

REPRODUCTION, DEVELOPMENT AND LIFE-HISTORY TRAITS

Craig M. YOUNG

INTRODUCTION

From the earliest days of deep-sea exploration, it was assumed that animals living in the presumably “hostile” environments of the deep sea should show life-history attributes and reproductive modes differing from those of their shallow-water counterparts. Shortly after the *Challenger* expedition returned from its circumnavigation of the globe, H.N. Moseley (1880) one of the naturalists of the expedition, summarized the current state of knowledge about conditions in the deep sea. He suggested, as had Wyville Thomson (1878) before him, that brooding (parental care of offspring) is a predominant reproductive strategy in deep water. This idea was supported by the finding of large egg sizes in echinoderms and cnidarians during the same expedition (Agassiz, 1881; Moseley, 1881), and set the stage for a generalization, ultimately formalized as Thorson’s Rule (Mileikovsky, 1971), which remained entrenched in the literature until very recent times, when numerous exceptions have been documented (reviewed by Young, 1994a; Pearse, 1994). A second idea first advanced by John Orton (1920) as a testable but untested hypothesis was that reproduction should be aperiodic in the constant thermal conditions of the deep sea. This hypothesis quickly became accepted as established fact and was questioned only when deep-sea seasonality and reproductive periodicity were documented after the 1960s (reviewed by Tyler, 1988).

Both Thorson’s Rule and Orton’s Rule were reasonable hypotheses when the deep sea was thought to be a completely monotonous habitat with no primary productivity, limited energy and virtually constant physical and chemical conditions. The predictive power of both proved inadequate once one began to understand something of the complexity, dynamics and variability of the deep-sea environment. Unexpected variability

has been demonstrated dramatically in the past two decades by the discovery of vents and seeps (see Chapter 4; Lonsdale, 1977; MacDonald et al., 1989), benthic storms (Chapter 2; Gardner and Sullivan, 1981; Hollister and McCave, 1984; Hollister and Nowell, 1991), turbidites (Chapter 2; McCave and Jones, 1988), and other major sources of disturbance. Nevertheless, the vertical gradients of environmental stability and of nutrient availability that provided impetus for the earliest predictions remain a useful framework for considering how natural selection has shaped the life-history attributes of deep-sea animals.

In this chapter, I provide a phyletic overview of known reproductive parameters and developmental modes of deep-sea invertebrates, then apply various predictions of life-history theory to deep-sea animals, considering which predictions are supported or refuted by the available data. Both chemosynthetic and non-chemosynthetic systems are discussed, though the emphasis is on the latter, as a comprehensive summary of reproduction at hydrothermal vents and cold methane seeps has recently been published (Tyler and Young, 1999). Space limits the present treatment to benthic invertebrates; for portals into the literature on life-history attributes of deep-sea fishes, the reader is referred to Stein and Percy (1982), Gordon and Duncan (1985) and Merrett (1987).

PHYLETIC OVERVIEW OF REPRODUCTION AND DEVELOPMENT

In his seminal review of evolutionary ecology in the deep sea, Sanders (1977) noted that deep-sea benthic sediments are dominated by polychaetes, crustaceans, molluscs (especially protobranch bivalves and gastropods) and echinoderms, the peracarid crustaceans

being the most speciose group. On hard substrata in the deep sea, cnidarians and sponges are especially abundant (Gage and Tyler, 1991) except at hydrothermal vents, where the hard-bottom fauna is dominated by polychaetes and molluscs (Grassle, 1986). As might be expected, the most speciose and abundant groups are also the best studied. I will discuss each of these major phyla in turn, then briefly consider a few others for which more limited information is available.

Annelida

Polychaete annelids are among the most abundant and diverse macrofaunal organisms in the deep sea (Hartman, 1965; Hartman and Fauchald, 1971). Most are deposit feeders depending directly on detrital material falling from above, and most live in the upper few centimeters of sediment. However, polychaetes are also well represented at hydrothermal vents and cold seeps, where they may take on bizarre life styles and spectacular forms. The giant tube worms of vents and seeps and the filamentous perviate pogonophorans are now recognized as polychaetes (family Siboglinidae) specialized for the use of chemosynthetic energy sources. Alvinellid polychaetes, which are common at hydrothermal vents, may be the most eurythermal metazoans (Cary et al., 1998). General aspects of polychaete life-history biology and development have been reviewed by Schroeder and Hermans (1975), Giangrande (1997) and Pernet et al. (2002).

Gonads, gametogenesis, and reproductive periodicity

Although many polychaetes are hermaphroditic, the majority of deep-sea forms that have been studied appear to have separate sexes. In polychaetes, the oocytes always originate within distinct ovaries, often found associated with the peritonea (Eckelbarger, 1986), but vitellogenesis, the stage of oogenesis in which oocytes are invested with yolk, may occur either within the ovary or while oocytes are floating freely within the coelom (Eckelbarger, 1986). In like manner, early spermatocytes released from the gonads often aggregate into plaques, then complete spermatogenesis while adrift in the coelom. Gametogenesis in the deep-sea polychaete *Pholoe anoculata* is coelomic in both sexes, with gametes concentrating near the acicula of the neuropodium (Blake, 1993). An unusual modification of the typical patterns occurs in the deep-sea cossurid *Cossura longocirrata*. In this species, oogenesis takes place in a single segment, which

releases mature oocytes into more posterior segments for storage, making the abdominal region appear beaded (Fournier and Peterson, 1991; Blake, 1993). In the large bathyal terebellid *Biremis blandi*, scattered oocytes may be found throughout the coelom, but the highest concentrations are in the ventral region, where they pool between the peritonea (Young, unpublished observations).

With a single exception, all deep-sea polychaetes that have been examined appear capable of reproducing throughout the year, though several species may have “fluctuating” reproductive cycles (as defined by A. Scheltema, 1987), in which there are high and low periods of spawning. One non-vent species, *Cossura longocirrata*, reproduces more in the summer than at other times of the year (Blake, 1993). All of the other fluctuating species are associated with vents (McHugh, 1989; McHugh and Tunnicliffe, 1994; Zal et al., 1995), and in every case sampling is inadequate to determine the period of the fluctuation. The only truly seasonal species is the non-vent spionid *Aurospio dibranchiata*, which occupies an impressively broad bathymetric range (300–3600 m). Notably, evidence for a seasonal gametogenic cycle came not only from the shallowest animals, but also from collections at 2000 m depth. No mature animals were found in spring collections, but animals collected in the summer and fall were ripe (Blake, 1993). However, these data must be regarded as preliminary, since only 13 of 425 individuals examined were found to bear any gametes at all.

Gamete structure and fertilization

Sperm of some deep-sea polychaetes are of the primitive type associated with free spawning and external fertilization (e.g., *Amphisamytha galapagensis*: McHugh and Tunnicliffe, 1994), but the variety of modified sperm described in the literature is striking (Table 12.1). A number of species have elongate sperm, often with limited mobility, which are probably indicative of either internal fertilization, fertilization in tubes, or pseudocopulation in gelatinous egg masses (Franzen, 1956; Jamieson and Rouse, 1989). The sperm of *Paralvinella pandorae* have a convoluted structure of unknown function near the mitochondrion, and the flagellum emerges at an acute angle near this structure (McHugh, 1989), suggesting that motility is limited. On the basis of this sperm structure, McHugh (1989) has speculated that sperm are transferred from the male to the female in bundles rather than being freely spawned. The sperm of *Paralvinella grasslei* lack acrosome,

Table 12.1
Studies of reproductive periodicity and gametes in deep-sea polychaetes

Species	Site	Depth (m)	Egg size ¹ (μm)	Sperm morphology	Periodicity ²	References
NON-VENT OR SEEP SPECIES						
<i>Auospio dibranchiata</i>	N. Carolina	300–3600	112	?	S	Blake (1993), Blake and Watling (1994)
<i>Bathynoe cascadiensis</i>	NE Pacific	2519–3021	?	?	C	Ruff (1991)
<i>Benthoscolex cubanus</i>	Bahamas	600	120	?	C	Emson et al. (1993)
<i>Cossura longocirrata</i>	N. Carolina	600–2000	180×80	?	F	Blake (1993)
<i>Euchone bansei</i>	NW Atlantic	1345–2495	100	?	C	Ruff and Brown (1989)
<i>Fauvelioeops glabra</i>	San Diego Trough	1240	?	?	C	Rokop (1977a)
<i>Hyalinoecia araucana</i>	Chile	600	?	?	?	Carrasco (1983)
<i>Microrbinia lineata</i>	N. Carolina	800–3000	344 (mean)	elongate, aberrant	?	Blake (1993)
<i>Nothria notialis</i>	Antarctic	800–900	large	?	C	Hartman (1967)
<i>Ophryotrocha labidon</i>	NW Atlantic	225–2100	73	?	C	Hilbig and Blake (1991)
<i>Ophryotrocha mandibulata</i>	NW Atlantic	2020–3015	48	?	?	Hilbig and Blake (1991)
<i>Ophryotrocha parlabidon</i>	NW Atlantic	225–2195	56.5	?	C	Hilbig and Blake (1991)
<i>Paronuphis antarctica</i>	Antarctic	800–900	?	?	C	Hartman (1967)
<i>Paedampharete acutiseris</i>	NW Atlantic	4626–4830	23?	?	C?	Russell (1987)
<i>Pholoe anoculata</i>	N. Carolina	583–2000	141	?	C	Blake (1993)
<i>Scalibregma inflatum</i>	N. Carolina	600	190	?	C	Blake (1993)
VENT AND SEEP SPECIES						
<i>Alvinella pompejana</i>	East Pacific Rise	2000	200	modified	P	Jollivet et al. (1998), Pradillon et al. (2001)
<i>Amphisamytha galapagensis</i>	NW Pacific	2447–2725	240	normal	C,F?	Zottoli (1983), McHugh and Tunnicliffe (1994)
<i>Branchiopolynoe seepensis</i>	Mid-Atlantic Ridge	1630–1685	390	elongate	A	Van Dover et al. (1999), Jollivet et al. (2000)
<i>Hesiocaeca methanicola</i>	Louisiana Slope	600	80	normal	C?	Eckelbarger et al. (2001)
<i>Lamellibrachia c.f. lymesii</i>	Louisiana Slope	600	105	elongate; bundles	A	Young et al. (1996b)
<i>Opisthotrochopodus</i> n. sp.	Mid-Atlantic Ridge	1700	390	elongate	A	Van Dover et al. (1999)
<i>Paralvinella pandorae</i>	Juan de Fuca Ridge	1570–2270	215	elongate, modified	C	McHugh (1989, 1995)
<i>Paralvinella palmiformis</i>	Juan de Fuca Ridge	1570–2270	260	modified	C,F	McHugh (1989)
<i>Paralvinella grasslei</i>	East Pacific Rise	2630	275	highly modified	F	Zal et al. (1995)
<i>Ridgeia piscesae</i>	Juan de Fuca Ridge	1853–2265	100	elongate; masses	C	Southward and Coates (1985)
<i>Riftia pachyptila</i>	East Pacific Rise	2500–2700	105	elongate; bundles	C	Cary et al. (1989), Gardiner and Jones (1985, 1993), Marsh et al. (2001)
<i>Seepiophilia jonesi</i>	Louisiana Slope	600	115	elongate; bundles	A	Young et al. (1996b)
<i>Methanoaricia dendrobranchiata</i>	Louisiana Slope	700	?	elongate	?	Eckelbarger and Young (2002)

¹ In most cases, egg sizes are the largest observed in histological sections and may not be representative of the actual sizes of eggs spawned.

² Periodicities are listed as either S, seasonal and synchronous; A, aseasonal, continuous, and asynchronous; and/or F, continuous breeding with fluctuating levels of gamete production.

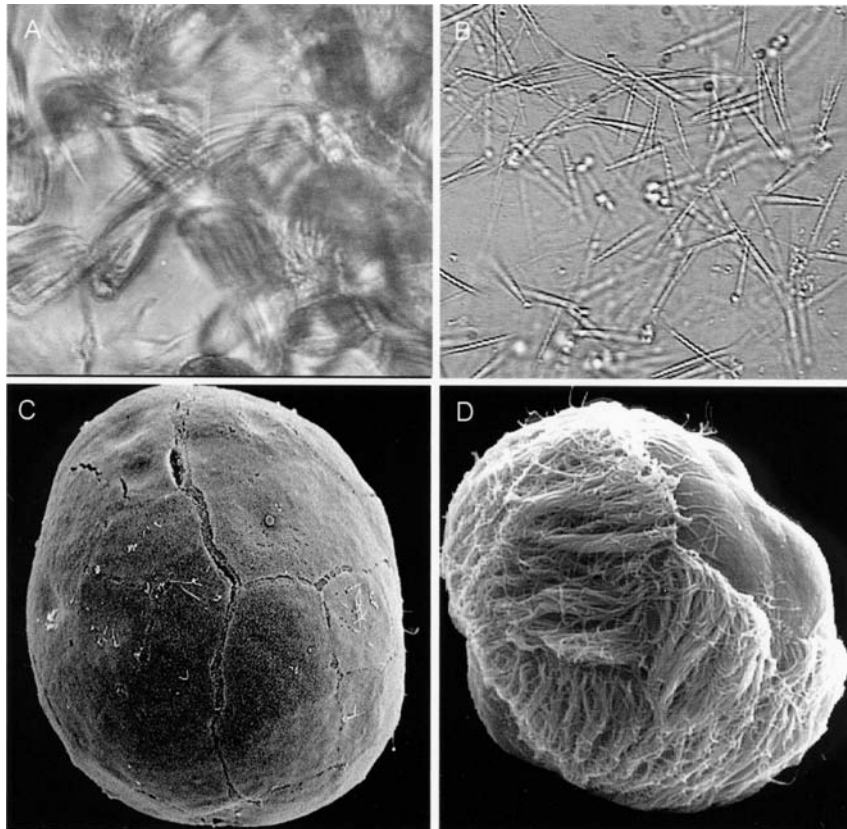


Fig. 12.1. Gametes and embryos of siboglinid tube worms. Sperm bundles (A) and free sperm (B) of *Riftia pachyptila* from 2500 m on the East Pacific Rise. Early larva (C) of *Riftia pachyptila*, showing newly formed cilia arising from trochoblast cells. Trochophore-like larva (D) of *Lamellibrachia* sp. from 600 m on the Louisiana slope.

flagellum and mitochondrion, but nevertheless have some mobility mediated by a flattened structure, apparently having an axoneme, which is believed to be homologous with the flagellum of a typical sperm (Zal et al., 1995). The egg of this species has a deep micropyle, which is interpreted as a mechanism that compensates for a sperm with no acrosome (Zal et al., 1995). *Alvinella pompejana* also has modified sperm (Jouin-Toulmond et al., 1997). Sperm of the orbinid polychaete *Methanoaricia dendrobranchiata*, a common inhabitant of *Bathymodiolus* beds at cold seeps on the Louisiana slope, achieve elongation with a huge acrosome (Eckelbarger and Young, 2002).

The reproductive system and fertilization mechanism of a scale worm, *Branchiopolynoe seepensis*, from Atlantic hydrothermal vents has been described in detail by Jollivet et al. (2000). This species is sexually dimorphic and the complex genital tract of the female includes specialized chambers to store eggs and also sperm received by copulation from the male genital

papillae. Upon leaving the ovaries, oocytes complete vitellogenesis in the coelom and are then collected by two pairs of ciliated coelomostomes, which lead to the proximal portions of the oviducts. The distal oviducts are enlarged to form spermathecae (seminal receptacles) that store sperm received by copulation from the males. Sperm are stored with their heads embedded in the thick epithelium of the spermatheca. The eggs pass through this chamber without being fertilized and are stored in an unpaired median ovisac until spawning. Jollivet et al. (2000), finding no fertilized eggs or embryos in the ovisac, infer that fertilization must occur at the time of spawning.

Perhaps the most modified of all polychaete sperm are found in the siboglinid (formerly vestimentiferan) tube worms associated with vents and seeps. All known siboglinid sperm are released in bundles or masses (Fig. 12.1). In at least one species, *Ridgeia piscesae*, sperm masses have been found attached to the vestimentum, near the gonopores of the female, suggesting

that fertilization may take place either internally or just outside the gonopores (Southward and Coates, 1985). Upon breaking out of the masses, individual sperm of this species undergo a transformation in which the acrosome migrates from its extreme terminal position to surround and cap the tip of the nucleus. Although sperm have been reported from the terminal part of the oviduct in *Riftia pachyptila* (Gardiner and Jones, 1985), there is growing evidence that these and other siboglinids are free spawners. Apparent spawning events have been observed repeatedly in *Riftia pachyptila* (Van Dover, 1994; L. Mullineaux, T. Shanks, R. Lutz, J. Childress, personal communications; C. Young, personal observations) as well as the cold-seep siboglinid *Lamellibrachia* sp. (C. Young, unpublished observations). In these putative spawning events, gametes are expelled in a puff as the animal withdraws partially or completely into its tube. It is not known whether all of these observations are of sperm bundles or if eggs are also released in puffs. However, it seems unlikely that the sperm of other species are transferred to females in the same manner as occurs in *Ridgeia*, as the sperm bundles of these other species separate into individual sperm (Fig. 12.1) shortly after they are diluted in seawater (Cary et al., 1989; Young et al., 1996b). The heads of siboglinid sperm are extremely elongate and consist of a helical mitochondrion wrapped around a helical nucleus (Gardiner and Jones, 1985). The terminal acrosome, which is columnar rather than conical in shape, seems to hold the bundles together on the apical ends, while the posterior end is held together by the individual flagellae, which beat as a unit until the bundle breaks apart. Upon dilution in seawater, the acrosome changes shape and is lost before fertilization (Young, personal observations). The individual sperm, as well as the sperm bundles, are motile in seawater.

Spawning has recently been observed in the so-called "ice worm", the hesionid *Hesiocaeca methanicola* that lives on exposed lumps of methane hydrate near cold seeps in the Gulf of Mexico (Fisher et al., 2000; Eckelbarger et al., 2001). Females apparently release eggs through nephridiopores, whereas males spawn their sperm through the cloaca, which is connected to the coelom by means of a ciliated duct (Eckelbarger et al., 2001). Fertilization in this species is indicated by a slight elevation of the fertilization membrane followed by production of unusually large polar bodies as the egg completes its maturation divisions.

Fecundity

Instantaneous fecundity has been estimated for only two species of non-vent deep-sea polychaetes, *Pholoe anoculata* and the orbinid *Microrbinia lineata*, both from the slope off North Carolina (Blake, 1993). The former has a fecundity of about 160 eggs and the latter bears only two large eggs in a single segment (Blake, 1993). These values are substantially lower than fecundities that have been reported for various polychaetes from hydrothermal vents, which range from less than 4000 in *Paralvinella grasslei* (Zal et al., 1995) through 230 000 in the much larger alvinellid polychaete *Alvinella pompejana* (Chevaldonné et al., 1997). The large hydrothermal-vent tube worm *Riftia pachyptila* holds as many as 700 000 ripe eggs in its ovisac, suggesting that as many eggs as this could be spawned at a time; but egg traps deployed *in situ* always yielded much smaller numbers (Young, unpublished data), suggesting that not all of these eggs are released at once. The smaller tube worm *Tevnia jerichonana*, also from the East Pacific Rise, is often the first colonist arriving at a newly formed vent habitat. Paradoxically, its fecundity is at least an order of magnitude lower than that of *Riftia pachyptila*, which generally arrives much later. Annual fecundities and lifetime fecundities cannot be estimated for any deep-sea polychaete because of inadequate information about longevity, spawning frequency, and the speed of the gametogenic cycle. It would not be surprising, however, if the annual fecundity of the continuously reproducing giant tube worm *Riftia pachyptila* greatly exceeds the fecundity of any lecithotrophic polychaete from shallow water.

Embryogenesis and larval development

Although the developmental modes of most deep-sea polychaetes remain completely unknown, a number of species are known to brood their young. Levin et al. (1994) listed eleven species of known brooders on the slopes of the Volcano 7 seamount in the eastern Pacific (Table 12.2). The mechanism of brooding varies among species, some brooding larvae in the tubes, others employing specialized brood pouches, and still others having the larvae attached directly to the segments of the mother, either laterally or dorsally (Levin et al., 1994). Because it is much easier to document brooding than other forms of reproduction, it is still not known whether brooding predominates among deep-sea polychaetes, or whether a majority of species have indirect development. Levin et al.

Table 12.2
Known and inferred modes and locations of development in deep-sea polychaetes¹

Species	Location	Depth (m)	Mode of development	Type of larva or location of broods	References
Acrocirridae sp. A	E. Pacific	730–3350	direct ²	brooded larvae attached dorsally	Levin et al. (1994)
<i>Ampharete</i> sp. A	E. Pacific	770–1800	direct ²	brooded in tube	Levin et al. (1994)
Ampharetidae sp. B	E. Pacific	770–1800	direct ²	brooded in tube	Levin et al. (1994)
<i>Aricidea quadrilobata</i>	E. Pacific	1300–1800	direct ²	brooded larvae attached dorsally	Levin et al. (1994)
<i>Aurospio dibranchiata</i>	N. Carolina	300–3600	indirect (?)	planktotrophic larva (?)	Blake (1993)
<i>Benthoscolex cubanus</i>	Bahamas	600	indirect (?)	planktotrophic larva (?)	Emson et al. (1993)
<i>Biremis blandi</i>	Bahamas	500–700	indirect	planktotrophic larva (?)	Young et al., unpublished
<i>Cirrophorus lyra</i>	E. Pacific	730–860	direct ²	brooded larvae attached laterally	Levin et al. (1994)
<i>Euchone bansei</i>	NW Atlantic	1345–2495	direct	unknown	Ruff and Brown (1989)
<i>Euchone incolor</i>	E. Pacific	770–3350	direct ²	larvae brooded dorsally and in tubes	Levin et al. (1994)
<i>Euphrosine</i> sp.	E. Pacific	1300–1800	direct ²	brooded larvae attached dorsally	Levin et al. (1994)
<i>Hyalinoecia araucana</i>	Chile	600	direct	brooded in tube	Carrasco (1983)
<i>Microrbinia lineata</i>	N. Carolina	800–3000	direct (?)	brooded embryos and larva	Blake (1993)
<i>Nothria notialis</i>	Antarctic	800–900	direct	brooded in capsules on tube	Hartman (1967)
Nephtyidae sp. C	E. Pacific	2970–3350	direct ²	brooded in dorsal brood pouches	Levin et al. (1994)
<i>Ophryotrocha mandibulata</i>	NW Atlantic	2020–3015	indirect (epitoky)	planktonic larva (?)	Hilbig and Blake (1991)
<i>Paronuphis antarctica</i>	Antarctic	800–900	direct	brooded in tube	Hartman (1967)
<i>Paedampharete acutiseris</i>	NW Atlantic	4626–4830	direct	unknown	Russell (1987)
<i>Protodorvillea</i> sp. A	E. Pacific	730–860	direct ²	brooded in dorsal brood pouches	Levin et al. (1994)
<i>Pholoe anoculata</i>	N. Carolina	583–2000	direct (?)	unknown	Blake (1993), Christie (1982)
Terebellidae	E. Pacific	1300–3350	direct ²	brooded in tube	Levin et al. (1994)
<i>Tharyx</i> sp. A.	E. Pacific	730–3350	direct ²	brooded in dorsal brood pouches	Levin et al. (1994)

VENT AND SEEP SPECIES

<i>Alvinella pompejana</i>	E. Pacific Rise (vent)	2500	indirect	lecithotrophic larva (?)	Jollivet et al. (1998), Pradillon et al. (2001)
<i>Amphisamytha galapagensis</i>	NW Pacific	2447–2725	indirect (?)	lecithotrophic, demersal larva	McHugh and Tunnicliffe (1994), Zottoli (1983)
<i>Branchipolynoe seepensis</i>	Mid-Atlantic Ridge (vent)	1700	indirect (?)	lecithotrophic larvae (?)	Van Dover et al. (1999), Jollivet et al. (2000)
<i>Hesiocaeca methanicola</i>	Gulf of Mexico (seep)	600	indirect	planktotrophic larvae	Eckelbarger et al. (2001)
<i>Lamellibrachia</i> cf. <i>luymesii</i>	Gulf of Mexico (seep)	600	indirect	lecithotrophic larvae	Young et al. (1996b)
<i>Opisthotrochopodus</i> n. sp.	Mid-Atlantic Ridge (vent)	1700	indirect (?)	lecithotrophic larvae (?)	Van Dover et al. (1999)

continued on next page

Table 12.2, *continued*

Species	Location	Depth (m)	Mode of development	Type of larva or location of broods	References
<i>Paralvinella grasslei</i>	East Pacific Rise (vent)	2630	indirect (?)	demersal larvae (?)	Zal et al. (1995)
<i>Paralvinella palmiformis</i>	Juan de Fuca Ridge (vent)	1570–2270	indirect (?)	lecithotrophic, demersal larvae (?)	McHugh (1989)
<i>Paralvinella pandorae</i>	Juan de Fuca Ridge (vent)	1570–2270	direct (?)	embryos brooded in tubes (?)	McHugh (1989)
<i>Ridgeia piscesae</i>	Juan de Fuca Ridge (vent)	1540	indirect	lecithotrophic larvae (?)	Jones and Gardiner (1989)
<i>Riftia pachyptila</i>	East Pacific Rise (vent)	2500–2700	indirect	lecithotrophic larvae	Marsh et al. (2001)
<i>Seepiophilia jonesi</i>	Gulf of Mexico (seep)	600	indirect	lecithotrophic larvae	Young et al. (1996b)

¹ In cases denoted by queries (?) definitive data are lacking, and the inference represents the best guess of the original author.

² Classified provisionally as a direct developer because a brooding mechanism has been documented; may exhibit mixed development in which larvae are released following a brooded embryonic period.

(1994) found evidence for brooding in only a single species on the North Carolina slope, but emphasized that absence of data does not imply that other brooders are not present. It is possible to distinguish between species with planktotrophic development and species relying on yolk (either pelagic lecithotrophs or brooded direct developers) on the basis of egg size (Schroeder and Hermans, 1975). However, the situation is further confused in polychaetes by the prevalence of mixed development, in which embryos are brooded either in or on the adult, or held in an egg mass initially, but then hatch as either planktotrophic or lecithotrophic larvae and complete their development in the plankton (reviewed by Wilson, 1991). Thus, in most instances where brooding has been observed in deep-sea species (Table 12.2), it is impossible to state with certainty whether the developmental mode is direct or if it involves a later larval stage. Indirect development has been inferred more commonly for seep and vent species than for species in non-chemosynthetic habitats, though evidence in many cases is circumstantial (e.g., McHugh, 1989; McHugh and Tunnicliffe, 1994; Zal et al., 1995). Early trochophore larvae of the free-spawning hesionid *Hesiocaeca methanicola* from seeps have been reared in the laboratory and found to be planktotrophic (Eckelbarger et al., 2001). Three species of siboglinids have now been reared to lecithotrophic larvae in the laboratory. *Lamellibrachia* sp. and *Escarpia* sp. from 600 m on the Louisiana slope develop into lecithotrophic trochophores (Fig. 12.1) from buoy-

ant eggs, and probably spend about three weeks in the plankton (Young et al., 1996b). *Riftia pachyptila* also has slightly buoyant eggs; these have been fertilized and the embryos reared in pressure vessels and on the sea floor to an early trochophore larval stage (Marsh et al., 2001). The yolk content and metabolic rate of the latter species suggests that it disperses for about five weeks (Marsh et al., 2001). Recent studies of the hot-vent polychaete *Alvinella pompejana* (Pradillon et al., 2001) show that embryos require temperatures around 10°C for successful development. Embryos dispersing at 2°C between vents apparently arrest development until sufficiently warm water is encountered. This is interpreted as a mechanism facilitating dispersal over very long distances. Despite the apparent prevalence of brooding in non-chemosynthetic polychaetes, there must be a number of species that produce larvae, as polychaetes are often among the most common organisms to appear in boxes of azoic mud deployed on or near the deep-sea floor and protected from invasion by burrowing adults or juveniles (Snelgrove et al., 1992, 1994).

