

Chapter 17

Lower Slope and Abyssal Benthic Decapods of the Eastern Pacific



M. K. Wicksten

Abstract A total of 119 species of decapod crustaceans have been reported from depths of 700 m or more in the eastern Pacific. From 1875 to 2000, decapods were caught mostly by trawls and dredges on muddy sea floors. Sampling has not been consistent and has been concentrated in certain geographic areas. Taxonomic confusion and potential misidentifications continue to create problems. Of the species in the area, 14 are considered to occur worldwide. The area from Alaska to northern California has the fewest species (8); the area from southwestern Mexico to Peru or Chile has the most (27). Of the taxonomic groups, the most speciose are the family Munidopsidae (31 species). Adaptations to the environment include loss of functional eyes, capacious carapaces, lack of strict food preferences, and antipredator behavior including ability to swim and association with other invertebrates. Reproduction is poorly known but seems to be asynchronous. Largely due to costs and difficulties in processing the catch, there are no extensive fisheries for deepwater decapods in the area.

Keywords Deep sea · Benthic crustaceans · Eastern Pacific · Decapoda

17.1 Introduction

A brief historical overview indicates that eastern Pacific decapods were collected as early as 1825–1827, when the HMS *Blossom* visited Monterey Bay. Further studies have continued on nearshore subtidal species, using scuba diving, trawls, dredging, and traps, and commercial fisheries for crabs and shrimps on the continental shelf. Records of decapod crustaceans below 700 m (the approximate lower limit of the oxygen minimum zone, OMZ) are scarce and almost always based on collections from trawls or dredges. In the eastern Pacific, the British expedition's ship HMS *Challenger* included a short stop at Valparaíso, Chile, and a visit to the Juan Fernández Islands in 1875; and later samples were taken in the Strait of Magellan.

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The most comprehensive study of deep-sea life was by the US fisheries steamer *Albatross* in 1890–1910. The participants used trawls to collect marine life from the area around the Galápagos Islands to San Francisco Bay, California. Reports of decapods from these collections included those by Faxon (1893, 1895) and Benedict (1910). Decapods of the Peru-Chile Trench and adjacent areas were studied by the cruises of the *Anton Bruhn* (Garth and Haig 1971). Other expeditions that collected decapods in that area included the cruise of the research vessel *Akademik Kurchatov* (Zarenkov 1976, carideans) and work by the Instituto del Mar del Perú (del Solar 1972; Haig 1974; Méndez 1981; Wicksten and Méndez 1982). McCauley (1972) trawled deep decapods to a depth of more than 3000 m as part of a survey of the effects of low-level radioactive wastes from the Hanford Site to the Columbia River and nearby ocean waters. Ambler (1980) described new species of squat lobsters taken off Oregon. Various deep-sea decapods were collected off Baja California during cruises by Scripps Institution of Oceanography, including specimens of *Glyphocrangon* (Wicksten 1979), *Bathystylodactylus* (Wicksten and Martin 2004), and new species of *Munidopsis* (Jones and Macpherson 2007). The University of Southern California received decapods collected during the California Department of Fish and Game's study of catches in sablefish traps (Wicksten 1982; Baba and Haig 1990).

Ongoing studies include works by M.E. Hendrickx and his colleagues in western Mexico including the Gulf of California, I. Wehrmann and colleagues in Costa Rica, and G. Guzmán and his colleagues off Chile. The biologists of the Monterey Bay Aquarium Institute (MBARI) have concentrated on the biota of the Monterey Submarine Canyon and nearby seamounts. Using the remotely operated vehicle (ROV) *Ventana*, they have obtained high-definition photographs of deep decapods showing living colors, behavior, and new ranges (Wicksten and Kuhnz 2015). Jeffrey Drazen and his colleagues at the University of Hawaii at Manoa have investigated the fishes and larger invertebrates in areas of manganese nodules along the Clarion-Clipperton Zone and the Peru Basin. New studies from the Exploration Vessel *Nautilus*, operated by the US National Oceanographic and Administration and the Ocean Exploration Trust and with the cooperation of the Charles Darwin Foundation, have combined use of a remotely operated vehicle with collections to provide new information on the deep fauna off the Galápagos Islands.

In 1989, I attempted a zoogeographic analysis of ranges of crustaceans living at 200 m or more in the entire eastern Pacific (Alaska to Cape Horn). Since that paper was published, new species (especially galatheoid anomurans) have been described, new records have been published, and additional information on color, habitat, physiology, and predator-prey relationships of these species have been reported. In situ color photographs now are available for some of the species. This new information has been compiled and included in the present contribution, updating the list of species occurring below 700 m depth.

17.2 Methods

Based on the contribution by Wicksten (1989), an updated list of species was elaborated containing new species and new records made available during the last 31 years. Aspects related to taxonomy, distributional range, habitat, functional anatomy, reproduction, larval stage, population densities, natural history, exploitation, and environmental disturbance are addressed.

17.3 Results

17.3.1 *Species in the Eastern Pacific*

A total of 120 species, not including species currently suspected of being undescribed, has been recorded (Table 17.1). For the purposes of this report, species are included for which the majority of their records were at 700 m or deeper. The species mentioned in this paper generally are confined to depths below the local oxygen minimum zone (OMZ). Some records are suspect. Rathbun (1904) reported *Pagurus capillatus* from only 4 m. This unlikely record could be the result of a misidentification or perhaps a specimen thrown overboard from a fishing vessel. Lithodid crabs of the genus *Paralomis* generally come from deep water, but the records of *Paralomis tuberipes* do not provide a depth. The area in which the holotype was collected was shallow, perhaps 15 m (F. Palero, pers. comm.) Identifications based on photographs or video stills from remotely operated vehicles often can be identified to genera, not species, because distinguishing features cannot be seen. Some species are known only from a single sample and thus there is no depth “range,” while others (e.g., *Pandalus platyceros*) have enormous ranges (0–1846 m, Wicksten 1989), which may reflect north-south distributional patterns or migration by age or sex. Depths in this chapter are given for settled adults and not pelagic larval stages.

Genera that contain species consistently found at 700 m or deeper include *Cerataspis*, *Benthesicymus*, *Bathypalaemonella*, *Bathystylodactylus*, *Nematocarcinus*, *Glyphocrangon*, *Parapagurus*, *Eiconaxius*, *Munidopsis*, and *Paralomis*. The deepest record from the eastern Pacific is for *Munidopsis verrucosus* at 4880 m (Jones and Macpherson 2007).

17.3.2 *Taxonomy*

Most shrimps have been identified on the basis of morphology. “Trans-ocean” (Atlantic and Pacific; eastern and western Pacific) species may in fact be separate species, but at present there is little or no genetic information for the vast majority of deep benthic decapods. Vereshchaka et al. (2019) revised the species assigned to

Table 17.1 List of species with geographic ranges and depths. If no source is provided, source is Wicksten (1989). Changes in names since 1989 are cited “as (old name) in (author, date).” The synonymies are not complete. See the latest reference for each species for further information

Order Decapoda

Suborder Dendrobranchiata

Infraorder Penaeoidea

Family Aristaedidae

1. *Cerataspis monstrosa* (Gray, 1828). Cosmopolitan, “north-west coast of U.S.A.” (Farfante and Kensley 1997 as *Plesiopenaeus armatus*); in eastern Pacific, Monterey Bay, Clarion-Clipperton Zone, 3477–5400 m, Peru Basin, 4120–4200 m (Wicksten and Kuhnz 2015; Amon et al. 2017; Drazen et al. 2019)

Family Benthescymidae

2. *Benthescymus laciniatus* (Rathbun, 1906). Azores, Canary Islands, Madagascar, Japan to Hawaiian Islands; in eastern Pacific, off Santa Catalina Island, California, off Baja California, Clarion-Clipperton Fracture Zone; 1471–4028 m (Farfante and Kensley 1997; Wicksten 2004, 2012)

