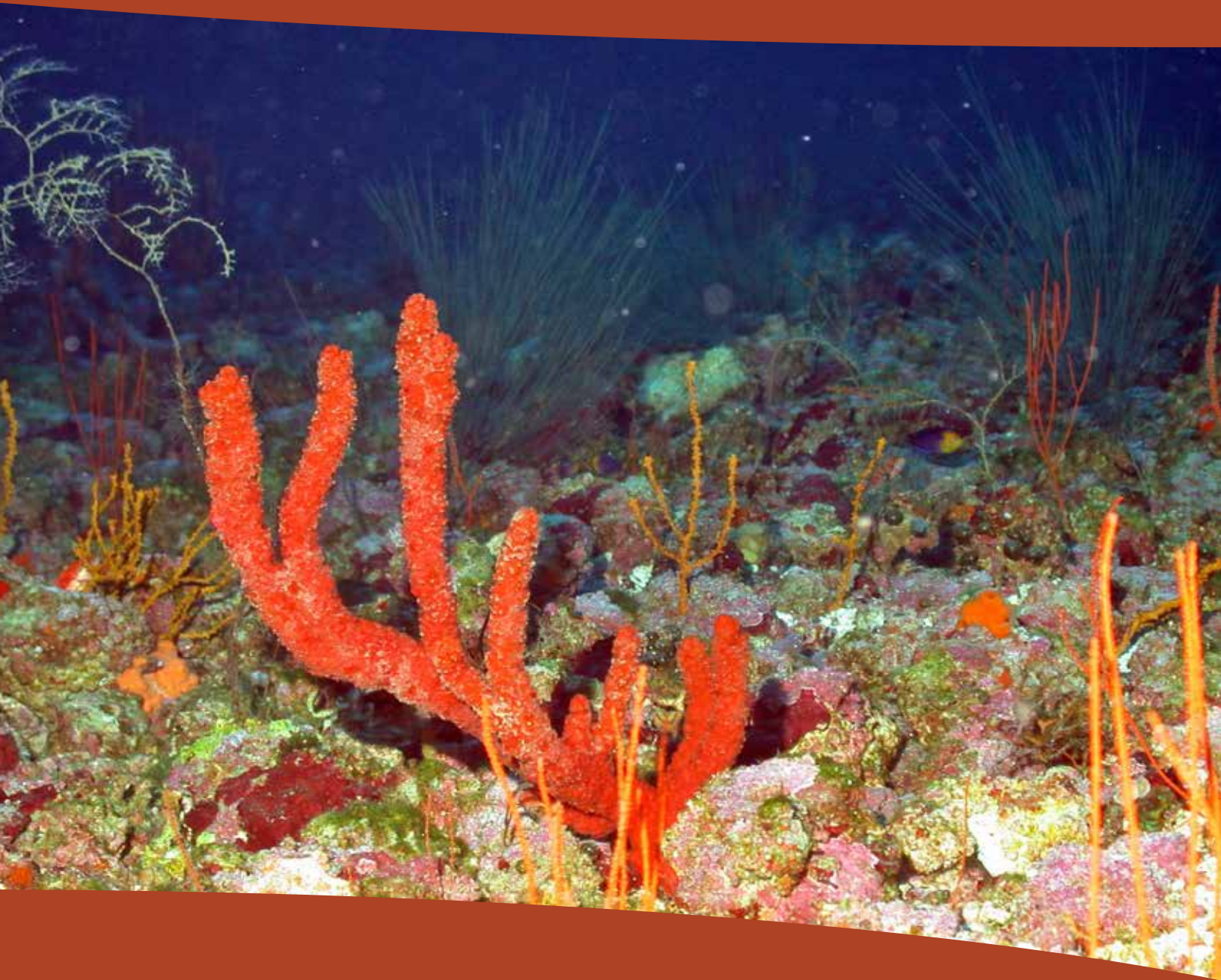


OIL IN OUR OCEANS

A Review of the Impacts of Oil Spills on Marine Invertebrates

Michele Blackburn, Celeste A. S. Mazzacano, Candace Fallon, and Scott Hoffman Black



THE XERCES SOCIETY
FOR INVERTEBRATE CONSERVATION

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The Xerces Society for Invertebrate Conservation

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The Xerces Society for Invertebrate Conservation is a nonprofit organization that protects wildlife through the conservation of invertebrates and their habitat. Established in 1971, the Society is at the forefront of invertebrate protection, harnessing the knowledge of scientists and the enthusiasm of citizens to implement conservation programs worldwide. The Society uses advocacy, education, and applied research to promote invertebrate conservation.

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Front Cover Photograph

The Flower Garden Banks National Marine Sanctuary contains some of the best remaining coral reefs in the Gulf of Mexico. Photograph: NOAA Photo Library, NURC/UNCW and NOAA/FGBNMS.

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Executive Summary

The overwhelming majority of marine biodiversity is represented by invertebrates, including sea stars, mussels, oysters, crabs, corals, and many thousands of other multicellular and unicellular animals. Despite this numerical dominance, marine invertebrates are extremely understudied. Marine invertebrates create and sustain invertebrate and vertebrate fisheries with huge commercial and recreational economic importance, they form extensive structures such as coral reefs and oyster beds that minimize wave action and protect shorelines from erosion and storm damage, and they are at the center of marine food webs.

More than 1.3 million metric tons of petroleum enters the sea annually. Human-induced sources of oil in marine habitats include spills, discharges of treated and untreated ballast water from oil tankers, effluents from oil refineries, oil/water separators on production platforms, and terrestrial sources such as effluent from sewage treatment plants and runoff from roads and parking lots. Oil spill damages are frequently presented only in terms of impacts on the so-called “charismatic megafauna” such as seals and seabirds and not in terms of impacts on invertebrate communities, which are often unknown or poorly assessed. Because marine invertebrates are fundamentally important in sustaining ocean biodiversity and are key components of multiple marine ecosystems from estuaries to the deep sea, it is important to understand the impacts of oil spills on both marine invertebrates and the animals that depend on them.

This report reviews the current science on the impacts of oil spills on marine invertebrates, with additional emphasis on the 2010 Deepwater Horizon oil spill in the Gulf of Mexico, which was the largest, deepest, and most prolonged offshore oil spill in U.S. history. In reviewing the current research, we summarize the effects of previous oil spills on a variety of habitats and invertebrate taxa worldwide, from the Gulf of Mexico to the Persian Gulf; identify knowledge gaps regarding marine invertebrate responses to oil spills and their subsequent recovery; and discuss marine invertebrate species and species groups of conservation concern in the Gulf of Mexico.

Importance of Marine Invertebrates

Marine invertebrates play important roles in water purification, habitat creation, and shoreline erosion control. They are critical food sources for a variety of marine wildlife, provide and sustain large commercial fisheries for humans, support lucrative tourist activities in coral reef snorkeling and fishing, and are important in the development of new pharmaceutical compounds. They are an integral part of marine food webs, comprising part or all of the diets of many fish, birds, and mammals. Zooplankton (tiny crustaceans and the embryos and larvae of other invertebrates) which are abundant in the water column form an important link in the marine food web, transferring energy captured by microscopic single-celled plants (phytoplankton) to higher-order consumers including fish, whales, and birds. Invertebrates inhabiting the substrate are an important food source for other invertebrates (lobsters, crabs, snails, octopuses), as well as birds, fish, and marine mammals. Marine invertebrates are also key prey items for sensitive species such as the federally endangered loggerhead sea turtles (*Caretta caretta*), blue and right whales (*Balaenoptera musculus* and *Eubalaena* spp.), and the proposed threatened rufa red knot (*Calidris canutus rufa*).

Lobster, crab, sea scallops, shrimp, squid, oysters, and sea cucumbers are also directly harvested

for commercial sale. Global wild shrimp production totals 3.4 million metric tons a year, and the global shrimp trade, valued at \$10 billion, is the largest commercial fishery in the world. U.S. oyster harvests yielded 28.5 million pounds valued at \$131.7 million in 2011, and in 2010 the commercial catch of blue crab (*Callinectes sapidus*) accounted for over 222 million pounds. The largest wild sea scallop fishery in the world is in U.S. waters. In 2010, 57 million pounds of sea scallop meat worth over \$449 million were harvested.

The commercial importance of marine invertebrates is not limited to consumption. Coral reefs have significant tourism value through scuba diving, snorkeling, recreational fishing, and boating. In the Florida Keys, reef-based tourism generates over \$1.2 billion annually; dive tourism in the Caribbean generated \$2 billion in 2000, and reefs in tourist areas of Indonesia have been valued at \$1 million per km². Because many marine invertebrates synthesize complex chemical compounds for defense, communication, competition, and prey capture, they have substantial economic importance as a source of novel chemicals. Approximately 30,000 natural products have been isolated from marine organisms, the majority of which are from invertebrates. These marine-derived products are used in a variety of pharmaceuticals, cosmetics, nutritional supplements, and pigments.

Marine invertebrates also create ecologically and commercially important habitats. Coral reefs support nine million (30%) of all ocean species, and catches from reef regions account for 10% of fish eaten by humans. Coral reefs form living breakwaters that dissipate wave energy, prevent erosion, and increase sedimentation rates near shorelines. Similarly, the dense beds formed by oysters not only create habitat that supports a diverse, abundant fauna in intertidal areas, but also stabilize sediment and protect shorelines from erosion. One hectare of oyster bed habitat can provide coastal protection valued at \$85,998 per year.



Invertebrates dominate the marine environment, both in sheer numbers of species and in providing the building blocks of the underwater ecosystem. Coral reefs in the Gulf of Mexico provide many benefits. (Photograph: National Oceanic and Atmospheric Administration, U.S. Department of Commerce.)

Impacts of Oil on Marine Invertebrates

The negative impacts of oil spills vary with the spill's location and magnitude as well as invertebrate life stage, habitat, sensitivity, feeding mode, and ability to avoid or process contaminants. The effects of oil on marine invertebrates in general include habitat degradation; smothering; fouling of gill structures; impaired reproduction, growth, development, feeding, immune response, and respiration; and disturbance of the food web.

Spilled oil disperses into different parts of the environment, from the water's surface through the water column to the sediment as well as the shoreline, and affects invertebrate communities in multiple habitats. Oil in the open water can cause immediate mortality in zooplankton. In addition, because zooplankton includes immature stages of invertebrates that inhabit the sediment (benthic habitat) as adults—such as sea urchins, sea stars, crabs, oysters, mussels, and marine worms—mortality may result in long-term decreases in biomass and changes in community composition. These early life stages are more sensitive to oil compared to adults, and thus zooplankton mortality has implications for recruitment of juveniles into existing adult populations. To compound the situation, benthic invertebrates are also adversely affected as adults by oil that is trapped and buried in sediments and/or in mussel and oyster beds, where it can persist essentially unchanged for years.

The following impacts on marine invertebrates of oil spills have been noted:

- ⇒ Echinoderms (sea urchins, sea stars, sea cucumbers) can be particularly sensitive to oil. Oiling of nearshore habitats has resulted in mass die-offs and strandings of sea urchins and sea stars, and early planktonic life stages exposed to oil may show impaired embryogenesis and larval growth.
- ⇒ Mollusks (mussels, oysters, and snails) are highly sensitive to oil. Oil ingested by mussels and oysters during filter-feeding accumulates in their fatty tissues and may be retained on the gills. Mussels and oysters have a limited capacity to metabolize oil, which prolongs their exposure and negatively impacts feeding, growth, reproduction, embryo development, and immune response. Snails and limpets in intertidal rocky shores and estuaries have shown high levels of mortality after oil spills and reduced recruitment of juveniles for years afterwards, and sublethal concentrations impair their mobility, foraging behavior, and reproduction.
- ⇒ Coral reefs are declining globally due to human-induced stressors, including oil spills. The effects of oil pollution on coral communities are severe and wide-ranging and include decreased growth; impaired reproduction and larval development; decreased recruitment of juveniles and reduced juvenile colonization capacity; and altered feeding and behavior. Stress responses in corals following oil spills include bleaching due to loss of symbiotic microorganisms; dead patches in reefs; and increased colonization by algae. Because corals are the building blocks of reef ecosystems, direct impacts of oil on corals lead to further alterations in the diverse communities of reef-dependent fish, invertebrates, and plants.
- ⇒ Crustaceans (crabs, amphipods, lobsters, and shrimp) suffer significantly reduced populations after oil spills, and large numbers may be seen stranded on the shore. Because many crustaceans burrow into sediment and feed on the surface, they are exposed to oil that can remain buried in sediments and associated with the surface layers for decades. This chronic exposure can impair feeding, mobility, development, and reproduction.
- ⇒ Polychaete worms display complex and varied responses to oil pollution. Following oil-spill-induced die-offs of marine invertebrates, some polychaete species may increase in abundance, some will rapidly colonize damaged habitat, and others suffer reduced populations.

While the effects of oil spills on invertebrate communities are often not specifically investigated for a long enough time period, multiple studies demonstrate severe acute and long-term impacts of oil on marine invertebrates. These studies highlight the need for additional and longer term studies on a greater number of species.

The Deepwater Horizon Oil Spill

The April 2010 disaster on the Deepwater Horizon rig and the subsequent underwater blowout of the well resulted in one of the largest, deepest, and most extensive offshore oil spills in U.S. history. Over a period of three months, between 4.6 and 4.9 million barrels (193 to 210 million gallons) of oil entered the Gulf of Mexico. This oil impacted almost every habitat in the northern Gulf, from the deep sea floor through the water column to the coastal wetlands, estuaries, beaches, barrier islands, tidal mud flats, and mangrove stands of five Gulf states.

The effects of the Deepwater Horizon spill on marine invertebrates were immediate and acute. Deepwater corals exposed to the oil plume were found dead or dying, and mussels and snails on shorelines were coated with oil and suffocated. Zooplankton in the water column were exposed to oil at levels known to cause mortality, and ingested oil was detected in exposed populations. Commercial fishing for crabs, shrimp, and oysters was suspended due to contamination. The timing of the Deepwater Horizon spill may have increased the severity of its impacts, as it corresponded with the spawning period of many coral, crabs, shrimp, and oysters, and the early life stages of these animals are more sensitive to oil.

While effects on local food webs and community-level responses have been largely overlooked and remain difficult to measure, potential ecosystem service losses related to the spill are of great concern. Long-term impacts persist, as invertebrates in impacted Gulf habitats continue to exhibit impaired disease resistance, decreased growth and reproduction, and slow population recovery. Oil remains trapped in sediments of both coastal marshes and deepwater habitats, where it is retained essentially unchanged and may extend impacts to invertebrates by as much as decades. There are additional concerns about the potential for permanent loss of invertebrate habitat in coastal areas, because the death of vegetation in oiled saltmarshes leads to increased erosion rates. The incredible diversity and natural variation in marine habitats and invertebrate fauna means that it is not possible to develop broad, universal relationships between oil inputs and associated impacts. Dedicated ongoing monitoring programs are needed in the Gulf of Mexico and other areas at high risk of oil pollution to assess baseline populations and community composition of invertebrates in unimpacted areas, determine oil spill impacts, monitor recovery, and understand the processes involved in ecosystem responses to pollution.

Marine Invertebrates at Risk in the Gulf of Mexico

The Gulf of Mexico is one of the world's most economically important and ecologically diverse marine systems. The Gulf's complex and varied habitats—wetlands, marshes, barrier islands, beaches, seagrass meadows, and coral and oyster reefs, as well as the pelagic (open water) and benthic (sediment) habitats to depths well in excess of 1,000 meters—provide the region with fisheries, tourism activities, and other ecosystem-supported benefits valued at an estimated \$19.7 billion per year. Underwater regions provide feeding grounds and critical nursery habitat for a diversity of resident and transient fauna, while the coastal and estuarine habitats support over 90% of all commercially and recreationally important species in the region during some stage in their life cycles.



An explosion on the Deepwater Horizon platform in April 2010 led to significant loss of human life. Over the next three months nearly 5 million barrels of crude oil flowed from the ruptured wellhead and into the Gulf of Mexico. (Photograph: United States Coast Guard.)

The Gulf of Mexico supports at least 15,419 species, 10% of which are found nowhere else on Earth. Invertebrates represent over 95% of all marine animals and populate a huge variety of habitats, but in general are much less well known than marine vertebrates. The exceptions are economically important species of crustaceans (crabs, lobsters), mollusks (oysters, mussels), and echinoderms (sea urchins). Because of enormous gaps in our knowledge of invertebrates and in the absence of historical or baseline data, it is difficult to fully understand the impacts of oil spills on this diverse fauna. As a first step in understanding which invertebrates are most at risk from oil spills, this report reviews some of the most imperiled major marine taxonomic groups, community types, and species in the Gulf of Mexico, including their current conservation status, ecology, distribution, threats, and research needs.

Corals may represent some of the most imperiled species in the Gulf of Mexico. In the aftermath of the Deepwater Horizon oil spill, it was predicted that ten coral species found in the Gulf that were previously identified by the International Union for Conservation of Nature (IUCN) as endangered or vulnerable may become more threatened. Two of these corals are already federally protected, and an additional seven have been proposed endangered or threatened by the National Marine Fisheries Service. Additional research into reproductive biology, disease etiology, and gene flow of these corals is needed, as is a better understanding of the effectiveness of restoration strategies.

Other major taxonomic groups, including crustaceans, echinoderms, and mollusks, appear relatively stable in the Gulf of Mexico, although numerous species (e.g., spiny lobsters, cone snails, and sea cucumbers) remain understudied (“data deficient”) and others have experienced notable declines. In

the 1980s, the long-spined sea urchin (*Diadema antillarum*) suffered a massive die-off of that was described as the most severe mortality event documented for a marine species. The die-off ultimately led to explosive algae growth that smothered already stressed reefs and inhibited larval coral settlement and growth. Recovery has been slow, and this sea urchin remains rare and functionally extinct throughout parts of its range. Another species that shows slow and limited recovery, despite bans on collections, is the queen conch (*Strombus gigas*), whose population has declined considerably due to overharvesting and poaching. The eastern oyster (*Crassostrea virginica*) is also a species of concern. Globally, oyster reefs are the single most impacted marine habitat due to overharvest, disease, sedimentation, pollution, and changing salinities. While oyster beds in the Gulf of Mexico are some of the healthiest and most productive in the world, the continued careful management of oysters in the Gulf is of critical ecological and economic importance.

Deepwater communities have been recognized as biodiversity hot spots, but coral assemblages in these areas are globally threatened, primarily due to destructive fishing practices. Because of their great depths and often inaccessible locations, little is known about the total number, extent, and location of deepwater coral communities and their ecology remains poorly studied and largely unknown. Deepwater corals are fragile, slow growing, and long-lived. Radiocarbon analyses indicate that some of these animals in the Gulf of Mexico have been growing continuously for at least the last two millennia. Such long-lived species are especially at risk from disturbances, as it may take decades or centuries for them to recover. Other important yet relatively understudied deep-sea ecosystems include cold seeps and hydrothermal vents. Sampling of mussel- and polychaete-dominated cold seeps in the northern Gulf discovered 66 associated taxa, 39 of which had not been previously reported in the Gulf of Mexico. Little is known about species interactions and community structure in these deepwater habitats, and recent findings of a high proportion of new species emphasize the importance of conservation efforts for deepwater benthic communities. There is a clear need for additional basic research on these and many other marine invertebrate communities and species, and detailed studies of their distribution, abundance, and ecology are a priority before their conservation needs can be fully understood and addressed.

Conclusions

Petroleum hydrocarbons and their degradation products have high acute and chronic toxicity to marine invertebrates. However, because of the extreme diversity of marine invertebrates and the relative lack of research and conservation attention they receive, we still know little about the ultimate ecosystem-level impacts of oil spills. More—and better—baseline data is needed on existing populations of ocean organisms, including invertebrates, so that we can better understand how these important animals are being affected not only by oil spills but also by multiple additional impacts such as other types of pollution, over-fishing, and climate change.

More research must also be focused specifically on marine invertebrates in the aftermath of oil spills to monitor immediate and long-term impacts as well as recovery. Any investigation of marine invertebrates following a spill event is generally confined to groups such as crabs and shrimp with direct economic value, but many other types of invertebrates that play critical roles in ocean and coastal food webs can be affected as well.

Spills occur when oil is transported, as well as during exploration and drilling activities, in spite of regulations intended to prevent such events. No amount of precautions can guarantee that a spill will not occur. Thus, if we are to protect marine wildlife, we must reduce our consumption of oil while following best practices to reduce the possibility and impact of oil spills.

Introduction

Oil spills pose a severe and ongoing threat to marine ecosystems and the invertebrate animals that sustain them. Invertebrates such as sea stars, mussels, oysters, and crabs represent the overwhelming majority of marine biodiversity (when considering multicellular marine fauna), but they are extremely understudied and the impacts of oil spills on these communities are often unknown or poorly assessed. Oil spill impacts are frequently presented only in terms of the so-called “charismatic megafauna” such as seals and seabirds. But without diverse, healthy communities of marine invertebrates, the ecosystems and food webs that sustain these larger animals could not exist. Marine invertebrates play key structural and functional roles in marine ecosystems and are already experiencing significant threats worldwide from global climate change, pollution, overharvesting, and damaging fishing practices. Because they sustain biodiversity at all higher levels within the ocean and are key components of multiple habitats from estuaries to the deep sea, it is important to understand the impacts of oil spills on marine invertebrates and the animals that depend on them. This understanding will enable us to develop informed conservation and restoration plans and effectively educate the public, policy makers, and agency officials on the negative impacts of oil spills to invertebrates, and may help ensure that marine invertebrates are a key part of the dialogue in future discussions of offshore drilling initiatives.

Over 100 million metric tons (31 billion gallons) of oil are transported by sea per day (Rodrigue et al. 2013) and more than 1.3 million metric tons (380 million gallons) of petroleum enters the sea annually, from multiple sources (NRC 2003). The principal sources of human-derived oil pollution in marine habitats are oil extraction and transportation, including tanker accidents as well as operational discharges. For example, washing ballast tanks account for 36,000 metric tons (11.2 million gallons) of oil per year entering oceans worldwide (note these discharges are illegal in North American waters); and consumer consumption of hydrocarbons produces spillages from car and boat owners, non-tank vessels, and runoff from impervious surfaces into water bodies (NRC 2003; Fingas 2013). Natural seepage of oil from the sea floor also contributes a significant portion of petroleum to the sea (over 45% of the 1.3 million metric tons [380 million gallons] released globally). However, these natural processes release oil at a low rate to which deep sea organisms are adapted and differ greatly from the sudden rapid release of huge quantities that occur in an oil spill or extraction accident.

In 1993, T. H. Suchanek published a comprehensive literature review on the impacts of oil pollution on marine invertebrates. Twenty years after this review, this report, *Oil in Our Oceans*, reviews the current state of knowledge of the impacts of oil spills on marine invertebrates, with additional emphasis on the unprecedented Deepwater Horizon oil spill in the Gulf of Mexico in 2010. We begin with an overview of the importance of marine invertebrates in food webs, commercial fisheries, coastal protection, and tourism and recreation. We then discuss the fate of oil in the sea and the acute and chronic impacts to marine species and ecosystems. We summarize the effects of previous oil spills on a variety of habitats and invertebrate taxa worldwide from the Gulf of Mexico to the Persian Gulf, and identify knowledge gaps regarding marine invertebrate responses to oil spills and their subsequent recovery. Finally, we discuss marine invertebrates of special conservation concern in the Gulf of Mexico.

Part 1

The Importance of Marine Invertebrates

Ecosystem Services

Marine invertebrates play important roles in water purification, habitat creation, shoreline erosion control, food webs, recreation activities, and derivation of pharmaceutical compounds (NRC 2013). These functions are already threatened by pollution, habitat degradation, and global climate change, and oil spills represent another persistent threat. Ecosystem services include food and medicines from marine organisms, regulation of ecosystem processes including improved water quality, non-material benefits such as aesthetic enjoyment and recreation, and supporting nutrient cycling and habitat creation (MEA 2005). The loss of any or all of these ecosystem services threatens regional and global economies. The following sections discuss the services provided by marine invertebrates in greater detail.

Marine Food Webs

Zooplankton

Plankton form a fundamental component of the biotic integrity of the world's oceans and are at the center of the marine food web. Comprised of different functional groups, planktonic organisms include phytoplankton, microscopic single-celled organisms (photosynthetic bacteria and protists); and zooplankton, small multicellular invertebrate animals and the larvae and eggs of larger animals including invertebrates such as crustaceans, annelid worms, and echinoderms. Zooplankton are the most abundant primary consumers in the water column, transferring the energy and nutrients captured by phytoplankton to secondary consumers on higher trophic levels (Fenchel 1988; Fredericksen et al. 2006; Falk-Petersen et al. 2009).

Plankton are a significant food source for much larger animals such as foraging fishes, whales, and birds (Sundby and Fossum 1990; Gaston et al. 1993; Hobson et al. 1994; Lough and Mountain 1996; Conway et al. 1998; Darling et al. 1998; Sommer et al. 2002; Dahl et al. 2003; Turner 2004; Lowry et al. 2004; Laidre et al. 2007). Planktonic krill and copepods provide sustenance for such charismatic megafauna as blue and right whales, Adelie and chinstrap penguins, and albatross (Moksnes et al. 1998; Pauly et al. 1998b; Clapham et al. 1999; Allsopp et al. 2007; Trivelpiece et al. 2011; Rasmuson 2012). Declines in plankton have implications for the entire food web. For example, a decrease in copepod abundance in the North Sea due to climate change is thought to have led to smaller sandeel fish populations, ultimately causing unprecedented breeding failures in seabirds such as guillemots, black-legged kittiwakes, terns, and skuas (Wanless et al. 2005; Dybas 2006).

Echinoderms

Echinoderms, including sea urchins, sea stars, and sea cucumbers, are an important food source for a variety of wildlife including fishes, lobsters, and sea otters (Engstrom 1982; Tegner and Levin 1983; Bingham and Braithwaite 1986; Harrold and Pearse 1987; McClintock 1994; Schiebling 1996). Sea cucumbers are important prey for numerous species of fish, sea stars, and crustaceans (Francour 1997), and are a major food source for the Pacific walrus (*Odobenus rosmarus divergens*) (Fay 1982). Sea urchins are key organisms in the food webs of benthic (substrate-dwelling) organisms and the adults, larvae, and embryos are important prey items for snails, sea stars, crustaceans, fish, birds, and sea otters (Tegner and Levin 1983; McClanahan and Muthiga 1989; Estes and Duggins 1995; Tegner and Dayton 2000; Hereu et al. 2005). In some areas, sea otter predation on urchins helps reduce their grazing pressure allowing proliferation of kelp bed forests, which are in turn utilized by a wide variety of other important invertebrates and marine species (Estes and Duggins 1995).

Crustaceans

Hermit crabs, king crabs, blue crabs, and fiddler crabs are important in the food web of coastal environments (Christofoletti et al. 2010; Yeager and Layman 2011; Rasmuson 2012), pelagic upwellings (Signa et al. 2008; Romanov et al. 2009), and the deep sea (Van Dover 2002; Jeng et al. 2004; Fisher et al. 2007; Wang et al. 2013). They provide food for mammals, shore birds, octopuses, fishes, and humans, and are a key prey item for endangered loggerhead sea turtles (Plotkin et al. 1993). Crabs, shrimp, and lobsters are eaten by fish such as Nassau grouper, gray triggerfish, and Pacific cod (Wilson et al. 1987; Baird and Ulanowicz 1989; Wilson et al. 1990; Heck and Coen 1995; Ebert and Ebert 2005; Boudreau and Worm



The aptly named blue crab (*Callinectes sapidus*) is an economically important species in the Gulf of Mexico. It is also a link in the food web, eating smaller animals and falling prey to larger fish and mammals. (Photograph: NOAA Photo Library.)

2012) and are the subject of large commercial fisheries (Miller et al. 2005; Romanov et al. 2009; Rasmuson 2012).

Small amphipod crustaceans are eaten by many top predators, including fishes, mammals, birds, and other invertebrates (Oliver et al. 1982, Oliver et al. 1984; Nerini 1984; Thomson and Martin 1984; Highsmith and Coyle 1992; Kock et al. 1994; Darling et al. 1998; Bocher et al. 2001; Moore et al. 2003; Watanabe et al. 2004; Coyle et al. 2007; Seitz et al. 2011). Amphipods are also a key component of deep-sea benthic environments. They are scavengers that process dead and decaying matter, recyclers of nutrients, and prey for substrate-feeding fishes (Dahl 1979; Collie 1985; Soliman 2007; Duffy et al. 2012). Bocher et al. (2001) examined the functional importance of the amphipod *Themisto gaudichaudii* in the pelagic food web. They found that breeding success of southern rockhopper penguins and several species of burrowing petrels was tied to availability of amphipods during the chick rearing season, and any reduction in amphipod abundance severely impacted seabird populations.

Mollusks

Marine mollusks such as snails, octopuses, squid, scallops, oysters, mussels, and clams provide food for sharks, otters, whales, and a variety of fishes. Clams are the primary food source for sea otters in the waters around southeast Alaska (Kvitek et al. 1993; Wolt et al. 2012). Cephalopods such as octopuses, squid, and nautilus are important food sources for a variety of seabirds, fishes, and mammals including swordfish, tuna, salmon, sharks, elephant seals, and whales (Thorpe et al. 2000; Watanabe et al. 2004; Hunsicker et al. 2010).

The corals *Lophelia pertusa* and *Leiopathes glaberrima* provide the structure that supports an assortment of anemones, as well as shelter for squat lobsters, in this image of Roberts Reef, a deepwater reef in the northern Gulf of Mexico. (Photograph: NOAA/Lophelia II 2010 Expedition, NOAA-OER/BOEMRE.)



Habitat Creation

Coral

Marine invertebrates form the core of coastal and deep sea food webs and create complex habitats that support a variety of other animals. The most notable of these are the corals that are the key structural and functional components of tropical and subtropical reef systems. Coral reefs sustain a biological productivity per square meter that is about 50–100 times greater than the surrounding waters and these habitats are among the most diverse and complex underwater communities known (IPIECA 1992; Harrison and Booth 2007; reviewed in Gibson et al. 2011). Coral reefs provide habitat to a vast array of marine organisms and contain up to nine million, or 30%, of all multicellular ocean species (Mather 2013). Nearly one third of the world's marine fish species are found on coral reefs (McAllister 1991) and the catch from reef areas constitutes approximately 10% of the fish consumed by humans (Smith 1978). The abundance, diversity, and resilience of coral communities can be used as an indicator of overall ecosystem health, and pollution can significantly damage coral communities and the services they provide (Loya and Rinkevich 1980; Loya 2004; Harrison and Booth 2007).

Bivalve Shellfish

The dense beds formed by bivalve shellfish such as mussels and oysters are also of critical ecological importance, since they stabilize sediment and provide physical structure and habitat to support an abundant and diverse fauna in intertidal areas (Valentine and Heck 1993; Carls and Harris 2005; Borthagaray and Carranza 2007; reviewed in Grabowski and Peterson 2007; Beck et al. 2009). Shellfish beds contain a complex network of microhabitats that are colonized and used by many other organisms, including macroalgae, fishes, and a diverse array of invertebrates that includes amphipods, other bivalves, gastropods, anemones, sea urchins, corals, polychaetes, crabs, and sea stars (Suchanek 1979; Kanter 1980; Bahr and Lanier 1981; Witman 1985; Jacobi 1987; Suchanek 1992; reviewed in Seed 1996; Borthagaray and Carranza 2007; Beck et al. 2009; Koivisto and Westerbom 2010). Healthy shellfish beds thus help support fisheries and provide food for a number of other species, including humans.

Commercial Fisheries

Many coastal and deep sea invertebrates are harvested globally for commercial sale, including lobster, crab, shrimp, squid, oysters, and sea cucumbers. As finfish resources dwindle worldwide the attention of global markets has turned increasingly to these invertebrate fisheries (Pauly et al. 1998a; Worm and Myers 2003; Frank et al. 2005; Anderson et al. 2011; Boudreau and Worm 2012), with an increase in reported catch from 2 to 12 million tonnes since 1950 (Anderson et al. 2011). Many of the newly targeted fisheries are on tropical coral reefs (Sadovy 2005) that can host thriving populations of commercially important species (Spurgeon 1992; Bryant et al. 1998; Nagelkerken et al. 2000; Fosså et al. 2002; Jonsson et al. 2004). Coral reefs may also support higher fish catches than nearby non-reef areas (Fosså et al. 2002). The potential net values for fisheries from coral reefs are estimated at \$5.7 billion per year (Cesar et al. 2003).

Echinoderm and cephalopod fisheries have seen the greatest increases (Anderson et al. 2011). In the English Channel alone, cephalopod catches increased from 8,000 to 23,000 tons—almost 300%—

over a twenty year period (Payne et al. 2006). Global wild shrimp production totals 3.4 million metric tons annually and the global shrimp trade is valued at \$10 billion, making it the largest commercial fishery in the world (Gillett 2008). Mollusks are also a key food source for humans, both in the U.S. and globally. U.S. harvests for 2011 included 28.5 million pounds of oysters, valued at \$131.7 million; over 331.3 million pounds of squid, valued at almost \$110.5 million; and 59.3 million pounds of bay and sea scallops, valued at \$587 million (NMFS 2012).

