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LIFESTYLES OF THE SPECIES-RICH AND FABULOUS: THE DEEP-SEA CRUSTACEANS

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Abstract

The lifestyles of deep-sea crustaceans that live below 200 m differ from their relatives in shallower waters. Crustacean groups in this realm range from megafaunal decapods through dominant macrofaunal peracarids to tiny meiofaunal-sized ostracodes and harpacticoid copepods. Their morphological adaptations may differ little from those found at shallower depths, but certain taxa are highly transformed by the selective environment of the abyss. Eyes and pigmentation are absent and antennae and legs are typically longer, sometimes exceeding 3 or more body lengths. Deep-sea crustaceans also have more spines on their body, which might reduce predation, but may also have other unknown uses such as changing their hydrodynamic profile. Among the peracarids, the isopods achieve the highest taxonomic and morphological diversity, often with strange shapes whose functional adaptations we cannot begin to determine. Although some deep-sea crustaceans show a comparative trend towards larger body size than in shallow water (deep-sea gigantism), because the smaller taxa are so abundant in the deep-sea, abyssal faunas have a smaller size on average than shallower faunas. Because the abyss is food-limited, crustaceans rely on carnivory or scavenging, and are adapted to avoid predation. Reproduction of the deep-sea crustaceans typically is accomplished through brooding and direct development or with lecithotrophic larvae, although a few taxa retain epipelagic larvae. Because deep-sea taxa live at low population densities, successful reproduction may include highly motile males that are presumably adapted for finding females. Many regions of the deep-sea, being far from the surface atmosphere, also have low oxygen availability and may trend toward dysoxia in areas where the pelagic oxygen minimum zone intersects the sea floor. In the face of limited food supplies and low oxygen levels, crustaceans have adapted their morphology and their feeding and reproductive behaviors to the extent that certain taxa thrive. Similar adaptations are seen in other deep-sea invertebrates, suggesting that the environment of the abyss has a significant impact on the lifestyles of all organisms that live there.

DEEP-SEA CRUSTACEANS

Readers may have encountered a few deep-sea crustaceans in their browsing of the literature, but these are probably idiosyncratic examples, such as giant deep-sea isopods in the genus *Bathynomus* or perhaps the "Yeti Crab" *Kiwa hirsuta*. The entire gamut of deep-sea crustaceans to be encountered is truly amazing, each with its own unique characteristics. This chapter provides an overview of the types of animals present and how they cope with the unusual challenges presented by deep-sea environments. The lifestyles of crustaceans in general are covered in other chapters, so habits unique to the deep sea are discussed here. The discussion employs deep-sea isopods as examples, not only because of our familiarity with them, but also because the asellotan isopods have evolved in the deep sea, and many families are endemic to that realm (Hessler and Thistle 1975, Lins et al. 2012). To be sure, most major crustacean groups are found in the deep sea, although a few are unusual both in morphology and lifestyle.

Definitions and Characteristics of Deep Sea

First, we need to know what is meant by the "deep sea." This question is complicated because many crustaceans and other animals show polar emergence or tropical submergence (Menzies and George 1969, Hessler 1970a, Hessler and Thistle 1975, Hall and Thatje 2009). Recently, we have discovered that even the tropics provide no real barriers to emergent deep-sea taxa (Wilson 2006). Setting these complications aside for the moment, we can use a physical benchmark as a guide. Some biologists set the deep-sea boundary at 1,000 meters because this is where light becomes nearly extinct in the open ocean. A practical depth of 200 m can be based on the distributions of deep-sea animals and long experience with taxa (Ekman 1953), especially in the North Atlantic Ocean (Gage and Tyler 1991). Light penetration near coastlines is limited by surface productivity and terriginous sediments, so light becomes attenuated fairly quickly. This upper limit is also below the usual permanent thermocline near the coast, which is another important physical parameter for deep-sea animals. As already implied, light and temperature are two important features of the deep sea. Other important parameters include organic matter and hydrodynamics. The sheer size of the deep sea is a major factor in the evolution of deep-sea faunas. General reviews may be found in Gage and Tyler (1991) and Rex and Etter (2011).

Types of Crustaceans in the Deep Sea

The entire range of lifestyles mentioned in other chapters of this volume is also present in the deep sea, so much of that detail applies here, too. Parasitic crustaceans and those living around hydrothermal vents are covered in other chapters, so these will be mentioned only in passing. The crustaceans that live in the deep sea, the subject of this chapter, include inhabitants of the vast benthic realm (benthos) and their relatives that live in the water column (nekton). The benthos is covered in this chapter, although a few pelagic forms are mentioned in relation to the benthos.

Benthos

Among the Crustacea, the deep sea is the domain of peracarid crustaceans at the macrofaunal scale (too small for most photographs, but with a body length larger than 0.25 mm) and ostracods and harpacticoid copepods at the meiofaunal scales (generally smaller than 0.25 mm).

The Isopoda (Fig. 11.1) are common in deep-sea samples and are one of the numerically dominant crustacean taxa in benthic assemblages (Sanders et al. 1965, Hessler and Jumars 1974). Many
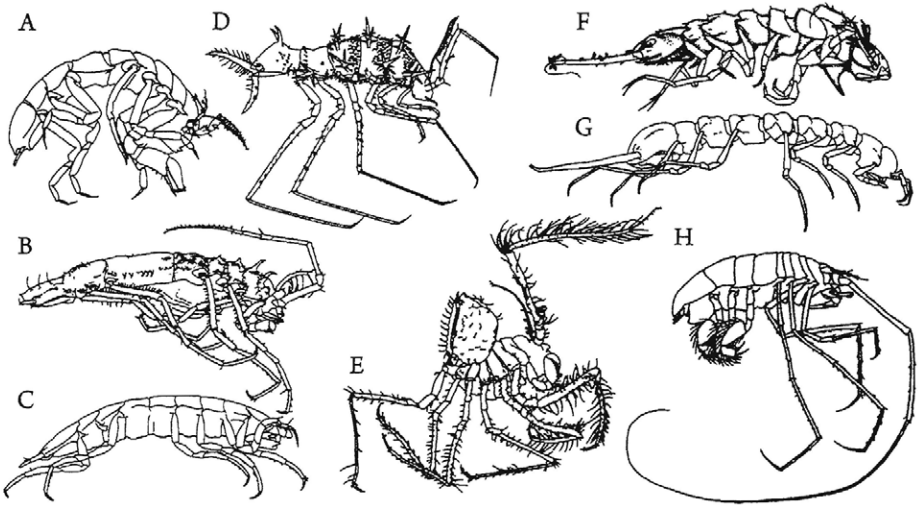
Fig. 11.1.
Abyssal isopods. Lateral views of several deep-sea *Asellota* to show the range of morphological diversity; most taxa differ considerably from related families found in shallow water. (A) *Chelator insignis* (Hansen 1916), (B) *Heteromesus ctenobasius* (Cunha and Wilson 2006), (C) *Xostylus* sp., (D) *Dendromunna compsa* (Lincoln and Boxshall 1983), (E) *Thylakogaster lobotourus* (Wilson and Hessler 1974), (F) *Macrostylis roaldi* (Riehl and Kaiser 2012), (G) *Vemathambema argentinensis* (Malyutina et al. 2001), and (H) *Eurycope cornuta* (Sars 1864). Modified from original publications, except for A, from Hessler 1970b; C, undescribed species from the Weddell Sea; E, from Cunha and Wilson 2003; and H, from Wilson and Hessler 1980.