2. *Daliscaris altus* (Bate, 1881). Indian Ocean, Philippines, Japan, to Fiji; in eastern Pacific, San Nicolas Island, California to Galápagos Islands, 916–4089 m (Farfante and Kensley 1999, as *Benthescymus altus*)

3. *Trichocaris tanneri* (Faxon, 1893). Off San Diego, California, to northern Chile, 484–2010 m (Hendrickx and Hernandez Payán 2017 as *Benthescymus tanneri*)

Family Solenoceridae

Haliporoides diomedea (Faxon, 1893). Gulf of Panama to southern Chile, 240–3455 m (Wicksten 1989)

Hymenopenaeus doris (Faxon, 1893). Mexico to northern Peru, 549–4802 m (Wicksten 1989)

Hymenopenaeus nereus (Faxon, 1893). Costa Rica to Ecuador; Clarion-Clipperton Zone, 330–4001 m; Peru Basin, 4120–4200 m (Hendrickx and Wicksten 2016; Drazen et al. 2019)

Suborder Pleocyemata

Suborder Pleyceomata

Infraorder Caridea

Family Acanthephyridae

Acanthephyra eximia (Smith, 1884): Cosmopolitan, in East Pacific at Erben Seamount off California, 200–3700 m (Crosnier and Forest 1973; Chace 1986); Costa Rica (Pequegnat and Wicksten 2006)

Family Nematocarcinidae

Nematocarcinus agassizii (Faxon, 1893). Gulf of California, Mexico to Peru including Cocos and Malpelo Island and Galápagos Islands, 230–1800 m (Hendrickx 1995a; Hernandez-Payán and Hendrickx 2016)

Nematocarcinus faxoni (Burukovsky, 2001). Southwestern Mexico to northern Peru, 799–2055 m (Hernandez-Payán and Hendrickx 2016)

Nematocarcinus proximus (Bate, 1888). Southern Indian Ocean, south of New Guinea, off Japan, off Juan Fernández Islands, southern Chile, 2514–2651 m (Chace 1986)

Nematocarcinus tenuipes (Bate, 1888). East Pacific Rise, 2558–2619 m (Komai and Segonzac 2005 as *Nematocarcinus ovalis*)

Segonzackomaius burukovskyi (Komai and Segonzac, 2005). East Pacific Rise, 2330–2612 m.

(continued)

Table 17.1 (continued)

Family Bathypalaemonellidae
<i>Bathypalaemonella delsolari</i> (Wicksten and Méndez, 1983). SW of Lobos de Tierra, Peru, 712–714 m
Family Stylodactylidae
<i>Bathystylodactylus echinus</i> (Wicksten and Martin, 2004). Off Magdalena Bay and Patton Escarpment, 3427–3689 m
Family Pandalidae
<i>Heterocarpus hostilis</i> (Faxon, 1893). NW of Cabo San Lucas, Baja California; SW Mexico; Isla del Coco, Costa Rica; to Supe, Peru, 890–1895 m (Wicksten and Hendrickx 2016)
<i>Heteronika nesisi</i> (Burukovsky, 1986). Western Baja California Mexico (Hendrickx 2019a, b).
<i>Pandalus amplus</i> (Bate, 1888). Washington to Gulf of California, 553–1986 m (Wicksten 2012, as <i>Pandalopsis amplus</i>)
<i>Pandalus tridens</i> (Rathbun, 1902). Pribilof Islands to San Nicolas Island, 5–1984 m (Wicksten 2012)
Family Thoridae
<i>Eualus biunguis</i> (Rathbun, 1902). Sea of Japan north to Bering Sea, south to Oregon, 90–2090 m (Butler 1980)
<i>Eualus macrophthalmus</i> (Rathbun, 1902). Unalaska to Point Sur, California, 110–1163 m (Butler 1980)
<i>Heptacarpus yaldwyni</i> (Wicksten, 1984). Off Salina Cruz, Mexico, 1052–1145 m
<i>Lebbeus bidentatus</i> (Zarenkov, 1976). Off Peru, 1680 m
<i>Lebbeus carinatus</i> (Zarenkov, 1976). Off Peru, 1850 m
<i>Lebbeus curvirostris</i> (Zarenkov, 1976). Off Peru, 1680–1860 m
<i>Lebbeus laurentae</i> (Wicksten 2010). West of Costa Rica (12°49'N 103°57'W), 2630 m
<i>Lebbeus scrippsi</i> (Wicksten and Méndez, 1982). SE Gulf of California, Peru to Chile, 768–1240 m (Hendrickx 2001)
<i>Lebbeus splendidus</i> (Wicksten and Méndez, 1982). Off Peru, 712–1100 m
<i>Lebbeus vicinus montereyensis</i> (Wicksten and Méndez, 1982). Monterey Bay, California to Gulf of California, 954–2086 m
<i>Lebbeus washingtonianus</i> (Rathbun, 1902). Northern Japan, across north Pacific to off San Clemente Island, California, 820–1808 (Komai and Takeda 2004)
Family Crangonidae
<i>Neocrangon abyssorum</i> (Rathbun, 1902). Bering Sea to Cortez Bank, California 97–2975 m (Wicksten 2012)
<i>Metacrangon procax</i> (Faxon, 1893). San Miguel Island, California to southern Peru, 830–1658 m (Wicksten 1989 as <i>Crangon lomae</i> , Wicksten 2012)
<i>Paracrangon areolata</i> (Faxon, 1893). SE Gulf of California; off Santa María Bay, Tres Marías Islands, Mexico to Peru, 1016–1650 m (Hendrickx 1996, 2001)
<i>Parapontophilus occidentalis</i> (Faxon, 1893). Off San Clemente Island (Wicksten 2012 as <i>Pontophilus gracilis occidentalis</i>), central Gulf of California to Peru, 1789–4082 m (Komai 2008; Hendrickx 2012b)
<i>Sclerocrangon atrox</i> (Faxon, 1893). Off Sinaloa (25° 15'N), Mexico to Peru, 1209–1238 m (Hendrickx 2012b)
Family Glyphocrangonidae
<i>Glyphocrangon alata</i> (Faxon, 1893). North of state of Michoacán, off Acapulco, Mexico to off Valparaiso, Chile, 600–1300 m (Hendrickx 2012b)

(continued)

Table 17.1 (continued)