Biomedical and Pharmaceutical Products

Marine invertebrates have substantial economic importance as a source of novel chemicals because many synthesize complex chemical compounds used in defense, communication, competition, and prey capture (Haefner 2003). Researchers recognized the potential for isolating novel biomedical compounds from marine invertebrates in the 1950s (Imhoff et al. 2011; Radjasa et al. 2011). In the last few decades approximately 30,000 natural products have been isolated from marine organisms, the majority from invertebrates (Haefner 2003; Radjasa et al. 2011). These compounds have been used in polymers and ceramics (Silva et al. 2012) and a wide variety of pharmaceuticals, cosmetics, nutritional supplements, enzymes, and pigments (Bruckner 2002).

Sea squirts, mollusks, sponges, and bryozoans have been especially useful in biomedical research (Gerwick and Moore 2012; Proksch et al. 2002; Radjasa et al. 2011). Sponges contain a wealth of biologically active compounds (Taylor et al. 2007); 36% of all described marine natural products are derived from these animals (Erwin et al. 2010). One of the first marine-derived anti-cancer agents, cytarabine, was developed from a sponge and is used to treat lymphoma and leukemia (Schwartzmann et al. 2001), and more than half of all natural products derived from marine organisms to combat the human immunodeficiency virus (HIV) come from sponges (Zhou et al. 2013).



The reefs created by oysters absorb wave energy and storm surges and increase sedimentation near shorelines, protecting coastal communities. One hectare of oyster reef habitat is estimated to provide \$85,998 of annual value in areas where property owners need coastal protection services (Photograph: Wikimedia Commons/Jstuby.)

There are currently two FDA-approved compounds in clinical use in the United States that are directly isolated from marine invertebrates: ecteinascidin 743, an anti-tumor drug derived from the sea squirt *Ecteinascidia turbinata*; and ziconotide, an analgesic isolated from the cone snail *Conus magnus* (Radjasa et al. 2011; Gerwick and Moore 2012). At least four other FDA approved synthetic agents have been derived from marine sponges and mollusks, although some compounds may actually be synthesized by bacterial symbionts and not the invertebrates themselves (Gerwick and Moore 2012). New research into invertebrate symbionts suggests that some of these unique bioactive compounds are a result of complex interactions between invertebrate hosts and a suite of microorganisms with potential applications for pharmaceutical uses (Proksch et al. 2002; Santiago-Vazquez et al. 2007; Taylor et al. 2007). An additional eleven natural products from marine invertebrates or their derivatives are currently undergoing clinical trials (Gerwick and Moore 2012). Other invertebrates, such as cnidarians (a group composed of corals, anemones, and jellyfish, among others), have also contributed to biomedical research. Green fluorescent protein (GFP), an extremely important marker protein used in cellular and molecular biology studies, originated from the jellyfish *Aequorea victoria* (Shimomura 2005; MacLachlan 2011). The potential for new bioproducts from marine invertebrates appears immense. The pharmaceutical industry average is one approved drug per 5,000–10,000 compounds tested, but compounds from the marine world have led to the development of one drug per 3,140 natural products tested (Gerwick and Moore 2012).

Water Filtration

Oysters and mussels effectively improve water clarity due to their filter-feeding activities, which reduces the amount of phytoplankton and suspended particulates (seston) (Cressman et al. 2003; Grizzle et al. 2006). This effectively decreases turbidity (Newell and Koch 2004), increases benthic algae (Newell et al. 2002), removes bacterial biomass (Cressman et al. 2003), and reduces nitrogen and other suspended particulate matter such as carbon, phosphorus, nitrogen, and silica (Dame et al. 1984; Cerco and Noel 2007; Pehler and Smyth 2011). Removal of these particulates from the water column helps increase light penetration in shallow calm waters, benefiting other nearby habitats that rely on photosynthetic organisms, such as eelgrass beds (Newell and Koch 2004). Under optimal temperature and salinity conditions, a single oyster may filter as much as 15 liters of water per hour, up to 1,500 times its body volume (Kumari and Solis 1995).

Shoreline Stabilization and Coastline Protection

The reefs created by corals and oysters protect shorelines and coastal communities by absorbing wave energy and storm surges. This has the additional benefit of minimizing coastal erosion and increasing sedimentation rates near shorelines (Birkeland 1997; Cesar et al. 1997; Costanza et al. 1997; Berg et al. 1998; Moberg and Folke 1999; Ahmed et al. 2005; Piazza et al. 2005; Coen et al. 2007; Barbier et al. 2011; Seavey et al. 2011). Coral reefs have been shown to absorb up to 90% of wind-generated wave action in their vicinity (UNEP-WCMC 2006). The current loss of coastal reefs due to pollution, disease, human development, and destructive fishing practices (Cesar et al. 2003; Mackenzie 2007; Wilberg et al. 2011) can have huge impacts on local economies, potentially requiring large investments in human-engineered defenses to replace the benefit from lost reefs (Grabowski et al. 2012). One hectare of oyster reef habitat is estimated to provide \$85,998 of annual value in areas where property owners need coastal protection services (Grabowski et al. 2012). Arkema et al. (2013) used various climate change models

and found that 16% of the U.S. coastline comprised high hazard areas that harbored 1.3 million people and represented \$300 billion in residential property value. With storm severity and frequency predicted to increase due to global climate change, the protective value of coral and oyster reefs will become increasingly important.

Tourism and Recreation

Coral reefs add significantly to the value of coastal tourism by supporting local economies through scuba diving, snorkeling, recreational fishing, and boating. Coastal tourism is one of the fastest growing sectors of the global tourism industry and a major source of employment in developing countries (UNEP-WCMC 2006). More than 100 countries have coastlines with coral reefs (Moberg and Folke 1999), offering a great potential for coral reef recreation. Out of the \$29.8 billion global net benefit of coral reefs, tourism and recreation account for 32% (\$9.6 billion total) (Cesar et al. 2003). In the Florida Keys, reef-based tourism generates over \$1.2 billion annually (UNEP-WCMC 2006). Similarly, dive tourism in the Caribbean brought in \$2 billion in 2000 (Collen et al. 2012) and in Indonesia, which has 50,000–100,000 km² of coral area, reefs in tourist areas have been valued at \$1 million per km² (Cesar 1996).



Photo: United States Navy, Navy Visual News Service (NVNS)

Part 2

Oil Impacts on Marine Invertebrates

The Fate of Spilled Oil

More than 1.3 million metric tons (380 million gallons) of petroleum enter the oceans each year (NRC 2003). Sources of oil in the marine environment include natural seeps, extraction, transportation, and consumption. All anthropogenic sources of oil combined account for about 53% of average annual discharges into marine waters worldwide, with the slow, sporadic releases from natural seeps accounting for the remainder (NRC 2003).

Natural seepages of crude oil on the seafloor have been discovered along continental margins in the Gulf of Mexico, the Atlantic Ocean, the Mediterranean Sea, and the east and west regions of the Pacific Ocean (Tyler et al. 2003; German et al. 2011). Around the North American continent, natural seeps appear to be restricted to the Gulf of Mexico and the Pacific Ocean off southern California.

Oil from human activities enters the marine environment through oil spills, discharges of treated and untreated ballast water from oil tankers, effluents from oil refineries, oil/water separators on production platforms, and terrestrial sources such as effluent from sewage treatment plants and runoff from impervious surfaces. In coastal areas, oil is mainly from road runoff, sewage, oil spills, and industry; in offshore zones, oil primarily enters the water from tanker spills and oil exploration and production facilities. Additional significant oil inputs include urban run-off into rivers and estuaries that discharge to the ocean, sewage effluent, oil spills from cargo ships, operational discharges from commercial vessels, and operation of recreational craft (NRC 2003; Fingas 2000; Fingas 2013). Oil and gas production and extraction processes contribute significantly to contaminants in the water column and sediments (benthos) around production facilities (NRC 2003), and have resulted in catastrophic spills from offshore platform facilities.

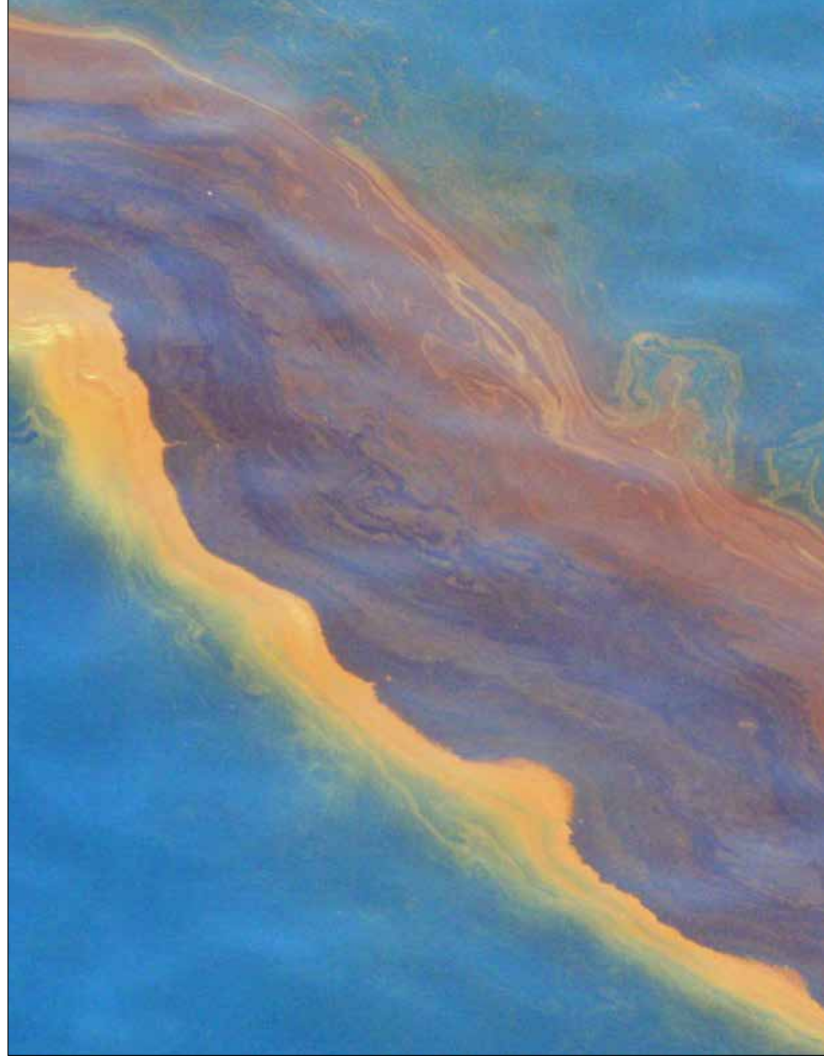
Physical and Chemical Weathering

Oil contains thousands of hydrocarbon molecules that differ in chemical structure, molecular weight, density, and ability to associate with either water or sediment. Crude (unrefined) oils of different densities and viscosities are processed into refined oils and the lighter (lower molecular weight) products used in industrial applications and engines. Oil is composed of compounds of carbon and hydrogen atoms, some arranged in long chains or rings, known as aromatic compounds. The mixture of hydrocarbons in oil range from smaller, volatile compounds (monocyclic aromatic hydrocarbons [MAH]) to very large, non-volatile compounds (polycyclic aromatic hydrocarbons [PAH]) (Fingas 2013). Both refined and unrefined oils contain a high proportion of highly toxic and carcinogenic compounds that include alkanes (paraffins), naphthenes (cycloalkanes), alkenes (olefins), dienes, alkynes, and benzenes

(O'Sullivan and Jacques 1998; NRC 2003; Fingas 2013). These compounds vary in their toxicity to marine invertebrates (Neff 2002). For example, aromatic compounds within oil, including MAHs, are the smaller and more volatile components of oil and include benzene, toluene, ethylbenzene, and xylene. Because of their chemical properties, MAHs are not persistent in seawater, bind weakly to marine sediments, and are not bioaccumulated to high concentrations by marine organisms (Kennicutt et al. 1988; Neff 2002; NRC 2003). Despite their known toxicity, these volatile compounds receive less attention than the more persistent PAHs in oil spill studies because of their lower affinity for incorporation into sediments and the tissues of marine organisms (Neff 2002). Polycyclic aromatic hydrocarbons are highly toxic and can persist for years in marine environments (Neff 2002), and thus have been the focus of many marine invertebrate toxicity studies and are therefore the focus of this review. The ultimate fate of oil in the ocean depends on the source, hydrocarbon composition, rate of release, and characteristics of the local ecosystem (Albers 2003; NRC 2003).

When oil spreads over the water's surface it undergoes physical and chemical changes known as weathering (NRC 2003). Physical processes involved in weathering include evaporation of volatile fractions into the atmosphere. The rate of evaporation depends on the type spilled and can range from 75% loss (light oil) to only 5% loss (heavy oil) within the first few days after a spill (Fingas 1999). The remaining oil undergoes transport processes such as advection (bulk fluid movement), spreading (oil slick), dispersion and entrainment (mixing by wind and water turbulence that moves oil into the water column), sinking and sedimentation (association with and binding to sediment particles), partitioning (separation of water-soluble and insoluble components of the oil), and stranding (washing onto the shore) (NRC 2003; Fingas 2013). Evaporation can help decrease the volume of spilled oil, but the mixing that creates emulsified oil (mousse) can actually increase the volume of the remaining oil three- to five-fold because emulsified oil contains 60–85% water. Most components of oil are not water soluble, so their dissolution and eventual degradation results in the loss of only about 1% of the volume. However, these soluble fractions are also highly toxic to aquatic life (O'Sullivan and Jacques 1998; Kingston 2002; Neff 2002; AMAP 2010; Fingas 2013). The poor solubility of higher molecular weight compounds, such as PAHs, enables them to bind to sediment particles, where they can create a "sediment sink" of pollutant that persists for years (Baumard et al. 1999). Oils that weather slowly can also strand on shorelines as tarballs and may persist for decades as relatively unaltered hydrocarbon sinks (Vandermeulen and Singh 1994).

Chemical weathering of oil involves the oxidation of constituent hydrocarbons to create a variety of "daughter" molecules (Burwood and Speers 1974; Garrett et al. 1998; Maki et al. 2001; Dutta and Harayama 2000; Lee 2003). Oxidation is mediated by energy from sunlight (photo-oxidation) and by certain bacteria and fungi (microbial oxidation) (Leahy and Colwell 1990; Swannell et al. 1996; Bruheim



An oil slick spreads across the surface of the Gulf of Mexico three weeks after the Deepwater Horizon disaster. When exposed to the weather, oil undergoes physical and chemical changes, and some of the volatile components evaporate. (Photograph: NOAA Photo Library.)



and Eimhjellen 1998; Atlas 1991; Head et al. 2006; Valentine et al. 2010, 2012; Redmond and Valentine 2012). Microbial oxidation of oil is an important part of natural remediation (Atlas 1991; Neff 2002; NRC 2003; Atlas and Hazen 2011), but it occurs slowly under anaerobic and/or cold conditions (Atlas et al. 1978; Kostka et al. 2011). Microbial oxidation is better understood in the laboratory (reviewed in Head et al. 2006), although field studies received renewed attention after the BP Deepwater Horizon oil spill in 2010 (Adcroft et al. 2010; Hazen et al. 2010; Valentine et al. 2010, 2012; Joye et al. 2011; Kessler et al. 2011; Kostka et al. 2011; Redmond and Valentine 2012). Microorganisms adapted to slow oil releases from natural seeps are unlikely to metabolize large inputs of spilled oil at a rate sufficient to be able to reduce the amount that ultimately reaches coastlines, estuaries, and the deep sea (NRC 2003; Camilli et al. 2010; Mendelsohn et al. 2012; Silliman et al. 2012; White et al. 2012; Montagna et al. 2013). For example, oil seeps in the northern Gulf of Mexico release about 200 metric tons of oil per day into the deep sea (MacDonald et al. 1993; Mitchell et al. 1999). In contrast, the Deepwater Horizon spill released 7,771 metric tons of oil per day across 86 days (Griffiths 2012), over 38 times the rate of natural seeps in the northern Gulf of Mexico. It is also worth noting that while oil represents an abundant carbon source for some microbes, hydrocarbon degradation in the ocean is limited by nutrient availability.

Photo-oxidation and microbial oxidation are both important in remediation of oil spills, but alteration of the “parent” oil molecules does not remove the risk to aquatic life as byproducts generated can be equally, or more, toxic to marine invertebrates (Newsted and Giesy 1987; Arfsten et al. 1996; Ankley et al. 1997; Pelletier et al. 1997; Erickson et al. 1999; Shelton et al. 1999; Albers 2003; Lee 2003; Bellas and Thor 2007; Kirby et al. 2007; Bellas et al. 2013). Toxicity of microbial oxidation byproducts has been demonstrated in the embryos and larvae of crabs, sea urchins, and marine worms (Shelton et al. 1999; Hamdoun et al. 2002). Amphipod and copepod crustaceans and oligochaete worms died when exposed to hydrocarbons in the presence of sunlight, suggesting that photo-oxidation created acutely toxic molecules (reviewed in Arfsten et al. 1996; Albers 2003; Bellas and Thor 2007). Similarly, oil toxicity to the larvae and embryos of mussels, oysters, and sea urchins was enhanced when oil was weathered artificially using UV light to stimulate photo-oxidation (Pelletier et al. 1997; Lyons et al. 2002; Saco-Álvarez et al. 2008; Bellas et al. 2013).

Persistence and Bioavailability of Spilled Oil

While weathering and oxidation contribute to oil dispersion and dissolution, persistence of oil in the environment is strongly affected by habitat. Rocky shores exposed to wave action and other physical disturbances are generally less sensitive to oil stranding compared to sheltered sites, such as muddy tidal flats, marshes, and mangrove swamps (Peterson et al. 2002). Because these sheltered habitats are also home to a diversity of sediment-dwelling bivalves and crustaceans, community-level impacts from oil exposure can persist for years (Hayes et al. 1993; Burns et al. 1993; Levings et al. 1994; Culbertson et al. 2007, 2008). Oil also penetrates into gravel-dominated, sheltered beaches and this deep infiltration, coupled with low rates of natural gravel replenishment, results in long-term oil persistence (Hayes and Michel 2001). This adversely affects small benthic organisms such as nematodes and copepods that are important in the marine food web (Gerlach 1978; Boucher 1985; Vranken and Heip 1986; Bodin 1988; Schmid-Araya and Schmid 2000). Though hydrocarbon availability to benthic organisms may decrease when it is bound to sediments (Maruya et al. 1996; Neff 2002), predicting the fate, distribution, bioavailability, and toxicity of such hydrocarbons is challenging and can vary with the physical and chemical characteristics of different marine habitats.

Oil may undergo bioaccumulation and/or biodegradation in living organisms (Albers 2003; NRC 2003), sometimes generating compounds that differ in toxicity from the parent molecules (Atlas 1991;

Martínez-Gómez et al. 2010). Biodegradation is primarily mediated by bacteria and fungi (see “Physical and Chemical Weathering”), but the digestive enzymes of polychaete worms may help solubilize ingested PAHs and make them more available to oil-degrading microbes, thereby enhancing bioremediation of oil-polluted sediments (Weston and Mayer 1998; Gilbert et al. 2001). Bioaccumulation occurs when fat-soluble hydrocarbons move directly across cell membranes or filter-feeding organisms ingest hydrocarbons bound to organic particles or sediment (Menon and Menon 1999; Baussant 2001; Neff 2002). Bioaccumulation in marine invertebrates depends on the type of oil released as well as an organism’s feeding strategy and ability to metabolize and excrete hydrocarbons (Stegeman 1985; Capuzzo 1996; Livingstone 1998; Neff 2002; Albers 2003; Meador 2003). For example, filter-feeding oysters and mussels may incorporate hydrocarbons at a greater rate than invertebrate grazers or predators and have higher levels of bioaccumulation, especially compared to marine vertebrates (Lech and Bend 1980; Widdows et al. 1982; Ba-Akdah 1996; Livingstone 1998; Neff 2002; Meador 2003; Martínez-Gómez et al. 2010).

Polycyclic aromatic hydrocarbon compounds in oil are of particular concern due to their persistence, bioaccumulation potential, and high toxicity to shellfish, plankton, and many other marine invertebrates, especially in the early life stages (Berthou et al. 1987; Cajaraville et al. 1992; Krishnakumar et al. 1994; Grundy et al. 1996; Pelletier et al. 1997; Dyrinda et al. 1998; Baussant et al. 2001; Le Floch et al. 2003; Meador 2003; Geffard et al. 2004; Fernandez et al. 2006b; Bellas and Thor 2007; Jeong and Cho 2007; Bellas et al. 2008, 2013; Saco-Álvarez et al. 2008; Hannam et al. 2010; Luna-Acosta et al. 2011; Grenvald et al. 2013). In a laboratory study, bivalves accumulated PAHs in their tissues at higher levels and eliminated them at a lower rate compared to fish (Law et al. 1997; Law and Hellou 1999; Baussant et al. 2001). Bioaccumulation of PAHs increases the body burden of toxicants and is associated with behavioral and physiological impairments (Neff et al. 1987; Neff 2002; Meador 2003). The incidence of tumors and other cellular pathologies in bottom-dwelling bivalves from contaminated coastal areas is thought to be linked to levels of fat-soluble contaminants such as PAHs (Neff and Haensly 1982; Berthou et al. 1987; Neff et al. 1987; McDowell and Shea 1997).

Ingested and absorbed hydrocarbons can be transferred through the food web to higher-level consumers (Varanasi et al. 1985; Baussant et al. 2001; Neff 2002; Albers 2003; Filipowicz et al. 2007; Allan et al. 2012), although biomagnification in fish and mammals at higher trophic levels is not well understood (Wan et al. 2007; Nfon et al. 2008). In some studies, PAH levels were greatest in phytoplankton and zooplankton (1,321 and 3,503 nanograms PAH per gram of lipid weight [ng/g lw]) and decreased through the food chain from invertebrates (66–770 ng/g lw) to birds (370 ng/g lw) and fish (43–247



Oil compounds are passed up through the food web via contaminated food items. Invertebrates have higher rates of bioaccumulation than vertebrates, and levels of polycyclic aromatic hydrocarbons have been shown to decrease as they are passed to birds. (Photograph: Wikimedia Commons/4028mdk09.)

ng/g lw) (Wan et al. 2007). Nevertheless, PAHs do move through the food web and PAH metabolites are known to be toxic to larger consumers (Stegeman and Lech 1991; Carrasco Navarro et al. 2012). Furthermore, because some marine invertebrates metabolize petroleum hydrocarbons slowly, relative to vertebrates (Livingstone 1998; Livingstone et al. 2000), invertebrate predators lower in the food chain may have proportionately higher body burdens of contaminants (reviewed in Meador 2003; Wang and Wang 2006; Filipowicz et al. 2007). Thus, PAH compounds may reach their highest levels of bioaccumulation in marine invertebrates at the base of the food web (Livingstone 1998; Wan et al. 2007), raising concerns for the loss or reduction of these important biota following an oil spill.

Impacts of Oil on Marine Invertebrates

Marine invertebrates typically receive little attention following oil spills unless a large die-off of lobsters, crabs, mussels, or another commercially important species is noted. Reports of affected wildlife are often limited to the most visible “charismatic megafauna,” including oiled seabirds, sea turtles, and mammals. However, oil has multiple adverse effects on marine invertebrates due to habitat degradation, oiling and smothering of individuals, acute and chronic toxicity, and disruption of the food web (Capuzzo 1987, 1990, 1996; Seymour and Geyer 1992; Lee and Page 1997; O’Sullivan and Jacques 1998; Peterson 2001; NRC 2003; Fingas 2013). Different marine invertebrate groups are exposed and respond to oil differently depending on their habitat, feeding mode, and ability to process ingested contaminants (Albers 2003; NRC 2003), and spills that are not immediately lethal can have short- (acute) or long-term (chronic) impacts on behavior, reproduction, growth and development, immune response, and respiration (Teal and Howarth 1984; Harvell et al. 1999; Albers 2003; Wootton et al. 2003; Auffret et al. 2004; Hannam et al. 2009; Hannam et al. 2010).

The extent and duration of damage to biota from oil spills is further affected by the type of oil spilled and its rate of release; prevailing seasonal meteorological and oceanographic conditions; the life stage of exposed fauna and their mobility within the habitat; habitat and substrate characteristics; and the spill response and mitigation activities (NRC 2003). Our understanding of the effects of oil pollution on the structure and function of marine communities and ecosystems is still limited, because these are complex, varying, and studied infrequently, and may be complicated by the presence of additional contaminants whose synergistic capabilities are unknown (Livingstone 1998; Livingstone et al. 2000; Thain et al. 2008). Studies are frequently undertaken in the laboratory rather than the field and experimental design, toxin concentrations, and exposure times are highly variable (reviewed in Sundt et al. 2011). The following sections describe the current state of our knowledge about the impacts of oil on marine invertebrates in general as well as on specific taxa groups.

Acute Impacts

An immediate effect of spilled oil is the physical smothering of oil as well as the uptake of toxic fractions across cell membranes that quickly kills large numbers of organisms. However, such die-offs can go unnoticed in the case of marine invertebrates unless they are seen floating or washed ashore. Massive mortality of intertidal and subtidal fauna was documented immediately after the barge *Florida* sank in Buzzards Bay, Massachusetts, in 1969. Heavy waves from storm action mixed the 700,000 liters of spilled fuel oil with water and sediments and killed many benthic invertebrates, including ampeliscid amphipods (Sanders et al. 1980). Large numbers of lobsters and surf clams washed up on beaches after the *North Cape* barge struck ground off of the coast of Rhode Island in 1996 and oil dispersed into

offshore areas and benthic ecosystems (Michel et al. 1997; French 1998). In the immediate aftermath of both the *Zoe Colocotroni* tanker spill off Puerto Rico in 1973 (Nadeau and Berquist 1977) and the *Sea Empress* spill off the south coast of Wales in 1996 (Moore et al. 1997; Edwards and White 1999), oiling of nearshore habitats resulted in large numbers of dead or dying invertebrates washing ashore, including mass strandings of sea urchins. The *Amoco Cadiz* spill in March 1978 off the coast of France caused mass mortality of limpets, sand clams, cockles, razor clams, sea urchins, and amphipods inhabiting the rocky shorelines and estuary sediments (Cross et al. 1978; Laubier 1980; reviewed in Maurin 1984). Oyster mortality from the *Amoco Cadiz* spill was as high as 50% at some sites, severely damaging an important commercial fishery in the region (Maurin 1984). The offshore oil plume created by the Deepwater Horizon oil spill in the Gulf of Mexico in 2010 coated deepwater corals in the area, leaving them dead or dying (Camilli et al. 2010; White et al. 2012).

Chronic Impacts

The ability of oil and its weathered byproducts to bind to and become buried in sediment results in long-term persistence in the environment and increases the exposure time of marine invertebrates (Krebs and Burns 1977; Teal et al. 1992; Burns et al. 1993; Owens et al. 1999; Reddy et al. 2002; Culbertson et al. 2007; Short et al. 2007). Many petroleum hydrocarbons are carcinogenic and/or mutagenic (Baussant et al. 2001; Albers 2003) and chronic exposure to oil and its weathered and metabolized byproducts can cause cellular damage and impair reproduction, growth, and development in marine invertebrates (Albers 2003; Meador 2003). Benthic (sediment-associated) species are exposed to sedimented hydrocarbons in and around the sediment–water interface for long periods and may thus accumulate higher levels of toxic hydrocarbons than pelagic species that inhabit the water column (Kirso et al. 2001; Meador 2003). In addition, sea urchins, crabs, and other organisms that live in the sediment as adults but are part of the pelagic zooplankton as embryos and larvae may be at increased risk of long-term population decreases as they are exposed to spilled and weathered oil in multiple habitats and life stages (Mathews et al. 1993; Price et al. 1993; Price et al. 1994; Bellas and Thor 2007).



Surface slicks quickly move oil into shoreline habitats. Washed ashore during a storm, emulsified oil remains on, and pooled below, vegetation. (Photograph: NOAA Photo Library.)

Impact of Oil on Marine Invertebrate Taxa Groups

Spilled oil partitions into different parts of the marine environment through dispersal, emulsification, sedimentation, and stranding, and the effects on invertebrate communities vary depending on the habitat(s) they occupy (Peterson et al. 1996; NRC 2003; Ihaksi et al. 2011). The two fundamental types of marine habitats are the pelagic zone (open water) and benthic zone (sediment); invertebrates are dominant inhabitants of both. Benthic and planktonic invertebrates are exposed to oil in different ways and vary in their ability to avoid exposure (Peterson et al. 1996). In addition, sensitivities to contaminants may vary significantly between species in the same habitat. Each oil spill event is unique and variations in the rate and quantity spilled, as well as environmental conditions around the spill site, make it difficult to apply generalizations regarding ultimate ecological effects (NRC 2003). The following sections discuss the impacts of oil spills on different groups of marine invertebrates, focusing first on the larger community-level response of the plankton and benthos.

Zooplankton

Plankton comprise the assemblage of small suspended organisms with limited mobility that drift with the currents. They are the primary component of the pelagic zone. Plankton contains both photosynthetic organisms (phytoplankton) as well as consumers (zooplankton). Zooplankton consist of a variety of small marine invertebrates that are split into two groups. Holoplankton spend their entire life cycle within the plankton community (krill, amphipods, and copepods) and meroplankton inhabit it temporarily during immature phases (eggs and larvae of sea urchins, sea stars, crustaceans, mollusks, corals, and marine worms). Zooplankton play a vital role in the marine food web by cycling nutrients and making them available to higher trophic levels (Turner 1984; Fenchel 1988; Frederiksen et al 2006; Falk-Petersen et al. 2009). They are a significant food source for vertebrates, including fish, birds, and whales (Turner 1984; Sundby and Fossum 1990; Gaston et al. 1993; Hobson et al. 1994; Lough and Mountain 1996; Conway et al. 1998; Darling et al. 1998; Sommer et al. 2002; Dahl et al. 2003; Turner 2004; Lowry et al. 2004; Laidre et al. 2007).

Because oil can float on the water's surface and disperse within the ocean as it weathers (NRC 2003), zooplankton are exposed to both floating oil slicks and to small dissolved droplets of oil in the water column (Cormack 1999; Almeda et al. 2013). Zooplankton at the air-sea interface are thought to be especially sensitive to oil spills due to their proximity to high concentrations of dissolved oil and to the additional toxicity of photo-degraded hydrocarbon products at this boundary (Bellas et al. 2013). In addition, chemical dispersants used after a spill to break up oil slicks may exacerbate the effects of oil exposure. A review by Lee et al. (2012) found that plankton communities (mainly represented by copepod studies) were impacted more severely by dispersant plus crude oil than by crude oil alone. This is often because the emulsified oil/dispersant mixture can be ingested and internalized into micro- and macro-invertebrates. The relatively limited mobility of zooplankton may render them less able than larger organisms to escape areas polluted by oil. A laboratory analysis of swimming behavior in calanoid copepods suggested they may have some ability to avoid oil-contaminated waters (Seuront 2010), but the ability of zooplankton to avoid massive oil spills under field conditions is problematic due to the strong influence of ocean currents on their movement and the rate of spread of oil slicks (NRC 2003; Almeda et al. 2013).

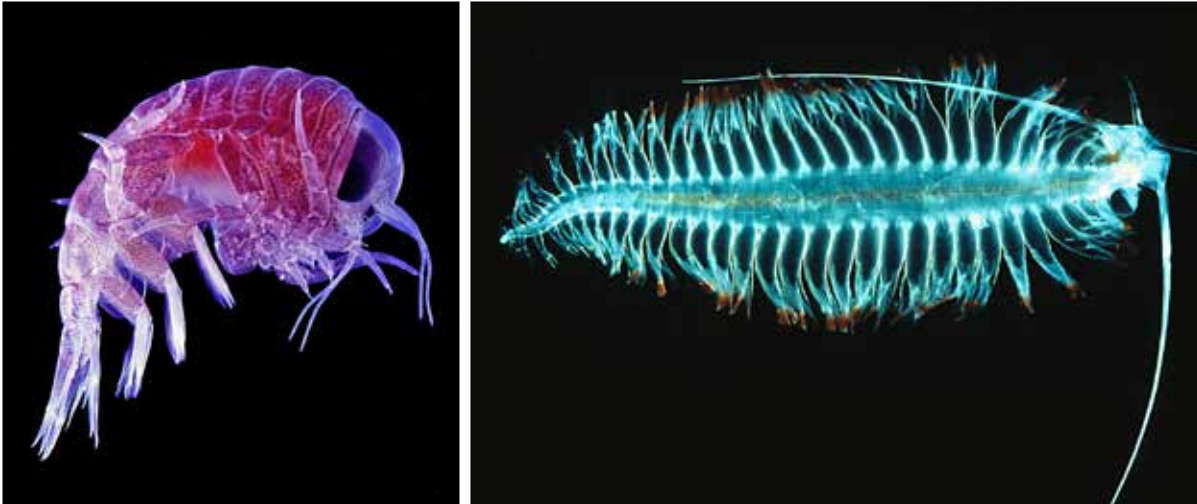
Negative impacts of oil on plankton include death from direct oiling as well as impaired feeding, growth, development, and reproduction (Geffard et al. 2002a; Bellas and Thor 2007; Saiz et al. 2009; Bellas et al. 2013; Grenvald et al. 2013). Zooplankton can be harmed by the uptake and transfer of pe-

roleum hydrocarbons during feeding, with additional impacts on higher trophic level consumers that rely on zooplankton as a food source (Runge et al. 2005; Wang and Wang 2006; Graham et al. 2010; Chanton et al. 2012; Almeda et al. 2013; Grenvald et al. 2013). Zooplankton bioaccumulate oil hydrocarbons, where they may have direct toxicity at high concentrations of pollutant, or may excrete them in their fecal pellets after sublethal exposure (Conover 1971; Johansson et al. 1980; Bellas and Thor 2007; Jensen et al. 2012; Lee et al. 2012; Almeda et al. 2013); thus, the movement and settlement of plankton and their waste products may further distribute oil molecules in water and sediment (Lee et al. 2012; Almeda et al. 2013).