of the endemic deep-sea families have no relatives in shallow water and are likely to have evolved in situ (Hessler et al. 1979). Although multiple independent colonizations of the deep sea are likely (Wilson 1981, Hessler and Wilson 1983, Lins et al. 2012), those taxa in many cases are taxonomically distinct from their closest shallow-water relatives.

The Tanaidacea also dominate deep-sea samples (Sanders et al. 1965, Hessler and Jumars 1974). The suborders Apseudomorpha and Tanaidomorpha occur both in the deep sea and shallow water, but the Neotanaidomorpha (Gardiner 1975) are restricted to the deep. Within the abundant and speciose Tanaidomorpha, those species that favor soft sediments are common in deep-sea samples (Larsen 2005), often exceeding isopods in abundance (Hessler and Jumars 1974, Larsen 2005). Amphipoda and Cumacea occur in deep-sea sediments but are much less abundant (Sanders et al. 1965, Hessler and Jumars 1974). The amphipods are much more evident as highly mobile scavengers (Britton and Morton 1994), although their real abundance in the sediments is substantially less than other crustaceans. Species of the rare deep-sea peracarid family Hirsutiidae (Jaume et al. 2006) have close relatives in anchialine caves. Little is known about their biology, although they are likely to live infaunally, similar to their tanaidacean relatives (Wilson 2009). Some authors have argued for a hypothetical link between the deep-sea and cavernicolous habitats (reviewed in Stock 1986), but evidence from misophrioid copepods (Boxshall and Jaume 1999, 2000) suggests that deep-water lineages that are also found in caves are the result of separate secondary colonization events.

The abundant and diverse copepods of the deep sea appear to live as they do in shallow water (Hicks and Coull 1983), and, indeed, some genera extend from shallow waters to the abyss (e.g., Veit-Köhler 2005). Among the copepods, the harpacticoids cannot be overlooked because their diversity is apparently immense (Fig. 11.2). The regional species richness of one basin, the northern

Gulf of Mexico, was estimated to be 2,200 species, which, if extrapolated to the area of the deep sea, gives a global species richness of 5.5×10^5 species (Baguley et al. 2006). Harpacticoids become relatively more abundant with increasing depth than do macrofauna (Thistle 2001), so the individual species are truly deep-sea organisms (Fig. 11.2).

The Ostracoda are common in meiofauna-sized samples in most places of the deep sea. They appear to have a lower diversity; for example, estimates for the Atlantic Ocean suggest a comparatively small number of 213 species (Dingle and Lord 1990). The Podocopida have been used extensively in palaeoceanographic studies owing to their calcareous shell (e.g., Benson et al. 1984, Cronin and Raymo 1997), thus, much of the information on this group comes from the stratigraphers rather than biologists. Like the harpacticoids, ostracods have congeners in shallow water (Neale 1988, Maddocks and Steinek 1987).

Decapod crustaceans (Fig. 11.3), although large and charismatic, are less important in deep-sea communities and occur primarily on the shelf and slope. The large malacostracans show declining diversity with depth (Hessler and Wilson 1983). Thalassinideans are thought to be restricted to waters shallower than 2,000 m owing to temperature tolerances (Dworschak 2000). Other decapod groups, however, are regularly encountered at greater depths. King crabs (Lithodidae) occur in excess of 4,000 m (Macpherson 1988), and parapagurid hermit crabs of the genus *Parapagurus* are found up to about 5,000 m (Lemaitre 1999). Some dendrobranchiate shrimps and brachyuran crabs, however, are found at hadal depths, the first being a spider crab, *Teratomaia*, collected from the Kermadec Trench by the *Galathea* expedition (Griffin and Tranter 1986), followed by more recent discoveries there of species of *Cerataspis* and *Benthesicymus* (Jamieson et al. 2009). A study of Decapoda from the southern Gulf of Mexico (Wicksten and Packard 2005) found that the greatest depths had few decapod species but that squat lobsters of the genus *Munidopsis* were diverse (25 species in the area) and common at most depths. In fact, the squat lobsters (Galatheoidea and Chirostyloidea) are the most frequently encountered anomurans in the deep sea, with more than 800 species worldwide (Baba et al. 2008). The average depth of occurrence is 588 m for chirostyloids (generally in association with corals) and 718 for galatheoids (generally free-living), although they can reach about 2,400 m and 5,400 m, respectively (Schnabel et al. 2011). The
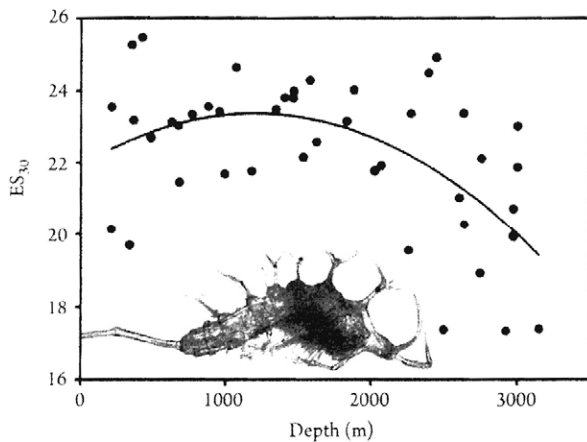