Arthropoda

Crustaceans, particularly peracaridans such as amphipods, tanaids, cumaceans and isopods, are very speciose and abundant in the deep sea (see Chapter 9). The abyssal sites sampled by Sanders and Grassle (1971) contained approximately 85–90 species of

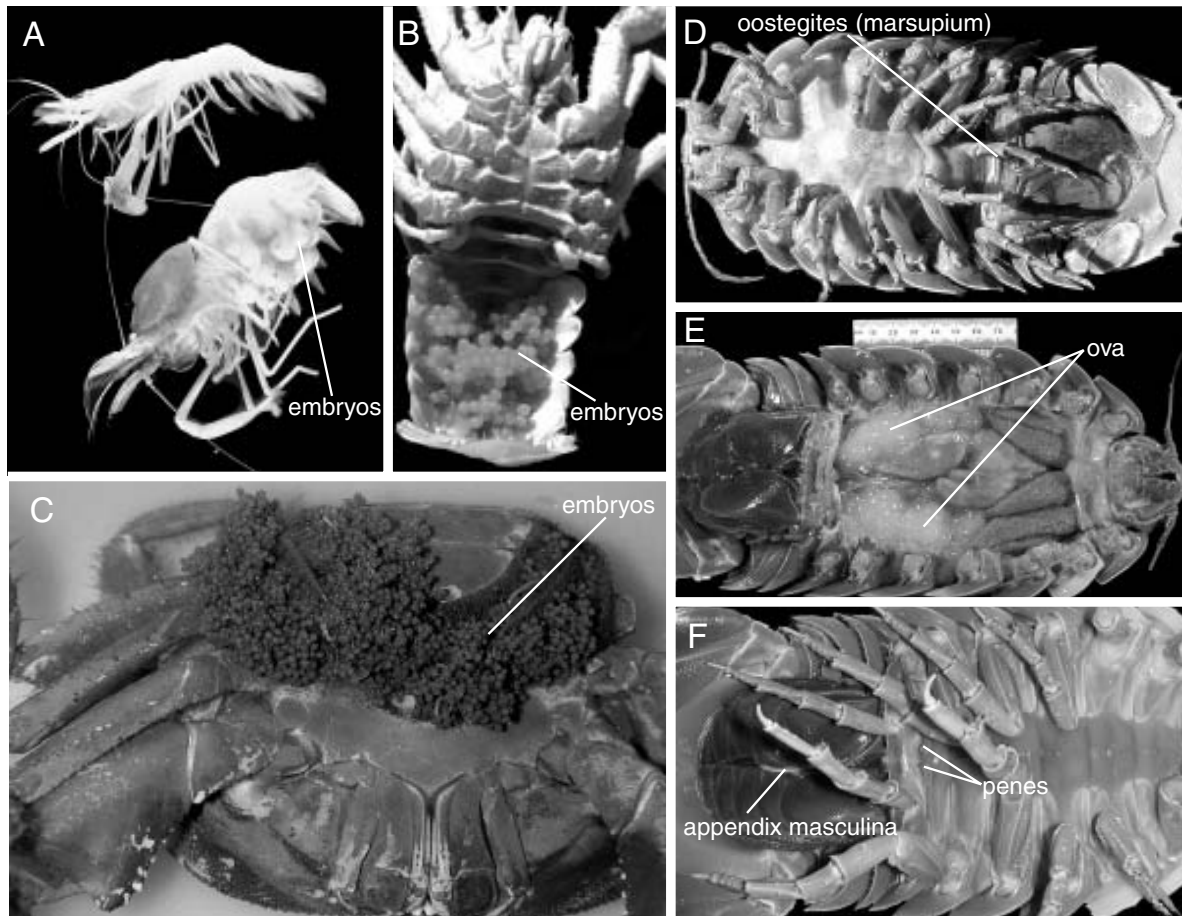


Fig. 12.2. A: Male (above) and female (below) wedding shrimp, from a bathyal hexactinellid sponge in the Bahamas. Note the extreme sexual dimorphism and the large embryos being brooded by the female. B: Galatheid crab of the genus *Munidopsis* from the Rockall Trough, showing very large eggs attached to the pleopods. C: Ventral view of a gravid female brachyuran crab, *Bythograea thermydron*, from hydrothermal vents on the East Pacific Rise. D: Female isopod, *Bathynomus giganteus*, from 800 m depth in the Gulf of Mexico. Oostegites (overlapping plates in the light colored region surrounded by walking legs) cover the brood of this large female, which measures nearly 20 cm in length. E: Female giant isopod, *Bathynomus giganteus*, dissected to show ovaries with very large (1 cm diameter) yolky eggs in the thoracic cavity. Note millimeter rule for scale. F: Ventral view of mature male *Bathynomus giganteus* showing external genitalia. Sperm are transferred to the female through paired penes on the last thoracic segment. The rod-like appendix masculina is also thought to have a role in sperm transfer.

peracarids in a sample of 1000 individuals, compared with 25 bivalve species and 3–5 species of ophiuroids, the next most speciose groups. Indeed, Hessler and Wilson (1983) estimated that peracarids comprise between one-third and one-half of all macrofaunal species in the deep sea. Caridean shrimps are among the most common organisms found at hydrothermal vents, especially in the Atlantic. Larger decapods such as geryonid, dromid and majid brachyurans and pagurid anomurans (hermit crabs) are especially common on the slope. Galatheid crabs (Fig. 12.2) are common at both bathyal and abyssal depths, whereas eryonids

are mostly restricted to the abyss. The importance of decapods at slope depths is well illustrated by the spider crab *Encephaloides armstrongi* (Creasey et al., 1997), which occurs at very high densities in the oxygen minimum layer of the Arabian Sea. So-called marriage shrimps commonly reside within the spongocoels of hexactinellid sponges in the deep sea. Each sponge commonly supports two individuals, a male and a female (Fig. 12.2). Cirripedes, including lepadiform, scalpellid and verruciform barnacles, live on hard substratum (often hard parts of other organisms such as crabs, sea urchins and hexactinellid sponge

stalks) at both bathyal and abyssal depths. Meiofaunal crustaceans, particularly harpacticoid copepods and ostracods, are very abundant in the deep-sea sediments.

Gonads, gametogenesis and reproductive periodicity

The gonads of decapod crustaceans are discrete, often paired or H-shaped organs that lie above the stomach within the cephalothorax and extrude gametes through gonopores on or near the bases of the pereopods. The gonads of peracarids originate under the abdominal pereonites (Johnson et al., 2001), but eventually may extend forward to the cephalothorax region as vitellogenesis proceeds (Bishop, 1994). Gonads of barnacles lie at the proximal end of the visceral mass in acorn barnacles and within the peduncle of stalked barnacles (Green et al., 1994).

Most crustaceans brood their embryos either to the juvenile stage or to a larval stage, so that reproductive periodicity has often been documented by simply noting the presence of brooded eggs or embryos. In decapods, the egg mass or sponge is found attached to the pleopods on the underside of the abdomen of ripe "berried" females (Fig. 12.2). In barnacles, the eggs are brooded as plaques or lamellae within the mantle cavity, and in peracarids (including amphipods, isopods, tanaids, mysids, cumaceans and a few lesser known groups) they are brooded in a thoracic brood chamber called a marsupium. The vast literature on brooding in peracarids has been recently reviewed by Johnson et al. (2001). In its most typical form, the peracarid marsupium is formed by overlapping plates (oostegites) which originate from the coxae of the walking legs. Harpacticoid copepods carry their embryos in a single brood sac attached to and trailing behind the abdomen.

The gametogenic process of deep-sea crustaceans appears identical to that of their shallow water relatives, no special adaptations for deep-sea gamete formation having been reported. The deep-sea red crab *Geryon quinquedens* has an oogenic cycle illustrating the general pattern seen in bathyal brachyurans that have been studied (Haefner, 1977). The ovary begins as a small colorless organ with no central lumen, and consisting mostly of connective tissue. The germinal epithelium is columnar and contains only small, previtellogenic oocytes (Haefner, 1977). As it begins to grow, the ovary becomes more opaque, and growing oocytes replace the central connective tissue. The early previtellogenic oocytes are small (14–53 μm) and the nuclei are highly vacuolated. Vitellogenic oocytes

containing cytoplasmic yolk granules are larger (74–278 μm) and have more compact nuclei. Each oocyte is surrounded by a single layer of follicle cells. The gonad grows and changes color as additional yolk is added to the expanding oocytes. Eventually, the mature ovum attains a diameter of 671 μm and the ovary fills the dorsal side of the ovary, completely obscuring the gut and hepatopancreas.

Wolff (1962) reported that the sex ratio of deep-sea asellote isopods is often biased significantly in favor of males. Indeed, of eleven families surveyed, all but one had a significantly skewed sex ratio. Wolff suggested that this pattern could be explained by gender-specific survivorship, as is known for some shallow-water isopods (Steel, 1961). Evidence for hermaphroditism has been found in four hadal tanaids collected from a depth of more than 6000 m (Wolff, 1956a), and Wilson (1981) reported a case of facultative hermaphroditism in a deep-sea isopod, *Eurycope iphthima*.

Table 12.3 gives a selection of studies of reproductive periodicity in deep-sea crustaceans. Although continuous breeding was predicted for deep-sea isopods early in the 20th century (Reibisch, 1927), the earliest data bearing directly on the subject of reproductive seasonality were anecdotal observations by Wolff (1962) and others who participated in the Danish *Galathea* Expedition between 1950 and 1952. In his monograph on the asellote isopods, Wolff (1962) noted that deep-sea asellote populations have fewer incubatory females (i.e., those with marsupium present) than did shallow-water isopods. Moreover, no brooding females at all were found among the samples of isopods ($n=40$) and tanaids ($n=30$) recovered from the hadal trenches during this expedition (Wolff, 1956a,b). Wolff (1962) considered several possible explanations for this pattern: 1) mortality may be greater for brooding females than for non-brooding ones; 2) brooding females may live deeper in the sediment, thereby avoiding the sampling equipment; 3) breeding occurs only once every few years; 4) the brooding period is much shorter than the preparatory period (the preparatory period is the moult stage when the marsupium is present, but the eggs have not been deposited in it). Although he had no access to seasonal samples from a given locality, he guessed that brooding should occupy a much longer period, perhaps 3–4 months, in deep water than the incubatory periods of 30 to 40 days known among shallow-water isopods, making the small proportion of incubating females even more surprising. After considering the various possibilities listed above,

Table 12.3
Reproductive periodicity and egg size in deep-sea crustaceans

Species	Site	Depth (m)	Egg size (μm)	Periodicity ¹	References
NON-VENT SPECIES					
MALACOSTRACA: PERACARIDA					
Mysidacea					
<i>Boreomysis tridens</i>	Rockall Trough	500–2500	1900–2100	S	Mauchline (1986)
<i>Erythrops microps</i>	Rockall Trough	500–1000	?	A	Mauchline (1986)
<i>Michthyops parva</i>	Rockall Trough	1500–2500	?	A	Mauchline (1986)
Cumacea					
<i>Diastylis stygia</i>	NW Atlantic	2065–2115	?	A	Blake and Watling (1994)
<i>Leucon jonesi</i>	Surinam	1500	?	A (?)	Bishop (1994)
Isopoda					
<i>Eurycope californiensis</i>	San Diego Trough	1171–1244	?	A	Rokop (1977b)
<i>Ilyarachna</i> sp.	NW Atlantic	1400–2178	?	A	Sanders and Hessler (1969)
<i>Ilyarachna profunda</i>	San Diego Trough	1171–1244	?	A	Rokop (1977b)
<i>Natatolana borealis</i>	Mediterranean	500	?	A,F	Kaïm-Malka (1997)
<i>Storhyngura birsteini</i>	Scotia Sea	1737–3804	?	S	George and Menzies (1967)
<i>Storhyngura scotia</i>	Scotia Sea	2450–2816	?	S (?)	George and Menzies (1967)
<i>Storhyngura robustissima</i>	Scotia Sea	884–1485	?	S (?)	George and Menzies (1967)
16 asellote species (pooled data)	N. Carolina Slope	515–5025	?	S (?)	George and Menzies (1968)
47 asellote species (pooled data)	Rockall Trough	1160–2925	?	A,F	Harrison (1988)
Amphipoda					
<i>Eusirus perdentatus</i>	Weddell Sea	176–799	2750	S	Klages (1993)
<i>Harpiniopsis excavata</i>	San Diego Trough	1171–1244	?	A	Rokop (1977a)
<i>Pseudoharpinia excavata</i>	San Diego Trough	1171–1244	?		Rokop (1977b)
CIRRIPEDIA					
<i>Poecilasma kaempferi</i>	Rockall Trough	2000	120	A	Green et al. (1994)
DECAPODA					
Dendrobranchiata:					
<i>Aristeus antennatus</i>	Mediterranean	400–800	336 (max)	S	Demestre and Fortuño (1992)
Caridea:					
<i>Plesionika acanthonotus</i>	Mediterranean	165–1550	530	S	Company and Sardà (1997)
<i>Plesionika edwardsi</i>	Mediterranean	256–512	590	S	Company and Sardà (1997)
<i>Plesionika giglioli</i>	Mediterranean	100–748	550	S	Company and Sardà (1997)
<i>Plesionika heterocarpus</i>	Mediterranean	82–699	530	A	Company and Sardà (1997)
<i>Plesionika martia</i>	Mediterranean	165–871	550	S	Company and Sardà (1997)
Macrura:					
<i>Stereomastis nana</i>	NE Atlantic	613–2642	700	A	Wenner (1978)
<i>Stereomastis sculpta</i>	NE Atlantic	486–2257	600	A	Wenner (1978)
Anomura:					
<i>Chirostylus</i> sp.	?	950	4280 ²	?	Van Dover and Williams (1991)
<i>Eumunida picta</i>	?	512	1556 ²	?	Van Dover and Williams (1991)
<i>Munida propinqua</i>	?	921	1001 ²	?	Van Dover and Williams (1991)

continued on next page

Table 12.3, *continued*

Species	Site	Depth (m)	Egg size (μm)	Periodicity ¹	References
<i>Munida quadrispina</i>	?	595	795 ²	?	Van Dover and Williams (1991)
<i>Munidopsis</i> spp. (35 species)	various	706–4390	2385–6560 ²	?	Van Dover and Williams (1991)
<i>Parapagurus pilosimanus</i>	Rockall Trough	350–5000	550	A	Tyler et al. (1985c)
Brachyura:					
<i>Benthescymus bartletti</i>	NW Atlantic	2000m	?	S (?)	Wenner (1980)
<i>Chaceon fenneri</i>	Gulf of Mexico	311–677	610	S	Erdman et al. (1991)
<i>Chaceon maritae</i>	SE Atlantic	400–900	680	A	Melville-Smith (1987)
<i>Chaceon quinquedens</i>	NW Atlantic	200–1600	820 (max)	S	Haefner (1977, 1978)
<i>Chaceon quinquedens</i>	Gulf of Mexico	860–1043	850	S	Erdman et al. (1991)
<i>Dorhynchus thompsoni</i>	Porcupine Seabight	1205–1250	320	S	Hartnoll and Rice (1984)
<i>Uroptychus nitidus</i>	?	592	2889	?	Van Dover and Williams (1991)

VENT SPECIES

DECAPODA:

Caridea:

<i>Alvinocaris lusca</i>	Galapagos Rift	2500	340×500	?	Van Dover et al. (1985)
<i>Chorocaris chacei</i>	Mid-Atlantic Ridge	840–3670	283	A,F (?)	Ramirez Llodra et al. (2000)
<i>Mirocaris fortunata</i>	Mid-Atlantic Ridge	840–3875	350	A,F (?)	Ramirez Llodra et al. (2000)
<i>Rimicaris exoculata</i>	Mid-Atlantic Ridge	2260–3875	320	A,F (?)	Ramirez Llodra et al. (2000)

Anomura:

<i>Munidopsis lentigo</i>	East Pacific Rise	2500	2200 (max)	?	Van Dover et al. (1985)
<i>Munidopsis subsquamosa</i>	East Pacific Rise	2500	2300 (max)	?	Van Dover et al. (1985)

Brachyura

<i>Bythograea thermydron</i>	East Pacific Rise	2500	480×540	?	Van Dover et al. (1985)
------------------------------	-------------------	------	---------	---	-------------------------

¹ Periodicities are listed as: S, seasonal and synchronous; A, aseasonal, continuous, and asynchronous; F, fluctuating levels of reproduction during continuous breeding.

² For comparative purposes, egg diameters were calculated from the egg volumes reported in the paper.

Wolff (1962, p. 221) concluded as follows with respect to abyssal isopods:

“However, in my opinion, the most likely explanation for the deficit of ovigerous females in the material presented here is to assume that the breeding in the bathyal and abyssal depths of the North Atlantic is to a certain extent seasonal, taking place in the winter months from which no material is available. The majority of the species originate from cold stenotherm shallow water ancestors which must be supposed to have had, as a rule, a seasonal breeding – as is the case with shallow-water species in the polar region today. As far as the asellotes are concerned, this mode of reproduction has also been maintained in the deep sea”.

Wolff (1956b) proposed a different hypothesis to

explain the absence of brooding females among hadal species, namely that these species live to advanced ages and reproduce infrequently, thereby reducing the likelihood that incubatory females will be collected in any given sample.

Some studies of deep-sea harpacticoids have shown a sex ratio biased strongly in favor of females (Hicks and Coull, 1983; Hicks and Marshall, 1985). This observation has been questioned by Thistle and Eckman (1990) who suggested that the skewed sex ratios may result either from gender-specific sampling bias or from males being more easily swept away by currents than females.

Empirical evidence to test Wolff’s prediction of deep-sea seasonality came several years later when George and Menzies collected limited samples of

isopods in the Scotia Sea (George and Menzies, 1967) and off North Carolina (George and Menzies, 1968). The evidence has been considered equivocal by most subsequent workers (e.g., Rokop, 1977b; Harrison, 1988; Bishop and Shalla, 1994), because many species were pooled and there was limited seasonal coverage of samples from any given region; nevertheless, the work stimulated interest in the possibility of seasonal reproduction in peracarids. Harrison (1988) pooled data for 47 asellote species in the Rockall Trough and concluded that there was no evidence for a distinct seasonal breeding pattern, though he did note a “fluctuating” breeding pattern in which more brooding females were found in some seasons than others. A fluctuating pattern of recruitment was also found in the cumacean *Diastylis stygia*, a species that recruits throughout the year in the northwest Atlantic (Blake and Watling, 1994). Strong evidence for seasonal breeding has been found at abyssal depth only for the mysid *Boreomysis tridens* (Mauchline, 1986), the Antarctic amphipod *Eusirus perdentatus* (Klages, 1993), and the cumacean *Leucon profundus* (Bishop and Shalla, 1994).

The careful study of reproduction in *Leucon profundus* by Bishop and Shalla (1994) sets a high standard that should be used in future studies of deep-sea peracarids. In this study, females were classified not only by the presence or absence of a brood, but also by the size and stage of the gonad and the developmental stages of brooded embryos. *Leucon profundus* was shown unequivocally to have a seasonal breeding cycle lasting approximately 14 months. This finding raises the possibility that other species in which brooding females have been found over much of the year may in fact be seasonal breeders with long reproductive cycles rather than aseasonal breeders with short brood times. This work raises an important challenge to virtually all previous studies; even though there are perhaps more observations of reproductive condition of peracarid crustaceans than most other groups of deep-sea animals, one still has only a very limited understanding of their breeding cycles and life histories.

Of the various caridean shrimp and other crustacea common at hydrothermal vents (Table 12.4), there is little evidence for periodic reproduction (reviewed by Tyler and Young, 1999). *Rimicaris exoculata*, probably the most abundant metazoan at vents on the mid-Atlantic ridge, appears to have multiple cohorts of eggs in its gonad, suggesting periodicity at the individual

level (Ramirez Llodra et al., 2000), but insufficient seasonal coverage is available to infer any sort of population-level synchrony. Extensive collections of these abundant carideans have yielded a surprisingly small number of berried females (P.A. Tyler, personal communication). As with abyssal isopods, there is no completely satisfying explanation for this pattern. One hypothesis that remains untested is that females brood their young far away from the vents in order to protect the embryos from elevated temperatures (Tyler and Young, 1999).

A number of crustaceans living at depths less than 1000 meters breed seasonally, as might be expected (Table 12.4). These include bathyal dendrobranchiate and caridean shrimps in the Mediterranean (Demestre and Fortuño, 1992; Company and Sardà, 1997) and some species of brachyurans in the northwest Atlantic and the Gulf of Mexico (Haefner, 1977; Hartnoll and Rice, 1984; Erdman et al., 1991). It is interesting that various species of the slope crab genus *Chaceon* found in the northeast Atlantic are seasonal breeders (Haefner, 1977, 1978; Erdman et al., 1991), but the congeneric *C. maritae*, living at comparable depths in the Southeast Atlantic, is aseasonal (Melville-Smith, 1987). There are insufficient data to infer seasonal reproduction in any abyssal brachyuran, though Wenner (1980) suggested that *Benthesicymus bartletti* from 2000 m may have a synchronous breeding pattern.

Most species of pandalid shrimp in shallow water are protandrous hermaphrodites, changing from male to female as they grow. King and Moffitt (1984) presented evidence that several species of deep-water tropical pandalids are fully dioecious and that they never undergo sex reversal. The reason for this difference between deep-sea and shallow species is not known.

Gamete structure and fertilization

Spermatozoa of all crustaceans are aflagellate and are modified for internal fertilization. There have been no detailed studies at the ultrastructural level of oogenesis or spermatogenesis in deep-sea crustaceans, though the general structure of the reproductive system is well known from gross dissections and paraffin histology. Spermatozoa are often packaged into sperm packets which are deposited in the oviducts of the female as sperm plugs. These have been commonly seen in the hydrothermal-vent crab *Bythograea thermydron* (G. Perovich, personal communication). The various studies of gonad morphology that have been conducted at the light-microscope level (e.g., Ramirez Llodra

Table 12.4
Studies of reproductive periodicity in deep-sea molluscs

Species	Site	Depth (m)	Egg size ¹ (µm)	Periodicity ²	References
APLACOPHORA					
<i>Prochaetoderma yongei</i>	NW Atlantic	1470–2030	226	A	Scheltema (1987)
GASTROPODA					
<i>Benthonella tenella</i>	NW Atlantic	3806–5042	82.5	A	Rex et al. (1979)
<i>Calliotropis ottoi</i>	Rockall Trough	990–2450	150–260	A	Colman and Tyler (1988)
<i>Colus jeffreysianus</i>	Rockall Trough	2200	170	A	Colman et al. (1986a)
SCAPHOPODA					
<i>Cadulus californicus</i>	San Diego Trough	1162–1244	240	S	Rokop (1977a)
BIVALVIA					
<i>Acharax alinae</i>	Lau Basin (vent)	?	600	A	Beninger and Le Penneec (1997)
<i>Batharca</i> sp.	San Diego Trough	1200–1240	~132	A	Rokop (1979)
<i>Bathymodiolus childressi</i>	Gulf of Mexico (seep)	500–700	90	S	Eckelbarger and Young (1999)
<i>Bathymodiolus elongatus</i>	Fiji Back-Arc Basin	?	50–60	A	Le Penneec and Beninger (1997)
<i>Bathymodiolus puteoserpentis</i>	Mid-Atlantic Ridge	3480	50–60	S	Le Penneec and Beninger (1997)
<i>Bathymodiolus thermophilus</i>	E. Pacific Rise (vent)	2500	50	A	Berg (1985)
<i>Bathymodiolus</i> n. sp.	Mid-Atlantic Ridge	840–865	50	S	Comtet and Desbruyères (1998)
<i>Calyptogena kilmeri</i>	Monterey Bay (seep)	900	180–237	S	Lisin et al. (1996)
<i>Calyptogena lauberi</i>	Tenryu Canyon (seep)	?	200	A	Fiala-Médioni and Le Penneec (1989)
<i>Calyptogena magnifica</i>	E. Pacific Rise (vent)	2500	309	A	Berg (1985)
<i>Calyptogena pacifica</i>	Monterey Bay (seep)	600	180–220	A (?)	Lisin et al. (1996)
<i>Ledella pustulosa</i>	NE Atlantic	2880–2921	120	S	Tyler et al. (1992a)
<i>Malletia cuneata</i>	NE Atlantic	2880–2921	240	A	Tyler et al. (1992a)
<i>Deminucula cancellata</i>	San Diego Trough	1200–1240	?	A	Rokop (1977a), Scheltema (1972)
<i>Nucula darella</i>	San Diego Trough	1200–1240	~154	A	Rokop (1979)
<i>Nuculana pontonia</i>	San Diego Trough	1200–1240	~176	A	Rokop (1979)
<i>Tindaria cervola</i>	San Diego Trough	1200–1240	?	A	Rokop (1979)
<i>Xylophaga</i> spp	W. Atlantic	600–2000	45	A	Turner (1973), Tyler and Young, unpublished
<i>Yoldiella jeffreysi</i>	NE Atlantic	2880–2921	120	A	Tyler et al. (1992a)

¹ In most cases, egg sizes are the maximum observed in histological studies and may not be representative of the actual sizes of eggs spawned.

² Periodicities are listed as either S, synchronous or seasonal; or A, aseasonal or continuous.

et al., 2000) suggest nothing about gametes in deep-sea Crustacea that differs from related species in shallow water (reviewed by Adiyodi and Subramoniam, 1983).

Fecundity

Fecundity has been studied mostly in slope decapods that have fishery importance (e.g., Clarke et al., 1991), though instantaneous fecundities have also been

reported for many deep-sea peracarids. For example, Wolff (1962) indicated that egg numbers in the asellote isopods range from 2 to 80, being correlated with the size of the brooding animal. Shallow-water isopods generally have much higher fecundities and smaller egg sizes (Zirwas, 1910).

The most comprehensive study of fecundity in deep-

sea crustaceans is that by Van Dover and Williams (1991) of 52 species of squat lobsters in the superfamily Galatheoidea, which related fecundity and egg size to depth of occurrence. They found a positive correlation between fecundity and body size, but no indication of reduced fecundity in deep-sea species that could not be explained by phylogenetic constraints. Hines (1988) reported that fecundity of two species of deep-sea geryonid crabs is significantly lower than those of shallow-water crabs with similar body sizes, but that reproductive output is in fact higher; the low fecundity values result from partitioning the reproductive effort into larger eggs. The reproductive effort of brachyuran crabs seems always to be limited by the amount of space available in the cephalothorax for yolk accumulation (Hines, 1982), and this rule applies equally well to the deep-sea forms as to those in shallow water (Hines, 1988). Ramirez Llodra et al. (2000) noted the same relationship between brood size and body size in deep-sea caridean shrimps whether they lived in mid-water or at Atlantic hydrothermal vents. It should be noted that closely related crustaceans having very different fecundities may be successful in the same deep-sea habitats. Perhaps the most striking example of this occurs in two congeneric vent-associated galatheids, *Munidopsis lentigo* and *M. subsquamosa*, both of which live at Pacific vents; they have fecundities of 13 eggs and 294 eggs, respectively (Van Dover et al., 1985).

Ramirez Llodra et al. (2000) examined fecundity of three caridean species from hydrothermal vents. One of these, *Mirocaris fortunata*, had highly variable fecundity, the number of eggs carried by a female ranging from 25 to 503. Based on a single berried female from each species, *Chorocaris chacei* and *Rimicaris exoculata* had much higher fecundities than *M. fortunata*, carrying 2510 and 988 eggs, respectively.

