

Seaweeds and Decapod Crustaceans on Gulf Deep Banks after the Macondo Oil Spill

DARRYL L. FELDER, BRENT P. THOMA, WILLIAM E. SCHMIDT, THOMAS SAUVAGE, SHERRY L. SELF-KRAYESKY, ANDREI CHISTOSERDOV, HEATHER D. BRACKEN-GRISSEY, AND SUZANNE FREDERICQ

The diversity of seaweeds and decapod crustaceans associated with rhodoliths on deep offshore banks in the northwestern Gulf of Mexico decreased dramatically after the Macondo blowout. Decapod crustacean communities declined in both abundance and diversity and exhibited major shifts in species dominance. Rhodoliths appear to serve as seedbanks for biological diversity because dead rhodolith rubble became covered by epi- and endolithic algae and microbes in laboratory microcosms. Decreased seaweed abundance in the field may relate to nutrient availability and microbial interactions. We hypothesize that declines of deep bank decapods largely reflect the loss of seaweed cover, which may have led to cascading effects on direct consumers and higher trophic levels. However, negative impacts of postspill increases in lipoclastic and chitinoclastic bacteria cannot be ruled out as possible contributors to overall decapod declines, although the evidence implicating these factors was limited only to decapod samples from nearby deeper soft substrates.

Keywords: conservation, plant–animal interactions, pollutants, coastal ecosystems, environmental health

Prior to the massive northern Gulf of Mexico spill from catastrophic failure of the Macondo well in April 2010, sampling of marine macroalgae (attached seaweeds) and benthic decapod crustaceans (e.g., shrimps, crabs, lobsters) had been initiated on deep banks (55–80 meters [m]) in the Gulf of Mexico, including two west of the spill site (Sackett and Ewing Banks). These studies, investigated under US Department of Energy and National Science Foundation (NSF) support, targeted diversity and endemism of Gulf of Mexico seaweeds (Fredericq et al. 2009) as the major group of macrophyte primary producers and decapod crustaceans (Felder et al. 2009) as a dominant group of benthic consumers on deep banks already postulated to be at risk from impacts of regional petroleum exploration and production. Ancillary to these sampling programs, trial benthic skimmer sampling (Pequegnat et al. 1970) of decapods on even deeper sedimentary substrata (500–1750 m) had also been undertaken to a limited extent. Owing to the availability of these data prior to the spill, follow-up studies were undertaken that allowed for some pre- and postspill comparisons of assemblages in these habitats. These studies were warranted by previous evidence of negative hydrocarbon spill impacts on benthic communities (e.g., Peterson et al. 2003, Roth and Baltz 2009).

Although both Sackett Bank (in the vicinity of 28 degrees [$^{\circ}$] 37.9 minutes [$'$] north [N], 89 $^{\circ}$ 33.4' west [W]) and Ewing

Bank (in the vicinity of 28 $^{\circ}$ 05.7'N, 91 $^{\circ}$ 01.2'W) are 115 and 270 kilometers, respectively, to the west of the Macondo site (figure 1) and, therefore, not in the areas most heavily and persistently oiled, surface data indicate that Sackett Bank was subjected to intermittent exposure from mid-May through August of 2010, whereas Ewing Bank is assumed to have been, at most, sporadically affected (NOAA 2010). It should also be pointed out that Sackett Bank, being farther east, is nearer the influence of the Mississippi River than is Ewing Bank. Despite the peripheral nature of these sites to the Macondo blowout event, our focus on them is prompted by our discovery in NSF-sponsored surveys from 2003–2006 that the seaweed and benthic decapod diversity and abundance on these banks exceeded those in comparable habitats sampled from throughout the Gulf of Mexico. Therefore, the diversity of potential indicator organisms in these hard-substratum habitats is exceptional, and the potential for observable acute or chronic impacts of the Macondo spill on bank populations is high.

At the outset of any such postevent analyses, it must be acknowledged that other large-scale environmental changes, in addition to the spill, also occurred in the region within the sampling period (2004–2013). These most conspicuously include potential impacts from major seasonal and annual variations in Mississippi River discharge (Rabalais

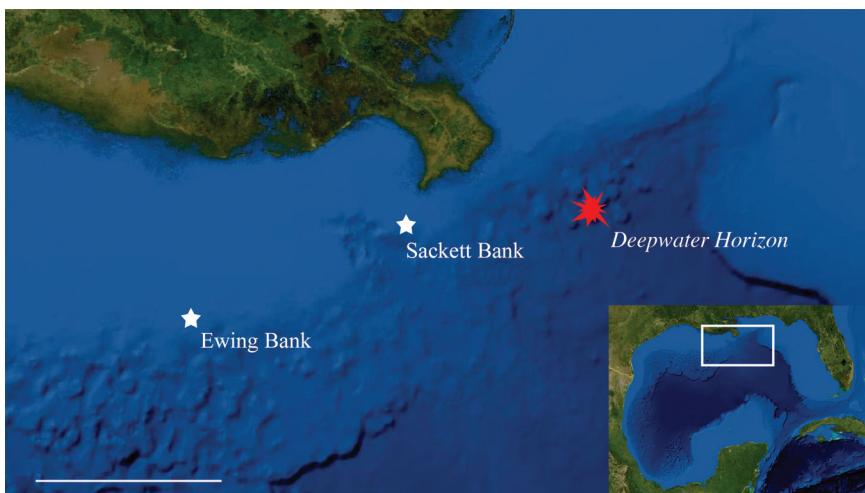


Figure 1. Map of collection sites. The scale bar represents 120 kilometers.

et al. 1996, Sklar and Browder 1998), Hurricane Katrina and smaller tropical storms in the region (Engle et al. 2009, Macauley et al. 2010), and annual expansions and contractions in a major northern Gulf of Mexico eutrophic zone that may impinge on the sampled sites (Diaz and Rosenberg 2008, Turner et al. 2012). Our data cannot isolate the effects of such events and separate them from potential spill impacts. Instead, we offer a summary of information accumulated over a timescale that spans these combined events and share selected observations and hypotheses based on field collections and lab studies that suggest what role the spill may have played in observed assemblage variations.