<i>Glyphocrangon rimapes</i> (Bate, 1983). Near Juan Fernández Islands, 2500 m
<i>Glyphocrangon sicaria</i> (Faxon, 1893). Costa Rica and Gulf of Panama, 1454–3310 m
<i>Glyphocrangon spinulosa</i> (Faxon, 1893). Cortez Basin, California, SE Gulf of California, to off Mariato Point, Panama, 956–1374 m (Hendrickx 2001, 2012b)
<i>Glyphocrangon taludensis</i> (Hendrickx, 2010). SW Mexico, 780–1879 m
<i>Glyphocrangon vicaria</i> (Faxon, 1893). San Clemente Basin, California, off Cedros Island and Cabo San Lucas, Baja California, Mexico; to Galápagos Islands, 1374–2441 m (Hendrickx 2012b)
Infraorder Astacidea
Family Nephropidae
<i>Nephropsis occidentalis</i> (Faxon, 1893). West coast of Baja California, Mexico to Chile, 550–1238 m (Manning 1970)
Infraorder Polychelida
Family Polychelidae
<i>Pentacheles laevis</i> (Bate, 1878). Cosmopolitan, in eastern Pacific, Mexico, Gulf of Panama, off Colombia, off Galápagos Islands, Nasca Ridge and Arica, Chile, 347–2505 m (Luke 1972 as <i>Polycheles granulatus</i> Galil 2000 (Hendrickx and Serrano 2012)
<i>Pentacheles validus</i> (A. Milne-Edwards, 1880). Cosmopolitan, off Juan Fernández Islands in eastern Pacific, 914–3365 m (Galil 2000)
<i>Polycheles tanneri</i> (Faxon, 1893). Gulf of Panama, off Galápagos Islands, Ecuador, Peru, 540–830 m (Galil 2000)
<i>Stereomastis nana</i> (Smith, 1884). Cosmopolitan, 300–4000 m (Galil 2000 as <i>Polycheles nanus</i>)
<i>Stereomastis pacifica</i> (Faxon, 1893). Noyo Canyon, California to off Valparaíso, Chile, 600–3380 m (Galil 2000; Wicksten 2012 as <i>Stereomastis sculptus pacificus</i>)
<i>Stereomastis suhmi</i> (Bate, 1878). Off Valparaíso, Chile, circum-Antarctic, 293–4000 m (Galil 2000 as <i>Polycheles suhmi</i>)
<i>Willemoesia inornata</i> (Faxon, 1893). Off Magdalena Bay, Baja California (Luke 1992); off Costa Rica, Gulf of Panama, Colombia, Ecuador, Chile, Galápagos and Juan Fernández Islands, 2380–4005 m (Wicksten 1989 as <i>W. challenger</i> , Galil 2000)
<i>Willemoesia pacifica</i> (Sund, 1920). Off Juan Fernández Islands, Kermadec Trench, off New Zealand, 2745–5000 m (Galil 2000)
Infraorder Axiidea
Family Axiidae
<i>Eiconaxius albatrossae</i> (Kensley, 1996). Pacific Panama, 851–1016 m (Komai and Tsuchida 2012). <i>Eiconaxius baja</i> Kensley 1996. Between Cortes Bank and San Clemente island, California; off northwestern Baja California (Pacific), 1098–1252 m (Komai and Tsuchida 2012)
Family Ctenochelidae
<i>Callianopsis goniophthalma</i> (Rathbun, 1902) Clarence Strait, Alaska to off Palos Verdes Peninsula, Los Angeles County, California; off Ahome Point, Sinaloa, Mexico, 483–1920 m (Hart 1982 as <i>Callianassa goniophthalma</i> ; Hendrickx 1995b; Wicksten 2012)
Family Calocarididae
<i>Calocaris investigatoris</i> (Anderson, 1896). Arabian Sea, Aleutian Islands to San Diego, California, 549–1733 m (Hart 1982)

(continued)

Table 17.1 (continued)

Infraorder Anomura
Family Chirostylidae
<i>Heteroptychus galapagos</i> (Baba and Wicksten, 2019). East Darwin Seamount, Galápagos Islands, 1012 m
<i>Heteroptychus nautilus</i> (Baba and Wicksten, 2019). East Wolf Seamount, 1049.4 m
<i>Uroptychus occidentalis</i> (Faxon, 1893). Gulf of Panama, 839 m; East Wolf Seamount, Galápagos Islands, 873 m (Baba and Wicksten 2019)
Family Sternostylidae
<i>Sternostylus defensus</i> (Benedict, 1902). Off Galápagos Islands, 717–873 m (Baba and Wicksten 2019)
<i>Sternostylus iaspis</i> (Baba and Haig, 1990). Southern Vancouver Island to Jasper Seamount, California, 600–1189 m (Wicksten, 2012 as <i>Gastroptychus iaspis</i>)
Family Munididae
<i>Munida curvipes</i> (Benedict, 1902). Off Chonos Archipelago, 1924 m
<i>Munida perlata</i> (Benedict, 1902). Southern Gulf of California, 1920–3292 m
<i>Munida propinqua</i> (Faxon, 1893). Gulf of Panama to Peru, 1290–1713 m
Family Munidopsidae
<i>Galacantha diomedea</i> (Faxon, 1893). San Clemente Island, California to off Constitución, Chile, 768–3790 m (Wicksten 1989 as <i>Munidopsis diomedea</i> ; Guzmán and Sellanes 2015)
<i>Galacantha rostrata</i> (Milne-Edwards, 1880). Off Acapulco, off Galápagos and Juan Fernández Islands, off Antofagasta, 1775–2492 m (Wicksten 1989 as <i>Munidopsis rostrata</i> ; Guzmán and Sellane, 2015)
<i>Munidopsis agassizii</i> (Faxon, 1893). Gulf of Panama, Peru, to Iquique, Chile, 384–1000 m (Guzmán and Sellanes 2015)
<i>Munidopsis albatrossae</i> (Pequegnat and Pequegnat, 1973). Oregon to central America, East Pacific Rise, 2550–2891 (Ambler 1980 as <i>M. aries</i> ; Jones and Macpherson 2007)
<i>Munidopsis alfredolaguardai</i> (Hendrickx and Ayon-Parente, 2013). Gulf of California to Chiloé, Chile, 480–1225 m (Guzmán and Sellanes 2015)
<i>Munidopsis antonii</i> (Filhol, 1884). Cosmopolitan, in eastern Pacific, from Bering Sea, off Oregon, central California, Costa Rica, Gulf of Panama, off Juan Fernández Islands, 3134–4100 m (Jones and Macpherson 2007 as <i>M. beringana</i>)
<i>Munidopsis barrerae</i> (Bahamonde, 1964). Off Peru to Los Vilos, Chile, 280–800 m (Guzmán and Sellanes 2015)
<i>Munidopsis bracteosa</i> (Jones and Macpherson, 2007). Mendocino Fracture Zone, Monterey Bay, California; 2441–2891 m
<i>Munidopsis cascadia</i> (Ambler, 1980). Cascadia Basin, off Oregon; Monterey Bay, California, 2743–2926 m (Jones and Macpherson 2007)
<i>Munidopsis cochlearis</i> (Khodkina, 1973). Southwest of Antofagasta, Chile, 4550 m
<i>Munidopsis follirostris</i> (Khodkina, 1973). North of Juan Fernández Islands, Chile, 1280 m
<i>Munidopsis granosicorium</i> (Williams and Baba, 1989). Off Strait of Juan de Fuca, 2020 m
<i>Munidopsis hamata</i> (Faxon, 1893). Baja California, Mexico to Chile, 390–1337 m (Guzmán and Sellanes 2015)
<i>Munidopsis hendersoniana</i> (Faxon, 1893). SW Coast of Mexico; Gulf of Panama, 1101–1869 m (Hendrickx 2017)
<i>Munidopsis hirsuta</i> (Jones and Macpherson, 2007). Off central California, 34 deg. 50 min. N, 123 deg. 00 min. W, 4100 m

(continued)

Table 17.1 (continued)