Fig. 11.2.
Harpacticoid copepods: depth distribution of species richness in the Gulf of Mexico, species expected in 30 randomly selected individuals from pooled replicate core samples. Harpacticoid insert is a species belonging to the family Anchorabolidae. Modified from Baguley et al. (2006), with permission from Elsevier; photo courtesy of D. Thistle.
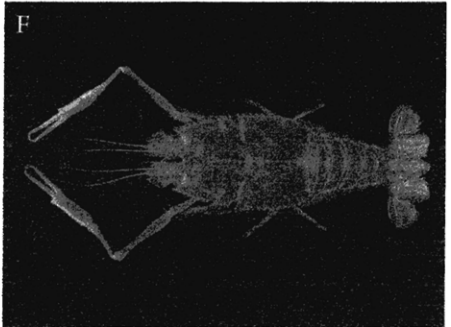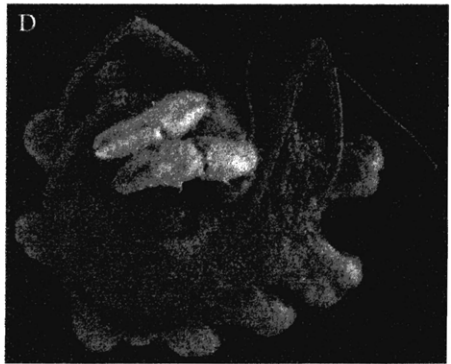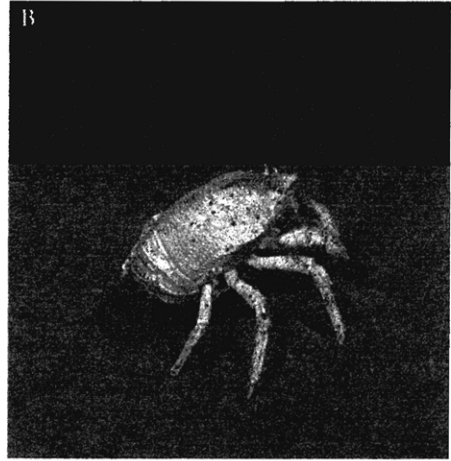
Fig. 11.3.
Deepwater decapods. (A) tanner crab (*Chionoecetes tanneri*); photo courtesy of Monterey Bay Aquarium Research Insitute (MBARI); (B) squat lobster (*Munidopsis albatrossae*); photo courtesy of MBARI; (C) king crab (*Paralomis* verrilli); photo courtesy of MBARI; (D) hermit crab (*Parapagurus latimanus* with zoanthid (*Epizoanthus* sp.), photo by S. Ahyong; (E) Clawed lobster (*Acanthacaris tenuimana*); photo courtesy of National Oceanic and Atmospheric Administration; and (F) blind lobster (*Polycheles amemiyai*); photo courtesy of T.Y. Chan. See color version of this figure in the centerfold.
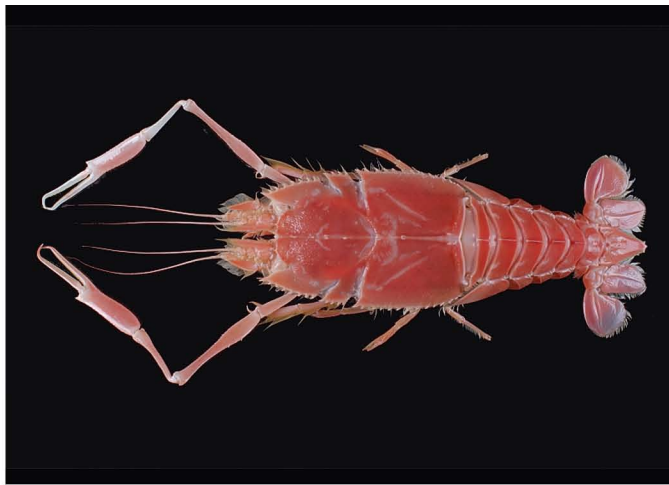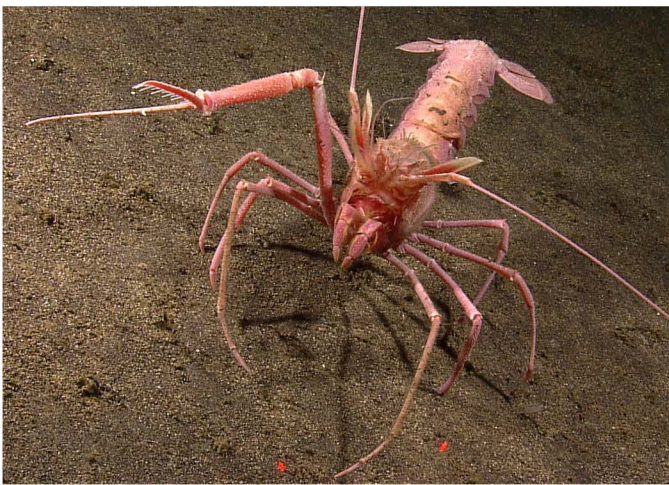
deep-sea endemic species of blind lobsters (Polychelidae), reaching depths of about 4,000 m (Galil 2000, Ahyong 2009), and deep-sea carrying crabs (Homolidae), reaching about 2,500 m (Guinot and Richer de Forges 1995), are relatively rare and few in number, with about 40 species and 70 species, respectively.

Stomatopoda are known from the deep sea but, being active predators, become rare into the abyss. The primary deep-water family, Bathysquillidae, is found between 200 and 1,500 m (Manning et al. 1990), although some members of the Squillidae regularly occur at slope depths as deep as 1,250 m (Ahyong 2013).

Barnacles are found on hard substrata and are limited to areas where the filter-feeding lifestyle is effective. More than 1,200 species of barnacles have been described from all depths, but mostly from shallow waters (Ahyong et al. 2011). When studied in detail, restricted regions like the deep sea around Taiwan can have nearly 20 species (Chan et al. 2008), and similar numbers are seen in New Zealand deep waters (Lörz et al. 2012). Leptostraca are rare in the deep sea and are limited to above 3,000 m as far as is known (Haney et al. 2001).