Embryogenesis and larval development

Peracarids have direct development, brooding their young to a stage that resembles a miniature adult. Apart from the study by Tso and Mok (1991) on development of the giant isopod *Bathynomus doederleini*, there have been few specific studies of embryology in deep-sea peracarids, though Bishop and Shalla (1994) carefully monitored changes in embryo number and size in the cumacean *Leucon profundus*. They found that embryogenesis was synchronous for the first eight months of development (their stages I–III), but a pattern of asynchronous development began with

the last two embryonic stages. Specifically, females with advanced embryos always contained a single stage V individual which was about to hatch, while the remaining embryos in the brood were still at stage IV. This observation suggests that large juveniles (manca stage) grow to full size one at a time and are released singly, the individuals in the brood hatching over a period of several months. A similar pattern of hatching has been found in the aseasonal congener *Leucon jonesi* (Bishop, 1994).

One of the first deep-sea larvae to be described in the literature was that of the deep-sea eryonid crab *Willemoesia suhmi*, a drawing of which appeared in the *Challenger* reports. Embryological development has since been described for several deep-sea decapods (e.g., Brattegard and Sankarankutty, 1967; Herring, 1974; Ingle, 1979; Sulkin and Van Heukelem, 1980; Williamson, 1982). In all cases, the patterns of development and the early larvae resembled closely those of shallow-water relatives. Caridean shrimps, including the very abundant vent shrimps *Chorocaris chacei*, *Mirocaris fortunata* and *Rimicaris exoculata*, have been studied extensively in recent years. Vereschaka (personal communication) has found embryos in the water column which he ascribes to *Rimicaris exoculata*, but there is some controversy about their identity. If this observation is correct, *R. exoculata* would be the only caridean that does not brood its embryos on the pleopods until hatching. However, this observation would help explain why very few berried vent shrimps have been collected. Larvae of Atlantic vent shrimps have been collected in midwater plankton samples near the mid-Atlantic Ridge, and postlarvae have been collected as far as 1000 km away, suggesting that dispersal potential is substantial (Herring and Dixon, 1998).

Fage (1956) reported that the eggs of pycnogonids (sea spiders) collected from a depth of more than 6000 m in the Banda Sea are brooded on the ovigerous legs of the males, in exactly the same manner as those of their shallow-water counterparts.

Mollusca

Deep-sea sediments contain a tremendous variety of gastropods (Clarke, 1962). Although some larger buccinids and pleurotomariids are encountered at slope depths (Harasewych, 2002), the deep-sea gastropod fauna is dominated by diminutive caenogastropod predators such as turrids. Ectoparasitic forms living as

epizoites on other organisms such as sea urchins are also common.

Bivalves are represented mostly by protobranchs (Allen, 1979; Zardus, 2002), though xylophagid bivalves are commonly found in waterlogged wood (Turner, 1973), and a number of other orders also live as infauna in the soft sediment. Deep-sea mussels and clams are among the most abundant animals living at cold seeps and hydrothermal vents (Van Dover, 2000).

Gonads, gametogenesis and reproductive periodicity

Prosobranch gastropods are mostly dioecious, though hermaphroditic species, especially protandric hermaphrodites, are known. The gonad is a discrete organ located on the upper part of the body whorl and connected to the outside by a gonoduct, which passes through the pericardium. In the more advanced forms, the gonoduct may be divided into pallial and cardiac portions, which in turn may be elaborated into various kinds of glands for the secretion of fluids, mucus or capsular material to protect the embryos. Scaphopods are all dioecious (Reynolds, 2002), as are aplacophorans and, with very few exceptions, bivalves. The gonad in mussels and clams is found dorsally, often in close association with the digestive gland.

Gametogenesis has been described at the ultrastructural level in only a few species of deep-sea molluscs, all from chemosynthetic ecosystems (Le Pennec and Beninger, 1997; Eckelbarger and Young, 1999). Eckelbarger and Young (1999) described oogenesis and spermatogenesis in the methanotrophic mussel *Bathymodiolus childressi*; the gametogenic mechanisms were shown to be similar to those of seasonally breeding shallow-water mussels. Spermatogenesis has also been described for the gastropod *Bathynnerita naticoidea* from the same habitat (Hodgson et al., 1998). Ongoing studies of gametogenesis in limpets from hydrothermal vents show that some species have rapid mechanisms of vitellogenesis virtually identical to those found in certain intertidal limpets (Eckelbarger, unpublished data).

Reproductive periodicity has been inferred from gonad histology in a number of deep-sea molluscs (Table 12.4), most of which have asynchronous gametogenesis indicative of continuous breeding. Seasonal breeders are found not only at relatively shallow slope depths (Rokop, 1977a; Eckelbarger and Young, 1999), but also at depths greater than 2000 m on the lower slope (Tyler et al., 1992a) and at 3480 m in a hydrothermal vent system on the Mid-Atlantic Ridge (Le Pennec

and Beninger, 1997). It is somewhat surprising that several species of mussels breed synchronously at vents and seeps, since these animals are presumably exposed to a continuous source of chemical energy that can be allocated to gonadal development.

Gamete structure and fertilization

Sperm have been described at the ultrastructural level for deep-sea gastropods from several families (Healy, 1988, 1989b, 1990; Hodgson et al., 1998) as well as for a midwater cephalopod, *Vampyroteuthis infernalis* (Healy, 1989a), and some chemosynthetic mussels (Eckelbarger and Young, 1999). In every case, the sperm structure was similar to that of shallow-water members of the same groups.

Transfer of spermatophores has been described in a deep-sea octopus (Lutz and Voight, 1994). Although no other specific studies of fertilization have been undertaken in deep-sea molluscs, it is presumed that deep-sea gastropods follow the strongly conservative patterns known for shallow-water taxa. Thus, archaeogastropods (with the exception of the Neritidae) spawn their gametes and fertilize externally, while other groups all fertilize internally by copulation.

Fecundity

Scheltema (1994) has reviewed the literature on fecundity in deep-sea molluscs. Instantaneous fecundity in bivalves ranges from two eggs in two species of pristogomid protobranchs on the continental slope (Sanders and Allen, 1973) to more than 30 000 eggs in opportunistic xylophagids that colonize wood (Turner, 1973). There are almost no reliable data on the fecundity of deep-sea gastropods despite reported counts of embryos in egg capsules (Gustafson et al., 1991), since the number of capsules produced by a single female is generally impossible to determine.

Embryogenesis and larval development

Egg masses from deep-sea snails have been found and described several times (Gustafson et al., 1991; Bouchet and Warén, 1994), but there are no descriptions of early embryology, nor has a complete sequence of larval development been reported for any deep-sea mollusc. The known patterns of larval development have been reviewed by Bouchet and Warén (1994) and Scheltema (1994). Most of what is known about larval development has been inferred from the apex of the adult shell, where the larval protoconch (in gastropods) or prodissoconch (in bivalves) is retained as a

permanent record of larval size and growth (Thorson, 1950; Jablonski and Lutz, 1983; Scheltema, 1994). The shell-apex method permits discrimination between species with non-planktotrophic and planktotrophic larvae, but does not resolve differences between species with pelagic lecithotrophic larvae and species that brood their young or hatch as juveniles from benthic egg capsules (Jablonski and Lutz, 1983). Despite this limitation, the method has been applied to a very large number of deep-sea species. Many such studies have focused on species from distinct geographical regions of the Atlantic (Bouchet, 1976b; Rex and Warén, 1982; Colman et al., 1986b) and on species from cold seeps and hydrothermal vents (reviewed by Gustafson and Lutz, 1994). A selection of these studies is summarized in Table 12.5. Although both planktotrophic and non-planktotrophic development are common among bathyal and abyssal molluscs, some groups have peak numbers of lecithotrophic species at slope depths (Rex and Warén, 1982), and others, exemplified in Fig. 12.3 by the Turridae (the most

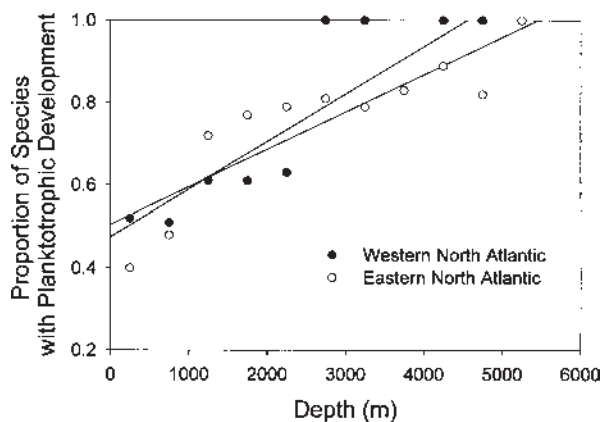


Fig. 12.3. The relationship between developmental mode and depth in deep-sea gastropods of the family Turridae. Redrawn from Potter and Rex (1992).

speciose family of gastropods in the deep sea), show a regular increase in the incidence of planktotrophy with increasing depth (Potter and Rex, 1992). Supporting evidence for planktotrophic larval development comes from the work of Bouchet (1976a) and Bouchet and Warén (1979), who have obtained the larvae of several species of abyssal gastropods in shallow-water plankton tows. Moreover, Bouchet and Fontes (1981) and Killingley and Rex (1985) have shown, by oxygen-isotope ratios in abyssal snail shells, that larvae develop at a warmer temperature than is found in the adult environment. A number of planktotrophic larvae from

deep-sea gastropods have eyes (Bouchet and Warén, 1994); but, in the only study of phototaxis in deep sea larvae, Bingham and Young (1993) showed that the eyed larvae of a bathyal snail, *Pelseneeria* sp., do not respond to unidirectional white light.

Bouchet and Warén (1994) have argued that planktotrophy in deep-sea gastropods is not only an ancestral condition (Strathmann, 1978), but also a plesiomorphic character constrained by phylogeny in most groups. They note that some species, particularly members of the exclusively deep-sea family Laubierinidae, produce very large veligers, males of which are neotonous and attain sexual maturity before settlement (Bouchet and Warén, 1994).

Knudsen (1961, 1970) provided detailed discussions of reproduction in non-chemosynthetic deep-sea bivalves, and the more recent literature in this field has since been reviewed (Knudsen, 1979; Schein, 1989; Scheltema (1994). Using criteria proposed by Ockelmann (1965) for inferring bivalve developmental mode from egg size, these studies suggest that pelagic lecithotrophy, not direct development or planktotrophy, prevails among sediment-dwelling deep-sea gastropods. The major exceptions appear to be in the Xylophagidae, which are nearly always associated with waterlogged wood or other plant material. Turner (1973) showed that some xylophagids have small eggs and wide dispersal, while Knudsen (1961) documented several species with large eggs that appear to brood their young on the outside of the shell (Fig. 12.4). The

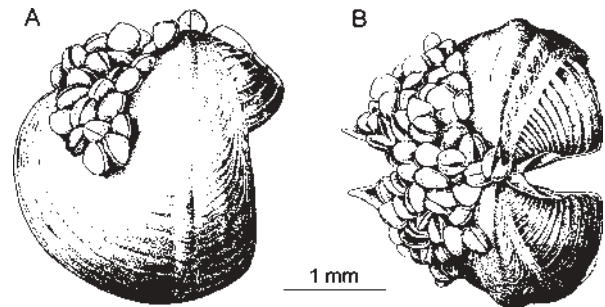


Fig. 12.4. Brooded juveniles on the valves of a bathyal xylophagid bivalve. Reproduced with permission from Knudsen (1961).

reasons for these divergent reproductive modes within a single family remain unexplained (Scheltema, 1994).

At hydrothermal vents, most molluscan species appear to have non-planktotrophic development, though planktotrophic species are also known (reviewed by Gustafson and Lutz, 1994). Craddock et al. (1997) predicted that non-planktotrophic species should have

Table 12.5
 Modes of larval development for deep-sea molluscs, as inferred from protoconch and prodossoconch sizes and morphologies

Taxon	Region	Depths (m)	Planktotrophic		Non-planktotrophic		References
			Families	Species	Families	Species	
NON-VENT AND SEEP SPECIES							
Archaeogastropoda	NW Atlantic	478–4970	0	0	–	22	Rex and Warén (1982)
Mesogastropoda	NW Atlantic	478–4970	–	12	–	21	Rex and Warén (1982)
Neogastropoda	NW Atlantic	478–4970	–	33	–	19	Rex and Warén (1982)
Gastropoda	NE Atlantic	2500–5300	15	(30%)	–	–	Bouchet and Warén (1979)
Gastropoda	Norwegian Sea	2500–4000	–	3	–	11	Bouchet and Warén (1979)
Prosobranch gastropods	NE Atlantic	various	–	10	–	B	Bouchet (1976b)
Prosobranch gastropods	NE Atlantic	2200–2900	–	6	–	8	Colman et al. (1986b)
Gastropoda	world	1000–5400	27	–	5	B	Bouchet and Warén (1994)
Bivalvia	Norwegian Sea	2500–4000	–	1	–	5	Bouchet and Warén (1979)
VENT AND SEEP SPECIES							
Gastropoda	Atlantic, Pacific	various	–	3	–	39	Gustafson and Lutz (1994)
Archaeogastropoda	Pacific	2500	–	0	–	4	Craddock et al. (1997)
Bivalvia	Atlantic, Pacific	various	1	5	–	2	Gustafson and Lutz (1994)

limited dispersal, but genetics did not bear out this prediction. However, Etter and Rex (1990) showed that genetic differentiation decreases concomitantly with a shift away from lecithotrophy along a depth gradient. Some of this confusion probably results from an inability to distinguish pelagic lecithotrophs from direct developers and some is probably because lecithotrophs living at low temperatures (and therefore having low metabolic rates) can disperse substantial distances without the benefit of feeding. Just as mode of development is not a good predictor of geographic range in deep-sea ascidians and echinoderms (Young et al., 1997), it may not predict dispersal potential or genetic differentiation in deep-sea molluscs.

Echinodermata

From the standpoint of reproduction, echinoderms are the best-studied group of deep-sea animals. Table 12.6 gives a summary of some reproductive parameters for all species studied. Most deep-sea echinoderms have separate sexes, though hermaphroditism is known among the holothurians (Tyler et al., 1992b) and occasional hermaphroditic echinoids have been observed (e.g., *Allocentrotus fragilis*, *Lytechinus euerces*: Young, personal observations). With few exceptions, the reproductive mechanisms and patterns found in shallow-water echinoderms are also represented among their deep-water relatives. Echinoderm reproduction has been thoroughly reviewed elsewhere (see Giese et al., 1991 as a convenient portal to the literature).

Gonads, gametogenesis and reproductive periodicity

Echinoderms were among the first deep-sea animals shown conclusively to have seasonal reproduction (Lightfoot et al., 1979; Tyler et al., 1982a) and recruitment (Schoener, 1968), though it is now known that seasonal breeding is the exception in this group rather than the rule. In the Rockall Trough, where numerous species have been examined in multiple seasons, only a small proportion of species breed seasonally (Table 12.6). However, at shallower bathyal depths on the Bahamian Slope, the majority of species are seasonal breeders. All known deep-sea species with seasonal breeding produce planktotrophic larvae, and all known species of continuous breeders produce non-planktotrophic larvae (Tyler and Young, 1993). Gonadal development is essentially the same as that of other echinoderms, proceeding through sequential

stages of gamete proliferation, vitellogenesis and gamete storage prior to spawning. However, in semi-continuous breeders such as *Echinus affinis*, the gonad contains multiple cohorts of gametes, and the cycle may take more than one year to complete (Tyler and Gage, 1984a).

Eckelbarger (1994b) has listed 34 species of bathyal and abyssal echinoderms whose ovaries have been examined by electron microscopy; but modified ovaries have been found only in four species of deep-sea holothuroids. In *Bathyplotes natans*, *Hansenothuria benti*, *Holothuria occidentalis* and *Mesothuria* sp., the inner epithelial cells of the oocytes resembled podocytes, cells which are generally associated with excretion in other invertebrates (Eckelbarger and Young, 1992; Tyler et al., 1994). In the case of sea-cucumber ovaries, it has been suggested that podocytes may function in exchange of nutrients between the genital haemal sinus and the ovary during vitellogenesis (Eckelbarger and Young, 1992).

Fecundity

Ramirez Llodra (2002) has reviewed the literature on fecundity in marine animals, including echinoderms in the deep sea. Fecundity has been estimated for many of the echinoid, asteroid and holothuroid species listed in Table 12.6. In general, deep-sea species follow the expected pattern (Vance, 1973) in which lecithotrophic species with large eggs have a smaller number of eggs than planktotrophic species. Thus, for example, the planktotrophic species *Plutonaster bifrons* produces about one million eggs (Tyler and Pain, 1982a), whereas co-occurring lecithotrophic starfish such as *Bathybiaster vexillifer* (Tyler et al., 1982b) and *Benthopecten simplex* (Pain et al., 1982a) produce only a small number of mature oocytes at any given time. Body size, gonad structure and depth all covary with fecundity in echinoderms. This is illustrated well in the forcipulate starfish of the Rockall Trough (Tyler et al., 1984). The brisingid starfish *Brisingella coronata* has an egg size (1250 µm) identical with that of the confamilial *Freyella spinosa*, yet the former has a fecundity of about 60 000 eggs and the latter produces only 2500 eggs. *Freyella* lives deeper (below 4000 m) than *Brisingella* (750–2450 m).

Gamete structure and fertilization

Eckelbarger et al. (1989c) and Eckelbarger (1994b) have reviewed the sperm morphology of deep-sea echinoderms. The majority have sperm of the primitive (Franzen, 1956) or ect-aquasperm (Rouse and

Table 12.6
Reproductive periodicity and egg sizes in deep-sea echinoderms

Species	Site	Depth (m)	Egg size (μm)	Periodicity ¹	References
ASTEROIDEA					
<i>Bathyiaster vexillifer</i>	Rockall Trough	2200	650	A	Tyler et al. (1982b)
<i>Benthopecten simplex</i>	Rockall Trough	2170–2300	950	A	Pain et al. (1982b)
<i>Brisinga endecacemos</i>	Rockall Trough	1860–2200	1250	A	Tyler et al. (1984)
<i>Brisingella coronata</i>	NE Atlantic	750–2200	1250	A	Tyler et al. (1984)
<i>Dytaster insignis</i>	Rockall Trough	2170–2910	120 (?)	S	Tyler et al. (1982a)
<i>Freyella spinosa</i>	Porcupine Abyssal Plain	4000–4212	1250	A	Tyler et al. (1984)
<i>Hymenaster gennaues</i>	Rockall Trough	2200	1100	A	Pain et al. (1982b)
<i>Hymenaster membranaceus</i>	Rockall Trough	1862–2300	1100	A	Pain et al. (1982b)
<i>Hyphalaster inermis</i>	Madeira Abyssal Plain	5000	650	A	Ramirez Llodra et al. (2002)
<i>Paragonaster subtilis</i>	Rockall Trough	2200	900	A	Tyler and Pain (1982b)
<i>Pectinaster filholi</i>	Rockall Trough	1752–2515	850	A	Pain et al. (1982b)
<i>Plutonaster bifrons</i>	Rockall Trough	2200	120	S	Tyler et al. (1982a)
<i>Pontaster tenuispinus</i>	Rockall Trough	588–1050	800	A	Pain et al. (1982b)
<i>Porcellanaster ceruleus</i>	Rockall Trough	2900	600	A	Madsen (1961), Tyler, unpublished.
<i>Pseudarchaster parelli</i>	Rockall Trough	2200	900	A	Tyler and Pain (1982b)
<i>Psilaster andromeda</i>	Rockall Trough	1050–2965	950	A	Tyler et al. (1982a)
<i>Styrachaster chuni</i>	Madeira Abyssal Plain	5000	650	A	Ramirez Llodra et al. (2002)
<i>Styrachaster horridus</i>	Madeira Abyssal Plain	5000	650	A	Ramirez Llodra et al. (2002)
<i>Xyloplax medusifformis</i>	New Zealand	1000	viviparous	?	Baker et al. (1986)
<i>Xyloplax turnerae</i>	Bahamas	2000	“large”	?	Rowe et al. (1988)
<i>Zoroaster fulgens</i>	Rockall Trough	2170–2450	950	A	Tyler et al. (1984)
OPHIUROIDEA					
<i>Amphiophiura bullata</i>	NW Atlantic	1330–4750	350	?	Schoener (1972)
<i>Amphilepis ingolfiana</i>	NW Atlantic	1330–4750	400	?	Schoener (1972)
<i>Homalophiura tessellata</i>	NW Atlantic	1330–4750	400	?	Schoener (1972)
<i>Ophiacantha bidentata</i>	Rockall Trough	2200	600	A	Tyler and Gage (1982)
<i>Ophiacantha normani</i>	San Diego Trough	1250	~430	A	Rokop (1974)
<i>Ophiocten gracilis</i>	Rockall Trough	1000	100	S	Sumida et al. (2000)
<i>Ophiomusium lymani</i>	NW Atlantic	1100–2000	600	S	Schoener (1968, 1972)
<i>Ophiomusium lymani</i>	Rockall Trough	2200	600	A, S	Gage and Tyler (1982b)
<i>Ophiura ljunghmani</i>	NW Atlantic	1330–3834	90	S	Schoener (1968, 1972)
<i>Ophiura ljunghmani</i>	Rockall Trough	2900	100	S	Tyler and Gage (1980), Gage and Tyler (1982a)
ECHINOIDEA					
<i>Alloccentrotus fragilis</i>	NE Pacific	50–1150	110	S	Booolootian et al. (1959)
<i>Araeosoma fenestratum</i>	Rockall Trough	631	1250	A	Tyler and Gage (1984b)
<i>Archaeopneustes hystrix</i>	Bahamas	300–625	~100	S	Young et al. (1997)
<i>Aspidodiadema jacobyi</i>	Bahamas	350–600	90	S	Young and George (2000)
<i>Brissopsis lyrifera</i>	Mediterranean	60–1000	80	S	Ferrand et al. (1988)
<i>Calveriosoma hystrix</i>	Rockall Trough	640–1075	1250	A	Tyler and Gage (1984b)
<i>Cidaris blakei</i>	Bahamas	500–750	110	S	Young, unpublished

continued on next page

Table 12.6, *continued*

Species	Site	Depth (m)	Egg size (μm)	Periodicity ¹	References
<i>Cidaris cidaris</i>	Rockall Trough	508–1500	110	S	Tyler and Gage (1984b)
<i>Echinus acutus</i>	Rockall Trough	500–1271	90 (?)	S	Gage et al. (1986)
<i>Echinus affinis</i>	Rockall Trough	2200	120	S	Tyler and Gage (1984a)
<i>Echinus elegans</i>	Rockall Trough	500–1271	90 (?)	S	Gage et al. (1986)
<i>Hygrosoma petersi</i>	Rockall Trough	990–2965	1150	A	Tyler and Gage (1984b)
<i>Linopneustes longispinus</i>	Bahamas	608–683	109	S	Young and Cameron (1989)
<i>Lytechinus euerces</i>	Bahamas	300–500	96	S	Young, unpublished
<i>Palaeobrissus hilgardi</i>	Bahamas	575–650	128	S	Young, unpublished
<i>Phormosoma placenta</i>	NE Atlantic, Bahamas	616–2240	1100	A	Tyler and Gage (1984b), Young and Cameron (1987)
<i>Poriodidaris purpurata</i>	Rockall Trough	990–1075	1500	A	Tyler and Gage (1984b)
<i>Salenia goesiana</i>	Bahamas	90–540	57	S	Young, unpublished
<i>Sperosoma grimaldi</i>	Rockall Trough	1210	1100	A	Tyler and Gage (1984b)
<i>Stylocidaris lineata</i>	Bahamas	600	120	S	Young et al. (1992)
HOLOTHUROIDEA					
<i>Bathyplotes natans</i>	NE Atlantic, Bahamas	625–1694	280	A	Tyler et al. (1994)
<i>Benthodytes sordida</i>	Porcupine Abyssal Plain	3680–4515	>1000	A (?)	Tyler and Billett (1987)
<i>Benthogone rosea</i>	Porcupine Seabight	1387–2120	750	A	Tyler et al. (1985b)
<i>Cherbonniera utriculus</i>	Rockall Trough	2878–4050	200	(S)	Tyler et al. (1987)
<i>Deima validum</i>	Porcupine Abyssal Plain	4080–4795	700	A (?)	Tyler and Billett (1987)
<i>Laetmogone violacea</i>	NE Atlantic	960–1506	350	A	Tyler et al. (1985b)
<i>Molpadia blakei</i>	Porcupine Abyssal Plain	1991–4510	200	A	Tyler et al. (1987)
<i>Oneirophanta mutabilis</i>	Porcupine Seabight	2900–4795	950	A (?)	Tyler and Billett (1987)
<i>Paroriza pallens</i>	NE Atlantic, Bahamas	900–1785	350	A	Tyler et al. (1992b)
<i>Paroriza prouhoi</i>	NE Atlantic	4080–4780	450	A	Tyler et al. (1992b)
<i>Peniagone azorica</i>	Rockall Trough	2220–2965	300	A	Tyler et al. (1985a)
<i>Peniagone diaphana</i>	Porcupine Abyssal Plain	3976–4780	300	A	Tyler et al. (1985a)
<i>Psychropotes depressa</i>	Porcupine Seabight	2405–2440	>750	A (?)	Tyler and Billett (1987)
<i>Psychropotes longicauda</i>	Porcupine Abyssal Plain	4043–4795	>3000	A (?)	Tyler and Billett (1987)
<i>Psychropotes semperiana</i>	Porcupine Abyssal Plain	5432–5440	>3000	A (?)	Tyler and Billett (1987)
<i>Ypsilothuria bitentaculata</i>	Rockall Trough	2175–2907	350	A	Tyler and Gage (1983)

¹ Periodicities are listed as either S, seasonal or synchronous; or A, aseasonal or continuous.

Jamieson, 1987) type, characterized by small spherical or conical nuclei. Such sperm are indicative of free spawning and external fertilization; both processes have been observed for more than 20 species of bathyal echinoderms (Young, 1994b). There is, however, an unexplained tendency toward gigantism in the sperm of deep-sea echinoderms (Fig. 12.5). For example, the sperm of soft-bodied echinothuriid sea urchins, which fertilize yolky eggs exceeding 1 mm in diameter (Tyler and Gage, 1984b; Young and Cameron, 1987; Cameron et al., 1988) are very elongate. These sperm

carry lipid bodies on the posterior end of the midpiece mitochondria (Eckelbarger et al., 1989a), a very rare feature in shallow-water sea urchins (an exception is the sand dollar *Echinarachnius parma*.) The lipid bodies are thought to serve as an energy store which permits the sperm to swim for an unusually long time after dilution (Young, 1994b), but could also provide some flotation, enabling the sperm to disperse upward with the rapidly floating eggs (Young and Cameron, 1987; Cameron et al., 1988). Sperm of even greater length are found in the deep-sea genus

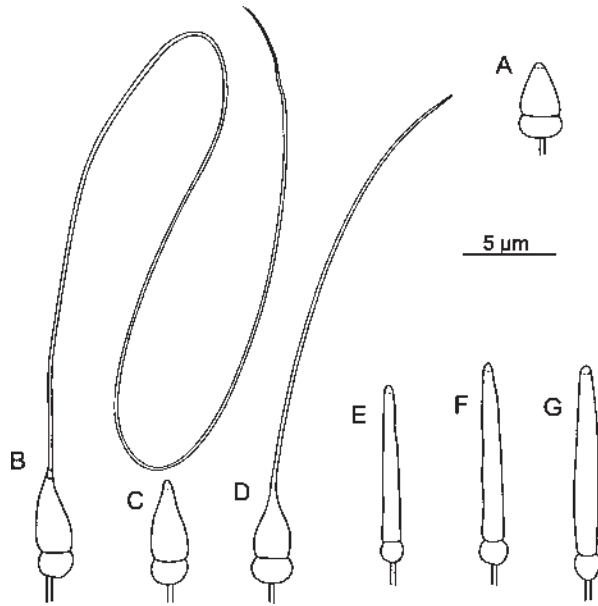


Fig. 12.5. Elongate and dimorphic sperm of deep-sea echinoids. The sperm of the arbaciid *Coelopleurus floridanus* (A) from the Bahamian slope is typical of a shallow-water echinoid. The elongate sperm from the genera *Araeosoma* (E,F) and *Phormosoma* (G) have lipid stores on the middle-piece, apparently to extend the swimming time. The elongate portion of the sperm head in *Aspidodiadema jacobyi* (D) consists of nuclear material, whereas the elongate anterior extension of the paraspermatozoan of *Phrissocystis multispina* (B) is a second flagellum. The euspermatozoan of *Phrissocystis* (C) is unmodified. Redrawn from Eckelbarger et al. (1989a-c).

