

Occurrence of anomuran crabs (Crustacea: Decapoda) in hydrothermal vent and cold-seep communities: a review

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Abstract.—Crabs of the family Lithodidae are frequently encountered in the vicinity of deep-sea hydrothermal vents and cold-seeps. Together with crabs of the families Galatheididae and Chirostylidae, they are the main contributors to the scavenging/predatory fauna of these highly productive areas, and a potential vector for the export of organic carbon to the surrounding deep-sea communities. A review of the literature indicates that anomuran crabs have been reported from such environments since their discovery, and occur virtually anywhere a reducing habitat is found. These three families are represented by at least eight genera, with at least 14 species occurring in hot vent areas, and eight in cold-seep associated communities.

Two species of lithodid crabs have recently been reported from the south Barbados accretionary prism cold-seeps at depths of 1200–1700 m (Macpherson 1994). In addition to the description of a new species, *Paralomis arethusa*, Macpherson mentioned that his new species and *Lithodes manningi* Macpherson, 1988, were the first records of the family Lithodidae to be found in hydrothermal vent and cold-seep areas. However, a review of the literature showed that occurrence of lithodid crabs in such environments has been known at least since 1985 (Suess et al. 1985). The taxonomic literature on deep-sea hydrothermal vent and cold-seep organisms often lacks ecological data, and ecological surveys frequently present vague taxonomic information. This review is intended to demonstrate that the Anomura are a particularly well represented group in deep-sea chemosynthetically-based ecosystems, and to present a literature survey of the species and accompanying information relevant to biogeographic studies.

Vents and seeps are environments where biomass and biological production are high compared to that of the surrounding abyssal plains, due to utilization of the expelled reduced compounds by chemoautotrophic microorganisms that constitute the first step of a trophic web independent from sea-surface production. Although organisms exclusively dependent on fluid emissions usually dominate these communities and live close to the expelled fluids, other inhabitants of the neighboring deep-sea environment are attracted by the high food supply and enter these environments. Like anomurans, most of these organisms are filter-feeders, scavengers, or predators. As top predators/scavengers, anomurans are rivalled only in some cases, in particular by the hydrothermal-endemic brachyuran crab family Bythograeidae.

Infraorder Anomura

Superfamily Paguroidea (sensu Forest 1987)

This superfamily comprises the Lithodidae and two families of hermit crabs. Pa-

guridae and Parapaguridae. Only one hermit crab has been reported to date from cold seeps of the Barbados accretionary prism, at depths of 1000–2000 m (K. Olu, pers. obs.), and another one from Monterey Bay seeps at 600–1000 m (J. P. Barry, pers. comm.). The Barbados specimen seems to belong to the genus *Parapagurus* (M. de Saint Laurent, pers. comm.). Although the Monterey Bay hermit crab has not been identified, it is possible that it is also a parapagurid, which are common at these depths.

Family Lithodidae

The first report of the occurrence of Lithodidae in hydrothermal vent or cold-seep habitats, is a "large crab," clearly a lithodid, illustrated in a sketch of the benthic community associated with cold-seeps along the lower Oregon subduction zone at 2037 m depth (Suess et al. 1985, Kulm et al. 1986). Subsequently, Carey et al. (1988) observed *Lopholithodes foraminatus* from a shallower part of this subduction zone. Whether the "large crab" and *L. foraminatus* are the same species is not stated. Tunnicliffe & Jensen (1987) proposed that the deeper water species from the lower zone could be the same *Paralomis* sp. they found at hydrothermal vents in the Juan de Fuca Ridge.

In total, four lithodid crabs have been identified to the species level from cold-seep areas, and the status of four others remains uncertain. The Lithodidae are represented at hydrothermal vents by two species and six occurrences not yet clearly assigned to species. Two of the described species (*Paralomis arethusa* and *P. jamsteci*) are until now known only from reducing environments. No lithodid species is definitely known from both vents and seeps.

Genus *Lithodes* Latreille, 1806

Lithodes manningi Macpherson, 1988

One specimen was collected at 1236 m depth in cold seeps of the Barbados accre-

tionary prism, and was identified by Macpherson (1994). The species is known from depths of 640–777 m in the Caribbean (Macpherson 1988).

Two species of lithodid crabs found at seeps of the Monterey Bay, at 600–1000 m, have been assigned tentatively to the genus *Lithodes* (J. P. Barry, pers. comm.). These crabs are not considered as seep-endemics.

Genus *Lopholithodes* Brandt, 1848

Lopholithodes foraminatus (Stimpson, 1859)

As previously mentioned, Carey et al. (1988) observed dense aggregations of *Lopholithodes foraminatus* while exploring apparently extinct seepage areas of the upper Oregon subduction zone, at a depth of ca. 250 m. There is no mention of this species at active seeps, but it could be the same species as the "large crab" observed at 2037 m by Suess et al. (1985). However, this occurrence would be much deeper than the known depth range of *L. foraminatus*, which is known from British Columbia to southern California, at 0–547 m (Hart 1982).

Genus *Neolithodes* Milne Edwards & Bouvier, 1894

Neolithodes diomedae (Benedict, 1894)

This species represents the first reported occurrence of Lithodidae in hydrothermal vents. Grassle (1986) described it as the most common crab found at the active hydrothermal vents, at 2000 m, in the Guaymas Basin, Gulf of California. It is known from southern California to South Georgia, at depths of 640–2450 m (Macpherson 1988).

Genus *Paralithodes* Brandt, 1848

Based on submersible observations, Sagalevich et al. (1992) reported *Paralithodes* sp., at 350–400 m, on the periphery of active hydrothermal vents on the summit of Piyp Volcano, in the Bering Sea, on dense populations of actinians.

Genus *Paralomis* White, 1856

This is the best represented of the lithodid genera in chemosynthetically-based communities. At least four species have been reported, including two exclusively from reducing habitats. Considering the numerous reports of "*Paralomis* sp." found in the literature, more species are likely to be discovered in the future.

