. Her evidence was based upon the occurrence of sexually mature females and also on length-frequency analysis. She found that deep-sea dredge hauls made in summer months yielded large numbers of young brittle stars, whereas in winter and spring few small specimens were taken. On the other hand, winter hauls had adults with well developed gonads, whereas samples taken in May lacked any such development.

Scheltema and Rodman (1966) found in a number of slope species of polychaetes that at least some individuals were in a reproductive condition at all times of the year.

Preliminary evidence from samples of *Nucula cancellata* collected at different times of year show that some portion of its population is in a reproductive state throughout the year. The importance of knowing the duration of reproduction was already pointed out in the previous section on reproductive potential.

### Mode of Reproduction

Thorson (1950), on the basis of very meager evidence, ventured the opinion that most deep-sea invertebrates would prove to have direct development and that consequently they would lack a planktonic dispersal stage. Though direct development is now known to be the rule for some

deep-sea taxa, this is clearly not so for many other invertebrate groups. Thus, whereas deep-sea isopods are known to develop directly, some bathyal ophiuroids (Schoener, in litt.) and many bathyal and abyssal bivalves (Ockelmann, 1965) have eggs of moderate to very small size, indicating a lecithotrophic or, more uncommonly, a planktotrophic development. Ockelmann (1965, p. 33, fig. 5) after carefully studying the prodissoconchs and egg size of a large number of species along the Atlantic coast of Europe, was able to demonstrate a positive correlation between increasing depth (up to 400 m) and the percentage of bivalve species having lecithotrophic development. The results of his study further showed that it was only among bivalves of the arctic shelfwaters that direct development was commonly found.

Ockelmann's concept is further extended to much greater depth by recent new data from two deep-sea expeditions. Knudsen (1967) has shown that of the 26 bathyal bivalve species collected during the John Murray Expedition, 58% had lecithotrophic development, 24% had direct development, and 8% are believed to produce planktotrophic larvae. The percentage of lecithotrophic development at abyssal depths is even higher. Results from the Galathea Expedition show that, among the 23 abyssal bivalve species for which the mode of reproduction is known (Knudsen, 1969, 1970), 78% had lecithotrophic development, 13% develop directly, and surprisingly, 9% appear to have planktotrophic larvae (i.e., two species, *Dacrydium panamensis* and *Abra profundorum*).

Turning now to the genus *Nucula* off the northeastern coast of the United States, a similar trend can be seen. Here, again, the difference in the mode of reproduction is evident from the characteristic size of the eggs (Fig 12). Two species, *Nucula delphinodonta* and *Nucula subovata*, have markedly larger eggs and direct development. The five remaining species including *Nucula proxima*, *Nucula annulata*, *Nucula granulosa*, *Nucula cancellata*, and *Nucula verrilli* have eggs ranging in diameter from 100 to 135  $\mu$  (Table 2). All five species apparently have lecithotrophic development. Thus among the four deep-water species, one has direct development; on the shelf one of three develops directly.

In general the evidence cited above tends further to strengthen Ockelmann's hypothesis that "lecithotrophic development with a short pelagic larval stage predominates among bivalves of the deep-sea" (Ockelmann, 1965, p. 35).

To date, however, there is but little direct evidence for the occurrence of larvae in the great depths of the ocean. Mileikovsky (1968) has recorded lamellibranch larvae from 1500 to 2000 meters in the region of the Kurile-Kamchatka Trench (p. 214, Table 4). Samples taken with closing nets from the deep-sea submarine Alvin have also contained lamellibranch veligers down to 1900 meters. According to the data of Mileikovsky, polychaete larvae can be found at depths exceeding 4000 meters.

Table 2

Relationship between mode of reproduction and geographic range among species of the bivalve genus *Nucula* known from off the northeastern coast of the United States

	Vertical distribution (m)	Egg diameter $\mu$	Probable development	Geographical distribution
SHELF SPECIES				
<i>Nucula proxima</i>	<200	100	Lecithotrophic	Western Atlantic: N E coast of U.S.
<i>Nucula annulata</i>	<200	120	Lecithotrophic	Western Atlantic N E coast of U.S.
<i>Nucula delphinodonta</i>	<200	190	Direct	Western Atlantic: N E coast of U.S.
SLOPE SPECIES				
<i>Nucula subovata</i>	530-1500	270	Direct	Western Atlantic N E coast of U.S.
<i>Nucula granulosa</i>	530-1500	120	Lecithotropic	Western Atlantic E coast of U.S. Eastern Atlantic: Bay of Biscay
<i>Nucula cancellata</i>	530-3860	135	Lecithotrophic	Western Atlantic: E coast of U.S. Eastern Atlantic: Bay of Biscay off W. Africa
ABYSSAL SPECIES				
<i>Nucula verrilli</i>	1960-3860	125	Lecithotrophic	Western Atlantic: N E coast of U.S. N E coast of Brazil Eastern Atlantic: off W. Africa

The widespread occurrence of lecithotrophic development in deep-sea benthic species can be significant to their dispersal. Even if the duration of larval development is only one or two days, the larvae may be transported for several kilometers. The velocities of deep-sea currents off the northeast coast of the United States have been investigated in recent years by Knauss (1965), Webster (1969), and Schmitz et.al (1970). Measurements on the slope and under the Gulf Stream have given values between 3 and 44 cm/sec. This means that during the course of 24 hours a neutrally buoyant particle may be carried from 2.6 to 38.0 kilometers per day.