The zooplankton community also contains the free-floating embryos and larvae of invertebrates that inhabit the sediment as adults. Their limited ability to swim renders them unable to escape oil-polluted waters. These early life stages of sea urchins, mollusks, and crustaceans are more sensitive to pollutants than adults and their survival is critical to the long-term health of the adult populations (Falk-Petersen 1979; Vashchenko 1980; Pelletier et al. 1997; Geffard et al. 2002a; Beiras and Saco-Álvarez 2006; Fernandez et al. 2006a, 2006b; Saco-Álvarez et al. 2008; Saiz et al. 2009; Anselmo et al. 2011; Bellas et al. 2013). The eggs and larvae of planktonic oysters exposed to oil show impaired development and decreased settlement of juveniles (Geffard et al. 2002a, 2002b; Beiras and Saco-Álvarez 2006; Choy et al. 2007). After the *Prestige* oil tanker spill off the northwest coast of Spain in November 2002, sea urchin (*Paracentrotus lividus*) embryo development was inhibited by as much as 50% when fuel oil content in the water was over 3.8%; oil levels below 1.9% did not appear to be toxic (Fernandez et al. 2006b). Oil-polluted seawater collected from coastal sites impacted by the *Prestige* spill was more toxic than contaminated sediment to embryos and larvae of bivalves and echinoderms, and oil impaired growth of sea urchin (*P. lividus*) and oyster (*Crassostrea gigas*) larvae and development of mussel embryos (*Mytilus galloprovincialis*) (Beiras and Saco-Álvarez 2006; Saco-Álvarez et al. 2008). Complete inhibition of sea urchin embryogenesis in eggs exposed to seawater samples collected in the impacted area was apparent even after the visible oil slick had disappeared (Beiras and Saco-Álvarez 2006). This was thought to be due to chrysene, a toxic PAH compound that dispersed in coastal waters in the weeks following the spill, demonstrating the ability of toxic petroleum compounds to persist and be transported within the environment.

Oil toxicity can decrease plankton biomass and change community composition (Johansson et al. 1980; Samain et al. 1980; Guzmán del Prío et al. 1986). Johansson et al. (1980) documented short-term impacts on zooplankton biomass in the month following the *Tsesis* oil spill off the coast of Sweden in 1977. While biomass levels were re-established within five days, the guts and feeding appendages of zooplankton were contaminated with oil for the three week duration of the study, suggesting the potential for even longer term population effects. High zooplankton mortality was reported in impacted areas off the north coast of Brittany during the 15 days following the *Amoco Cadiz* oil spill and the population in nearshore areas continued to be impacted for 30 days (Samain et al. 1980). The subsurface release of oil during the Ixtoc I oil well spill in the Gulf of Mexico in 1979 caused a four-fold decrease in zooplankton concentrations for three years afterwards compared to the same area a decade earlier (Guzmán del Prío et al. 1986). In contrast, Batten et al. (1998) concluded that plankton communities were not significantly impacted after the 1996 *Sea Empress* wreck in the entrance to Milford Haven in southwest Wales, but Edwards and White (1999) reported a reduction in copepod egg viability in April 1996 (two months following the spill), with complete recovery of copepod populations by November 1996. The sheer magnitude of the Ixtoc I spill compared with the *Sea Empress* as well as the location and duration of the spills may explain the differences observed in long-term plankton response. The Ixtoc I well released 1,260,000 gallons of oil per day for the first two months of the spill and eventually released around 480,000 metric tons over a 10-month period in offshore waters, while the *Sea Empress* spilled a total of 72,000 metric tons over a one-week period in nearshore waters.

Studies on the long-term effects of oil contamination on plankton are limited because few regions



Zooplankton are the primary component of the pelagic zone. Holoplankton spend their entire life cycle within the plankton community and meroplankton inhabit it temporarily during immature phases. Zooplankton come in many forms. Shown here are an amphipod (left) and a polychaete worm (right). (Photographs: Wikimedia Commons/Uwe Kils.)

have comprehensive pre-spill data on plankton communities to use for comparison and the large degree of natural variability in plankton populations and the effects of ocean processes and climate on their distribution can further complicate detection of impacts (Richardson and Schoeman 2004; Runge et al. 2005; Cowen et al. 2006; reviewed in Penela-Arenaz et al. 2009; Letessier et al. 2011; Grenvald et al. 2013). Moreover, monitoring must start immediately after a spill and continue beyond the time recovery is noted. Existing research has shown substantial short- and long-term toxicity of oil and its weathered by-products to eggs, larvae, and mature zooplankton following large oil spills, but comprehensive long-term research programs are needed in order to understand the full range of effects of oil pollution on planktonic systems.

Benthic Invertebrate Taxa

Benthic invertebrates are a diverse community of animals that live on or within sediments, such as crustaceans, worms, and mollusks. They occur from intertidal coastal areas to the deep sea; some are mobile while others live a sessile (non-motile) existence on the seafloor. Benthic invertebrates can be separated into two major size classes: meiofauna, which range in size from 50–500 μm and include copepods and nematode worms, and macrofauna, comprising organisms larger than 500 μm . Species in either size class may live primarily on the surface of sediment or substrate (epifauna) or burrow into or below the sediment/water interface (infauna). Both infaunal and epifaunal invertebrates are important food sources for larger bottom-feeding invertebrates, as well as fish such as flounder, snapper, and juvenile pink and chum salmon (Kaczynski et al. 1973; Feller and Kaczynski 1975; Sedberry and Cuellar 1993; Link et al. 2002; Latour et al. 2008; Wells et al. 2008).

When oil washes ashore it coats intertidal benthic invertebrates and their habitats (Cross et al. 1978; Sanders 1978; Lee and Page 1997; NRC 2003). Most oil floats, but some is emulsified or dissolved in the water column, where it can attach to suspended particles and sink to the bottom (Meador 2003; NRC 2003). Oil bound to sediment may become more bioavailable to organisms when it is periodically suspended in the water column due to waves or storm disturbances. Because many benthic invertebrates are relatively sessile they can have longer-term exposure and accumulate higher levels of persistent, sed-

iment-bound contaminants (Gray et al. 1990; NRC 2003; reviewed in Peterson et al. 2003b).

In response to oil exposure, benthic invertebrates can either move, tolerate the pollutant (with associated impacts on overall health and fitness), or die (Gray et al. 1988; Lee and Page 1997). Response to oil differs depending on invertebrate life history and feeding behavior as well as the ability to metabolize toxins, especially PAH compounds (Varanasi et al. 1985). Transfer of hydrocarbons to benthic invertebrates depends on their bioavailability and persistence (NRC 2003). Marine bivalves such as mussels and oysters ingest oiled organic particles during filter-feeding and take in oil dissolved in the water column across their gills (Varanasi et al. 1985; NRC 2003). Toxic PAH compounds have been shown to accumulate in filter-feeders (Menon and Menon 1999) and cellular pathologies observed in the tissues of benthic bivalves may be linked to chronic oil exposure to, and uptake from, contaminated sediments (Neff and Haensly 1982; Berthou et al. 1987). In contrast, populations of polychaetes, oligochaetes, and nematodes can be enhanced in oiled sediments when there are low concentrations of hydrocarbon pollutants (Sanders et al. 1980; reviewed in Peterson et al. 1996; Jewett et al. 1999).

This differential exposure and toxicity can lead to longer-term alterations in the structure and biodiversity of benthic communities (Southward and Southward 1978; Dean et al. 1996; Dauvin 1998; Jewett et al. 1999; Carls and Harris 2005; Culbertson et al. 2007). The effects of oil on the relatively immobile infauna such as bivalves, amphipods, and polychaetes are important because these groups dominate soft-bottom benthic communities in oceans and estuaries (Sanders et al. 1980; Poggiale and Dauvin 2001). These are important because they contribute to the diets of large vertebrates, including fishes, walrus, and whales (Highsmith and Coyle 1992; Nelson et al. 1994; Coyle et al. 2007). Their burrowing activity also mixes sediments, recycles nutrients, and at low oil concentrations, accelerates the weathering of sediment-bound oil (McElroy et al. 1990; Grossi et al. 2002). In the aftermath of oil spills, amphipod and echinoderm populations may completely disappear or be severely reduced (Dauvin 1982; Peterson et al. 1996) and opportunistic species—especially polychaetes—can thrive in the impacted areas (Sanders 1978; Sanders et al. 1980; Peterson et al. 1996; Fukuyama et al. 1998; Jewett et al. 1999). Deposit-feeding and burrowing benthic invertebrates are impacted by chronic exposure to hydrocarbons in polluted sediments (Culbertson et al. 2007; Hale et al. 2011) and their populations can continue to fluctuate as they respond by building shallower burrows to avoid sediment-bound oil, leading to greater exposure on the surface, reduced mobility, and increased susceptibility to predation (Culbertson et al. 2007).

Benthic infaunal invertebrates live within the small spaces of sediment particles where oil is trapped, leading to greater impacts from oil spills. However, because these small invertebrates are elusive, negative impacts to populations of these animals can go completely unnoticed in the absence of targeted surveys, unless large numbers of dead individuals float to the surface or are specifically sampled by trawling after spills. For example, tube-forming amphipods experienced mass mortality following the *Florida* spill off the coast of Massachusetts in 1969 (Cross et al. 1978) when oil impacted nearshore benthic habitats. In this case, the immediate death of these relatively inconspicuous soft-bodied crustaceans was noted before the animals had decomposed only because of the huge numbers that died both after the spill and from continued oiling by contaminated sediments (Sanders et al. 1980). In contrast, larger benthic species can be detected much more easily, as was seen when an unprecedented number of dead lobsters, crabs, and other invertebrates washed ashore following the *North Cape* fuel oil spill offshore of Rhode Island in 1996 (Michel et al. 1997; French 1998; reviewed in NRC 2003).

Echinodermata

The phylum Echinodermata contains approximately 7,000 species that occupy nearly every marine habitat from shallow waters to abyssal depths and includes sea lilies, feather stars, sea stars, sea urchins, sea

cucumbers, and sand dollars. Most are exclusively benthic as adults (either motile or attached to hard substrates), while their eggs and larvae float freely as plankton before settling into a benthic lifestyle. Echinoderms increase biodiversity of coral reefs and kelp ecosystems, stir up sediment, and mobilize nutrients. They are an important food source for a variety of wildlife including fishes, lobsters, and sea otters (Engstrom 1982; Tegner and Levin 1983; Bingham and Braithwaite 1986; Harrold and Pearse, 1987; McClintock 1994; Schiebling 1996). They have commercial significance as a fishery, since sea cucumbers and sea urchins are considered a delicacy in some parts of the world (Conand 2000; Akamine 2004). Sea cucumbers are efficient deposit feeders and may be important in the remediation of wastes produced in the aquaculture of fish and mussels. This reduces the impacts on the benthos and in turn produces a valuable food source for human consumption (Inui et al. 1991; Wu 1995; Slater and Carton 2007). Echinoderms may be particularly sensitive to marine pollution, since many studies have shown consistent acute impacts on echinoderms in benthic community responses to oil spills (Moore et al. 1997; Edwards and White 1999; Mignucci-Giannoni 1999; Barillé-Boyer et al. 2004). Given their importance as key predators and grazers within marine benthic communities, oil-spill impacts on echinoderm populations might lead to dramatic changes in ecosystem structure.

Sea Urchins

Sea urchins are key organisms in benthic marine food webs, where they help structure community composition. They graze and scavenge algae, dead fish, sponges, and barnacles and serve as an important prey item for otters and other predators. They also compete with abalone for grazing opportunities



Dead or damaged sea urchins have been found after oil spills in several countries, including France, Wales, and the United States. Purple sea urchin (*Strongylocentrotus purpuratus*). (Photograph: Wikimedia Commons/David Monniaux.)

(Harrold and Pearse 1987; Estes and Duggins 1995; Tegner and Dayton 2000; Hereu et al. 2005). Their soft bodies are surrounded by a round, spiny shell (or “test”) that provides protection from predators and they have small tubular projections (tube feet) that function in locomotion, feeding, and respiration. Sea urchins can use their tube feet to attach to the substrate and to right themselves when overturned. Adult sea urchins are eaten by crabs, sea stars, snails, sea otters, birds, and fish, while their planktonic embryos and larvae are a food source for fish, shrimp, and crustaceans (Tegner and Levin 1983; McClanahan and Muthiga 1989; Estes and Duggins 1995; Tegner and Dayton 2000; Hereu et al. 2005). Some are known to be important in regulating the abundance and distribution of macroalgae in coastal communities (Kitching and Thain 1983; Hereu et al. 2005), and their interactions with sea otters, abalone, and kelp strongly influence the ecology of kelp bed communities in temperate coastal waters (reviewed in Estes and Duggins 1995). Oil-mediated disturbances in these complex communities can affect individual sea urchin behaviors (Axiak and Saliba 1981) and disrupt overall ecosystem dynamics (Barillé-Boyer et al. 2004).

The damaging effects of oil on the early planktonic life stages of sea urchins were discussed previously (see “Zooplankton” on page 23). Although far less has been reported on the effects of oil on adult sea urchins, several field studies have documented immediate acute impacts on adult sea urchin populations following large oil spills that reach nearshore and intertidal benthic habitats. When assessing the effects of marine pollution on benthic macrofauna as a whole, sea urchins as a group consistently show large declines (reviewed in Suchanek 1993; Peterson et al. 1996; Barillé-Boyer et al. 2004). In the 10 months following the *General M.C. Meigs* spill off the northwest coast of Washington state in 1972, dead purple sea urchins (*Strongylocentrotus purpuratus*), or live urchins missing spines, were seen in all impacted areas (Clark et al. 1973). Acute impacts on sea urchins were also reported in the days after



Sea stars are a remarkably diverse group in both habitat and form, from the simple five-armed forms frequently found on beaches and in tidal pools to the many-armed basket star entwining the branches of this deepwater gorgonian coral. (Photograph: NOAA Photo Library, NURC/UNCW and NOAA/FGBNMS.)

the *Zoe Colocotroni* tanker accident off of Puerto Rico in 1973 (Nadeau and Berquist 1977) and in the weeks following the 1996 *Sea Empress* spill off the south coast of Wales (Moore et al. 1997; Edwards and White 1999). In both cases, oiling of nearshore habitats resulted in large numbers of dead or dying invertebrates being washed ashore, including mass strandings of sea urchins. Although such die-offs on beaches and shorelines can be disease related, in the case of the *Sea Empress* spill, high concentrations of hydrocarbons were detected in the tissues of dead urchins, clearly implicating oil pollution as the causative agent (Edwards and White 1999). Sublethal impacts of oil on adult behaviors and physiology can also contribute to ongoing mortality. In one study, sea urchin righting response (effort by the animal to right itself with its tube feet after being turned over) was compromised by oil in a dose-dependent fashion, with the greatest delay in righting response seen after 96 hours of exposure to 32 ppm of crude oil (Axiak and Saliba 1981). Delayed, or inhibited, righting responses increases vulnerability to predators and interferes with mobility, reproduction, and feeding.

Sea urchin populations that experience mass mortality from oil exposure may take years to recover, during which time community composition can be substantially altered. Sea urchins in intertidal pools along the Atlantic coastline of France, documented prior to the *Erika* spill in November 1999, were found dead in their burrows in the month following the spill (Barillé-Boyer et al. 2004). Close monitoring of oil-impacted intertidal pools found that recolonization of sea urchins did not occur until two years later and it took three years for urchin densities to reach pre-spill levels. A dramatic growth of algae was noted during the prolonged absence of these influential grazers. Invasive and opportunistic species also appeared during this period (Barillé-Boyer et al. 2004), illustrating the significant impacts of the removal of a key species group on community composition.

Sea Stars

About 2,000 species of sea stars (also called starfish or asteroids) are currently known. The most familiar species have five-arms, although some species may have up to 40 arms (Lawrence 2013). Sea stars are important ocean predators. Their tiny, suction-cupped tube feet can pry open the shells of oysters, clams, and mussels, while their calcified skin provides armor-like protection. Like their relatives the sea urchin, sea stars are keystone species that influence the structure and biodiversity of intertidal and subtidal benthic ecosystems (Paine et al. 1985; Menge et al. 1994; Gaymer and Himmelman 2008).

Acute oil toxicity to sea stars following several major oil spills resulted in significant die-offs (Mignucci-Giannoni 1999; Joly-Turquin et al. 2009). Numerous species of intertidal sea stars were found stranded on shore following the grounding of the barge *Morris J. Berman* that spilled 3.6 million liters of Bunker C oil off Punta Escambrón in San Juan, Puerto Rico, in 1994. Echinoderms were the invertebrate group most affected by this spill and sea stars and sea urchins accounted for 58% of all phyla affected (Mignucci-Giannoni 1999). This figure probably underestimates the actual mortality because it is likely that many more marine invertebrates, including sea stars, died offshore but were not recovered (Mignucci-Giannoni 1999). Similarly, large numbers of the starfish *Asterias rubens* were found dead and washed ashore on a polluted coastline in the days following the *Erika* oil spill off France in 1994 (Joly-Turquin et al. 2009).

Multiple sublethal impacts of oil pollution on sea stars have been documented in laboratory studies, including detrimental effects on growth, locomotion, ability to detect prey, and feeding behavior (Ordzie and Garofalo 1981; O'Clair and Rice 1985; Temara et al. 1999). The magnitude of these effects differed depending on the type of oil and/or sea star species. Feeding responses in the common sea star (*A. forbesi*) were impaired during a six hour sublethal exposure to 0.1–0.5 ppm crude oil and dispersant (Corexit® 9527), both separately and as mixtures (Ordzie and Garofalo 1981). In the sea star *Evasterias troschelii*, growth and feeding rates were depressed during a 28 day exposure to the water-soluble fraction (WSF) of crude oil at and above 0.2 ppm, and at the highest concentrations (0.97 and 1.31 ppm

WSF) they ceased feeding, suffered loss of arms, or died (O'Clair and Rice 1985). Temara et al. (1999) found foraging behavior and prey localization by the sea star *Coscinasterias muricata* was impacted by exposure to 10% crude oil. It is often difficult to demonstrate or measure the impact of reduced predation by keystone predators such as sea stars (Paine et al. 1985; Menge et al. 1994; Gaymer and Himmelman 2008), but these animals are known to be important in structuring ecosystem biodiversity. Moreover, their morbidity and death following oil spills has implications for altered predator-prey relationships that could produce cascading changes in food webs and benthic community dynamics.

Mollusca

The Mollusca is a diverse and abundant group of at least 50,000 marine, freshwater, and terrestrial species. Mollusks are important inhabitants of every ecosystem in which they are found, from hydrothermal and hydrocarbon seeps of the deep sea up through the benthos, the pelagic ocean, coastal estuaries, rivers, and terrestrial habitats from sea level to mountain tops. All mollusks are soft bodied, although some taxa have a protective, calcium-rich, external shell. Marine mollusks include familiar and economically important groups such as snails, octopuses, squid, scallops, oysters, mussels, and clams. Oysters, mussels, and other filter-feeding mollusks provide vital ecological services by improving water quality and clarity for other aquatic life (Dame et al. 1984; Ostroumov 2005; Beck et al. 2009). Squid, scallops, and oysters are a key food source for humans and in some areas may constitute a large part of commercial fishery harvests.

Bivalves

The bodies of bivalve mollusks are enclosed by two protective external shells, connected by a strong elastic ligament that acts as a hinge. Bivalves are found in marine and freshwater environments and include clams, oysters, scallops, and mussels. Most adult marine bivalves inhabit the benthos, where they may burrow into soft-sediment burrows (e.g., clams), be attached to the substrate by strong filaments (byssal threads; e.g., mussels), or live on top of the substrate and be capable of localized movements (e.g., scallops) (Dame 2012). Oysters and mussels are important ecosystem engineers, creating beds that provide habitat and foraging areas for invertebrates and fishes (Suchanek 1978; Borthagaray and Carranza 2007; Beck et al. 2009). Oil spills pose a significant threat to oysters and mussels because they are sessile and unable to escape impacted areas and, as filter feeders, they integrate environmental pollutants but have a limited capacity to metabolize them (Farrington and Tripp 1995; Peterson 2001; Neff 2002; reviewed in Meador 2003; Jeong and Cho 2005, 2007).

Mussels

Mussels often occur in dense intertidal aggregations in coastal oceans and estuaries, where their beds help protect the shoreline from erosion by breaking the impact of moving waves and provide habitat for other invertebrates and fish (Suchanek 1978; Bertness 1984; Jones et al. 1994; Tokeshi 1995; Prado and Castilla 2006; Borsje et al. 2011). Marine mussels live in a variety of benthic habitats from shallow estuaries to cold deep sea environments. Some mussels are keystone species in estuarine ecosystems because of their high rates of production and active processing and filtering of nutrients (Suchanek 1978; Hall-Spencer and Moore 2000; Carmichael et al. 2012c). Others live in the deep sea, where they are associated with cold seeps and hydrothermal vents and utilize oxidized methane or reduced sulfur compounds produced by microbes as an energy source (Fisher et al. 2007). Mussels are ecosystem engineers (Borthagaray and Carranza 2007) and the habitat formed by mussel beds creates small spaces for other aquatic organisms to feed, live, and shelter (Sebens 1985; Witman 1985; Jacobi 1987). They can effectively trap and contain contaminants for many years (Farrington and Tripp 1995; Fukuyama et al.

1998; Carls et al. 2001; Carls and Harris 2005).

Mussels ingest contaminants during filter-feeding and can accumulate them in their tissues at concentrations above those found in the surrounding seawater (Widdows et al. 1982; Neff et al. 1987; Livingstone et al. 2000; Baussant et al. 2001; Neff 2002; Tronczyński et al. 2004; Sundt et al. 2011). Ingested toxins, such as PAHs, may be retained on the gills or integrated into lipid-rich tissues (O'Sullivan and Jacques 1998; Baussant et al. 2001). These toxins can continue to accumulate because of the efficiency of mussel feeding and their limited capacity to metabolize PAHs (Livingstone 1998; Livingstone et al. 2000; Baussant et al. 2001). Chronic exposure to oil has been shown to reduce overall condition, decrease growth and feeding rates, and depress immune response, which may result in population declines (Widdows et al. 1982, 1987, 1995; Cajaraville et al. 1992; Babcock et al. 1998; Donkin et al. 2003; Le Floch et al. 2003; Widdows and Staff 2006; Culbertson et al. 2008). Accumulation of PAHs has been shown to disrupt cellular immunity (Krishnakumar et al. 1994; Grundy et al. 1996; Dyrnda et al. 1998; Hannam et al. 2010), byssal thread attachment (Eisler 1975; Lindén 1977), and the ability to tolerate exposure to air (Thomas et al. 1999b). Mussels (*Mytilus galloprovincialis*) exposed to sublethal doses of benzo[a]pyrene (19 mg/L), a PAH commonly found in the environment following oil spills, showed significant DNA damage within 48 hours, which continued to increase through 72 hours of exposure (Banni et al. 2010). Additional studies have shown that accumulated PAHs cause DNA damage in mussels (Pérez-Cadahía et al. 2004; Laffon et al. 2006).

Some studies have suggested mussels tolerate higher levels of oil pollution (Large et al. 2002; Thomas et al. 1999a), but others have found that any observed tolerance declines with increasing duration of exposure to oil (Cajaraville et al. 1992; Culbertson et al. 2008). Because many marine animals rely on mussels as a food source, the reduction in overall health of mussels chronically exposed to oil (which could affect their nutritive value) combined with increased mortality and population declines could have a large impact on the marine food web. For example, chronic exposure of *Mytilus trossulus* to oil from the *Exxon Valdez* in intertidal habitats may have impacted the sea otters (*Enhydra lutris*) that rely on them for food (Carls and Harris 2005). Intertidal oil was retained in sediments following the *Exxon Valdez* spill and was biologically available at toxic levels for an extended period (Short et al. 2004). As a result, both the sediments and the mussel community may experience long-term contamination as wave action and storms regularly suspend PAHs that are taken up by mussels and transferred to vertebrate predators (Fukuyama et al. 1998; Carls et al. 2004; Carls and Harris 2005; Culbertson et al. 2008). Intensive efforts were made to clean beaches in the year following the spill, but oil exposure coupled with vigorous cleanup (high-pressure hot water washes) damaged intertidal environments. It took years to re-establish previous mussel abundance (Houghton et al. 1997; Peterson 2001; NRC 2003). On the other hand, sites left to recover naturally can continually expose mussels to contaminated sediments (Babcock et al. 1996; Hayes and Michel 1999; Carls et al. 2001; Carls and Harris 2005; Payne et al. 2005). Spilled



Around deepwater cold seeps, mussels form dense beds that provide shelter to shrimps and other animals. In intertidal zones, mussels form similarly dense beds but are vulnerable to pollution from oil spills. (Photograph: NOAA Photo Library, Expedition to the Deep Slope 2007, NOAA-OE.)

oil is not only immediately toxic to mussels but also negatively impacts mussel feeding and development when trapped in sediments or mussel beds. Studies document impacts persisting for several decades following a spill, underscoring the need for continued monitoring of the status and recovery of oil-exposed mussel populations and the diversity of wildlife that relies on them for habitat or food (Bodkin et al. 2002, 2012; Carls et al. 2004; Carls and Harris 2005; Culbertson et al. 2008).

Oysters

Oyster beds create reef-like habitat for communities of polychaete worms, crustaceans, and other invertebrates that in turn provide food for fishes and other marine wildlife (Zimmerman et al. 1989; Peterson et al. 2003a; Beck et al. 2009; Grabowski et al. 2012). Oyster beds occur in estuaries along continental margins throughout the world, where they have important functional roles in protecting and stabilizing shorelines (Beck et al. 2009, 2011). Suspension feeding by oysters removes accumulated organic matter such as algae and pollutants from estuaries, and helps control the growth of excess algae in habitats that are affected by eutrophication (enrichment with excess nutrients) (Dame et al. 1984; Grabowski and Peterson 2007). The loss of natural breakwaters and wave attenuators, such as oyster beds and coastal marshes, has been implicated in recent coastline damage following massive storms, highlighting the importance of maintaining healthy coastal oyster communities in protecting people and coastlines (Day et al. 2007; Arkema et al. 2013). A recent global assessment of oyster beds showed an estimated loss of as much as 85% of oyster reef habitat in several ecoregions around the world (Kirby 2004; Beck et al. 2011). Commercial harvesting has contributed to oyster bed declines, and the condition of some beds is so poor that they are functionally extinct (i.e., no longer able to provide ecosystem services, with losses close to 99% [Beck et al. 2011]).

Oysters have substantial economic importance worldwide and are harvested in the wild and from aquaculture systems (Beck et al. 2009; FAO 2013b). In North America, oyster reefs support important commercial fisheries from the Gulf of Mexico through the Atlantic coast and up to the Gulf of St. Lawrence (Stanley and Sellers 1986). The east and Gulf coasts of North America provide more than 75% of the global harvest by augmenting oyster beds through seeding programs and bed-building projects (LDWF 2011, 2012; FAO 2013b). In 2001, U.S. oyster harvests yielded 28.5 million pounds valued at \$131.7 million (NMFS 2012). However, due to a range of anthropogenic stressors, including overharvesting, habitat alteration and destruction, and pollution, oyster reefs are suffering dramatic declines worldwide (Beck et al. 2011). As is the case for mussels, oil spills pose a significant threat to oysters because they can bioaccumulate hydrocarbons in much higher concentrations than observed in other marine organisms (Neff 2002; reviewed in Meador 2003; Tronczyński et al. 2004).

Oyster reefs may be directly fouled by oil when floating slicks are transported by winds and ocean currents to nearshore habitats (Teal and Howarth 1984; Tronczyński et al. 2004; Bado-Nilles et al. 2008). Oysters filter nutrients and other materials, and can take up pollutants from water and sediments (Dame et al. 1984; Neff 2002; Croxton et al. 2012). Oysters may accumulate PAHs from oil in their tissues, but because they have a limited capacity to metabolize these compounds, the toxic effects of PAHs and the impacts on reef health may be protracted (Fisher et al. 2000; Neff 2002; reviewed in Meador 2003; Auffret et al. 2004; Croxton et al. 2012). Similar to mussels, both acute and chronic exposure to oil have been shown to negatively affect adult oyster reproduction, feeding, and growth (Berthou et al. 1987; Jeong and Cho 2007). Long-term exposure to PAHs at 200 µg/L suppressed feeding in adult *Crassostrea gigas* oysters, possibly as a mechanism to reduce the amount of toxin taken in, and was accompanied by a reduction in growth rates (Jeong and Cho 2007). Oyster mortality was estimated at 50% in the most impacted sites in the first three months following the *Amoco Cadiz* spill in March 1978 off the coast of France (Berthou et al. 1987). Surviving oysters accumulated hydrocarbons at levels up to several thousand ppm, and by two years post-exposure, hydrocarbons persisted in their tissues at high levels (100 ppm) (Neff and Haensly 1982; Neff et al. 1985). These oysters were found to have poor nutritional status

and altered patterns of metabolism compared with oysters at unimpacted sites (Neff and Haensly 1982). In addition, atrophy in the gonads of flat oysters was seen after the *Amoco Cadiz* spill indicating that reproduction and spawning did not occur in the following year (Berthou et al. 1987).

Oil contamination has negative impacts on the early life stages of oysters (see “Zooplankton” on page 23), including weakened immunity (Lacoste et al. 2001; Luna-Acosta et al. 2011). In a study by Luna-Acosta et al. (2011), enzyme activity related to immune defense was inhibited in the gills of juvenile oysters following exposure to PAHs. Compromised immunity can render an entire reef more susceptible to pathogens and disease (Chu et al. 1993; Chu and Hale 1994; Bado-Nilles et al. 2008), and several studies have specifically examined the role of PAHs in impairing the cellular immune responses of adult oysters (Sami et al. 1992; Auffret et al. 2004; Jeong and Cho 2005; Bado-Nilles et al. 2008; Croxton et al. 2012). Oysters that ingested PAHs via feeding on oil-contaminated diatoms had an impaired immune system due to damage of immune response cells (hemocytes) (Croxton et al. 2012).

Gastropods

Gastropods comprise about 80% of all living mollusks, with 62,000 described freshwater, marine, and terrestrial species. Familiar marine gastropods include abalones, limpets, conchs, nudibranchs, sea hares, cowries, and whelks. Most aquatic gastropods are benthic, although some are planktonic. Gastropods have a soft body protected by a single, often coiled, shell, although some land and sea slug groups have lost their external shell. Depending on species, gastropods may scavenge dead plant or animal matter, graze on algae and plants, or prey on other organisms. A few species are external or internal parasites of other invertebrates. They have substantial economic importance: periwinkles (*Littorina*), queen conchs (*Strombus gigas*), abalones (*Haliotis*), and turban shells (*Turbo*) are harvested for human consumption. In 2011, more than 900,000 pounds of queen conch, valued at over \$1.7 million, were harvested from U.S. waters (NOAA 2013c). Shells are also used in jewelry-making and defensive compounds extracted from cone shells (*Conus*) have promise in the pharmaceutical industry for the manufacture of pain relievers (Haefner 2003; Libes 2009).

Gastropods are common inhabitants of near-shore benthic environments, including intertidal rocky shores and estuaries (Beesley et al. 1998), and are often impacted by urban pollutants from land and oil spills that reach shore (Gundlach and Hayes 1978; Sanders et al. 1980; Peterson 2001; Barillé-Boyer et al. 2004; Juanes et al. 2007). Petroleum hydrocarbons can impair gastropod mobility and foraging behavior at sublethal doses (Hyland and Miller 1979; MacFarlane et al. 2004), while acute exposure has caused high levels of mortality after oil spills (Sanders et al. 1980; Gundlach and Hayes 1978; Peterson 2001; Barillé-Boyer et al. 2004; Juanes et al. 2007). The *Amoco Cadiz* spill in 1978 off the coast of France severely oiled the coastline. Periwinkles (*Littorina obtusata* and *L. littorea*), limpets (*Patella vulgata*), and topshells (*Gibbula cineraria*, *G. umbilicalis*, and *Calliostoma zizyphinum*) were found dead or dying at the base of rocks in subsequent weeks (Cross et al. 1978).