Paralomis arethusa Macpherson, 1994

Paralomis arethusa is one of two lithodid crabs known from cold-seep communities of the Barbados accretionary prism at 1691 m depth. This species is known only from this location (Macpherson 1994).

Paralomis cubensis Chace, 1939

Sassen et al. (1993) produced a photograph of a "crab" (clearly a lithodid) crawling on tubeworms and mussels at the Green Canyon methane seep, on the upper continental slope of the Gulf of Mexico, at 620 m. It was subsequently identified as *Paralomis cubensis*. It is considered as a "vagrant" species of the Gulf of Mexico seeps by Carney (1994), and is not commonly in direct contact with the seep community. *P. cubensis* is known from east Florida to Brazil, at 329–730 m (Macpherson 1988).

Paralomis jamsteci Takeda & Hashimoto, 1990

In hydrothermal areas of the Okinawa Trough, lithodid crabs have been observed on the Minami-Ensei Knoll, at 700 m, where a new species was described as *Paralomis jamsteci* (Hashimoto et al. 1990, Takeda & Hashimoto 1990). This species is living among mytilid beds, near vent openings (Hashimoto et al. 1995). Two other yet unidentified species of *Paralomis* also occur at the Minami-Ensei vents (Hashimoto et al. 1995).

Paralomis multispina (Benedict, 1894)

Horikoshi & Ishii (1985), Hashimoto et al. (1987, 1989), and Ohta (1990b) have described cold-seep communities of Sagami Bay in Japan, at depths of 900–1200 m, where large *Paralomis multispina* and the clams *Calyptogena soyoae* are the dominant species. *P. multispina* is known from Japan to California, at 500–1665 m (Hart 1982).

Paralomis verrilli (Benedict, 1894)

Paralomis verrilli is believed to be the species found at hydrothermal vents of the Iheya Ridge, at 1400 m, in the Mid-Okinawa Trough (S. Ohta, pers. comm.; Ohta 1990a; Kim & Ohta 1991; Hashimoto et al. 1995). Although still to be confirmed, this occurrence would not be surprising as *P. verrilli* is usually found at depths of ca. 1500–3500 m around Japan and from the Bering Sea to California (S. Ohta, pers. comm.). Crabs tentatively assigned to this species were also reported from the Sagami Bay cold-seeps, but in much lower numbers than the dominant *P. multispina* (J. Hashimoto, pers. comm.).

Additional occurrences of Paralomis species.—Several authors have reported the occurrence of lithodid crabs as belonging to the genus *Paralomis*. Most reports have been based on collected specimens. Two yet unidentified species of *Paralomis* occur at the Minami-Ensei vents (Mid-Okinawa Trough), living on mytilids or around bacterial mats, together with the vent endemic *P. jamsteci* (Hashimoto et al. 1995). In the hydrothermal areas of the North-Fiji back-arc basin (2000 m) the "white-coloured lithodid crabs" observed by Jollivet et al. (1989), were later identified as belonging to the genus *Paralomis*, and have also been sampled at 1800 m in venting areas of the Lau back-arc basin (Desbruyères et al. 1994). On the Juan de Fuca ridge in the northern Pacific, the lithodid crab observed and sampled at 1600 m on the Axial Seamount hydrothermal vent area by Tunnicliffe & Jensen (1987), is a species of *Par-*

alomis that co-occurs with the brachyuran majid crab *Macroregonia macrochira*. These authors suggested that this lithodid might be the same species found at the Oregon cold-seeps by Suess et al. (1985). This *Paralomis* sp. and *Paralomis verrilli* (if confirmed) would then be the only lithodid species that occur in both vent and seep environments. Galkin & Moskalev (1990b) also observed a crab closely related to *Paralomis* on the Juan de Fuca ridge.

Remarks on Lithodidae.—The Lithodidae do not seem to be physiologically dependent on the chemosynthetic production of vents or seeps. E. Escobar-Briones (pers. comm.) recently observed that although *Neolithodes diomedae* was seen near bacterial mats and hydrothermal vent structures in the Guaymas Basin, it appears to mainly feed on organic matter of photoautotrophic origin. The opportunistic behavior of this deep-sea scavenger is, however, believed to contribute to the export of hydrothermal material to the surrounding abyssal environment. In other hydrothermal and cold-seep settings, direct evidence exists of lithodid crabs feeding on chemoautotrophic symbiont-containing fauna. Tunnicliffe & Jensen (1987) reported that pieces of vestimentiferan tubes were found in the stomachs of *Paralomis* sp. at Axial Seamount vents. Observations of *P. multispina* and *P. jamsteci* feeding upon live vesicomylid and mytilid bivalves are mentioned by Hashimoto et al. (1989) and Takeda & Hashimoto (1990) in Sagami Bay cold-seeps and Okinawa vents. Suess et al. (1985) described a large lithodid in the Oregon seeps as actively feeding on vesicomylid clams. The *Lithodes* spp. from Monterey Bay seep communities are known to have attacked unsuccessfully vesicomylid clams (J. P. Barry, pers. comm.). Another type of feeding has been proposed for *P. multispina* by Horikoshi & Ishii (1985), who observed this crab actively scooping up and "feeding" on the black reduced mud within the clam beds of Sagami Bay cold-seeps. Most frequently, the Lithodidae occur in greatest densities at vents

and seeps. As there appears to be no other advantage in getting close to such a toxic milieu than the increased food-supply (particularly near hydrothermal vents with high concentrations of hydrogen sulfide and heavy metals, low oxygenation and pH), they can be considered at least to partially feed on chemosynthetically-derived material.

Cold-seep Lithodidae described to date range in depths from 250 to 2037 m. However, one occurrence is known from cold-seep communities of the Nankai Trough, Japan subduction zone, at 3800 m (M. Sibuet, pers. comm.). At hydrothermal vents, the depth range is 350–2000 m. The geographical distribution of these observations is worldwide, with some noticeable exceptions: no Lithodidae have ever been observed near hydrothermal vent areas of the East Pacific Rise (EPR), the Galápagos Rift, nor the Mid-Atlantic Ridge. The crab mentioned by Guinot & Macpherson (1987) from the EPR at 12°35'N, although probably a lithodid, cannot be assigned to a hydrothermal context. It was indeed observed on an off-axis seamount located 18 km from the ridge axis and even farther from the nearest known vent site in this area (P. Chevaldonné, pers. obs.).