The deep bank seaweed community

Offshore benthic seaweeds in the northwestern Gulf of Mexico are associated with unique deep bank habitats, known as *salt domes* or *diapirs*, that are peculiar to that part of the Gulf. Prior to the Macondo spill, these hard banks harbored the highest known levels of seaweed diversity in the northern Gulf of Mexico (Fredericq et al. 2009, 2014). This important component of the photosynthetic community produces oxygen, acts as a carbon dioxide sink, consolidates substrata, provides food and shelter for both invertebrate and vertebrate animals, and may induce the settlement and metamorphosis of some invertebrates. On these hard bank slopes, red algal nodules (rhodoliths) and unconsolidated carbonate rubble are the major contributors of calcium carbonate (CaCO_3). Under normal, healthy environmental conditions, this rubble is completely or partially covered by a great diversity of epilithic crustose and erect red, brown, and green seaweeds. The life histories, growth, maturation, and reproduction of this marine flora depend on numerous abiotic factors, both physical (e.g., flow regimen, light penetration, temperature, substratum conditions) and chemical (e.g., nutrient availability, exposure to hydrocarbon contaminants), as well as biotic factors (e.g., herbivory, bacteria with associated morphogenetic substances). The combination

of these factors determines the diversity, abundance, population structure and seasonal turnover of the seaweed assemblages in the deep northwestern Gulf of Mexico bank habitats.

Six postspill cruises conducted from December 2010 to October 2013 at Ewing and Sackett Banks, sites at which rich algal assemblages were previously documented, revealed a dramatic die-off of seaweeds. Unconsolidated rubble and rhodoliths dredged at depths of 55–75 m appeared either bleached and mostly denuded of fleshy algae or sparsely covered by a few crust-forming species (figure 2). The few seaweed taxa we collected in our first postspill expedition (December 2010) included calcified, crust-forming corallines, other crustose

Peyssonneliaceae (Rhodophyta), and the otherwise rare gelatinous nonulvophycean green alga *Verdigellas*. Our most recent surveys of Ewing Bank (October 2013) revealed about 10 visibly evident species, whereas in our prespill samples, we typically counted more than 60 species (Fredericq et al. 2014).

Rhodoliths in the northwestern Gulf of Mexico are predominantly composed of two major categories of CaCO_3 rubble. The first is biogenic in origin and is formed by encrusting, nongeniculate red algal species (rhodoliths, *sensu stricto*), and the second is autogenic in origin, resulting from the differential erosion processes of diapir salt (halite); the ensuing rubble surface becomes secondarily settled by algae (figure 3). In the autogenic rubble formation, the diapir salt contains trace amounts of impurities—notably, calcium sulfate (CaSO_4 ; anhydrite and gypsum)—and when underground water dissolves away the salt fraction, the remaining anhydrite part forms a somewhat insoluble barrier that is then acted on by anaerobic bacteria that convert CaSO_4 to CaCO_3 . The composite sedimentary overlayer of CaCO_3 , gypsum, and anhydrite above a diapir is known geologically as *caprock* (Gore 1992). Anaerobic bacteria obtain the carbon necessary to reduce anhydrite to limestone from hydrocarbons in petroleum products that accumulate in pockets along the edge of the salt dome banks on the continental shelf (Rezak et al. 1985). It is the banks' caprock slopes and peaks that, today, are covered by unconsolidated rubble and rhodoliths (Minnery 1990).

Rhodolith ecosystems are common constituents of the modern and fossil marine environments in which they are found from the poles to the tropics, from shallow subtidal habitats to offshore banks on continental shelves, and they are especially common in clear tropical waters at depths of 50–286 m (Foster 2001, Pereira-Filho et al. 2012); however, knowledge of their biodiversity and ecosystem functioning, particularly for those found in the northwestern Gulf of Mexico, is gravely deficient. For example, in Buster and Holmes (2011), the terms *rhodolith*, *algal nodule*, and



Figure 2. Dredged, bleached, and mostly bare rhodoliths collected at Ewing Bank on 26 August 2012. The width of the image is 15 centimeters. Photograph: Suzanne Fredericq.

and planktonic primary producers and particulate organic matter from terrestrial sources), may help explain the high number of species in this exceptional ecosystem. The functional ecology of such complex habitats has received little attention, in contrast to other marine ecosystems, such as seagrass beds, kelp forests, or coral reefs. This may be in part because rhodoliths are particularly problematic to identify (Broom et al. 2009). The deposition of CaCO_3 by marine algae is an essential process in the global carbon cycle, and rhodoliths are recognized as foremost carbonate builders when they form extensive beds; however, despite its dominance in marine environments, algal calcification (and dissolution) has received relatively little attention for its impact on the global carbon cycle (Lee and Carpenter 2001).

Sampling of rhodoliths and their recovery in microcosms

Bare or partly algal-denuded unconsolidated rubble or rhodoliths sampled as live rocks at Ewing and Sackett Banks in April 2011 and subsequent field collections were brought to our laboratory at the University of Louisiana at Lafayette and maintained in a series of approximately 75-liter closed microcosm tanks, each equipped with a SeaClone 100 protein skimmer (Instant Ocean, Blacksburg, Virginia) and a 24-inch double-bright 600-lumen lights LED (light-emitting diode) lighting system (Marineland, Blacksburg, Virginia). The protein skimmer provided filtration and a flow of 1200 liters per hour. The LED photosynthetically available radiation (PAR) in the microcosms was about 30 micromol (μmol) photons per square meter (m^2) per day, a measurement approximating *in situ* light PAR or irradiance levels

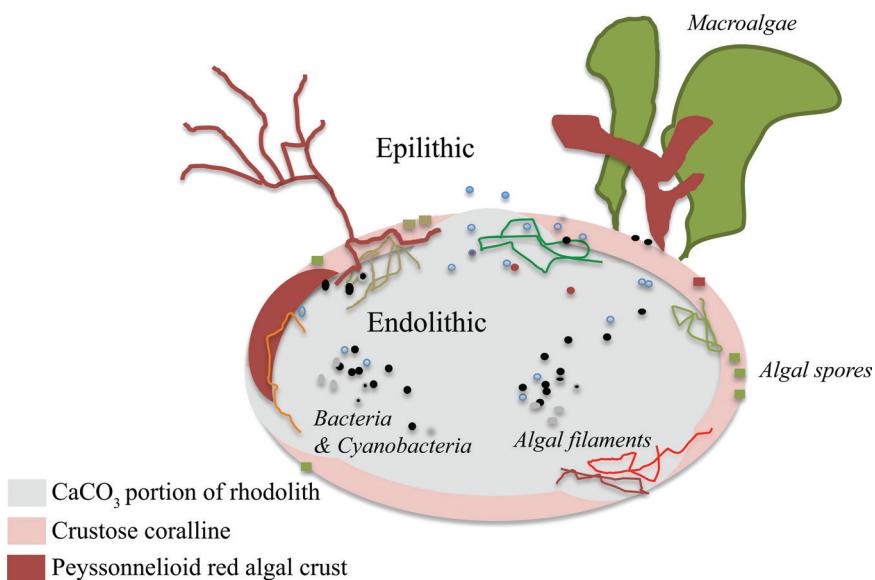


Figure 3. The typical prespill rhodolith interior and exterior portion from Ewing Bank. Abbreviation: CaCO_3 , calcium carbonate.

unconsolidated rubble are not mentioned. However, rhodolith beds off Louisiana can be seen clearly, both *in situ* and on box dredge retrieval, in our series of videos posted at <http://youtube.com/nemastoma2>.

