Chapter 10
Unusual Habitats and Organisms Associated with the Cold Seeps of the Gulf of Mexico

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10.1 Unusual Habitats

10.1.1 Geological Setting

The northern Gulf of Mexico continental slope is part of perhaps the most dynamic and structurally complex passive margin in today's oceans. The geologic framework promotes expulsion of fluids and gases from the deep subsurface to the modern seafloor. This framework results from the deposition of enormous volumes

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of river-borne sediment over thick and malleable salt deposits. As part of the Triassic rifting that separated North America, Africa, and South America, the Gulf of Mexico was created. During the mid-to-late Jurassic (~175–145 million years ago) a thick salt unit, the Louann Salt, was deposited in the Gulf (Brooks et al. 1987). This period was characterized by an arid climate. At that time the embryonic Gulf was composed of a complex of individual basins and structural arches, much like the present Red Sea and its gulfs. A high evaporation rate and restricted marine basins led to the creation of thick salt deposits. After salt formation, the Gulf became a shallow basin with extensive algal-rich carbonate tidal flats, similar to today's Persian Gulf and its flanking environments. These late Jurassic and early Cretaceous deposits (~150–100 million years ago), now deeply buried, are known source rocks for a significant part of Gulf's rich oil reserves (Salvador 1987). From the late Cretaceous period which followed to modern times, rivers draining the North American continental interior have delivered large volumes of sediment to the northwestern and northern Gulf. The initiation of this siliciclastic sedimentation during late Cretaceous times corresponded to the rise of the Rocky Mountains in western North America. As a consequence of this massive influx of sediment, underlying salt deposits were deformed into diapirs, tabular salt masses, salt tongues, thrust sheets, and many other geometries (Humphris 1979; Peel et al. 1995). Salt deformation is still an on-going process. Thickening of the southward building siliciclastic sediment wedge and on-going salt deformation create both deep-seated and shallow faults (Brooks et al. 1987; Aharon et al. 1992). These faults function as migration pathways for hydrocarbons generated in the deep subsurface to shallower subsurface reservoirs (Kennicutt et al. 1988). In addition, when these faults provide a clear migration route to the seafloor, they are manifest as hydrocarbon seeps or more dynamic fluid vents.

Across the northern Gulf's continental slope, the major geomorphic elements are smooth, intraslope sedimentary basins separated and bordered by higher relief areas of complex seafloor consisting of ridges and domes usually supported by salt in the shallow subsurface (Fig. 10.1, Plate 20). Features resulting from fluid and gas expulsion are of a much smaller scale than the intraslope basins and bordering ridges and domes. These seep- and vent-related features and the faults that function as the hydrocarbon conduits are concentrated along the flanks of the intraslope sedimentary basins. Features such as mounds of various types, mud volcanoes, mud flows, pockmarks, brine pools, and asphalt seeps result from the expulsion process (Roberts 2001). Using the vast 3D-seismic database that has been developed in support of oil and gas exploration and production in the northern Gulf of Mexico, many sites of fluid-gas expulsion have been localized on the seafloor. As is illustrated by the surface reflectivity map of Fig. 10.2, which was generated from 3D-seismic data, the areas of seepage are "bright spots" of high reflectivity. They are distinct from the surrounding seafloor and result from hard bottom conditions. These sites may take on many forms, including some of the more spectacular occurrences of brine pools, asphalt seeps, and barite chimneys. The presence of such a diversity of geological settings helps to establish the Gulf of Mexico as an excellent natural laboratory for the study of seep systems that may serve as a reference for future work in other known and as-yet-to-be discovered seep systems around the world.

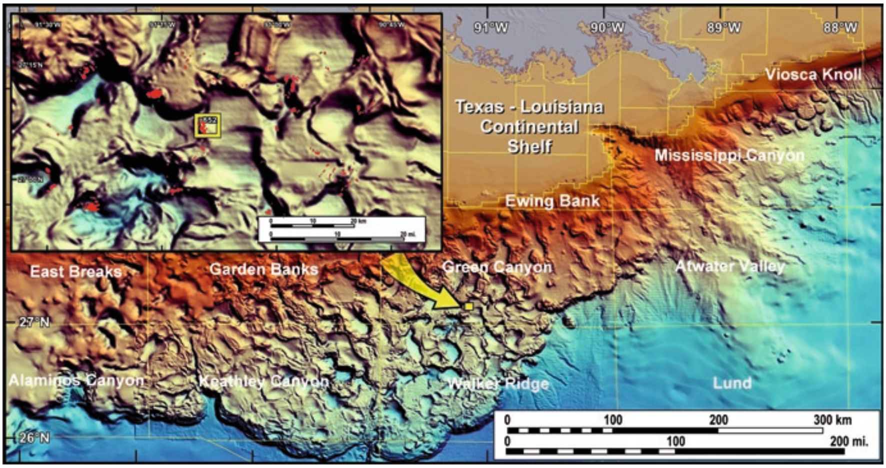

Fig. 10.1 Multibeam bathymetry of the northern Gulf's continental slope, which has been enhanced for a 3D-effect, illustrates the complex of intraslope sedimentary basins (smooth areas) and flanking rough topography comprised of domes and ridges. A color plate of this figure can be found in Appendix (Plate 20)