Superfamily Galattheoidea

This superfamily includes four families, two of which are represented at deep-sea hydrothermal vents and cold seeps.

Family Galatheidae

Galatheid crabs have been found associated with hydrothermal environments since the first submersible expeditions explored the Galápagos Rift vents (Corliss & Ballard 1977). They have also been known to occur in cold-seep settings since the discovery of this type of community (Paull et al. 1984). Galatheids are familiar members of vent and seep communities but often do not attract as much attention as other spectacular organisms such as the Vestimentifera and

large bivalves. Also, because most galatheid crabs appear similar, to the non-specialists, observations on them are numerous but often vague. Only three of the 11 definite species known so far have been reported from cold-seep communities, and one, *Munidopsis crassa*, from both hydrothermal and seep environments. Reports of the latter, however, seem suspect as one is from the Mid-Atlantic Ridge, and another from the Peru margin. Many occurrences are mentioned only as "galatheid crabs," so much more species are likely to be described in the future.

Genus *Munida* Leach, 1820

Munida magniantennulata Baba & Türkay, 1992

This species was originally described from three specimens collected at hydrothermal vents of the Lau back-arc basin in the southwest Pacific, at a depth of 1750–2000 m (Baba & de Saint Laurent 1992, Baba & Türkay 1992). It was subsequently found in collections from a non-vent environment off Australia (Baba 1994).

Munida microphthalma Milne Edwards, 1880

In the seepage areas of the Barbados accretionary prism, at 1700–2000 m, two different species of Galatheididae have been observed (K. Olu, pers. obs.). Only one has been collected and identified as *M. microphthalma* (M. de Saint Laurent, pers. comm.). Joilivet et al. (1990) earlier reported *Munidopsis* sp. from the same area. They either misidentified *M. microphthalma* from their towed camera pictures, or observed the second and bigger species, which might be a *Munidopsis*. *Munida microphthalma* has been reported from the Atlantic, south of Iceland to Ascension Island, in the Gulf of Mexico, the Caribbean, and the Bay of Biscaya, at depths of 194–2129 m (Wenner 1982).

Genus *Munidopsis* Whiteaves, 1874

This is the most commonly encountered galatheid genus in reducing environments, including at least 10 species, of which six are known so far only from hydrothermal vents. Many authors have reported *Munidopsis* sp. or *Munidopsis*-like galatheid crabs, so again, the list of species is likely to expand.

Munidopsis alvisca Williams, 1988

This so far exclusively hydrothermal-associated species was described by Williams (1988) from widely separated venting areas. *Munidopsis alvisca* occurs at the periphery of hydrothermal areas on the Explorer and Juan de Fuca ridges, at 1545–1800 m, in the northeastern Pacific, and at 2000 m in the Guaymas Basin, Gulf of California (Khodkina 1991). Van Dover et al. (1990) also reported a galatheid crab which might be *M. alvisca*, from vents of the Escanaba Trough on the Gorda Ridge.

Munidopsis beringana Benedict, 1902

A galatheid sampled from cold-seeps of the Middle America Trench at 3700–4000 m west of Mexico has been assigned to *Munidopsis beringana* (E. Macpherson, pers. comm.). The galatheid crabs observed at shallower seep communities (2900 m) might belong to this same species (K. Olu, pers. obs.). There is still some doubt on the determination of this species, as the collected specimens present some variations from other *M. beringana*. This occurrence is also out of the known geographical and depth range of this species, usually found from the Bering Sea to Oregon, at 2800–3276 m (Ambler 1980).

Munidopsis crassa Smith, 1885

As previously mentioned, this species is believed to be present both in cold-seep and hydrothermal settings. Segonzac (1992) reported it from the Snake Pit hydrothermal area, at 3480 m, on the Mid-Atlantic Ridge.

Olu et al. (1996) recently reported *Munidopsis crassa* from cold-seeps of the Peru margin, at 3000–3600 m, although unidentified galatheids were also observed at 5040 m. A comparative examination of Atlantic and Peru specimens is needed to confirm these findings. *M. crassa* was previously only known from the Atlantic, at 2679–5315 m (Wenner 1982).

Munidopsis diomedea (Faxon, 1895)

Munidopsis diomedea was observed near hydrothermal vents of the Guaymas Basin, Gulf of California, at 2000 m depth (Khodkina 1991), along with *M. alvisca*. One of these two species might be the *Munidopsis* sp. mentioned by Lutz (1992) from cold seepages in the same area. *M. diomedea* is common in the Gulf of California, and is known from California to Chile, at 768–3790 m (Haig & Wicksten 1975).

Munidopsis lauensis Baba & de Saint Laurent, 1992

Munidopsis lauensis occurs with *Munida magniantennulata* at deep-sea vents of the Lau back-arc basin, in southwest Pacific, at 1750 m. It is also found at 2000 m in hydrothermal sites of the nearby North-Fiji back-arc basin (Baba & de Saint Laurent 1992). To date, this species is exclusively known from hydrothermal areas.

Munidopsis lentigo Williams & Van Dover, 1983

This hydrothermal vent endemic is considered a "high temperature" species (Williams & Van Dover 1983) as it seems to be the galatheid that lives closest to high temperature fluid venting. It has been found only at vent sites of the East Pacific Rise at 21°N, 2600 m depth.

Munidopsis marianica Williams & Baba, 1989

Munidopsis marianica is another apparently vent-endemic from the 3600–3700 m

deep hydrothermal sites of the Mariana back-arc basin, western Pacific, where it lives in 10–25°C waters among dense carpets of actinians (Williams & Baba 1989, Hessler & Lonsdale 1991).