Rhodoliths are well known as important ecosystem engineers (Foster et al. 2007) and provide a structurally complex habitat associated with high biodiversity. The physical complexity of rhodoliths accommodates many microhabitats for diverse assemblages of algae, invertebrates, and other taxa, which, combined with a complex food web that derives energy from a diversity of carbon sources (including sessile

measured with a LI-COR Biosciences (Lincoln, Nebraska) biospherical PAR sensor incorporated in a CTD (for conductivity, temperature, and depth) rosette and water sampler (e.g., at a 57-m depth on 25 August 2012; at 10:10 A.M., PAR = 22 μmol photons per m^2 per day, and at 4:40 P.M., PAR = 30 μmol photons per m^2 per day). Each of the closed microcosms was initially filled with *in situ* water collected with CTD rosette Niskin bottles. For some tanks, the collected seawater was used untreated, whereas for others, it was sterilized with an ultraviolet filter (Aquanetics Systems, San Diego, California) in order to reduce or eliminate the seeding



Figure 4. Microcosm showing biogenic and autogenic rhodolith algal community recovery, photographed on 27 November 2012, from bare rhodoliths collected on 26 August 2012. The width of microcosm is 30 centimeters.
Photograph: Suzanne Fredericq.

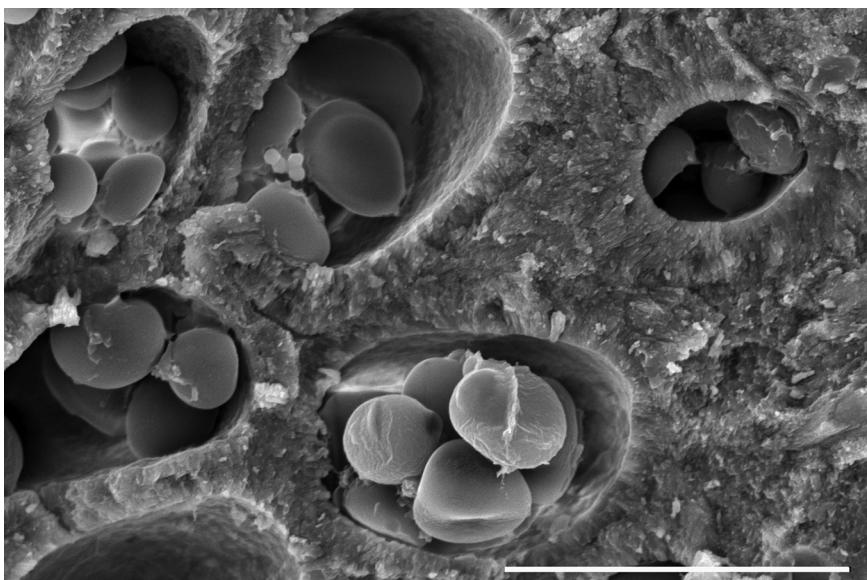


Figure 5. Newly found life history stages of the dinoflagellate *Prorocentrum* sp. growing inside calcium carbonate-encrusted cells of the rhodolith-forming coraline red alga *Lithothamnion* sp. The scale bar represents 20 micrometers.
Micrograph: Sherry L. Self-Krayesky.

of water column microorganisms, including potential algal spores. Although not quantitatively measured, both treatments resulted within 3 weeks in the gradual regeneration of conspicuous red, green, and brown seaweed germlings from the bare, apparently dead rhodolith rubble (figure 4). Interestingly, species composition in these microcosms reflected prespill macroalgal assemblages observed in the past at these sampling sites. We hypothesize that alternative

resting stages of algae are currently present within the rhodoliths substratum in the Gulf, as part of the microbiota, but is repressed in the field at the time of the postspill sampling (Fredericq et al. 2014). When placed in our tanks, conspicuous algal growths were released from unidentified factors limiting their development in the field. We are currently conducting environmental DNA sequencing to characterize the prokaryotic and eukaryotic organisms associated with the rhodolith microbiota and in the adjacent water column. Fredericq and colleagues (2014) hypothesized that deepwater rhodoliths in the northwestern Gulf of Mexico might play an overlooked function as marine seedbanks, in analogy to land plant seedbanks (Hoffmann and Santelices 1991), providing a refuge and ensuring resilience for biological diversity following natural stochastic events or anthropogenic disturbances, such as the Macondo oil spill. Calcium carbonate substrata in general are well known to be essential in the life cycle of some seaweeds in which the heteromorphic stage of the sporophyte individual (in which meiosis occurs) is often a small crust, disk, or aggregation of creeping filaments that does not resemble the larger gametophyte individual and that may produce resting spores (Hawkes 1990).

We have already documented that seaweed propagules, germlings, and bacteria settle on glass slides from the microcosm ambient seawater in our August 2011 Ewing Bank sample and that seaweed propagules and bacteria growing within (endolithic) or on (epilithic) the rubble substratum from the same tank were clearly visible with epifluorescence microscopy (Fredericq et al. 2014). More recently, scanning electron microscope (SEM) images of calcareous inner cells of an undescribed rhodolith-forming coraline *Lithothamnion* sp. (Hapalidaceae, Corallinales) collected in August 2012

and Oct 2013 on Ewing Bank revealed previously unknown endolithic life history stages of the toxic, bloom-forming dinoflagellate *Prorocentrum* sp. (confirmed molecularly in our laboratory with *cob1* as *Prorocentrum* 'lima'; figure 5). Additional research will demonstrate whether endolithic dinoflagellate stages are stimulated by oil spills or whether they are part of the normal life cycle of *Prorocentrum* worldwide.