Gastropods such as the flat periwinkle (*Littorina obtusata*) are common in intertidal environments. The 1978 *Amoco Cadiz* wreck severely oiled hundreds of miles of France's coastline, killing large numbers of periwinkles, limpets, and other inhabitants of the rocky coast. (Photograph: Sandy Rae/Flickr.)





Coral polyps, with tentacles extended. Each polyp creates and lives within a stony, calcium-rich exoskeleton. These combine to form the coral reef framework that supports a diverse association of marine plants and animals. (Photograph: NOAA Photo Library, NURC/UNCW and NOAA/FGBNMS.)

Immediate mortality of several gastropod species (primarily *Littorina* spp.) was observed on a heavily oiled, intertidal coral reef flat after the Bahía las Minas refinery spill in 1986 on the Caribbean coast of Panama (Garrity and Levings 1990), and decreased abundance and reduced juvenile recruitment was detected three years following the spill. Gastropods were also killed after the *Erika* oil tanker ran aground in 1999 off the coast of France. In that incident, a storm transported the oil to the shore where it killed gastropods inhabiting intertidal rock pools. Trochid gastropods that were members of the original community were absent from intertidal pools two years later (Barillé-Boyer et al. 2004). After the 1999 *Laura D'Amato* tanker spill in Australia's Sydney Harbor, surveys of intertidal invertebrate communities on surrounding rocky shorelines indicated that populations of the intertidal gastropod *Austrocochlea porcata* were heavily impacted (MacFarlane and Burchett 2003). A year after the spill the abundance of this intertidal gastropod remained low and opportunistic species increased in abundance (MacFarlane and Burchett 2003).

Laboratory studies further confirm the acute and long-term impacts of oil on gastropod physiology and behavior. After the *Laura D'Amato* spill the intertidal gastropod *A. porcata* showed significant mortality after a 96 hour exposure to crude oil, with an LC_{50} (concentration at which 50% of the test population dies) of 11.7 ppm (Reid and MacFarlane 2003). This concentration is lower than 15–30 ppm measured at coastal sites that were intermediately oiled due to the 1969 *Florida* spill off the coast of Massachusetts—and up to 100 times lower than oil concentrations detected in an oiled salt marsh (Krebs and Burns 1977). Oil exposure affects gastropod feeding. Eisler (1975) demonstrated that predation on uncontaminated mussel prey was three times higher than predation on mussel prey that had been exposed to sublethal concentrations of crude oil (10 mL/L) for 28 days. Reproduction may also be affected. Eisler (1975) also found that predatory gastropods exposed to crude oil showed a three-fold reduction in egg case deposition relative to untreated controls.

Cnidaria

Animals in the phylum Cnidaria, such as sea anemones, corals, and jellyfish, are mostly found in shallow waters, with sessile forms commonly seen in tide pools on rocky coasts (Ruppert and Barnes 1994). Members of this phylum display remarkable colors and a variety of elaborately branched structures. This is reflected in the name Cnidaria, which means “flower animals.”

Different groups have different life histories. They create and/or inhabit coral formations in tropical and subtropical waters as well as deep sea environments (Ruppert and Barnes 1994). Adults can be sessile, like the corals that live as non-motile polyps, or free-swimming medusa that use pulsing movements of their bell- or umbrella-shaped bodies to travel through the water column. Sea anemones are primarily sessile, solitary benthic animals that attach to rocks and shells. Other species burrow in the mud or sand or hitchhike on animals such as hermit crabs, while stony corals may live as individual polyps or in large colonial aggregations that are the structural basis for coral reefs.

Cnidaria generally have a mouth surrounded by tentacles armed with microscopic stinging cells called nematocysts. They are generally passive predators that use their tentacles to capture small prey items in passing currents, though larger prey such as fish may fall victim to jellyfish tentacles.

Some cnidarians rely on currents to disperse their eggs and sperm, with the subsequent embryos and larvae residing in the plankton. Others brood their larvae before releasing them into the plankton, while yet others may reproduce by fragmentation or budding. Larval Cnidaria eventually settle on reefs or other substrates as juvenile polyps (e.g., corals) or develop into free-living medusae (e.g., some jellyfish).

The most familiar group of cnidarians is the Anthozoa, which includes stony corals, soft corals, and blue corals, as well as sea anemones, sea whips, sea fans, and sea pens. Anthozoans do not have a medusal stage. Instead, the sperm and egg unite to form a planula and attach to a suitable substrate where further development occurs.

Corals and Coral Reefs

The best-known anthozoans—and the group that has received the most research attention following oil spills—are the corals and coral reef communities. Stony corals, which secrete a hard, calcium-rich exoskeleton, are found in shallow tropical and subtropical seas as well as in the deep sea. Both shallow and deepwater corals rely on currents to disperse their eggs, sperm, and/or larvae, and to supply them with food. Shallow water corals have symbiotic algal microorganisms called zooxanthellae. The corals provide the zooxanthellae with protection, nutrients, and exposure to sunlight, while the zooxanthellae provide oxygen and supplemental energy. Shallow water reefs are highly productive systems that provide habitat and food for a diversity of marine life (McCloskey 1970; Hatcher 1988; McAllister 1991; Nagelkerken et al. 2000; Hughes et al. 2002; Harrison and Booth 2007; Knowlton et al. 2010; reviewed in Gibson et al. 2011), including mussels, crabs, oysters, and sea stars (McCloskey 1970), and habitat for commercially important fishes, including yellow snapper (Sorokin 1990; Spurgeon 1992; Nagelkerken et al. 2000). Deepwater corals lack associated zooxanthellae, but still support diverse communities of snails, oysters, clams, worms, sponges, and commercially important fishes (Fosså et al. 2002; Jonsson et al. 2004; Rogers 2004; Costello et al. 2005; Reed et al. 2006; Henry and Roberts 2007). Soft corals, including sea pens, sea fans, and sea whips, are also important members of the coral reef community, and provide additional structural components. Their biomass can exceed the coverage of their stony counterparts (Benayahu and Loya 1977, 1981; Tursch and Tursch 1982; Riegl et al. 1995; Fabricius 1997).

The economic value of coral reefs has been assessed at about \$30 billion annually (Conservation International 2008). Costanza et al. (1997) estimated the value of benefits provided by coral reefs to be \$607,500 per km² of reef per year, although this might be an underestimate as new medical and indus-

trial uses of coral are discovered. Due to the high diversity of organisms reefs support, the potential of finding a new drug from a reef-dependent species may be 300 to 400 times more likely than discovering one from a terrestrial ecosystem (Bruckner 2002a). Compounds with anti-tumor, anti-inflammatory, and wound-healing potential have been extracted from various coral reef-associated animals like sponges and soft corals, and coral skeletons have been used in bone grafts (Spurgeon 1992; Carté 1996; Libes 2009). Part of the value of reefs is their ability to serve as natural barriers that protect coastlines and coastal communities from storm surges (McAllister 1991; Cesar 1996; Berg et al. 1998). The loss of near-shore reefs that help attenuate waves leaves shorelines exposed to damaging erosional forces (Birkeland 1997; Cesar et al. 1997; Berg et al. 1998; Moberg and Folke 1999; Barbier et al. 2011).

Despite their economic importance, coral reefs worldwide are suffering from unsustainable uses and human-induced disturbances that affect their resilience and capacity to supply ecological goods and services. These disturbances include destructive fishing methods, collection of fish and other animals for the aquarium trade, coral mining for lime production, sedimentation due to deforestation, climate and ocean changes, pollution, and oil spills (Brown 1987; Wilkinson 1993; Hawkins and Roberts 1994; Dulvy et al. 1995; Kuhlmann 1988; Moberg and Folke 1999; Munday 2004; Mangi and Roberts 2006; Haapkylä et al. 2007; Harrison and Booth 2007). A significant fraction of the estimated 62,000 metric tons of oil spilled into the world's oceans per year (NRC 2003) is released into reef ecosystems (Ramade and Roche 2006, cited in Haapkylä et al. 2007) and chronic oil pollution in coastal waters is a serious threat to coral communities (Loya and Rinkevich 1980; Southward et al. 1982; Bak 1987; Burns and Knap 1989; Guzmán et al. 1991). Toxic PAHs are present chronically in coral reef systems as a result of tanker accidents, ballast releases, and urban runoff (Loya and Rinkevich 1980; Haynes and Johnson 2000; NRC 2003; Shigenaka 2001; Shigenaka et al. 2010). Due to their nearshore location, shallow water corals are at additional risk from tanker accidents, oil refinery operations, and oil exploration and extraction activities (IPIECA 1992; Guzmán and Holst 1993).

The impact of oil on coral ecosystems depends on many physical, chemical, and biological factors (Shigenaka et al. 2010). Oil slicks that form above subtidal reefs can smother corals in intertidal seas when they are exposed during low tides (Johannes et al. 1972; Shigenaka 2001; Haapkylä et al. 2007; Shigenaka et al. 2010). Subtidal corals can come into contact with spilled oil as a result of wave action or turbulence that mixes the oil into the water column when oil adsorbs onto particles and sinks (Payne and Phillips 1985; Shigenaka et al. 2010). Application of chemical oil dispersants can translocate oil further from the source, increasing its potential to contact corals (Haapkylä et al. 2007). Moreover, oil re-suspended from sediments may impact reefs as oiled sediment particles and detritus settle on, or are consumed by, coral polyps (Burns and Knap 1989; Guzmán and Holst 1993; Shigenaka et al. 2010). Consequently, contaminated prey and detritus is a potential route of oil exposure for corals, though this has not been studied extensively (Loya and Rinkevich 1980; O'Sullivan and Jacques 1998; Shigenaka et al. 2010).

Despite their importance, corals are often examined only as a part of the larger coastal ecosystem community following oil spills and may be omitted entirely from impact studies (Gooding 1971 [tanker *R. C. Stoner*, Wake Island, September 1967]; Nadeau and Berquist 1977; Page et al. 1979 [*Zoe Colocotroni*, Puerto Rico, March 1973]; NOAA 1995 [Barge *Morris J. Berman*, Puerto Rico, January 1994]). Nonetheless, multiple field studies after spill events have found impacts of chronic oil pollution on coral communities including impaired reproduction, larval development, and juvenile recruitment (reviewed in Loya and Rinkevich 1980). Re-oiling from contaminated sediment in oiled mangroves is thought to be responsible for negative impacts on coral regeneration, growth, and juvenile recruitment (Cubit et al. 1987; Guzmán and Holst 1993; Michel et al. 1993; Burns et al. 1994). Following the 1986 Bahia Las Minas refinery spill in Panama, the cover, size, and diversity of live corals decreased in both subtidal and intertidal reefs in these sheltered coastal waters (Guzmán et al. 1991). In addition, Jackson et al. (1989) studied long-term impacts on corals in the 18 months following the Bahia Las Minas spill and observed



Coral reefs are impacted by a variety of human activities, including overfishing, mining for lime, and coral collection. This reef is covered by an abandoned fishing net. Oil spills add another stressor to already disturbed habitats. (Photograph: NOAA, NURC/UNCW and NOAA/FGBNMS.)

signs of stress responses including bleaching (loss of symbiotic zooxanthellae) and swelling of tissues. They also observed dead areas with loss of coral tissue, colonization by macroalgae, and reef areas contaminated with globules of oil.

Several laboratory studies have shown detrimental impacts of oil on the individual polyps of reef-forming corals, including decreased growth and reproduction (Rinkevich and Loya 1979; Loya and Rinkevich 1980; Peters et al. 1981; Dodge et al. 1984; Bak 1987; Guzmán and Holst 1993; Guzmán et al. 1994; Harrison 1994), impaired larval development and reduced colonization capacity (Rinkevich and Loya 1979; Harrison et al. 1984; Kushmaro et al. 1997; Negri and Heyward 2000). Negative impacts on feeding and behavior were also found (Loya and Rinkevich 1979). Gross cellular damage can also result from sublethal exposure to oil (Peters et al. 1981; Harrison et al. 1990; Rougée et al. 2006). Exposure of the coral *Manicina areolata* to oil at 0.1 and 0.5 ppm for three months caused substantial tissue abnormalities, including impaired development of reproductive tissues and degeneration and loss of symbiotic zooxanthellae (Peters et al. 1981). Other studies have found differing sensitivities of coral to oil pollution (Lewis 1971; Johannes 1975; Loya and Rinkevich 1980; Dodge et al. 1984). This was attributed to physiological differences among species of coral, the types of oils and dispersants studied, differences in exposure times and dosages, and the length of time corals were monitored for recovery.

The dispersants used to help break up oil slicks following a spill can increase availability of oil particles in the water column (Lunel 1995; Chapman et al. 2007) and increase exposure of filter-feeding corals (IPIECA 1992). In addition, mixtures of oil and dispersants may be more toxic to corals than oil alone (Cook and Knap 1983; Ballou et al. 1989; Guzmán et al. 1991; Negri and Heyward 2000; Ward et

al. 2003; Shafir et al. 2007; Goodbody-Gringley et al. 2013). Crude oil and dispersant chemicals inhibited metamorphosis and fertilization in corals when tested separately, but impairment of larval development was magnified when oil and dispersant were both present (Negri and Heyward 2000). Similarly, settlement and survival of coral larvae decreased with separate treatments of oil and dispersant, while oil plus chemical dispersant resulted in settlement failure and complete larval mortality (Goodbody-Gringley et al. 2013).

The acute and chronic impacts of oil on corals further threatens an ecosystem already in serious decline from multiple stressors (IPIECA 1992; Sebens 1994; Brown 1997; Pandolfi et al. 2003; Chabanet et al. 2005). Corals are the building blocks of reef ecosystems, hence oil-mediated impacts on corals themselves will be accompanied by a wide range of associated impacts affecting the diversity of associated fish, invertebrates, and plants, effectively altering the entire ecology of the reef system (Reimer 1975; Maragos et al. 1996; Shigenaka et al. 2010; NRC 2012).

Crustacea

Marine crustaceans include crabs, lobsters, krill, amphipods, copepods, barnacles, and shrimp, and are found from shorelines and deep sea to open water and estuaries. Most are free living and mobile, while others (e.g., barnacles) attach to rocks and other substrates. Planktonic crustaceans (krill and copepods) are an important part of pelagic food webs, providing sustenance to large vertebrate and invertebrate predators (Moksnes et al. 1998; Pauly et al. 1998b; Rasmuson 2012). Benthic crustaceans, such as amphipods, crabs, shrimp, and lobsters, provide food for foraging fishes (Wilson et al. 1987; Baird and Ulanowicz 1989; Wilson et al. 1990; Highsmith and Coyle 1992; Heck and Coen 1995) and support large commercial fisheries (Miller et al. 2005; Rasmuson 2012).

Many crustaceans live in the benthos of coastal areas or deep seas as adults while others are exclusively estuarine-dependent species in nearshore environments (Guillory et al. 2001; Zimmerman et al. 2002; Rakocinski and McCall 2005; Fisher et al. 2007; Romanov et al. 2009; Rasmuson 2012). Crustaceans may be exposed to oil in the water column through direct contact, feeding, or while burrowing in oiled sediments (Krebs and Burns 1977; Burger et al. 1991; Culbertson et al. 2007; Cormack et al. 2011). Crustaceans are sensitive to marine pollutants (Krebs and Burns 1977; Brodersen 1987; Burger et al. 1992; Peterson et al. 1996; Culbertson et al. 2007) and members of this group have experienced large die-offs following oil spills (Cross et al. 1978; Sanders et al. 1980; Teal and Howarth 1984). Notable kills were reported after the 1978 *Amoco Cadiz* spill off the coast of France (Vandermeulen and Singh 1994), the 1989 *Exxon Valdez* spill in Alaska (Jewett et al. 1999), and the 1996 *North Cape* spill off the coast of Rhode Island (Michel et al. 1997; French 1988; McCay et al. 2001). The following sections address the impacts of oil spills on benthic crustaceans; for impacts on planktonic crustaceans, see “Zooplankton” on page 23.

Crabs

Marine crabs, such as hermit crabs, king crabs, blue crabs, and fiddler crabs, are an important part of the food web in a variety of ocean habitats, from coastal environments to the open ocean and the deep sea (Van Dover 2002; Jeng et al. 2004; Fisher et al. 2007; Signa et al. 2008; Romanov et al. 2009; Christofolletti et al. 2010; Yeager and Layman 2011; Rasmuson 2012; Wang et al. 2013). They feed on algae, detritus, bacteria, worms, mollusks, and other crustaceans, and provide food for a number of fish, octopuses, shorebirds, and mammals, as well as the endangered loggerhead sea turtle (Plotkin et al. 1993). Their burrowing activities in benthic environments contribute to sediment turnover (bioturbation), which increases oxygenation and nutrient availability in underlying sediments (Robertson 1986; Smith et al.

1991; Cormack et al. 2011). Crabs are important inhabitants of coastal ecosystems because they are benthic detritivores with strong ecological links between marine, marsh, and terrestrial environments (Kristensen 2008). They are also a lucrative fishery globally. In 2010, the worldwide commercial catch of blue crab (*Callinectes sapidus*) was over 110,000 metric tons (FAO 2013a), and, in the U.S., the fishery was ranked the fifth largest in value, earning an estimated \$206 million (NMFS 2010).

Crabs may be impacted by oil spills through direct physical smothering and by the acute toxicity of oil adhering to body surfaces (O'Sullivan and Jacques 1998). Oil spills can cause significant reductions to benthic crab populations (Krebs and Burns 1977; Cross et al. 1978; Michel et al. 1997; French 1998). Crabs ingest oil from contaminated water or sediment and experience fouling and clogging of gills or impaired feeding. This leads to behavioral changes, reduced feeding, and long-term ecosystem-level impacts (Cross et al. 1978; O'Sullivan and Jacques 1998; Barth 2007; Culbertson et al. 2007; Kristensen 2008). For example, exposure of the shore crab *Carcinus maenas* to 200 µg/L of the PAH pyrene over a period of 28 days significantly increased the time needed to break the shells of their prey (Dissanayake et al. 2010). Furthermore, chemical dispersants that emulsify the oil and create smaller droplets within the water column and benthos may allow for more efficient diffusion of oil into crab tissues than oil alone, resulting in a higher body burden (Chase et al. 2013). Higher body burdens of oil can impact crab behavior and reduce fitness, ultimately disrupting the roles they provide as ecosystem engineers and impacting predators of crabs (Krebs and Burns 1977; Culbertson et al. 2007; Kristensen 2008).

Many instances of massive acute mortality among crabs after oil spills have been noted. Oil released during the 1996 *North Cape* spill off the coast of Rhode Island killed millions of hermit and rock crabs that were found stranded on the shore (Michel et al. 1997; French 1998). Similar acute mortality among crabs (*Carcinus maenus*) was seen after the 1978 *Amoco Cadiz* spill off the coast of France. In severely oiled intertidal habitats, the gills of killed individuals were coated with oil (Cross et al. 1978). On the coast of Massachusetts, numerous fiddler crabs (*Uca pugnax*) were found dead or dying in heavily oiled salt marshes following the 1969 *Florida* barge spill. Surviving crabs had abnormal mobility and burrowing behavior, likely due to feeding on oiled sediments (Krebs and Burns 1977). Following the 1991 Gulf War oil spill along the Saudi Arabian coast, almost all of the burrowing crabs in heavily oiled marshes died. Burrows were visibly oiled to depths of 30 cm and no crabs were present in the burrows a year after the spill (Hayes et al. 1993).

The detrimental impacts of oil spills on crab populations can continue for many years after a spill. Fiddler crab densities were lower after the *Florida* spill at sites where sediment PAH concentrations exceeded 200 ppm and recruitment of juvenile crabs in oiled marshes was reduced throughout a seven year study (Krebs and Burns 1977). Residues from the *Florida* were detected in crabs analyzed 20 years



Hermit crab in the Flower Garden Banks National Marine Sanctuary, Gulf of Mexico. (Photograph: NOAA Photo Library.)

after the spill and in sediments analyzed 30 years after the spill. Crabs in contaminated sediments had impaired feeding and mobility (Teal et al. 1992; Reddy et al. 2002; Culbertson et al. 2007). Contaminated fiddler crabs acquired a body burden of oil pollutants so high that, because of their limited metabolic capacity, it would likely not be cleared from their tissues within their life span (Burns 1976). Eleven years after the 1991 Gulf War spill, oil remained in the marshes at quantities of at more than 30 grams of hydrocarbons per kilogram of sediment or substrate (g/kg). This was trapped under mats of bacteria that utilized hydrocarbons as an energy source. The reduction in crab burrows beneath these mats likely contributed to mat growth, since bioturbation from crab activity mixes sediments and limits bacterial growth (Hoffman 1994; Barth 2007; Kristensen 2008). Crab burrows were noted in areas where the bacterial mats were breaking up. In 1999, oil concentration was measured at 22 g/kg sediments and only 3 burrows per square meter were detected. Just two years later, oil concentration had fallen to 5.7 g/kg sediment and burrow density increased to 41 per square meter. The persistence of oil in the marsh sediments and long-term impairment of crab physiology and behavior demonstrates the extended impact of near-shore spills. Such oil-induced reductions in crab populations have long-term impacts on the ecology of entire salt marsh and coastal water communities due to the importance of crab larvae and adults as food for foraging fishes and shorebirds (Morgan 1990; Iribarne and Martinez 1999; Mazumder et al. 2006).

Amphipods

Marine amphipods are small crustaceans (5–50 mm) whose abundance and diversity in shallow and deepwater environments can surpass all other crustaceans and even all other invertebrate groups (Thomas 1993; Cartes and Sorbe, 1999; Poggiale and Dauvin 2001). Amphipods are a key component of deep sea benthic environments, both as scavengers that process dead and decaying matter and make nutrients available to other trophic levels, and as prey for benthic-feeding fishes (Dahl 1979; Collie 1985; Soliman 2007; Duffy et al. 2012). They are mostly free-living and can be found burrowing in sediments, suspended or swimming above the substrate, or living in fixed or mobile tubes (Thomas 1993). Others are cryptic, inhabiting crevices in live coral and sponges (Richards et al. 2012) or seeking refuge among seaweeds (Duffy and Hay 1991). Amphipods play many roles in the marine food web as scavengers, herbivores, predators, or prey for many top predators, including other invertebrates, fishes, mammals, and birds (Oliver et al. 1982, 1984; Nerini 1984; Highsmith and Coyle 1992; Kock et al. 1994; Bocher et al. 2001; Watanabe et al. 2004; Coyle et al. 2007; Seitz et al. 2011).

Significant negative impacts on amphipod populations have been frequently observed following oil spills (Sanders et al. 1980; Dauvin 1982; Elmgren et al. 1983; Jewett and Dean 1997). Amphipod populations in several families were depressed for up to six years at sites impacted by the 1989 *Exxon Valdez* spill in Prince William Sound, Alaska (Jewett and Dean 1997). These effects were likely due to oil persisting in cold sediments; amphipods in the laboratory exposed to intertidal sediment samples collected from oiled beaches in 1990 showed significant mortality (Wolfe et al. 1996). After the 1978 *Amoco Cadiz* spill off the Atlantic coast of France, ampeliscid amphipods were completely absent from sites where they had been the dominant population (Dauvin 1982). Recolonization of impacted areas was low and amphipod densities did not reach pre-spill levels for 11 years, which likely had impacts on amphipod-eating fish (Dauvin 1989). After the 1977 *Tsesis* oil spill in the Baltic Sea, amphipods (*Pontoporeia* spp.) at oiled sites were reduced to less than 5% of their pre-spill biomass. Surviving females produced significantly greater numbers of abnormal larvae and population recovery was not detected for almost three years after the spill (Elmgren et al. 1983). Amphipods may be especially sensitive to the effects of local pollution because of their low dispersal rate due to limited mobility and lack of a planktonic larval stage (Lindén 1976; Dauvin 1989, 1998; Thomas 1993; Ramos-Gómez et al. 2009; Molisani et al. 2013). These large, oil-induced amphipod die-offs and subsequent slow recolonization rates can

have long-term impacts on food web dynamics (Dauvin 1989, 1998). For example, based on their importance as a food resource for fish, it was calculated that the estimated loss of 1,500 tons of *Pontoporeia* spp. that occurred during the three years following the *Tsesis* spill could have caused a loss of 100 tons of fish production (Elmgren et al. 1983).

Laboratory studies have also found acute and chronic impacts of oil exposure on amphipod development and reproduction. In acute 48-hour toxicity trials, larval amphipods were almost 700 times more sensitive than adults to crude oil (larval $LC_{50} = 0.8 \mu\text{l/L}$; adult $LC_{50} = 550 \mu\text{l/L}$) (Lindén 1976). Exposure to sublethal concentrations of oil impaired reproduction and newly hatched larvae from surviving embryos were found dead or adhering to a film of oil (Lindén 1976). The dramatic sensitivity to oil pollution seen in both field and laboratory studies could make amphipods an “umbrella” group that demonstrate the potential impacts of oil on the other less visible and often overlooked small invertebrates that inhabit benthic environments (Jewett and Dean 1997; Fukuyama et al. 1998).

Polychaetes

Polychaetes are segmented worms with tubular bodies covered with fleshy, bristled protrusions. They are among the most common and abundant benthic invertebrates inhabiting coasts, estuaries, coral reefs, and the deep sea (Kohn and Lloyd 1973; Maurer and Vargas 1984; Carpenter 1986; Klumpp et al. 1988; Dauvin et al. 1994; Lauerman et al. 1996; Mackie et al. 1997; Hutchings 1998; Laguionie-Marchais et al. 2013). Polychaetes have diverse lifestyles. Some burrow into the sediment, others are sessile tube-dwellers, and some are free-living and planktonic. Polychaetes are omnivorous, consuming algae, invertebrates, or detritus on the seafloor (Fauchald and Jumars 1979; Tenore 1981; Alongi and Hanson 1985; Gaston 1987; Manokaran et al. 2013). They support marine food webs in coastal waters as well as



Feathery “branches” of the polychaete Christmas tree worm (*Spirobranchus giganteus*) have a dual purpose, collecting food and acting as respiratory organs. The remainder of the worm lives in a hole bored into the substrate. (Photograph: NOAA Photo Library.)

the deep sea and are prey for benthic-feeding fishes (Thijssen et al. 1974; Martin and Christiansen 1997; Besy et al. 1999; Drazen et al. 2008a, 2008b).

The responses of polychaete populations to oil spills are complex and varied. Some species increase in abundance, and some, such as *Capitella capitata*, may be the first colonizers in the aftermath of oil-spill die-offs (Sanders 1978; Sanders et al. 1980; Fukuyama et al. 1998; Peterson et al. 1996). Others can contribute to biodegradation of oil in sediments and some have different abilities to metabolize contaminants (Bauer et al. 1988; Driscoll and McElroy 1997). A study to assess impacts of the *Exxon Valdez* oil spill on benthic communities in, and adjacent to, eelgrass beds in Prince William Sound, Alaska, found that some of the most well-represented groups at oiled sites included nine families of polychaetes: Amphictenidae, Nereidae, Opheliidae, Sabellidae, and Sigalionidae at depths less than 3 meters; Maldanidae, Nephtyidae, and Syllidae at 6 to 20 meters depth; and Spionidae at all depths (Jewett et al. 1999). In contrast to the mass mortality seen among many benthic invertebrates following the *Amoco Cadiz* spill off the coast of France in 1978, polychaetes (*Arenicola*) appeared to tolerate high levels of hydrocarbons in the sediments and were seen actively deposit-feeding (Cross et al. 1978; Laubier 1980). After the 1969 *Florida* spill in Buzzards Bay, Massachusetts, the polychaete *Capitella capitata* became established in impacted areas at high densities (up to 200,000 individuals/m²). These densities decreased after several months as other species of benthic invertebrates replaced them, but although benthic community richness slowly increased, in heavily oiled sites the communities remained unstable for at least three years following the spill (Sanders 1978; Sanders et al. 1980).

Populations of the polychaete *Harmothoe sarsi* responded quite differently after the 1977 *Tsesis* oil spill in the Baltic Sea and were reduced to less than 5% of their pre-spill biomass (Elmgren et al. 1983). The response of *H. sarsi* compared with *C. capitata* may be a consequence of their different feeding strategies and trophic relationships in benthic environments. *Capitella capitata* thrives in the absence of competition and is a non-selective deposit feeder consuming detritus and algae and benefiting from organic pollution (Sanders et al. 1980; Tenore 1981; Tenore and Chesney 1985; Peterson et al. 1996). In contrast, *H. sarsi* is a predatory polychaete that feeds primarily on benthic amphipods, especially those



The impact of and recovery from an oil spill depends on a number of factors, including the type and quantity of oil and the habitat that is affected. The tidal zone in Brittany, France, was heavily oiled following the *Amoco Cadiz* grounding in 1978. (Photograph: NOAA Photo Library.)

in the genus *Pontoporeia* (Sarvala 1971; Abrams et al. 1990). *Pontoporeia affinis* populations declined drastically after the *Tsesis* oil spill and concomitant declines in *H. sarsi* populations may have been due to loss of their primary food source (Elmgren et al. 1983).

The burrowing behavior of sediment-dwelling polychaetes may play an important role in the fate of oil contaminants in sediment (Bauer et al. 1988; Christensen et al. 2002; Granberg et al. 2005; Cuny et al. 2007). Polychaete burrowing aids bioturbation (sediment mixing), which not only increases oxygen levels and nutrient availability (Kristensen et al. 1985; Gilbert et al. 1994; Kristensen and Kostka 2005), but also favors development of oil-degrading bacterial communities within their burrows (Bauer et al. 1988; Christensen et al. 2002; Granberg et al. 2005; Cuny et al. 2007; Timmerman et al. 2008). For example, the polychaetes *Nereis diversicolor* and *N. virens* influenced aerobic microbial degradation of PAHs through the aeration of sediment within their burrows (Chung and King 1999, 2001; Wenzhofer and Glud 2004; Cuny et al. 2007). Digestive fluids of some polychaetes (e.g., *N. virens*) act as natural surfactants that contribute to the solubilization of PAH compounds, increasing their availability for microbial degradation and enhancing bioremediation of oil-polluted sediments (Weston and Mayer 1998; Gilbert et al. 2001).

Recovery and Recolonization

Signs and symptoms of oil contamination can persist for many years after a spill in sheltered habitats such as oiled salt marshes and mangrove swamps. Here, detrimental effects may be evident for decades (Cormack 1999; Kingston 2002; NRC 2003; reviewed in Moore 2006; Fingas 2013). There is little agreement on what qualifies as “biological recovery” of an oil-impacted ecosystem and such determinations are further complicated by the dynamic nature of marine ecosystems and the impacts of other anthropogenic disturbances (Roemmich and McGowan 1995; Sell et al. 1995; McGowan et al. 1998; Scheffer et al. 2001; Kingston 2002). There is also an unfortunate lack of long-term studies that could reveal indirect or protracted impacts (Hawkins et al. 2002; Peterson et al. 2003b).

Recolonization rates of oil-impacted habitats are affected by the type of organisms in the community, time of year, availability of colonists and/or juvenile recruits, climatic conditions, and biological interactions among colonists (Capuzzo 1987, 1990; Kingston 2002). Marine animals with a pelagic phase can move across large distances and enable a more rapid recovery to pre-spill abundances (Obrebski 1979; Elmgren and Frithsen 1982; Dauvin 1989; Günther 1992; Kingston 2002). However, many taxa have more restricted habitat needs and/or limited mobility and planktonic organisms, including the larvae of many species that are benthic as adults, may not be able to physically avoid floating oil slicks (Guzmán del Prío et al. 1986; Peters et al. 1997; Shigenaka 2001; Almeda et al. 2013). In addition, oil can persist for decades as evidenced by the 1970 spill from the barge *Arrow* into Chedabucto Bay, Nova Scotia. Oil found in underlying sediments sampled 20 years later was virtually undegraded or unweathered and contained many of the same PAH compounds as the original oil (Vandermeulen and Singh 1994). Some reviews indicate that recovery from oil spills occurs within three years (Moore 2006; Penela-Arenaz et al. 2009), while others find that recovery requires up to ten years (Kingston 2002; Fingas 2013; Peterson et al. 2012).

The ecological effect of oil in the marine environment is a function of many factors, including oil type, release rates, oil fate processes, habitat type, local weather and oceanographic conditions, and distribution and type of organisms being impacted. The rate of recovery of affected areas can differ substantially in different habitats. In general, exposed rocky shores recovered from oil spills within three to four years, while sheltered habitats may require 12 years or more to recover (Page et al. 1983; Baker

1999; Kingston 2002; NOAA 2002b; NRC 2003; Fingas 2013). Strong wave action in exposed habitats can help remove contamination and some shorter-lived animals may be better able to recolonize such shores quickly (Sanders et al. 1980; Peterson 2001; Kingston 2002). The complexity of marine ecosystems makes it difficult to predict how an oil spill will move through the system and ultimately affect community composition and ecosystem services (Fingas 2013; NRC 2012, 2013).