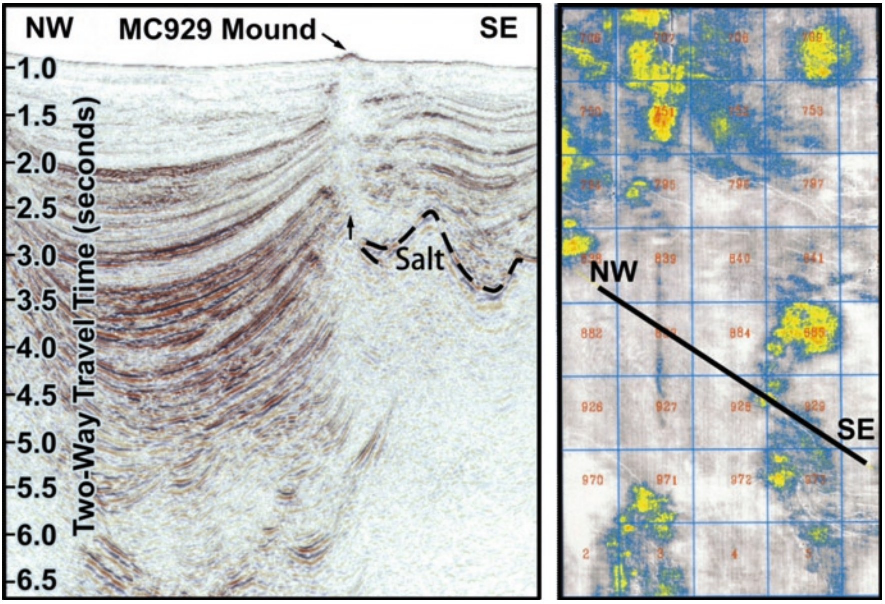

Fig. 10.2 The 3D-seismic surface reflectively map of this figure illustrates a series of seafloor "bright spots" that represent hydrocarbon seep sites. These surface reflectively anomalies are arranged at the flanks of sedimentary basins. The NW-SE oriented seismic cross section illustrates a thick sedimentary basin and the MC 929 mound on the flank of the basin. A distinct vertical fluid-gas migration pathway is shown as an acoustically amorphous zone from the edge of subsurface salt to the seafloor. The MC 929 mound has resulted from the expulsion process. A color plate of this figure can be found in Appendix (Plate 21)

10.1.2 Brine Pools

Hypersaline brine is present on the seafloor of the Gulf of Mexico in numerous locations. This brine is formed from the interaction of pore waters with relatively shallow salt bodies (Reilly et al. 1996). The mobile salt compresses the overlying sediment layers resulting in de-watering of the sediments and a subsequent increase in both salinity and hydrocarbon concentration as the fluids migrate towards the surface, or laterally along density gradients in areas of high bathymetric relief (Roberts and Carney 1997). When these fluids reach the seafloor they may form streams of brine usually in the form of darkly colored anoxic sediments, but may also pool in local depressions formed by salt withdrawal or pockmark craters. The degree of mixing with the overlying seawater is a function of the salinity of the brine and seepage rate with very slow seepage resulting in gradients of salinity such as found at the Orca Basin (Brooks et al. 1990), and high salinity leading to distinct density interfaces such as the brine pool NR1 in Green Canyon lease block 233 (MacDonald et al. 1990) and the brine lake in Alaminos Canyon 601 (Roberts et al. 2007).

The Orca Basin site is a diffuse brine basin descending from 2,000 to 2,400 m depth (Brooks et al. 1990). Below approximately 2,200 m, the salinity gradually increases until it reaches over 200 ppt at the bottom of the basin with very gradual mixing by diffusion with the overlying water column. The megafauna surrounding the basin decreases as the salinity increases and oxygen concentration declines until the community is dominated almost exclusively by hexactinellid sponges with a few holothurians (*Benthodytes typica*) also occasionally present. At salinities above 65 ppt, even these organisms are excluded and the epibenthos appeared entirely depauperate.