<i>Munidopsis hystrix</i> (Faxon, 1893). Anacapa Island, California to Peru, 552–1243 m (Wicksten 2012)
<i>Munidopsis kensmithi</i> (Jones and Macpherson, 2007). Central California, 34 deg. 50 min. N, 123 deg. 00 min. W, 4100 m; photograph off Monterey Bay, California (MBARI photo files); Lamont Guyot, East Mariana Basin, 4833 m (Dong et al. 2017)
<i>Munidopsis lignaria</i> (Williams and Baba, 1989): Cascadia Basin off Oregon, East Pacific Rise off south central Mexico, 2030–2875 m (Ambler 1980 as <i>Munidopsis ciliata</i>)
<i>Munidopsis nitida</i> (A. Milne-Edwards, 1880). Gulf of Mexico, Caribbean, Indian Ocean, Japan; in eastern Pacific, Gulf of Panama and off Cocos Island, 1245–2363 m (Ambler 1980 as <i>Munidopsis ciliata</i> , Baba 2005)
<i>Munidopsis opalescens</i> (Benedict, 1902). Straits of Magellan, Chilean Patagonia, subantarctic islands, 922 m (Guzmán and Sellanes 2015)
<i>Munidopsis palmatus</i> (Khodkina, 1973). Gulf of California, Chile, 1225–1240 m (Hendrickx 2001)
<i>Munidopsis panamae</i> (Baba, 2005). Gulf of Panama, 3800 m
<i>Munidopsis producta</i> (Baba, 2005). Bay of Panama, Mariato Point to Cocos Island, 3260–3680 m (Faxon 1895 as <i>Munidopsis subsquamosa aculeata</i> ; Henderson 1888 as <i>Munidopsis aculeata</i> ; Guzmán and Sellanes 2015 as <i>M. subsquamosa</i>)
<i>Munidopsis quadrata</i> (Faxon, 1893). Queen Charlotte Islands, Canada to off Tres Mariás Islands; Antofagasta to Constitución, Chile, 245–1574 m (Guzmán and Sellanes 2015)
<i>Munidopsis scotti</i> (Jones and Macpherson, 2007). Juan de Fuca Ridge, 2715 m
<i>Munidopsis segonzaci</i> (Jones and Macpherson, 2007). Central California, 34°50'N, 123°W, 4100 m.
<i>Munidopsis tiburon</i> (Jones and Macpherson, 2007). Oregon (Ambler 1980 as <i>Munidopsis</i> sp.), Vance Seamount and Monterey Bay Canyon, California, 1829–2029 m
<i>Munidopsis tuftsi</i> (Ambler, 1980). Tufts Abyssal Plain, northern Pacific, 3500–3858 m
<i>Munidopsis verrilli</i> (Benedict, 1902). Oregon, Monterey Bay to “Cerros” (= Cedros) Island; western Pacific in Makassar Strait and Tasmania, 732–4169 m (Baba 2005)
<i>Munidopsis verrucosus</i> (Khodkina, 1973). Aleutian Islands to Antofagasta, Chile, 3932–4880 m (Jones and Macpherson 2007)
<i>Munidopsis vicina</i> (Faxon, 1893). Off Alaska Peninsula, Gulf of Panama, Cocos Island, 936–3885 m (Wicksten 2012; Baba 2005)
<i>Munidopsis yaquinensis</i> (Ambler, 1980): Off Oregon, 2763–2377 m
Family Paguridae
<i>Pagurus capillatus</i> (Benedict, 1892). Chukchi Sea, Bering Sea off Santa Cruz, California, 4–1189 m (Wicksten 2012).
Family Parapaguridae
<i>Parapagurus foraminosus</i> (Lemaitre, 1999). Off Baja California to Ecuador, Cocos and Galápagos Islands, 915–2807 m
<i>Parapagurus holthuisi</i> (Lemaitre, 1989). Gulf of California to Chile, 1410–3340 m (Garth and Haig 1971 as <i>Parapagurus abyssorum</i>)
<i>Parapagurus benedicti</i> (de St. Laurent, 1972). Alaska to off Juan Fernández Islands, 415–2012 m (McLaughlin 1974; Wicksten 2012 as <i>Parapagurus pilosimanus benedicti</i>)
<i>Probebebi mirabilis</i> (Boone, 1926): Costa Rica to Peru, 1145–3995 (Wicksten 1989)
Family Lithodidae
<i>Lithodes couesi</i> (Benedict, 1895). Japan, Okhotsk Sea, Bering Sea, Alaska south to Tortugas Bay, Baja California, Mexico, 384–1125 m (Martin et al. 1997)

(continued)

Table 17.1 (continued)

<i>Lithodes panamensis</i> (Faxon, 1893). Costa Rica, Gulf of Panama, off Peru, 760–838 m. (Macpherson and Wehrtmann 2010). (Unconfirmed record off Cabo San Lucas, Mexico, Hendrickx and Harvey 1999)
<i>Lithodes wiracocha</i> (Haig, 1974). Off Costa Rica, SW of Banco de Mancora, Peru, 620 m (Macpherson and Wehrtmann 2010)
<i>Neolithodes diomedae</i> (Benedict, 1894). Monterey Bay and Sur Ridge, California; off Panama to Peru, 830–1300 m (Barry et al. 2016)
<i>Paralomis aspera</i> (Faxon, 1893). West coast of Baja California and SW of Manzanillo, Mexico, Panama to northern Peru, 560–1397 m (Hendrickx 2019a, b)
<i>Paralomis chilensis</i> (Andrade, 1980). Off Coquimbo to off Los Vilos, Chile, 400–420 m.
<i>Paralomis diomedae</i> (Faxon, 1893). California, Costa Rica to northern Peru, 458–830 m (Macpherson and Wehrtmann 2010)
<i>Paralomis inca</i> (Haig, 1974). Peru to Chile, 620–744 m
<i>Paralomis longipes</i> (Faxon, 1893). Off Cocos Island to Peru, 760–1409 m
<i>Paralomis multispina</i> (Benedict, 1895). Japan, Alaska to San Diego, California, 500–1665 m (Sakai 1971)
<i>Paralomis otsuae</i> (Wilson, 1990). West coast of Baja California, off Jalisco, western Mexico; Peru to Mejillones del Sur, Chile, 80–2054 m (Hendrickx 2019a, b)
<i>Paralomis papillata</i> (Benedict, 1895). “Off Lower California, or perhaps south of the region” (Benedict 1895), off Costa Rica, Peru 712–744 m (Macpherson and Wehrtmann 2010)
<i>Paralomis phrixa</i> (Macpherson, 1991). Northern Peru and off Tasmania, 1815–1860 m
<i>Paralomis sonne</i> (Guzmán, 2009). Off Antofagasta, Chile, 1775 m
<i>Paralomis verrilli</i> (Benedict, 1895). Sea of Okhotsk to Cortez Bank, California, 1238–2379 m
Infraorder Brachyura
Family Homolodromiidae
<i>Homolodromia robertsi</i> (Garth, 1973). off Peru, 800 m
Family Dorippidae
<i>Ethusina faxonii</i> (Rathbun, 1933). Western Mexico to Peru, 2999–4081 m
<i>Ethusina robusta</i> (Miers, 1886). Bay of Panama to Galápagos Islands and coast of Ecuador, 1618–3334 m
Family Cymonomidae
<i>Cymonomus menziesi</i> (Garth in Garth and Haig, 1971). Peru, 1005–1124 m
Family Epialtidae
<i>Rochinia cornuta</i> (Rathbun, 1898). Off Galápagos Islands, 718–1160 m
Family Trichopeltariidae
<i>Trichopeltarion corallinum</i> (Faxon, 1893). SE Gulf of California; off Acapulco to Peru, 834–1280 m (Hendrickx 2001)
<i>Trichopeltarion hystricosus</i> (Garth in Garth and Haig, 1971). Peru to Chile, 907–935 m

Benthescycymus, changing *B. altus* to *Dalicularis altus* and *B. tanneri* to *Trichocaris tanneri* but a more recent revision changed the name of the latter species to *Benthoecetes tanneri* (WoRMS editorial board (2020). Pequegnat and Wicksten (2006) used morphology to compare specimens of *Acanthephyra eximia* taken in the Gulf of Mexico with those from western Costa Rica, but did not find any observable differences between them, nor did Chace (1986) in his treatment of Pacific

Oplophoridae. *Pandalus ampla*, reported from both the Atlantic and Pacific Oceans, may be a species complex (Komai 1994). Burukovsky (2001) redefined the species of *Nematocarcinus* so that some supposedly cosmopolitan species have since been divided into related species. Krygier and Pearcy (1981) reported *Nematocarcinus exilis* off Oregon, but this specimen needs to be re-examined. *Lebbeus washingtonianus* may be a highly variable species or a species complex (Komai and Takeda 2004). Komai et al. (2004) noted that *L. washingtonianus* had been reported from the eastern Pacific and from a single location in the Okinawa Trough, but the habitat and depth of these records were different. They suggested that the identification was uncertain and that the specimens be re-examined. There are photographs of what probably are *Lebbeus* spp. taken by ROV's off Monterey Bay, Costa Rica, and the Galápagos Islands, but these cannot be identified to species without specimens (MKW unpublished). A shrimp identified as *Bathypalaemonella serratipalma* was photographed off the Galápagos Islands (L. Watling pers. comm.), but it was not compared to the eastern Pacific *B. delsolari*.