In sensitive environments such as marshes and mangrove swamps, response and cleanup actions after a spill can cause substantial physical disturbance and additional damage. Inappropriate cleanup can increase erosion, damage marsh vegetation, or force oil into sediments through trampling, and overall increase recovery times for both flora and fauna (Webb 1993; Fingas 2013). In exceptional cases, where there are heavy deposits of oil or extensive subsurface penetration on salt marshes, shore treatment may be effective in advancing recovery (Sell et al. 1995; Fingas 2013). Because each oil spill comprises a unique set of chemical, physical, and biological characteristics, there is no one appropriate response method that can be applied to all oil spills (NRC 2003, 2005; Fingas 2013).

The use of dispersants following an oil spill has both benefits and disadvantages. Dispersant use increases the amount of oil that physically mixes into the water column thereby reducing the potential for a surface slick to contaminate shoreline habitats and coastal wildlife, or come into contact with planktonic organisms on the water surface (NRC 2005; Fingas 2013). However, by facilitating movement of oil into the water column, dispersants increase the potential exposure of water-column and benthic biota to spilled oil (NRC 2005, 2012; Fingas 2013). Furthermore, the use of dispersants does not preclude the possibility of oil plus dispersant reaching sensitive nearshore environments and invertebrates (NRC 2005, 2012, 2013; Bik et al. 2012; Carmichael et al. 2012a; Silliman et al. 2012; Fingas 2013; Montagna et al. 2013; Sammarco et al. 2013). Dispersant application represents a conscious decision to increase the oil burden from a spill on one component of the ecosystem (i.e., the water column) while reducing the burden on another (i.e., coastal wetlands) (NRC 2005; Fingas 2013). In some instances, aggressive cleanup techniques such as high-pressure hot-water washes used to remove oil from shorelines may delay recovery of affected intertidal communities such as gastropods, mussels, and clams (Sell et al. 1995; Houghton et al. 1997; Peterson 2001; NRC 2003). Selection of response actions often considers protection of environmentally sensitive environments, but may neglect the potential impacts on marine invertebrates from such mitigation strategies (NRC 2012; Fingas 2013). The survival of all invertebrates should be considered after an oil spill to understand impacts or guide cleanup methods. Unfortunately, efforts are often focused on commercially and economically important species, leaving a gap in understanding of other ecologically important invertebrates that are the foundation of marine food webs (NRC 2012, 2013).



Photo: United States Coast Guard

Case Studies: A History of Significant Marine Oil Spills Prior to the Deepwater Horizon, with Special Emphasis on Impacts to Invertebrates.

1969: Sinking of the barge *Florida*

In 1969, the barge *Florida* sank in Buzzards Bay, Massachusetts, spilling 700,000 liters of Number 2 fuel oil. Heavy wave action from a storm that followed the spill mixed the oil with water and sediments and increased impacts on wildlife (reviewed in Kingston 2002). Oil moved into sensitive sheltered marshes where it killed crabs, amphipods, worms, mollusks, and other benthic invertebrates (Sanders 1978; Burns and Teal 1979; Sanders et al. 1980). Analysis of benthic communities in the five years following the spill showed large fluctuations in invertebrate species and incomplete recovery (Sanders et al. 1980). Populations of the opportunistic polychaete *Capitella capitata* dominated in oiled areas, but were eventually replaced by a succession of changing invertebrate communities (Sanders 1978; Sanders et al. 1980). The dominance of *C. capitata* from December 1969 to July 1970 was followed by establishment of the polychaete *Mediomastus ambiseta* during the second and third years following the spill, after which other polychaete worms, gastropods, small bivalves, and clams began to colonize impacted sites (Sanders 1978). Impacted marshes showed large fluctuations in species abundances and composition for at least five years after the spill, with polychaetes and gastropods dominant at sites sampled in 1971 and 1972. By comparison, community composition of unoiled marshes in the same region remained relatively stable (Sanders 1978; Sanders et al. 1980). This rapid turnover in oiled areas suggests continuing stress on marsh biota, as described by the Intermediate Disturbance Hypothesis, in which species turnover is accelerated in habitats experiencing ongoing chronic disturbances such as pollution due to the ongoing colonization of new niches followed by local extirpation and recolonization by different species (Connell 1978).

Examination of impacts to marsh biota beyond this five-year study focused mainly on crabs (Krebs and Burns 1977; Culbertson et al. 2007). Depression of fiddler crab (*Uca pugnax*) populations in oiled marshes was correlated with oil persistence and continued for over seven years after the spill (Krebs and Burns 1977). Larval crabs were more affected by residual oil than adults and long-term impacts on juvenile recruitment were thought to be due to oil exposure during sensitive molt periods (Krebs and Burns 1977). Polycyclic aromatic hydrocarbons from the oil spill persisted for 30 years in marsh sediments (Reddy et al. 2002) and fiddler crabs in these habitats continued to exhibit slowed escape responses and lower feeding rates more than 37 years after the spill (Culbertson et al. 2007). These continued impacts on fiddler crab populations can have long-term consequences for the saltmarsh ecosystem since adult crabs are an important food source for shorebirds and reductions in crab populations can also reduce the abundance of larvae, which are prey for foraging fishes (Morgan 1990; Iribarne and Martinez 1999; Mazumder et al. 2006).

1970: Grounding of the tanker *Arrow*

The tanker *Arrow* ran aground off the coast of Nova Scotia in 1970, spilling 10,000 tons of Bunker C oil into Chedabucto Bay. Oil was driven by wind into nearshore areas where it eventually oiled 200 km of coastline, but the presence of sea ice prevented investigation of spill impacts until the following year (re-

viewed in Teal and Howarth 1984; Lee et al. 1999). Impacts to benthic invertebrates were documented for up to 20 years after the spill, with most post-spill research focused on long-term impacts on intertidal clams. Six years after the spill, soft-shelled clams (*Mya arenaria*) in Chedabucto Bay were still being exposed to oil trapped in sediments and their populations were consistently lower at oiled locations than at reference sites (Teal et al. 1978; Thomas 1978). In this same time period, dead clams from oiled sites analyzed for contaminants had 650 µg/g of oil in their tissues. Live clams had 150–350 µg/g of oil in tissue samples and exhibited decreased growth rates (Gilfillan and Vandermeulen 1978; Thomas 1978) and impaired growth was seen for as long as nine years after the spill (MacDonald and Thomas 1982).

Substantial quantities of oil persisted in the environment for many years. Oil and tar mats were detected in two locations in Chedabucto Bay 20 years after this spill (Vandermeulen and Singh 1994). With limited weathering and sedimentation some tar mats were only slightly changed in composition from the original oil. Tar residues found trapped in beach cobble 20 years post-spill also remained relatively unweathered when compared with the reference Arrow Bunker C oil (Vandermeulen and Singh 1994). Oil residues and oily sheens were visible 30 years after the spill and sediment samples were contaminated with oil at concentrations ranging from 300 to 23,000 ppm (Lee et al. 2003). Although benthic invertebrates, such as green crabs (*Carcinus maenus*), soft-shelled clam (*M. arenaria*), common periwinkle (*Littorina littorea*), amphipods (*Gammarus oceanicus*), and sand worms (*Nereis* and *Arenicola* sp.), were seen in areas where oil from the *Arrow* persisted, sediment collected from these areas has significant toxicity to amphipods suggesting that the health of resident invertebrate communities was still being affected (Lee et al. 2003).



In March 1978, the *Amoco Cadiz* ran aground on Portsals Rocks, three miles from the coast of Brittany, France. The tanker foundered in heavy seas and was broken apart, releasing 220,000 tons of oil into the coastal waters. More than 200 miles of coastline were contaminated. The disaster was seen by millions on daily television news broadcasts across Europe and came to symbolize the damage caused by oil spills. (Photograph: NOAA Photo Library.)

1977: Grounding of the tanker *Tsesis*

The *Tsesis* oil tanker spilled around 252,000 gallons of fuel oil along the coast of Sweden in the Baltic Sea in October 1977. The decrease in zooplankton biomass observed recovered within five days of the spill but the guts and feeding appendages of zooplankton were contaminated with oil for at least three weeks afterwards (Johansson et al. 1980). Unfortunately, observations of zooplankton were done only for one month and do not capture the possibility of longer-term population effects.

Benthic invertebrate abundance was also reduced after the spill. Major groups included ostracods, harpacticoid copepods, and flatworms (class Turbellaria). Nematode abundance, however, appeared unaffected (Elmgren et al. 1983). Within 16 days of the spill, populations of benthic macrofauna including amphipods (*Pontoporeia* spp.) and polychaete worms (*Harmothoe sarsi*) were reduced to less than 5% of pre-spill biomasses at the most impacted site. Live female egg-bearing amphipods were found to have significantly more abnormal embryos when compared to those from a reference site (Elmgren et al. 1983). Oil originating from the *Tsesis* was detected in the tissues of *Macoma balthica* clams from a site that was not visibly oiled, indicating that the spill's impacts were more widespread than originally believed (Elmgren et al. 1983). By November 1979, densities of benthic meiofaunal organisms had increased to levels comparable to a reference site, but species diversity had not yet recovered. Oiled sites were dominated by nematodes and increased numbers of harpacticoid copepods, but Turbellaria, ostracods, and kinorhynchans (small worm-like invertebrates) were rare (Elmgren et al. 1983). Amphipod biomass was still depressed in the most impacted areas three years after the spill. Because they are a preferred food for commercially important fish such as herring (Casini et al. 2004), this extended reduction in amphipod abundance could have long term impacts on the food web (Elmgren et al. 1983).

1978: Grounding of the tanker *Amoco Cadiz*

The *Amoco Cadiz* ran aground off the northwest coast of France in March 1978, spilling about 220,000 tons of oil into coastal waters over several days. Adverse weather conditions following the spill pushed the oil onshore and into sediments, negatively impacting the diverse biota of local estuaries (Neff and Haensly 1982). The rich community of benthic invertebrates supported by the fine sand habitat of the Bay of Morlaix was severely impacted by heavy oiling (Cross et al. 1978), and impacts to oysters (Berthou et al. 1987) and zooplankton (Samain et al. 1980) were well documented following the spill. High mortality of zooplankton was reported in impacted areas off the north coast of Brittany 15 days after the spill (Samain et al. 1980) and impacts to zooplankton continued to be detected for 30 days post spill in nearshore areas where oil remained. Negative impacts were detected a year later as storms caused release of oil from contaminated environments (Samain et al. 1980).

In nearshore benthic environments, many echinoderms and mollusks died and continued to wash ashore for several weeks following the spill. These included heart urchins (*Echinocardium cordatum*), razor clams (*Ensis siliqua* and *Pharus legumen*), and mussels (*Mytilus edulis*) (Cross et al. 1978; Laubier 1980). Almost the entire intertidal fauna of exposed mud flats was damaged by oil in the days after the spill (Boucher 1980). Mass mortality of periwinkles (*Littorina obtusata* and *L. littorea*) and limpets (*Patella vulgata*) occurred in the rocky bottom along the shore, and sand clams and cockles in estuary sediments died (Cross et al. 1978; Maurin 1984). Limpets were released from their rocks and overturned and topshells (*Gibbula cineraria*, *G. umbilicalis*, and *Calliostoma zizyphinum*) were found dead or dying (Cross et al. 1978). Crabs (*Carcinus maenus*) from severely oiled rocky intertidal habitats were found dead and dying in the days following the spill and subsequent dissection showed oil coating their gills (Cross et al. 1978). Sand community biomass fell immediately after the spill and within two years the

original community was replaced by a small number of opportunistic benthic invertebrate species characteristic of eutrophic conditions. Polychaetes dominated and invaded habitat that had been occupied previously by amphipods (Laubier 1980; Dauvin 1982).

Oysters, an important commercial fishery in the region, were covered in a layer of oil immediately after the spill and mortality rates as high as 50% were detected at severely impacted sites in the Aber Benoit area for up to three months afterwards (Maurin 1984; Berthou et al. 1987). Resuspension of oiled sediments in subsequent years due to storm action resulted in continuing recontamination of oyster beds (Berthou et al. 1987). Atrophy in the gonads of flat oysters was noted, indicating that reproduction and spawning did not occur in the following year (Berthou et al. 1987). Oysters in the most impacted areas accumulated hydrocarbons at levels up to several thousand parts per million soon after being exposed, and oil persisted at high levels (100 ppm) in oyster tissues two years later (Neff and Haensly 1982; Neff et al. 1985). These oysters had poor nutritional status and altered metabolism compared with those at unimpacted sites (Neff and Haensly 1982).

Similarly, ampeliscid amphipods, a common member of many soft-bottom benthic communities in cold temperate waters (Poggiale and Dauvin 2001), were completely absent from sites where they had been the dominant population (Dauvin 1982). It took eleven years for amphipods to recolonize impacted areas and reach pre-spill densities. It is likely that amphipod-dependent fish species were impacted during this span (Dauvin 1989). Substantial long-term community-level alterations were reported in the years following the spill, notably the suppression of sensitive benthic species (Dauvin 1998).

1989: Blowout of the platform Ixtoc I

The Ixtoc I platform blowout in 1979 released an estimated 475,000 metric tons (140 million gallons) of oil into the Bay of Campeche in the southern Gulf of Mexico over a period of almost 10 months. The platform sank to the bottom of the Gulf following an explosion and fire. The oil that entered the water column from the sunken platform eventually reached the surface where it formed a 1–4-cm-thick layer



Oil plume spreading from the Ixtoc I platform blowout. (Photograph: NOAA Photo Library.)

covering an area 0.7–5.0 km wide and 60 km long (Jernelöv and Lindén 1981). After 60 days of continuous release, oil drifting on currents reached Texas beaches, coating them with a moderate to heavy oiling and impacting over 150 miles of shoreline during August and September 1979 (ERCO 1982; Hooper 1981). Clean-up response in Texas relied on the ability of barrier island beaches to naturally impede oil from reaching areas further inland, and booming, a containment method that involves using a temporary floating barrier, was used to protect sensitive marshes.

Apart from minor oiling along inlets and shorelines, no major impacts to estuarine habitats or species were reported. Unfortunately, as with many oil spills, no long-term studies were done to monitor effects on impacted ecosystems in either Texas or Mexico. Pre-spill benthic sampling of intertidal and subtidal populations was conducted prior to oil coming ashore in Texas, followed by post-spill sampling in September 1979 (Thebeau et al. 1981). This study found distinct post-spill reductions in populations of the most common benthic taxa at most sites surveyed (including significant reductions in haustoriid amphipods) and increases in populations of opportunistic polychaetes. Gastropods, mollusks, and crustaceans were also impacted post-spill. Researchers were reluctant to attribute impacts solely to the spill, suggesting that natural phenomena such as tropical storms in early-mid September could have contributed to population reductions (Thebeau et al. 1981). However, lack of continued sampling makes it impossible to know if there were long-term population effects from the spill.

Longer-term effects reported in offshore communities showed that zooplankton abundance suffered a four-fold decrease for three years after the Ixtoc I spill compared to pre-spill numbers obtained in the region a decade earlier (Guzmán del Prío et al. 1986). Oil from this spill remains in the ecosystem as evidenced by small tar balls that still wash ashore more than 30 years later (Tunnell 2011). Assertions have been made that the majority of Gulf species and habitats seem to have recovered (Tunnell 2011). Unfortunately, in the absence of long-term comprehensive studies and a deficiency of pre-spill baseline data, it is difficult to draw definitive conclusions on the impacts of this spill on marine invertebrate communities.



Intensive cleaning efforts during the immediate aftermath of the *Exxon Valdez* spill were unable to remove oil from between the rocks on the shores of Prince William Sound. (Photograph: NOAA Photo Library.)

1989: Grounding of the supertanker *Exxon Valdez*

The *Exxon Valdez* supertanker grounded on Bligh Reef in northeastern Prince William Sound, Alaska, in 1989. At the time, this spill was the largest in U.S. history. Eleven million gallons of oil spilled, of which 5 million gallons were ultimately distributed over approximately 400 miles of shoreline and intertidal habitats (Gundlach et al. 1990). Oil from the *Exxon Valdez* coated rock surfaces and penetrated soft sediments causing widespread mortality and morbidity among the coastal and intertidal mussels, echinoderms, amphipods, and crabs of Prince William Sound and the Gulf of Alaska (Jewett et al. 1994; Dean et al. 1996; Spies et al. 1996; Jewett and Dean 1997; Coats and Shigenaka 2005). Immediate impacts on intertidal communities occurred due to direct oiling, and oil trapped in sediments remained a chronic source of exposure for many years (Fukuyama et al. 1998; Hayes and Michel 1999; see review by Peterson 2001; Carls and Harris 2005; Bodkin et al. 2012).

In the year following the spill, amphipods were less abundant at oil-impacted sites compared with reference sites, and populations of amphipods in several families were still depressed at impacted sites six years later (Jewett and Dean 1997; Peterson 2001). A study to assess impacts on benthic communities in, and adjacent, to eelgrass beds in Prince William Sound found that some of the most well-represented groups at oiled sites were opportunistic polychaetes (Jewett et al. 1999; Peterson 2001). This indicated that the more sensitive invertebrate groups had not yet recolonized and/or were unable to successfully compete for space and resources (Sanders 1978; Sanders et al. 1980; see review by Peterson et al. 1996; Fukuyama et al. 1998).

Despite intensive efforts to clean beaches in the year following the spill, only about 10% of the oil was removed (Mearns 1996) and the methods used were blamed for some of the damage reported in intertidal environments. High-pressure washes with hot water removed seaweeds and gastropods such as periwinkles (*Littorina sitkana*) and drills (*Nucella* spp.) from rocks, and subsequent recolonization was slow compared with untreated oiled sites (Houghton et al. 1997; Peterson 2001). Oil persisting in the environment continued to exert negative impacts on wildlife. Survival and growth of clams (*Protothaca staminea*) was reduced 5–6 years after the spill at sites contaminated by residual oil, and soft shell clams (*Mya arenaria*) and mussels (*Mytilus trossulus*) in a heavily oiled location in Prince William Sound in 1989 showed metabolic stress due to PAH exposure 11 years after the spill (Houghton et al. 1997; Fukuyama et al. 2000; Downs et al. 2002).

Oil trapped in intertidal sediments in Prince William Sound degraded slowly and was biologically available to organisms at toxic levels for at least two decades (Carls and Harris 2005; Bodkin et al. 2012). Surveys done more than 10 years post-spill at 100 beaches in western Prince William Sound that were heavily to moderately oiled in 1989 found buried oil at 28 sites along the coastline (Short et al. 2004). These slow rates of hydrocarbon loss from sheltered habitats greatly extended the exposure period of intertidal communities to toxins (Babcock et al. 1996; Hayes and Michel 1999; Carls et al. 2001; Carls and Harris 2005; Payne et al. 2005). Exposure duration to oil differed greatly depending on location. For example, mussel populations were exposed to oil for months where oil was present only in the water column, but exposure persisted for as much as 10 to 20 years at sites where oil remained in sediment (Babcock et al. 1996; Carls et al. 2001; Carls et al. 2004; Carls and Harris 2005; Bodkin et al. 2012). Wave action and storms periodically resuspend buried oil, releasing compounds that were taken up by local mussel populations (Fukuyama et al. 1998; Carls et al. 2004; Carls and Harris 2005).

While a preponderance of studies showed long-term damage to benthic communities as a result of the spill with data demonstrating at least a decade or more of negative impacts due to the persistence of oil in sediments (Babcock et al. 1996; Fukuyama et al. 1998; Hayes and Michel 1999; Carls et al. 2001; Peterson 2001; Bodkin et al. 2002; Carls et al. 2004; Carls and Harris 2005; Bodkin et al. 2012), there is a lack of consensus about recovery and continuing impacts. Recovery within one to two years was

reported for shores in Prince William Sound (Boehm et al. 1995; Hoff and Shigenaka 1999; Page et al. 2005) but many of the longer term studies described above show that oil persisted in sediments at levels that negatively affected wildlife. Furthermore, long-term impacts have been demonstrated on sea otters and birds foraging in oiled intertidal areas and on clams and mussels with accumulated tissue hydrocarbons, with reductions in abundance, slower growth, and reduced use of oiled habitats for up to 20 years following the spill (Peterson 2001; Bodkin et al. 2002; Bodkin et al. 2012).

1991: Deliberate oil releases during the Gulf War

During the 1991 Gulf War, Iraqi forces deliberately released crude oil from oil tankers, oil terminals, and oil refineries in Iraq and Kuwait. Between January and March 1991 an estimated 10.8 million barrels of oil spilled into the Persian Gulf (MEPA 1993). In the months that followed, almost 1 million barrels of this oil washed ashore along the coast of Kuwait and Saudi Arabia. With the war ongoing, no investigation of affected sites was possible until late 1991, so the immediate acute impacts of the spill on marine biota were not assessed (Mathews et al. 1993). However, it was clear that oiling occurred in sensitive shoreline habitats and offshore ecosystems, and corals and offshore zooplankton communities were affected (Readman et al. 1992; Hayes et al. 1993; Mathews et al. 1993; Price et al. 1993; Barth 2007; reviewed in Shigenaka et al. 2010). Most research following this spill focused on impacts to fish and macrofauna, including commercially important shrimp and ecologically sensitive corals. A few studies also reported impacts to small benthic invertebrates such as ostracods and amphipods (Kado et al. 1993; Mathews et al. 1993; Price et al. 1993; Mostafawi 2001). As is the case with many oil spills, monitoring efforts waned as the oil and its immediate effects become less visible.

Surveys conducted after the war in November and December 1991 indicated that offshore benthic ecosystems at a water depth of at least 54 m were heavily impacted by sediment oiling. Notably, ostracod abundance and diversity decreased and their shells were visibly oiled (Mostafawi 2001). In 1992, significant damage was seen in coral (*Platygyra* spp. and *Porites* spp.) near an oil release point, resulting in the death of coral colonies (reviewed in Shigenaka et al. 2010). In February 1992, sampling of benthic invertebrates at oil-polluted beaches and marshes found lower percentages of live organisms at oiled sites compared with reference sites, especially for gastropods and bivalves (Kado et al. 1993). Sand collected from these contaminated sites significantly impaired the development of sea urchin embryos in the laboratory. Oil contamination was still present in the nearshore surface waters of Kuwait and Saudi Arabia in August 1992 and the sea-surface layer, where eggs and larvae of marine animals are often concentrated, showed significant toxicity to heart urchin larvae in laboratory tests (Price et al. 1994). Egg and larval abundances on spawning grounds of commercially important shrimp were about an order of magnitude lower in 1992 than in earlier years and the fishery was suspended as harvest fell from nearly 4,000 tons in 1989 to about 25 tons in the first half of 1992 (Mathews et al. 1993; Price et al. 1993).

Two and a half years after the spill, sediment at beaches within the spill path had oil concentrations high enough to cause continued leaching to the nearshore area and impact local benthic infauna, as indicated by amphipod toxicity tests (Randolph et al. 1998). Long-term impacts were also seen where oil persisted in salt marshes during the dozen years following the spill. Almost all of the burrowing crabs in the area died and burrows were visibly oiled to depths of 30 cm. No crabs were present in the burrows a year after the spill (Hayes et al. 1993). Slow recolonization occurred in areas where oil concentrations decreased over time, but some of the heavily oiled marshes showed little recovery, and oil remained trapped even a decade after the spill (Barth 2007).

1996: Grounding of the barge *North Cape*

The *North Cape* barge struck ground during a storm off the coast of Rhode Island in January 1996, spilling an estimated 828,000 gallons of No. 2 fuel oil into Block Island Sound. The oil was dispersed by wind and waves into the water and offshore areas, where it affected benthic ecosystems (Michel et al. 1997). The spill was particularly devastating for nearshore crustaceans and surf clams, which were found dead or dying on the beaches (Michel et al. 1997; French 1998). About three million lobsters washed ashore after the spill (French 1998) and their numbers were still depressed at impacted sites seven months post-spill (Michel et al. 1997). A later damage assessment estimated that a total of nine million lobsters had been killed (McCay et al. 2001). An estimated 150.6 million surf clams were killed, along with large numbers of blue mussels, bay scallops, rock crabs, and hermit crabs (McCay et al. 2001). Significant restoration was undertaken to compensate for losses in commercially important shellfish populations, and restoration plans for scallop, clam, and lobster were developed (NOAA 2002a). Actions implemented in the years following the spill included creating nurseries or protected and caged sanctuaries in retention ponds (DeAngelis et al. 2009). Continued monitoring has enabled adaptive management to improve restoration. However, while success has been demonstrated in scallop restoration efforts, oyster reefs have seen only limited recruitment and larval settlement (DeAngelis et al. 2009).

Other acute impacts included the death of worms, amphipods, and other invertebrates (French 1998; NOAA 2002a). In heavily oiled salt marshes, contaminated sediment caused the death of an estimated 6.6 billion organisms (NOAA 2002a). Long-term impacts to zooplankton communities were not studied in any detail because it was assumed these resources would not be as predominant during the winter, as few benthic invertebrates spawn during that time. Plankton sampling carried out in July and August after the spill confirmed this, as typical historical abundances were noted (Michel et al. 1997).

Part 3

The Deepwater Horizon Disaster

On 20 April, 2010, the drilling rig Deepwater Horizon caught fire and exploded. In addition to the loss of life and injuries suffered by the crew, this tragedy released a massive quantity of oil. The Deepwater Horizon rig sank two days after the explosion, leaving the ruptured wellhead gushing tens of thousands of barrels of oil each day (Griffiths 2012). Ultimately, an estimated 4.6 to 4.9 million barrels (193 to 201 million gallons) of oil was spilled into the Gulf of Mexico before the well was capped more than twelve weeks later on 15 July, 2010 (Griffiths 2012; NRC 2013). This was one of the largest and most extensive offshore oil spill events in U.S. history (National Commission 2011), and oil and dispersants impacted multiple coastal and offshore ecosystems in the Gulf of Mexico (NOAA NRDA 2012). Oil impacted the deep sea floor (White et al. 2012; Montagna et al. 2013), the pelagic water column (Camilli et al. 2010; Graham et al. 2010; Chanton et al. 2012), and the highly productive coastal wetlands and estuaries along the northern Gulf of Mexico (Bik et al. 2012; Silliman et al. 2012). The spill was unprecedented in both its scale and the ocean depths at which it occurred (National Commission 2011), and it severely impacted a region known for its high levels of biodiversity (Felder and Camp 2009) and economically vital fisheries (NMFS 2012; NRC 2012).

The Gulf of Mexico Ecosystem

The Gulf of Mexico is one of the most important marine ecosystems in the world from both an ecologic and economic standpoint (Zimmerman et al. 2002; Baltz and Yáñez-Arancibia 2009; Craig 2010; Fautin et al. 2010) and one of the most biodiverse marine systems on Earth (Felder and Camp 2009; Fautin et al. 2010; German et al. 2011). The Gulf is home to wetlands, marshes, barrier islands, beaches, seagrass meadows, and coral and oyster reefs (Kilgen and Dugas 1989; Yáñez-Arancibia and Day 2004; Cordes et al. 2008; Fautin et al. 2010; Sammarco et al. 2012). The rich biodiversity in these complex and varied habitats provides the region with ecosystem services and tourism activities that generate an estimated \$19.7 billion per year (National Commission 2011; NRC 2012). The Gulf's underwater regions provide feeding grounds, critical nursery habitat, and high productivity for a diversity of resident and transient fauna (Minello and Zimmerman 1991; Minello et al. 2003; Upton 2011), while coastal and estuarine habitats support over 90% of all commercially and recreationally important species in the region during some stage in their life cycle (Gunter 1967; Zimmerman et al. 2002; Glancy et al. 2003; Lellis-Dibble et al. 2008).

Gulf of Mexico ecosystems are of special concern because so many economically important fisheries depend on the marshes and estuaries for spawning areas, nurseries, and feeding (Minello and Zimmerman 1991; Beck et al. 2001; Deegan et al. 2002; Minello et al. 2003; Upton 2011). As a result, the Gulf of Mexico produces the largest volume and value of seafood in the U.S., with the exception of Alaska (LDWF 2011; Upton 2011). Invertebrate fisheries in the region include blue crab (*Callinectes sapi-*



Fire boat response crews battle the blazing remnants of the Deepwater Horizon oil rig the day after it exploded off the coast of New Orleans. The rig collapsed and sank the following day, rupturing the wellhead, which spewed oil into the Gulf of Mexico at a rate of tens of thousands of barrels per day for nearly three months. (Photograph: U.S. Coast Guard.)

dus), white shrimp (*Litopenaeus setiferus*), brown shrimp (*Farfantepenaeus aztecus*), and eastern oyster (*Crassostrea virginica*) (Lassuy 1983; Muncy 1984; Perry and McIlwain 1986; Stanley and Sellers 1986). In 2008, the U.S. Gulf coast seafood industry harvested a total of 1,273 million pounds of shrimp, crabs, oysters, and fish, with an estimated commercial value of \$662 million (finfish: \$146 million; shellfish: \$516 million) and supporting over 213,000 jobs with a related income of \$5.5 billion (NMFS 2009; Upton 2011). The highest fishery values were for shrimp (\$366 million) followed by oysters (\$60 million) and blue crab (\$39 million) (NMFS 2009; Upton 2011). Gulf catches are estimated to account for 68% of total U.S. shrimp harvest (212 million pounds), 64% of U.S. oyster harvest (18.2 million pounds), and 28% of U.S. blue crab harvest (55 million pounds) (NMFS 2012). These high catches are linked to the region's extensive network of wetlands and estuaries that serve as nurseries for these species (Minello and Zimmerman 1991; Beck et al. 2001; Deegan et al. 2002; Minello et al. 2003; LDWF 2011; Upton 2011).

Because of the great depths at which oil from the Deepwater Horizon spill was deposited, deep-sea habitats in the Gulf were also at risk. Deep-sea habitats support a diverse fauna (Grassle 1991; Jensen and Frederiksen 1992; Brooke and Schroeder 2007; Fisher et al. 2007; Haedrich et al. 2008; German et

al. 2011) that provide vital functions including biomass production (Grassle and Maciolek 1992; Wei et al. 2012), habitat provision for other invertebrates including mollusks, sponges, tube worms and other polychaetes, and crustaceans (Kennicutt et al. 1988; Pequegnat et al. 1990; Brooke and Schroeder 2007; Fisher et al. 2007; Cordes et al. 2008), sediment bioturbation and stabilization, organic matter decomposition (Dahl 1979; Soliman 2007; Duffy et al. 2012), and energy flow to higher trophic levels (Collie 1985; Mortensen et al. 1995). Potential ecosystem service losses related to the spill are of great concern (Danovaro et al. 2008; Montagna et al. 2013). Deep-sea biota are already at risk from oil and gas exploration, trawl fishing that destroys corals and bottom habitat, and eutrophication from agricultural run-off that creates algal blooms and oxygen depletion zones—and oil pollution exacerbates these stressors and decreases the resiliency of the system (Rogers 1999; Camilli et al. 2010; Diercks et al. 2010; Kessler et al. 2011; White et al. 2012; NRC 2012; Montagna et al. 2013).

Impacts of the Deepwater Horizon Oil Spill on Marine Invertebrates

Routes of Exposure

The Deepwater Horizon spill released oil at a greater depth (5,000 feet) and in a larger volume than ever seen in previous spills in U.S. history (National Commission 2011; NRC 2013). An aquatic life inventory done before the spill found 15,400 marine species in this Large Marine Ecosystem (Felder and Camp 2009) and the deep sea surrounding the location of the exploded well is characterized as being the most biodiverse region of the Gulf at depths of 1,000–3,000 meters (Felder and Camp 2009; Costello et al. 2010). Because the spill occurred during the spawning period for many Gulf animals, the oil-sensitive embryos and larvae of invertebrates are likely to have been especially impacted (Perry and McIlwain 1986; Guillory et al. 2001; Zimmerman et al. 2002; LDWF 2011), since they lack both mobility to avoid contaminated areas and the body mass and metabolic mechanisms to survive oil exposure (Brodersen et al. 1977; Peters et al. 1997; Negri and Heyward 2000; Cherr and Griffin 2001; Beiras and Saco-Álvarez 2006).

Oil also impacted organisms in offshore and coastal areas of the Gulf of Mexico (Graham et al. 2010; Allan et al. 2012; Bik et al. 2012; White et al. 2012). Because the spill occurred 40 miles off the coast of Louisiana, oil did not immediately wash ashore allowing data on many regional fauna to be collected before they were contacted by oil (NOAA NRDA 2012). Two distinct pathways for oil movement were identified: The smaller oil particles created by chemical dispersant use (0.78 million gallons Corexit® 9500), which sank and moved in the deep-sea currents (Camilli et al. 2010; National Commission 2010), and the surface slick that moved toward shore with wind and currents. Surface slicks were treated with over 1 million gallons of chemical dispersants (National Commission 2010; NOAA NRDA 2012). Chemical dispersants are toxic to marine invertebrates. Although the long-term impacts of dispersants used in the Deepwater Horizon oil spill have yet to be determined, Corexit® 9500 has been shown to inhibit settlement and survival of coral larvae in laboratory studies (Goodbody-Gringley et al. 2013) and could negatively impact coral reefs. Furthermore, laboratory studies have shown the addition of dispersant significantly increased the toxicity of oil to Gulf of Mexico phytoplankton communities (Ozhan and Bargu 2014). Because they are primary producers, impacts on phytoplankton communities also impact zooplankton that depend on them for food (Falk-Petersen et al. 2009; Chanton et al. 2012; Gilde and Pinckney 2012).