Aspidodiadema (Fig. 12.5). The sperm nucleus of *Aspidodiadema jacobyi* from the Bahamian slope is 29 µm long, approximately an order of magnitude longer than a typical echinoid sperm (Eckelbarger et al., 1989b). Similarly elongate nuclei have been observed in *A. arcitum* from the Hawaiian slope (Young, unpublished data). The reason for these very long sperm heads is unknown; *Aspidodiadema* spp. freely spawn small (90 µm) eggs and fertilize them externally, apparently in the same manner as other echinoids with much smaller primitive-type sperm.

The Hawaiian deep-water echinoid *Phrissocystis multispina* is the only echinoderm known to have sperm dimorphism, and also the only known species with bipolar-tailed sperm (Eckelbarger et al., 1989b). Males produce not only normal-looking euspermatozoa, but also paraspermatzoa with two tails (Fig. 12.5), both of which originate from centrioles on the posterior end of the nucleus, but one pointing forward and one aft. As fertilization has not been observed in this species, the different roles of the two sperm types have not been

discovered. The unusual concentricycloid asteroids of the genus *Xyloplax*, considered by some to constitute a separate phylum of echinoderms, apparently fertilize internally and consequently have sperm of a modified type. These unusual filiform sperm have been described in detail by Healy et al. (1988).

The mechanisms and problems of external fertilization in deep-sea echinoderms have been discussed by Young (1994b). Free spawning, often in response to chemical spawning inducers such as potassium chloride, has been observed in many species, though very few spawning events have been observed *in situ*. A number of Bahamian-slope species, including *Aspidodiadema jacobyi* (Young, unpublished), *Cidaris blakei* (Young, 1994b), *Salenia goesiana* (Young, unpublished) and *Stylocidaris lineata* (Young et al., 1992) form tight aggregations or pairs during the breeding season, apparently to cope with the problem of isolation at spawning (Fig. 12.6). Other species, including seasonally breeding spatangoids and cassiduloids, move about in herds during the entire year. Hermaphroditic holothurians in the genus *Paroriza* apparently pair for extended periods of time (Fig. 12.6; Tyler et al., 1992b; Mauviel and Sibuet, 1985).

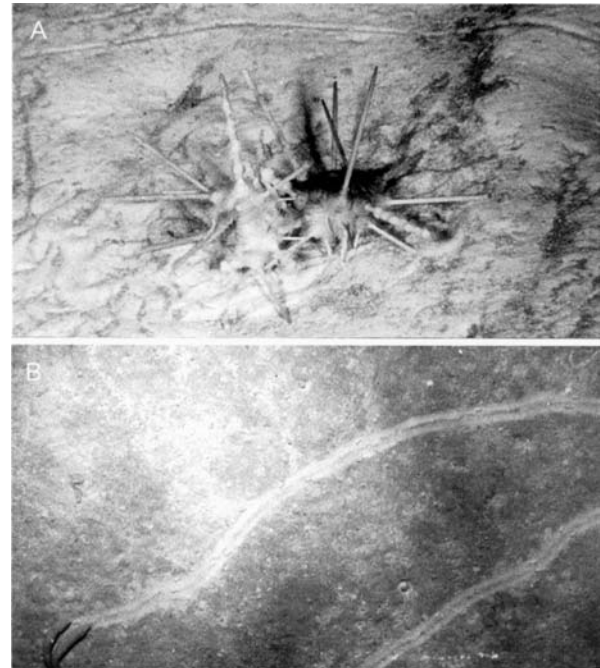


Fig. 12.6. Reproductive pairing in deep-sea echinoderms. A: a pair of ripe *Stylocidaris lineata* from the Bahamian Slope (Young et al., 1992). B: two individuals of *Paroriza* sp. leaving a long trail across the sea floor in the North Atlantic. Reproduced by permission from Mauviel and Sibuet (1985).

Embryogenesis and larval development

Early predictions notwithstanding, only two deep-sea echinoderm species, the holothurian *Oneirophanta mutabilis* (Hansen, 1968) and the concentricycloid *Xyloplax medusiformis* (Rowe et al., 1988), are known to brood their young internally, though it is likely that many ophiuroids and a few asteroids will also eventually be found to brood. Although a number of shallow-water or eurybathic species from Antarctica are known to be brooders (Thomson, 1878; Agassiz, 1881; Sladen, 1889), all other species of strictly bathyal or abyssal echinoderms, including many which were once assumed on the basis of egg size to be brooders (Agassiz, 1881; Thorson, 1946; Madsen, 1961) reproduce with either pelagic lecithotrophic larvae or planktotrophic larvae (Pearse, 1994; Young, 1994a). The lecithotrophs, exemplified by the echinothuriid echinoids (Tyler and Gage, 1984a), elasipod holothurians (Tyler and Billett, 1987) and porcellanasterid sea stars (Madsen, 1961; Ramirez Llodra et al., 2002), have yolky eggs approaching or exceeding 1 mm in diameter. Although it is clear from morphology and observation that these large eggs float (Young and Cameron, 1987; Cameron et al., 1988) and that these species do not retain their large eggs, lecithotrophic larvae have not been described for any deep-sea echinoderm. Indeed, Tyler and Billett (1987) have suggested that the large eggs of elasipod holothurians are direct developers which bypass a larval stage and develop directly into swimming juveniles of the sort commonly found in mid-water trawls (Gebruk et al., 1997).

Planktotrophic larvae have been reared for a number of echinoderm species living at bathyal depths, including the ophiuroid *Ophiocten gracilis* (Mortensen, 1898; Tyler and Gage, 1982) and the echinoid *Cidaris cidaris* from European waters (Prouho, 1888), the echinoid *Laganum diploporum* from Japan (Mortensen, 1921), and nine species of echinoids from the Bahamian slope: *Archaeopneustes hystrix* (Young et al., 1996c), *Aspidodiadema jacobyi* (Young et al., 1989; Young and George, 2000), *Cidaris blakei* (Young, unpublished), *Coelopleurus floridanus* (Young, unpublished), *Conolampas sigsbei* (C.M. Young and P.A. Tyler, unpublished), *Linopneustes longispinus* (Young and Cameron, 1989), *Lytechinus euerces* (Young et al., 1996c), *Palaeobrissus hilgardi* (C.M. Young and J.L. Cameron, unpublished) and *Stylocidaris lineata* (Young et al., 1996c, 1997). With the exception of *Aspidodiadema jacobyi* (Young and George, 2000), all of the larvae described are morphologically similar

to shallow-water members of the taxa to which they belong.

The larvae of *Aspidodiadema jacobyi* are unusual in several ways. Like typical planktotrophs, they develop from a small egg (90 μm) but, unlike other species, development of a mouth is delayed for the first 21 days, as the blastocoel becomes filled with yolky cells from the vegetal plate (Young et al., 1989). The yolky cells permit dispersal and perhaps vertical migration (Young et al., 1996c) for up to two months before planktonic food is required (Young et al., 1989). Eventually, the larva becomes a very large and complicated echinopluteus having 12 arms, a long posterior process and convoluted ciliary lobes (Young and George, 2000).

Cnidaria

In the deep sea, benthic cnidarians including various octocorals, scleractinian corals and actinian and zoanthic sea anemones, are particularly common on hard substrata such as seamounts and boulders, and on the volcanic rocks at some hydrothermal vents. Many species that require a firm surface have adopted an epizoid lifestyle, often becoming specialized for life on a single species of echinoderm, sponge or gorgonian. The most common cnidarians on soft bottoms are pennatulids (sea pens), which anchor their rachises in the sediment like a root.

Gonads, gametogenesis and reproductive periodicity

Aspects of reproduction have recently been described for several deep-sea pennatulid octocorals. *Kophobelemnion stelliferum*, a sea pen from the Porcupine Seabight in the northeast Atlantic, produces large eggs (800 μm), has separate sexes and apparently breeds continuously (Rice et al., 1992). Members of the cosmopolitan pennatulid genus *Umbellula* have eggs of a similar size which originate on the mesenterial filament, then complete oogenesis while floating freely in the gastrovascular cavity (Tyler et al., 1995). Ultrastructural details of gametogenesis have been described for *Pennatula aculeata*, a species that lives in relatively shallow (110 m) water and to a depth of at least 1500 m (Eckelbarger et al., 1998). Females of this species contained oocytes of all sizes and at all stages of oogenesis, suggesting that breeding is aperiodic. Sperm were packaged in sperm cysts, each of which contained spermatocytes at a comparable stage of development. The sperm remain packaged

in these cysts until after spawning, possibly as a mechanism for reducing sperm dilution (Eckelbarger et al., 1998).

Bronsdon et al. (1993, 1997) contrasted the reproductive patterns of two epizoic anemones, *Ampiphanthus inornata* which lives attached to gorgonians at depths between 2100 and 2300 m, and *Kadosactis commensalis*, which lives on sea cucumbers between 4500 and 4900 m. The shallower species breeds seasonally, releasing eggs in the spring, whereas the deeper-dwelling species has asynchronous breeding and probably spawns throughout the year. A species pair of zoanthid anemones which live epizoically on hermit crabs have also been studied at similar depths. In this case, however, the shallow species (*Epizoanthus paguriphilus* at 770–1065 m) and the deep one (*Epizoanthus abyssorum* at 3749 to 4400 m), are both continuous breeders (Muirhead et al., 1986).

Van-Praët and Duchateau (1984) and Van-Praët (1990) also provided evidence for seasonal reproduction in an abyssal sea anemone, *Paracalliactis stephensoni*. The timing and duration of reproduction has also been related to depth and seasonal flux of organic matter in congeneric actinians of the genus *Phelliactis* (Van-Praët et al., 1990). Both species are dioecious and produce large eggs. *Phelliactis hertwigii* lives between 719 and 1448 m in the Porcupine Seabight and produces an egg 180 µm in diameter. Gametogenesis takes 8–9 months and spawning occurs in October or November of each year. *Phelliactis robusta* lives at a greater depth (1600–2173 m) in the Bay of Biscay and produces a slightly larger egg (220 µm). Its gametogenesis takes 15–19 months and it spawns in April or May. These contrasting life cycles appear to be correlated with differences between the two habitats in the timing and intensity of phytodetritus flux (Van-Praët et al., 1990). Despite intense recent interest in deep-sea scleractinian corals such as *Lophelia pertusa*, there are no published data on the reproduction of these species, although fecundity appears to be very low (Waller and Tyler, pers. comm.).

Embryogenesis and larval development

Brooded planula larvae of two deep-water hydrocorals, *Cryptohelia pudica* and *Errina labiata*, were observed by Moseley (1881) during the *Challenger* expedition. Both male and female gametes of hydrozoans, actinians and octocorals were also described by

the *Challenger* authors (von Kölliker, 1880; Hertwig, 1882; Allmann, 1883). Danielssen and Koren (1884) reported a developing embryo from inside the polyp of *Umbellula encrinus*, but no evidence of brooding has been reported since and it has been suggested (Tyler et al., 1995) that the earlier workers mistook a parasitic flatworm for an embryo.

The only study of larval biology in a deep-water cnidarian is of the alcyonacean *Anthomastus ritteri* from California (Cordes et al., 2001). A large individual of this species broods more than 4000 yolky embryos in its gastrovascular cavity. Larvae are released as fully formed demersal planulae capable of settlement within two days, but also capable of delaying metamorphosis for more than four months (Cordes et al., 2001).

Other phyla

Porifera

Hexactinellids dominate the sponge fauna of bathyal and abyssal depths, yet hexactinellid larvae have been described for only a single species from relatively shallow water, and embryos have only been observed in a few cases (M. Maldonado and C.M. Young, unpublished observations). Witte (1996) described reproduction in three deep-sea demosponges from 2300 m in the Norwegian Sea. One of these reproduced seasonally, the onset of yolk formation correlating closely with the maximum flux of particles collected in sediment traps.

Nemertea

Seven species of pelagic nemertean worms living at depths between 250 and 3250 m in the eastern Pacific had eggs substantially larger (0.5–1 mm diameter) than those typical of shallow-water nemerteans (Norenburg and Roe, 1998). Females tended to be larger than males, and the sex ratio was apparently biased toward females in all but one species. The polystyliferan nemerteans in this assemblage transfer yolk to the oocytes through cytoplasmic bridges attached to nurse cells, a vitellogenic mechanism unknown among shallow-water nemerteans. Reproduction was iteroparous in all species, though only two species of the genus *Phallone-mertes* showed evidence of seasonal reproductive peaks (Norenburg and Roe, 1998).

Echiura

Selenka (1885) reported multiple dwarf males attached to a single female of the echiuran worm *Bonellia*

sumhi dredged from a depth of 2451 m off Nova Scotia. This observation suggests that this species reproduces in the same way as its shallow-water congeners, which produce larvae that settle preferentially on the female worm.

Bryozoa

On the basis of skeletal morphology, it appears that some deep-sea bryozoans brood embryos and release coronate larvae similar to those of shallow-water ascophorans (Davidson, 1880). Although there has been considerable taxonomic work on deep-water bryozoans in recent years, beginning with the bryozoan volume of the *Galathea* reports (Hayward, 1981), there have been no studies specifically directed at reproduction.

Brachiopoda

Larvae of the deep-sea inarticulate brachiopod *Pelagodiscus atlanticus*, which lives at depths ranging from 365 m to 4435 m, were collected from shallow water by Ashworth (1915). Other inarticulate larvae have been taken in plankton samples between 1000 and 3000 m (Simroth, 1897; Eichler, 1911). There have been no recent studies of reproduction in deep-sea brachiopods.

Hemichordata

Enteropneust worms are relatively common in the deep sea, though reproduction has only been examined in a single species. The very elongate "spaghetti worm," *Saxipendium coronatum*, lives draped over rocks in areas of diffuse hydrothermal flow at about 2500 m depth on the East Pacific Rise. Most individuals that have been collected are male, suggesting a strongly biased sex ratio. The testes, which are easily visible through the transparent body wall, occur in series along most of the trunk of the worm, giving the worm the appearance of a double pearl necklace. The sperm ultrastructure, as described by Franzen et al. (1985), reveals mushroom-shaped primitive sperm suggestive of external fertilization. Franzen et al. (1985) also reported small eggs, from which they inferred planktotrophic development. However, a recent re-examination of this species (Young, unpublished data) reveals very large floating eggs suggestive of either lecithotrophic larval development (a developmental mode unknown in the enteropneusts) or pelagic direct development. Giant larvae (up to 22 mm diameter) of an enteropneust known as *Planktosphaera pelagica* have been collected from oceanic waters in both the Atlantic and Pacific (Spengel, 1932; Hadfield and

Young, 1983). Although the adults remain unknown, it is generally thought that these are the larvae of an unknown enteropneust from the deep sea.

Chordata

Colonial ascidians collected from deep water have often been found to contain brooded larvae, like their shallow-water relatives (e.g., Herdman, 1886). A few deep-water solitary ascidians, including *Hypobythius calycodes* (Moseley, 1876) and some species of carnivorous octacnemid ascidians (Young and E. Vázquez, unpublished data) produce eggs much larger than those of any known shallow-water solitary ascidian. It is not known whether these gigantic eggs (nearly 1 mm in diameter) develop directly, bypassing the larval stage, or if they develop by means of lecithotrophic tadpoles like the majority of shallow-water solitary ascidians. Larval development has been described for only a single bathyal species, *Bathypera feminalba* (Young and Vázquez, 1995). Tadpoles of this species were very similar to those of shallow-water species in the same family.

LIFE-HISTORY TRAITS IN THE DEEP SEA: PREDICTIONS AND EVIDENCE

Life-history theory predicts traits that maximize fitness of an organism in the particular environment where it lives. These include brood size, size of young, age distribution of reproductive effort, the interaction of reproductive effort with adult mortality, and variation in all of these traits among the progeny of an individual (Stearns, 1976). In the context of marine organisms, "brood size" is generally called "fecundity" and "size of young" may be equated with egg size, which often determines the mode of development. Most marine animals reproduce until they die, so the "age distribution of reproductive effort" is often equivalent to age at first reproduction. To these one may add a number of traits that are especially germane for marine animals, including developmental mode, degree of parental protection, and various traits that assure successful fertilization (the "breeding strategy": Young, 1999), including mating systems, spawning behaviors, sperm chemotaxis and pheromonal communication.

An extensive literature on life-history traits considers differences that are expected between species or populations occupying stable vs. unstable environments. Although there is considerable habitat variation at bathyal and abyssal depths, extensive regions (e.g., abyssal

plains) are much more stable than most shallow-water habitats, and indeed are perhaps among the most stable and predictable environments on the planet (see Chapter 2). Because depth is roughly correlated with gradients in nutrient availability and habitat stability, it is useful to consider what life-history traits would be favored by natural selection at various depths in the sea. It is also interesting to consider how life histories might differ between normal (heterotrophic) deep-sea systems and autotrophic systems such as hydrothermal vents and cold seeps.

Environmental stability is not the only selective pressure in the deep sea that is expected to influence life-history traits. On the abyssal plain, low population densities, spatially uniform habitats, low temperature and limited food are all expected to influence life-histories, as are the extreme physical and chemical conditions found at hydrothermal vents.

Partitioning of energy between somatic and reproductive needs

Background

A fundamental idea in many life-history theories is the principle of allocation, a zero-sum game in which an organism has a fixed amount of energy and material to allocate among various reproductive tissues, somatic tissues and activities (Fisher, 1930; Williams, 1966). Theories about allocation are roughly divisible into deterministic models such as the familiar r - K selection idea of MacArthur and Wilson (1967) and stochastic models, such as the bet-hedging theories of Cohen (1966), Holgate (1967), Mountford (1968), Murphy (1968), Schaffer (1974) and others. These various models have been reviewed and summarized by Pianka (1970), Stearns (1976) and Todd (1986).

In the r -selection/ K -selection dichotomy (MacArthur and Wilson, 1967), so-called “ r -strategists” are organisms living in environments (e.g., hydrothermal vents), where mortality is caused largely by unpredictable events. Such organisms are expected to invest more energy in reproduction so as to spread the risk of mortality among habitats and times. “ K -strategists” are organisms living in stable environments (e.g., the abyssal plain) where density-dependent mortality (e.g., from competitive interactions) occurs as the environment reaches carrying capacity. Such organisms are expected to allocate more of their energy to growth, efficiency, persistence, and competitive ability than to producing offspring which could ultimately

be competitors. Proponents of the theory emphasize that most species occupy places along a continuum of r and K selection, but that a distinct dichotomy still exists between two very different kinds of animals (Pianka, 1970). However, Pianka (1970) also noted that aquatic organisms in general do not conform to the r / K dichotomy.

The stochastic “bet-hedging” life-history models have become more popular in recent years than deterministic models such as r - K selection, particularly for marine organisms with pelagic larvae and type III (Deevey, 1947) survivorship curves (Todd, 1986). These models predict the same combinations of life-history traits as r / K selection theory, but argue that these combinations should be found under circumstances opposite to those predicted by r / K selection. Specifically, the stochastic models predict short life, high reproductive potential and semelparity for species living in environments where the probability of juvenile (or larval) survivorship is quite constant and the opposite traits (long life, low reproductive output, iteroparity) where juvenile survival is variable.

Predictions

The r / K selection theory would predict that species in stable, food-limited habitats in the deep sea should tend toward the K end of the continuum, while vent species living in geologically unpredictable habitats should be r -strategists. The “bet-hedging” models are difficult to test for deep-sea animals because there are no data on the temporal variability of juvenile or larval survival. If juveniles or larvae develop in the relatively constant conditions of the abyssal plain or in the predator-poor abyssopelagic zone, then the “bet-hedging” models would predict a combination of traits similar to “ r -selection”. If, on the other hand, abyssal animals send their larvae into the upper water column where mortality processes are more severe and variable, then a combination of traits similar to K -selection would be expected. The latter traits would also be predicted for stochastically unpredictable hydrothermal vent habitats.

Evidence

Grassle and Sanders (1973) and Sanders (1979) considered the available evidence for a K -selected life-history strategy in the deep sea. Experimental tests of this hypothesis subsequently came from colonization experiments in which defaunated sediments were deployed in trays on the sea floor (Grassle, 1977; Desbruyères et al., 1980; Levin and Smith, 1984;

Grassle and Morse-Porteous, 1987; reviewed by Smith and Hessler, 1987) or deposited directly on the sea floor in mounds resembling the fecal deposits of burrowing infauna (Kukert and Smith, 1992). Results from these experiments have been variable. Most of the sediment-tray experiments indicated that colonization rates are significantly slower in the deep sea than in shallow water (Grassle, 1977; Levin and Smith, 1984; Grassle and Morse-Porteous, 1987; Snelgrove et al., 1994). In all of these studies, it took a very long time for the community to return to background levels. Both Desbruyères et al. (1980) and Kukert and Smith (1992) documented much higher rates of recolonization. However, in the study by Desbruyères et al., most of the colonists were polychaetes not represented in background samples; and some of the colonization in the study by Kukert and Smith is likely to have been invasion by adult burrowing, not larval settlement.

Can any of these colonization data be interpreted as evidence that species found in the deep sea allocate more energy to growth and maintenance than to colonization of new habitats by larval dispersal? Strictly speaking, recruitment rate is not a life-history trait that can be influenced by natural selection, but some factors contributing to recruitment rate (e.g., fecundity, larval defense mechanisms, larval habitat selection behaviors) are. One must therefore exercise extreme caution in making the leap from gamete production to colonization rate, as variable pelagic processes may result in large losses of animals with high fecundity or, conversely, occasional high recruitment of animals which invest relatively little in reproduction. Moreover, experiments deployed at different times may yield very different results for species with seasonal recruitment processes. The situation is further confused by the inclusion of some ophiuroids (Gage and Tyler, 1982b) and bivalves (Gage et al., 1980) with apparently continuous reproduction which still recruit seasonally or sporadically (Gage, 1991). In a community that contains several species with different periods of annual recruitment, slow colonization rates are not surprising; indeed, they would be expected in some proportion of experiments deployed at varying times of the year and lasting for only about two years. Thus, low colonization rates may be indicative of low investment of gametes, but should not be taken as direct evidence of K-selection. Finally, the use of colonization data to evaluate life-history strategy assumes that species with K-selected traits normally

live at population equilibrium, and hence require little ability to colonize disturbed or newly available habitats. This point has been questioned by Caswell (1982), who stated categorically and with the support of population models that life-history traits cannot be used to distinguish equilibrium and non-equilibrium populations.

In making their case for K-selection in the deep sea, Grassle and Sanders (1973) noted that many deep-sea animals, particularly the highly diverse peracarid crustaceans (isopods, amphipods, tanaids, cumaceans, mysids), typically have low fecundity and some parental protection, and lack a pelagic larval stage. However, the K-selected traits of parental protection and direct development are also universal among shallow-water peracarids, suggesting that these traits are phylogenetically constrained (Eckelbarger and Watling, 1995). Sanders (1977) noted that brittle stars and some other deep-sea animals have high fecundity and produce pelagic larvae, but he supposed that these species must occupy peripheral deep-sea habitats such as slopes and boreal seas, where conditions are less stable and biological accommodation (and K-selection) is less likely to occur. It is now known that many deep-sea animals do in fact produce abundant pelagic larvae (reviewed by Young, 1994a) and that settlement rates of such animals may sometimes be very high in the deep sea (see Gage and Tyler, 1981, for an example of high ophiuroid settlement).

Turner (1973, 1977) provided dramatic demonstrations of apparently r-selected deep-sea species associated with ephemeral and patchy habitats such as waterlogged wood. Regardless of what time of year wood is deployed in the deep sea, xylophagid molluscs and associated polychaetes invade it and grow quickly to reproductive maturity (Tyler and Young, unpublished data). The speed and reliability of the colonization process indicates that there must be a "soup" of larvae always ready to invade wood as it becomes available. This is classic r-selection; indeed, it is one of the most extreme examples of a "weedy" or r-selected species anywhere in nature.

Rex (1979) provided evidence for a depth-related shift along the r-K continuum in *Alvania pelagica*, a gastropod common at shelf and slope depths in the western Atlantic. He inferred longevity and the relative amounts of energy devoted to growth and reproduction from careful measurements of the protoconchs and body whorls of the shell. The results indicated a clear shift to greater K-selection occurring below the

shelf/slope break where the environment becomes more stable. Slope snails seem to allocate more energy to growth and less to reproduction than conspecifics on the shelf. A similar analysis within the protobranch bivalve genus *Nucula* was conducted by Scheltema (1972) over a depth gradient from the shelf to the abyss. He showed that species from the abyss allocated much less energy to reproduction than did their shallow congeners, and also that abyssal species tended to have lower fecundities and larger eggs. All of these observations are consistent with the predicted shift from r- to K-selection with increasing depth and environmental stability. However, the opposite may hold true for brachyuran crabs. Hines (1988) noted that deep-sea brachyurans in the genus *Chaceon* (formerly *Geryon*) have higher reproductive outputs than shallow-water crabs of comparable sizes, but that their fecundities were lower because of larger egg sizes.

The r-K selection theory predicts that animals should grow slowly, mature late, and live to a greater age in more stable environments. The most dramatic and oft-cited example of this is in the deep-sea protobranch bivalve *Tindaria callistiformis* from 3.8 km depth, which, on the basis of radioisotopic dating and shell sculpturing are estimated to attain reproductive maturity in about 50 years and to live for more than a century (Turekian et al., 1975). Gage and Tyler (1991) have discussed potential sources of error in this life span estimate, which has a confidence interval of 76 years. Similar longevities have been inferred for shallow-water bivalves using a variety of techniques (Breen and Shields, 1983; Jones et al., 1978), so long-lived clams are not unique to the very stable habitats of the abyss. Moreover, analysis of isotopes in deep-sea clams on the Galapagos Rise reveals very fast growth rates and shorter life spans (Turekian et al., 1979). Analysis of size-frequency data of protobranch bivalves in the Rockall Trough indicate that growth rates are fairly rapid, and that clams there live for only about eight years (Gage, 1985), which is similar to the expected longevity of a small clam from inshore waters (Gage and Tyler, 1991). Grassle (1977) found reproductively mature protobranchs (*Deminucula cancellata*) in colonization trays that had only been on the sea floor for about two years. Similar data from sediment trays indicate that the aplacophoran mollusc *Prochaetoderma yongei* attains full adult size in only two months and reproductive maturity in less than a year (Scheltema, 1987). Taken

together, these data do not support the contention that deep-sea bivalves live longer, mature later, or grow slower than shallow-water species.

Gage and Tyler (1985) have analysed growth and longevity in the sea urchin *Echinus affinis* from a depth of 2200 meters on the Hebridean Slope. This species lives for up to 28 years and attains reproductive maturity after about five years. A shallow-water congener, *Echinus esculentus*, lives for only up to 12 years and attains maturity after about 1.5–2.5 years (Nichols et al., 1985). Other echinoids from various shallow temperate and tropical seas are likewise shorter-lived and attain reproductive maturity much faster (Ebert, 1982) than *E. affinis*. The limited data on echinoids are consistent with a shift toward K-strategy in the deep sea. However, other predicted attributes of a K-adapted species do not apply to *Echinus affinis*. This species has high fecundity, small egg size (Tyler and Gage, 1984a), produces a pelagic larva (Young and Tyler, 1993) and sometimes recruits in very large numbers (Gage and Tyler, 1985).