Records of lobster-like decapods need further confirmation. A previous report of *Eiconaxius acutifrons* by Wicksten (1982) from California is now identified as *E. baja* Kensley, 1996 (Komai and Tsuchida 2012). If confirmed, a record of *Willemoesia leptodactyla* off Punta San Juan, Peru, would be the first record of this species from the eastern Pacific (Luke 1992). Photographs in the “benthic invertebrate guide” for the ship *Okeanos Explorer* (NOAA 2019) in the central Pacific show a squat lobster identified as *Gastroptychus* cf. *iaspis*. I examined a paratype of *Sternostylus iaspis* and concluded that the pattern of spines on the carapace and chelae of *S. iaspis* are markedly different from those of the (as yet unidentified) squat lobster in the central Pacific. As of this writing, *S. iaspis* is known only from the eastern Pacific.

There is general agreement that many members of the superfamilies Galatheoidea and Chirostyloidea need to be studied further and may in fact be species complexes. The taxonomy of species of *Munidopsis* is particularly confusing. For example, *Munidopsis bairdii* and *M. antonii* currently are considered to be cosmopolitan species, but there has been no genetic comparison of specimens from different oceans (E. Macpherson pers. comm.). *Munidopsis subsquamosa*, considered to be a cosmopolitan species, recently has been determined in the eastern Pacific to be a different species, *M. producta* (Baba 2005). Specimens reported as *M. subsquamosa* from Oregon (Ambler 1980) and off Chile (Guzmán and Sellanes 2015) need to be re-examined (Baba 2005). Presumably the same species has been reported in the eastern Pacific as *Munidopsis subsquamosa aculeata* by Faxon (1895) and *Munidopsis aculeata* Henderson, 1888. There has been extensive recent revision of species of the Chirostylidae based on morphological work (Baba 2005; Baba et al. 2018) and new genetic studies (Jones and Macpherson 2007). Some species formerly assigned to the genus *Gastroptychus* have been re-examined and assigned to the genus *Sternoptychus* (Baba et al. 2018), including *Sternoptychus iaspis* in the eastern Pacific.

The nomenclature of the various crab-like decapods has remained relatively stable since 1989, although there are new records and range extensions. Lemaitre (1989, 1999) revised the deep-sea hermit crabs of the genus *Parapagurus*.

17.3.3 Ranges

Ranges of eastern Pacific decapods known from more than a single location are provided (Table 17.2). If a species only has been reported from latitudinally isolated locations (e.g., from Monterey Bay, California, and off Chile), then those two reports are listed separately instead of giving the range as “Monterey Bay to Chile.” For the majority of the species, there are few or no numerical data, so the system largely is based on the presence or absence of specimens. Records from the Clarion-Clipperton Zone, Peru Basin, Eastern Pacific Rise, and Juan de Fuca Ridge are included.

The huge spread of the Indo-Pacific region has many more species than the eastern Pacific, especially in the Chirostylidae (Baba and Schnabel 2018) and other members of the Galatheoidea (as Galatheidae in older literature). The biota of the eastern Pacific is isolated and less diverse than that of the western and central Pacific (Macpherson et al. 2010). The eastern Pacific is separated from the central Pacific by as much as 8000 km: Easter Island lies over 1850 km west of the Juan Fernandez Islands; Hawaii is nearly 5000 km from California. This vast distance is known as the “Eastern Pacific Barrier” and probably limits the dispersal of species between these two areas. The lack of records in abyssal and lower slope areas may be due to a lack of study. Wicksten and Kuhnz (2015) first reported the common and widespread abyssal shrimp *Cerataspis monstrosa* off California, when photographs and video stills from ROV’s and improved cameras became available. Species reported to be worldwide or trans-Pacific tend to be abyssal species (living as deep as 2000 m or more), as are species that range from Alaska or California to Peru or Chile. At least four species range across the north Pacific from Japan to California, perhaps able to “island hop” along submerged spurs or slopes across the length of the Aleutian Archipelago.

Previous work suggests differentiation in species assemblages by latitude (Wicksten 1989; Macpherson et al. 2010; Guzmán and Sellanes 2015). The area from southwestern Mexico to Peru is particularly rich in species. These ranges seem to correspond to patterns of modern currents or possibly ancient geologic events or climate changes, such as the closing of the seaway across Central America. Ranges of many species are based only on a single specimen or a few crustaceans from one isolated locality: for example, Jones and Macpherson (2007) described three new species of *Munidopsis* from a single site in California. Some areas (south of the Columbia River, Oregon to Monterey Bay, California; much of western Central America, or most areas 1500 m deep or more) remain poorly studied or not sampled at all. At present, there is no definitive evidence that any deep benthic decapods are endemic to a particular island chain, vent system, or seamount.

Table 17.2 Range of decapod crustaceans with more than one record in different sectors of the eastern Pacific

World-wide, trans-Pacific or in more than one ocean	Alaska or Canada to Chile	Oregon or California to Western Mexico, Costa Rica or Panama	Japan and Russia into Eastern Pacific
<i>Cerataspis monstrosa</i> (as <i>Plesiopenaeus armatus</i>)	<i>Parapagurus benedicti</i>	<i>Lebbeus vicinus montereyensis</i>	<i>Eualus biunguis</i>
<i>Benthescycymus laciniatus</i>	<i>Munidopsis quadrata</i>	<i>Glyphocrangon spinulosa</i>	<i>Lebbeus Washingtonianus</i>
<i>Acanthephyra eximia</i>	<i>Munidopsis verrucosus</i>	<i>Glyphocrangon vicaria</i>	<i>Lithodes couesi</i>
<i>Nematocarcinus proximatus</i>	<i>Munidopsis vicina</i>	<i>Munidopsis albatrossae</i>	
<i>Pandalus ampla</i>		<i>Munidopsis challengerii</i>	
<i>Pentacheles laevis</i>	Alaska, Washington or Oregon to California	<i>Munidopsis lignaria</i>	California to Peru or Chile
<i>Pentacheles validus</i>	<i>Pandalus tridens</i>	<i>Paralomis multispina</i>	<i>Bentheocetes tanneri</i>
<i>Polycheles nanus</i>	<i>Eualus biunguis</i>	<i>Munidopsis hystrix</i>	<i>Metacrangon procax</i>
<i>Calocaris investigataris</i>	<i>Paralomis verrilli</i>	<i>Neocrangon abyssorum</i>	<i>Parapontophilus occidentalis</i>
<i>Munidopsis antonii</i>		<i>Sternostylus iaspis</i>	<i>Polycheles pacificus</i>
<i>Munidopsis kensmithi</i>		<i>Munidopsis cascadia</i>	<i>Galacantha diomedae</i>
<i>Munidopsis nitida</i>		<i>Pagurus capillatus</i>	<i>Neolithodes diomedae</i>
<i>Munidopsis subsquamosa species complex</i>		<i>Munidopsis tiburon</i>	<i>Paralomis diomedae</i>
<i>Munidopsis verrilli</i>			
Southwestern Mexico and Gulf of California to Panama and Ecuador	Southwestern Mexico to Peru or Chile	Costa Rica or Panama to Ecuador, Peru or Chile	Circum-Antarctic or Southern Chile
<i>Munidopsis hendersoniana</i>	<i>Hymenopenaeus doris</i>	<i>Haliporides diomedae</i>	<i>Willemoesia pacifica</i>
<i>Parapagurus foraminatus</i>	<i>Glyphocrangon alata</i>	<i>Glyphocrangon sicario</i>	<i>Polycheles suhmi</i>
	<i>Sclerocrangon atrox</i>	<i>Hymenopenaeus nereus</i>	<i>Munidopsis opalescens</i>
	<i>Nematocarcinus agassizi</i>	<i>Polycheles tanneri</i>	
	<i>Nematocarcinus faxoni</i>	<i>Munida propinqua</i>	
	<i>Lebbeus scrippsi</i>	<i>Munidopsis agassizi</i>	
	<i>Paracrangon areolata</i>	<i>Munidopsis alfredolaguardai</i>	
	<i>Willemoesia inornata</i>	<i>Paralomis phrixa</i>	