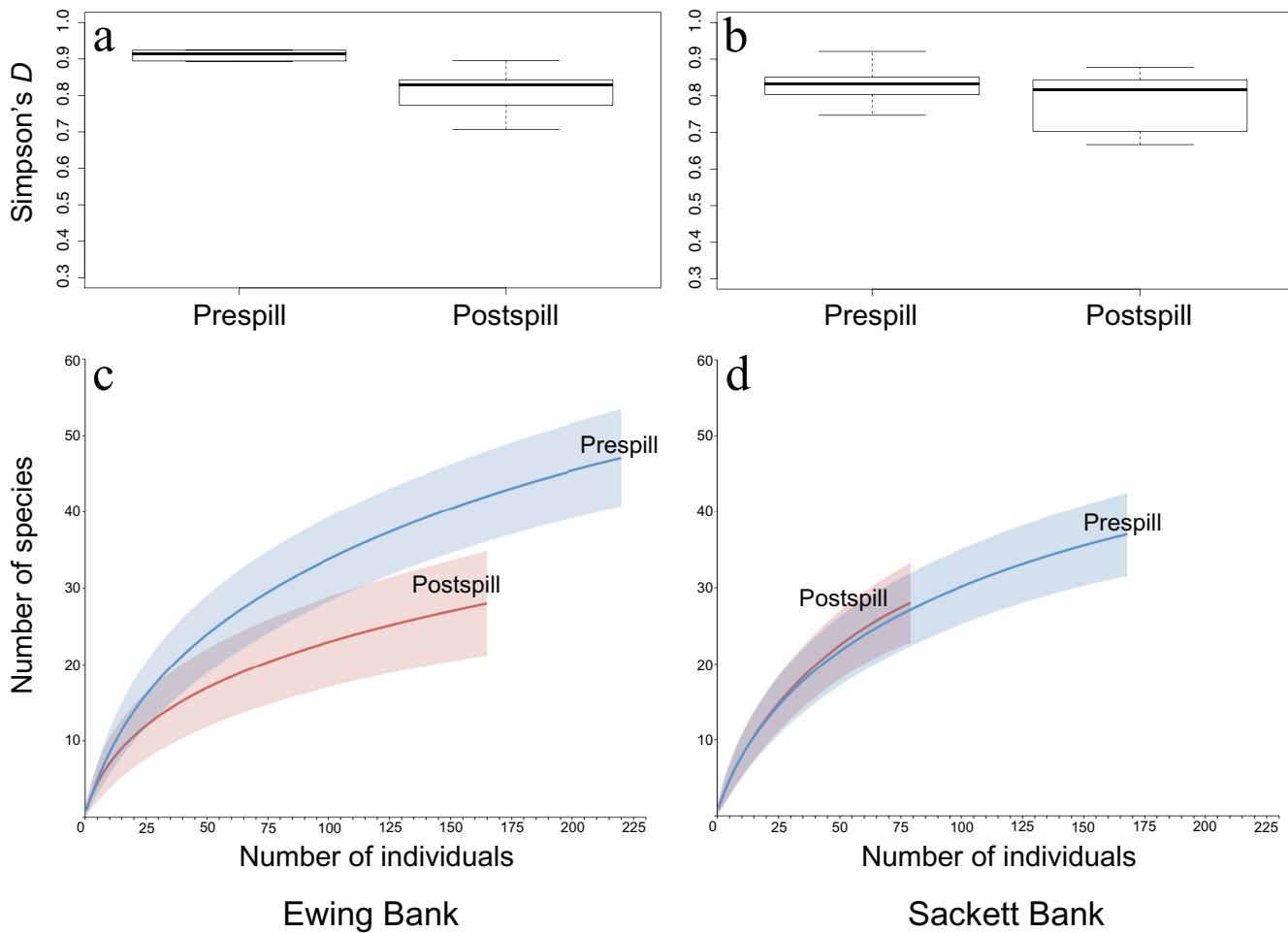


Figure 6. (a, b) Simpson's diversity index (D) and (c, d) rarefaction curves calculated from six samples with highest diversity in pre- and postspill conditions on both Ewing and Sackett Bank. The Simpson's D values were calculated in R using vegan (version 2.0-7; R Foundation for Statistical Computing, Vienna, Austria; <http://CRAN.R-project.org/package=vegan>), and the rarefaction values were calculated in EstimateS (version 9.1.0; R. K. Colwell, University of Connecticut, Storrs; <http://purl.oclc.org/estimates>).

The deep bank decapod crustacean community

The benthic decapod assemblage, sampled simultaneously with the box dredge methods used for seaweeds and rhodoliths, showed a strong decline in abundance on both banks in postspill (2010–2012) samples relative to prespill (2004–2006) samples. A significant decrease was also observed in both diversity and richness on Ewing Bank ($p < .05$; figure 6), with species richness and diversity (Simpson's D) on Ewing Bank depressed on average by 42% and 12%, respectively. Although both richness and diversity were also depressed on Sackett Bank (29% and 9%, respectively), its pre- and postspill assemblage compositions were not found to be significantly different. This could reflect a decapod assemblage on Sackett Bank that was, even prior to the spill, adapted to periodic perturbations because of its relative proximity to Mississippi River discharge. This is suggested by consistently lower levels of species richness in prespill samples from Sackett Bank than in those from

Ewing Bank (rarefied species richness values of 2.63 and 6.39, respectively).

The overall decline in diversity and richness of decapod assemblages on both deep banks was accompanied by changes in relative abundance of formerly dominant species, although more strikingly so on Ewing than on Sackett Bank. This may again attest to Sackett Bank's being the more frequently perturbed community. On Ewing Bank, populations of two previously dominant brachyuran crabs, *Melybia thalamita* (figure 7a) and *Palicus affinis*, declined markedly in postspill samples, whereas a resilient, yet to be named, regionally endemic hermit crab, *Phimochirus* sp. (figure 7b) came to dominate the postspill decapod community there at a relative abundance more than five times that seen in prespill assemblages.

Remarkably, four specimens representing two species of spider crabs, *Nemausa acuticornis* and *Macrocoeloma concavum* (figure 7c, 7d), and a small galatheid squat lobster,



Figure 7. (a) A female of *Melybia thalamita* with an 8.8-millimeter (mm)-wide carapace, which was the dominant decapod crustacean on Ewing Bank prior to the spill but which is rare in collections since. (b) A male of *Phimochirus* sp. with a 6.3-mm-long carapace shield; this species was present among Ewing Bank decapods prior to the spill but dominated assemblage diversity and abundance in postspill sampling. (c) A female of *Nemausa acuticornis* with a 28.0-mm-wide carapace and (d) a male of *Macrocoeloma concavum* with a 19.2-mm-wide carapace, both of which were introduced to microcosms in August 2012 as undetected early stages on rhodoliths from Ewing Bank and matured over the following 6 months without introduction of extraneous food. Photographs: Darryl L. Felder.