The path of oil movement was such that it may have impacted almost all habitats of the northern Gulf of Mexico from the deep sea through the water column to the shorelines and estuaries (Camilli et al. 2010; Graham et al. 2010; Barron 2012; Bik et al. 2012; Chanton et al. 2012; Lehr et al. 2010; Mendelssohn et al. 2012; Silliman et al. 2012; NOAA NRDA 2012; Montagna et al. 2013; Sammarco et al. 2013). The deep-sea oil plume was carried by slow-moving currents at a depth of about 3,600 feet (1,100 m) southwest of the blowout site (Camilli et al. 2010). Efforts to plug the well resulted in the deposition of drilling mud on the ocean floor, which contributed to the overall environmental impacts in the deep sea (Neff et al. 1987; Kennicutt et al. 1996; UAC 2010). Multiple inputs of oil, drilling mud, and dispersants pose significant threats to the deepwater corals, tube worms, small burrowing benthic invertebrates, and bivalves that thrive in this environment (Peterson et al. 1996; Cordes et al. 2006; Cordes et al. 2008; White et al. 2012; Montagna et al. 2013). The spill eventually reached the nearshore habitats of the northern Gulf of Mexico, oiling nearly 1,100 linear miles of shoreline in Texas, Louisiana, Mississippi, Alabama and Florida. Some 220 miles of shoreline were heavily oiled and 140 miles moderately oiled, with the remaining shorelines lightly oiled and/or continuing to receive tar balls (DeLaune and Wright 2011; OSAT 2011; Bik et al. 2012; Mendelssohn et al. 2012; NOAA NRDA 2012; Silliman et al. 2012; NRC 2013).

The Gulf's coastal waters support many commercial shrimp, crab, and oyster fisheries, and the submerged aquatic vegetation in estuaries, such as eelgrass beds, is essential habitat for juvenile and adult shellfish (Gunter 1967; Zimmerman et al. 2002; Glancy et al. 2003; Lellis-Dibble et al. 2008; Brown 2012; NOAA NRDA 2012). Shellfish spawned during the spill period and the oil slick covered a significant portion of their spawning grounds. Consequently, crabs, shrimp, and oysters were exposed



The coast of the Gulf of Mexico includes a diversity of wetlands and other sensitive habitats. In the weeks after the collapse of the Deepwater Horizon rig, oil contaminated many hundreds of miles of intertidal areas. (Photograph: NOAA Photo Library.)



Extensive clean up was necessary on beaches and other intertidal areas in the months following the Deepwater Horizon blowout. Booms made out of plastic pom-poms line the sand at Fourchon Beach, Louisiana. (Photograph: NOAA Photo Library.)

to oil at all life stages (Perry and McIlwain 1986; Guillory et al. 2001; Zimmerman et al. 2002; LDWF 2011; NOAA NRDA 2012; Sammarco et al. 2013). Coastal oiling killed mussels and snails in Louisiana saltmarshes (NOAA NRDA 2012; NRC 2012; Silliman et al. 2012). The eggs and larvae released from shallow water coral reefs off the coasts of Florida and Texas during spawning were also threatened.

The most acutely damaged coastal areas were the marshes, where oil was trapped in sediments and oiled vegetation died. These oiled saltmarshes also showed erosion rates more than twice that of unoiled marshes in the year after the spill creating concerns about permanent habitat loss in ecosystems already experiencing high rates of decline and degradation (Kennish 2002; Lotze et al. 2006; Blum and Roberts 2009; Waycott et al. 2009; DeLaune and Wright 2011; Gulf Coast Ecosystem Recovery Task Force 2011; Mendelssohn et al. 2012; NRC 2012; Peterson et al. 2012; Silliman et al. 2012). Sand beaches, barrier islands, tidal mud flats, and mangrove stands were oiled, threatening productive nearshore nursery grounds and intertidal species (NOAA NRDA 2012). Samples from crabs, shrimp, and oysters in contaminated marshes had PAH concentrations over 3,800 times higher than the U.S. Environmental Protection Agency's (EPA) acceptable threshold for human consumption. Sediment from Louisiana's Atchafalaya wetlands was contaminated with 18 different PAH compounds that exceeded EPA's screening levels, with impacts detected from June 2010 to at least March 2011 (EPA 2006; EPA 2011; Sammarco et al. 2013). Fishery closures in the Gulf after the spill affected 88,522 square miles of ocean, including over 36% of the Gulf of Mexico Exclusive Economic Zone (EEZ), a sea zone from the coast out to 200 nautical miles in which a state has special rights over exploration and use of marine resources. These closures resulted in a staggering loss of income, jobs, food, and recreational opportunities and impacted a fishing industry worth an estimated \$5.5 billion. Projected losses for commercial and recreational fisheries in the Gulf are an estimated \$147 million between 2011 and 2013 (IEM 2010; Upton 2011; NRC 2012; NMFS 2013a).

Invertebrate Taxa Impacted by the Deepwater Horizon Oil Spill

Research on the effects of the Deepwater Horizon oil spill focused mostly on the physical transport and flow rate of oil (Camilli et al. 2010; Crone and Tolstoy 2010; Hsieh 2010; Maltrud et al. 2010; McNutt et al. 2011, Socolofsky et al. 2011; Camilli et al. 2010; Carmichael et al. 2012a; reviewed in McNutt et al. 2012; Reddy et al. 2012; Ryerson et al. 2012), the microbial degradation of spilled oil (Adcroft et al. 2010; Hazen et al. 2010; Valentine et al. 2010; Joye et al. 2011; Kessler et al. 2011; Redmond and Valentine 2012; Valentine et al. 2012), and acute damages from the spill (Allan et al. 2012; Bik et al. 2012; NOAA NRDA 2012; Silliman et al. 2012; White et al. 2012).

Effects on local food webs or community-level responses were largely overlooked and remain difficult to measure (Machlis and McNutt 2010; Bik et al. 2012). An incomplete understanding of complex ecosystem interactions in the Gulf and the diversity of Gulf habitats made it difficult to know the true extent of damage following the spill (NOAA NRDA 2012), and elucidation of the entire range of impacts on invertebrates will require better understanding of ecosystem interactions and dedicated long-term studies.

Wildlife in the northern Gulf of Mexico was exposed to relatively fresh surface oil during the spill. Oil exposure continues from weathered oil still present in sediments of beaches, marshes, nearshore areas, and the deep sea (White et al. 2012; Bik et al. 2012; Carmichael et al. 2012a; Silliman et al. 2012; Montagna et al. 2013; Sammarco et al. 2013). Despite the disappearance of visible oil at some coastal sites, there were significant impacts on benthic ecosystems at coastal areas around Alabama and Louisiana. Communities that included the small arthropods, annelids, and nematodes that are important in food webs, nutrient cycling, and sediment stabilization were lost after the spill and apparently replaced by fungal taxa (Bik et al. 2012). Organisms in impacted Gulf habitats will likely continue to be affected by decreased disease resistance, reduced growth and reproduction, and slower population recovery (Teal and Howarth 1984; Livingstone 1998; Carls and Harris 2005; Culbertson et al. 2008; DeLaune and Wright 2011; Mendelssohn et al. 2012; NOAA NRDA 2012; Silliman et al. 2012). Economically important invertebrate fisheries may be most at risk from oil spill impacts because these relatively sessile benthic organisms can suffer increased exposure and higher rates of mortality compared to more mobile fish species (Teal and Howarth 1984; Meador 2003; Sammarco et al. 2013). The following sections address the effects of the Deepwater Horizon oil spill on these groups in detail.

Oysters

The eastern oyster (*Crassostrea virginica*) is a valuable component of coastal ecosystems along the northern Gulf of Mexico coast and was thus a focus for many studies on the effects of the Deepwater Horizon oil spill (Bahr and Lanier 1981; Beck et al. 2009; IEM 2010; Beck et al. 2011; Gulf Coast Ecosystem Recovery Task Force 2011; Upton 2011; NMFS 2012; NOAA NRDA 2012; NRC 2012). Oyster beds provide habitat, water filtration, and shoreline protection to coastal ecosystems, and Gulf oysters account for nearly two-thirds of the nation's oyster fishery (LDWF 2011; Upton 2011; EPA 2012; NMFS 2012). Louisiana is the national leader in oyster production with annual dockside sales of over \$35 million (LDWF 2011). In 2009, the Louisiana oyster fishery harvested approximately 14 million pounds (LDWF 2010). However, after the spill in 2010, the oyster harvest fell to an all-time low of 6.8 million pounds, partially due to fishery closures as a result of oil contamination and public health concerns (LDWF 2010, 2012).

Oil hydrocarbons can cause reproductive failure, immune suppression, and reduction in feeding and growth in oysters (Berthou et al. 1987; Auffret et al. 2004; Jeong and Cho 2007; Bado-Nilles et al. 2008; Croxton et al. 2012). Adult oysters are immobile and unable to avoid oil pollution, and their ex-

posure is increased as they accumulate contaminants in their soft tissues and via filter-feeding (Berthou et al. 1987; Jeong and Cho 2007; Meador 2003; Croxton et al. 2012; NOAA NRDA 2012). Planktonic eggs and larvae exposed to oil show impaired development and decreased recruitment of juveniles into oyster beds (Geffard et al. 2002a, 2002b; Gagnaire et al. 2006b; Choy et al. 2007). The timing of oyster spawning coincided with the Deepwater Horizon oil spill, and oyster beds and nearshore areas important for spawning in the northern Gulf were exposed as slicks moved ashore (Allan et al. 2012; NOAA NRDA 2012; Carmichael et al. 2012b; Sammarco et al. 2013). Mitigation responses in coastal areas further impacted oyster populations (Allan et al. 2012; Carmichael et al. 2012b; NOAA NRDA 2012). After the spill, fresh water from the Mississippi River was released into estuaries in an attempt to keep the oil from reaching coastal estuaries (LDWF 2011; Carmichael et al. 2012b; NOAA NRDA 2012). While these discharges may have kept some oil offshore, they also altered the pH and decreased the salinity in oyster habitats below tolerance levels and caused significant mortality (Gagnaire et al. 2006; LDWF 2011; Carmichael et al. 2012b; Dickinson et al. 2012). Although oyster health may be impacted by different cumulative events, including hypoxia and disease, direct and indirect effects of oil and oil response measures following the Deepwater Horizon oil spill is estimated to have contributed up to a 50% loss of Louisiana's annual oyster crop (LDWF 2011; Upton 2011).

Impacts to adult and larval oysters and reef habitats are still being assessed to understand effects of the Deepwater Horizon oil spill, including nutritional, reproductive, and immunological status of oysters from impacted sites (La Peyre et al. 2011; Casas et al. 2012; NOAA NRDA 2012). Deepwater Horizon Trustees (groups in charge of recovering damages from parties responsible for the spill) are



A trawl full of oysters collected for oil analysis. Following the Deepwater Horizon accident, extensive testing of shellfish was undertaken to ensure safety of the commercial fisheries. (Photograph: NOAA Photo Library.)

examining oysters at more than 150 sites from Louisiana to Florida and comparing the data to baseline data from pre-existing sampling programs (e.g., Mussel Watch) (Deepwater Horizon Trustee Early Restoration Plan 2012; NOAA NRDA 2012). Assessments include accumulation of contaminants in adult oysters; survival, biomass, and recruitment and settlement of juveniles in oyster beds; and larval abundance in water samples taken from spawning grounds (NOAA NRDA 2012). Closure of oyster harvest for much of the season in 2010 allowed the fishery to recover in 2011 and 2012, but recruitment failures continue to threaten the long-term health of the industry (LDWF 2012). Oyster stock assessments conducted after the spill showed a dramatic absence of seed oysters, suggesting a high incidence of larval mortality since the fall 2010 spawning period (LDWF 2011, 2012). The 2010, 2011, and 2012 stock assessments in Louisiana's primary oyster grounds yielded troubling evidence of reproductive failures (LDWF 2010, 2011, 2012). While a variety of environmental and anthropogenic stressors can affect the health and resilience of oysters and oyster reefs, the timing and magnitude of the observed decreases in oyster abundance, with 2012 numbers down 62% from 2011 and down 95% from the 2002–2011 10-year average, show the dramatic impact of the spill (LDWF 2012).

Blue Crabs

Blue crabs (*Callinectes sapidus*) are fundamental components of estuarine food webs in the Gulf of Mexico (Plotkin et al. 1993; Zimmerman et al. 2002; Wells et al. 2008) as well as the most economically important crab species for the region. In 2008, 41.6 million pounds of blue crabs were caught in the Gulf of Mexico, a harvest with a commercial value of \$39 million (Upton 2011). In 2011, Louisiana provided approximately 28% (55 million pounds) of the nation's blue crab landings, an increase of 34% from 2010 harvest levels when fisheries closed after the Deepwater Horizon spill (NMFS 2012). Gulf blue crabs are an estuarine-dependent species with an almost entirely coastal distribution (Perry and McIlwain 1986). This renders them good indicators of estuary health (Zimmerman et al. 2002; Gelpi et al. 2009). Different life stages inhabit planktonic, nektonic, and benthic habitats (Guillory et al. 2001; Rakocinski and McCall 2005), thus all life stages came in contact with oil in both nearshore estuaries as juveniles and as spawning adults in the Gulf of Mexico (Zimmerman et al. 2002; Rakocinski and McCall 2005; NOAA NRDA 2012).

Following the spill, a large portion of the offshore blue crab larval grounds in the northern Gulf received surface oiling (Perry et al. 2010; NOAA NRDA 2012; Sammarco et al. 2013). Oil droplets were found inside the shells of larval crabs from the Gulf raising concerns for both the developing crabs and the animals that feed on them. Final reports on this issue have not yet been published (Perry et al. 2011). Although some critical nursery habitat in local estuaries and marshes was impacted by oil (Mendelssohn et al. 2012; Silliman et al. 2012; Sammarco et al. 2013) there were no documented reports of blue crab die-offs (see NOAA NRDA 2012 impact assessment). It is thought that continuing exposure of larval crabs to surface and subsurface oil are likely to impact populations in the long-term (Lee 1975, 2013; Heck and Spitzer 2001) and oiled nursery habitat in the Mississippi Delta may also impact blue crab populations until the marshes recover (Mendelssohn et al. 2012; Silliman et al. 2012; Sammarco et al. 2013). A significant post-spill decline in blue crabs was observed in lightly oiled marshes in Alabama in 2010 but populations were reported to be recovered to pre-spill abundances in 2011 (Moody et al. 2013). Based on the extent of heavy oiling of both coastal and offshore habitats used by this species there is a significant threat for injuries to blue crab populations, which are vulnerable to loss of marsh nursery habitat and pollution (Perry and McIlwain 1986; Guillory et al. 2001; Zimmerman et al. 2002; Perry and Graham 2011; NOAA NRDA 2012; Sammarco et al. 2013).

Research is still underway on the impacts of the oil spill on these animals and much remains to be formally published from either the trustee assessment (NOAA NRDA 2012; Perry and Graham 2011) or

from independent scientific studies. Oil spill trustees, through the NOAA Natural Resources Damage Assessment (NOAA NRDA 2012) investigation, are conducting toxicity tests and monitoring larvae and egg-bearing females to determine the impact of oil on early life history stages of blue crabs. More work is needed on populations at a greater number of sites and at more heavily oiled sites over multiple years to understand impacts and recovery in other areas affected by the spill. Ongoing impacts of the Deepwater Horizon oil spill are likely to result in loss of recruitment that can threaten the sustainability of the blue crab fishery and the organisms that rely on them (Coglianese 2010; IEM 2010).

Shrimp

The Gulf of Mexico regional shrimp harvest is the largest in the U.S. Over 212 million pounds were harvested in 2011, representing 68% of the national total (NMFS 2012). The major commercial species in the Gulf of Mexico include brown, white, and pink shrimp, which account for \$130 million in revenue for Louisiana alone (IEM 2010; Upton 2011). Shrimp inhabit both coastal and offshore coastal areas within the Gulf during different phases of their life cycle, with the shallow waters of estuaries supporting commercially important species (Muncy 1984; Upton 2011; NOAA NRDA 2012). Impacts to the shrimp industry and economic health of the region as a consequence of the spill and closure of the fishery resulted in a harvest that decreased by 35.6 million pounds of shrimp in 2010 compared with 2009. This represents a 27% decrease relative to pre-spill levels (Upton 2011).

The Deepwater Horizon spill happened during spring spawning and at a time when juvenile shrimp move out into the Gulf (Muncy 1984; Flores-Coto et al. 2010; IEM 2010; Allan et al. 2012; NOAA NRDA 2012). Shrimp eggs carried offshore by ocean currents and larvae migrating towards the protective estuarine nursery grounds are likely to have encountered oil dissolved in the water column or in surface slicks (Flores-Coto et al. 2010; IEM 2010; Allan et al. 2012; NOAA NRDA 2012; Sammarco et al. 2013). Important nursery habitat for juvenile shrimp was impacted as the oil reached sensitive nearshore estuarine areas (Allan et al. 2012; NOAA NRDA 2012; Mendelssohn et al. 2012; Silliman et al. 2012; Sammarco et al. 2013). Oil-mediated damage to sensitive early life stages jeopardizes recruitment of shrimp the following year, affecting the entire population (IEM 2010).

The ability of coastal marsh habitats to trap oil hydrocarbons within sediments can extend exposure and recovery time frames by decades (Carls and Harris 2005; Culbertson et al. 2007; Culbertson et al. 2008; Mendelssohn et al. 2012), and oiling of Gulf marshes may impact the long-term health of estuarine-dependent shrimp species until the habitat recovers (Tunnell 2011). Toxicity testing on grass shrimp is planned as part of the NOAA Natural Resources Damage Assessment (NOAA NRDA 2012) to understand and quantify the extent of impacts due to exposure to Deepwater Horizon oil.

Shallow-Water and Mesophotic Coral Reefs

Mesophotic coral ecosystems (MCE) are extensions of shallow water corals that continue further into the depths of the ocean (Kahng et al. 2010). They are light-dependent coral communities in the deepest part of the photic zone (30–150 m depth; Lesser et al. 2009; Kahng et al. 2010). These ecosystems include both stony and soft corals as well as sponges, gastropods, bivalves, and other invertebrates (Hinderstein et al. 2010; Kahng et al. 2010). Isolated communities of shallow water and mesophotic corals occur in many areas of the continental shelf and outer edge of the continental slope of the Gulf of Mexico. The most extensive reefs in U.S. waters are off Texas and Florida and include the Florida Middle Grounds, Dry Tortugas, East and West Flower Garden Banks (FGB), Stetson Banks, and Sonnier Banks (Rezak et al. 1990; Sammarco et al. 2012). The Flower Garden Banks in the western Gulf of Mexico is a National

Marine Sanctuary that has been designated an environmental treasure; its shallow water and mesophotic reefs support a diverse assemblage of fishes, sponges, hydroids, sea whips, and many other marine invertebrates (Thompson et al. 1999; Kahng et al. 2010). The coral reefs protected in the sanctuary are the healthiest in the western hemisphere (Thompson et al. 1999). Despite its sanctuary status, the Flower Garden Banks co-exist with extensive oil and gas exploration and drilling in the northern Gulf of Mexico, placing them in ongoing jeopardy from oil spills (Craig 2010).

Coral reefs can be exposed to oil through smothering, contact with particles mixed into the water column and sediments, and through filter feeding activities. Such exposure can interfere with reproduction, metamorphosis, recruitment, or settlement processes (Johannes et al. 1972; Loya and Rinkevich 1979, 1980; Fadlallah 1983; Payne and Phillips 1985; IPIECA 1992; Guzmán and Holst 1993; Negri and Heyward 2000; Shigenaka 2001; Haapkylä et al. 2007; Shigenaka et al. 2010). The Flower Garden Banks are 300 miles from the Deepwater Horizon well, and surface oil did not appear to directly impact the sanctuary (NOAA NRDA 2012). However, coral embryos and larvae are planktonic and while it is unclear whether the surface oil or the deepwater plume impacted these

planktonic stages, which ultimately settle in the Flower Garden Banks and other reefs in the Gulf, it is likely that they were subjected to oil within the water column during their movement through Gulf currents (Edmunds et al. 2001; NOAA NRDA 2012). In fact, coral reef ecosystem health in the Gulf area is dependent upon connectivity of ocean currents and the dispersal of coral species from other Gulf reefs (Gittings et al. 1992; Lugo-Fernández et al. 2001; Sammarco et al. 2012), so exposure of some proportion of the juvenile population seems likely. Due to the sensitive nature of these ecosystems, the NOAA Natural Resources Damage Assessment (NOAA NRDA 2012) continues to look at possible exposure pathways and long-term impacts.

The chemical emulsifiers dispersed the oil over greater distances increasing both the potential for contact with corals (Loya and Rinkevich 1980; Haapkylä et al. 2007) and toxicity of exposure (Loya and Rinkevich 1980; Epstein et al. 2000; Goodbody-Gringley et al. 2013). Chemical dispersants are known to be toxic to some corals; larvae of the proposed endangered coral *Montastraea faveolata* showed complete mortality following exposure to Corexit® 9500 in laboratory tests, while exposure to oil plus Corexit® 9500 resulted in higher mortality than exposure to oil alone (91% vs. 80%) (Goodbody-Gringley et al. 2013). This study and others raise concerns that response methods involving dispersants could affect the health and survival of corals (Ballou et al. 1989; Guzmán et al. 1991; Negri and Heyward 2000; Ward et al. 2003; Goodbody-Gringley et al. 2013). Research on the impacts of the Deepwater Horizon oil spill is still in progress, while hundreds of tissue, water, oil and sediment samples collected in, and around, shallow and mesophotic coral are being evaluated (NOAA NRDA 2012). As coral reefs continue to be lost globally, protecting these communities from additional stressors is important to the long-term health of coral reefs and the local economies they sustain (IPIECA 1992; Sebens 1994; Brown 1997; Pandolfi et al. 2003; Chabanet et al. 2005).



The Flower Garden Banks National Marine Sanctuary in the Gulf of Mexico encompasses the healthiest coral reef communities in the Americas. (Photograph: NOAA Photo Library.)

Plankton

Planktonic invertebrates were exposed to oil from the broken wellhead that mixed with ocean water and passed through the water column up to the surface (Camilli et al. 2010; Diercks et al. 2010; Graham et al. 2010; Chanton et al. 2012). Immediately following the spill, phytoplankton were impacted both by direct exposure to oil and by a loss of energy for photosynthesis, since the resulting slick reduced sunlight penetration into the water (NOAA NRDA 2012). Because phytoplankton are consumed by zooplankton, zooplankton may have suffered from loss of food in addition to the direct toxicity of oil exposure (Graham et al. 2010; Chanton et al. 2012; Gilde and Pinckney 2012; NOAA NRDA 2012; Ozhan and Bargu 2014). Oil was present in such high concentrations in surface and subsurface waters after the Deepwater Horizon spill that it was rapidly taken up by zooplankton (Diercks et al. 2010; Allan et al. 2012). Oil persisted in these organisms, as the isotopic signatures of the Deepwater Horizon oil could be detected against background levels in samples taken from June 2010 to May 2011 (Graham et al. 2010; Chanton et al. 2012). Moreover, mesozooplankton (>200 μm size) collected in 2010 in the northern Gulf of Mexico system showed evidence of exposure to PAHs from the Deepwater Horizon oil spill (Mitra et al. 2012).

Many studies have shown that oil, especially the PAH components, is acutely toxic to plankton and can alter swimming ability, reproduction, and affect respiration (Johansson et al. 1980; Samain et al. 1980; Guzmán del Prío et al. 1986; Mathews et al. 1993; Price et al. 1993; Price et al. 1994; Bellas and Thor 2007; Saiz et al. 2009; Seuront 2011; Bellas et al. 2013; Grenvald et al. 2013). Many of the Gulf's commercially important benthic species, such as blue crab and shrimp (Muncy 1984; Perry and McIlwain 1986; Heck and Spitzer 2001; Flores-Coto et al. 2010), have planktonic larvae, and the damaging effects of the oil spill on these specific components of the plankton have already been discussed.

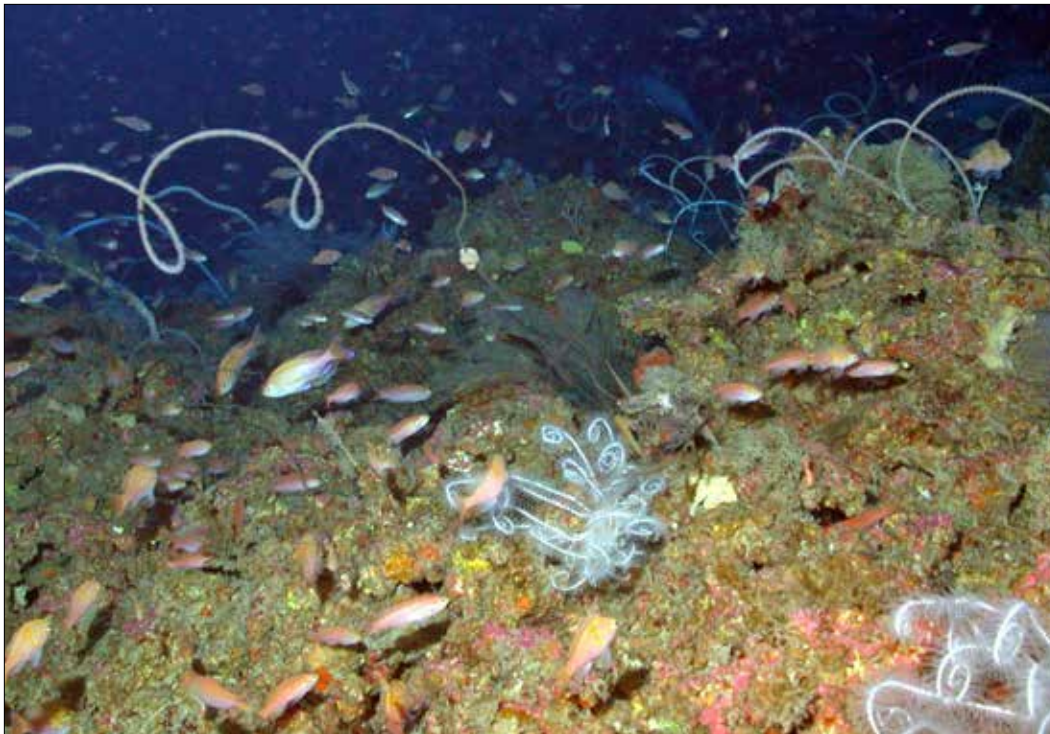
Multiple food web alterations were likely following the spill, as plankton are central components of coastal and offshore food webs (Turner 1984; Turner 1986; Turner and Roff 1993; Turner 2004) and help sustain commercially important fisheries in the Gulf of Mexico (Stoecker and Govoni 1984; Guillory et al. 2001; McCawley et al. 2003; Wells et al. 2008). The microbial, phytoplankton, and zooplankton communities exposed to Deepwater Horizon oil underwent rapid changes. As a result, phytoplankton may have been temporarily enhanced in the northern Gulf of Mexico due to loss of predatory pressure from zooplankton consumers (Abbriano et al. 2011). Studies of radiocarbon isotopes from the Deepwater Horizon well oil in the coastal and offshore planktonic food webs of the northern Gulf of Mexico suggest that oil compounds were transferred by microbial consumers to zooplankton (Graham et al. 2010; Chanton et al. 2012). Zooplankton are important food for early life stages of foraging fishes, crab, and shrimp, and their population declines may have impacted food availability for these groups (Stoecker and Govoni 1984; Guillory et al. 2001; Szedlmayer and Lee 2004). The bioaccumulation of PAHs could transfer contaminant to higher trophic levels (Stegeman and Lech 1991; Fisk et al. 2001; Wan et al. 2007; Hallanger et al. 2011; Almeda et al. 2013).

Zooplankton may be able to excrete PAHs within a period of days (Berrojalbiz et al. 2009) and a review by Abbriano et al. (2011) on the plankton response following the Deepwater Horizon oil spill suggests that, given their high reproductive capacity and short generation times, zooplankton may not show significant damages from oil pollution. However, PAHs were found in zooplankton collected in August and early September 2010, weeks after the Deepwater Horizon well was finally capped in mid-July (Mitra et al. 2012). Considering the rapid turnover rate of zooplankton populations in the Gulf's warm waters, this suggests that PAHs persisted in the environment even after oil stopped flowing from the well and/or that adult zooplankton transferred accumulated PAHs to subsequent generations (Mitra et al. 2012). Long-term effects on plankton may be difficult to detect and can be masked by the large degree of natural variability in plankton populations and the effects of ocean processes and climate on their distribution (Richardson and Schoeman 2004; Runge et al. 2005; reviewed in Penela-Arenaz

et al. 2009; Letessier et al. 2011; Grenvald et al. 2013). However, existing research indicates that zooplankton experience acute and chronic impacts from oil spills and that populations require long-term studies to understand the full magnitude of the damage (Samain et al. 1980; Fisk et al. 2001; Guzmán del Prío et al. 1986; Pelletier et al. 1997; Fernandez et al. 2006b; Lee et al. 2012; Almeda et al. 2013; Bellas et al. 2013; Goodbody-Gringley et al. 2013). It is not yet known whether bioaccumulation and transfer of contaminants to higher trophic levels will affect organisms in the long-term. Pre-spill data are being used as a reference point to understand the effects of oil and determine if impacts at the plankton level will affect the health of commercially important species in the next several years (NOAA NRDA 2012).

Deep-Sea Invertebrates

The deep sea is the largest biome in the Gulf of Mexico, but the difficulty of access makes it the most understudied region of the world's oceans (Thistle 2003; NRC 2012). The deep-sea ecosystem supports a diverse fauna (Grassle 1991; Jensen and Frederiksen 1992; Brooke and Schroeder 2007; Haedrich et al. 2008; German et al. 2011) whose health is critical to countless ecologically and commercially important species in the region. Deep-sea organisms provide a large amount of biomass (Grassle and Maciolek 1992; Wei et al. 2012), and deepwater corals create essential habitat for other invertebrates including mollusks, sponges, tube worms and other polychaetes, and crustaceans (Kennicutt et al. 1988; Pequegnat et al. 1990; Brooke and Schroeder 2007; Fisher et al. 2007; Cordes et al. 2008). These organisms contribute to sediment bioturbation and stabilization, as well as organic matter decomposition (Dahl 1979; Soliman 2007; Duffy et al. 2012). They also provide energy to higher trophic levels (Collie 1985; Mortensen et al. 1995).



The diversity of life in deep-sea environments is greatly understudied. Corals provide essential habitat for fish and many other inhabitants. (Photograph: NOAA Photo Library, NURC/UNCW and NOAA/FGBNMS.)



Deepwater invertebrates such as these mussels and tube worms are threatened by not only the oil released by the Deepwater Horizon well blowout but also spilled drilling mud and dispersant chemicals. (Photograph: NOAA Photo Library, Aquapix and Expedition to the Deep Slope 2007.)

Limited baseline data on organisms in deep-sea benthic habitats in the Gulf was gathered through a project affiliated with the Census of Marine Life to assess deepwater communities prior to oil exploration in the deep sea. Unfortunately, no such surveys had been done around the Deepwater Horizon well site prior to the spill (Rowe and Kennicutt 2008; Knowlton et al. 2010; Snelgrove 2010). The deep sea at depths of 1,000 to 3,000 meters (3,280 to 9,842 feet) is characterized as being one of the most biodiverse regions of the Gulf, and with the Deepwater Horizon well located at 1,525 meters, there is the potential for ecosystem service losses in the deep sea near the blowout site (Snelgrove et al. 1997; Rogers 1999; Rogers 2004; Fisher et al. 2007; Felder and Camp 2009; NRC 2012, 2013).

The deep-sea habitat around the exploded well was affected not only by oil but also by response efforts that resulted in the deposition of drilling mud on the ocean floor and introduced chemical dispersants (Neff et al. 1987; Kennicutt et al. 1996; NRC 2003; UAC 2010). These contaminants may pose significant threats to the health of the deepwater corals, tube worms, benthic amphipods, and bivalves (Peterson et al. 1996; Cordes et al. 2006; Cordes et al. 2008; Soliman and Wicksten 2007; White et al. 2012; Montagna et al. 2013). However, lack of knowledge of the species diversity, population abundances, and the full range of ecosystem functions they provide makes it difficult to completely assess impacts of large releases of oil on these systems, especially when it occurs at such great depth (NOAA NRDA 2012; NRC 2012; Wei et al. 2012).