Some crustaceans are parasitic on crustaceans or other deep-sea species. Rhizocephalans might be parasitic on most deep-sea decapods and are common on king crabs and squat lobsters (Boyko and Williams 2011). The cryptoniscid isopods appear in deep-sea samples containing other peracarid crustaceans (we are uncertain which species they were infesting) and are hyperparasitic in some cases, such as *Liriopsis* living on a rhizocephalan host that infests the king crab *Paralomis* (Peresan and Roccatagliata 2005). Tantulocarida, whose adults are sometimes mistaken for cryptoniscids, infest deep-sea peracarids, sometimes at a high frequency (Boxshall and Lincoln 1987). Gnathiid isopods, ectoparasites of fishes, occur in the deep sea (Svavarsson 1999), but we have no information on host preferences among the suite of deep-sea fishes because pranizas (the juvenile state that infests fishes) have not been recorded from deep-sea fishes.

BIOLOGY

Morphological Adaptations

Inferring the adaptations of deep-sea crustaceans uses the logical process of deduction (Fitzhugh 2006) or hypothetical inference, where an explanatory theory is inferred based on patterns in the evidence. Because we have little empirical evidence for practically anything we might want to know about the behavior of deep-sea crustaceans, the function of a structure might be inferred from mechanical or hydrodynamic properties of morphology (e.g., Fig. 11.4). Once the structure is understood, a hypothesis might be inferred regarding the behavioral function of that morphology, although we may still not know the structure's biological role. Our hypotheses may seem plausible, but once behavioral evidence is available, we could be embarrassed by the discrepancy between theory and reality. A good example comes from a deep-sea isopod collected in shallow water in New Harbor, off McMurdo Sound in the Ross Sea, Antarctica. This animal, belonging to the genus *Notopais* (previously *Echinozone*) was originally thought to behave similarly to other Munnopsidae that swim with their last three walking legs (Hessler and Strömberg 1989, Wilson 1989, Hessler 1993). A substantial number of species of munnopsids are holopelagic (Osborn 2009). Indeed, *Notopais* has large paddle-like posterior legs, as do most other members of this family. Consequently, this genus was thought to be benthopelagic based on its apparent swimming equipment. At McMurdo Station, when the animal was placed in an aquarium with a soft sediment floor, we were astonished to see the animal use its large "swimming" legs to excavate a depression and push its wedge-shaped posterior into the sediment. When buried, only the long antennae and two pairs of walking legs
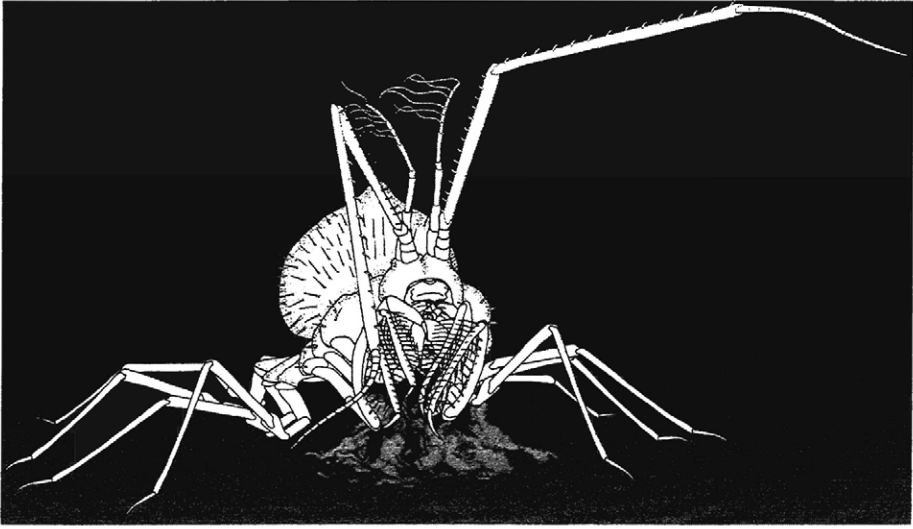
Fig. 11.4.
Thylakogaster on the deep-sea floor. An artist's impression of what one of the stranger asellotan isopods might look like in its natural environment. From G.D.F. Wilson.

protruded from a dimple in the sediment. *Notopais* did swim like other munnopsids, but only reluctantly when evicted from its sedimentary burrow (Hessler and Strömberg 1989) and then for only a few strokes. The isopod would quickly lose interest in swimming and drop back to the mud where it dug itself in. Clearly, theories based only on mechanics need corroborative behavioral evidence; they should not be used as evidence themselves.

   Although much of our information on deep-sea crustaceans is inferential or hypothetical, clear patterns emerge, and, in a few instances, we have direct evidence. Deep-sea crustaceans often have morphologies that seem bizarre to us, especially among the asellote isopods. One explanation might be perceptual—we are accustomed to the appearance of shallow-water animals, so those that live in an infrequently sampled environment may seem unfamiliar and strange. Another explanation might come from the absence of light. Because crustaceans have been released from the need for crypsis in visible wavelengths, they may have evolved shapes that maximize fitness for other adaptive modalities. The length of antennae sometimes exceeds 3–5 body lengths, as in the holopelagic Munnopsidae (Isopoda; Wilson 1982, Osborn 2009), but highly elongate appendages are also common among many other groups, such as the epibenthic families Dendrotionidae and Haplomunnidae (Wilson 1976). Eyes disappear with increasing depth in deep-sea crustaceans, and this occurs independently in many different lineages (Hessler and Wilson 1983). Associated with this is a loss of coloration of any sort, although crustaceans living in the bathyal zone (200–2,000 m) may retain red coloration (e.g., Fig 11.3), which is perceptually black at those depths.