There have been no explicit analyses comparing “r-selected” and “K-selected” traits of deep-sea animals from vents and seeps with animals that rely on allochthonous food in the “normal” deep sea. The predictions would be ambiguous in any case, since the food supply of vent/seep animals is more predictable and constant, yet the environment itself may remain stable for much less time.

“Bet hedging” models are currently difficult to evaluate for deep-sea habitats because there are no data whatsoever on juvenile vs. adult survival probabilities in the deep sea. It would seem reasonable to assume that juvenile survival is less variable in the stable deep sea than in temporally more variable shallow systems. However, Jumars and Gallagher (1983) have argued that, in the virtual absence of physical disturbance, predation becomes the most important source of mortality and that predation pressure should be more intense on younger animals because more mouth sizes would be able to ingest them. An extreme case of heavy juvenile mortality has been documented in the ophiuroid *Ophiocten gracilis* (Gage and Tyler, 1981). Also, Gage et al. (1980) and Gage and Tyler (1981) have invoked temporally variable juvenile mortality as a possible explanation for apparent seasonal recruitment in species that reproduce continuously.

In summary, there is evidence for a depth-related increase in certain K-selected traits within species and families of a few taxa, but there is also abundant

evidence to suggest that the opportunistic r-strategy is well represented in the deep sea. As in shallow water, the deep sea contains enough spatial and temporal variability to allow exploitation by species with various strategies of energy allocation.

Age distribution of reproductive effort

Background

In his classic paper linking life-history traits with population growth, Cole (1954) focused on the demographic advantages and disadvantages of one-time reproduction (semelparity) and repeated reproduction (iteroparity). His major finding, often known as “Cole’s result” was that semelparous animals that reproduce early in life produce as many offspring over many generations (i.e., are “as fit”) as iteroparous animals that produce more offspring over the course of an individual’s life, but begin reproduction later in life. This result has been challenged as an oversimplification (Charnov and Schaffer, 1973) but the fact remains that both kinds of organisms are successful in the real world. Todd (1986) noted that virtually all intertidal invertebrates are iteroparous and used this observation in support of the bet-hedging models that predict iteroparity for habitats where organisms have variable survival in the early life-history stages.

Predictions

“Bet-hedging” models predict that semelparity should increase as a function of environmental stability; thus, “normal” deep-sea habitats should select for semelparity, particularly among species that do not produce pelagic larvae. The r/K-selection theory, by contrast, predicts a predominance of long-lived, iteroparous species in stable deep-sea habitats.

Evidence

The most extensive work on reproductive patterns in the deep sea is that of Tyler, Gage and their colleagues in the Rockall Trough. Of the many species of echinoderms, molluscs, cnidarians and other invertebrates they have studied, virtually all reproduce over a wide range of body sizes, a feature indicative of iteroparity. Moreover, the majority of deep-sea species for which seasonal samples have been obtained appear to reproduce more or less continuously, probably over a number of annual cycles. The large number of observations on echinoderm reproduction on the Bahamian Slope also indicate iteroparity in all species. However, Turner’s observations on xylophagid

bivalves living in wood are in stark contrast, as these species attain reproductive maturity quickly and must reproduce before they consume their own habitat. Not all xylophagids seem to follow this pattern. Knudsen (1961) found juveniles attached in some way to the adults of nine species. Although this was interpreted as evidence of brooding, the young might also have settled on the adults after a period of dispersal. Thus, although at first sight it seems that some xylophagids might not be opportunistic and iteroparous, definitive information is not available. Other kinds of opportunistic species which probably have semelparous reproduction include some cocculinid limpets which colonize palm fronds and wood (Young and Tyler, unpublished data), and sipunculans which recruit opportunistically into fibrous substrata (M.A. Rice, P.A. Tyler and C.M. Young, unpublished data). The latter appear to live longer than a year and can reproduce several times in laboratory culture. However, sipunculans differ from xylophagids ecologically in that they do not destroy their own habitat. Before concluding that iteroparity is more common than semelparity in the deep sea, it should be noted that semelparity is much more difficult to document than iteroparity in infrequent deep-sea sampling programs; indeed, it is probably common for semelparous species to have life spans shorter than typical sampling intervals.

Not all small-bodied animals are semelparous in the deep sea. Wolff (1956a) found that the females of at least two species of hadal tanaids “... pass through several egg-bearing periods lasting probably at least three months” and that “these periods may occur only once every second or third year, provided that the female reaches an age of, say 15–20 years.” Wolff (1962) also found evidence of iteroparity in asellote isopods, and Bishop reported multiple cohorts of gametes in the gonads of abyssal cumaceans, a clear indication of iteroparity.

If Jumars and Gallagher (1983) are correct about the importance of juvenile predation, then the “bet-hedging” models correctly predict iteroparity; if not, then the predominance of iteroparity in the deep sea is best explained as a K-selected life-history trait. Empirical evaluation of these models requires demographic data, which, with the exception of a few echinoderms and bivalves in the Rockall Trough, remain scarce for deep-sea animals (Gage and Tyler, 1991).

At vents and seeps, many of the larger animals, including alvinellid polychaetes, siboglinid tube worms

and bivalves, appear to reproduce over a wide range of body sizes, suggesting that reproduction is either continuous or iteroparous (reviewed by Tyler and Young, 1999). To date, no semelparous species have been documented at vents or seeps, but it seems likely that some of the abundant small gastropods might be opportunistic and semelparous.

Seasonal vs. continuous breeding

Background

At the individual level, gametogenesis may proceed rapidly or slowly depending on the mechanisms of yolk deposition, and with either single or multiple cohorts of eggs developing at any given time (reviewed by Eckelbarger, 1994a). The mechanism of vitellogenesis may be absolutely conserved in some groups, but in others, selection can modify the timing and speed of gametogenesis to produce life cycles that reflect the environmental cycles in which the animal lives. Some tropical animals, which live in environments with virtually constant temperature and daylength breed semi-continuously (reviewed by Giese and Pearse, 1974; Young, 1999), but the vast majority of shallow-water animals in both temperate and tropical latitudes are periodic, synchronous breeders with annual reproductive cycles being the most common (Giese and Pearse, 1974).

Predictions

Moseley (1880) thought that there might be some seasonality in the deep sea, but his tentative suggestion was soon overshadowed by an influential paper by Orton (1920) predicting that deep-sea animals living at constant temperature should reproduce continuously. Although Orton advanced this idea as a testable hypothesis, it was not tested for many decades. During the intervening period, it became practically canonized in the deep-sea literature, in part because seasonal samples were hard to obtain, but also because the dynamic nature of the deep sea was not fully appreciated by biologists.

Evidence

Tables 12.1 to 12.4 list by major group all bathyal and abyssal species for which gametogenesis has been studied sufficiently well to infer periodicity of reproduction. Only a small amount of evidence comes from populations sampled regularly for reproductive parameters throughout the years. Constraints in ship-time, so that different seasons are sampled in different

years, often make it necessary to piece data together to make a composite year. It is not uncommon to find data sets with many months missing. As a poor alternative to seasonal sampling, patterns of reproductive periodicity have often been inferred from single gonad samples. This may be done by examining the cohort structure of gametes; the presence of multiple egg sizes and few mature gametes is suggestive of semi-continuous reproduction, particularly when numerous individuals of the population show a similar pattern. On the other hand, population-wide synchrony in which all individuals have a single gamete cohort is indicative of periodic, synchronized reproduction.

It is clear from the data that the majority of deep-sea species have aseasonal reproduction, but that seasonal reproduction also occurs at all latitudes and to depths of several thousand meters. Seasonal reproduction is known among sponges, cnidarians, peracarid and decapod crustaceans, molluscs, and echinoderms. Vent species are mostly continuous breeders. However, preliminary evidence suggests that some bivalves living at relatively shallow hydrothermal vents may breed seasonally (Comtet and Desbruyères, 1998; Comtet et al., 1999) as do many animals at cold seeps. The factors that drive seasonality remain unknown, as these animals may obtain all of the carbon and energy needed for maintenance from chemosynthetic sources. It is possible that they use phytodetritus as an energy source for gonad development, while relying on methane for maintenance and construction of somatic tissue.

Because the very existence of seasonal breeding came as a great surprise when it was first documented in the deep sea, it has perhaps received undue attention. It must be kept in mind that the vast majority of deep-sea animals, particularly at abyssal depths, reproduce aperiodically or continuously and therefore require no periodic cues for the entrainment of their gametogenic cycles.

Environmental control of gametogenesis

Background

Among marine animals, the timing of reproduction is almost invariably controlled on two different temporal scales: a long scale associated with initiation and progression of gametogenesis, and a shorter scale associated with spawning. Factors that entrain seasonal cycles of gametogenesis in shallow water include predictable changes in the natural light regime (e.g., sunrise, sunset, increasing daylength), and predictable

variability in salinity, diet and energy availability (Giese and Pearse, 1974). Most of the periodic cues known to control reproduction in shallow water (e.g., daylength, sunrise, temperature, lunar period, salinity, wave action) are not available in the deep sea. Nevertheless, there are seasonal changes even at abyssal depths that could possibly entrain reproductive cycles (reviewed by Tyler, 1988). Some of these factors, all of which remain untested as controllers of gametogenesis or spawning, include eddy kinetic energy, spring or summer falls of phytodetritus, and turbulence during benthic storms.

Predictions

Phytodetritus on the sea floor might qualify as a reliable cue for the entrainment of gametogenesis, particularly in temperate habitats where food may not only entrain reproduction, but also provide the energy needed for gamete production. A number of workers have suggested that phytoplankton detritus is probably the main controller of gametogenesis (Tyler, 1988; Tyler et al., 1994; Campos-Creasey et al., 1994).

The phytodetrital entrainment hypothesis gives rise to three predictions about the distribution of seasonal or periodic reproduction among deep-sea invertebrates: 1) If phytoplankton entrains gametogenesis, then one would expect more seasonality at the sea floor underlying highly productive temperate seas than in oligotrophic tropical regions, where the seasonal signal should be less intense; 2) one would expect more seasonality at bathyal depths than at abyssal depths; and 3) seasonal reproduction should be more common among animals living in non-chemosynthetic systems than in vent or seep animals, since the latter should have food available to them throughout the year.

Evidence

Latitudinal and depth comparisons of reproductive periodicity are easiest with the Echinodermata, since this phylum has been most extensively studied. At least one common deep-sea group, the echinoid family Echinothuriidae, reproduce continuously at all depths and latitudes where they occur. This suggests that reproductive periodicity, as well as mode of larval development, may be phylogenetically constrained for this group. The data show that seasonal breeders are present among echinoderms at both temperate and tropical latitudes and to a depth of about 3000 m. However, the few data available for greater depths suggest that seasonal reproduction may indeed become less common. When tropical and temperate latitudes

are compared, it appears that seasonal breeders are more common in tropical seas than in the temperate ones, a pattern not predicted by the phytodetrital entrainment hypothesis. However, the comparison is not entirely valid, since the only data set for tropical seas is for Bahamian Slope echinoids at depths less than 1000 m, whereas most data for temperate species are from greater depths. Greater geographic and bathymetric coverage is needed before these correlative tests are fully satisfactory.

In the past few years, my laboratory has undertaken experimental studies (as yet unpublished) to determine if detrital food entrains reproductive cycles in bathyal echinoids. Although the data remain preliminary, laboratory experiments and also experiments in field enclosures suggest that the timing of reproduction can be shifted at least slightly by providing excess food at certain times of year. Food quantity and quality control fecundity and egg quality in bathyal echinoids (S. George and Young, unpublished data), but can also shift the speed of the gametogenic process. Thus, evidence is beginning to accrue to support the hypothesis that the timing of food falls can control the onset or completion of gametogenesis.

Tyler et al. (1994) showed that *Plutonaster bifrons*, a seasonally breeding sea star from the Rockall Trough, shifts its diet to phytodetritus when this food source is available, whereas a continuously breeding starfish, *Bathybiaster vexillifer*, is predatory and therefore one trophic link away from the direct influence of the seasonal phytodetrital pulse. *Echinus affinis*, an echinoid from lower bathyal depths, shows a seasonal change in gut contents which reflects the composition of the sea-floor phytodetritus (Campos-Creasey et al., 1994). This species breeds annually in mid-winter, releasing eggs several months before phytodetritus becomes available to plankton at bathypelagic depths (Tyler and Gage, 1984a). If larval development is very slow, it is conceivable that planktotrophic larvae may be using this detritus as a food source. However, one does not know how long larvae take to reach the feeding stage in this species.

Fertilization success and the control of spawning

Background

Successful reproduction requires that eggs and sperm be mature and present at exactly the same time. Sperm generally have a short swimming time, and must occur at relatively high concentrations in order

for fertilization to occur (reviewed by Levitan, 1995). In shallow water, fertilization success is assured by breeding behaviors that bring animals into close proximity (e.g., Run et al., 1988), by environmental cues that assure simultaneous release of gametes (reviewed by Giese and Kanatani, 1987), and, at least in some species, by chemical communication (e.g., Miller, 1989). Internal fertilization is the most secure method of assuring that eggs and sperm come together. In some species this follows copulation, and in others sperm are collected and maintained by the female until the eggs are ready to be fertilized. Internal fertilization occurs in many gastropod molluscs, in peracarid, cirripede and decapod crustaceans, in bryozoans, in colonial ascidians, and in many polychaetes. Among free spawners, the timing of gamete release is often controlled by photoperiodic cues such as sunrise and lunar period. Epidemic spawning, wherein the gametes of one individual provide a signal that stimulates spawning in another, is commonly thought to facilitate spawning throughout the animal kingdom (Thorson, 1946). However, evidence for epidemic spawning remains equivocal for most species (Young, 1999), and only a few experimental studies (e.g., Starr et al., 1990) have shown its importance in shallow-water animals.

Fertilization success may also be facilitated by gamete modifications that reduce dilution by water currents, or that increase gamete longevity (Eckelbarger, 1994b).

Predictions

Because photoperiodic spawning cues are absent in the deep sea and many animals occur at low population densities, an increase in the incidence of internal fertilization is expected. Among species that fertilize externally, behavioral mechanisms such as spawning aggregation and an increase in the importance of pheromonal communication have been predicted (Young, 1999). Gamete modifications are also expected (Eckelbarger et al., 1989c; Eckelbarger, 1994b).

Evidence

Internal fertilization is the rule among deep-sea peracarids, which are the most diverse animals in the deep sea, and also predominates among the deep-sea gastropods, which include many diminutive species that lay egg masses with developing embryos. Many of the polychaetes living at hydrothermal vents have sperm that are clearly modified for internal fertilization. For example, the alvinellid and polynoid polychaetes

have spermathecae for receiving exogenous sperm from other individuals and storing the sperm until eggs are ready to be fertilized (Zal et al., 1994; Jollivet et al., 2000). Internal fertilization also appears likely in a vent siboglinid tube worm, *Ridgeia piscesae*. In this species, sticky masses of sperm are apparently captured on the vestimentum of the female worm, then transferred into the gonoducts (Southward and Coates, 1985). Although other siboglinids release unusual helical sperm in bundles (Cary et al., 1989), evidence suggests that they all fertilize externally (Van Dover, 1994; Young et al., 1996b).

Elongate and modified sperm are much more common among deep-sea free-spawning echinoderms than among their shallow-water relatives (reviewed by Eckelbarger et al., 1989c), and elongate sperm have also been described for a hydrothermal-vent bivalve (Beninger and Le Pennec, 1997). Some modifications, such as lipid reserves associated with the mitochondria of echinothuriid sea-urchin sperm (Eckelbarger et al., 1989b) appear to increase sperm longevity, whereas others, such as the bipolar tailed, dimorphic sperm of *Phrissocystis multispina* (Eckelbarger et al., 1989a), may reduce dilution. The release of sperm in swimming bundles by hydrothermal-vent and cold-seep siboglinids may also help to maintain high sperm concentrations in environment where buoyant, turbulent water could easily carry individual sperm away from the spawning females.

Many deep-sea echinoderms apparently facilitate fertilization by living in perennial herds (Young, 1994b), but others occur as scattered individuals, often at very low population densities. Many of the latter, including species of echinoids, holothuroids and ophiuroids, form pairs (Fig. 12.6) and other small-scale aggregations prior to spawning (Tyler et al., 1992b; Young et al., 1992; Young, 1994b, 1999). Indeed, breeding aggregations have been documented in many more deep-sea species than shallow-water ones, a pattern that is particularly striking when sampling bias is taken into account. Wilson (1975) posed the following hypothesis on the basis of his own work with insects:

“It is plausible (but unproved) that swarming is most advantageous to members of rare species and to those living in environments where the optimal time for mating is unpredictable.”

Pairing behavior in rare deep-sea echinoderms that live in an environment with few spawning cues lends credible support to Wilson's hypothesis.

Starr et al. (1994) demonstrated that phytodetritus can stimulate larval release in animals living in relatively shallow water but below the euphotic zone; but, to date, natural spawning cues have only been documented for a single deep-sea animal: a vesicomid clam living at cold seeps in Sagami Bay, Japan (Fujiwara et al., 1998). In this species, spawning was correlated with small natural temperature rises in the environment, and was induced experimentally in an elegant experiment wherein seawater was artificially heated *in situ*.

Fecundity and egg size

Background

The relationships among parental investment, egg size, and fecundity in marine invertebrates have received much attention. It is assumed that an animal of any particular body size should have a fixed amount of energy available for reproduction and that this energy allotment may be divided into many small eggs with little energy invested per egg, or into fewer large eggs with more energy per egg. A portion of the available energy may also be used for parental protection of broods, for auxiliary structures such as egg capsules, or for assuring successful fertilization. Among shallow-water free-spawning invertebrates, the former strategy is most common, especially among species with relatively large body sizes (e.g., Menge, 1975). Broadcasting many small eggs with no parental protection and little yolk requires high fecundity to compensate for high mortality during a long planktonic life (Thorson, 1950; Chia, 1974). These tradeoffs were first formalized for marine invertebrates by Vance (1973), whose classic model was immediately challenged (Underwood, 1974; Strathmann, 1974) and has been updated many times since (Christensen and Fenchel, 1979; Havenhand, 1993). Recently, there has been discussion about the potential role of fertilization processes in driving the evolution of egg size (Levitan, 1995), though this idea has not yet been accepted as fully as Vance's initial premise that egg size evolves because of limitations in fecundity and mortality during the larval stage.

Vance's model and most subsequent formulations predict that the very large and small egg sizes are evolutionarily stable, and that few eggs of intermediate size will be found. Thus, species tend to have either very large yolky eggs and lecithotrophic development,

or very small eggs with planktotrophic larval development. In all of these models, it is assumed that a species has a fixed amount of energy to allocate to reproduction, that an animal with small body size will have less energy for reproduction than one with large body size, and that mortality in the plankton will be greater for small eggs than large eggs.

Predictions

What egg sizes are to be expected in the deep sea? With the dramatic exceptions of a number of very large amphipods, isopods and pycnogonids, deep-sea animals tend to be smaller on average than related animals in coastal and littoral environments, a pattern that may be related to energy limitation in deep water (Rex and Etter, 1998). Small animals are expected to produce small numbers of large eggs not only because they have inadequate energy to invest in large fecundity, but also because space for brooding embryos may be limited (Strathmann and Strathmann, 1982). Thus, in the deep sea, models of reproductive partitioning predict large egg size, short or non-existent larval periods, and significant investment in parental care. Even in megafauna with large body sizes, limited energy in the environment might reduce the amount of energy that can be devoted to reproduction, thus driving the species toward decreased fecundity and large egg size. On the other hand, if mortality in the plankton is less important in the deep sea than in shallow water, then animals with small body size could perhaps reproduce successfully with low fecundities and smaller egg sizes than their shallow-water counterparts.

Reproductive output, which is sometimes but not always reflected in fecundity, is predicted to decrease with depth because of food limitation in deep water.

Evidence

The relationships among egg size, fecundity and depth have been examined for galatheid crabs (Van Dover and Williams, 1991), caridean shrimps (Ramirez Llodra et al., 2000), protobranch bivalves (Scheltema, 1994), and echinoderms (Pearse, 1994). Van Dover and Williams plotted the mean egg volume against depth for 52 species of galatheids ranging from intertidal to abyssal depths (Fig. 12.7). There was a general positive correlation between egg volume and depth. Statistical analysis within genera showed that this trend was significant in *Galathea* spp. and *Munidopsis* spp., but not in *Munida* spp. Apparent depth-related trends in fecundity in other groups of crustaceans are often caused by body-size differences or by a shift to larger

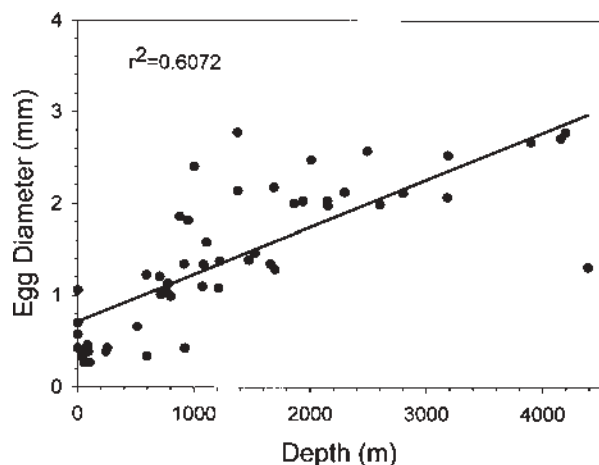


Fig. 12.7. The relationship between egg size and depth in deep-sea galatheids. Redrawn from Van Dover and Williams (1991).

egg sizes at greater depths (e.g., King and Butler, 1985; Mauchline, 1988; Company and Sardà, 1997). In Scheltema's (1994) review of fecundity data for bivalves, there is no obvious bathymetric trend in fecundity; indeed, two of the protobranch species with the lowest fecundities occur on the upper slope.

Sewell and Young (1997) have recently assembled all available data on echinoderm egg sizes for an additional test of the prediction by Vance's model that egg sizes should fall into a bimodal distribution. Combining data from all depths, they found clear bimodality in several echinoderm classes, though the pattern was obscured in taxa that brood their young or have other kinds of parental care. The bimodality remains when species occurring at depths less than 500 m are removed from the data set, suggesting that planktonic mortality is important in the deep sea, just as it is in shallow water.

Developmental mode

The reasons why larvae are present in some life cycles but not others have received considerable theoretical consideration in recent years (e.g., Strathmann, 1978, 1985, 1993; Wray and Raff, 1991; Wray, 1995; Hall and Wake, 1999; Hickman, 1999; Pechenik, 1999). Pechenik (1999) has reviewed in detail the advantages and disadvantages of having a larval form in the life cycle, and made some predictions about the environments where larvae are likely to have evolved or been lost. Many of the arguments relate to the advantages and disadvantages of dispersal. Potential advantages of dispersal include: 1) reducing competition between adults and their offspring; 2) minimizing

competition among siblings; 3) colonization of new habitats; 4) decreasing predation by benthic predators; 5) reducing the negative effects of inbreeding; and 6) spreading the risk of mortality in spatially and temporally variable environments. The fossil record provides several examples where molluscan clades with larval development survived longer in geological time than species with more limited dispersal (Jablonski and Lutz, 1983). However, there is still no solid evidence that there is selection for larvae as dispersal agents *per se* (Pechenik, 1999). Studies that have attempted to assess the advantages of dispersal on different scales have generally concluded that only moderate dispersal is advantageous, even in shallow water where there is considerable temporal variability in habitats (Palmer and Strathmann, 1981; Strathmann, 1985; Hedgecock, 1986).

Predictions

Thorson (1946, 1950) predicted that deep-sea animals should brood their young or have direct development. He reasoned that planktotrophic larval development should be impossible in deep water because larvae would have to migrate too far before encountering food items required to complete development. This idea, which Mileikovsky (1971) named "Thorson's Rule", is so logically appealing that it became a virtual paradigm for deep-sea reproduction.

If larvae evolved primarily for dispersal, then one might predict that larval development should be less common in the deep sea, where conditions tend to be more stable and habitats more continuous than in shallow water.

Evidence

Although brooding was once predicted to be the predominant mode of development among deep-sea animals (Thorson, 1950), recent analysis of the egg-size data in North Atlantic echinoderms shows that pelagic lecithotrophy, rather than brooding, is the main reproductive mode in both deep and polar seas (Pearse, 1994). Many authors have assumed that large egg sizes indicate brooding (Madsen, 1961; Tyler and Gage, 1984b); but, to date, very few brooding echinoderms have been found at abyssal or bathyal depths. The notable exception is the holothurian *Oneirophanta mutabilis* (Hansen, 1968), the only deep-sea elaspod holothurian known to brood its young. All other deep-sea holothurians that have been studied apparently produce pelagic lecithotrophic larvae (Tyler and Billett, 1985, 1987; Tyler et al., 1985a, 1992b;

Sewell et al., 1998). Planktotrophic development is found in a number of north Atlantic echinoderms, including the sea stars *Plutonaster bifrons* and *Psilaster andromeda* (Tyler and Pain, 1982a), the echinoids *Cidaris cidaris* (Prouho, 1888) and *Echinus affinis* (Tyler and Gage, 1984a), and the ophiuroids *Ophiocten gracilis* (Sumida et al., 2000) and *Ophiura ljunghmani* (Tyler and Gage, 1980). However, these represent only a small fraction of the species studied; the remainder have pelagic lecithotrophic development. In tropical seas, planktotrophic development is very common among echinoids (e.g., Young and Cameron, 1989; Young and George, 2000), though pelagic lecithotrophic development remains the most common mode of development in asteroids and holothuroids. Lecithotrophic echinoderm eggs that have been studied are buoyant and probably move great distances up into the water column. For example, the eggs of soft-bodied echinothuriid echinoids, which are more than 1 mm in diameter, float at a rate that should carry them to the surface from 1000 m depth in about 4 days (Young and Cameron, 1987; Cameron et al., 1988).

Many gastropods in the deep sea lay egg masses (Table 12.5), but some hatch in the capsule and emerge as crawl-away juveniles (Bouchet and Warén, 1994); the proportion of species that hatch from the egg mass to disperse in the water column as either lecithotrophic or planktotrophic pelagic larvae is unknown. Most of what is known concerning the development of deep-sea molluscs has been inferred from the dimensions of the protoconch (gastropods) or prodissoconch (bivalves) at the apex of the adult shell (Rex and Warén, 1982; Scheltema, 1994; Gustafson and Lutz, 1994), although also some deep-sea larvae have been captured in near-surface plankton hauls (Bouchet, 1976b). Xylophagid bivalves in the deep sea have very small eggs, planktotrophic larvae, and high fecundity, as might be expected for weedy species that rapidly colonize isolated and ephemeral substrata (Turner, 1973). Most vent and seep molluscs, including a myriad of tiny limpets, are apparently lecithotrophic, though some of the large-bodied mussels probably produce planktotrophic larvae (Gustafson and Lutz, 1994).

One could argue that brooding is the most typical reproductive mode in the deep sea, since peracarid crustaceans brood and are also the most speciose group in the deep sea. However, from an evolutionary standpoint, one cannot argue that there has been selection for brooding in the deep sea, since without exception

shallow water peracarids also brood their young. Thus, it appears that these animals are constrained phylogenetically to brooding as a developmental strategy. Decapod crustaceans, including brachyuran crabs and caridean shrimps, generally produce planktonic larvae, many of which are probably planktotrophic. The larva of an abyssal eryonid crab was described at the time of the *Challenger* expedition (von Willemoes-Suhm, 1876). The abundant vent shrimp on the Mid-Atlantic Ridge, *Rimicaris exoculata*, is known to produce larvae, some of which have been captured in plankton trawls many hundreds of meters above the bottom (Herring and Dixon, 1998).