(continued)

Table 17.2 (continued)

Southwestern Mexico and Gulf of California to Panama and Ecuador	Southwestern Mexico to Peru or Chile	Costa Rica or Panama to Ecuador, Peru or Chile	Circum-Antarctic or Southern Chile
	<i>Nephropsis occidentalis</i>	<i>Munidopsis barrerei</i>	
	<i>Galacantha rostrata</i>	<i>Munidopsis producta</i>	
	<i>Munidopsis hamata</i>	<i>Probeebei mirabilis</i>	
	<i>Munidopsis palmatus</i>	<i>Ethusina robusta</i>	
	<i>Parapagurus holthuisi</i>	<i>Trachycarcinus hystricosus</i>	
	<i>Paralomis aspera</i>	<i>Paralomis inca</i>	
	<i>Paralomis otsuae</i>	<i>Paralomis longipes</i>	
	<i>Paralomis papillata</i>		
	<i>Trachycarcinus corallinus</i>		
	<i>Ethusina faxoni</i>		

The eastern Pacific, Indo-Pacific, and Atlantic contain species that seem to be cosmopolitan or belong to closely related clades, such as the *Munidopsis subsquamosa* complex. Such clades suggest interconnectivity until fairly recently. The closing of the Isthmus of Panama between the Caribbean and the eastern Pacific may have occurred in stages. The latest estimate gives an estimated time of complete closing by an estimated 2.8 million years ago (O’Dea et al. 2017). This closing resulted in many sibling species in the nearshore Caribbean and tropical eastern Pacific. How this closing affected the deep biota is less well understood. In comparison to the western Atlantic and Caribbean, the eastern Pacific exceeds the western Atlantic in species of the Lithodidae and Thoridae but has only one of the Nephropidae and fewer of the Glyphocrangonidae and Polychelidae than the western Atlantic-Caribbean. The large crabs of the family Geryonidae, common inhabitants of the western Atlantic, are not known from the eastern Pacific. Thirty-nine species of the Munidopsidae (including *Galacantha*) have been reported for the entire eastern Pacific, as opposed to 25 in the Gulf of Mexico alone (Wicksten and Packard 2005). Whether these totals reflect differences in sampling effort or habitat diversity remain unknown. Recent descriptions of many new species by Jones and Macpherson (2017), among others, have added greatly to the number of eastern Pacific species and suggest that species diversity is poorly known and likely to be underestimated.

17.3.4 Habitats

Most early studies of deep-sea benthic animals were done by trawling, which usually is conducted on soft substrates. Shrimps and lobsters that usually are caught or seen on muddy or silty sea floors include the abyssal species *Cerataspis monstrosa*,

Benthescymus laciniatus, and *Willemoesia* spp.; *Haliporoides diomedea*, which buries itself in soft substrates (Hendrickx 1995a, b); *Nephropsis occidentalis* (Manning 1970; Hendrickx 2003); and *Glyphocrangon* spp. Most records of *Nematocarcinus* spp. come from muddy areas, but recent ROV photographs also show them among rocks or manganese nodules (J. Drazen, pers. comm.). *Nematocarcinus burukovskyi* and *N. ovalis* have been photographed at or near hydrothermal vents but also at a distance from them and are not considered to be obligate vent associates (Komai and Segonzac 2005). Recent photographs by Drazen et al. (2019) show *Cerataspis monstrosa*, *Hymenopenaeus nereus*, *Benthescymus* sp., *Probeebei mirabilis*, and an unidentified species of *Munidopsis* in a field of manganese nodules.

Eastern Pacific decapods are affected by the oxygen minimum zone (OMZ), a consistent feature along much of the eastern Pacific. The upper depth of the OMZ varies considerably, from less than 50 m off Peru to 200–600 m off California and Oregon. The lower limit also is variable, from 600–700 m off Chile and Peru to about 1100 m off North America (Helly and Levin 2004). Hypoxia is most severe off western Mexico and Central and South America, to less than 0.2 ml oxygen per liter, with North America usually above the 0.2 ml limit. The El Niño climatic condition also can have a great influence, deepening the OMZ off Peru and Chile by more than 100 m but also having severe effects on pelagic organisms at lesser depths (Arntz et al. 2006). In the southern Gulf of California, there is no macrofauna inhabiting areas between approximately 150–500 m due to severe hypoxic or anaerobic conditions (Hendrickx 2003). Hendrickx and Hernandez Payán (2017) noted that both *Nematocarcinus agassizii* and *N. faxoni* are restricted to zones deeper than the core of the OMZ, as are *Nephropsis occidentalis* and *Stereomastis pacificus* (Papiol et al. 2016; Hendrickx and Serrano 2012).

17.3.5 Functional Anatomy

As in shallow-water species, decapods living on muddy sea floors generally have elongate dactyls that serve as stilts. Species of *Nematocarcinus* are rightly called “thread leg” shrimps, for their hairlike legs provide a minimum support for these shrimps at depth. Species of the Benthescymidae have very thin legs as well as poorly calcified exoskeletons. Squat lobsters and lithodids living on rocks usually have sturdy appendages and may have spinules on their dactyls. The spinules may aid in gripping a host coral or the substrate. Lithodid crabs and burrowing species of *Glyphocrangon* and the Munidopsidae generally have sturdy exoskeletons. Deep-sea crabs generally do not have swimming paddles or flat digging appendages, which can be characteristic of decapods of the continental shelf (e.g., the swimming crabs, family Portunidae, and the frog crabs, family Raninidae).

Garth and Haig (1971) noted that the crab *Lophorochinia parabranchia*, living within the OMZ of the Peru-Chile Trench, had greatly swollen gill chambers and enlarged excurrent openings. *Lithodes couesi* also has inflated branchial chambers

and large exhalent openings and scaphognathites (Somerton 1981). Species of *Munidopsis* represent the largest group of decapod crustaceans below the OMZ (Hendrickx 2012a). *Bentheocetes tanneri*, *Glyphocrangon spinulosa*, and *Nephropsis occidentalis* also have been reported from conditions of low oxygen (Hendrickx 2003). Their particular adaptations to these conditions remain unstudied.

Many deep decapods have no or reduced vision. Members of the Polychelidae and Munidopsidae do not have pigmented eyes. *Cymonomus menziesii* has long eyestalks but no cornea. Crustaceans living in dim light may have superpositional eyes, in which screening pigments in the ommatidia are concentrated and allow light to pass through to more than one ommatidium before striking the rhabdome, which contains rhodopsin. These eyes are adapted to very low light but have less visual acuity and capability for image formation than is found in light-adapted eyes. In the Atlantic lobster, *Nephrops norvegicus*, the superposition compound eyes are large and able to adjust their sensitivity to spectral and temporal changes through movement of pigments. As in some other deep crustaceans, exposure to ambient surface light intensities can damage the retina layer, but such damage does not cause a noticeable impact on survival (Gaten et al. 2013).

In contrast, the abyssal anomurans *Probeebei mirabilis* and *Parapagurus holthuisi* (as *P. abyssorum*) have pigmented eyes that seem to be functional (Garth and Haig 1971). Hiller-Adams and Case (1988) stated benthic crustaceans living at greater depths tend to have larger eyes than those in lesser pelagic depths, and Warrant and Locket (2004) suggested that the better nutrition of the sea floor would favor agile crustaceans with larger eyes. Frank et al. (2012) found that the Atlantic chirostyliid squat lobster *Gastroptychus spinifer*, which has large eyes, had greatest sensitivity in the blue region of the spectrum and could detect greenish bioluminescence. Although this squat lobster itself is not bioluminescent, it might be able to detect the difference between bioluminescence produced by zooplankton which it eats and that of the pennatulaceans and zoanthids on which it lives.