Galathea rostrata, which were not evident when macrofaunal decapods were thoroughly sorted from postspill dredge samples of rhodoliths, grew to maturity in the microcosms. These individuals apparently grew from recently settled megalopae or early crabs that occupied the interstices of rhodoliths collected and maintained in the laboratory with *in situ*-collected seawater. Unfed, they subsisted on the seaweeds that subsequently flourished in nutrient-fortified seawater of the microcosm. These specimens, all three representing species that were relatively common in field samples prior to the spill, provide evidence that recruitment has continued on the banks. Furthermore, they establish that sampled rhodoliths harbor the seeds of recovery in food chains for these animals; they appeared to thrive solely on the seaweed vegetation and associated epibionts found in lab microcosms.

Although the abundance and diversity of decapods on both banks were reduced under postspill conditions, definitive evidence of Macondo oil from the spill on either bank

is lacking, although some samples of rhodoliths from Ewing Bank taken in December 2010 smelled conspicuously of petroleum (less so on a return to the site in April 2011). Given evidence from surface data, our observations of petroleum residue on Ewing Bank and the results of previous studies on the effects of hydrocarbon exposure on macro-invertebrates (e.g., Goodbody-Gringley et al. 2013, Powers et al. 2013), we suspect that hydrocarbon exposure may have, at some scale, caused localized mortalities, reduced the fecundity of surviving females, or reduced recruitment.

Changes in decapod assemblages could be an indirect result of massive hydrocarbon influxes' altering microbial communities that, in turn, negatively affected resident decapod populations or potential larval recruits in the water column. However, we found no evidence of cuticular lesions, which were previously linked to microbial activities (e.g., Bullis et al. 1988, Chistoserdov et al. 2012), or heavy manganous gill precipitates on decapods from the bank samples, despite

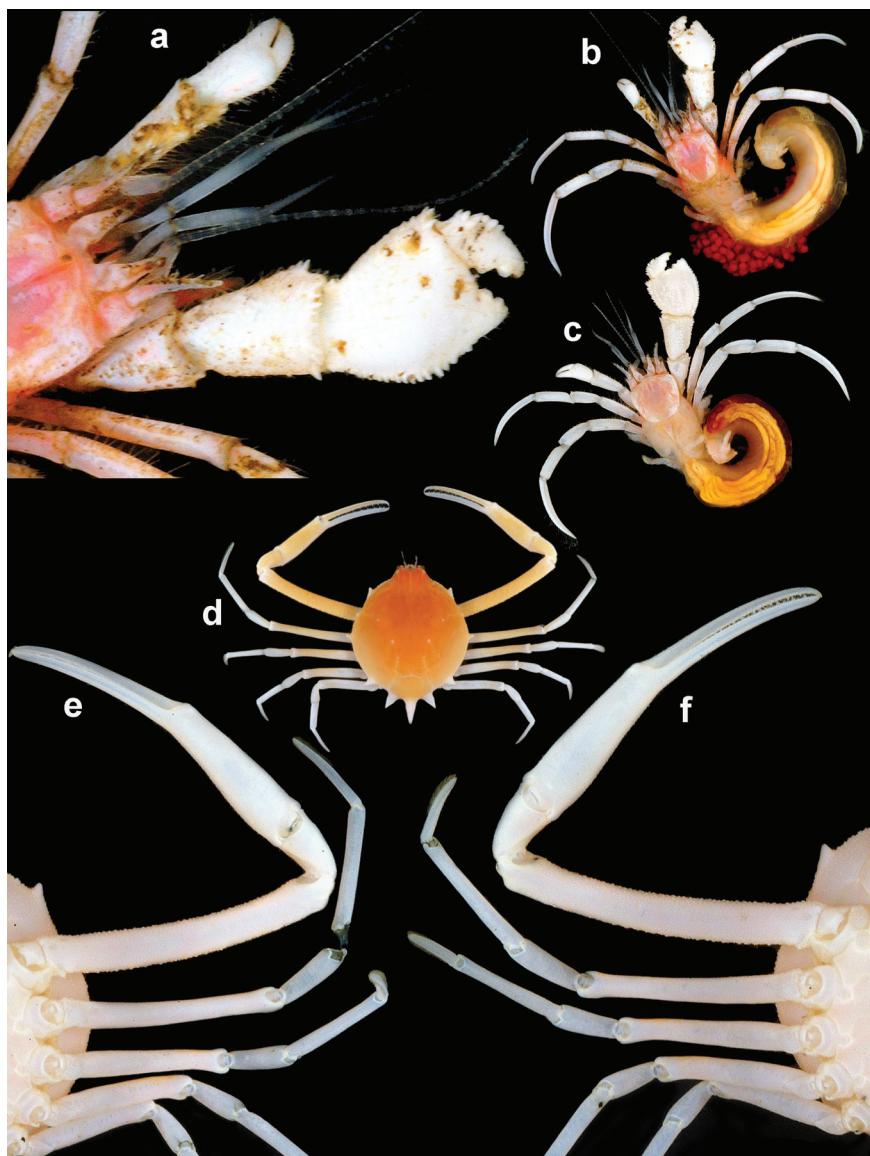


Figure 8. (a, b) An egg-bearing female of the deep-sea hermit crab *Sympagurus acinops* with a 3.6-millimeter (mm)-long carapace shield, collected in April 2011 near a depth of 1250 meters (m), 29 kilometers (km) east-northeast of the spill. Multiple early lesions are evident on its chelipeds and eyestalks. In panel (a), the distal margin of the carpus has fully eroded on the minor cheliped. (c) A female of *S. acinops* with a 4.1-mm-long carapace shield representing a typical prespill specimen devoid of lesions, collected from the northwestern Gulf of Mexico in August 2008 near a depth of 900 m, 295 km west-southwest of the spill. (d-f) A male of the purse crab *Myropis quinquespinosa* with a 21.6-mm-wide carapace, collected in April 2011 near a depth of 83 m, 74 km northwest of the spill. Multiple small dark lesions are most evident ventrally, including a major joint lesion that caused (e) disarticulation of the dactylus from the leg on the animal's left side and (e, f) incipient lesions evident as dark spots or a darkening of multiple joint membranes. Photographs: Darryl L. Felder.