Developmental modes of deep-sea infaunal polychaetes have been inferred from egg size in a number of studies (Table 12.1). Planktotrophy, lecithotrophy and brooding strategies are all present in these species, though lecithotrophic development again predominates and phylogenetic patterns of developmental mode are generally conserved. At hydrothermal vents and cold seeps, a number of polychaetes have been studied, most of which probably have larval development. Deep-sea perviate pogonophorans, now considered polychaetes, brood their embryos in their tubes, eventually releasing larval forms that are probably short-lived and demersal (Baake, 1976), but the related siboglinid polychaetes from vents and seeps produce small yolky eggs (100–115 μm) which develop into lecithotrophic trochophore larvae (Young et al., 1996b; Marsh et al., 2001). Wax esters confer buoyancy on these eggs despite their small size (Marsh et al., 2001).

Larval dispersal and migration

Background

Both the role of dispersal in evolution and the functions of dispersal in the life cycles of individual animals remain somewhat controversial, but most arguments revolve around the genetic advantages of outcrossing and the spread of risk among spatially and temporally heterogeneous environments (Strathmann, 1974; Palmer and Strathmann, 1981). Dispersal could also be important for reducing competition when resources are limiting locally. In the marine environment, most species disperse by means of microscopic larvae. Larvae may disperse for very long distances or they may have short lives and limited dispersal. With few known exceptions, those shallow-water species that disperse for long distances have feeding (planktotrophic) larvae, whereas most philopatric dispersers have lecithotrophic

larvae or direct development (reviewed by Jablonski and Lutz, 1983). Planktotrophic development requires that larvae find food before they exhaust the energy and nutrients sequestered by the mother in the egg, so most planktotrophic animals depend either directly or indirectly upon phytoplankton. Those species that do not produce larvae, including peracarid crustaceans, must disperse as adults or juveniles.

It is generally supposed that dispersal should be less crucial for the maintenance of genetic diversity in stable habitats than in habitats where there is a high likelihood of environmental change and a commensurate requirement for adaptive change in the genome. However, Hamilton and May (1977) have disputed this point with a model showing the population-wide importance of successfully competing for distant sites. Long-distance dispersal should not be advantageous where densities remain too low to foster competition among siblings or between siblings and offspring. Disadvantages of larval dispersal include high planktonic mortality and the improbability of locating a site as good as that of one's parents.

Predictions

One might predict that long-distance dispersal of larvae would not be favored by natural selection on the abyssal plain because great expanses of uniform substratum would make colonization of new habitats unnecessary. Moreover, in habitats like seamounts where a small area of suitable substratum is surrounded by extensive areas of marginal or unsuitable habitat, selection should favor only limited dispersal. Large eggs, parental protection and lecithotrophic development should be found in those deep-sea habitats where dispersal is not critical to the survival of the species. However, in ephemeral deep-sea habitats such as hydrothermal vents, the temporal variability of the system might compensate for the danger of gamete loss to unsuitable habitat, favoring the evolution of larval dispersal mechanisms.

Because the density of living phytoplankton declines rapidly below the deep chlorophyll maximum at about 200 m, and they are virtually absent below the permanent thermocline, it has been predicted that planktotrophy should not be a viable strategy for deep-sea animals (Thorson, 1946, 1950). Thorson argued that it would be impossible for a microscopic larva to migrate all the way to the euphotic zone without feeding, and Scheltema (1994) provided calculations in support of this contention.

Etter and Caswell (1994) used a cellular automaton model to explore the advantages of dispersal in habitats with various levels of disturbance in a competitive system. The model predicts that long-distance dispersal would only be advantageous at certain disturbance frequencies, and that the range of these frequencies would be influenced by reproductive output, competition and the intensity of disturbance. If it is assumed that the frequency of disturbance decreases as a function of depth down the slope, then the greatest advantages to dispersal may be expected at some intermediate depth, which would correspond to an intermediate level of disturbance.

Evidence

As indicated in Tables 12.1 to 12.6, planktotrophic larvae are produced by animals in many phyla living at slope depths and planktotrophy is common in some groups (notably prosobranch gastropods) even at abyssal depths. The mechanisms of nutrition for these larvae remain generally unknown. They may use nutritional resources available at depth (bacteria, dissolved organic matter, detrital seston) or they may migrate to a depth where sufficient food is available. Both possibilities have been discussed in the literature and explored experimentally. Young et al. (1997) presented a mathematical model incorporating swimming speeds, respiration rates and plankton concentrations to predict the likelihood that larvae could reach the euphotic zone by migrating from bathyal depths. When run with reasonable parameter estimates taken from deep-water echinoderm larvae where data were available and shallow-water larvae when the former were not available, the model showed that migration could be possible for many species if they were respiring at low rates and swimming at high (but realistic) speeds. However, larvae of some of these species cannot tolerate the temperatures or pressures found at or near the level where phytoplankton are abundant (Young and Cameron, 1989; Young and Tyler, 1993; Young et al., 1996a, 1997; Tyler and Dixon, 2000). Preliminary data (W. Jaeckle, A. Pile, I. Bosch and C. Young, unpublished) show that larvae of bathyal echinoderms can absorb dissolved organic matter and remove heterotrophic bacteria from the water column at relatively high rates. These various pieces of indirect evidence indicate that planktotrophic development may be a viable developmental strategy in the deep sea, even for species that cannot migrate to the euphotic zone.

Compelling evidence that some larvae migrate

ontogenetically to the euphotic zone comes from the work of Ashworth (1915) and Bouchet (1976a,b), both of whom collected deep-sea larvae among the shallow-water plankton. Bouchet and Fontes (1981) and Killingley and Rex (1985) analysed oxygen isotopes in protoconchs; these data indicated that the carbonate in protoconchs was deposited at a warmer temperature than in the teloconchs.

Genetic studies of hydrothermal vent animals generally have demonstrated a high level of genetic exchange among remote sites, suggesting the strong possibility of larval dispersal (reviewed by Jollivet, 1993; Mullineaux and France, 1995; Vrijenhoek, 1997; Tyler and Young, 1999). Indeed, larvae from many phyla have been collected in vent plumes (Mullineaux et al., 1995, 1996), larval development has been inferred from shell apices of many vent molluscs (Gustafson and Lutz, 1994); and a handful of vent and seep species have been reared in the laboratory from larvae (Young et al., 1996b; Epifanio et al., 1999; Marsh et al., 2001; Pradillon et al., 2001). The swimming behavior of larvae of the vent crab *Bythograea thermydron* suggests that it disperses quite passively for long distances, then begins walking when it encounters the warm water of a vent. Similarly, the embryos of an alvinellid polychaete, *Alvinella pompejana*, undergo arrested development at 2°C, then resume cleavages when encountering warmer temperatures (Pradillon et al., 2001). Using data on lipid reserves, metabolism and currents, dispersal distance has been estimated for the siboglinid polychaete *Riftia pachyptila* (Marsh et al., 2001). The lecithotrophic larvae of this species are capable of drifting for about 38 days. At 9°N on the East Pacific Rise, this dispersal time is sometimes enough to permit dispersal over the transform faults that separate ridge segments.

Young et al. (1999) analysed the geographic ranges of deep-sea echinoderms and ascidians with known modes of larval dispersal. They found that the standard relationship between geographic range and mode of development (planktotrophs disperse farther and have broader ranges than lecithotrophs: see Jablonski and Lutz, 1983) breaks down in deep water. This is probably because lecithotrophs can drift much longer distances in the cold temperatures of the deep sea than in warmer surface waters. Some of the species with the broadest ranges were elaspod holothurians, which produce lecithotrophic larvae, but also are capable of pelagic dispersal in the juvenile and adult stages.

Etter and Caswell (1994) tested the prediction of

their dispersal/disturbance model by examining the relative proportions at various depths of gastropod species with planktotrophic and nonplanktotrophic development (Rex and Warén, 1982). In the western Atlantic, the proportion of prosobranch gastropods with planktotrophic development increases with depth to 2000 m, where the number of planktotrophic and nonplanktotrophic species is approximately the same (Rex and Warén, 1982). This pattern fits the predictions of the model well, suggesting that disturbance frequency might interact with other factors influencing the evolution of larval dispersal in the deep sea.

CONCLUSIONS

It is now recognized that the deep sea is not a single, continuous habitat, but rather a mosaic of habitats in which many species have particular specialized requirements (Tyler, 1995). The insular, dynamic, often ephemeral, vent and seep habitats with abundant sources of autochthonous nutrition contrast markedly with stable, nutrient-poor and extensive abyssal plains where all energy is allochthonous in origin. Likewise, the continental slopes and rises contain many different habitats, each characterized by specific topographic features, food levels, and physical characteristics, and each occupied by distinct assemblages of species adapted to those conditions. It is not surprising therefore that reproductive modes and life-history traits of animals, as revealed by more than a century of study, show a rich assortment of tactics and strategies for responding to the diversity of habitats in the deep sea. With few exceptions, the reproductive strategies and tactics found in shallow-water systems are also represented in the deep sea, though there remain clear shifts in the relative importance of different strategies with depth. As in most other ecological systems, generalizations become harder to make as one learns more about the details.

REFERENCES

- Adiyodi, R.G. and Subramoniam, T., 1983. Arthropoda–Crustacea. In: K.G. Adiyodi and R.G. Adiyodi (Editors), *Reproductive Biology of Invertebrates, Vol. 1: Oogenesis, Oviposition and Oosorption*. Wiley, Chichester, pp. 443–495.
- Agassiz, A., 1881. Echinoidea. *Reports of the Scientific Research of the Voyage of HMS Challenger, Zoology*, 3(9): 1–321. 65 Plates.
- Allen, J.A., 1979. The adaptations and radiation of deep-sea bivalves. *Sarsia*, 64: 19–27.

- Allmann, G.J., 1883. Hyroida, Part 1. *Reports of the Scientific Research of the Voyage of HMS Challenger, Zoology*, 7(20): 1–54. 20 Plates.
- Ashworth, J.H., 1915. On larvae of *Lingula* and *Pelagodiscus*. *Trans. R. Soc. Edinburgh*, 51: 45–70.
- Baake, T., 1976. The early embryos of *Siboglinum fiordicum* Webb (Pogonophora) reared in the laboratory. *Sarsia*, 60: 1–11.
- Baker, A.N., Rowe, F.W.E. and Clark, H.E.S., 1986. A new class of Echinodermata from New Zealand. *Nature*, 321: 862–864.
- Beninger, P.G. and Le Pennec, M., 1997. Reproductive characteristics of a primitive bivalve from a deep-sea reducing environment: giant gametes and their significance in *Acharax alinae* (Cryptodonta: Solemyidae). *Mar. Ecol. Prog. Ser.*, 157: 195–206.
- Berg Jr., C.J., 1985. Reproductive strategies of mollusks from abyssal hydrothermal vent communities. *Biol. Soc. Wash. Bull.*, 6: 185–197.
- Bingham, B.L. and Young, C.M., 1993. Larval phototaxis in barnacles and snails associated with bathyal sea urchins. *Deep-Sea Res.*, 40: 1–12.
- Bishop, J.D.D., 1994. The growth, development and reproduction of a deep-sea cumacean (Crustacea: Peracarida). *Zool. J. Linn. Soc.*, 74: 359–380.
- Bishop, J.D.D. and Shalla, S.H., 1994. Discrete seasonal reproduction in an abyssal peracarid crustacean. *Deep-Sea Res.*, 41: 1789–1800.
- Blake, J.A., 1993. Life history analysis of five dominant infaunal polychaete species from the continental slope off North Carolina. *J. Mar. Biol. Assoc. UK*, 73: 123–141.
- Blake, J.A. and Watling, L., 1994. Life history studies of deep-sea benthic infauna: Polychaeta, Aplousobranchia, and Cumacea from the continental slope off Massachusetts. In: C.M. Young and K.J. Eckelbarger (Editors), *Reproduction, Larval Biology and Recruitment of the Deep-Sea Benthos*. Columbia University Press, New York, pp. 243–260.
- Booolootian, R.A., Giese, A.C., Tucker, J.S. and Farmanfarmaian, A., 1959. A contribution to the biology of a deep-sea echinoid, *Allocentrotus fragilis* (Jackson). *Biol. Bull.*, 16: 362–372.
- Bouchet, P., 1976a. Mise en évidence d'une migration de larves véligères entre l'étage abyssal et la surface. *C. R. Acad. Sci. Paris*, 283: 821–824.
- Bouchet, P., 1976b. Mise en évidence de stades larvaires planctoniques chez des Gastéropodes prosobranches des étages bathyal et abyssal. *Bull. Mus. Natl. Hist. Nat. Zool.*, 277: 947–972.
- Bouchet, P. and Fontes, J.C., 1981. Migrations verticales des larves de Gastéropodes abyssaux: arguments nouveaux dus à l'analyse isotopique de la coquille larvaire et postlarvaire. *C. R. Acad. Sci. Paris*, 292(3): 1005–1008.
- Bouchet, P. and Warén, A., 1979. Planktotrophic larval development in deep-water gastropods. *Sarsia*, 64: 37–40.
- Bouchet, P. and Warén, A., 1994. Ontogenetic migration and dispersal of deep-sea gastropod larvae. In: C.M. Young and K.J. Eckelbarger (Editors), *Reproduction, Larval Biology and Recruitment of the Deep-Sea Benthos*. Columbia University Press, New York, pp. 98–117.
- Brattegard, T. and Sankarankutty, C., 1967. On the prezoa and zoea of *Geryon tridens* Krøyer (Crustacea: Decapoda). *Sarsia*, 26: 7–12.
- Breen, P.A. and Shields, T.L., 1983. Age and size structure in five populations of geoduck clams (*Panope generosa*) in British Columbia. *Can. Tech. Rep. Fish. Aquat. Sci.*, 1169: 1–66.
- Bronsdon, S.K., Tyler, P.A., Rice, A.L. and Gage, J.D., 1993. Reproductive biology of two epizoic anemones from the deep north-eastern Atlantic Ocean. *J. Mar. Biol. Assoc. UK*, 73: 531–542.
- Bronsdon, S.K., Rogers, A.D., Tyler, P.A., Rice, A.L. and Gage, J.D., 1997. Genetic study of the extent and consequences of sexual and asexual reproduction in the deep-sea epizoic anemones *Amphianthus inornata* and *Kadosactis commensalis* (Cnidaria: Anthozoa). *Mar. Biol.*, 128: 231–239.
- Cameron, J.L., Young, C.M. and McEuen, F.S., 1988. Floating lecithotrophic eggs from the bathyal echinothuriid sea urchin *Araeosoma fenestratum*. In: R.D. Burke, P.V. Mladenov, P. Lambert and R.L. Parsley (Editors), *Echinoderm Biology*. Balkema, Rotterdam, pp. 177–180.
- Campos-Creasey, L.S., Tyler, P.A., Gage, J.D. and John, A.W.G., 1994. Evidence for coupling the vertical flux of phytodetritus to the diet and seasonal life history of the deep-sea echinoid *Echinus affinis*. *Deep-Sea Res.*, 41: 369–388.
- Carrasco, F.D., 1983. Description of adults and larvae of a new deep water species of *Hyalinoecia* (Polychaeta, Onuphidae) from the Southeastern Pacific Ocean. *J. Nat. Hist.*, 17: 87–93.
- Cary, S.C., Felbeck, H. and Holland, N.D., 1989. Observations on the reproductive biology of the hydrothermal vent tube worm *Riftia pachyptila*. *Mar. Ecol. Prog. Ser.*, 52: 89–94.
- Cary, S.C., Shank, T.M. and Stein, J., 1998. Worms bask in extreme temperatures. *Nature*, 391: 545–546.
- Caswell, H., 1982. Life history theory and the equilibrium status of populations. *Am. Nat.*, 120: 317–339.
- Charnov, E.L. and Schaffer, W.M., 1973. Life history consequences of natural selection: Cole's result revisited. *Am. Nat.*, 107: 791–793.
- Chevaldonné, P., Jollivet, D., Vangriesheim, A. and Desbruyères, D., 1997. Hydrothermal-vent alvinellid polychaete dispersal in the eastern Pacific. 1. Influence of vent site distribution, bottom currents, and biological patterns. *Limnol. Oceanogr.*, 42: 67–80.
- Chia, F.-S., 1974. Classification and adaptive significance of developmental patterns in marine invertebrates. *Thalassia Jugosl.*, 10: 121–130.
- Christensen, F.B. and Fenchel, T.M., 1979. Evolution of marine invertebrate reproductive patterns. *Theor. Popul. Biol.*, 16: 267–282.
- Christie, G., 1982. The reproductive cycles of two species of *Pholoe* (Polychaeta: Segalionidae) off the Northumberland coast. *Sarsia*, 67: 283–292.
- Clarke, A., Hopkins, C.C.E. and Nilssen, E.M., 1991. Egg size and reproductive output in the deep-water prawn *Pandalus borealis* Krøyer, 1838. *Funct. Ecol.*, 5: 724–730.
- Clarke, A.H., 1962. On the composition, zoogeography, origin and age of the deep-sea mollusk fauna. *Deep-Sea Res.*, 9: 291–306.
- Cohen, D., 1966. Optimizing reproduction in a randomly varying environment. *J. Theor. Biol.*, 12: 119–129.
- Cole, L.C., 1954. The population consequences of life history phenomena. *Q. Rev. Biol.*, 29: 103–137.
- Colman, J.G. and Tyler, P.A., 1988. The egg capsules of *Colus jeffreysianus* (Fischer, 1868) (Prosobranchia: Neogastropoda) from the Rockall Trough, North East Atlantic. *Sarsia*, 73: 139–145.
- Colman, J.G., Tyler, P.A. and Gage, J.D., 1986a. The reproductive

- biology of *Colus jeffreysianus* (Gastropoda: Prosobranchia) from 2200 m in the NE Atlantic. *J. Molluscan Stud.*, 52: 45–54.
- Colman, J.G., Tyler, P.A. and Gage, J.D., 1986b. Larval development of deep-sea gastropods (Prosobranchia: Neogastropoda) from the Rockall Trough. *J. Mar. Biol. Assoc. UK*, 66: 951–965.
- Company, J.B. and Sardà, F., 1997. Reproductive patterns and population characteristics in five deep-water pandalid shrimps in the Western Mediterranean along a depth gradient (150–1100 m). *Mar. Ecol. Prog. Ser.*, 148: 49–58.
- Comtet, T. and Desbruyères, D., 1998. Population structure and recruitment in mytilid bivalves from the Lucky Strike and Menez Gwen hydrothermal fields (37°17'N and 37°50'N) on the Mid-Atlantic Ridge. *Mar. Ecol. Prog. Ser.*, 163: 165–177.
- Comtet, T., Le Pennec, M. and Desbruyères, D., 1999. Evidence of a sexual pause in *Bathymodiolus azoricus* (Bivalvia: Mytilidae) from hydrothermal vents of the Mid-Atlantic Ridge. *J. Mar. Biol. Assoc. UK*, 79: 1149–1150.
- Cordes, E.E., Nybakken, J.W. and VanDykhuizen, G., 2001. Reproduction and growth of *Anthomastus ritteri* (Octocorallia: Alcyonacea) from Monterey Bay, California, U.S.A. *Mar. Biol.*, 138: 491–501.
- Craddock, C., Lutz, R.A. and Vrijenhoek, R.C., 1997. Patterns of dispersal and larval development of archaeogastropod limpets at hydrothermal vents in the eastern Pacific. *J. Exp. Mar. Biol. Ecol.*, 210: 37–51.
- Creasey, S., Rogers, A.D., Tyler, P.A., Young, C.M. and Gage, J.D., 1997. The population biology and genetics of the deep-sea spider crab, *Encephaloides armstrongi* Wood-Mason 1891 (Decapoda: Majidae). *Philos. Trans. R. Soc. London Ser. B*, 352: 365–379.
- Danielssen, D.C. and Koren, J., 1884. Pennatulida. In: *Den Norske Nordhavs-Expedition 1876–1878 Zoologi*, Part 12, with 12 plates and 1 map. Grøndahl Bogtrykkeri, Cristiania, Norway, pp. 1–83.
- Davidson, T., 1880. Brachiopoda. *Reports of the Scientific Research of the Voyage of HMS Challenger, Zoology*, 1(1): 1–67. 4 Plates.
- Deevey, E.S., 1947. Life tables of natural populations of animals. *Q. Rev. Biol.*, 22: 283–314.
- Demestre, M. and Fortuño, J.-M., 1992. Reproduction of the deep-water shrimp *Aristeus antenatus* (Decapoda: Dendrobranchiata). *Mar. Ecol. Prog. Ser.*, 84: 41–51.
- Desbruyères, D., Bevas, J.Y. and Khripounoff, A., 1980. Un cas de colonisation rapide d'une sédiment profond. *Oceanol. Acta*, 3: 285–291.
- Ebert, T.A., 1982. Longevity, life history, and relative body wall size in sea urchins. *Ecol. Monogr.*, 52: 353–394.
- Eckelbarger, K.J., 1986. Vitellogenic mechanisms and the allocation of energy to offspring in polychaetes. *Bull. Mar. Sci.*, 39: 426–443.
- Eckelbarger, K.J., 1994a. Diversity of metazoan ovaries and vitellogenic mechanisms: implications for life history theory. *Proc. Biol. Soc. Wash.*, 107: 193–218.
- Eckelbarger, K.J., 1994b. Ultrastructural features of gonads and gametes in deep-sea invertebrates. In: C.M. Young and K.J. Eckelbarger (Editors), *Reproduction, Larval Biology and Recruitment of the Deep-Sea Benthos*. Columbia University Press, New York, pp. 137–157.
- Eckelbarger, K.J. and Watling, L., 1995. Role of phylogenetic constraints in determining reproductive patterns in deep-sea invertebrates. *Invert. Biol.*, 114: 256–269.
- Eckelbarger, K.J. and Young, C.M., 1992. Ovarian ultrastructure and vitellogenesis in ten species of shallow-water and bathyal sea cucumbers (Echinodermata: Holothuroidea). *J. Mar. Biol. Assoc. UK*, 72: 759–781.
- Eckelbarger, K.J. and Young, C.M., 1999. Ultrastructure of gametogenesis in a chemosynthetic mytilid bivalve (*Bathymodiolus childressi*) from a bathyal, methane seep environment (northern Gulf of Mexico). *Mar. Biol.*, 135: 635–646.
- Eckelbarger, K.J. and Young, C.M., 2002. Spermiogenesis and modified sperm morphology in the “seepworm” *Methanoaricia dendrobranchiata* (Polychaeta: Orbiniidae) from a methane seep environment in the Gulf of Mexico: implications for fertilization biology. *Biol. Bull.*, 203: 134–143.
- Eckelbarger, K.J., Young, C.M. and Cameron, J.L., 1989a. Modified sperm ultrastructure in four species of soft-bodied echinoids (Echinodermata: Echinothuriidae) from the bathyal zone of the deep sea. *Biol. Bull.*, 177: 230–236.
- Eckelbarger, K.J., Young, C.M. and Cameron, J.L., 1989b. Ultrastructure and development of dimorphic sperm in the abyssal echinoid *Phrissocystis multispina* (Echinodermata: Echioidea): implications for deep-sea reproductive biology. *Biol. Bull.*, 176: 257–271.
- Eckelbarger, K.J., Young, C.M. and Cameron, J.L., 1989c. Modified sperm in echinoderms from the bathyal and abyssal zones of the deep sea. In: J. Ryland and P.A. Tyler (Editors), *23rd European Marine Biology Symposium: Reproduction, Genetics and Distributions of Marine Organisms*. Olsen and Olsen, Fredensborg, Denmark, pp. 67–74.
- Eckelbarger, K.J., Tyler, P.A. and Langton, R.W., 1998. Gonadal morphology and gametogenesis in the sea pen *Pennatula aculeata* (Anthozoa: Pennatulacea) from the Gulf of Maine. *Mar. Biol.*, 123: 677–690.
- Eckelbarger, K.J., Young, C.M., Ramirez Llodra, E., Brooke, S. and Tyler, P.A., 2001. Gametogenesis, spawning behavior, and early development in the “iceworm” *Hesiocaeca methanicola* (Polychaeta: Hesioniidae) from methane hydrates in the Gulf of Mexico. *Mar. Biol.*, 138: 761–775.
- Eichler, P., 1911. Die Brachiopoden der deutschen Sudpolar Expedition. *Dtsch. Sudp. Exped. Bd. Xii Zool. Iv. Bd.*, with 3 plates, pp. 384–385.
- Emson, R.H., Young, C.M. and Paterson, G.L.J., 1993. A fire worm with a sheltered life: studies of *Benthoscolex cubanus* Hartman (Amphinomidae), an internal associate of the bathyal sea urchin *Archaeopneustes hystrix* (A. Agassiz, 1880). *J. Nat. Hist.*, 27: 1013–1028.
- Epifanio, C.E., Perovich, G., Dittel, A.I. and Cary, S.C., 1999. Development and behavior of megalopa larvae and juveniles of the hydrothermal vent crab *Bythograea therydron*. *Mar. Ecol. Prog. Ser.*, 185: 147–154.
- Erdman, R.B., Blake, N.J., Lindberg, W.J., Lockhart, F.D., Perry, H.M. and Waller, R.S., 1991. Comparative reproduction of the deep-sea crabs *Chaceon fenneri* and *C. quinquedens* (Brachyura: Geryonidae) from the northeast Gulf of Mexico. *Invertebr. Reprod. Dev.*, 19: 175–184.
- Etter, R.J. and Caswell, H., 1994. The advantages of dispersal in a patchy environment: effects of disturbance in a cellular automaton model. In: C.M. Young and K.J. Eckelbarger (Editors), *Reproduction, Larval Biology and Recruitment of the Deep-Sea Benthos*. Columbia University Press, New York, pp. 284–305.
- Etter, R.J. and Rex, M.A., 1990. Population differentiation