When illuminated or brought to the surface, deep-sea decapods may be bright red. Faxon (1895) illustrated six red benthic species by watercolors immediately after collection. Photographs show the same coloration in *Cerataspis monstrosa* (<https://www.ncddc.noaa.gov/oceanosanimalguide/Dendrobranchiata005.html>) and *AcanthePHYra eximia* (Baba et al. 1985). Many species of *Munidopsis* are white. Deep-sea fishes may be able to detect the colors from pigmentation at depth, so red colors, invisible at that depth, could serve in visual camouflage. Carotenoid (red) pigments also may be involved in physiological functions that remain unstudied.

Deep decapods, like shallow-water ones, have sensory setae of a wide variety of shapes and functions. Many have tactile setae on the pereopods and chemosensory setae (aesthetascs) on the first antennae. Decapods in general have gustatory setae on the inner mouthparts. The function of small peg setae, spinules, and other sensors remains unknown but might include detection of vibrations or currents. Many have long, whiplike second antennae that may serve in determining individual distance from conspecifics or moving through tight spaces.

17.3.6 *Reproduction, Larval Stages, and Population Densities*

Reproduction in deep decapods seems to be year-round. Photographs of lithodid crabs (*Paralomis* sp. and *Neolithodes agassizii*) show that adult females may be much smaller than the males holding them in the “mating embrace” (MBARI photo files). Some species produce large numbers of small eggs. The eastern Pacific *Nematocarcinus agassizii* and *N. faxoni* can carry up to 10,000 eggs (Hendrickx and Hernandez Payán 2017). Wenner (1979a) found that western Atlantic *Nematocarcinus* spp. produced as many as 15,573 eggs per female. *Pandalus platyceros* females carry a mean egg count of 2028 eggs per female (Butler 1970). *Stereomastis pacificus* had eggs approximately 1 mm in largest dimension. This size is similar to those of *S. sculpta*, a related Atlantic species, which carried as many as 19,080 eggs (Wicksten 1981). A female *Lithodes couesi* can carry as many as 5000 eggs but usually close to 4000 (Somerton 1981). *Parapagurus foraminosus* carries as many as 2716 eggs that increase in diameter during development (Ayon Parente and Hendrickx 2009). Penaeoid shrimp females do not carry eggs ventrally, and so reproduction must be estimated by examination of the gonads.

Other decapods carry fewer, larger eggs. *Lebbeus scrippsi* females carried 32–66 eggs (Hendrickx 2001). *Glyphocrangon alata* females carry 28–51 eggs; *G. spinulosa*, 11–16; and *G. vicaria*, 10–29 (Wicksten 1979). The few species of *Munidopsis* that have been studied have few large eggs and abbreviated development, but the larvae may be able to float for extended periods in nutritionally poor water (Jones and Macpherson 2007). Female *Galacantha diomedae* carry from 11 to 126 large eggs (Hendrickx and Papiol 2019). A specimen of *Uroptychus nitidus* from the Gulf of Mexico carried 35 eggs (MKW, unpublished data).

Larval stages of deep decapods are poorly known and may be unidentifiable. Size distribution of larvae of *S. pacificus* taken in an Isaacs-Kidd midwater trawl (mesh size 3 mm) suggested that there were at least five larval stages, previously called the “Eryoneicus” larvae. The largest larval stages had a total length of 60 mm or more, as much as 0.8 times the total length of reproducing adults (Wicksten 1981). *Cerataspis monstrosa* produces a bizarre larval form that only recently was matched with the adult (Bracken-Grissom et al. 2012). *Pandalus ampla* has five zoeal stages and one postlarva (Park et al. 2004). In *Galacantha diomedae*, the large eggs contain advanced embryos at stage 5, consistent with extended, lecithotrophic embryonic development and a reduced pelagic larval stage (Hendrickx and Papiol 2019).

Decapods have few indicators of lifespan other than the obvious—big ones probably are older than smaller ones. Brachyurans show obvious sexual dimorphism in the shape of the abdomen and often the length of the chelipeds relative to the body and the gape between the fingers of the chela. *Pandalus dispar* and *Pandalus platyceros* from the northern Pacific generally live no more than 4 years, which may be typical of pandalids (Butler 1980).

Populations of deep benthic decapods can be patchy. Arana et al. (2003) found that groups of *Haliporoides diomedae* were separated by a submarine canyon.

Hendrickx and Hernandez Payán (2017) found that populations of *Nematocarcinus faxoni* varied from 1 to 800 animals per hectare in the Gulf of California and Pacific side of Baja California. *Nematocarcinus agassizii* was encountered less frequently but also varied in density, from 1 to 50 animals per hectare. The densities of both species declined with depth, with *N. agassizii* having its lowest values at the 1701–2100 m interval and *N. faxoni* at 1301–500 m. *Galacantha diomedeeae* occurred at maximum densities of 71 squat lobsters per hectare (Hendrickx and Papiol 2019).

Drazen et al. (2019) reported on scavenging decapods seen from baited camera traps and in camera transects in the Peru Basin. The shrimp *Hymenopenaeus nereus* was present in 63% of the images, showing up to 15 shrimp at once (average of 9 shrimp per view). This abundance was similar to that seen for the species in the eastern Clarion-Clipperton Zone (Leitner et al. 2017). The hermit crab *Probeebei mirabilis* appeared in 29% of the images and in all deployments, with 1 to 9 crabs per view. The large number of these crabs seemed to be “unique” among abyssal scavenger studies. This large number of hermit crabs may not be an isolated occurrence. More than 300 *Sympagurus pictus* were taken in a single trawl in the Gulf of Mexico (MKW unpublished data). Such great numbers were not collected at any other station during 1964–2004 and seem likely to represent a short-term aggregation, perhaps at a sunken food source.

17.3.7 Natural History

There is very little natural history information available for deep slope and abyssal decapods. I have included published information on related species living in the Gulf of Mexico and western Atlantic, unpublished information from communications with colleagues, my own field notes, and information from preserved specimens in the Biodiversity Research and Teaching Collections of Texas A&M University.

There is a general assumption that deep decapods feed on small benthic invertebrates, debris, mucus, bacterial mats, or other nutritional sources that they glean from the substrate. Two squat lobster species (*Munidopsis verrilli* and *Munidopsis bracteosa*) and the lithodid crab *Neolithodes diomedeeae* have been collected or photographed at carcasses of dead whales (Jones and Macpherson 2007, MBARI photo files). Papiol and Hendrickx (2015) reported that *Bentheocetes tanneri* often fed on benthic or benthopelagic prey, especially the squat lobster *Pleuroncodes planipes* and oplophorid shrimps. Wenner (1979a, b) reported that *Nematocarcinus ensifer* and *N. rotundus* from the western Atlantic were omnivorous, feeding on fish parts, foraminiferans, polychaetes, and detritus. *Glyphocrangon* spp. from the western Atlantic also were omnivores, feeding on gastropods, fish scales, polychaetes, and unidentified detritus (Thompson 1963; Gore 1985). *Glyphocrangon sculpta* off Ireland was photographed more or less passively moving with the current across the sea floor, where it fed on bivalves, foraminiferans, and small infaunal crustaceans

(Lampitt and Burnham 1983). In situ photographs of *Bathystylocodactylus* cf. *inflatus* from the western Pacific and an unidentified *Bathystylocodactylus* from the Clarion-Clipperton Zone show the shrimps with their setose second appendages extended laterally, probably filter-feeding on small particles carried by a current (Amon et al. 2017; Wicksten et al. 2017). Krygier and Pearcy (1981) captured a single *Neocrangon abyssorum* (as *Crangon abyssorum*) in a midwater trawl at a distance of more than 1500 m from the sea floor and suggested that it might forage off the sea floor. *Stereomastis pacificus* has been taken in baited sablefish traps (Wicksten 1981), and *Cerataspis monstrosa*, *Hymenopenaeus nereus*, and an unidentified species of *Benthescycymus* were attracted to baited traps in the Peru Basin (Drazen et al. 2019). Lithodid crabs in general are detritivores or feed on mollusks, barnacles, and smaller crustaceans. Species of *Munida* may scavenge, feed on smaller crustaceans, or use setose maxillipeds to sweep detritus from the sea floor. A squat lobster (*Sternostylus* sp.) was photographed gleaning small particles from the water (L. Kuhnz MBARI pers. comm.). A large lithodid crab, probably *Neolithodes agassizii*, was photographed feeding on an ophiuroid in the western Atlantic (D. Wagner, NOAA, *Okeanos Explorer* expedition 18-06).