Munidopsis sonne Baba, 1995

Munidopsis sonne is only known from two specimens collected at active vents of the North Fiji Basin, at 1992 m (Baba 1995).

Munidopsis starmer Baba & de Saint Laurent, 1992

Munidopsis starmer also seems restricted to hydrothermal vents (Baba & de Saint Laurent 1992) and occurs at vent sites of the North-Fiji Basin, at 2750 m. In the same area, *M. lauensis*, *M. sonne*, and two species of Chirostylidae are also present.

Munidopsis subsquamosa Henderson, 1885

Munidopsis subsquamosa is believed to be a complex of deep-sea cosmopolitan species (Van Dover 1986), which explains its considerable geographic range. Although this complex clearly needs a complete re-examination and taxonomic work at the molecular level, we will simply call it here *M. subsquamosa*. It was the first galatheid species observed in a chemosynthetically-based community, and is found at almost every vent location in the eastern Pacific, in a depth of ca. 2600 m (de Saint Laurent 1984, Hessler et al. 1985, Van Dover et al. 1985). At 21°N on the East Pacific Rise (EPR), it occurs with *M. lentigo*, but inhabits colder waters. It is the only species observed at 13°N (EPR) and sites of the Galápagos Rift, and has also been collected from the EPR at 10–12°N (Van Dover & Hessler 1990) and 9°50'N (Kaartvedt et al. 1994). At the latter location, Lutz (1992) suggested that there might be two different species of *Munidopsis*.

Additional occurrences of Munidopsis

species.—Many reports of “*Munidopsis* sp.” exist from a great variety of hydrothermal and seepage areas. Hydrothermal occurrences include the EPR at 17–20°S (Van Dover & Hessler 1990); three locations in the Mid-Okinawa back-arc basin, the Iheya Ridge at 1400 m (Ohta 1990a, Kim & Ohta 1991), the Izena Calderon at 1400 m (Hashimoto et al. 1995), and the Minami-Ensei Knoll at 700 m (Hashimoto et al. 1990, 1995); Manus back-arc basin in the southwest Pacific at 2500 m (Galkin 1992); TAG area on the Mid-Atlantic Ridge (Galkin & Moskaliev 1990a); and Broken Spur area farther north on this same ridge (Murton et al. 1995). Reports from cold-seeps include the Nankai Trough in the Japanese Trench at 3800 m (Laubier et al. 1986), carbonate seeps of Enshu-nada, Japan, at 1000–1220 m (Ohta et al. 1995), and the Laurentian Fan at 3850 m (Mayer et al. 1988).

In Monterey Bay, cold-seep communities occur at two different bathymetric levels, at 3000–3600 m (Embley et al. 1990) and 600–1000 m (J. P. Barry, pers. comm.). At least two different species have been observed so far, possibly of two different genera. At deeper sites, a single species has been found and tentatively assigned to the genus *Munidopsis* by Embley et al. (1990), but could also be a species of *Munida* according to J. P. Barry (pers. comm.). At shallower seeps (600–1000 m), two different species of Galatheidae are known, one of which might be the same species observed deeper, and the other apparently is a seep endemic that might belong to the genus *Munidopsis* (J. P. Barry, pers. comm.).

In the Gulf of Mexico seep communities, MacDonald et al. (1989) reported a possibly undescribed species of *Munidopsis* from the Bush Hill site, at 540 m, on the Louisiana Slope. At different seepage depths on the slope (400–1000 m and 2200 m), Carney (1994) indicated two *Munidopsis* spp. (including one seep endemic), different from the “background” galatheids. One of these is probably the Bush Hill species. *Muni-*

dopsis spp. are much more common than the chirostylid *Eumunida picta* that also occurs at the 400–1000 m sites, and they live in close association with mytilid bivalves and vestimentiferan tubeworms. At 3270 m, in cold-seeps of the Florida Escarpment, Hecker (1985) has reported a large and numerous white *Munidopsis* sp. that has not been seen far outside the seep communities.

Unconfirmed reports of *Munidopsis*-like galatheids include those from the hydrothermal vents of the Piyp volcano, at 800 m, in the Bering Sea (Sagalevich et al. 1992). In the region of the Barbados accretionary prism, *Munidopsis*-like galatheids have also been observed associated with cold seeps on mud volcanoes, at 4710–4980 m (K. Olu, pers. obs.), and galatheids tentatively assigned to *Munidopsis* were reported by Jollivet et al. (1990), at shallower cold-seep sites (1000–2000 m), in the southern part of the prism.

Family Chirostylidae

Chirostylid crabs are represented in chemosynthetic communities by two genera and three species. This family is frequently overlooked by non-specialist observers when reporting the occurrence of “galatheids.”

Genus *Eumunida* Smith, 1883

Eumunida picta Smith, 1883

This species is considered as a rare vagrant in cold-seeps of the Louisiana slope, at 400–1000 m depth (Carney 1994). It has been reported from Massachusetts to Colombia, at 200–600 m (de Saint Laurent & Macpherson 1990).

Genus *Uroptychus* Henderson, 1888

Baba & de Saint Laurent (1992) have described two new species only known from vents of the North-Fiji Basin.

Uroptychus bicavus Baba & de Saint
Laurent, 1992

Uroptychus bicavus is known from a
depth of 2750 m.

Uroptychus thermalis Baba & de Saint
Laurent, 1992

Uroptychus thermalis occurs at depth of
2000 m.

Additional occurrences of Galatheoidea.—Several authors have reported the occurrence of "galatheid crabs" or "squat lobsters" that cannot be assigned with certainty to a family. These reports are from hydrothermal areas of the EPR at 21°30'S (Renard et al. 1985), 23°30'S and 26°S (Marchig & Gundlach 1987), the Gulf of Aden (Juniper et al. 1990) and the Edison Seamount in the southwestern Pacific (Herzig et al. 1994), and from cold seeps of Enshu-nada, Japan, at 1000–1220 m (Ohta et al. 1995).