- decreases with depth in deep-sea gastropods. *Deep-Sea Res.*, 37: 1251–1261.
- Fage, L., 1956. Les pycnogonides du genre *Nymphon*. *Galathea Rep.*, 2: 159–165.
- Ferrand, J.G., Vadon, C., Doumenc, D. and Guille, A., 1988. The effect of depth on the reproductive cycle of *Brissopsis lyrifera* (Echinoidea, Echinodermata) in the Gulf of Lions, Mediterranean Sea. *Mar. Biol.*, 99: 387–392.
- Fiala-Médioni, A. and Le Pennec, M., 1989. Adaptive features of the bivalve molluscs associated with fluid venting in the subduction zones off Japan. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 71: 161–167.
- Fisher, C.R., MacDonald, I.R., Sassen, R., Young, C.M., Macko, S.A., Hourdez, S., Carney, R.S., Yoye, S. and McMullin, E., 2000. Methane ice worms: *Hesiocaeca methanicola* colonizing fossil fuel reserves. *Naturwissenschaften*, 87: 184–187.
- Fisher, R.A., 1930. *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford, 291 pp.
- Fournier, J.A. and Peterson, M.E., 1991. *Cossura longocirrata*: redescription and distribution, with notes on reproductive biology and a comparison of described species of *Cossura* (Polychaeta: Cossuridae). *Ophelia*, Supplement 5: 63–80.
- Franzen, A., 1956. On spermiogenesis, morphology of the spermatozoon, and biology of fertilization among invertebrates. *Zool. Bidrag Uppsala*, 31: 355–480.
- Franzen, A., Woodwick, K.H. and Sensenbaugh, T., 1985. Spermiogenesis and ultrastructure of spermatozoa in *Saxipendium coronatum* (Hemichordata, Enteropneusta), with consideration of their relation to reproduction and dispersal. *Zoomorphology*, 105: 302–307.
- Fujiwara, Y., Tsukahara, J., Hashimoto, J. and Fujikura, K., 1998. In situ spawning of a deep-sea vesicomid clam: evidence for an environmental cue. *Deep-Sea Res.*, 45: 1881–1889.
- Gage, J.D., 1985. The analysis of population dynamics in deep-sea benthos. In: P.E. Gibbs (Editor), *Proceedings of the Nineteenth European Marine Biology Symposium*. Cambridge University Press, Cambridge, pp. 247–260.
- Gage, J.D., 1991. Biological rates in the deep sea: a perspective from studies on processes in the benthic boundary layer. *Rev. Aquat. Sci.*, 5: 49–100.
- Gage, J.D. and Tyler, P.A., 1981. Non-viable seasonal settlement of larvae of the upper bathyal brittlestar *Ophiocten gracilis* in the Rockall Trough. *Mar. Biol.*, 64: 163–174.
- Gage, J.D. and Tyler, P.A., 1982a. Reproduction and growth in the deep-sea brittle star *Ophiura ljunmani* (Lyman). *Oceanol. Acta*, 3: 177–185.
- Gage, J.D. and Tyler, P.A., 1982b. Growth and reproduction of the deep-sea brittlestar *Ophiomusium lymani* Wyville Thomson. *Oceanol. Acta*, 5: 73–83.
- Gage, J.D. and Tyler, P.A., 1985. Growth and recruitment of the deep-sea urchin *Echinus affinis*. *Mar. Biol.*, 90: 41–53.
- Gage, J.D. and Tyler, P.A., 1991. *Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor*. Cambridge University Press, Cambridge, 504 pp.
- Gage, J.D., Lightfoot, R.H., Pearson, M. and Tyler, P.A., 1980. An introduction to a sample time-series of abyssal macrobenthos: methods and principal sources of variability. *Oceanol. Acta*, 3: 169–176.
- Gage, J.D., Tyler, P.A. and Nichols, D., 1986. Reproduction and growth of *Echinus acutus* var. *norvegicus* Duben and Koren and *E. elegans* Duben and Koren on the continental slope off Scotland. *J. Exp. Mar. Biol. Ecol.*, 101: 61–83.
- Gardiner, S.L. and Jones, M.L., 1985. Ultrastructure of spermiogenesis in the vestimentiferan tube worm *Riftia pachyptila* (Pogonophora: Obturata). *Trans. Am. Microsc. Soc.*, 104: 19–44.
- Gardiner, S.L. and Jones, M.L., 1993. Vestimentifera. In: F.W. Harrison and M.E. Rice (Editors), *Microscopic Anatomy of Invertebrates*, Vol. 12. Wiley-Liss, New York, pp. 371–460.
- Gardner, W.D. and Sullivan, L.G., 1981. Benthic storms: temporal variability in a deep-ocean nepheloid layer. *Science*, 213: 329–331.
- Gebruk, A.V., Tyler, P.A. and Billett, D.S.M., 1997. Pelagic juveniles of the deep-sea elapsidid holothurians: new records and review. *Ophelia*, 46: 153–164.
- George, R.Y. and Menzies, R.J., 1967. Indication of cyclic reproductive activity in abyssal organisms. *Nature*, 215: 878.
- George, R.Y. and Menzies, R.J., 1968. Further evidence for seasonal breeding cycles in deep sea. *Nature*, 220: 80–81.
- Giangrande, A., 1997. Polychaete reproductive patterns, life cycles and life histories: an overview. *Oceanogr. Mar. Biol. Annu. Rev.*, 35: 323–386.
- Giese, A.C. and Kanatani, H., 1987. Maturation and spawning. In: A.C. Giese, J.S. Pearse and V.B. Pearse (Editors), *Reproduction of Marine Invertebrates, Vol. IX, Seeking Unity in Diversity*. Blackwell Press, Palo Alto; and Boxwood Press, Pacific Grove, CA, pp. 251–331.
- Giese, A.C. and Pearse, J.S., 1974. Introduction: general principles. In: A.C. Giese and J.S. Pearse (Editors), *Reproduction of Marine Invertebrates I. Acoelomate and Pseudocoelomate Metazoans*. Academic Press, New York, pp. 1–49.
- Giese, A.C., Pearse, J.S. and Pearse, V.B. (Editors), 1991. *Reproduction of Marine Invertebrates, Vol. VI: Echinodermata*. Boxwood Press, Pacific Grove, CA; and Academic Press, San Diego.
- Gordon, J.D.M. and Duncan, J.A.R., 1985. The ecology of the deep-sea benthic and benthopelagic fish on the slopes of the Rockall Trough, northeast Atlantic Ocean. *Prog. Oceanogr.*, 15: 37–69.
- Grassle, J.F., 1977. Slow recolonization of deep-sea sediment. *Nature*, 265: 618–619.
- Grassle, J.F., 1986. The ecology of deep-sea hydrothermal vent communities. *Adv. Mar. Biol.*, 23: 301–362.
- Grassle, J.F. and Morse-Porteous, L.S., 1987. Macrofaunal colonization of disturbed deep-sea environments and the structure of deep-sea benthic communities. *Deep-Sea Res.*, 34A: 1911–1950.
- Grassle, J.F. and Sanders, H.L., 1973. Life histories and the role of disturbance. *Deep-Sea Res.*, 23: 643–659.
- Green, A., Tyler, P.A., Angel, M.V. and Gage, J.D., 1994. Gametogenesis in deep and surface-dwelling oceanic stalked barnacles from the NE Atlantic Ocean. *J. Exp. Mar. Biol. Ecol.*, 184: 143–158.
- Gustafson, R.G. and Lutz, R.A., 1994. Molluscan life history traits at deep-sea hydrothermal vents and cold methane/sulfide seeps. In: C.M. Young and K.J. Eckelbarger (Editors), *Reproduction, Larval Biology and Recruitment of the Deep-Sea Benthos*. Columbia University Press, New York, pp. 76–97.
- Gustafson, R.G., Littlewood, D.T.J. and Lutz, R.A., 1991. Gastropod

- egg capsules and their contents from deep-sea hydrothermal vent environments. *Biol. Bull.*, 180: 34–55.
- Hadfield, M.G. and Young, R.E., 1983. Planctosphaera (Hemichordata: Enteropneusta) in the Pacific Ocean. *Mar. Biol.*, 73: 151–153.
- Haefner Jr., P.A., 1977. Reproductive biology of the female deep-sea red crab, *Geryon quinquedens*, from the Chesapeake Bight. *Fish. Bull.*, 75: 91–102.
- Haefner Jr., P.A., 1978. Seasonal aspects of the biology, distribution and relative abundance of the deep-sea red crab *Geryon quinquedens* Smith, in the vicinity of the Norfolk canyon, Western North Atlantic. *Proc. Natl. Shellfish. Assoc.*, 68: 49–62.
- Hall, B.K. and Wake, M.H., 1999. Introduction: larval development, evolution and ecology. In: B.K. Hall and M. Wake (Editors), *The Origin and Evolution of Larval Forms*. Academic Press, San Diego, pp. 1–21.
- Hamilton, W.D. and May, R.D., 1977. Dispersal in stable habitats. *Nature*, 269: 578–581.
- Hansen, B., 1968. Brood protection in the deep-sea holothurian *Oneirophanta mutabilis* Theel. *Nature*, 217: 1062–1063.
- Harasewych, M.G., 2002. Pleurotomarioidean gastropods. *Adv. Mar. Biol.*, 42: 235–292.
- Harrison, K., 1988. Seasonal reproduction in deep-sea Crustacea (Isopoda: Asellota). *J. Nat. Hist.*, 22: 175–197.
- Hartman, O., 1965. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic Areas. *Alan Hancock Foundation Occas. Pap.*, 28: 1–378.
- Hartman, O., 1967. Larval development of benthic invertebrates in Antarctic Seas: early development of *Nothria notialis* (Monro) and *Paronuphis antarctica* (Monro) in Bransfield Strait, Antarctic Peninsula. *Proceedings of the Symposium on Pacific–Antarctic Sciences. JARE Sci. Rep.*, Special Issue No. 1: 205–208.
- Hartman, O. and Fauchald, K., 1971. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic Areas. *Alan Hancock Foundation Monogr. Mar. Biol.*, 6: 1–327.
- Hartnoll, R.G. and Rice, A.L., 1984. Further studies on the biology of the deep-sea spider crab *Dorhynchus thomsoni*: instar sequence and the annual cycle. In: P.E. Gibbs (Editor), *Proceedings of the 19th European Marine Biology Symposium*. Cambridge University Press, Cambridge, pp. 231–241.
- Havenhand, J.N., 1993. Egg to juvenile period, generation time, and the evolution of larval type in marine invertebrates. *Mar. Ecol. Prog. Ser.*, 97: 247–260.
- Hayward, P.J., 1981. The Cheilostomata of the deep sea. *Galathea Rep.*, 15: 21–68.
- Healy, J.M., 1988. Ultrastructural observations on the spermatozoa of *Pleurotomaria africana* Tomlin (Gastropoda). *J. Molluscan Stud.*, 54: 309–316.
- Healy, J.M., 1989a. Spermatozoa of the deep-sea cephalopod *Vampyroteuthis infernalis* Chun: ultrastructure and possible phylogenetic significance. *Philos. Trans. R. Soc. London Ser. B*, 323: 589–608.
- Healy, J.M., 1989b. Spermatozeugmata of *Abyssochrysis*: ultrastructure, development and relevance to the systematic position of the Abyssochrysididae (Prosobranchia, Caenogastropoda). *Bull. Mus. Natl. Hist. Nat. Paris*, 11: 509–533.
- Healy, J.M., 1990. Taxonomic affinities of the deep-sea genus *Provanna* (Caenogastropoda): new evidence from sperm ultrastructure. *J. Molluscan Stud.*, 56: 119–122.
- Healy, J.M., Rowe, F.W.E. and Anderson, D.T., 1988. Spermatozoa and spermiogenesis in *Xyloplax* (Class Concentricycloidea): a new type of spermatozoon in the Echinodermata. *Zool. Scr.*, 17: 297–310.
- Hedgecock, D., 1986. Is gene flow from pelagic larval dispersal important in the adaptation and evolution of marine invertebrates? *Bull. Mar. Sci.*, 39: 550–564.
- Herdman, W.A., 1886. Tunicata, part 2. *Reports of the Scientific Research of the Voyage of HMS Challenger; Zoology*, 14(38): 1–432. 49 Plates.
- Herring, P.J., 1974. Observations on the embryonic development of some deep-living decapod crustaceans with particular reference to *Acanthephyra*. *Mar. Biol.*, 25: 25–33.
- Herring, P.J. and Dixon, D.R., 1998. Extensive deep-sea dispersal of postlarval shrimp from a hydrothermal vent. *Deep-Sea Res.*, 45: 2105–2118.
- Hertwig, R., 1882. Actiniaria. *Reports of the Scientific Research of the Voyage of HMS Challenger; Zoology*, 6(15): 1–136. 14 Plates.
- Hessler, R.R. and Wilson, G.D.F., 1983. The origin and biogeography of the malacostracan crustaceans in the deep sea. In: R.W. Sims, J.H. Price and P.E.S. Whalley (Editors), *Evolution, Time and Space: The Emergence of the Biosphere*. Academic Press, London, pp. 227–254.
- Hickman, C.S., 1999. Larvae in invertebrate development and evolution. In: B.K. Hall and M. Wake (Editors), *The Origin and Evolution of Larval Forms*. Academic Press, San Diego, pp. 22–60.
- Hicks, G.R.F. and Coull, B.C., 1983. The ecology of marine meiobenthic copepods. *Oceanogr. Mar. Biol. Annu. Rev.*, 21: 67–175.
- Hicks, G.R.F. and Marshall, B.A., 1985. Sex selective predation of deep-sea, meiobenthic copepods by pectinacean bivalves and its influence on copepod sex ratios. *N. Z. J. Mar. Freshwater Res.*, 19: 227–231.
- Hilbig, B. and Blake, J.A., 1991. Dorvilleidae (Annelida: Polychaeta) from the U.S. Atlantic slope and rise. Description of two new genera and 14 new species, with a generic revision of *Ophyrotrocha*. *Zool. Scr.*, 20: 147–183.
- Hines, A.H., 1982. Allometric constraints and variables of reproductive effort in Brachyuran crabs. *Mar. Biol.*, 69: 309–320.
- Hines, A.H., 1988. Fecundity and reproductive output in two species of deep-sea crabs, *Geryon fenneri* and *G. quinquedens* (Decapoda: Brachyura). *J. Crustacean Biol.*, 8: 557–562.
- Hodgson, A.N., Eckelbarger, K.J. and Young, C.M., 1998. Sperm morphology and spermiogenesis in the methane-seep mollusk *Bathynnerita naticoidea* (Gastropoda: Neritacea) from the Louisiana Slope. *Invertebr. Biol.*, 117: 199–207.
- Holgate, P., 1967. Population survival and life history phenomena. *J. Theor. Biol.*, 14: 1–10.
- Hollister, C.D. and McCave, I.N., 1984. Sedimentation under deep-sea storms. *Nature*, 309: 220–225.
- Hollister, C.D. and Nowell, A.R.M., 1991. HEBBLE epilogue. *Mar. Geol.*, 99: 445–460.
- Ingle, R.W., 1979. The larval and post-larval development of the brachyuran crab *Geryon tridens* Krøyer (Family Geryonidae) reared in the laboratory. *Bull. Br. Mus. Nat. Hist. Zool.*, 36: 217–232.

- Jablonski, D. and Lutz, R.A., 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. *Biol. Rev.*, 58: 21–89.
- Jamieson, B.G.M. and Rouse, G.W., 1989. The spermatozoa of the Polychaeta (Annelida): an ultrastructural review. *Biol. Rev.*, 64: 93–157.
- Johnson, W.S., Stevens, M. and Watling, L., 2001. Reproduction and development of marine peracarideans. *Adv. Mar. Biol.*, 39: 105–260.
- Jollivet, D., 1993. *Distribution et Évolution de la Faune Associée aux Sources Hydrothermales Profondes à 13°N sur la Dorsale du Pacifique Orientale: le Cas Particulier des Polychètes Alvinellida*. Thèse de Doctorat nouveau régime, Université de Bretagne Occidentale, 357 pp.
- Jollivet, D., Chevaldonné, P. and Planque, B., 1998. Hydrothermal vent alvinellid polychaete dispersal in the eastern Pacific. 2. A metapopulation model based on habitat shifts. *Evolution*, 53: 1128–1142.
- Jollivet, D., Empis, A., Baker, M.C., Hourdez, S., Comtet, T., Jouin-Toulmond, C., Desbruyères, D. and Tyler, P.A., 2000. Reproductive biology, sexual dimorphism, and population structure of the deep-sea hydrothermal vent scale-worm, *Branchiopolynoe seepensis* (Polychaeta: Polynoidae). *J. Mar. Biol. Assoc. UK*, 80: 55–65.
- Jones, D.S., Thompson, I. and Ambrose, W.G., 1978. Age and growth rate determinations for the Atlantic surf clam *Spisula solidissima* (Bivalvia: Mactracea), based on internal growth lines in shell cross-sections. *Mar. Biol.*, 47: 63–70.
- Jones, M.L. and Gardiner, S.L., 1989. On the early development of the vestimentiferan tube worm *Ridgeia* sp. and observations on the nervous system and trophosome of *Ridgeia* sp. and *Riftia pachyptila*. *Biol. Bull.*, 177: 254–276.
- Jouin-Toulmond, C., Zal, F.D. and Hourdez, S., 1997. Genital apparatus and ultrastructure of the spermatozoa in *Alvinella pompejana* (Annelida: Polychaeta). *Cah. Biol. Mar.*, 38: 128–129.
- Jumars, P.A. and Gallagher, E.D., 1983. Deep-sea community structure: three plays on the benthic proscenium. In: W.G. Ernst and J.G. Morin (Editors), *The Environment of the Deep Sea*. Prentice-Hall, Englewood Cliffs, NJ, pp. 215–255.
- Kaïm-Malka, R.A., 1997. Biology and life cycle of *Natatolana borealis* Lilj. 1851, a scavenging isopod from the continental slope of the Mediterranean. *Deep-Sea Res.*, 44: 2045–2067.
- Killingley, J.S. and Rex, M.A., 1985. Mode of larval development in some deep-sea gastropods indicated by oxygen-18 values of their carbonate shells. *Deep-Sea Res.*, 32A: 809–818.
- King, M.G. and Butler, A.J., 1985. Relationship of life-history patterns to depth in deep-water caridean shrimps (Crustacea: Natantia). *Mar. Biol.*, 86: 129–138.
- King, M.G. and Moffitt, R.B., 1984. The sexuality of tropical deep-water shrimps (Decapoda: Pandalidae). *J. Crustacean Biol.*, 4: 567–571.
- Klages, M., 1993. Distribution, reproduction and population dynamics of the Antarctic gammaridean amphipod, *Eusirus perdentatus* Chevreux, 1912 (Crustacea). *Antarct. Sci.*, 5: 349–359.
- Knudsen, J., 1961. The bathyal and abyssal *Xylophaga* (Pholadidae, Bivalvia). *Galathea Rep.*, 5: 163–209.
- Knudsen, J., 1970. The systematics and biology of abyssal and hadal Bivalvia. *Galathea Rep.*, 11: 7–241.
- Knudsen, J., 1979. Deep sea bivalves. In: S.V.D. Spoel, A.C.V. Bruggen and J. Lever (Editors), *Pathways in Malacology*. Scheltema, Holkema, Utrecht, pp. 195–224.
- Kukert, H. and Smith, C.R., 1992. Disturbance, colonization and succession in a deep-sea sediment community: artificial-mound experiments. *Deep-Sea Res.*, 39: 1349–1371.
- Le Pennec, M. and Beninger, P.G., 1997. Ultrastructural characteristics of spermatogenesis in three species of deep-sea hydrothermal vent mytilids. *Can. J. Zool.*, 75: 308–316.
- Levin, L.A. and Smith, C.R., 1984. Response of background fauna to disturbance and enrichment in the deep sea: a sediment tray experiment. *Deep-Sea Res.*, 31A: 1277–1285.
- Levin, L.A., Plaia, G.R. and Huggett, C.L., 1994. The influence of natural organic enhancement on life histories and community structure of bathyal polychaetes. In: C.M. Young and K.J. Eckelbarger (Editors), *Reproduction, Larval Biology and Recruitment of the Deep-Sea Benthos*. Columbia University Press, New York, pp. 261–283.
- Levitani, D.R., 1995. The ecology of fertilization in free-spawning invertebrates. In: L.R. McEdward (Editor), *Ecology of Marine Invertebrate Larvae*. CRC Press, Boca Raton, FL, pp. 123–156.
- Lightfoot, R.H., Tyler, P.A. and Gage, J.D., 1979. Seasonal reproduction in deep-sea bivalves and brittlestars. *Deep-Sea Res.*, 26A: 967–973.
- Lisin, S.E., Hannan, E.E., Kochevar, R.E., Harrold, C. and Barry, J.P., 1996. Temporal variation in gametogenic cycles of vesicomycid clams. *Invertebr. Reprod. Dev.*, 31: 307–318.
- Lonsdale, P.F., 1977. Clustering of suspension-feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centers. *Deep-Sea Res.*, 24: 857–863.
- Lutz, R.A. and Voight, J.R., 1994. Close encounter in the deep. *Nature*, 371: 563.
- MacArthur, R.H. and Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ, 216 pp.
- MacDonald, I.R., Boland, G.S., Baker, J.S., Brooks, J.M., Kennicutt II, M.C. and Bidigare, R.R., 1989. Gulf of Mexico hydrocarbon seep communities II. Spatial distribution of seep organisms and hydrocarbons at Bush Hill. *Mar. Biol.*, 101: 235–247.
- Madsen, F.J., 1961. On the zoogeography and origin of the abyssal fauna. *Galathea Rep.*, 4: 177–218.
- Marsh, A.G., Mullineaux, L.S., Young, C.M. and Manahan, D.T., 2001. Larval dispersal potential of the tubeworm *Riftia pachyptila* at deep-sea hydrothermal vents. *Nature*, 411: 77–80.
- Mauchline, J., 1986. The biology of the deep-sea species of Mysidacea (Crustacea) of the Rockall Trough. *J. Mar. Biol. Assoc. UK*, 66: 803–824.
- Mauchline, J., 1988. Egg size and brood sizes of oceanic pelagic crustaceans. *Mar. Ecol. Prog. Ser.*, 43: 251–258.
- Mauviel, A. and Sibuet, M., 1985. Repartition des traces animales et importance de la bioturbation. In: L. Laubier and C. Monniot (Editors), *Peuplements Profonds du Golfe de Gascogne*. Institut Français de Recherche pour l'Exploration de la Mer, Brest, France, pp. 157–173.
- McCave, I.N. and Jones, K.P.N., 1988. Deposition of ungraded muds from high density non-turbulent turbidity currents. *Nature*, 333: 250–252.
- McHugh, D., 1989. Population structure and reproductive biology of two sympatric hydrothermal vent polychaetes, *Paralvinella pandorae* and *P. palmiformis*. *Mar. Biol.*, 103: 95–106.
- McHugh, D., 1995. Unusual sperm morphology in a deep-sea

- hydrothermal-vent polychaete, *Paralvinella pandorae* (Alvinellidae). *Invertebr. Biol.*, 114: 1161–1168.
- McHugh, D. and Tunnicliffe, V., 1994. Ecology and reproductive biology of the hydrothermal vent polychaete *Amphisamytha galapagensis* (Ampharetidae). *Mar. Ecol. Prog. Ser.*, 106: 111–120.
- Melville-Smith, R., 1987. The reproductive biology of *Geryon maritae* (Decapoda, Brachyura) off south west Africa/Namibia. *Crustaceana*, 53: 259–275.
- Menge, B.L., 1975. Brood or broadcast? The adaptive significance of different reproductive strategies in the two intertidal sea stars *Leptasterias hexactis* and *Pisaster ochraceus*. *Mar. Biol.*, 31: 87–100.
- Merrett, N.R., 1987. A zone of faunal change in assemblages of abyssal demersal fish in the eastern North Atlantic: a response to seasonality in production? *Biol. Oceanogr.*, 5: 137–151.
- Mileikovsky, S.A., 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance. *Mar. Biol.*, 10: 193–213.
- Miller, R.L., 1989. Evidence for the presence of sexual pheromones in free-spawning starfish. *J. Exp. Mar. Biol. Ecol.*, 130: 205–221.
- Mortensen, T., 1898. Die Echinodermenlarven der Plankton-Expedition nebst einer systematischen Revision der bisher bekannten Echinodermenlarven. *Ergeb. Plankton-Exp.*, 2j: 1–120.
- Mortensen, T., 1921. *Studies of the Development and Larval Forms of Echinoderms*. G.E.C. Gad, Copenhagen, 266 pp.
- Moseley, H.N., 1876. On deep-sea ascidians &c. *Linn. Soc. Trans. Ser. ii*, 1: 287.
- Moseley, H.N., 1880. Deep-sea dredgings and life in the deep sea. *Nature*, 21: 543–547, 569–572, 591–593.
- Moseley, H.N., 1881. Hydroid, Alcyonarian and Madreporarian Corals. *Reports of the Scientific Research of the Voyage of HMS Challenger, Zoology*, 2(7): 1–248. 32 Plates.
- Mountford, M.D., 1968. The significance of litter size. *J. Anim. Ecol.*, 37: 363–367.
- Muirhead, A., Tyler, P.A. and Thurston, M.H., 1986. Reproductive biology and growth of the genus *Epizoanthus* (Zoanthidea) from the north-east Atlantic. *J. Mar. Biol. Assoc. UK*, 66: 131–143.
- Mullineaux, L.S. and France, S.C., 1995. Dispersal mechanisms of deep-sea hydrothermal vent fauna. *Geophys. Monogr.*, 91: 408–424.
- Mullineaux, L.S., Wiebe, P.H. and Baker, E.T., 1995. Larvae of benthic invertebrates in hydrothermal vent plumes over the Juan de Fuca Ridge. *Mar. Biol.*, 122: 585–596.
- Mullineaux, L.S., Kim, S.L., Pooley, A. and Lutz, R.A., 1996. Identification of archaeogastropod larvae from a hydrothermal vent community. *Mar. Biol.*, 124: 551–560.
- Murphy, G.I., 1968. Pattern in life-history and environment. *Am. Nat.*, 102: 391–403.
- Nichols, D., Sime, A.A.T. and Bishop, G.M., 1985. Growth in populations of the sea-urchin *Echinus esculentus* L. (Echinodermata: Echinoidea) from the English Channel and Firth of Clyde. *J. Exp. Mar. Biol. Ecol.*, 86: 219–228.
- Norenburg, J.L. and Roe, P., 1998. Reproductive biology of several species of recently collected pelagic nemerteans. *Hydrobiologia*, 365: 73–91.
- Ockelmann, K.W., 1965. Developmental types in marine bivalves and their distribution along the Atlantic Coast of Europe. In: L.R. Cox and J.F. Peake (Editors), *Proceedings of the 1st European Malacological Congress, London 1962*, pp. 25–35.
- Orton, J.H., 1920. Sea temperature, breeding and distribution in marine animals. *J. Mar. Biol. Assoc. UK*, 12: 339–366.
- Pain, S.L., Tyler, P.A. and Gage, J.D., 1982a. The reproductive biology of the deep-sea asteroids *Benthopecten simplex* (Perrier), *Pectinaster filholi* Perrier, and *Postaster tenuispinus* Duben & Koren (Phanerozoia: Benthopectinidae) from the Rockall Trough. *J. Exp. Mar. Biol. Ecol.*, 65: 195–211.
- Pain, S.L., Tyler, P.A. and Gage, J.D., 1982b. The reproductive biology of *Hymenaster membranaceus* from the Rockall Trough, North-East Atlantic Ocean, with notes on *H. gennaeus*. *Mar. Biol.*, 70: 41–50.
- Palmer, A.R. and Strathmann, R.R., 1981. Scale of dispersal in varying environments and its implications for life histories of marine invertebrates. *Oecologia*, 48: 308–318.
- Pearse, J.S., 1994. Cold-water echinoderms break “Thorson’s Rule”. In: C.M. Young and K.J. Eckelbarger (Editors), *Reproduction, Larval Biology and Recruitment of the Deep-Sea Benthos*. Columbia University Press, New York, pp. 26–39.
- Pechenik, J.A., 1999. On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Mar. Ecol. Prog. Ser.*, 177: 269–292.
- Pernet, B., Qian, P.-Y., Rouse, G.W., Young, C.M. and Eckelbarger, K.J., 2002. Phylum Annelida: Polychaeta. In: C.M. Young, M.A. Sewell and M.E. Rice (Editors), *Atlas of Marine Invertebrate Larvae*. Academic Press, London, pp. 207–243.
- Pianka, E.R., 1970. On r- and K-selection. *Am. Nat.*, 100: 592–597.
- Potter, E. and Rex, M.A., 1992. Parallel development-depth trends in deep-sea turrid snails from the Eastern and Western North Atlantic. *Nautilus*, 106: 72–75.
- Pradillon, F., Shillito, B., Young, C.M. and Gaill, F., 2001. Developmental arrest in vent worm embryos. *Nature*, 413: 698–699.
- Prouho, H., 1888. Recherches sur le *Dorocidaris papillata* et quelques autres échinides de la Méditerranée. *Arch. Zool. Exp. Gen.*, 2: 213–380.
- Ramirez Llodra, E., 2002. Fecundity: characteristics and role in life history strategies of marine invertebrates. *Adv. Mar. Biol.*, 43: 78–172.
- Ramirez Llodra, E., Tyler, P.A. and Copley, J.T.P., 2000. Reproductive biology of three caridean shrimp, *Rimicaris exoculata*, *Chorocaris chacei* and *Mirocaris fortunata* (Caridea: Decapoda), from hydrothermal vents. *J. Mar. Biol. Assoc. UK*, 80: 473–484.
- Ramirez Llodra, E., Tyler, P.A. and Billett, D.S.M., 2002. Reproductive biology of porcellanasterid asteroids from three abyssal sites in the Northeast Atlantic with contrasting food input. *Mar. Biol.*, 140.
- Reibisch, J., 1927. Amphipoda: Flohkrebse. *Handb. Zool. Berlin*, 3(1): 767–808.
- Rex, M.A., 1979. r- and K-selection in a deep-sea gastropod. *Sarsia*, 64: 29–32.
- Rex, M.A. and Etter, R.J., 1998. Bathymetric patterns of body size: implications for deep-sea biodiversity. *Deep-Sea Res. II*, 45: 103–127.
- Rex, M.A. and Warén, A., 1982. Planktotrophic development in deep-sea prosobranch snails from the western North Atlantic. *Deep-Sea Res.*, 29: 171–184.
- Rex, M.A., Van Ummersen, C.A. and Turner, R.D., 1979.