The most well-known brine pool of the Gulf is the brine pool NR1. This feature is a crater filled with a slowly seeping dense brine of approximately 120 ppt. The brine maintains a temperature anomaly to the seafloor and is supersaturated in methane (Joye et al. 2005), with visible bubble streams emanating from the center of the pool at times (MacDonald et al. 1990). The pool is surrounded by a ring of *Bathymodiolus childressi* mussels. The mussels of the inner edge of the bed appear to be in better physiological condition, while the mussels of the outer edges of the pool are generally larger but have lower glycogen content and slower growth rates (Nix et al. 1995; Smith et al. 2000). The communities associated with the mussel beds are highly homogenous and consist primarily of the commensal gastropod *Bathynerita naticoidea*, the "snot worm" *Methanoaricia dendrobranchiata*, an undescribed galatheoid *Munidopsis* sp. 1, and the shrimp *Alvinocaris stactophila* (Bergquist et al. 2005).

The Brine Lake in Alaminos Canyon 601 is a larger feature that also contains a distinct interface at the surface of the pool (Plate 23a). It is a highly distinct feature on the seafloor (Fig. 10.3, Plate 22) that was first described from a dive of the deep submergence vehicle *Alvin* in June 2006 (Roberts et al. 2007). The brine interface and the shoreline were quite distinct, but there also appeared to be two former

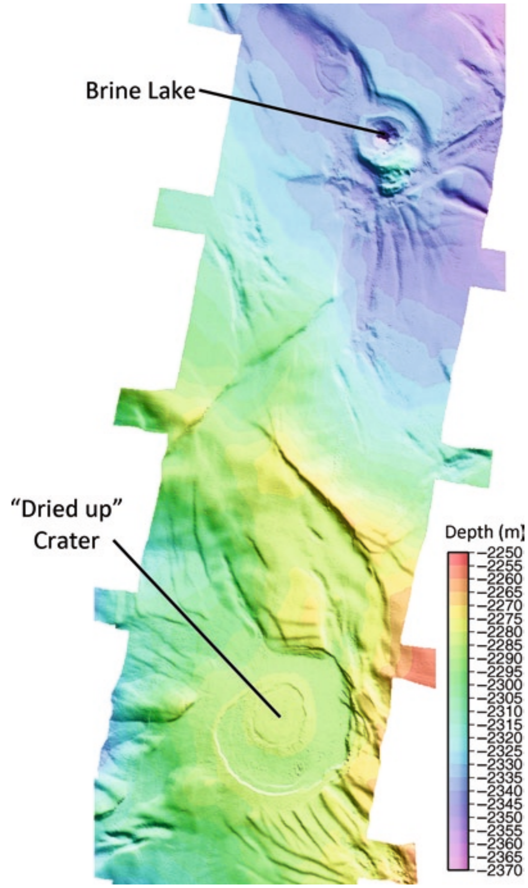

Fig. 10.3 Multibeam bathymetry of the Alaminos Canyon 601 lease block. Bathymetry data acquired by the Hugin AUV operated by C&C Technologies as part of the Expedition to the Deep Slope study funded by the U.S. Minerals Management Service and NOAA Office of Ocean Exploration. In the northern section of the image, the well-defined depression of the brine lake is apparent. In the southern section of the image, the outline of the dried up brine lake can be seen along with possible flows from large expulsion events or drainage of the brine from the crater at the top of the feature. A color plate of this figure can be found in Appendix (Plate 22)

shorelines where the lake contained greater volumes of fluids in the recent geologic past. There were occasional mussel beds composed of *Bathymodiolus brooksi* surrounding the lake interspersed with beds of the heart urchin (spatangid echinoid) *Sarsiaster greigi* (Plate 25). The sediments beneath these communities exhibited low sulfate reduction rates, but high concentrations of hydrogen sulfide. There was also a new species of octopus collected from the shoreline of the Lake that appeared in a well-publicized photograph from Roberts et al. (2007). The fluids of the lake have a salinity of up to 90‰ and exhibited low rates of anaerobic methane oxidation and sulfate reduction. There were barite “rafts” suspended within the brine throughout the lake, suggesting that the majority of the abundant barium contained in seeping pore fluids undergoes rapid precipitation when coming in contact with the sulfate contained in the brine lake.

During another Gulf of Mexico research cruise with the ROV Jason II in July 2007, the large feature to the south of the brine lake was investigated (Fig. 10.3, Plate 22). This 200 m diameter crater was apparent on the AUV multibeam survey conducted, but was not visited during the 2006 cruise. The ROV conducted a survey around the perimeter of the lake, which was a distinct shoreline with small brine pools and brine-stained sediments. On the northern edge of this second feature was an extensive mussel bed estimated to be nearly 3,000 m^2, among the largest continuous biogenic habitats ever observed in the Gulf of Mexico. Although by all appearances this was another brine lake, when a brine sample was attempted near the northern shore of the lake, the sinking bottle encountered the bottom almost immediately. As the ROV transited across the center of the “lake” the brine disappeared as the sediments became more oxidized, including areas of an apparent iron-oxide crust (Plate 23). These observations suggest that this feature is a large crater that fills with brine during active periods that are punctuated by dormant phases (like the one observed) when the lake would “dry up.” This could occur either through slow diffusive mixing of the brine with the overlying seawater, or perhaps by a catastrophic failure of the shoreline following the accumulation of a thick layer of dense brine.