The scale of the Deepwater Horizon spill and depth of oil release render it a unique and relatively uninvestigated category of oil spill (National Commission 2011; NOAA NRDA 2012). Analysis of the fate of hydrocarbons in the oil plume from the blowout indicate that the increased dissolution as oil

under pressure moved from a depth of 1,100 meters through the water column resulted in the appearance of high levels of toxic PAHs in subsurface waters (Camilli et al. 2010; Diercks et al. 2010). Direct movement of oil into deep-sea ecosystems and bottom sediments has been confirmed: oil trapped within a subsurface plume entered deepwater sediments by multiple pathways including direct sinking, adsorption onto water column particles and drilling mud from the capping of the well, and incorporation into zooplankton fecal pellets that subsequently sank (Camilli et al. 2010; UAC 2010; Lee et al. 2012; Lee 2013; Montagna et al. 2013). The full extent of impacts and risks to marine invertebrates at these depths, however, remain unknown (Camilli et al. 2010; White et al. 2012; Montagna et al. 2013). Oil binding to sediments in these cold waters will be available in essentially unchanged form to deepwater organisms and may persist for many years (NRC 2003; Camilli et al. 2010; White et al. 2012; Montagna et al. 2013). Oil weathering through biodegradation by microorganisms is less well known for the deep sea compared with shallow marine systems. Due to the presence of natural seeps, petroleum-degrading microbes are ubiquitous in the Gulf (Redmond and Valentine 2012; Valentine et al. 2010; Valentine et al. 2012). Although the number of microbes increased in the wake of the Deepwater Horizon spill and oil biodegradation was detected within a deepwater plume, the amount of oil released was more than double the rate contributed by natural seeps, vastly exceeding microbial oxidation capacities (Adcroft et al. 2010; Camilli et al. 2010; Diercks et al. 2010; Hazen et al. 2010; Valentine et al. 2010; Edwards et al. 2011; Joye et al. 2011; Kessler et al. 2011; Redmond and Valentine 2012; Valentine et al. 2012).

Potential impacts of oiling on deepwater communities include physical smothering, exposure through the food web (uptake of oiled plankton, detritus), settlement of particle-bound oil droplets to the benthos, and oxygen depletion (hypoxia) in bottom waters due to the increased oxygen demand from oil-metabolizing bacteria (NRC 2003; Adcroft et al. 2010; Lehr et al. 2010; Kessler et al. 2011; White et al. 2012; Wei et al. 2012; Montagna et al. 2013). Changes as a result of hypoxia include reduced species diversity and an overall community shift as more tolerant nematode and annelid worms replace less tolerant echinoderms and crustaceans (Levin 2003; Levin and Sibuet 2012). Recent work has documented reductions in deep-sea benthos that correlate with sediment PAH concentrations (Montagna et al. 2013). Significant reductions in faunal abundance and diversity were observed 3 km from the blow-out location in all directions, covering an area 24 km², and moderate reductions in diversity were seen up to 8.5 km to the northeast and 17 km to the southwest, with diversity increasing with increased distance from the well. Tolerant and opportunistic nematodes were also found in high abundance as more sensitive benthic species were lost (Montagna et al. 2013). It is unknown how long these communities will take to recover, but earlier work indicates that recolonization of deep-sea benthos can take several years or longer (Grassle 1977).

Given the magnitude and depth of the Deepwater Horizon oil spill, damage to deepwater coral reefs is a major concern (NRC 2012; White et al. 2012). Deepwater coral communities may be indicators of oil pollution impacts because even if no direct hydrocarbon deposition occurs on the reefs, corals filter and trap particulate material from the water. In the case of deep-sea hard-bottom coral communities, very little historical image data are available and the location and composition of many of these communities is unknown. Limited visual observations at these depths found that at least one deep-sea coral community has been impacted by the oil spill and showed signs of recent damage. The oil covering these communities was confirmed to be from the Deepwater Horizon oil well (White et al. 2012). Impacts of oil spills to deepwater communities are difficult to document because of the depth of these communities and because each spill presents a unique set of physical, chemical, and biological conditions. However, recovery of some deepwater species such as black corals may take decades to centuries due to their slow growth and the extreme age of many of these animals (Prouty et al. 2011; Wagner et al. 2012). Damages to the ecosystem services and natural resources of the Gulf's deep sea are a real and grave consequence of the spill that may threaten the long-term health of the region (Danovaro et al. 2008; Joye and MacDonald 2010; NRC 2012; White et al. 2012; Wei et al. 2012; Montagna et al. 2013).

Data Gaps and Continuing Research Needs

Although they comprise over 95% of all marine animals and populate a huge variety of habitats, marine invertebrates are much less well-known than the vertebrates that rely on them for food and shelter. Invertebrates of economic importance such as some crustaceans, mollusks, and echinoderms have been better studied, but these represent only a tiny proportion of more than 150,000 described marine invertebrate species, leaving enormous gaps in our knowledge (Collen et al. 2012). The damage assessment for the Deepwater Horizon oil spill is the largest ever conducted. Given its scope and ecological complexity, studies of impacts, recovery rates, and changes in ecosystem services may continue for years. Long-term impacts from the Deepwater Horizon oil spill on marine ecosystems are not yet known and the conclusions of the Natural Resource Damage Assessment conducted by oil spill trustees are not expected for several years (NOAA NRDA 2012). Unfortunately, in the absence of historical or baseline data on multiple species and ecosystems, it is difficult to fully understand the immediate and long-term impacts of oil spills on this productive and diverse invertebrate fauna.

Few studies have documented long-term impacts of oil spills and dispersants on invertebrate populations and more research is needed to fully understand the impacts of oil on marine invertebrates in multiple habitats. The large numbers of organisms in the plankton, combined with their rapid turnover time, has led some investigators to conclude that oil impacts on this fauna will be short lived. However, because so many marine animals rely on plankton for food, and because much of the zooplankton is comprised of sensitive early life stages of benthic marine invertebrates, such blanket statements are unjustified. The long-term effects of oil spills on planktonic invertebrates are relatively unknown because current studies are often limited in frequency and scope and usually only started immediately after a spill. Compounding this, such studies are often discontinued as soon as plankton populations appear to show any recovery. Research has shown that oil from the Deepwater Horizon spill was transferred to zooplankton (Graham et al. 2010; Chanton et al. 2012), and modeling is being done to further evaluate the transport of oil through the food chain and impacts on marine organisms (NOAA NRDA 2012; NRC 2013).

More data is needed on the impacts of oil spills on benthic invertebrates, especially filter-feeding organisms such as shellfish. These animals are not only affected immediately by oiling and smothering but also by chronic exposure from oiled sediments that may continue for decades. Toxicity testing on species such as shrimp, blue crab, eastern oyster, and fiddler crab will be done under NOAA's Natural Resources Damage Assessment. The comprehensive testing will include the effects of exposure to oil droplets and oiled sediment, the effects of ingesting oil-contaminated food particles or prey animals, and the relative toxicities of oil and chemical dispersants (Hemmer et al. 2010; 2011; NOAA NRDA 2012; NRC 2013). Response metrics being examined include survival, growth, reproduction, development, tissue damage, gene expression, immunological responses, and behavior, with special attention to sensitive early life stages and/or spawning adults (Hemmer et al. 2010; 2011; NOAA NRDA 2012; Perry et al. 2011). Nearshore shallow water corals are another understudied group and, given their ecological importance and sensitivity, further investigation of these organisms and the communities they sustain is needed.

Direct movement of oil into deep-sea ecosystems and bottom sediments has been confirmed but the full extent of impacts and risks to marine invertebrates at these depths remains unknown (Camilli et al. 2010; White et al. 2012; Montagna et al. 2013). Negative impacts of oil deposited on the seafloor have been demonstrated for deep-sea corals and benthic invertebrates (White et al. 2012; Montagna et al. 2013) and further studies on the impacts to deep-sea corals will continue under the NOAA Natural Resources Damage Assessment (NOAA NRDA 2012). Studies on the effects of oil spills on deep-sea ecosystems are hampered by our continuing lack of knowledge about a large proportion of the biota in



Sediment samples were gathered after the Deepwater Horizon spill to measure contamination levels. Long-term monitoring is required to understand the ongoing impacts to shellfish from exposure to oil in sediment. (Photograph: NOAA Photo Library.)

these habitats. Great strides have been made in deep-sea investigations of marine life, but an increased effort to census the biodiversity of deep-sea benthic environments, especially deepwater corals, is needed to realistically evaluate the impacts of oil spills (Rogers 1999, 2004; Cordes et al. 2008; Sulak et al. 2008; Becker et al. 2009; Felder and Camp 2009; NRC 2012, 2013).

Many questions remain about the acute and sublethal effects associated with oil cleanup and mitigation response and the recovery of marine invertebrates and their habitat following response efforts (Fingas 2013; NRC 2013). A significant unknown aspect of the Deepwater Horizon spill is the impact of chemical dispersants introduced at the unprecedented depth of 1,500 m into an ecosystem whose biota is little-known (NRC 2012; NRC 2013). More long-term research is required to understand the impacts of dispersants and other response methods that can result in increased toxicity to marine organisms (NRC 2005; Fingas 2013; NRC 2013) in order to realistically evaluate the relative risks and environmental trade-offs of mitigation activities (Fingas 2013) and develop response plans that weigh the net environmental benefits and risks to marine invertebrates and ecosystems (Sell et al. 1995; NRC 2005; NRC 2012; NRC 2013). Risk assessments should consider the effects of a variety of factors on invertebrate populations, including the type of oil spilled; the rate of oil release; seasonal, meteorological, and oceanographic conditions; the life stage of exposed fauna and their mobility within the habitat; the type of habitat and substratum; and the response and mitigation activities implemented (NRC 2003; Peterson et al. 2003b; NRC 2005; NRC 2012; Fingas 2013).

Part 4

Marine Invertebrates at Risk in the Gulf of Mexico

Despite the fact that invertebrates dominate global ecosystems, comprise nearly 80% of all known multicellular species on Earth, and perform a host of integral roles in all ecosystems, the vast majority are poorly described and studied. We currently know the status of less than 1% of described invertebrate species, and of those species whose status is known, one in five is thought to be at risk of extinction (Collen et al. 2012). These numbers are alarming and point to a glaring need for additional research and careful consideration of these animals in conservation planning.

Marine invertebrates represent over 95% of all marine animals and populate a huge variety of habitats from shallow-water coral reefs to deep-sea chemosynthetic vents and abyssal plains. Despite this, they are even less well understood than their terrestrial counterparts. Observing and inventorying marine life poses numerous unique challenges to researchers and most studies tend to focus on the larger, more charismatic species. Regions that are especially difficult to access, such as deep-sea ecosystems, are in particular need of assessment.

Widespread threats from climate change, exploitation, habitat degradation, and other natural and anthropogenic sources are increasingly putting marine invertebrates at risk, although the full extent of these impacts on marine communities are largely unknown. Comprehensive species assessments are vital to understanding the status and conservation needs of many of these animals, and the current paucity of data poses real challenges to researchers and managers who would include these species in conservation efforts. To address some of these needs, the status of 1,306 marine invertebrates has been evaluated using the International Union for Conservation of Nature's (IUCN) Red List criteria. Approximately one quarter of these species is threatened with extinction (Collen et al. 2012). However, given the fact that there are over 150,000 described marine invertebrates (Collen et al. 2012) enormous gaps in our knowledge remain.

Prior to the year 2000, the majority of species on the IUCN Red List were terrestrial and less than 1% of species were marine. To address the critical need to assess the status of marine species, the IUCN created the Global Marine Species Assessment in 2005, which was subsequently formalized as the Marine Biodiversity Unit of the IUCN Global Species Programme. By April 2013, the Marine Biodiversity Unit had assessed over 11,000 species, including global populations of invertebrates such as reef-building corals and bivalves, commercial sea cucumbers, and cone snails. A regional initiative between the IUCN and the Harte Research Institute (HRI) is helping to ensure that Red List assessments are completed for selected Gulf of Mexico invertebrates.

The Gulf of Mexico is the ninth largest body of water in the world and one of the planet's most biodiverse marine water bodies, supporting a documented 15,419 species (Felder and Camp 2009). Ten percent of these species are endemic and are found nowhere else on Earth (Campagna et al. 2011). One reason for the Gulf's remarkable species diversity is its great variety of ecosystems. The Gulf's coastline includes more than 1,600 miles of U.S. shoreline. Within this distance are over 50% of the United States' continental wetlands. These include lagoons, estuaries, shallow-water coral reefs, seagrass meadows, and almost all the country's remaining mangrove habitats. (One of the largest mangrove swamps in



The Gulf of Mexico is one of the planet's most diverse marine regions. Over 15,000 species are known to live there. Corals, such as the federally protected staghorn coral (*Acropora cervicornis*) shown here, are some of the most imperiled marine species. (Photograph: Albert Kok, Wikimedia Commons.)

the world is on Florida's southwest coast.) Beyond the coastline, the ocean floor is a patchwork of sea-mounts, deep-sea coral-sponge communities, expansive sandy plains, and natural hydrocarbon vents. Perhaps surprisingly, this biodiversity coexists with major U.S. industries, including commercial fisheries (85% of all shrimp harvests and 60% of all oysters in the U.S.) and over 4,500 oil and gas platforms. The Flower Garden Banks National Marine Sanctuary, which boasts one of the healthiest reefs in the world, is ringed by oil and gas production platforms.

This coexistence is not necessarily a happy one. Corals are some of the most imperiled marine invertebrates documented in the Gulf, with two species currently protected under the Endangered Species Act (ESA). Seven additional Gulf coral species have recently been proposed as endangered or threatened under the ESA and their status is currently being reviewed by the National Marine Fisheries Service (NMFS). All nine of these corals have been identified as critically endangered, endangered, or vulnerable by the IUCN (Campagna et al. 2011; see Appendix I). Ivory tree coral (*Oculina varicosa*), a deep water coral found throughout the Gulf, has also been classified as vulnerable by the IUCN. Eleven additional coral species that occur in the Gulf of Mexico have been classified as critically imperiled or imperiled in the state of Florida (NatureServe 2013; see Appendix I). Coral reefs are some of the most productive, diverse ecosystems on the planet and their loss threatens the existence of hundreds of species that rely on their services. In Florida alone, 110 coral reef-associated species have been identified as being in great need of conservation, more than 100 of which are found in the Gulf of Mexico (FFWCC 2011a, see Appendix II).

In addition to corals, major groups of conservation concern in the Gulf of Mexico include mollusks, echinoderms (sea urchins and sea cucumbers), sponges, and crustaceans. The queen conch, a long over-harvested species with plummeting populations in some regions, is a federal candidate species and is protected under the Convention on International Trade in Endangered Species (CITES). Other potentially imperiled species include eastern oysters and the Florida cone snail. Oyster reefs are recognized as one of the most imperiled ecosystems in the world. The Gulf of Mexico supports the largest oyster harvest in the U.S. and careful management of this important resource will be vital in maintaining this status.

Given the sheer number and diversity of marine invertebrates in Gulf waters and the fact that so little is known about most of these species, it is extremely difficult to determine which species may be imperiled. Deep-water communities, including deep-water corals, worm- and mussel-associated cold seeps, and sponge gardens, are recognized as biodiversity hot spots (Bongiorni et al. 2010; Prouty et al. 2011; Quattrini et al. 2013) and yet we know relatively little about the ecology, distribution, or abundance of species in these communities. Deep-water coral assemblages, thought to be globally threatened (Rogers 2004; Schroeder et al. 2005; Brooke and Schroeder 2007), are especially fragile, slow-growing, and long-lived, and may be particularly at risk. Detailed studies on numerous marine invertebrate groups, including sea cucumbers, anemones, octocorals, and sponges, is a priority before their conservation needs can be fully understood and addressed.

The conservation status of these species of concern has come into greater question in the aftermath of the 2010 Deepwater Horizon oil well blowout. While numerous studies have emerged regarding

The structures built by corals provide feeding grounds and shelter for thousands of other species and support commercial fisheries. (Photograph: NOAA Photo Library, NURC/UNCW and NOAA/FGBNMS.)



the effects of the spill and subsequent restoration efforts on vertebrates, relatively little is known about its impacts on marine invertebrates. It is to be expected that some of the greatest impacts may be on long-lived and sessile species whose populations cannot rebound quickly or easily escape to other habitats. Now, four years after the spill, it appears that the effects of this spill may be worse for poorly known benthic and deep-sea organisms, such as deepwater corals, which may be thousands of years old (White et al. 2012).

Campagna et al. (2011) predicted that species identified as "endangered" or "vulnerable" by the IUCN may become even more threatened as a result of the oil blowout. Using this as a first step in understanding which invertebrates are most at risk from the spill, we have reviewed some of the most imperiled major marine taxonomic groups, community types, and species in the Gulf of Mexico, including details on their current conservation status, ecology, distribution, threats, and research needs. We begin by reviewing some of the most imperiled coral species in the Gulf of Mexico, including the two that are federally protected. Following this, we discuss several major marine taxonomic groups and community types that occur in the Gulf of Mexico that are known to be sensitive and may be priorities for conservation action. We conclude by outlining some of the major gaps in knowledge regarding these species and offer some recommendations for future research.

Corals

Coral reefs comprise some of the most biodiverse communities on the planet and have often been referred to as the rainforests of the sea. They provide habitat to a vast array of marine organisms and support up to nine million species (Mather 2013). Despite their global importance, coral reefs are in serious decline worldwide and represent one of the most endangered marine communities (Bellwood et al. 2004; Haapkylä et al. 2007). One-third of zooxanthellate (those containing dinoflagellate algal symbionts) reef-building corals are thought to be at risk of extinction, largely as a result of climate change (Carpenter et al. 2008; Collen et al. 2012). Climate change can cause severe fluctuations in temperature that lead to numerous harmful effects to corals, including bleaching, increased susceptibility to disease, increased severity of storms, and ocean acidification (IUCN 2013). Most coral reefs are also impacted by invasive species and a multitude of local anthropogenic threats, including over exploitation, pollution, nutrient enrichment from wastewater runoff, and destructive fishing practices. The combined effects of these have resulted in worldwide loss of reef structure and an impaired ability of these ecosystems to sustain complex ecological interactions (Carpenter et al. 2008).

An analysis of the state of coral reef ecosystems in the United States and the Freely Associated States (FAS) in the Pacific (which include the Republic of Palau, the Federated States of Micronesia, and the Republic of the Marshall Islands) determined that approximately half of all coral reef ecosystems under U.S. or FAS jurisdiction are considered to be in 'poor' or 'fair' condition and have declined over time due to both natural and anthropogenic threats (Waddell and Clarke 2008). Reefs in the Gulf have been particularly devastated in recent years by a number of impacts, including global warming, coastal development, invasive species, overharvesting, harmful tourism activities, and the removal of key herbivores such as sea urchins. The majority of key resources (such as water quality, living coral cover, and reef fish populations) in this region were reported to be in poor or fair condition (Waddell and Clarke 2008). Indeed, the last three decades have seen unprecedented declines in coral reef cover from disease outbreaks, large tropical storms, and the loss of major algal consumers, leading to massive ecological shifts in reef structure and function that have ultimately turned coral-dominated reefs into reefs dominated by macroalgae (Gardner et al. 2003; Bellwood et al. 2004; Hughes et al. 2010; DeBose et al. 2013).

The combined effects of all these impacts, and the continued downward trend of many coral reef

populations, are troubling. The Gulf of Mexico alone is home to sixty reef-building corals that provide important habitat and resources to hundreds of other invertebrate and fish species. The IUCN recently assessed all sixty of these species and found ten to be threatened or near threatened (Campagna et al. 2011), including two federally protected species of *Acropora*. Dramatic population declines over the last 30 years for all ten species led to a petition to list 83 species of corals as threatened or endangered under the ESA (CBD 2009). In February 2010, NMFS issued a Notice of 90-Day Finding: Petition to List 83 Species of Corals as Threatened or Endangered under the ESA (NOAA 2010). It determined 82 of the 83 species petitioned warranted formal review, including nine of the species that are found in the Gulf of Mexico. All nine of these species were subsequently proposed for listing as threatened or endangered under the ESA by the NMFS. A final decision is expected in June 2014 (NOAA 2013a).

Below, we profile ten coral species that are particularly at risk in the Gulf of Mexico. These species have been organized alphabetically by family and include the two federally protected species and the seven proposed species. Each profile includes the conservation and taxonomic status, distribution, habitat, ecology, population trends, and threats. (For more extensive profiles of each of the listed/proposed species see NOAA's Status Review Report [Brainard et al. 2011].) We provide conservation statuses according to six different entities, including NatureServe, the Endangered Species Act, the IUCN Red List, CITES, and the Florida Fish and Wildlife Conservation Commission (FFWCC).

Family Acroporidae

Acropora is the most abundant and species-rich genus of corals in the world (Bruckner and Hourigan 2000). Out of more than 110 species of *Acropora* worldwide, only three (*A. palmata*, *A. cervicornis*, and *A. prolifera*) exist in the Gulf of Mexico and Caribbean region (Felder and Camp 2009). Two of these species, elkhorn coral (*A. palmata*) and staghorn coral (*A. cervicornis*), dominate coral reef ecosystems in the Caribbean, favoring warm, shallow water and providing most of the three dimensional structure on these reefs. These ecosystem giants are important biogenic habitat for many species of fish and invertebrates. Since the 1970s these two species have experienced catastrophic population declines (Bellwood et al. 2004; CBD 2004; ABRT 2005; Kappel 2005) due to the combined effects of disease, thermally induced bleaching, predation, competition, storm damage, and anthropogenic activities. The number of obligate species that depend on these corals is unknown, as is the extent of biodiversity loss that would result from their extinction. Their decline, however, has already had major ecological impacts on shallow-water reef communities in the region (Carpenter et al. 2008).

Caribbean acroporid corals are especially sensitive to cold water, which has likely limited their distribution in the Gulf of Mexico. However, the influence of the warm Loop Current, which enters the Gulf of Mexico from the south and follows an intense clockwise flow, has allowed several reef-building species to extend northward. In 2003, Zimmer et al. (2006) discovered a colony of elkhorn coral at the West Flower Garden Bank in 21.6 m of water. Two years later, they found another colony at the East Flower Garden Bank at a depth of 23.5 m, the deepest record for this species in the Caribbean and western Atlantic region. The discovery of these species so far north from their previously known ranges has led Precht and Aronson (2004) to suggest staghorn and elkhorn coral are expanding their ranges up the coast of Florida and into the northern Gulf of Mexico as a result of rising sea temperatures.

While the newly discovered populations of elkhorn coral in the northern Gulf appear to be healthy, devastating declines of both elkhorn and staghorn corals throughout the Caribbean and Florida prompted their listing as threatened species under the Endangered Species Act on May 9, 2006 (NOAA 2008a). NMFS has recently proposed a rule to reclassify these species as endangered due to ongoing threats and population declines (NOAA 2012a).

Elkhorn coral, *Acropora palmata*

CONSERVATION STATUS

U.S. Endangered Species Act: threatened (5/9/2006); proposed endangered

FFWCC List: Biologically vulnerable

U.S. State: NatureServe, S1 Critically imperiled (Florida)

NatureServe (global): G3 Vulnerable

IUCN Red List: Critically endangered

CITES: Appendix II

In a recent ESA report to Congress (NOAA 2013b), the status of this species was reviewed and shown to still be declining. It has been given a recovery priority number of 3 out of 10 (1 being the highest priority). However, a recovery plan for this species is still under development. In December 2012, NMFS proposed that this species be reclassified from threatened to endangered. Determinations are pending, and a final listing is expected in June 2014.



Elkhorn coral (*Acropora palmata*). (Photograph: Paul Asman and Jill Lenoble, Wikimedia Commons; Creative Commons 2.0.)

Critical Habitat

In November 2008, NMFS designated critical habitat for both elkhorn and staghorn coral at four sites in the Caribbean and off the south coast of Florida including the Florida Keys and the Dry Tortugas.

Protected Areas and Conservation Actions

In the Gulf of Mexico, this species is present in several MPAs, including the Florida Keys National Marine Sanctuary, Dry Tortugas National Park, and Flower Garden Banks National Marine Sanctuary. The Florida Keys National Marine Sanctuary has developed a coral management plan that includes zoning and channel markings for sensitive species and targeted restoration efforts (NOAA 2013b). The recently discovered colonies of elkhorn coral in the East and West Flower Garden Banks are not currently included in the elkhorn critical habitat areas described by NOAA (2008b) and should be considered for inclusion.

Research Needs

More information is needed to assist the recovery of acroporids. This includes research into reproductive biology, disease etiology, gene flow and genetic diversity, linkages between declines and natural versus anthropogenic disturbances, and effectiveness of restoration strategies (Bruckner 2002; Aronson et al. 2008b). Given the recent discovery of elkhorn coral in the northern Gulf of Mexico, studies could also investigate long-distance dispersal and migration of larvae and the potential of deeper colonies to serve as a refuge for the species (Zimmer et al. 2006). The overall health and vulnerability of these northern colonies should also be addressed given the decline of this species in the Caribbean and Florida.

DESCRIPTION AND TAXONOMIC STATUS

Taxonomic issues: None

Elkhorn coral is the largest of all species of *Acropora* (NOAA 2008a). Colonies are structurally

complex and individuals are characterized by many large, antler-like branches.

DISTRIBUTION

Elkhorn coral is widespread but restricted to shallow tropical hard-bottom communities (Aronson et al. 2008b, NatureServe 2013). It is usually found at depths of less than 20 m on outer reef slopes with exposure to wave action (Aronson et al. 2008b, NOAA 2008a).

This species is known from the western Gulf of Mexico, the Caribbean, Florida, and the Bahamas (Aronson et al. 2008b). Previously, the northernmost record for this species was at Fowey Rocks, just north of Biscayne National Park, Florida (Porter 1987). However, this species appears to be expanding northward along the Florida peninsula and into the northern parts of the Gulf of Mexico (Precht and Aronson 2004). In 2003 and 2005 two elkhorn coral colonies were discovered in the East and West Flower Garden Banks in the northern Gulf of Mexico (Zimmer et al. 2006). At 23.5 m, the colony at the East Flower Garden Banks is the deepest reported record from the Caribbean and western Atlantic (Zimmer et al. 2006).

HABITAT AND ECOLOGY

This species requires clear, well-circulated water, and has a salinity tolerance range between 18 and 40 parts per thousand (ppt), with upper temperature limits cited at 35.8°C (NatureServe 2013).

Juveniles are uncommon for this species and localized recruitment generally occurs by asexual fragmentation (Hughes and Connell 1999, Bak et al. 2009). Although recruits to reef populations are usually rare (Guzmán et al. 1991; Bak et al. 2009), they are critical to maintaining the genetic diversity of future populations (Albright et al. 2010). Spawning season is in August or September with synchronized release of gametes into the water column, followed by external development of planulae larvae (ABRT 2005).

Zooxanthellate corals are carnivorous and can capture zooplankton with their tentacles; they receive supplementary nutrients through their photosynthetic symbionts.

POPULATION TREND

Research on this species indicates a drastic decline. There has been an estimated 80–98% global decline in individuals of this population since 1980 (Aronson et al. 2008b).

THREATS

Despite its wide distribution, this species is considered highly threatened and ecologically fragile due to a number of threats, including high sensitivity to temperature, salinity, sedimentation, and eutrophication and extreme susceptibility to bleaching, disease, anchor damage, and boat groundings (NatureServe 2013). Low sexual recruitment further threatens this species. Populations in southern Florida have declined dramatically since the turn of the century due to land use practices, disease, and catastrophic storm events such as hurricanes.

Disease

The greatest source of regionwide mortality for staghorn corals has been disease, including white pox disease (Rogers and Muller 2012), white band disease, and black band disease (NOAA 2013b). White pox disease, caused by the human pathogen *Serratia marcescens*, has been particularly devastating for elkhorn coral in recent decades (Patterson et al 2002). During a disease outbreak in 2003, a unique strain of these bacteria was identified from both diseased elkhorn coral and untreated human sewage, potentially linking wastewater with disease outbreaks. Further compounding this issue, both the coral-eating snail *Coralliophila abbreviata* (which preferentially feeds on *Acropora*) and nonhost corals have been shown to potentially function as reservoirs or vectors of this pathogen (Sutherland et al. 2011). White

band disease has been one of the most significant causes of mortality to acroporid species throughout the western Atlantic, Gulf of Mexico, and Caribbean (Bruckner 2002; Kline and Vollmer 2011; Gignoux-Wolfsohn et al. 2012). Populations of elkhorn coral, staghorn coral, and the hybrid fused staghorn coral (*A. prolifera*) declined as much as 95% in the 1980s and early 1990s from direct mortality by white band disease (Bruckner 2002). Rising sea temperatures may cause an increase in the incidence and severity of these diseases, particularly in areas with abundant coral cover (Bruno et al. 2007), potentially leading to greater outbreaks that can cause dramatic changes in the function and structure of coral reef ecosystems in the Gulf.

Ocean acidification

Coral animals are marine calcifiers that secrete calcium carbonate to create reef structure. As atmospheric carbon dioxide levels rise, more carbon dioxide is absorbed into the world's oceans, leading to ocean acidification. This phenomenon is well known to have deleterious effects on established coral colonies.

Successful sexual reproduction in most reef-building corals, including elkhorn coral, depends on a three-stage process of external fertilization, larval settlement, and subsequent growth and survival. These early life-history stages are vulnerable to changes in water chemistry. As atmospheric carbon dioxide levels and consequent ocean acidification continue to increase, the status of already imperiled calcifying animals such as corals can worsen. Albright et al. (2010) found that all three of these stages were negatively impacted by increases in carbon dioxide levels, suggesting that ocean acidification can severely compromise sexual reproduction and the ability of coral reefs to recover from other disturbances such as hurricanes and disease.

Oil spills

Oil spills have been shown to have negative effects on this species. Elkhorn coral suffered much more than other common species at a heavily oiled Panama reef in the first two years following the massive oil spill at Bahía las Minas due to a ruptured storage tank in 1986, experiencing nearly complete elimination and suggesting that branching corals are more sensitive to human disturbances than other species (Guzmán et al. 1991). Oil in coral tissues and sedimentation have been found to inhibit fertilization, gonad development, and reproduction in broadcaster species (Guzmán and Holst 1993), and spills that occur during spawning season may further inhibit reproductive ability if gametes encounter oil on the water surface (Guzmán et al. 1991).

Predation

The primary predators of elkhorn coral are coral-eating snails (particularly *Coralliophila abbreviata*), the bearded fireworm *Hermodice carunculata*, and damselfish. Predation may directly cause mortality or injuries that lead to invasion of other biota, such as algae or boring sponges (ABRT 2005). For example, both elkhorn and staghorn corals are susceptible to *Cliona* bioeroding sponges, which actively invade and kill live corals (ABRT 2005). These sponges then take up residence in the dead coral structure. The degree of invasion by *Cliona* and other bioeroding sponges has also been linked to human sewage pollution (Rose and Risk 1985; Schonberg and Ortiz 2008), highlighting the need for close monitoring of water quality near coral reefs.



Staghorn coral (*Acropora cervicornis*). (Photograph: Nick Hobgood, Wikimedia Commons.)

Staghorn coral, *Acropora cervicornis*

CONSERVATION STATUS

U.S. Endangered Species Act: threatened (5/9/2006); proposed endangered

FFWCC List: Biologically vulnerable

U.S. State: NatureServe, S1 Critically imperiled (Florida)

NatureServe (global): G3 Vulnerable

IUCN Red List: Critically endangered

CITES: Appendix II

In the most recent ESA biennial report to Congress (NOAA 2013e), the status of this species was found to still be declining. It has been given a recovery priority number of 3 out of 10 (1 being the highest priority). However, a recovery plan for this species is still under development. In December 2012, NMFS proposed reclassifying this species as endangered. Final decisions are pending.

Critical Habitat

In November 2008, NMFS designated critical habitat for both elkhorn and staghorn coral at four sites in the Caribbean and off the south coast of Florida including the Florida Keys and the Dry Tortugas.

Protected Areas and Conservation Actions

In the Gulf of Mexico, this species is present in the Florida Keys National Marine Sanctuary and Dry Tortugas National Park. The Florida Keys National Marine Sanctuary has developed a management plan for the Sanctuary's corals, including protective activities such as zoning and channel markings, as well as restoration efforts (NOAA 2013d).

Research Needs

More information is needed to assist the recovery of acroporids including research into taxonomy, population trends, ecology and habitat status, threats, restoration activities, proper protection and recovery, and disease etiology and management (Aronson et al. 2008a). In addition, more information is required on survival and fecundity, sexual and asexual recruitment, juvenile population dynamics, recruitment, and survivorship, as well as studies of populations showing signs of recovery (Bruckner 2002).

DESCRIPTION AND TAXONOMIC STATUS

Taxonomic issues: None.

Colonies of this species are antler-like with cylindrical, straight, or slightly curved branches.

DISTRIBUTION

This species is widespread in the tropical western Atlantic (NatureServe 2013) and is found in the southern Gulf of Mexico. Like elkhorn coral, this species appears to be moving north due to warming sea temperatures. In 1998, numerous expansive thickets of staghorn coral were found off the Florida coast at Ft. Lauderdale, where they had not been previously observed (Precht and Aronson 2004).