A compilation made from the data of Clarke (1962) shows that 35% of all Atlantic bivalve species from depths of over 2000 m have an amphi-Atlantic geographical distribution. The figure is, however, heavily biased toward species with a restricted range because so many bivalves are known from only a single collection (vide Knudsen, 1970, p. 185). When more data are available they will probably show a greater percentage of deep-sea bivalves having wide geographical distributions. On the other hand the Asellote

isopods, reproducing exclusively by direct development, will probably have less than five percent of their species with amphi-Atlantic geographical distribution.

Returning now to the genus *Nucula* off the northeastern North American continent (Table 1) it is known that all shelf species from this region are confined in their distribution to the western Atlantic. Because of their depth restriction it is apparently not possible for lecithotrophic species to disperse across the Atlantic Basin in a stepwise fashion. Of the deep-water species, however, all with lecithotrophic development are found both in the eastern and western Atlantic Ocean and apparently extend their range by means of pelagic larvae. Only the one directly developing species is restricted to the western Atlantic.

Summarizing, although the data on the mode of reproduction among deep-sea benthic invertebrates is quite scanty, there is enough evidence to conclude that a positive correlation exists between the wide geographic range of taxa and the occurrence of a larval dispersal stage.

It should be very evident from what has been written in this brief discourse that there are very few facts known concerning the reproduction of life history of deep-sea benthic organisms. Yet such knowledge is basic to further understanding the dynamics of bathyal and abyssal communities!

### Summary

1. There is a wide range in the reproductive potential among deep-sea species, ranging from but a few eggs as in the isopods to many thousands of eggs as found in some echinoderms. Among protobranch bivalves of the genus *Nucula* there is evidence suggesting that deep-sea species must either survive better, live longer, or reproduce more continuously than their counterparts on the shelf.

2. Practically nothing is known concerning periodicity or synchrony of reproduction in more deep-sea forms.

3. There appears to be a positive correlation between the geographic range of species and the occurrence of a larval dispersal stage.

### BIBLIOGRAPHY

- Bruun, A.F., 1957 Deep Sea and Abyssal Depths. Chapter 22. In: Treatise on Marine Ecology and Paleoecology. Ed. J.W. Hedgpeth. Geol. Soc. Amer. Mem., 671:641-672
- Chanley, P., 1968. Larval development in the class Bivalvia. Symp. on the Mollusca, (Cochin) Mar. Biol. Assn. India, II: 457-481.
- Clarke, A.H., 1962. Annotated list and bibliography of the abyssal marine molluscs of the world. Bull. Nat. Mus. Canada 181:1-114.
- Deevey, E.S. 1947. Life tables for natural populations of animals. Quart. Rev. Biol., 22:283-314.



- George, R.Y. and R. J. Menzies, 1967. Indications of cyclic reproductive activity in abyssal organisms. *Nature* (London), 215:878.
- George R. Y. and R. J. Menzies, 1968. Further evidence for seasonal breeding cycles in deep sea. *Nature* (London), 220:80-81.
- Hampson, G.R., (1971). A species pair of the genus *Nucula* (Pelecypoda) from the eastern coast of the United States. *Proc. Malacal. Soc. Lond.* 39:333-342.
- Knauss, J.A., 1965. A technique for measuring deep-ocean currents close to the bottom with an unattached current meter and some preliminary results. *J. Mar. Sci.*, 23:237-245.
- Knudsen J., 1967. The deep sea Bivalvia. The John Murray Expedition 1933-34. *Sci. Rept.*, 11 (3):237-343.
- Knudsen, J., 1969. Remarks on the biology of abyssal bivalves. (*Proc. Third Europ. Malac. Congr.*) *Malacologia* 9 (1):271-272.
- Knudsen, J., 1970. The systematics and biology of abyssal and hadal Bivalvia. *Galathea Rept.*, 11:7-241.
- MacArthur, R.H. and E.O Wilson, 1967. The theory of island biogeography, Princeton Univ. Press, Princeton, N.J. 203 pp.
- Mileikovsky, S.A., 1968. Some common features in the drift of pelagic larvae and juvenile stages of bottom invertebrates with marine currents in temperate regions. *Sarsia*, 34:209-216.
- Ockelmann, K.W., 1965. Developmental types in marine bivalves and their distribution along the Atlantic coast of Europe. *Proc. First Europ. Malacal. Congr.*, 1962, pp. 25-35.
- Pianka, E.R., 1970. On r- and K selection *Amer. Nat.* 104 (940):592-597.
- Sanders, H.L., 1968. Marine benthic diversity: A comparative study. *Amer. Nat.* 102:243-282.
- Sanders, H.L. and R.R. Hessler, 1969. Ecology of the deep-sea benthos. *Science* (N.Y.), 163:1419-1424.
- Scheltema, R. S. and J. Rodman, 1966. Reproduction of the deep-sea benthos. W.H.O.I. Ref. No. 66-3 pp. 68-69. (Unpublished manuscript.)
- Schmitz, W.J., A.R. Robinson and F.C. Fuglister, 1970. Bottom velocity observations directly under the Gulf Stream. *Science*, 170:1192-1194.
- Schener, 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.
- Thorson, G., 1950 Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.*, 25:1-45.
- Webster, F., 1969. Vertical profiles of horizontal ocean currents. *Deep-Sea Res.*, 16:85-98.