10.1.3 Asphalt Flows

In addition to the brine pools and lakes of the Gulf of Mexico, another recently discovered anomalous geological feature are the asphalt seeps of the Gulf. These features were first described from a series of sites in the Chapapote Knolls region of the southern Gulf (MacDonald et al. 2004). The asphalt flows at this site covered large areas of the seafloor and resembled volcanic lava flows. In the vicinity of the flows and within the cracks of the asphalt were siboglinid tubeworms similar in appearance to *Escarpia laminata* from the northern Gulf as well as symbiotic vesicomyid and bathymodioline bivalves.

The source of the heavy asphaltine hydrocarbons is a matter of some debate. It was suggested that the abundance of asphalt at the seafloor was a result of rapid transport from a deep-seated source by supercritical fluid (Hovland et al. 2005). This hypothesis relies on a narrow fault running directly to the crust-sediment interface 13 km below the seafloor where fluids may become heated over 400°C. The buoyant fluid could transport relatively unaltered hydrocarbons to the surface where they would rapid devolatize and form a hardened crust and lava-like appearance while maintaining a heated core of fluid and liquid hydrocarbons. This process relies on the fluids and hydrocarbons remaining over 100°C at the seafloor under pressures over 280 ATM (2,800 m water depth).

The alternative hypothesis for the formation of the Chapopote asphalt flows is the hydrocarbon trap-leakage model (Ding et al. 2008). This involves the presence of a shallow coarse sand reservoir that accumulates hydrocarbons along with intrusions of these hydrocarbons into the overlying thin sediment layers and subsequent leakage to the seafloor. In this large shallow reservoir, only 100–200 m below the seafloor, the hydrocarbons mature through chemical, physical, or biological removal of lighter hydrocarbons. The hydrocarbons are able to appear at the seafloor as asphalt because of the very short, direct connections provided by salt-related faulting of the overlying trap.

During the surveys of the northern Gulf of Mexico in 2007, an asphalt site was discovered at 950 m in Garden Banks 647. The asphalt flows were not as extensive as the Chapopote site, but isolated flows were abundant and spread throughout an area of approximately 500 by 700 m. These were associated with authigenic carbonates, gorgonian corals (*Placogorgia* sp. and *Villogorgia* sp.), and siboglinid tubeworms (*Seepiophila jonesi* and *Escarpia laminata*). Upon collection of one of the tubeworms, a thin string of hydrocarbons came out of the sediments attached to the posterior, buried portion of the tube suggesting that heavy hydrocarbons were abundant in the shallow subsurface even if they were not visible on the seafloor. Some of the asphalt nodules were collected and left on the lab bench following sampling. As they warmed to 20–25°C overnight, one of the nodules cracked and a thick, viscous tar leaked out of the outer crust (see Plate 23c). The shallow depth of this site, the presence of abundant hydrocarbons in surface sediments, and the large area over which evidence of asphalt seepage was apparent support the hydrocarbon trap-leakage model rather than the supercritical fluid hypothesis for asphalt seep formation.

10.1.4 Barite Chimneys

At most hydrocarbon seep sites the bottom is largely composed of Ca-Mg carbonate that forms as a by-product of the chemistry created from microbial oxidation of hydrocarbons. However, in the case of the Mississippi Canyon (MC) 929 mound, imaged on the seismic profile and surface reflectivity map of Fig. 10.2, the hard bottom is composed of primarily barium sulfate or barite (Roberts and Aharon 1994). At selected sites, along with hydrocarbons, barium-rich waters are fluxed from an anaerobic subsurface environment to the aerobic sediment-seawater interface where barite is precipitated. Barite cones (see Plate 23d) have developed over the top of the MC 929 mound along with broad areas of sheet-like barite deposition on the surrounding seafloor. Bathymodiolin mussels are found on the cones as well as scattered on the surrounding seafloor. Associated with these mussels is a very low diversity community consisting of gastropods (primarily *Cataegis meroglypta* and *Bathynerita naticoidea*), a few species of polychaetes (*Nereis* sp. being the most abundant) and unusually high abundances of chitons (*Ischnochiton mexicanus* and *Lepidopleura* spp.) (EEC unpublished data).