our having observed an episode of these abnormalities in populations of several decapod species collected on nearby soft sediments of deeper waters (figures 8 and 9; Felder et al. 2012). Lesions on these soft-sediment decapods, common

on freshly caught specimens in benthic skimmer samples collected in April and August 2011 from near the spill site, often penetrated well into or totally through the endocuticle, sometimes at joint membranes of appendages at which they could be of sufficient severity to cause appendage loss and, almost certainly, some mortalities. The occasional occurrence of at least superficial lesions on decapod specimens is neither unexpected nor necessarily pathogenic, and we sometimes observe these to result from physical injuries, molting complications, or ectoparasitic infestations prior to capture. In preserved specimens, we conclude that these may alternatively occur as artifacts of spackling or surface desiccation from being frozen (freezer burn) prior to alcohol preservation, which makes comparisons of fresh collections with archived materials in alcohol very difficult. However, multiple, deeply penetrating, dark-margin pits were not noted in prespill samples from our northern Gulf of Mexico study areas (in field notes or archives), nor were any observed lesions so severe as to have cleaved appendage articles at joint membranes (figure 8f). Furthermore, occurrences of such lesions were episodic: They occurred in April and August 2011 samples but were absent in three sample periods thereafter (through October 2013), despite our heightened attention and detailed search for them. Finally, despite the difficulty of equating and judging the pathogenicity of lesions in archived samples, we did attempt preliminary scoring of the total frequency of cuticular scarring (lesions and otherwise) among preserved specimens the deepwater caridean shrimp of the genus *Glyphocrangon* from the northern Gulf of Mexico. We found 8.6% of 58 specimens from before the spill to bear such scar or lesion markings, compared with 20% of 30 specimens taken after the spill, which reflects a nearly threefold increase.

In many cases, manganese gill precipitates, observed in elevated frequency and severity among deeper-water soft-sediment decapods following the spill (especially in populations of *Glyphocrangon* and polychelid lobsters that also bore cuticular lesions), appeared to be severe enough to compromise respiratory efficiency (figure 9d). If these same abnormalities or lesions in fact occurred in bank decapods and

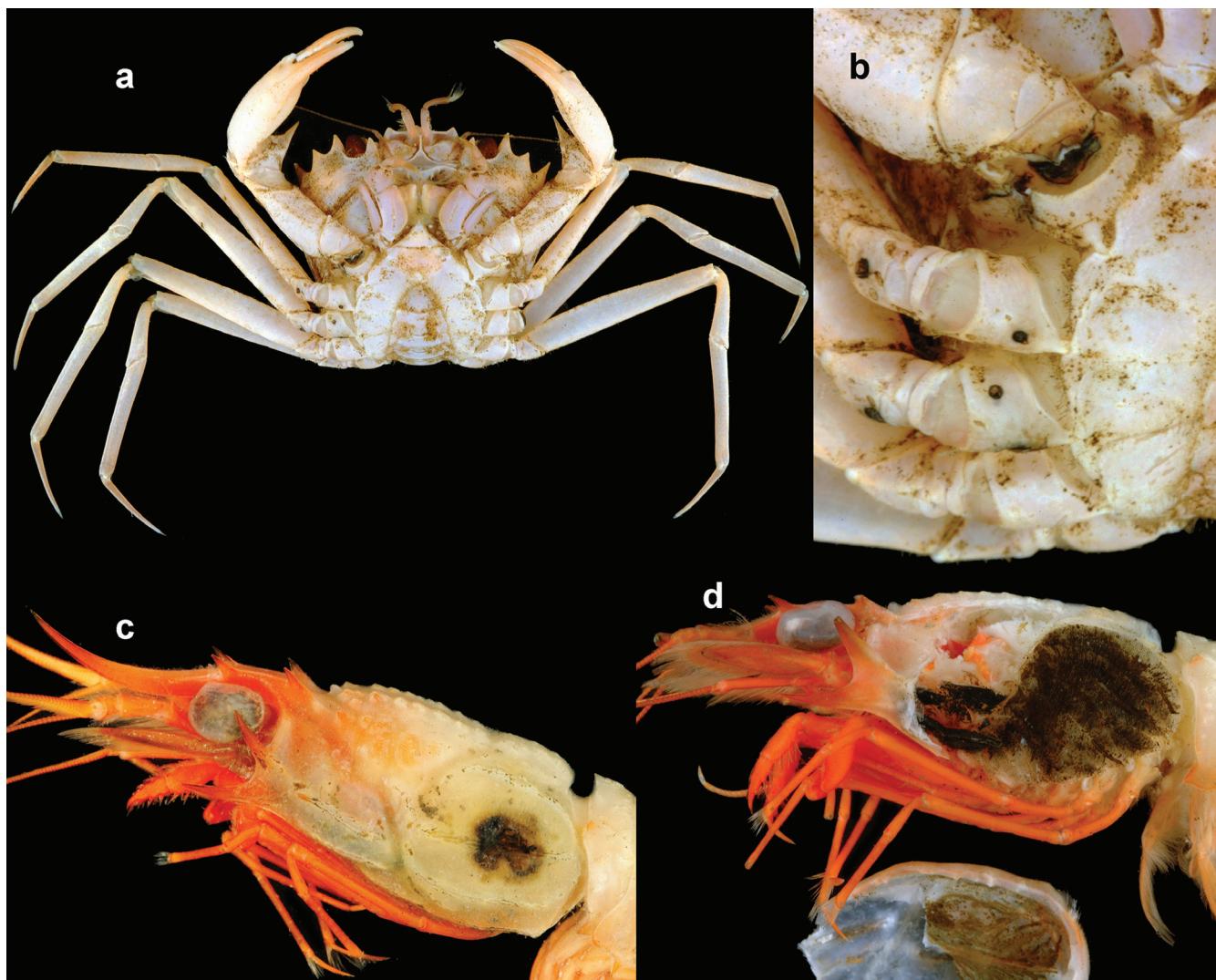


Figure 9. (a, b) A juvenile female of the deep-sea red crab *Chaceon quinquedens* with a 28.0-millimeter (mm)-wide carapace, collected in August 2011, near a depth of 1735 meters (m), 49 kilometers (km) east of the spill site. Multiple dark lesions are visible, especially on the joint membranes. (a) The second walking leg is lost, and the basis is capped by a large dark lesion on the animal's left side. (b) The large joint lesion at the base of cheliped on the animal's right side. (c, d) Specimens of the deep-sea shrimp *Glyphocrangon longirostris* collected in April 2011 near a depth of 1250 m, 110 km west-southwest of the spill site. (c) A male with a 15.2-mm-long carapace showing a large dark lesion penetrating the gill cavity wall. (d) A female with an 18.3-mm-long carapace, showing gills heavily covered by dark manganese precipitate (confirmed by elemental analysis). Photographs: Darryl L. Felder.

resulted in diseased or moribund decapods there, they could easily have gone undetected, given intense predation by bank fish populations and could therefore have gone unrepresented in our short-tow dredge samples from the banks. But again, on those occasions on which we could sample bank decapods, we were able to detect only the decline in abundance and diversity, rather than any direct evidence of pathology to account for it.