Deep decapods may have consistent associations with other invertebrates. *Bathypalaemonella serratipalma* associates with soft corals (Wicksten and Heathman 2015). Unidentified *Lebbeus* species live on hexactinellid sponges (Fig. 17.1). Species of the small lobster *Eiconaxius* are commensals of hexactinellid sponges (Kensley 1996; Komai and Tsuchida 2012). Members of the family Chirostylidae seem consistently to associate with antipatharians or alcyonaceans. *Uroptychus occidentalis*, like the Atlantic *U. nitidus*, lives on *Chrysogorgia* spp. (Baba and Wicksten 2017, 2019); *Heteroptychus nautilus*, on bamboo corals (Isididae) (Baba and Wicksten 2019); *Sternostylus iaspis*, on gorgonians and antipatharians (Wicksten 2012); and *S. defensus*, on antipatharians (Baba and Wicksten 2019). The nature of the associations between these shrimps, lobsters, or anomurans



Fig. 17.1 *Lebbeus* sp. on hexactinellid sponge *Staurocalyptus* sp., Davidson Seamount, 35.721 degrees N, 122.724 degrees W. 1315 m. Photo courtesy of MBARI 2006

and their sponge or cnidarian hosts is uncertain. Crustaceans may use their host as a perch off the sea floor, from which they can capture zooplankton, a safe refuge from predators, or a source of mucus and tissue on which they feed. They might also drive off potential predators on their host or remove debris adhering to it (Wagner et al. 2012). The hermit crab *Parapagurus benedicti*, like the related Atlantic *P. pilosimanus*, can inhabit a shell overgrown by zoanthids (M. Wicksten, field notes). *Parapagurus foraminosus* occupies shells of *Bathybembix bairdii*, often covered by an unidentified sea anemone (Actiniaria) (Hendrickx and Ayón Parente 2009). These cnidarians may discourage potential predators of the crab and at the same time gain locomotion. Juvenile *Neolithodes diomedea* are found on or beneath the elapodid holothurian *Scotoplanes* sp., where they may take shelter from predators (Barry et al. 2016). The caprellid amphipod *Caprella unguina* clings to the legs of *Paralomis multispina* (Wicksten 1982). *Paralomis longipes* and other lithodid crabs may have stalked barnacles attached to the exoskeleton (Haig 1974).

Deep decapods can be parasitized. *Nematocarcinus* spp. and *Glyphocrangon* spp. may be parasitized by isopods (Wenner 1979a; Markham 2016). *Munidopsis antonii*, *M. depressa*, and *M. beringana* are parasitized by bopyrid isopods (Román-Contreras 2008). *Lithodes couesi* can be parasitized by the rhizocephalan cirriped *Briarosaccus callosus* (Somerton 1981). *Lithodes couesi* can be parasitized by a dinoflagellate, *Hematodinium* sp. (Jensen et al. 2010).

Predators on deep decapods probably include each other, especially larval stages. Squids and octopuses live at depths and are likely to prey on decapods. Small sharks and benthic fishes of the families Macrouridae, Ophidiidae, and others prey on crustaceans and whatever else they can catch (Fitch and Lavenberg 1968). Deep decapods can escape from predators by a rapid tail flip and swimming backward, as is found in many shrimps and squat lobsters (superfamily Galatheoidea), digging into the sea floor or hiding. Species of *Glyphocrangon* have locking ball and socket joints on the last three abdominal somites and telson as well as sharp teeth, ridges, and nodules on the exoskeleton (Rice 1981). These armored shrimps can arch the body so that the carapace and abdomen touch (Anderson and Bullis 1970). Large lithodid crabs may escape predation by means of a “size refugium”—they are too big for most predators to attack. *Galacantha rostrata* and *G. diomedea* have formidable dorsal spines, as do some juvenile lithodids.

17.3.8 Exploitation and Environmental Disturbance

Most fishing for decapods occurs on the continental shelf and upper slope, at depths at much less than 700 m. The cost of operating gear below 500 m has been a major factor in limiting fisheries, and so many deepwater species either are incidental catch or part of exploratory fisheries (Hendrickx 1995a, b; Hendrickx and Hernandez Payán 2017). Wehrtmann et al. (2012) compiled a comprehensive report on deepwater fisheries of the Central and South America. Most of these fisheries were for shrimps of the family Pandalidae (*Heterocarpus affinis* from

Mexico to Peru, *H. reedei* in Chile). Of these, *H. affinis* seems to have the greatest potential for a fishery but off Costa Rica; *H. affinis* is fished “only in negligible quantities.” The lower slope species considered for fisheries in western Mexico include the carideans *Pandalus amplus* and *Nematocarcinus* spp. and the penaeoid *Bentheocetes tanneri*. The penaeoid *Haliporus diomedea* gradually increased in landings in Chile from the 1970s and then decreased as of 2012. The lithodid crab *Paralomis longipes* has been taken in traps off Peru, but as of 2012, the landings had declined considerably. *Bentheocetes tanneri*, with a thin exoskeleton, was deemed to be too fragile to be easily caught and transported. *Pandalus platyceros* has been caught in traps and trawls from Alaska to southern California and has been considered for a potential fishery off western Mexico (Butler 1970; Sunada 1984; Flores et al. 2004). Prized as seafood, the “spot prawn” currently sells for at least \$37.95/pound (454 g) and thus is a luxury item. Lost fishing gear, including traps used to catch prawns, is a concern because it may become entangled with corals or sponges on the sea floor (Etnoyer et al. 2013).

The effects of manganese mining can include removal of hard substrate, creation of large sediment plume, and immediate mortality of resident species. Drazen et al. (2019) visited experimentally plowed areas in the Peru Basin. Using camera transects and baited traps, they found that fish density was lower in the first years following disturbance but increased over time. Twenty-six years after disturbance, there are no differences in overall fish densities between reference and experimental areas, but the dominant fish species still exhibited lower densities in the plowed habitat. The scavenging community was dominated by fishes, shrimps, and the hermit crab *Probeebi mirabilis*. Almost nothing is known about the lifespans and recruitment of these decapods, and one can only speculate that extensive disturbance in their habitat would have a negative effect on them.

New evidence points to the damaging effects of plastics on marine animals, even deep-sea crustaceans. Jamieson et al. (2019) found that 72% of the deep-sea amphipods (Lyssianassidae) collected in deep-sea trenches (including the Peru-Chile Trench) at 7000–10,890 m contained microplastics. Amphipods being common scavengers and likely to enter the food chain for larger crustaceans, fishes, and cephalopods, it seems likely that these pollutants also pose a threat to deep-sea decapods.

Pandalid shrimps, lithodid crabs, and *Munidopsis* spp. have been photographed clinging to shipwrecks and sunken cargo containers (MBARI file photographs, M. Wicksten unpublished.) The photographs from ROV's generally do not show the interior of these structures, where rust, obstructions, and layers of anoxic sediments tend to accumulate. These metal structures at least for a time can offer a raised hard area that acts as an “artificial reef,” but their lifespan is limited by the time it takes for them to rust, fall apart, and sink down into a silty sea floor.

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