10.2 Seep Organisms

10.2.1 Tubeworms

The diversity of vestimentiferan siboglinid tubeworms in the Gulf of Mexico is the highest in the world, with currently five to six species reported (see Fig. 10.4 and Plate 24 for images of *Escarpia laminata* and *Lamellibrachia luymesi*). Three species are found at the shallow sites between approximately 500 and 1,000 m (*Seepiophila jonesi*, *L. luymesi*, and an undescribed species of escarpiid, the latter being very uncommon), and two or three others at depths greater than approximately 1,200 m (*E. laminata*, and one or two species of undescribed *Lamellibrachia*, one common, the other one rare). The common *Lamellibrachia* species on the lower slope appears morphologically distinct, but does not exhibit significant genetic differentiation from *L. luymesi* in the 16S or COI sequences obtained to date (Miglietta et al. in press). Microsatellite data indicate that there is sufficient gene flow among the upper slope (<1,000 m) seep sites in the Gulf of Mexico to prevent genetic drift among populations of *L. luymesi* and *S. jonesi* (McMullin 2003), but additional data is required to examine patterns in gene flow among the populations of the upper and lower continental slope species.

Although there appears to be high gene flow among populations of tubeworms in the Gulf of Mexico, there is an apparent structure in the populations of the symbionts. In the Gulf of Mexico, there are three main clades of sulfide-oxidizing symbionts at the sites surveyed to date, according to depth and/or location: one was found in the Upper Louisiana Slope (550–650 m), another was found at Alaminos Canyon (2,200 m), and the last one at the Florida Escarpment (3,300 m; McMullin et al. 2003). Tubeworm symbionts are transmitted environmentally rather than vertically from one generation to the next (Nelson and Fisher 2000; Nussbaumer et al. 2006). The relationship among symbiont types is not congruent with host phylogeny since at some sites, different siboglinid species may harbor the same symbiont phylotype (e.g. *Lamellibrachia* sp. and *Escarpia laminata* at Alaminos Canyon). This suggests that there is no specific choice of symbiont by the host but rather the acquisition of the local strain of the symbionts from the environment.

Lamellibrachia luymesi was originally described from off the coast of Guyana, and based on morphological characters the common shallow-water species in the Gulf of Mexico has been identified as *L. luymesi* (Gardiner and Hourdez 2003). Two specimens of another species, *L. victori*, were collected off Uruguay (Mañe-Garzon and Montero 1985). Based on morphological characters alone, this species could actually correspond to *L. luymesi* since the morphological variability observed in *L. luymesi* encompasses the morphological characters and proportions described for *L. victori*. Another species of *Lamellibrachia* has been collected off the coast of Chile, although the taxonomic identification of this species remains unresolved at this time (Sellanes et al. 2008). A species of