Hypotheses: Nutrient or microbial connections in declines of seaweeds and consumers?

The pathways by which marine bacteria interact with both multi- and unicellular eukaryotic algae are extremely diverse

(e.g., Barott and Rowher 2012). The reasons for most of the macroalgal biomass decline and disappearance following the Macondo oil spill—impacts of which appear to be long lasting with little recovery as of October 2013—are currently unknown and require an ecosystem-wide investigation that is specially focused on the less visible component of primary producers, such as endolithic algae, resting spores and carbonate dwellers, heteromorphic life history stages, and their interplay with bacterial communities involved in elemental cycling within and surrounding the rhodoliths.

Oil is composed of hydrocarbons and other organic compounds containing nitrogen, sulfur, and metals (e.g., iron,

nickel, copper) that may have stimulated components of microbial communities to the detriment of other organisms. We can hypothesize that the introduction of oil into porous bedrock stimulated anaerobic sulfate reducers, leading to the production of hydrogen sulfide, a weak acid known as *hydro-sulfuric acid* when it is dissolved in water. It is possible that, under these conditions, the conspicuous vegetative component of the algal life cycle may have died, leaving onsite epilithic or endolithic resting stages (e.g., spores, propagules, endolithic stages) at the surface and within rhodoliths; these, when placed in our laboratory microcosms under controlled conditions, have been triggered to germinate, revealing algal diversity currently repressed in the northwestern Gulf of Mexico. The heavy fractions of oil may have been retained in the underlying sediment where they would potentially ooze sulfide with long-term negative impacts on macroalgal assemblages and higher trophic levels that depend on them as a resource or habitat. Our collections of pre- and postspill rhodoliths preserved in silicagel for DNA analysis will be particularly important to assess any shift in bacterial communities toward sulfate reducers. Another hypothesis involves oil-induced stress on the algal community component, known to lead to their increased dimethylsulfoniopropionate (DMSP) production. This sulfur-containing molecule, metabolized by anaerobic prokaryotes (Van der Maarel and Hansen 1997), may also have contributed to sulfide production, further stressing the remaining macroalgae.

Whether prokaryotes and algal communities act independently or synergistically in the northwestern Gulf to promote environmental health, ecosystem stability, productivity, resilience, or biological adaptation in response to rapid environmental change is currently poorly understood. Because of our extensive pre-Macondo-spill database and DNA-preserved specimens of rhodolith-associated seaweeds in the northwestern Gulf of Mexico, we have an exceptional point of reference for comparing pre- and postspill collections from a particular offshore site for integrating taxonomic, phylogenetic, and environmental barcoding approaches with newer, seasonal collections from the same sites to infer the ecosystem function of rhodolith beds. An important question is whether specific endolithic algal communities drive specific bacterial communities or vice versa? Crustose coralline algae generally encourage benign microbial communities, whereas turf algae and fleshy macroalgae are known to promote heterotrophic microbial diversity (Barott et al. 2012). These interesting points may have many implications for important ecological cues, such as spore settlement on the rhodoliths.

The use of cost-effective, state of the art, next-generation sequencing tools will accelerate the discovery, characterization, and phenology of currently unknown microbial and eukaryotic diversity associated with rhodolith beds and will also enhance our understanding of the synergistic processes occurring between these organisms at the ecological level. Linking rhodolith-habitat eukaryotic biodiversity with the functional composition of the coexisting microbial

organisms to uncover potential patterns of association at the community level will illuminate how the interaction between pro- and eukaryotes influences overlooked biodiversity in the deep bank ecosystem. Furthermore, the interplay of bacterial and algal communities found in proximity to (e.g., in ambient seawater) and within rhodoliths (i.e., as endoliths) and their function for higher trophic levels in the northwestern Gulf of Mexico is currently unknown. Because crustose corallines are generally known to release chemosensory compounds that have been implicated in the larval settlement and morphogenesis of a range of invertebrates, especially reef-building corals (e.g., Hadfield and Paul 2001), mollusks (Roberts 2001), cnidarians, crustaceans, echinoderms (Riosmena-Rodríguez and Medina-Lopez 2011), sponges (Ávila and Riosmena-Rodríguez 2011), and gorgonians (Georgiadis et al. 2009), we hypothesize that coralline-dominated rhodoliths in the northwestern Gulf of Mexico may likewise be implicated in controlling the dynamics of their microbiota as well (i.e., through cryptobiosis or seed-bank dormancy during environmental stress).

It has been shown elsewhere that the algal component of the photosynthetic community exudes organic matter (e.g., Smith et al. 2006) that is used by prokaryotes sharing an environment and that these bacteria, in turn, cycle key biogeochemical elements necessary to these primary producers and other eukaryotic colonizers. In addition to the release of chemically diverse organic carbon in their direct environment, algae, as was previously mentioned, also produce DMSP intracellularly as osmolyte, an antioxidant and grazing deterrent (e.g., Sunda et al. 2002), with the excess leaking out of the cell and selectively enriching the surrounding bacteria involved in the metabolism of this sulfur-containing molecule (such as marine roseobacters; Buchan et al. 2005) or methylotrophs (Schäfer 2007).

Furthermore, we currently do not understand the bottom-up (nutrient-driven) and top-down (algal consumption by herbivores) factors that affect algal growth at these depths, factors that may explain the suppression of or variation in algal diversity and abundance observed in field collections on deep northwestern Gulf of Mexico hard banks. An ecophysiological approach using multiple stable isotope and nutrient content analyses of freshly collected seaweed vouchers and invertebrates (and of prespill specimens from the same deep bank sites) are urgently needed to assess spatiotemporal variation of nutrient regimes, nutrient sources, and exposure to oil and dispersant in order to assess which abiotic factors and trophic-level interactions may influence seaweed community development and, indirectly, the primary and secondary consumers that depend on the seaweeds for their survival.