   The presence of spines on the dorsal surface or elsewhere on the body is a recurring morphological theme in deep-sea benthic crustaceans. Deep-sea epibenthic groups seem to have members that are especially spiny, from decapods (e.g., Lithodidae) to the asellotan isopods (Fig. 11.1) and copepods (Fig. 11.2). We can only speculate what purpose the spines might have, although one might observe that the spines increase the effective size of an animal without the extra cost of growth. Spines in shallow-water taxa are correlated with inferred predation pressure (Wallerstein and Brusca 1982, Bollache et al. 2006). Although some authors suggest this is also true for deep-sea taxa, we have few empirical data to support it. Other likely means of predator avoidance are found

in the use of biocoenoses by hermit crabs that protect the soft pleon. Most species use empty gastropod shells, but others use scaphopods, hollow wood, or even zoanthid colonies (*Epizoanthus* spp.) in the case of several parapagurid species (Williams and McDermott 2004).

Certain crustaceans, especially asellotan isopods, have especially unusual anatomies. *Thylakogaster* (family Haplomunnidae; Wilson and Hessler 1974) is probably the most peculiar genus among the isopods: species in this genus have a spiny inflated pleon that is reflexed over the back of the body, combined with second and third legs that are elongate, curved, and form a basket of spinose setae underneath the mouth and first pereopods. Like many deep-sea isopods, the antennae are especially long, and the posterior legs are especially thin and elongated. Because these animals have not been seen alive in their natural environment, one can only speculate on their behavior, other than they are likely to be epibenthic, possibly using the basket of spines to process sediment for food items (Fig. 11.4). Related taxa are similarly strange: *Dendromunna* species (Dendrotionidae) have elongate limbs on a narrow tubular thorax that has lateral projecting tergites to attach the legs, with a dorsal surface furnished with mace-like spiny projections (Fig. 11.1D). Among the Munnopsidae, isopod species in the genera *Paropsurus* and *Bathyopsurus* are much larger than most deep-sea isopods (body length 30–60 mm, not including legs or antennae), with inflated natasomes (posterior thoracic somites and pleon in one unit) and paddle-like swimming legs that are rotated laterally. These animals are so odd that one was identified from a deep-sea photograph as a possible deep-sea arachnid (Thiel and Schriever 1989); since then, *Paropsurus* has become much better known, especially at sites near Monterey Bay, California, in the Eastern Pacific (Fig. 11.5).

Some taxa are obviously infaunal: macrostylid isopods have been observed to be excellent burrowers, tanaids are well known as tube dwellers, and deep-sea cumaceans are shallow burrowers that leave their anterior carapace projecting above the substratum. The latter two taxa have mostly the same morphology regardless of whether they occur in shallow or deep seas. Similarly, deep-sea thalassinideans (Gebiidea, Axiidea) have body plans that are identical to those of their shallow-water counterparts.

The benthic boundary layer in the deep-sea is less turbulent than in shallow-water habitats. As a consequence, epibenthic lifestyles are common, especially because the highest value nutrition can be sourced from only the upper few millimeters of the sea floor. Nevertheless, erosive current velocities at the seafloor in some regions might have multiple impacts on deep-sea animals. In areas subject to benthic storms that can reach velocities that erode the sea floor (Thistle et al. 1985), lifestyles shift from epifaunal to predominantly infaunal forms (Thistle and Wilson 1987, 1996).

Some decapods, especially those living in chemosynthetic environments (cold-seeps and hydrothermal vents), "farm" sulfur-oxidizing bacteria as food. Squat lobsters, such as *Kiwa* and *Shinkaia*, and some parapagurid hermit crabs have dense patches of setae on which bacteria are grown and regularly harvested (Goffredi et al. 2008, Tsuchida et al. 2011). For the recently discovered *Kiwa puravida*, these chemosynthetic bacteria are its main food source (Thurber et al. 2011).

Size Structure

Although a few giants are known, such as the frequently noted *Bathynomus* species or the numerically rare megafaunal decapods, most crustaceans in the deep sea are meiofaunal sized (below 250 microns) or at the scale of the macrofauna (modal sizes below 10 mm), similar to most other deep-sea fauna. Although adults might achieve centimeter sizes, juveniles are typically tiny and are barely outside the meiofaunal range (Thiel 1975).

Size has important consequences in abyssal habitats. Because the average deep-sea crustacean is small, it lives in a substantially different physical environment in the deep sea than in shallow water. At typically low temperatures in the abyss (<4°C), sea water is more viscous and dense than
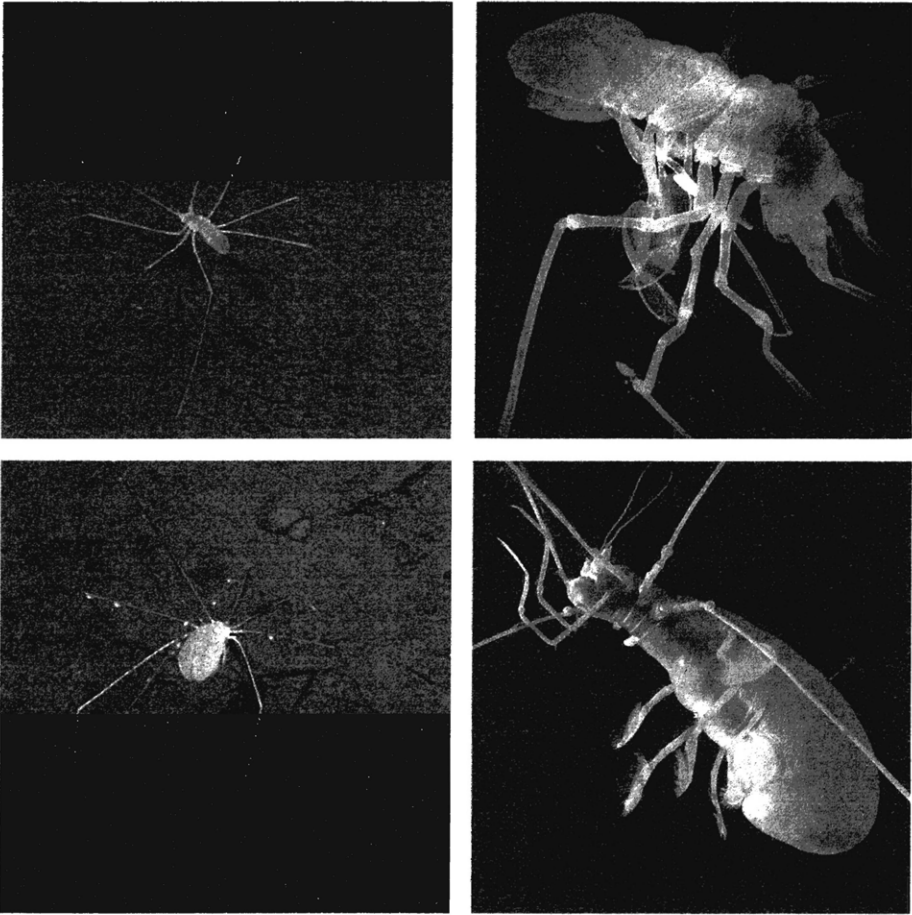
Fig. 11.5.
Benthopelagic isopods. Seafloor (left) and laboratory photographs (right) of two benthopelagic isopods found off the California coast: *Munnopsurus* (top) and *Paropsurus* (bottom). See color version of this figure in the centerfold. Photos courtesy of K. Osborn and MBARI.