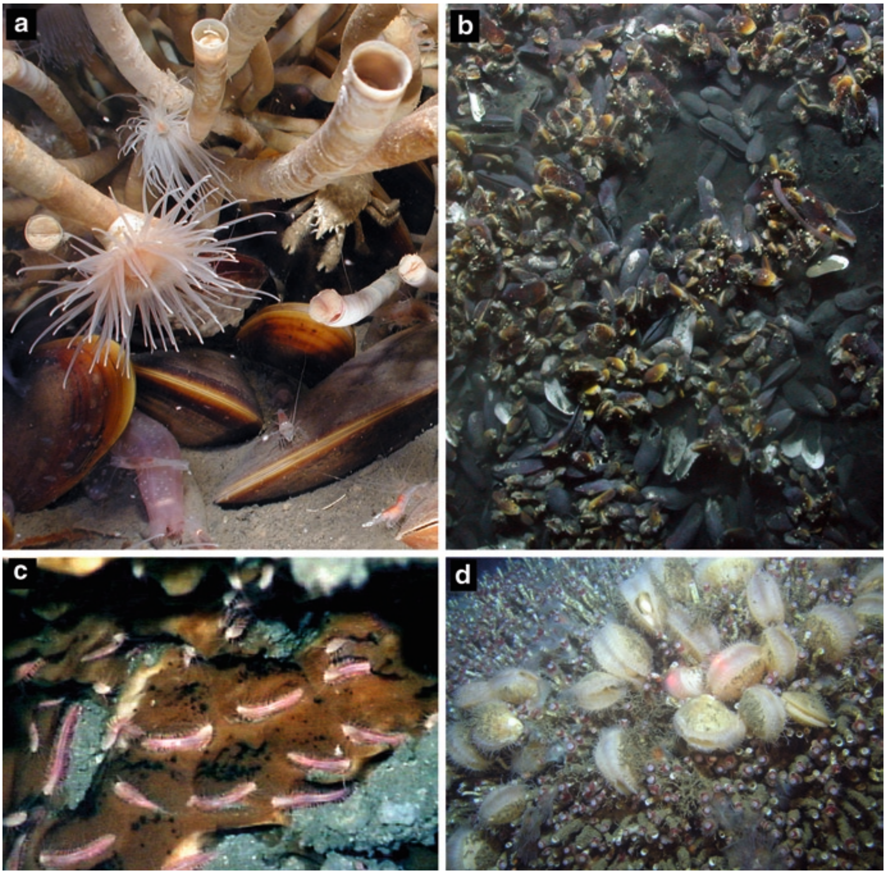

Fig. 10.4 Fauna of the Gulf of Mexico seeps. (**a**) Habitat formed by the vestimentiferan *Escarpia laminata* and the mussel *Bathymodiolus brooksi* from Alaminos Canyon 818 at approximately 2,750 m depth. Also shown are the shrimp *Alvinocaris muricola*, the galatheid crab *Munidopsis* sp., and the holoturian *Chirodota heheva*. (**b**) A small portion of the 3,000 m^2 mussel bed at the southern crater in Alaminos Canyon 601. The mussels are primarily *Bathymodiolus brooksi* and a worm-like individual of *Chirodota heheva* is present in the upper right corner. This part of the mussel bed lies at the shoreline of the crater where there are still pools of brine. (**c**) The iceworm *Hesiocaeca methanicola* on an outcropping piece of methane hydrate at 525 m depth in Green Canyon 234. (**d**) The tubeworm-associated clam *Acesta oophagia* enclosing the tips of the tubeworm *Lamellibrachia luymesi* at approximately 460 m in Mississippi Canyon 751 (Images A and B courtesy of the Expedition to the Deep Slope investigators, image C courtesy of Chuck Fisher and Erik Cordes, image D courtesy of the Lophelia II: Reefs, Rigs, and Wrecks investigators). A color plate of this figure can be found in Appendix (Plate 24)

Lamellibrachia closely related to the Gulf of Mexico *L. luymesi* has also been found in the Mediterranean (Southward et al. submitted). Based on all of this evidence, *L. luymesi* could be very widespread and inhabit a much larger bathymetric range than previously thought.

A study of communities of the Barbados Accretionary prism also revealed the presence of tubeworms, *Escarpia* cf. *laminata*, and *Lamellibrachia* sp. (Olu et al. 1996). In the REGAB area off Western Africa, another species of *Escarpia* (*E. southwardae*) forms dense bushes in areas with abundant hard substrata (Andersen et al. 2004). Interestingly, this species is genetically indistinguishable from *E. laminata* in the Gulf of Mexico based on COI data (Andersen et al. 2004). In addition, *E. spicata* from the Pacific coast of North America is also nearly identical in COI sequence to these two species (McMullin et al. 2003). It is possible that there is ongoing genetic dispersal throughout this wide biogeographic province. Although connectivity among all of these widely dispersed sites is unlikely, additional exploration for stepping-stone seep sites along the South American margin may help resolve this issue.

The close relatedness of all of these species groups suggests that larvae may be able (either currently or in the past) to travel wide distances over their lifespan. Siboglinids appear to have internal fertilization with the presence of spermathecae observed in females along with the release of fertilized embryos (Hilario et al. 2005). The eggs develop into trochophore larvae that can spend up to several weeks in the water column, potentially permitting a wide dispersal and colonization of active seep sites (Young et al. 1996). This is corroborated by evidence that the larvae of *L. luymesi* are capable of surviving in temperatures as high as 17°C (CM Young 2009, personal communication), and the presence of siboglinid sequences collected in the plankton at depths as shallow as 5 m in the Mediterranean (Marie et al. 2006). This would allow rapid transport of larvae in the higher velocity currents of the surface layers of the ocean and could potentially lead to gene flow among the *Lamellibrachia* and *Escarpia* species throughout the Atlantic and potentially around South America to the Pacific.

Alternatively, there is simply a lack of resolution in the majority of the genetic markers commonly used for phylogeography in this group. It is possible that the evolutionary rate has decreased in at least some lineages of vesitmentiferan tubeworms. Interestingly, the groups for which the genetic markers commonly used fail to discriminate closely related species all inhabit cold seep areas, a type of environment usually stable over thousands of years. These species are characterized by very long life-spans (several hundreds of years), which results in an overlap of many generations of worms, all potentially able to interbreed. This may in fact reduce the apparent mutation rate.