One hypothesis is that the decline of resident decapods on deep banks may relate largely to the loss of seaweed cover, which could have led to cascading effects on both direct consumers and higher trophic levels. However, at this time, we can only speculate on the connection of this potential trophic deregulation to the Macondo spill or to other

precipitous environmental perturbations from the same time period. However, perhaps decapods are also vulnerable to oil spills by way of insult to their protective epicuticle, and the kinds of lesions observed in our deep skimmer samples from soft sediments may also have occurred more widely throughout the decapod assemblage, remaining undetected in the absence of comprehensive seasonal monitoring. Oil and dispersants used to combat oil spills could have directly or indirectly (by way of altered microbial communities) affected the integument of crustaceans by compromising the integrity of their epicuticle, which serves as a physical barrier between the environment and the more permeable inner layers of the exoskeleton. Natural populations of lipoclastic microbes, massively enhanced in density by the presence of dispersed oil in the water column or in benthic sediments, could potentially attack crustacean epicuticular surfaces, as well as the dispersed oil. The thinning of waxy epicuticle by hydrocarbon solubilization or microbial erosion may give chitinivorous bacteria and other microorganisms access to the chitin and protein of exocuticles and endocuticles, potentially leading to the development of lesions known commonly as *shell disease*.

Shell disease has been studied extensively in economically important crustaceans, such as the American lobster (*Homarus americanus*; e.g., Laufer et al. 2005a, Chistoserdov et al. 2005, 2012) and the European edible crab (*Cancer pagurus*; e.g., Vogan et al. 2001) and, to a lesser extent, in the blue crab (*Callinectes sapidus*; Noga et al. 1998, 2000), deep-sea geryonid crabs (Bullis et al. 1988), commercial mud crabs (Andersen et al. 2000), grapsoid crabs (Li 2004), nephropid and spiny lobsters (Porter et al. 2001, Freeman and MacDiarmid 2009, Mancuso et al. 2010), and several species of caridean and penaeid shrimp (Lavilla-Pitogo and de la Peña 1998, Goarant et al. 2000, Jayasree 2006). Clearly, it can and has previously caused dramatic losses in commercial fisheries and could, under some circumstances, potentially affect deep bank decapod assemblages or, perhaps, even nearshore commercial crab and shrimp fisheries of the northern Gulf of Mexico.

However, definitive evidence of a link between shell disease mortalities and spilled hydrocarbons has yet to be provided. The presence of environmental pollutants, in some cases, correlates with shell disease (Ziskowski 1996) and, in others, does not (Powell and Rowley 2005), although alkylphenols have recently received particular attention as potential environmental triggers of the disease in the American lobster (Laufer et al. 2005b). At the present, in the absence of further research to test our hypotheses, we are limited to much the same level of speculation as in previous spill cases. For example, a comparatively small spill off Rhode Island involved the release of 828,000 gallons of home heating oil (Cobb et al. 1999). Dramatic lobster mortality was observed following this incident, coincident with an onslaught of shell disease. No connection between the spill and the disease episode was ever scientifically established, but lobster fishermen and the local populace were firmly convinced that the spilled oil

caused this event. Although the oil likely contributed to an increase in disease vulnerability during a few years following the spill, it was more widely accepted that the likely overall trigger of this disease in the American lobster was global warming's impact on bottom temperatures in Long Island Sound (Wilson and Swanson 2005). Similarly, the decline of decapod assemblages on Louisiana's deep banks coincides with a period in which the surrounding waters were subject to a massive hydrocarbon and dispersant release and a cascade of chemical and microbial processes involving the degradation of these materials.

Oil and dispersant unquestionably triggered dramatic changes in the Gulf microbial community, inducing an increase of bacteria belonging to the genus *Colwellia* and the order Oceanospirillales (Bælum et al. 2012), both of which represent lipoclastic and chitinolytic groups (Cottrell et al. 2000). One of the most prominent obligate oil degraders, *Alcanivorax borkumensis*, of order Oceanospirillales, possesses a powerful lipase (Martins dos Santos et al. 2010). Even so, although such observations suggest a role in etiology of potential decapod crustacean shell disease, we can only hypothesize a link to mortalities and measurable population declines, and we cannot exclude other potential population impacts of river flow, regional hypoxia, and storm disturbance.

Seedbank hypothesis

The consideration of rhodoliths as seedbanks for biological diversity, sources of community regeneration, and an important ecosystem unit for the cycling of elements is a novel concept (Fredericq et al. 2014) and an unanticipated outgrowth of our postspill monitoring program. Research on carbonate components of relict continental margin sediments is typically focused on the negative effects of endolithic microborers, endolithic algae, or fungi on hermatypic corals as agents of substratum erosion (Tribollet and Golubic 2005) or pathogenic agents (Yarden et al. 2007). Previous studies on endolithic microborer communities have shown that the arrangement of the endolithic biota in carbonate substrata is dynamic (Wisshak et al. 2005) and can shift because of a decrease in seawater pH (Tribollet et al. 2009) or an alteration in available organic material (Carreiro-Silva et al. 2009) in the ambient water. We hypothesize that rhodolith endo- and epilithic biota in the northwestern Gulf of Mexico likewise constitute a very dynamic ecosystem and that their continued study will lead to a deeper general understanding of benthic marine interactions. For example, one noteworthy research finding emanating from our ongoing postspill investigations of Ewing Bank rhodolith beds is that newly discovered life history stages of a bloom-forming *Prorocentrum* dinoflagellate may reside inside deep bank rhodoliths. Future scanning electron microscopy observations should reveal where a particular transitional, sessile stage of *Prorocentrum* fits in the developmental sequence that leads to the free-living, flagellated, bloom-forming stage in the northwestern Gulf of Mexico.

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Darryl L. Felder (dlf4517@louisiana.edu), Brent P. Thoma (brent.thoma@gmail.com), William E. Schmidt, Thomas Sauvage, Sherry L. Self-Krayesky, Andrei Chistoserdov, and Suzanne Fredericq (slf9209@louisiana.edu) are affiliated with the Department of Biology, and DLF and BPT are also affiliated with the Laboratory for Crustacean Research at the University of Louisiana at Lafayette. Heather D. Bracken-Grissom is affiliated with the Department of Biology at Florida International University, in Miami, Florida.