in warmer waters. High viscosity combined with the small size of most deep-sea crustaceans would give them a low Reynolds number, which places substantial limits on rapid movements such as swimming (Vogel 1996, Yen 2013). Rapid swimming is possible but is energetically less favorable.

Small size would seem to be metabolically favorable for deep-sea organisms living in an environment where food availability is a large constraint on lifestyle. Although the typical approach to investigating this assertion is to compare sizes of animals from shallow and deep habitats within taxocenes, many deep-sea animals are not necessarily smaller than their relatives from shallow water. This is certainly true for the asellote isopods that dominate deep-sea macrofaunal crustacean assemblages (Wolff 1962) and for the numerically superabundant meiofaunal harpacticoid copepods and ostracods (Thiel 1975). In fact, Wolff (1962) found, in surveying size in larger genera of the Asellota ranging from shallow depths to the abyssal zone, a limited positive correlation between size and depth. Gigantism has been noted in many crustacean groups, such as mysids, euphausiids, decapods, tanaids, isopods, and amphipods (reviewed in Timofeev 2001). Nevertheless, the abundance of larger animals is significantly lower and decreases more rapidly than for groups of smaller animals, which results in a substantial decrease in average body size with depth (Thiel 1975, Rex et al. 2006).
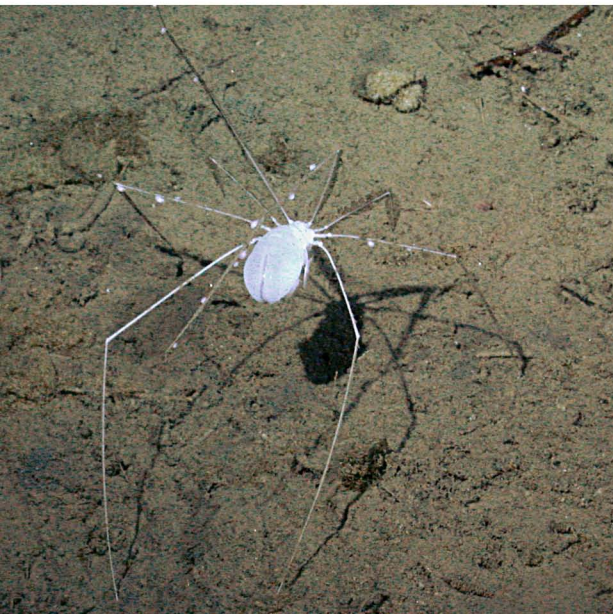
What Do Deep-sea Crustaceans Eat?

What is on the dinner table for a crustacean living in the abyss? For the larger crustaceans, this would mean other members of the fauna (Drazen et al. 2008) or falls of large animals (Smith and Baco 2003). The majority of deep-sea crustaceans, however, have been assumed to be deposit feeders (Thiel 1979, Hessler and Jumars 1974, Flach and Heip 1996, Thistle 2003), which implies that the animals ingest sediment directly and extract nutrients as the material passes through the gut. Menzies (1962) summarized that 90% of the isopods fed "wholly or in part" on bottom deposits. Certainly, when deep-sea isopods are examined, sediment appears in the gut, which leads to the inference that they are grazing on the surface sediment for nutrition. Deep-sea sediments are typically low in labile organic compounds (Gage 2003), so eating sediment randomly is not a good strategy. Most biologists think that feeding activity is mostly limited to the sediment surface that accumulates material of variable food quality falling from the water column. The rain of material from the water column, however, is mostly of low quality owing to remineralization processes that take place during transit from the sea surface to the deep seafloor. The average organic carbon content of the surface sediments is closely related to depth; this relationship is sufficiently good that investigators have used surface productivity and depth to calculate available organic carbon at the seafloor (Biggs et al. 2608, Wei et al. 2010). Most detrital-feeding crustaceans select relatively high organic content particles that have recently settled to the sea floor (Gage 2003). In some instances, the particles settle in dense aggregations owing to surface bursts in productivity. Most research has shown that large megafaunal organisms like echinoderms (Gage 2003) or testate protozoans (Gooday et al. 1993) benefit from phytodetritus accumulations, but, in one instance, large populations of spider crabs (presumed to be *Encephaloides armstrongi*) off the coast of Oman live off phytoplankton-derived detritus to the extent that they (along with an abundant brittlestar) deplete organic matter from the sediments (Smallwood et al. 1999). Interestingly, these spider crabs also live in or around the oxygen minimum zone (OMZ) associated with the high detrital input from the water column.

Much of the biomass on the seafloor has sediment surrounding it in the form of protistans. Snider et al. (1984) observed that, on a volumetric basis, deep-sea meiofauna consists mostly of protistans such as agglutinating foraminiferans and komokiaceans. Feeding on large testate protists is a likely prospect for many deep-sea crustaceans because foraminiferal protoplasm constitutes a high proportion of deep-sea biomass (Gooday et al. 1992, Svavarsson and Davidsdóttir 1994). Some deep-sea isopods are known to select and consume foraminiferans specifically (Svavarsson and Davidsdóttir 1994, Cartes et al. 2001).

Large particles like fecal pellets and dead animals might sink to the sea floor quickly, bringing relatively high-quality food (Gage 2003). At the large end of the scale, whale falls may provide a rich source of nutrition for long periods of time, creating a center of biotic activity that can last for years (Smith and Baco 2003). Entire local ecosystems are based on whale falls, including isopods, amphipods, squat lobsters, and other small crustaceans (Smith and Baco 2003).