10.2.2 Mussels

The bathymodiolin mussels are also very diverse in the Gulf of Mexico, with a total of at least five species (Gustafson et al. 1998). *Bathymodiolus childressi* occurs at depths ranging from 500 to at least 2,300 m. Two other *Bathymodiolus* species (*B. brooksi* and *B. heckerae*) exclusively occur at deeper sites with depth ranges between 1,080–3,300 and 2,200–3,300 m, respectively (Cordes et al. 2009, see Fig. 10.4 and Plate 24 for images of *B. brooksi*). *Tamu fisheri* has only been collected at shallow sites (500–600 m), and *Idas macdonaldi* has been reported from a single site (GB 386; Gustafson et al. 1998). All of these species are symbiotic with either sulfide-oxidizing, methanotrophic, or both types of bacteria (see chapter 6, this volume). Such a diversity of metabolic types suggests an ability to occupy different ecological niches and avoid competition while co-occurring at the same sites. On the Mid-Atlantic Ridge, Won et al. (2003) showed that co-occurring *Bathymodiolus* species (*B. azoricus* and *B. puteoserpentis*) shared the same sulfide-oxidizing symbiont phylotype, and also harbor very similar methanotrophic symbionts. Based on electron micrographs, the authors suggest that *Bathymodiolus* may continuously acquire symbionts from their environment. Kádár et al. (2005) published data that support this view. These authors showed that the Mid-Atlantic Ridge species *B. azoricus* could lose its symbionts by starving it from sulfide and later re-acquire them when exposed to sulfide again. In the Gulf of Mexico however, when different species of *Bathymodiolus* co-occur, they harbor distinct phylotypes of symbionts. This indicates that, unlike vestimentiferan tubeworms, *Bathymodiolus* species seem to be able to more precisely select their symbionts from the environment.

Bathymodiolus childressi is one of the rare species found at both shallow and deep sites, which prompted interest in the study of the relatedness between shallow and deep populations. An initial study based on allozyme data indicated a clear difference between the two populations separated by 1,700 m of water depth (Craddock et al. 1995). Allozyme markers, however, can be under selection and a specific allelic form may provide a better fitness in deeper populations. Later, Carney et al. (2006) used two mitochondrial and six nuclear markers (including microsatellites, assumed to be neutral), and showed that all the populations studied were interbreeding regardless of depth and distance. A study of spawning and development of *B. childressi* from the shallow water site Brine Pool NR-1 suggests that larvae may spend over a year in the water column (Arellano and Young 2009). This probably provides this species of mussel with a very high dispersive capability, at least throughout the Gulf of Mexico.

Interestingly, genetic comparisons to mussels collected at other sites within the Atlantic Equatorial Belt region (AEB: including the Gulf of Mexico, Blake Ridge, Barbados accretionary prism, Mauritanian margin, and the Gulf of Guinea) revealed the presence of species closely related to *B. childressi* and *B. heckerae* outside of the Gulf of Mexico (Cordes et al. 2007). A genetic study using the mitochondrial COI marker, and the nuclear ITS2 marker confirmed the close relatedness of the different populations, raising questions about possible recent genetic exchange (Olu-Le Roy et al. 2007b). These species complexes are amphi-Atlantic, i.e. found in either side of the Atlantic but not on the Mid-Atlantic Ridge, where two other species of *Bathymodiolus* (*B. azoricus* and *B. puteoserpentis*) inhabit the diffuse areas around hydrothermal vents. This suggests some gene flow in the recent past between the two sides of the Atlantic that may be possible, given the long larval duration estimated for *B. childressi* in the Gulf of Mexico (Arellano and Young 2009).

10.2.3 Iceworms

Another interesting species with a direct tie to seep productivity is the iceworm, *Hesiocaeca methanicola* (see Fig. 10.4c and Plate 24). Iceworms are hesionid polychaetes that inhabit the surface of methane hydrates on the upper Louisiana slope (Desbruyères and Toulmond 1998). They were first discovered living in very high densities (up to 2,500 individuals per square meter) within small depressions carved into an outcropping of methane hydrate (Fisher et al. 2000). The iceworms apparently create these depressions by fanning their parapodia and increasing the water movement over the surface of the clathrate. This may facilitate the sublimation of the hydrate and increase the dissolved methane and sulfide available to free-living microbes from which they likely derive the majority of their nutrition (Fisher et al. 2000). A few small individuals of the same species have occasionally been found in mussel collections at shallow and deep sites of the Gulf of Mexico (Cordes et al. 2007, submitted).

10.2.4 Alvinocaridid Shrimp

The shrimp family Alvinocarididae is endemic to hydrothermal vents and cold seeps worldwide. In the Gulf of Mexico, *Alvinocaris stactophila* is only found at shallow sites (depths around 500–650 m, Carney 1994; Bergquist et al. 2003; Cordes et al. 2006) while a different species, *A. muricola* (see Fig. 10.4a and Plate 24), is encountered at deep sites where they are associated with the tubeworms *Escarpia laminata* and *Lamellibrachia* sp. (Cordes et al. 2007, submitted). A species referred to as *A.* cf. *muricola* was also reported from the Barbados southern seeps at depths of 1,200 and 1,700 m (Olu et al. 1996). Olu-Le Roy et al. (2007a) also report a closely related species in the REGAB pockmark (3,160-m deep) off West Africa, associated with the tubeworms *E. southwardae*. Sequencing of the COI gene for the populations from the Gulf of Mexico, REGAB, and Logatchev (on the Mid-Atlantic Ridge) revealed that they form a monophyletic clade of closely related species (Zelnio and Hourdez 2009). At Blake Ridge cold seeps, however, another species occupies a similar niche (Van Dover et al. 2003). Based on COI, this species is more closely related to another Alvinocarid genus, *Opaepele* (see Zelnio and Hourdez 2009). Similar to the genetic patterns detected in tubeworms and mussels, this suggests either recent or on-going gene flow between the different areas through their larval stage. Interestingly, a recent dive on an experimental wood pile located 300 m away from the Logatchev vent field revealed the presence of *Alvinocaris* sp. on this concentrated biomass source (SH, personal observation). This clearly indicates that habitats other than hydrothermal vents and cold seeps may serve as stepping stones between otherwise isolated populations of *Alvinocaris*.