Remarks on Galatheidae and Chirostyliidae.—Like Lithodidae, Galatheidae and Chirostyliidae are generally not considered to be dependent on the chemically reduced fluids emitted at vents and seeps. Their representatives are often restricted to the periphery of the sites, where they are believed to be opportunistic species taking advantage of increased productivity. However, there is a significant number of species that seem to be endemic to hydrothermal vents or cold-seeps, and some of them even appear to be adapted to this harsh environment, not just the periphery. Van Dover (1986) observed that gravid females of the hydrothermal *Munidopsis subsquamosa* seemed to live under higher temperature conditions than males. Although this species is not restricted to vent areas, this behaviour was interpreted as a possible adaptation to improve reproductive efficiency. Galatheids also seem to adapt relatively well to hypoxic conditions, such as those encountered in reducing habitats. In some British Columbia fjords, for instance, dense aggregations of *Munida quadrispina* are consistently found

at low oxygen levels, where most other invertebrates of the fjords cannot compete for food and space (Burd & Brinkhurst 1984). Stable isotope analyses led Van Dover & Fry (1989) and E. Escobar-Briones (pers. comm.) to characterize *Munidopsis subsquamosa* and *M. alvisca*, of the Galápagos and Guaymas hydrothermal vents, as having a mixed diet partly including a sulfur-based source of carbon. Similar analyses on the Iheya Ridge *Munidopsis* sp. also show at least a partial nutritional dependence on chemosynthetic processes (Kim et al. 1989, Kim & Sakai 1991). At the Monterey Bay cold-seeps, an apparently seep endemic galatheid is found grazing on mats of the filamentous bacteria *Beggiatoa*, and is even covered with the bacterial filaments (J. P. Barry, pers. comm.).

Galatheids and chirostylids might also act as vectors for the export of organic matter of hydrothermal origin in the deep sea. They might disperse more efficiently than lithodids, due to their swimming abilities, and can also easily detect new food sources. Two shark carcasses placed 100 m from a vent site at 13°N on the EPR (Fig. 1) attracted hundreds of *Munidopsis subsquamosa* within a day (D. Desbruyères, pers. comm.). These characteristics might also favor dispersal of non-planktonic developmental stages of vent and seep species. Carney (1994) reported that *Munidopsis* sp. of the Gulf of Mexico seepage areas are often covered with juvenile mussels, and may be an important means of post-settlement dispersal for seep endemic sessile taxa. Such phoretic processes might also occur in hydrothermal polychaetes (Tunnicliffe & Jensen 1987, Zal et al. 1995).

Galatheidae are found in virtually every hydrothermal or cold-seep environment, as well as in other types of reducing habitats such as whale carcasses (Bennett et al. 1994, Wada et al. 1994) or decomposing wood (Williams & Baba 1989). They do not seem to be limited by depth, as their occurrence is reported from as deep as 5040 m, in the deepest cold-seep communities



Fig. 1. Attraction of *Munidopsis subquamosa*, a galatheid crab commonly found in deep-sea hydrothermal vents of the eastern Pacific, to shark carcasses deposited 100 m from a vent site at 13°N, on the East Pacific Rise (2600 m).

(Olu et al. 1996). They are also associated with the shallowest occurrence of vestimentiferans known to date, at 82 m, in the cold-seep site of Kagoshima Bay, Japan (Hashimoto et al. 1993).

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Literature Cited

- Ambler, J. W. 1980. Species of *Munidopsis* (Crustacea, Galatheidae) occurring off Oregon and in adjacent waters.—*Fishery Bulletin* 78:13–34.
- Baba, K. 1994. Deep-sea galatheid crustaceans (Anomura: Galatheidae) collected by the "Cidaris I" expedition off central Queensland, Australia.—*Memoirs of the Queensland Museum* 35:1–21.
- . 1995. A new squat lobster (Decapoda: Anomura: Galatheidae) from an active thermal vent area in the North Fiji Basin, SW Pacific.—*Crustacean Research* 24:188–193.
- , & M. de Saint Laurent. 1992. Chirostyliid and galatheid crustaceans (Decapoda: Anomura) from active thermal vent areas in the southwest Pacific.—*Scientia Marina* 56:321–332.
- , & M. Türkay. 1992. *Munida magniantennulata*, a new deepsea decapod crustacean from active thermal vent areas of Valu-Fa-Ridge in the Lau Basin, SW-Pacific (Anomura: Galatheidae).—*Senckenbergiana Maritima* 22:203–210.
- Benedict, J. E. 1894. Descriptions of new genera and species of crabs of the family Lithodidae, with notes on the young of *Lithodes camtschaticus* and *Lithodes brevipes*.—*Proceedings of the United States National Museum* 17:479–488.
- . 1902. Descriptions of a new genus and forty-six new species of crustaceans of the family Galatheidae, with a list of the known marine species.—*Proceedings of the United States National Museum* 26:243–344.
- Bennett, B. A., C. R. Smith, B. Glaser, & H. L. Maybaum. 1994. Faunal community structure of a chemoautotrophic assemblage on whale bones in the deep northeast Pacific Ocean.—*Marine Ecology Progress Series* 108:205–223.
- Brandt, J. F. 1848. Die Gattung *Lithodes* Latreille nebst vier neuen ihr verwandten von Wosnesenski entdecken, als Typen einer besondern Unterabtheilung (Tribus Lithodea) der Edwards'schen Anomuren.—*Bulletin de la Classe Physico-Mathématique de l'Académie Impériale des Sciences de Saint-Petersbourg* 7:171–175.
- Carey, A. G., Jr., D. L. Stein, G. L. Taghon, & A. E. DeBevoise. 1988. Biology and ecology of the Oregon continental shelf edge associated with the accretionary prism. Pp. 137–149 in M. P. De Luca & I. Babb, eds., *Global venting, mid-water, and benthic ecological processes*. NOAA, Groton, Connecticut, 442 p.
- Carney, R. S. 1994. Consideration of the oasis analogy for chemosynthetic communities at Gulf of Mexico hydrocarbon vents.—*Geo-Marine Letters* 14:149–159.
- Chace, F. A., Jr. 1939. Reports on the scientific results of the first Atlantis Expedition to the West Indies, under the joint auspices of the University of Havana and Harvard University. Preliminary descriptions of one new genus and seventeen new species of decapod and stomatopod Crustacea.—*Memorias de la Sociedad Cubana de Historia Natural* 13:31–54.
- Corliss, J. B., & R. D. Ballard. 1977. Oases of life in the cold abyss.—*National Geographic* 152:440–453.
- Desbruyères, D., A. M. Alayse, S. Ohta, & the scientific parties of BIOLAU and STARMER cruises. 1994. Deep-sea hydrothermal communities in Southwestern Pacific back-arc basins (the North Fiji and Lau Basins): composition, microdistribution and food web.—*Marine Geology* 116:227–242.
- Embley, R. W., et al. 1990. Geological setting of chemosynthetic communities in the Monterey Fan Valley system.—*Deep-Sea Research* 37:1651–1667.
- Faxon, W. 1895. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission steamer "Albatross," during 1891 during Lieut.-Commander Z. L. Tanner, U. S. N., commanding. XV. The stalk-eyed Crustacea.—*Bulletin of the Museum of Comparative Zoology at Harvard College* 18:1–292.
- Forest, J. 1987. Les Pylochelidae ou "pagures symétriques" (Crustacea: Coenobitoidea). Résultats des campagnes MUSORSTOM.—*Mémoires du Muséum National d'Histoire Naturelle, Série A, Zoologie* 137:1–274.
- Galkin, S. V. 1992. Bottom fauna of the Manus Basin