The scavenging guild of deep-sea crustaceans is important in the transfer of surface production to the deep seafloor and for mobilizing the nutrients of recently fallen carcasses of larger animals (Gage 2003, Britton and Morton 1994). The largest members of this group are amphipods *Alicella gigantea* and *Eurythenes gryllus* and the isopod *Bathynomus giganteus* (Shulenberger and Hessler 1974, Barradas-Ortiz et al. 2003), but many smaller amphipods and isopods are active as scavengers, such as amphipods related to *Orchomene* (Tamburri and Barry 1999) and smaller cirolanids in the genus *Natatolana* (Wong and Moore 1995). Many other larger swimming shrimp, such as *Acanthephyra* and *Benthesicymus*, king crabs such as *Neolithodes grimaldii*, and squat lobsters are also known to come to food falls or bait where they can be photographed (Gage 2003, Lovrich and Thiel 2011). Many species of the squat lobster

(genus *Munidopsis*), which occur mostly below 500 m down to the abyssal plain, are thought to be scavengers (Hoyoux et al. 2009). Even the greatest depths are no barrier for crustacean scavengers, for example amphipods from the genus *Hirondellea* reported from the Philippine Trench; Wolff 1976a, Hessler et al. 1978), and the spider crab *Teratomaia* and dendrobranchiate shrimps *Benthesicymus* and *Cerataspis* in the Kermadec Trench (Griffin and Tranter 1986, Jamieson et al. 2009).

Other important types of food-related habitats are wood falls and clumps of plant detritus (e.g., seagrass) that get transported to the deep sea. Although wood falls are best known as a habitat for the wood-boring clam *Xylophaga* (Turner 1973), they are also important habitats for other crustaceans, including amphipods (Larsen 2007), isopods, barnacles (Wolff 1976b), ostracods (Maddocks and Steineck 1987), munidopsid squat lobsters, pylochelid hermit crabs, and thalassinidean shrimps (Hoyoux et al. 2009, Lovrich and Thiel 2011). Wolff (1976b) observed that the isopod families Ischnomesidae and Nannoniscidae can be found living in or on seagrass detritus at abyssal depths. At least some decapods, such as the munidopsid squat lobster *Munidopsis andamanica*, consume the wood and biofilm directly and extract nutrition by the action of a specialized gut microflora (Hoyoux et al. 2009). Many hermit crabs, such as the pagurid *Xylopagurus* and the pylochelid hermit crabs (e.g., *Bathycheles* and *Xylocheles*) even use wood sections for housing, rather than the more typical gastropod or scaphopod shell (Lemaitre 1995).

Fatty acids, sterols, and lipids might give a window into what deep-sea animals eat through inferences about the source of these compounds (Drazen et al. 2008). For example, MacAvoy et al. (2003) found, using the carbon isotope signatures of fatty acids, that the isopod *B. giganteus* did not feed on sources from photosynthetic production, which implies that their food was sourced from chemoautotrophic production at the many cold-seeps in the Gulf of Mexico. A direct approach was pioneered by Blankenship and Yayanos (2005) in which polymerase chain reaction (PCR) analysis of the gut contents of two abyssal scavenging amphipods, *Scopelocheirus schellenbergi* and *E. gryllus*, showed that their diet was considerably more diverse than previously thought. They found that *S. schellenbergi* and *E. gryllus* feed on a variety of invertebrates (including other amphipod species) that were unlikely to be consumed as carrion, so these presumed scavengers may also be predators.

Predator Avoidance

A consequence of living in a food-poor environment is that each organism is also a likely food item. Thistle's (2003) suggestion that "larvae, juveniles and meiofauna of all life stages should experience more intense predation than do macrofaunal and megafaunal adults" is a corollary of Dayton and Hessler's (1972) view that deposit feeders might also crop living prey facultatively. Although we have little information on predation pressures for deep-sea crustaceans, size frequency analysis of large samples shows that this pressure exists. Some deep-sea isopods, when a large number of specimens are available for examination, show distinctly bimodal distributions, with a large peak of juveniles and a more widely spread out peak of adults (e.g., Hessler 1970a, Wilson 1981). Although this has been considered evidence of periodic reproduction, the appearance of these patterns in fully abyssal environments where yearly periodicity is low suggests that something else is influencing the pattern. If one posits that adults are relatively long-lived, which is possible because the size frequency data suggest that many isopod species are iteroparous, then the juveniles could grow rapidly to the subadult state, at which point growth slows down. In such a system, bimodality arises because early instars become less frequent at larger sizes, but the mode of adults results from accumulation of those individuals that have survived size-specific predation to achieve larger and more long-lived sizes. The dip in the size frequency from the smaller sizes, then, may be owing to predation pressure on juveniles.

The Reproductive Consequences of Living in the Deep Sea

Reproductive requirements can have a large impact on the lifestyle and morphology of deep-sea crustaceans. Feeding and reproduction are closely linked because successful brooding in the female requires a substantial input of energy. In some cases, the species can be seen to be facultatively either male or female depending on circumstances, perhaps owing to nutrition and growth (*Eurycope diadela* in Wilson 1983). Most data for isopods have come from the larger species, such as the rather atypical benthopelagic scavenger *B. giganteus* (Barradas-Ortiz et al. 2003): this species shows a strong relationship between seasonal food supply and reproductive activity. Although many deep-sea crustaceans probably reproduce aseasonally (Young 2003), certain species have been found to have synchronous releases of young, such as the cumacean *Leucon profundus* (Bishop and Shalla 1994). Although not synchronous, some taxa can have patterns of breeding intensity, such as isopods in the northeastern Atlantic (Harrison 1988), which appear to respond to the yearly spring bloom in surface waters by having a high proportion of females brooding young in the winter. Summertime increases in peracarid crustaceans have been observed at bathyal depths as well as in the western Mediterranean (Cartes et al. 2001).

Because population sizes are small in the deep sea, meeting the opposite sex at the right time might be a challenge for successful reproduction. In the numerically abundant and diverse isopod suborder Asellota, the female is able to mate at any time after the early juvenile instar and to store the sperm until the eggs are released into the brood pouch (reviewed in Wilson 1991); this might be an adaptation to the low probability of finding mates at low population densities.