10.2.5 Tubeworm-Associated Clams

Acesta oophaga (see Fig. 10.4d and Plate 24) was initially thought to be an ecophenotypic variant of *A. bullisi* that grows attached to the tubeworm *Lamellibrachia luymesi*, with a notch in the valves to accommodate the siboglinid's tube (Kohl and Vokes 1994). Later morphological and genetic examination revealed that it was a distinct species, with a shorter and thicker shell, and that the notch in the shell was a normal occurrence for the species (Järnegren et al. 2007). In an earlier study, Järnegren et al. (2005) showed that young *A. oophaga* do not possess a notch, settle near the opening of the tube, with their hinge facing up. At that stage, the bivalves rely on filter-feeding only. Once a little bit larger, the animal turn their shells and eventually grow enclosing the worm's tube opening. The clams are preferentially found on female *Lamellibrachia* (85% of the observations for a tubeworm aggregation with an even sex-ratio), and their stable isotope signatures suggest that as adults a proportion of the diet of the individuals on female worms consists of the embryos released by the tubeworms.

10.2.6 Other Species

The distributional patterns of other seep-associated species also indicate a strong connection between the Gulf of Mexico fauna and other deep-sea areas in the Atlantic. The galatheid *Munidopsis geyeri* is known from the Gulf of Mexico including the Florida Escarpment, the Columbia and Venezuela Basins, and has also been sampled at the seeps of the African margin (MacPherson and Segonzac 2005). The commensal polynoid scale-worm found in *Bathymodiolus* aff. *heckerae* from Africa is genetically similar to *Branchipolynoe seepensis* occurring at the Florida Escarpment (Olu-Le Roy et al. 2007b, D. Jollivet unpublished data). However, the species found in *Tamu fisheri* from the upper slope sites in the Gulf of Mexico is clearly genetically and morphologically distinct (SH, unpublished data). Another polynoid polychaete found at both the shallow and deep seeps of the Gulf of Mexico, *Harmothoe* sp., are genetically indistinguishable based on COI sequences (Cordes et al. submitted).

There are also a few examples of wide distribution in the echinoderms of the seeps in the Equatorial Atlantic Belt. *Ophioctenella acies* is a brittle star that has been found in extremely high abundances in mussel beds from the seeps of the lower slope of the Gulf of Mexico, the Blake Ridge, South Barbados, and also at numerous sites along the mid-Atlantic Ridge (Stöhr and Segonzac 2005). This is one of the first species to be present at all of these habitats and raises the potential for more species to be discovered that cross the seep-vent habitat boundary. The sea cucumber *Chirodota heheva* (see Fig. 10.4b and Plate 24) is considered to be a common resident at seep sites in the Gulf of Mexico and off the southeast coast of the USA, and is also found at anthropogenic habitats (Pawson and Vance 2004), while the same species was reported from the REGAB area off Western Africa (Olu-Le Roy et al. 2007a). *Sarsiaster greigii*, an irregular sea urchin, has been found partially buried in seep sediments, often leaving long trails of apparently reduced sediments behind at the seeps of the Blake Ridge and the deep Gulf of Mexico (van Dover et al 2003; Lessard-Pilon et al. submitted). All of these observations of broad distributions provide evidence for a high dispersal capacity in these seep inhabitants, and allow us to begin to assemble a picture of the biogeography of the cold seep fauna of the world.

10.3 Summary

The seeps of the Gulf of Mexico constitute an incredibly complex but well studied ecosystem that may serve as a model for a variety of other similar settings as they are discovered around the world (Fisher et al. 2007; Cordes et al. 2009). This is particularly relevant given our increasing understanding of the connectivity among deep-water seep ecosystems within the Atlantic basin and world-wide. Even within the familiar setting of the Gulf of Mexico, new discoveries continue to shape our conception of the cold seep ecosystem. New habitat types, new species, and new biogeochemical processes continue to influence our perception of cold seeps, the deep sea, and ecological processes in general. Due to the large volume of existing information on the seeps of the Gulf of Mexico, these new discoveries may be more rapidly interpreted and make the Gulf a relatively accessible and tractable natural laboratory for the further understanding of the complex cold seep ecosystem.

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