- hydrothermal—*Okeanologiya* 22:1102–1110 (In Russian with English summary)
- & L. I. Moskalov 1990a. Hydrothermal fauna of the Mid Atlantic Ridge—*Okeanologiya* 30:624–627
- & ——— 1990b. Faunal composition at hydrothermal vents of the Juan de Fuca Ridge. Pp. 157–166. *In* A. P. Lisitsin, ed. *Geological processes and hydrothermalism on the Juan de Fuca Ridge*. Nauka, Moscow (in Russian)
- Grassle J. F. 1986. The ecology of deep-sea hydrothermal vent communities—*Advances in Marine Biology* 23:301–362
- Guinot D. & E. Macpherson 1987. Une faune de mer qui n'en est pas une—*L'Univers du Vivant* 24:111–114
- Haug J. & M. K. Wicksten 1975. First record and range extensions of crabs in California waters—*Bulletin of the Southern California Academy of Sciences* 74:100–104
- Hart J. I. L. 1982. Crabs and their relatives of British Columbia. British Columbia Provincial Museum Handbook 40. Ministry of Provincial Secretary and Government Services, Victoria. British Columbia 267 p.
- Hashimoto J., K. Fujikura & H. Hotta 1990. Observations of deep-sea biological communities at the Minami Ensei knoll—*JAMSTECR Deep-sea Research* 6:167–179 (In Japanese with English summary)
- , T. Miura, K. Iijukura & J. Otsake 1995. Discovery of vestimentid and tube-worms in the euphotic zone—*Zoological Science* 10:106–1067
- , S. Ohta, K. Iijukura & T. Miura 1995. Microdistribution pattern and biogeography of the hydrothermal vent communities of the Minami Ensei Knoll in the Mid-Casawa Trough, Western Pacific—*Deep Sea Research* 42:577–598
- , T. Tanaka, H. Hotta, S. Matsuzawa & H. Sakai 1990. Deep-sea communities dominated by the giant clam *Calypso-gena yoae* along the slope of Hatsushima Island, Sagami Bay, central Japan—*Palaeogeography Palaeoclimatology Palaeoecology* 71:179–192
- , J. F. Tanaka, S. Matsuzawa & H. Hotta 1987. Surveys of the deep-sea communities dominated by the giant clam *Calypso-gena yoae* along the slope of Hatsushima Island, Sagami Bay—*JAMSTECR Deepsea Research Special Issue* 3:37–50 (in Japanese with English summary)
- Hecker B. 1985. Fauna of a cold sulfur seep in the Gulf of Mexico: comparison with hydrothermal vent communities and evolutionary implications—*Bulletin of the Biological Society of Washington* 6:467–472
- Henderson J. R. 1988. Diagnoses of the new species of Galatheida collected during the Challenger expedition—*Annals and Magazine of Natural History Series 5* 16:407–421
- 1888. Report on the Anomura collected by H.M.S. Challenger during the years 1873–1876—*Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–1876 (LXIX)* 26:1–221
- Herzig P. et al. 1994. Submarine volcanism and hydrothermal venting studied in Papua New Guinea—*Fos Transactions American Geophysical Union* 75:513–516
- Hessler R. R. & P. F. Lonsdale 1991. Biogeography of Mariana Trough hydrothermal vent communities—*Deep-Sea Research* 38:155–199
- , W. M. Smith Jr. & C. H. Keller 1985. Spatial and temporal variation of giant clams, tube worms, and mussels at deep-sea hydrothermal vents—*Bulletin of the Biological Society of Washington* 6:41–428
- Horikoshi M. & T. Ishii 1985. Mode of occurrence of *Calypso-gena yoae* observed from the Japanese submarine cable Shinkai 2000 in Sagami Bay—*Deep-Sea Newsletter* 1:14–16
- Jollivet D., J. C. Fauvel, R. Riboulard, D. Desbruyeres & G. Blanc 1990. Composition and spatial organization of a cold seep community on the south Barbados tectonic prism: tectonic, geochemical and sedimentary context—*Progress in Oceanography* 24:25–45
- et al. 1989. Premières observations de communautés animales associées à hydrothermalisme artificiel du bassin Nord djien—*Comptes Rendus de l'Académie des Sciences de Paris, Série III* 309:501–505
- Jumper S. K., V. Tunnicliffe & D. Desbruyeres 1990. Regional scale features of the northeast Pacific East Pacific Rise and out of Aden vent communities. Pp. 265–278. *In* R. McMurtry, ed. *Gorda Ridge and floor spreading: the United States Exclusive Economic Zone*. *Proceedings of the National Academy of Sciences* 87:1000–1004
- Kaattvedt C., L. van Doren & J. M. Lineaux P. H. Wiené & S. M. Boulben 1994. Amphipods on a deep-sea hydrothermal vent chimney—*Deep Sea Research* 41:179–199
- Knodkna I. V. 1991. Deep-sea species of the genus *Mutuoopsis* (Decapoda: Alpheoidea: Galatheididae) from the hydrothermal vents of the Pacific—*Zoologicheskii Zhurnal* 77:77–79 (In Russian with English summary)
- Kuo D. S. & S. Ohta 1991. Comparative observations and comparison of biological communities of the two hydrothermal vents on the Iheya Ridge of the Mid-Casawa Trough—*JAMSTECR Deepsea Research* 7:221–233 (in Japanese with English summary)
- , E. Otsake & H. Sakai 1991. Carbon isotopic ratios