- Reproductive pattern in the abyssal snail *Benthonella tenella* (Jeffreys). In: S.E. Stancyk (Editor), *Reproductive Ecology of Marine Invertebrates*. University of South Carolina Press, Columbia, pp. 173–188.
- Reynolds, P.D., 2002. The Scaphopoda. *Adv. Mar. Biol.*, 42: 135–234.
- Rice, A.L., Tyler, P.A. and Paterson, G.L.J., 1992. The pennatulid *Kophobelemnion stelliferum* (Cnidaria: Octocorallia) in the Porcupine Seabight (North-east Atlantic Ocean). *J. Mar. Biol. Assoc. UK*, 72: 417–434.
- Rokop, F.J., 1974. Reproductive patterns in the deep-sea benthos. *Science*, 186: 743–745.
- Rokop, F.J., 1977a. Seasonal reproduction of the brachiopod *Frieleia halli* and the scaphopod *Cadulus californicus* at bathyal depths in the deep sea. *Mar. Biol.*, 43: 237–246.
- Rokop, F.J., 1977b. Patterns of reproduction in the deep-sea benthic crustaceans: a reevaluation. *Deep-Sea Res.*, 24: 683–691.
- Rokop, F.J., 1979. Year-round reproduction in the deep-sea bivalve molluscs. In: S.E. Stancyk (Editor), *Reproductive Ecology of Marine Invertebrates*. University of South Carolina Press, pp. 189–198.
- Rouse, G.W. and Jamieson, B.G.M., 1987. An ultrastructural study of the spermatozoa of the polychaetes *Eurythoe complanata* (Amphinomidae), *Clymenella* sp. and *Micromaldane* sp. (Maldanidae) with definition of sperm types in relation to reproductive biology. *J. Submicrosc. Cytol.*, 19: 573–584.
- Rowe, F.W.E., Baker, A.N. and Clark, H.E.S., 1988. The morphology, development and taxonomic status of *Xyloplax* Baker, Rowe and Clark 1986 (Echinodermata, Concentricycloidea) with the description of a new species. *Proc. R. Soc. London Ser. B*, 233: 431–459.
- Ruff, R.E., 1991. A new species of *Bathynoe* (Polychaeta: Polynoidae) from the northeast Pacific Ocean commensal with two species of deep-water asteroids. *Ophelia*, Supplement 5: 219–230.
- Ruff, R.E. and Brown, B., 1989. A new species of *Euchone* (Polychaeta: Sabellidae) from the north-west Atlantic with comments on ontogenetic variability. *Proc. Biol. Soc. Wash.*, 102: 753–760.
- Run, J.-Q., Chen, C.-P., Chang, K.-H. and Chia, F.-S., 1988. Mating behaviour and reproductive cycle of *Archaster typicus* (Echinodermata: Asteroidea). *Mar. Biol.*, 99: 247–253.
- Russell, D.E., 1987. *Paedampharete acutiseriis*, a new genus and species of Ampharetidae (Polychaeta) from the North Atlantic HEBBLE area, exhibiting progenesis and broad intraspecific variation. *Bull. Biol. Soc. Wash.*, 7: 140–151.
- Sanders, H.L., 1977. Evolutionary ecology and the deep-sea benthos. The changing scene in natural sciences, 1776–1976. *Acad. Nat. Sci. Spec. Publ.*, 12: 223–243.
- Sanders, H.L., 1979. Evolutionary ecology and life history patterns in the deep sea. *Sarsia*, 64: 1–7.
- Sanders, H.L. and Allen, J.A., 1973. Studies on deep-sea Protobranchia (Bivalvia); prologue and Pristiglomidae. *Bull. Mus. Comp. Zool. Harvard*, 145: 237–262.
- Sanders, H.L. and Grassle, J.F., 1971. The interactions of diversity, distribution and mode of reproduction among major groupings of the deep-sea benthos. *Proceedings of the Joint Oceanographic Assembly (Tokyo, 1970)*, pp. 260–262.
- Sanders, H.L. and Hessler, R.R., 1969. Ecology of the deep-sea benthos. *Science*, 163: 1419–1424.
- Schaffer, W.M., 1974. Selection for optimal life histories: the effects of age structure. *Ecology*, 55: 291–303.
- Schein, E., 1989. Pectinidae (Mollusca, Bivalvia) bathyaux et abyssaux des campagnes BIOGAS (Golf de Gascogne). Systematique et biogéographique. *Ann. Inst. Oceanogr. Paris*, 65: 59–129.
- Scheltema, A.H., 1987. Reproduction and rapid growth in a deep-sea aplacophoran mollusc, *Prochaetoderma yongei*. *Mar. Ecol. Prog. Ser.*, 37: 171–180.
- Scheltema, R.S., 1972. Reproduction and dispersal of bottom dwelling deep-sea invertebrates: a speculative summary. In: R.W. Bauer (Editor), *Barobiology and the Experimental Biology of the Deep Sea*. School of Public Health, University of North Carolina, Chapel Hill, pp. 56–68.
- Scheltema, R.S., 1994. Adaptations for reproduction among deep-sea benthic molluscs: an appraisal of the existing evidence. In: C.M. Young and K.J. Eckelbarger (Editors), *Reproduction, Larval Biology and Recruitment of the Deep-Sea Benthos*. Columbia University Press, New York, pp. 44–75.
- 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.*, 17: 193–199.
- Schroeder, P.C. and Hermans, C.O., 1975. Annelida: Polychaeta. In: A.C. Giese and J.S. Pearse (Editors), *Reproduction of Marine Invertebrates, Vol. III: Annelids and Echiurans*. Academic Press, New York, pp. 1–213.
- Selenka, E., 1885. Gephyrea. *Reports of the Scientific Research of the Voyage of HMS Challenger, Zoology*, 13: 1–14. 4 Plates.
- Sewell, M.A. and Young, C.M., 1997. Are echinoderm egg size distributions bimodal? *Biol. Bull.*, 193: 297–305.
- Sewell, M.A., Tyler, P.A., Young, C.M. and Conand, C., 1998. Ovarian development in the class Holothuroidea: a reassessment of the “tubule recruitment model”. *Biol. Bull.*, 192: 17–26.
- Simroth, H., 1897. Die Brachiopoden der Plankton-Expedition. *Ergeb. Plankton-Exped.*, Bd. ii: 1–19.
- Sladen, W.P., 1889. Asteroidea. *Reports of the Scientific Research of the Voyage of HMS Challenger, Zoology*, 30: 1–893. 118 Plates.
- Smith, C.R. and Hessler, R.R., 1987. Colonization and succession in deep-sea ecosystems. *Trend Ecol. Evol.*, 2: 359–363.
- Snelgrove, P.V.R., Grassle, J.F. and Petrecca, R.F., 1992. The role of food patches in maintaining high deep-sea diversity: field experiments with hydrodynamically unbiased colonization trays. *Limnol. Oceanogr.*, 37: 1543–1550.
- Snelgrove, P.V.R., Grassle, J.F. and Petrecca, R.F., 1994. Macrofaunal response to artificial enrichments and depressions in a deep-sea habitat. *J. Mar. Res.*, 52: 345–369.
- Southward, E.C. and Coates, K.A., 1985. Sperm masses and sperm transfer in a vestimentiferan, *Ridgeia piscesae* Jones, 1985 (Pogonophora: Obturata). *Can. J. Zool.*, 67: 2776–2781.
- Spengel, J.W., 1932. *Planctosphaera pelagica*. *Sci. Results 'Michael Sars' North Atlantic Deep-Sea Exped.*, 5: 1–27.
- Starr, M., Himmelman, J.H. and Therriault, J.C., 1990. Direct coupling of marine invertebrate spawning with phytoplankton blooms. *Science*, 247: 1071–1074.
- Starr, M., Therriault, J.C., Conan, G.Y., Comeau, M. and Robichaud, G., 1994. Larval release in a sub-euphotic zone invertebrate triggered by sinking phytoplankton particles. *J. Plankton Res.*, 6: 1137–1147.

- Stearns, S.C., 1976. Life-history tactics: a review of the ideas. *Q. Rev. Biol.*, 51: 3–47.
- Steel, E.A., 1961. Some observations on the life history of *Asellus aquaticus* (L) and *Asellus meridianus* Racovitza (Crustacea: Isopoda). *Proc. Zool. Soc. London*, 137(1): 71–87.
- Stein, D.L. and Percy, W.G., 1982. Aspects of the reproduction, early life history, and biology of macrourid fishes off Oregon, U.S.A. *Deep-Sea Res.*, 29A: 1313–1329.
- Strathmann, R.R., 1974. The spread of sibling larvae of sedentary marine invertebrates. *Am. Nat.*, 108: 29–44.
- Strathmann, R.R., 1978. The evolution and loss of feeding larval stages of marine invertebrates. *Evolution*, 32: 894–906.
- Strathmann, R.R., 1985. Feeding and non-feeding larval development and life-history evolution in marine invertebrates. *Annu. Rev. Ecol. Syst.*, 16: 339–361.
- Strathmann, R.R., 1993. Hypotheses on the origins of marine larvae. *Annu. Rev. Ecol. Syst.*, 24: 89–117.
- Strathmann, R.R. and Strathmann, M.F., 1982. The relation between adult size and brooding in marine invertebrates. *Am. Nat.*, 119: 91–101.
- Sulkin, S.D. and Van Heukelem, W.F., 1980. Ecological and evolutionary significance of nutritional flexibility in planktotrophic larvae of the deep sea red crab *Geryon quinquegens* and the stone crab *Menippe mercenaria*. *Mar. Ecol. Prog. Ser.*, 2: 91–95.
- Sumida, P.Y.G., Tyler, P.A., Lampitt, R.S. and Gage, J.D., 2000. Reproduction, dispersal and settlement of the bathyal ophiuroid *Ophiocten gracilis* in the NE Atlantic Ocean. *Mar. Biol.*, 137: 623–630.
- Thistle, D. and Eckman, J.E., 1990. The effect of a biologically produced structure on the benthic copepods of a deep-sea site. *Deep-Sea Res.*, 37: 541–554.
- Thomson, C.W., 1878. Notice of some peculiarities in the mode of propagation of certain echinoderms of the Southern Sea. *J. Linn. Soc. London*, 13: 55–79.
- Thorson, G., 1946. Reproduction and larval development of Danish marine bottom invertebrates. *Medd. Dan. Fisk. Havunders. Ser. Plankton*, 4: 1–523.
- Thorson, G., 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.*, 25: 1–45.
- Todd, C.D., 1986. Reproductive strategies of north temperate rocky shore invertebrates. In: P.G. Moore and R. Seed (Editors), *The Ecology of Rocky Coasts*. Columbia University Press, New York, pp. 203–219.
- Tso, S.F. and Mok, H.K., 1991. Development, reproduction and nutrition of the giant isopod *Bathynomus doederleini* Ortman, 1894 (Isopoda, Flabellifera, Cirolanidae). *Crustaceana*, 61: 141–154.
- Turekian, K.K., Cochran, D.P., Kharkar, D.P., Cerrato, R.M., Vaisnys, J.R., Sanders, H.L., Grassle, J.F. and Allen, J.A., 1975. Slow growth rate of deep-sea clam determined by ²²⁸Ra chronology. *Proc. Natl. Acad. Sci. USA.*, 180: 2829–2832.
- Turekian, K.K., Cochran, J.K. and Nozaki, Y., 1979. Growth rate of a clam from the Galapagos hot spring field using natural radionuclide ratios. *Nature*, 280: 385–387.
- Turner, R.D., 1973. Wood-boring bivalves, opportunistic species in the deep sea. *Science*, 180: 1377–1379.
- Turner, R.D., 1977. Wood, mollusks, and deep-sea food chains. *Bull. Am. Malacol. Union*, (1976): 13–19.
- Tyler, P.A., 1988. Seasonality in the deep sea. *Oceanogr. Mar. Biol. Annu. Rev.*, 26: 227–258.
- Tyler, P.A., 1995. Conditions for the existence of life at the deep-sea floor: an update. *Oceanogr. Mar. Biol. Annu. Rev.*, 33: 221–244.
- Tyler, P.A. and Billett, D.S.M., 1985. The life history biology of *Peniagone azorica* and *P. diaphana* (Echinodermata: Holothurioidea) from the NE Atlantic. *Mar. Biol.*, 89: 71–81.
- Tyler, P.A. and Billett, D.S.M., 1987. The reproductive ecology of elapsipodid holothurians from the N.E. Atlantic. *Biol. Oceanogr.*, 5: 273–296.
- Tyler, P.A. and Dixon, D.R., 2000. Temperature/pressure tolerance of the first larval stage of *Mirocaris fortunata* from Lucky Strike hydrothermal vent field. *J. Mar. Biol. Assoc. UK*, 80: 739–740.
- Tyler, P.A. and Gage, J.D., 1980. Reproduction and growth in the deep-sea brittlestar *Ophiura ljunghmani* (Lyman). *Oceanol. Acta*, 3: 177–185.
- Tyler, P.A. and Gage, J.D., 1982. *Ophiopluteus ramosus* the larval form of *Ophiocten gracilis* (Echinodermata: Ophiuroidea). *J. Mar. Biol. Assoc. UK*, 62: 485–486.
- Tyler, P.A. and Gage, J.D., 1983. The reproductive biology of *Ypsilothuria talismani* (Holothuroidea: Dendrochirota) from the N.E. Atlantic. *J. Mar. Biol. Assoc. UK*, 63: 609–616.
- Tyler, P.A. and Gage, J.D., 1984a. Seasonal reproduction of *Echinus affinis* (Echinodermata: Echinoidea) in the Rockall Trough, northeast Atlantic Ocean. *Deep-Sea Res.*, 31: 387–402.
- Tyler, P.A. and Gage, J.D., 1984b. The reproductive biology of echinothuriid and cidarid sea urchins from the deep sea (Rockall Trough, North-East Atlantic Ocean). *Mar. Biol.*, 80: 63–74.
- Tyler, P.A. and Pain, S.L., 1982a. The reproductive biology of *Plutonaster bifrons*, *Dytaster insignis* and *Psilaster andromeda* (Asteroidea: Astropectinidae) from the Rockall Trough. *J. Mar. Biol. Assoc. UK*, 62: 869–887.
- Tyler, P.A. and Pain, S.L., 1982b. Observations of gametogenesis in the deep-sea asteroids *Paragonaster subtilis* and *Pseudarchaster parelii* (Phanerozoia: Goniasteridae). *Int. J. Invertebr. Reprod.*, 5: 269–272.
- Tyler, P.A. and Young, C.M., 1993. Reproduction in marine invertebrates in ‘stable’ environments. *Invertebr. Reprod. Dev.*, 22: 185–192.
- Tyler, P.A. and Young, C.M., 1999. Reproduction and dispersal at vents and cold seeps. *J. Mar. Biol. Assoc. UK*, 79: 193–208.
- Tyler, P.A., Grant, A., Pain, S.L. and Gage, J.D., 1982a. Is annual reproduction in deep-sea echinoderms a response to variability in their environment? *Nature*, 300: 747–749.
- Tyler, P.A., Pain, S.L. and Gage, J.D., 1982b. The reproductive biology of the deep-sea asteroid *Bathybiaster vexillifer*. *J. Mar. Biol. Assoc. UK*, 62: 57–69.
- Tyler, P.A., Pain, S.L., Gage, J.D. and Billett, D.S.M., 1984. The reproductive biology of deep-sea forcipulate seastars (Asteroidea: Echinodermata) from the N.E. Atlantic Ocean. *J. Mar. Biol. Assoc. UK*, 64: 587–601.
- Tyler, P.A., Gage, J.D. and Billett, D.S.M., 1985a. Life-history biology of *Peniagone azorica* and *P. diaphana* (Echinodermata: Holothurioidea) from the north-east Atlantic Ocean. *Mar. Biol.*, 89: 71–81.
- Tyler, P.A., Muirhead, A., Billett, D.S.M. and Gage, J.D., 1985b. The reproductive biology of the deep-sea holothurians *Laetmogone violacea* and *Benthogone rosea* (Elasipodida: Holothurioidea). *Mar. Ecol. Prog. Ser.*, 23: 269–277.
- Tyler, P.A., Muirhead, A. and Colman, J.G., 1985c. Observations on continuous reproduction in large deep-sea epibenthos. In: P.E.

- Gibbs (Editor), *Proceedings of the Nineteenth European Marine Biology Symposium*. Cambridge University Press, Cambridge, pp. 223–330.
- Tyler, P.A., Billett, D.S.M. and Gage, J.D., 1987. The ecology and reproductive biology of *Cherbonniera utriculus* and *Molpadia blakei* from the N.E. Atlantic. *J. Mar. Biol. Assoc. UK*, 67: 385–397.
- Tyler, P.A., Harvey, R., Giles, L.A. and Gage, J.D., 1992a. Reproductive strategies and diet in deep-sea nuculanid protobranchs (Bivalvia: Nuculoidea) from the Rockall Trough. *Mar. Biol.*, 114: 571–580.
- Tyler, P.A., Young, C.M., Billett, D.S.M. and Giles, L.A., 1992b. Pairing behaviour, reproduction and diet in the deep-sea holothurian genus *Paroriza* (Holothuroidea: Synallactidae). *J. Mar. Biol. Assoc. UK*, 72: 447–462.
- Tyler, P.A., Eckelbarger, K.J. and Billett, D.S.M., 1994. Reproduction in the holothurian *Bathylotes natans* (Holothuroidea: Synallactidae) from bathyal depths in the northeast and western Atlantic. *J. Mar. Biol. Assoc. UK*, 74: 383–402.
- Tyler, P.A., Bronsdon, S.K., Young, C.M. and Rice, A.L., 1995. Ecology and gametogenic biology of the genus *Umbellula* (Pennatulacea) in the North Atlantic Ocean. *Int. Rev. Gesamten Hydrobiol.*, 80: 187–199.
- Underwood, A.J., 1974. On models for reproductive strategy in marine benthic invertebrates. *Am. Nat.*, 108: 874–878.
- Van Dover, C.L., 1994. In situ spawning of hydrothermal vent tubeworms (*Riftia pachyptila*). *Biol. Bull.*, 186: 134–135.
- Van Dover, C.L., 2000. *The Ecology of Deep-Sea Hydrothermal Vents*. Princeton University Press, Princeton, NJ, 424 pp.
- Van Dover, C.L. and Williams, A.B., 1991. Egg size in squat lobsters (Galatheoidea): constraint and freedom. In: A. Wenner and A. Kuris (Editors), *Crustacean Egg Production*. Balkema, Rotterdam, pp. 143–156.
- Van Dover, C.L., Factor, J.R., Williams, A.B. and Berg Jr., C.J., 1985. Reproductive patterns of decapod crustaceans from hydrothermal vents. *Bull. Biol. Soc. Wash.*, 6: 223–227.
- Van Dover, C.L., Trask, J., Gross, J. and Knowlton, A., 1999. Reproductive biology of free-living and commensal polynoid polychaetes at the Lucky Strike hydrothermal vent field (Mid-Atlantic Ridge). *Mar. Ecol. Prog. Ser.*, 181: 201–214.
- Van-Praët, M., 1990. Gametogenesis and the reproductive cycle in the deep-sea anemone *Paracalliactis stephensoni* (Cnidaria: Actiniaria). *J. Mar. Biol. Assoc. UK*, 70: 163–172.
- Van-Praët, M. and Duchateau, G., 1984. Mise en évidence chez une actinie abyssale (*Paracalliactis stephensoni*) d'un cycle saisonnier de reproduction. *C. R. Acad. Sci.*, 299: 687–690.
- Van-Praët, M., Rice, A.L. and Thurston, M.H., 1990. Reproduction in two deep-sea anemones (Actiniaria); *Phelliactis hertwigi* and *P. robusta*. *Prog. Oceanogr.*, 24: 207–222.
- Vance, R.R., 1973. On reproductive strategies in marine benthic invertebrates. *Am. Nat.*, 107: 339–352.
- von Kölliker, A., 1880. Pennatulida. *Reports of the Scientific Research of the Voyage of HMS Challenger*, Zoology, 1(2): 1–41. 11 Plates.
- von Willemoes-Suhm, R., 1876. Preliminary report to Prof. Wyville Thomson, F.R.S., director of the civilian scientific staff, on observations made during the earlier part of the voyage of H.M.S. Challenger. *Proc. R. Soc. London*, 24: 569–585.
- Vrijenhoek, R.C., 1997. Gene flow and genetic diversity in naturally fragmented metapopulations of deep-sea hydrothermal vent animals. *J. Hered.*, 88: 285–293.
- Wenner, E.L., 1978. Some aspects of the biology of deep-sea lobsters of the family Polychelidae (Crustacea, Decapoda) from the Western North Atlantic. *Fish. Bull.*, 77: 435–444.
- Wenner, E.L., 1980. Notes on the biology of a deep-sea penaeid, *Benthescymus bartletti* Smith. *Crustaceana*, 38: 290–294.
- Williams, G.C., 1966. *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. Princeton University Press, Princeton, NJ, 307 pp.
- Williamson, D.I., 1982. The larval characters of *Dorhynchus thomsoni* Thomson (Crustacea, Brachyura, Majoidea) and their evolution. *J. Nat. Hist.*, 16: 727–744.
- Wilson, E.O., 1975. *Sociobiology: The New Synthesis*. Belknap Press, Cambridge, MA, 697 pp.
- Wilson, G.D.F., 1981. Taxonomy and postmarsupial development of a dominant deep-sea erysopid isopod. *Proc. Biol. Soc. Wash.*, 94: 276–294.
- Wilson, W.H., 1991. Sexual reproductive modes in polychaetes: classification and diversity. *Bull. Mar. Sci.*, 48: 500–516.
- Witte, U., 1996. Seasonal reproduction in deep-sea sponges triggered by vertical particle flux? *Mar. Biol.*, 124: 571–581.
- Wolff, T., 1956a. Crustacea Tanaidacea from depths exceeding 6000 m. *Galathea Rep.*, 2: 187–241.
- Wolff, T., 1956b. Isopoda from depths exceeding 6000 m. *Galathea Rep.*, 2: 85–167.
- Wolff, T., 1962. The systematics and biology of bathyal and abyssal isopoda asellota. *Galathea Rep.*, 6: 1–320. 19 Plates.
- Wray, G.A., 1995. Evolution of larvae and developmental modes. In: L.R. McEdward (Editor), *Ecology of Marine Invertebrate Larvae*. CRC Press, Boca Raton, FL, pp. 413–447.
- Wray, G.A. and Raff, R.A., 1991. The evolution of developmental strategy in marine invertebrates. *Trend Ecol. Evol.*, 6: 45–50.
- Young, C.M., 1994a. A tale of two dogmas: the early history of deep-sea reproductive biology. In: C.M. Young and K.J. Eckelbarger (Editors), *Reproduction, Larval Biology and Recruitment of the Deep-Sea Benthos*. Columbia University Press, New York, pp. 1–25.
- Young, C.M., 1994b. The biology of external fertilization in deep-sea echinoderms. In: C.M. Young and K.J. Eckelbarger (Editors), *Reproduction, Larval Biology and Recruitment of the Deep-Sea Benthos*. Columbia University Press, New York, pp. 179–200.
- Young, C.M., 1999. Synchrony and sociality: breeding strategies in constant and variable environments. In: M. Whitfield, J. Matthews and C. Reynolds (Editors), *Aquatic Life Cycle Strategies: Survival in a Variable Environment*. Marine Biological Association of the United Kingdom, Plymouth, pp. 1–14.
- Young, C.M. and Cameron, J.L., 1987. Laboratory and in situ flotation rates of lecithotrophic eggs from the bathyal echinoid *Phormosoma placenta*. *Deep-Sea Res.*, 34: 1629–1639.
- Young, C.M. and Cameron, J.L., 1989. Developmental rate as a function of depth in the bathyal echinoid *Linopneustes longispinus*. In: J.S. Ryland and P.A. Tyler (Editors), *Reproduction, Genetics and Distributions of Marine Organisms*. Olsen and Olsen, Fredensborg, Denmark, pp. 225–234.
- Young, C.M. and George, S.B., 2000. Larval development of the tropical deep-sea echinoid *Aspidodiadema jacobyi*: phylogenetic implications. *Biol. Bull.*, 198: 387–395.
- Young, C.M. and Tyler, P.A., 1993. Embryos of the deep-sea echinoid

- Echinus affinis* require high pressure for development. *Limnol. Oceanogr.*, 38: 178–181.
- Young, C.M. and Vázquez, E., 1995. Morphology, larval development, and distribution of *Bathypora feminalba* n. sp. (Asciacea: Pyuridae), a deep-water ascidian from the fjords and sounds of British Columbia. *Invertebr. Biol.*, 114: 89–106.
- Young, C.M., Cameron, J.L. and Eckelbarger, K.J., 1989. Extended pre-feeding period in a planktotrophic echinoid larva from the bathyal zone of the deep sea. *J. Mar. Biol. Assoc. UK*, 69: 695–702.
- Young, C.M., Tyler, P.A., Cameron, J.L. and Rumrill, S., 1992. Seasonal breeding aggregations in low-density populations of the bathyal echinoid *Stylocidaris lineata*. *Mar. Biol.*, 113: 603–612.
- Young, C.M., Tyler, P.A. and Gage, J.D., 1996a. Vertical distribution correlates with pressure tolerances of early embryos in the deep-sea asteroid *Plutonaster bifrons*. *J. Mar. Biol. Assoc. UK*, 76: 749–757.
- Young, C.M., Vázquez, E., Metaxas, A. and Tyler, P.A., 1996b. Embryology of vestimentiferan tube worms from deep-sea methane/sulfide seeps. *Nature*, 381: 514–515.
- Young, C.M., Devin, M.G., Jaekle, W.B., Ekaratne, S.U.K. and George, S.B., 1996c. The potential for ontogenetic vertical migration in larvae of deep-sea echinoids. *Oceanol. Acta*, 19: 263–271.
- Young, C.M., Ekaratne, S.U.K. and Cameron, J.L., 1997. Thermal tolerances of embryos and planktotrophic larvae of *Archaeopneustes hystrix* (A. Agassiz) (Spatangoidea) and *Stylocidaris lineata* (Mortensen) (Cidaroida), bathyal echinoids from the Bahamian Slope. *J. Exp. Mar. Biol. Ecol.*, 223: 65–76.
- Young, C.M., Sewell, M.A., Tyler, P.A. and Metaxas, A., 1999. Biogeographic and bathymetric ranges of Atlantic deep-sea echinoderms and ascidians: the role of larval dispersal. *Biodiv. Conserv.*, 6: 1507–1522.
- Zal, F.D., Desbruyères, D. and Jouin-Toulmond, C., 1994. Sexual dimorphism in *Paralvinella grasslei*, a polychaete annelid from deep-sea hydrothermal vents. *C. R. Acad. Sci. Ser. C*, 317: 42–48.
- Zal, F.D., Jollivet, D., Chevaldonné, P. and Desbruyères, D., 1995. Reproductive biology and population structure of the deep-sea hydrothermal vent worm *Paralvinella grasslei* (Polychaeta: Alvinellidae) at 13°N on the East Pacific Rise. *Mar. Biol.*, 122: 637–648.
- Zardus, J.D., 2002. Biology of protobranch bivalves. *Adv. Mar. Biol.*, 42: 1–65.
- Zirwas, C., 1910. *Die Isopoden der Nordsee*. Inaug.-Dissert. Univ. Kiel, pp. 71–118.
- Zottoli, R., 1983. *Amphisamytha galapagensis*, a new species of ampharetid polychaete from the vicinity of abyssal hydrothermal vents in the Galapagos Rift, and the role of this species in rift ecosystems. *Proc. Biol. Soc. Wash.*, 96: 379–391.