The greatest morphological impact of reproduction on lifestyle can be seen in the Tanaidacea, which have several adaptations that allow them to survive in the deep sea (Gardiner 1975, Johnson et al. 2001) but that are also present in shallow-water species. Many tanaid males have degenerate mouthparts as adults and have substantial adaptations for swimming and chemoreception (Larsen 2005). The Tanaidacea also have a sex ratio that is highly skewed toward females, so that males are exceedingly rare. This has also been observed in the isopod family Macrostylidae (Riehl et al. 2012).

Most deep-sea crustaceans brood their young. Of course, brooding direct-developing young defines the Peracarida (Johnson et al. 2001), but most other crustaceans brood their young as well (summarized in Young 2003) either as eggs attached to the body wall or pleopods (most decapods), in sacs (harpacticoids), or in lamellae in the mantle cavity (barnacles). Barnacles, particularly pedunculate Scalpellidae, after a period of brooding show variation in their length of the dispersal phase possibly related to adaptations to different habitats (Buhl-Mortensen and Høeg 2006). The deep-living species release advanced cyprid larvae during a short dispersal phase, whereas the species found on seamounts or the upper slope require a longer planktonic phase and so release lecithotrophic nauplii. Long developmental times in deep-sea barnacles may allow larvae to be dispersed over a great geographical distance via deep-sea currents (Chan et al. 2010).

Some deep-sea crustaceans retain pelagic larvae, in which hatchlings must rise through several kilometers of possibly dangerous water column to reach the feeding grounds in the lighted zone. Most decapods have pelagic larvae, including squat lobsters, hermit crabs, and king crabs. The length of the larval phase (and numbers of stages), however, is highly variable. For instance, among squat lobsters, munidopsids and chirostylids have large yolky eggs with reduced numbers of larval stages compared to munidids and eumunidids, which produce tiny eggs and have unabbreviated development (Baba et al. 2011). Lithodids typically produce large yolky eggs and lecithotrophic larvae (Hall and Thatje 2011). The Polychelidae have an especially modified long-lived eryoneicus larva that was originally thought to represent the adults of other species (Galil 2000).

Fecundity typically is lower than in relatives from shallow water (Young 2003), although parasitic groups like the Tantulocarida can brood hundreds of embryos (Boxshall and Lincoln 1987),

probably in response to a short parasitic attachment period (the adults are shed with the host's exuvium) and the need to infect new hosts.

Respiration

Some natantians have been observed to have a definite decline in respiration with increasing depth (Childress 1975), and this may be a general observation for most deep-water crustaceans. Most crustaceans, as part of the deep-sea fauna, can tolerate low oxygen tensions, down to around 0.5 mL L^{-1}, below which species diversity shows substantial declines (Levin 2003). The OMZ (400–1,000 m) off Oman, with oxygen tensions of 0.15–0.20 mL L^{-1}, has an abundant species of the amphipod *Ampelisca* (Levin et al. 2000), suggesting that even the higher limit is not absolute. Comparisons of deep-water species living in or near OMZs shows that, rather than relying on anaerobiosis, they have highly efficient mechanisms for extracting oxygen (Childress and Siebel 1998). Some adaptations, such as the raised pleotelson in species of the isopod genus *Thylakogaster* (Fig. 11.1E), could be a method of placing the respiratory surfaces (pleopods) higher above the benthic interface.

Squat lobsters, too, can be common in OMZs, and at least some can oxyregulate, maintaining rates of oxygen consumption independent of environmental oxygen levels (Zainal et al. 1992, Lovrich and Thiel 2011). Additionally, the larger body size of individuals of a given species may increase tolerance to low oxygen tensions. Individuals of *Munidopsis scobina* from the Arabian Sea, sampled near the core of the OMZ, were larger than those from a neighboring site with a higher oxygen concentration (Creasey et al. 2000).

COMPARISONS WITH OTHER DEEP-SEA ANIMALS

Many biological constraints on crustacean life in the abyss will also apply to other taxa. Thus, most other invertebrates are macrofaunal- or meiofaunal-sized (Thiel 1975, Rex et al. 2006), favor direct development, produce few offspring (Young 2003), and are detritivores or micropredators. The connection between reproduction and nutrition applies for other taxa as well, such as bivalves and ophiuroids.

One group, the gastropod mollusks, seem to have a pattern that deviates from other deep-sea invertebrates (Rex et al. 2005a). Deep-sea snails show a diversity pattern that parallels that of the larger malacostracans: that of declining diversity with depth. Many gastropod species have planktonic or demersal larvae, with the consequence that the greater depths may form a biogeographic sink for populations that live in the bathyal realms (Rex et al. 2005b).

FUTURE DIRECTIONS

Despite the broad ambit of research on deep-sea crustacean lifestyles, several fruitful areas for more research are identifiable. Biochemical research on food sources should generate better understanding of how and what deep-sea crustaceans eat. Direct studies of gut contents can give limited information, although expanding the toolkit to lipid analysis (Drazen et al. 2008), radionuclide analysis, and genetic methods should be fruitful. Blankenship and Yayanos (2005) were successful in detecting a broad range of food sources from genetic analysis of deep-sea scavenging amphipods' gut contents. Their results showed a nonoverlapping set of sources between scavengers and a filter feeder (a bivalve mollusk).

Large samples of a single species in which all instars have been collected should give a better insight into population dynamics. Unfortunately, most samplers or traps are either biased or do not obtain large samples. For benthic crustaceans, the best results are obtained by repeated sampling using a large-area quantitative sampler, such as a box corer.

Direct in situ behavioral observation may seem to be a remote possibility, but new technologies such as autonomous vehicles (e.g., the MBARI Rover; McGill et al. 2009) combined with high-magnification digital imaging might provide conclusive data on how deep-sea crustaceans live.

CONCLUSIONS

Empirical evidence for most aspects of the lifestyles of deep-sea crustaceans is scarce to absent, but a few generalizations can be made. Most deep-sea crustaceans are either predators or choosy detritivores, are blind but often have highly elongated limbs and antennae, reproduce by direct-developing brooded embryos, and are, on average, less than a millimeter long. They might have unusual shapes compared to shallow-water crustaceans, but they also give us new insights on the malleability of the crustacean body plan to adapt to a challenging environment.

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