- of deep-sea hydrothermal vent animals at the Mid-Okinawa Trough.—*Ocean Research* 13: 19–30.
- , J. Hashimoto, F. Yanagisawa, & S. Ohta. 1989. Sulfur isotopic ratios of hydrothermal vent-animals at Ogasawara Arc and Mid-Okinawa Trough—evidence for microbial origin of hydrogen sulfide at low-temperature submarine hydrothermal areas.—*Geochemical Journal* 23:195–208.
- Kulm, L. D., et al. 1986. Oregon subduction zone: venting, fauna, and carbonates.—*Science* 231: 561–566.
- Latreille, P. A. 1806. *Genera Crustaceorum et Insectorum secundum Ordinem naturalem in Familiis disposita, iconibus exemplis plurimis explicata*.—Apud Amand Koenig Bibliopolam, Parisiis et Argentorati 1:1–302.
- Laubier, L., S. Ohta, & M. Sibuet. 1986. Découverte de communautés animales profondes durant la campagne franco-japonaise KAIKO de plongées dans les fosses de subduction autour du Japon.—*Comptes Rendus de l'Académie des Sciences de Paris, Série III* 303:25–29.
- Leach, W. E. 1820. *Gafatécadées*.—*Dictionnaire des Sciences Naturelles, Paris* 18:48–56.
- Lutz, R. A. 1992. The biology of deep-sea vents and seeps—Alvin's Magical Mystery Tour.—*Oceanus* 34:75–83.
- MacDonald, I. R., G. S. Boland, J. S. Baker, J. M. Brooks, M. C. Kennicutt II, & R. R. Bidigare. 1989. Gulf of Mexico hydrocarbon seep communities II. Spatial distribution of seep organisms and hydrocarbons at Bush Hill.—*Marine Biology* 101:235–247.
- Macpherson, E. 1988. Revision of the family Lithodidae Samouelle, 1819 (Crustacea, Decapoda, Anomura) in the Atlantic Ocean.—*Monografias de Zoologia Marina* 2:9–153.
- . 1994. Occurrence of two lithodid crabs (Crustacea: Decapoda: Lithodidae) in the cold seep zone of the South Barbados accretionary prism.—*Proceedings of the Biological Society of Washington* 107:465–468.
- Marchig, V., & H. Gundlach. 1987. Ore formation at rapidly diverging plate margins results of cruise GEOMETEP 4.—*BGR Circular* 4:3–22.
- Mayer, L. A., A. N. Shor, J. Hughes Clarke, & D. J. W. Piper. 1988. Dense biological communities at 3850 m on the Laurentian Fan and their relationship to the deposits of the 1929 Grand Banks earthquake.—*Deep-Sea Research* 35: 1235–1246.
- Milne Edwards, A. 1880. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico and in the Caribbean Sea, 1877, 78, 79, by the U.S. Coast Survey Steamer Blake, Lieut. Commander C. D. Sigsbee, U. S. N., and Commander J. R. Bartlett, U. S. N., Commanding. VIII. Etudes préliminaires sur les crustacés.—*Bulletin of the Museum of Comparative Zoology at Harvard College* 8:1–68.
- , & E. L. Bouvier. 1894. *Neolithodes*, genre nouveau de la sous-famille des Lithodines.—*Bulletin de la Société Zoologique de France* 19: 120–122.
- Murton, B. J., Van Dover, C. L., & Southward, E. 1995. Geological setting and ecology of the Broken Spur hydrothermal vent field: 29°10'N on the Mid-Atlantic Ridge. Pp. 33–41 in L. M. Parson, C. L. Walker, & D. R. Dixon, eds., *Hydrothermal vents and processes*. Geological Society, London, 411 p.
- Ohta, S. 1990a. Deep-sea submersible survey of the hydrothermal vent community on the northeastern slope of the Iheya ridge, the Okinawa Trough.—*JAMSTECTR Deepsea Research* 6: 145–156 (in Japanese with English summary).
- . 1990b. Ecological observations and remarks on the cold seep communities in Sagami Bay, central Japan.—*JAMSTECTR Deepsea Research* 5:181–195 (in Japanese with English summary).
- . 1995. Search for the chemosynthetic ecosystem in the bathyal zone of Enshu-nada. Report of the observations of the dive 771 of "Shinkai 2000".—*JAMSTEC Journal of Deep Sea Research* 11:219–225 (in Japanese with English summary).
- Olu, K., A. Duperret, M. Sibuet, J. P. Foucher, & A. Fiala-Médioni. 1996. Structure and spatial distribution of cold seep communities along the Peruvian active margin: relationship with geological and fluid patterns.—*Marine Ecology Progress Series* 132:109–125.
- Paull, C. K., et al. 1984. Biological communities at the Florida Escarpment resemble hydrothermal vent taxa.—*Science* 226:965–967.
- Renard, V., R. Hékinian, J. Francheteau, R. D. Ballard, & H. Backer. 1985. Submersible observations at the axis of the ultra-fast-spreading East Pacific Rise (17°30' to 21°30'S).—*Earth and Planetary Science Letters* 75:339–353.
- Sagalevich, A. M., P. V. Torokhov, V. V. Matveyenkov, S. V. Galkin, & L. I. Moskalev. 1992. Hydrothermal manifestations at Piyp submarine volcano, Bering Sea.—*International Geology Review* 34:1200–1209.
- Saint Laurent, M. de. 1884. Crustacés décapodes d'un site hydrothermal actif de la dorsale du Pacifique oriental (13° Nord), en provenance de la campagne française Biocytherm.—*Comptes Rendus de l'Académie des Sciences de Paris, Série III* 299:355–360.
- , & E. Macpherson. 1990. Les espèces du gen-

- re *Eumunida* Smith, 1883 (Crustacea: Decapoda: Chirostyliidae).—*Journal of Natural History* 24:647–666.
- Sassen, R., J. M. Brooks, I. R. MacDonald, M. C. Kennicutt II, N. L. Guinasso Jr., & A. G. Requejo. 1993. Association of oil seeps and chemosynthetic communities with oil discoveries, upper continental slope, Gulf of Mexico.—*Transactions of the Gulf Coast Association of Geological Societies* 43:349–355.
- Segonzac, M. 1992. Les peuplements associés à l'hydrothermalisme océanique du Snake Pit (dorsale médio-atlantique; 23°N, 3480 m): composition et microdistribution de la mégafaune.—*Comptes Rendus de l'Académie des Sciences de Paris, Série III* 314:593–600.
- Smith, S. I. 1883. Preliminary report on the Brachyura and Anomura dredged in deep water off the south coast of New England by the United States Fish Commission in 1880, 1881 and 1882.—*Proceedings of the United States National Museum* 6:1–57.
- . 1885. On some new or little known decapod crustacea from recent Fish Commission dredging off the east coast of the United States.—*Proceedings of the United States National Museum* 7:493–511.
- Stimpson, W. 1859. Notes on North American Crustacea in the Museum of the Smithsonian Institution I.—*Annals of the Lyceum of Natural History of New York* 7:49–93.
- Suess, E., et al. 1985. Biological communities at vent sites along the subduction zone off Oregon.—*Bulletin of the Biological Society of Washington* 6:475–484.
- Takeda, M., & J. Hashimoto. 1990. A new species of the genus *Paralomis* (Crustacea, Decapoda, Lithodidae) from the Minami-Ensei Knoll in the mid-Okinawa trough.—*Bulletin of the National Science Museum, Tokyo, Series A* 16:79–88.
- Tunnicliffe, V., & R. G. Jensen. 1987. Distribution and behaviour of the spider crab *Macroregonia macrochira* Sakai (Brachyura) around the hydrothermal vents of the northeast Pacific.—*Canadian Journal of Zoology* 65:2443–2449.
- Van Dover, C. L. 1986. A comparison of stable isotope ratios ($^{18}\text{O}/^{16}\text{O}$ and $^{13}\text{C}/^{12}\text{C}$) between two species of hydrothermal vent decapods (*Alvinocaris lusca* and *Munidopsis subsquamosa*).—*Marine Ecology Progress Series* 31:295–299.
- , J. R. Factor, A. B. Williams, & C. J. Berg Jr. 1985. Reproductive patterns of decapod crustaceans from hydrothermal vents.—*Bulletin of the Biological Society of Washington* 6:223–227.
- , & B. Fry. 1989. Stable isotopic compositions of hydrothermal vent organisms.—*Marine Biology* 102:257–263.
- , J. F. Grassle, & M. Boudrias. 1990. Hydrothermal vent fauna of Escanaba Trough (Gorda Ridge). Pp. 285–287 in G. R. McMurray, ed., *Gorda Ridge: a seafloor spreading center in the United States Exclusive Economic Zone*. Springer-Verlag, New York.
- , & R. R. Hessler. 1990. Spatial variation in faunal composition of hydrothermal vent communities on the East Pacific Rise and Galapagos spreading center. Pp. 253–264 in G. R. McMurray, ed., *Gorda Ridge: a seafloor spreading center in the United States Exclusive Economic Zone*. Springer-Verlag, New York.
- Wada, H., T. Naganuma, K. Fujioka, H. Kitazato, K. Kawamura, & Y. Akazawa. 1994. The discovery of the Torishima Whale Bone Animal Community (TOWBAC) and its meaning: the results of revisit dives by the "Shinkai 6500."—*JAMSTEC Journal of Deep Sea Research* 10:37–47 (in Japanese with English summary).
- Wenner, E. L. 1982. Notes on the distribution and biology of Galatheidae and Chirostyliidae (Decapoda: Anomura) from the Middle Atlantic Bight.—*Journal of Crustacean Biology* 2:360–377.
- White, A. 1856. Some remarks on Crustacea of the genus *Lithodes* with a brief description of a species apparently hitherto unrecorded.—*Proceedings of the Zoological Society of London* 1856: 132–135.
- Whiteaves, J. F. 1874. On recent deep-sea dredging operations in the Gulf of St. Lawrence.—*American Journal of Science, Series 3* 7:210–219.
- Williams, A. B. 1988. New marine decapod crustaceans from waters influenced by hydrothermal discharge, brine, and hydrocarbon seepage.—*Fishery Bulletin* 86:263–287.
- , & K. Baba. 1989. New squat lobsters (Galatheidae) from the Pacific Ocean: Mariana back-arc basin, East Pacific Rise, and Cascadia Basin.—*Fishery Bulletin* 87:899–910.
- , & C. L. Van Dover. 1983. A new species of *Munidopsis* from submarine thermal vents of the East Pacific Rise at 21°N (Anomura: Galatheidae).—*Proceedings of the Biological Society of Washington* 96:481–488.
- Zal, E., D. Jollivet, P. Chevaldonné, & D. Desbruyères. 1995. Reproductive biology and population structure of the deep-sea hydrothermal vent worm *Paralvinella grasslei* (Polychaeta: Alvinellidae) at 13°N on the East Pacific Rise.—*Marine Biology* 122:637–648.