HABITAT AND ECOLOGY

This species occurs on numerous classes of marine hard-bottom communities, including low-relief hard-bottom areas, patch reefs, spur and groove reefs, fringing reefs, transitional reefs, and deeper intermediate reefs. It is characterized by fragmentation, low sexual recruitment, and rapid growth. This species typically grows in fore- and back-reef areas (either facing the open ocean or located on the back wall) with water 4–14 m deep (NOAA 2008a) and is commonly found in lagoons and the upper- to mid-reef slopes, at depths of 1–24 m (Aronson et al. 2008a). It occupies the same general habitat as elkhorn coral (see previous profile).

Spawning occurs in late August with external larval development. Staghorn coral recruits mainly by localized dispersal of asexual fragments rather than larval settlement (Hughes and Connell 1999; Bak et al. 2009). Reproductive strategies and characteristics are similar to those of elkhorn coral.

POPULATION TREND

This species has been noted to be experiencing a short-term (within 10 years or three generations) decline of 10–30% (NatureServe 2013). This species is critically endangered according to IUCN Red List criteria due to a population reduction exceeding 80% over the last few years; this reduction has been caused primarily by disease, climate change, and other anthropogenic factors (Aronson et al. 2008a).

THREATS

Staghorn coral is considered extremely threatened due to high sensitivity to environmental perturbations and widespread decline in the western Atlantic. Threats include sedimentation, eutrophication, disease, bleaching, salinity, and mechanical damage. NatureServe (2013) cites thermal events, anchor damage, and diseases as the cause for declining populations in south Florida and the Caribbean. The primary predators of staghorn coral are the marine snail *Coralliophila abbreviata* and the fireworm *Hermodice carunculata*.

Disease

Staghorn coral is particularly susceptible to disease, especially white band disease, which has severely impacted staghorn populations in recent years (Kline and Vollmer 2011). The quick and devastating impact this disease has had on staghorns can be attributed to a combined transmission both by animal vectors (the coral-eating snail *C. abbreviata*) and through the water column (Gignoux-Wolfsohn et al. 2012).

Oil spills

There are no known documented impacts from oil spills for this particular species. However, staghorn coral may suffer from the same negative effects that have been documented for elkhorn coral and corals in general (see section above on elkhorn coral).



A patch of Lamarck's sheet coral (*Agaricia lamarcki*). (Photograph: NOAA Photo Library.)

Family Agaricidae

The *Agaricia* genus is restricted to the western Atlantic (CBD 2009). There are seven species of this genus in the Gulf of Mexico (Felder and Camp 2009).

Lamarck's sheet coral, *Agaricia lamarcki*

CONSERVATION STATUS

U.S. Endangered Species Act: Proposed threatened

FFWCC List: Biologically vulnerable

U.S. State: N/A

NatureServe (global): N/A

IUCN Red List: Vulnerable

CITES: Appendix II

Critical Habitat

None designated for this species.

Protected Areas and Conservation Actions

In the Gulf of Mexico, this species is present in several Marine Protected Areas, including the Florida Keys National Marine Sanctuary, Dry Tortugas National Park, and the Flower Garden Banks National Marine Sanctuary.

Research Needs

There is relatively little information available for this species. There is a need for more quantitative information on the status of the populations and rates of recovery in deepwater habitats. In addition, research is needed in taxonomy, population trends, ecology, threats, restoration action, recovery management, and disease management (Aronson et al. 2008c).

DESCRIPTION AND TAXONOMIC STATUS

Taxonomic issues: This species has no known taxonomic issues. It is morphologically similar in appearance to *A. grahamae*.

Colonies form large flat plates that commonly overlap and are arranged in whorls (Aronson et al. 2008c; CBD 2009). They are usually brown with white margins (NOAA 2012b).

DISTRIBUTION

This species occurs in the Caribbean and the Gulf of Mexico, around the coast of Florida and the Bahamas. It is common in intermediate to deep waters, and is the dominant species at the base of the reefs in the southern and western Caribbean (Aronson et al. 2008c). On Pulley Ridge off the northwest tip of the Florida Straits, this species is one of the dominant zooxanthellate scleractinians (Waddell and Clarke 2008). This species is most common at depths of 5 to 25 m, particularly between 10 and 15 m in highly turbid waters (Aronson et al. 2008c).

HABITAT AND ECOLOGY

Lamarck's sheet coral can be found in water depths of 5 to 76 m and is most common in deep waters or

areas with reduced light; it is rarely found in shallow reef environments (Brainard et al. 2011). Reproductive data on Lamarck's sheet coral is lacking, but other members in its genus are gonochoric brooders that release larvae in the spring and summer (Brainard et al. 2011). This species has low recruitment rates and is a relatively long-lived species, with a half-life of 17 years and some colonies living more than a century (Brainard et al. 2011).

POPULATION TREND

This species is thought to be vulnerable. Declines in its population due to coral bleaching and disease have been reported throughout the region. The estimated decline of both destroyed and declining reefs is on the order of 38% over three generations (30 years) (Aronson et al. 2008c).

THREATS

Lamarck's sheet coral is primarily threatened by thermal stress and coral bleaching. It is also susceptible to white plague, black band disease, and high sedimentation.

Bleaching

The primary long-term threat to this species has been coral bleaching, to which this species is particularly susceptible due to its thin tissues and limited ability to cope with temperature changes (Fitt and Warner 1995; Aronson et al. 2008c; Brainard et al. 2011).

Disease

This species is susceptible to white plague and black band disease and mortality rates due to these have increased dramatically since 2001 (Aronson et al. 2008c). It is possible that this species' ability to recover from these diseases is inhibited due to its morphology. The overlapping nature of its branches may spread disease more readily across the reef (Aronson et al. 2008c).

Oil spills

There are no known documented impacts from oil spills for this particular species. However, Lamarck's sheet coral may suffer from the same negative effects that have been documented for corals in general.

Family Faviidae

There are three species within the family Faviidae that we profile in this section, all of which were once considered to be a single species complex: boulder star coral (*Montastraea annularis*), mountainous star coral (*M. faveolata*), and star coral (*M. franksi*).

Boulder star coral, *Montastraea annularis*

CONSERVATION STATUS

U.S. Endangered Species Act: Proposed endangered

FFWCC List: Biologically vulnerable; Keystone species

U.S. State: NatureServe, S2 Imperiled (Florida)

NatureServe (global): G5

IUCN Red List: Endangered

CITES: Appendix II

Critical Habitat

None designated for this species.

Protected Areas and Conservation Actions

In the Gulf of Mexico, this species is present in several MPAs, including the Florida Keys National Marine Sanctuary, Dry Tortugas National Park, and the Flower Garden Banks National Marine Sanctuary.

Research Needs

Additional studies are needed on colony density, coverage, and size-frequency distributions from reef community classes for each species (NatureServe 2013). In addition, research on the taxonomy, population trends, ecology, habitat status, threats, and restoration actions is needed, and identification of new or expanded protected areas is a priority (Aronson et al. 2008f).

DESCRIPTION AND TAXONOMIC STATUS

Taxonomic issues: Until 1994, this species was lumped with mountainous star coral and star coral and referred to as the “*Montastraea annularis* species complex” (CBD 2009). All three are now recognized as separate species, but much of the research conducted prior to this time does not distinguish among the three.

Colonies of boulder star coral grow in columns and live colonies generally lack ridges or bumps on their surfaces, which helps distinguish it from other species in the complex (Brainard et al. 2011).

Boulder star coral (*Montastraea annularis*). (Photograph: NOAA Photo Library.)



DISTRIBUTION

This species is widespread in distribution in the tropical western Atlantic and is abundant on most classes of reef communities (NatureServe 2013). It can be found in the Caribbean and the Gulf of Mexico, and around the coasts of Florida, the Bahamas, and Bermuda (Aronson et al. 2008f).

HABITAT AND ECOLOGY

Boulder star coral is often one of the most abundant reef corals in depths ranging from 1 to 10 m (Aronson et al. 2008f). Spawning takes place from mid-August to September but recruits are usually rare, as successful recruitment of this species is infrequent and episodic (Guzmán et al. 1991).

POPULATION TREND

This species has undergone a decline of over 50% in the last 30 years (Aronson et al. 2008f).

THREATS

Species threats listed include chronic sedimentation, disease, bleaching, and eutrophication but it is moderately tolerant to environmental perturbation and high salinity. According to NatureServe (2013), incidence of disease and bleaching are well documented. Hurricane damage, bioerosion by sponges, and the loss of habitat due to algal overgrowth and sedimentation at critical recruitment stages are also threats (Aronson et al. 2008f). Boulder star coral is also impacted by predation by the stoplight parrotfish (*Sparisoma viride*) (Aronson et al. 2008f). The scope for recovery is somewhat limited due to the extreme longevity of this species, long generation times, and its low rates of recruitment (Aronson et al. 2008f).

Bleaching

Coral bleaching is one of the primary threats to this species (Aronson et al. 2008f). Croquer and Weil (2009) found a significant relationship between coral bleaching and the prevalence of two virulent diseases affecting the *Montastraea annularis* species complex. If bleaching events become more intense and frequent, disease-related mortality of Caribbean coral-reef builders could increase. Coral bleaching has also been linked to reproductive failure in this species one year after bleaching, with reduced reproductive output after two years (Mendes and Woodley 2002).

Disease

Boulder star coral is very slow growing. A 500-year-old colony may be severely reduced within months by disease, and take decades to recover (Carpenter et al. 2008). It is particularly susceptible to white plague, yellow band, and black band disease (Aronson et al. 2008f). Yellow band disease primarily affects slow-growing massive species such as this genus (Bruckner and Bruckner 2006).

Oil spills

When this species spawns, its gametes tend to rise to the surface, where they may be more likely to encounter, and be negatively impacted by, oil (Guzmán et al. 1991).

Mountainous star coral, *Montastraea faveolata*

CONSERVATION STATUS

U.S. Endangered Species Act: Proposed endangered

FFWCC List: Biologically vulnerable; Keystone species

U.S. State: N/A

NatureServe (global): N/A

IUCN Red List: Endangered

CITES: Appendix II

Critical Habitat

None designated for this species.

Protected Areas and Conservation Actions

In the Gulf of Mexico, this species is present in the Florida Keys National Marine Sanctuary, Dry Tortugas National Park, and the Flower Garden Banks National Marine Sanctuary.

Research Needs

Additional research on taxonomy, population trends, ecology, habitat status, threats, and restoration actions is needed, as is identification of new or expanded protected areas (Aronson et al. 2008g).

DESCRIPTION AND TAXONOMIC STATUS

Taxonomic issues: Until 1994, this species was lumped with boulder star coral and star coral and referred to as the “*Montastraea annularis* species complex” (CBD 2009). All three are now recognized as separate species, but much of the research conducted prior to this time does not distinguish among the three.

This species forms head or sheet colonies, with active growth typically found at the colony edge (CBD 2009).

DISTRIBUTION

This species is found throughout the Caribbean and Gulf of Mexico, and around Florida and the Bahamas (Aronson et al. 2008g).

HABITAT AND ECOLOGY

Species in the *M. annularis* species complex are hermaphroditic spawners that release gametes in the summer (Richmond and Hunter 1990).

POPULATION TREND

Mountainous star coral is believed to have undergone a decline exceeding 50% over the past 30 years due to bleaching and disease, among other factors (Aronson et al. 2008g).



Mountainous star coral (*Montastraea faveolata*). (Photograph: NOAA Photo Library.)

THREATS

The major threats to this species are infectious diseases and bleaching. Other threats include predation by parrotfish, hurricane damage, and loss of habitat at the recruitment stage due to algal overgrowth and sedimentation, as well as more localized impacts (Aronson et al. 2008g). Current rates of mortality are exceeding growth and recruitment, and the chances of recovery are limited due to the species' extreme longevity, low recruitment rates, and long generation times.

Bleaching

Coral bleaching is a major threat to this species. The *Montastraea annularis* complex as a whole has been shown to be highly to moderately susceptible to bleaching (as reviewed in Brainard et al. 2011).

Disease

Yellow band disease has been shown to severely compromise reproductive output of this species (Weil et al. 2009). As with acroporid corals, nutrient enrichment (such as from wastewater runoff) has been found to exacerbate coral diseases, including yellow band disease (CBD 2009). A study of this species in the Florida Keys during and after the 2005 mass bleaching event found that corals with greater bleaching intensities later developed white plague infections, suggesting that this species is susceptible to loss of disease resistance during intense bleaching events (CBD 2009).

Oil spills

Goodbody-Gringley et al. (2013) investigated the potential effects of an oil spill on coral larvae from the Florida Keys by examining the effects of exposure to fresh and weathered Deepwater Horizon oil and dispersants. Using short-term assays to monitor larval settlement rates, survivorship, and behavioral responses, mountainous star coral planulae decreased significantly after exposure to increased concentrations of Deepwater Horizon crude oil, weathered oil, water-accommodated fractions, chemically enhanced water-accommodated fractions (CEWAF), and Corexit® 9500. Higher concentrations of CEWAF and Corexit® resulted in settlement failure and complete larval mortality. The authors suggest that based on these results, the use of dispersants to mitigate oil spills in vicinity of coral reefs should be avoided.

Star coral, *Montastraea franksi*

CONSERVATION STATUS

U.S. Endangered Species Act: Proposed endangered

FFWCC List: N/A

U.S. State: N/A

NatureServe (global): N/A

IUCN Red List: Vulnerable

CITES: Appendix II

Critical Habitat

None designated for this species.

Protected Areas and Conservation Actions

In the Gulf of Mexico, this species is present in several MPAs, including the Florida Keys National Marine Sanctuary, Dry Tortugas National Park, and the Flower Garden Banks National Marine Sanctuary.

Research Needs

Research in taxonomy, population trends, ecology, habitat status, threats, and restoration actions is needed, and identification of new or expanded protected areas is a priority (Aronson et al. 2008h). There is a need for more quantitative information on the status of populations in deeper water habitats (Aronson et al. 2008h).

DESCRIPTION AND TAXONOMIC STATUS

Taxonomic issues: Until 1994, this species was lumped with boulder star coral and mountainous star coral and referred to as the “*Montastraea annularis* species complex” (CBD 2009). All three are now recognized as separate species, but much of the research conducted prior to this time does not distinguish among the three.

Colonies of this star coral can be massive, flat and encrusting, or columnar, with characteristically bumpy appearances that help differentiate the species from boulder star and mountainous star corals (Dawson 2006; CBD 2009). Colors vary between gray, green, yellow, and brown.

DISTRIBUTION

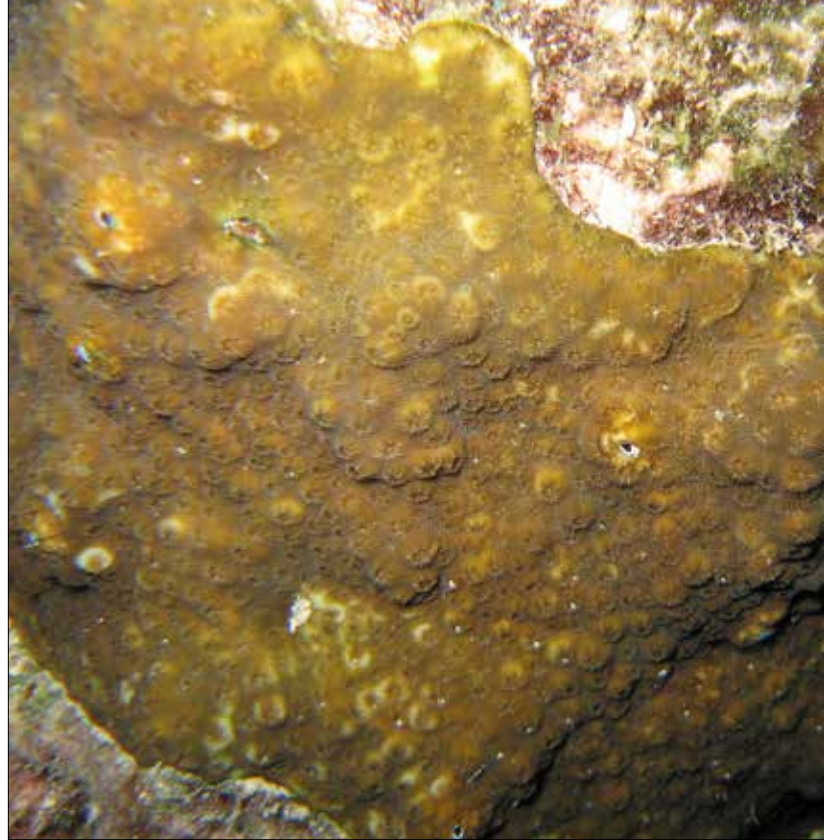
This species is found throughout the Caribbean and Gulf of Mexico, and around Florida, Bermuda, and the Bahamas (Aronson et al. 2008h). It is the dominant coral species at the East and West Florida Garden Banks reefs (Waddell and Clarke 2008).

HABITAT AND ECOLOGY

This star coral is found at depths of 5–50 m, and is often the most abundant coral between 15 and 30 m in fore-reef environments (Aronson et al. 2008h). This species is a hermaphrodite that spawns in the summer (Richmond and Hunter 1990).

POPULATION TREND

This species has seen significant declines in recent decades, with accelerating losses of cover in U.S.



An encrusting form of star coral (*Montastraea franksi*). (Photograph: NOAA Photo Library.)

waters since 2002 (Aronson et al. 2008h; CBD 2009). Vulnerability to disease and habitat degradation increases the likelihood of this species being lost within one generation. The species is projected to lose 38% of its population in the next three decades (Aronson et al. 2008h; CBD 2009).

THREATS

The major threats to this species are infectious diseases (such as plague, yellow band disease, and black band disease) and bleaching (Aronson et al. 2008h). Nutrient enrichment has been found to exacerbate coral disease, including yellow band disease in this species (CBD 2009). Loss of habitat during the recruitment phase due to algal overgrowth and sedimentation is also a concern (Aronson et al. 2008h). This species' extremely low productivity, recent dramatic population declines, and restriction to the highly disturbed and degraded greater Caribbean region all contribute to its higher estimated extinction risk (Brainard et al. 2011).

Oil spills

No specific studies on the effects of oil spills on this species are known. However, research on the effect of crude oil and dispersants on sibling species *M. faveolata* demonstrated significant impacts to coral planulae, including settlement failure and larval mortality (Goodbody-Gringley et al. 2013).



Pillar coral (*Dendrogyra cylindrus*). (Photograph: NOAA Photo Library.)

Family Meandrinidae

Pillar coral, *Dendrogyra cylindrus*

CONSERVATION STATUS

U.S. Endangered Species Act: Proposed Endangered

FFWCC List: Biologically vulnerable

U.S. State: Florida state, threatened; NatureServe, S1 Critically imperiled (Florida)

NatureServe (global): G3 Vulnerable

IUCN Red List: Vulnerable

CITES: Appendix II

Critical Habitat

None designated for this species.

Protected Areas and Conservation Actions

In the Gulf of Mexico, this species is present in several MPAs, including the Florida Keys National Marine Sanctuary and Dry Tortugas National Park.

Research Needs

Further inventory is needed in the Gulf of Mexico to determine its distribution (NatureServe 2013). Additional research into this species' ecology and conservation would aid conservation and management actions. Continued enforcement of bans on collecting coral and anchoring boats on reefs is needed (Neely et al. 2013). Extant populations should be included in marine protected areas (NatureServe 2013).

DESCRIPTION AND TAXONOMIC STATUS

Taxonomic issues: None

As its name suggests, this species forms colonies of cylindrical pillars approximately 1 m in height (Neely et al. 2013) that are usually closely fastened to the underlying substrate (FFWCC 2011b). Colonies that do not fasten to the substrate tend to fall over, which may be a limiting factor in colony size (FFWCC 2011b). These corals are usually light brown in color and may have a furry appearance, owing to the extended tentacles of the polyps during daylight (FFWCC 2011b).

DISTRIBUTION

This species is moderately widespread throughout the tropical western Atlantic but limited to shallower reef communities (NatureServe 2013). It can be found throughout the Caribbean and southern Gulf of Mexico, and around Florida and the Bahamas (Aronson et al. 2008d). It is regionally rare in the Florida Keys (Neely et al. 2013) and is most often found at high-relief spur and groove reefs (FFWCC 2011b).

HABITAT AND ECOLOGY

This species is a gonochoric spawner with separate male and female colonies (Richmond and Hunter 1990). Spawning takes place in mid-August (Neely et al. 2013; NatureServe 2013) and has been observed to match the spawning period of *Acropora* spp. in the Florida Keys National Marine Sanctuary (Bak et al. 2013).

POPULATION TREND

The IUCN assessment notes that specific population trends are unknown (Aronson et al. 2008d). However, declines in habitat quality of 38% over three generation lengths (30 years) can be used as a proxy for population reduction (Aronson et al. 2008d). Pillar coral has been assessed a relatively high extinction risk due to overall low population density, natural rarity, lack of observed sexual recruitment, and susceptibility to disease mortality (Brainard et al. 2011).

THREATS

Pillar coral is highly fragile and is imperiled due to low population density, poor reproductive rates, low recruitment, high susceptibility to sedimentation, and slow growth (Brainard et al. 2011; FFWCC 2011b; NatureServe 2013). It is also sensitive to eutrophication and boat groundings (NatureServe 2013). Additional threats include hurricane and storm damage, bioerosion by sponges, damage by anchors, climate change, habitat loss or reduction in habitat quality, and predation by damselfish (FFWCC 2011b).

Bleaching

This species is susceptible to coral bleaching. After the bleaching event that devastated Caribbean coral reefs in 2005, a study investigating the extent of bleaching on coral species at 12 sites off the east coast of Puerto Rico showed 100% bleaching frequency for pillar coral (Waddell and Clarke 2008).

Disease

This species is highly susceptible to white plague and yellow band disease (Bruckner and Bruckner 2006; Aronson et al. 2008d; CBD 2009).

Low reproductive rates and recruitment

This species' method of reproduction may be a threat to its persistence. Because it exists in such low densities in Florida, broadcast spawning may not be sufficient for successful fertilization (there is a low probability of gametes fertilizing and recruiting) (FFWCC 2011b). In addition, this species has low juvenile survivorship (Aronson et al. 2008d) and no juvenile pillar corals were detected on reefs in the Florida Keys during surveys from 1999 to 2009 (FFWCC 2011b).

Oil spills

There are no known documented impacts from oil spills on this particular species.

Taxonomic distinctness

Pillar coral is the only species in its genus and one of only ten species in the family Meandrinidae. Further declines in this species could cause the extinction of an entire evolutionary line.

Elliptical star coral, *Dichocoenia stokesii*

CONSERVATION STATUS

U.S. Endangered Species Act: Proposed threatened

FFWCC List: Biologically vulnerable

U.S. State: N/A

NatureServe (global): N/A

IUCN Red List: Vulnerable

CITES: Appendix II

Critical Habitat

None designated for this species.

Protected Areas and Conservation Actions

In the Gulf of Mexico, this species is present in the Florida Keys National Marine Sanctuary, Dry Tortugas National Park, and the Flower Garden Banks National Marine Sanctuary.

Research Needs

Additional research is needed on taxonomy, population trends, ecology, threats, restoration, identification and expansion of protected areas, and recovery management (Aronson et al. 2008e).

DESCRIPTION AND TAXONOMIC STATUS

Taxonomic issues: Some researchers treat *Dichocoenia stokesii* and its sibling species *D. stellaris* as one species (*D. stokesii*), but the IUCN differentiates them as two species (CBD 2009). Further taxonomic work is needed to clarify the status (Aronson et al. 2008e).

Colonies of elliptical star coral are usually orange-brown and form either massive spheres or thick plates (Brainard et al. 2011).

DISTRIBUTION

This species occurs in the Caribbean and Gulf of Mexico, and around Florida, the Bahamas, and Bermuda (Aronson et al. 2008e).

HABITAT AND ECOLOGY

This species typically occurs at depths of 3 to 20 m on most classes of marine hard-bottom communities within its range (NatureServe 2013). Little information on reproductive ecology is available, but elliptical star coral is reported to be a gonochoric spawner with low recruitment rates and slow colony growth (Brainard et al. 2011; NatureServe 2013).

POPULATION TREND

Specific population trends for this species are unknown, but declines in habitat quality of 38% over three generations (30 years) are a proxy for population reduction (Aronson et al. 2008e). Upper Florida Keys populations have declined substantially in recent years due to disease outbreaks (Brainard et al. 2011).



Elliptical star coral (*Dichocoenia stokesii*). (Photograph: NOAA Photo Library.)

THREATS

This species is sensitive to disease, bleaching, sedimentation, and storm damage.

Disease

Elliptical star coral is highly susceptible to disease, especially white plague, and to a lesser extent black band disease (Santavy et al. 2005; Voss and Richardson 2006; Aronson et al. 2008e). White plague type II led to mass mortalities of the species in the northern Florida Keys between 1995 and 2002, and the average number of colonies per site declined by almost 75%. No evidence of coral recruitment was found during the seven-year period (Richardson and Voss 2005).

Oil spills

There are no known documented impacts from oil spills on this particular species.



Rough cactus coral (*Mycetophyllia ferox*). (Photograph: NOAA Photo Library.)

Family Mussidae

Rough cactus coral, *Mycetophyllia ferox*

CONSERVATION STATUS

U.S. Endangered Species Act: Proposed endangered

FFWCC List: Biologically vulnerable

U.S. State: N/A

NatureServe (global): N/A

IUCN Red List: Vulnerable

CITES: Appendix II

Critical Habitat

None designated for this species.

Protected Areas and Conservation Actions

In the Gulf of Mexico, this species is present in several MPAs, including the Florida Keys National Marine Sanctuary and Dry Tortugas National Park.

Research Needs

Research on taxonomy, population trends, ecology, habitat status, threats, and restoration actions is needed, and identification and expansion of protected areas is a priority (Aronson et al. 2008i).

DESCRIPTION AND TAXONOMIC STATUS

Taxonomic issues: None

Colonies of this species are composed of encrusting plates with interconnecting valleys, usually in gray and brown colors (Brainard et al. 2011).

DISTRIBUTION

This species is found in the Caribbean, the southern Gulf of Mexico, and around Florida and the Bahamas (Aronson et al. 2008i).

HABITAT AND ECOLOGY

Rough cactus coral is most commonly found in fore-reef environments at 5–30 m depths, although it can also occur in some deeper back-reef and lagoon habitats (Aronson et al. 2008i). This species is a hermaphroditic brooder that releases its larvae in the winter and spring (Richmond and Hunter 1990).

POPULATION TREND

The population trend of rough cactus coral is unknown. However, declines in habitat quality of 38% over three generation lengths (30 years) can be used as a proxy for population decline in this species (Aronson et al. 2008i). Long-term monitoring on species presence/absence from permanent stations in the Florida Keys shows dramatic declines in population. Rough cactus coral was recorded at 20 of 97 stations in 1996 but only four stations in 2009 (Brainard et al. 2011).

THREATS

Rough coral cactus is extremely rare and recent observed declines in abundance are due primarily to bleaching and disease, as well as degradation of coral reef habitat and high sedimentation (Aronson et al. 2008i; Brainard et al. 2011).

Bleaching

No bleached colonies were observed during the mass 2005 bleaching event in Florida (Brainard et al. 2011), although this species sustained high mortality off Puerto Rico and Grenada due to the bleaching event and a subsequent outbreak of plague (Aronson et al. 2008i).

Disease

Rough cactus coral is susceptible to white plague (Porter et al. 2001; Santavy et al. 2005) and black band disease. Outbreaks of white plague were first identified in Florida in 1975 and again in the early 1980s (Aronson et al. 2008i). High rates of mortality have been associated with a more virulent form of white plague, which has affected the species since the late 1990s in other locations throughout the Caribbean (Aronson et al. 2008i).

Oil spills

There are no known documented impacts to this particular species by oil spills.

Sensitive Species Groups

Crustaceans

Over 2,500 species of crustaceans are known from the Gulf of Mexico (Tunnell 2011), including economically important species of shrimp, lobster, and crab. The conservation status of most marine crustaceans is poorly understood. However, crustaceans in general are vulnerable to habitat degradation, pollution, urban and agricultural development, and overfishing.

Oil spills can be particularly devastating for crustaceans and can physically impact individuals by choking gills, adhering to body surfaces, or impeding feeding. Oil contamination disturbs or alters behavior (O'Sullivan and Jacques 1998). Brodersen (1987) noted a type of narcosis in the larvae of red king crab and kelp shrimp when exposed to the water soluble fraction of oil, which could cause larvae to sink in the water column and be eaten, injured, or buried. Amphipods are highly sensitive to oil and may experience temporary, local extirpation following a spill (Suchanek 1993; Jewett et al. 1999; Schlacher et al. 2011). Oil and dispersant droplets from the Deepwater Horizon spill have been found within the shells of blue crab larvae (Earth Gauge 2010) and the eggs of some crustaceans may have encountered floating oil (Tunnell 2011).

The IUCN recently completed a global review of lobster species and did not determine any species in the Gulf of Mexico to be threatened. However, a large number of these species remain data deficient and their conservation status may be updated when additional research is completed. For example, the Caribbean spiny lobster (*Panulirus argus*) is a commercially important species in Florida and the Ca-



Squat lobster (*Eumunida picta*) perched on a thicket of the deepwater coral, *Lophelia pertusa*. (Photograph: NOAA Photo Library; courtesy of Lophelia II 2012 Expedition, NOAA-OER/BOEMRE.)

ribbean and is thought to be exploited or overharvested throughout its range (Butler et al. 2011; Collen et al. 2012). Florida fisheries for this species are believed to be relatively stable but additional research is needed to determine harvest impacts. Due to these gaps in knowledge regarding fishing effort, the Caribbean spiny lobster is currently ranked as data deficient according to IUCN listing criteria and it is possible this species will be up-listed to an IUCN threat category when additional information is obtained (Butler et al. 2011).

Echinoderms

Echinoderms are strictly marine species and are found in all seas at all depths. They include sea stars, brittle stars, urchins, sea cucumbers, and sea lilies. The Gulf of Mexico is home to a relatively high diversity of echinoderms, with 522 species, of which 6% are endemic (Felder and Camp 2009).

In many parts of the world there have been huge declines in commercially important echinoderm species such as sea cucumbers and urchins, prompting the IUCN to identify this group as needing further evaluation. A recent assessment of the order Aspidochirotrida found none of the sea cucumbers in the Gulf of Mexico to be threatened (Purcell et al. in review). It should be noted, though, that like most marine invertebrates, many of the species reviewed were considered data deficient. Restricted range endemics from groups such as sea cucumbers are highly susceptible to marine pollution and may suffer high risks of extinction (Collen et al. 2012). In the Gulf of Mexico, eight endemics belong to the sea cucumber family Holothuroidea (Felder and Camp 2009). At least two of these, *Chiriodata heheva* and *Ophioctenella acies*, ingest mud during feeding (Carney 2010) and may be particularly sensitive to high levels of pollutants in sediments.



Ophiuroids may be locally abundant in deepwater ecosystems, but little is known about them. Here they are entwining gorgonian corals. (Photograph: NOAA Photo Library; Lophelia II 2012 Expedition, NOAA-OER/BOEMRE.)

Echinoderms are known to be extremely sensitive to any reduction in water quality (Nelson-Smith 1973) and can be very susceptible to toxicity in the environment because they absorb water and nutrients through their body wall (Suchanek 1993; Peterson et al. 1996). Studies of the effects of multiple oil spills on echinoderm populations have shown overall declines in population (Jewett et al. 1994; Braddock et al. 1995). Sea stars, for example, can die or undergo degraded functions as a result of cilia becoming coated with oil (Earth Gauge 2010). Joly-Turquin et al. (2009) found that contaminated food was an important route of polycyclic aromatic hydrocarbon (PAH) contamination of the common starfish (*Asterias rubens*). It is unclear, however, whether volatile and soluble oil fractions have greater direct effects on echinoderms than compounds obtained this way.

Echinoderms can be relatively abundant on deep-sea floors but they are a rare component of chemosynthetic ecosystems (Carney 2010) that derive energy from hydrothermal vents. In the Gulf of Mexico several species appear to have a strong dependence on chemosynthetic habitats, including two species of holothuroids (*Chirodota hydrothermica* and *C. heheva*) and the ophiuroid *Ophioctenella acies* (Carney 2010). Little is known about these organisms. Deepwater ophiuroids, in particular, are in urgent need of comprehensive studies (Felder and Camp 2009).

The Florida Fish and Wildlife Conservation Commission (2011a) lists five echinoderms as “species of conservation concern” in the Gulf of Mexico due to their biological vulnerability or rarity (see Appendix II). An additional 22 species are “taxa of concern,” meaning that despite limited information on these species there is evidence of or expert consensus about population declines, rarity, or limited habitat requirements.

While echinoderms on the whole appear to be either stable or of unknown status in the Gulf of Mexico, there are exceptions. Perhaps the best known case of an echinoderm in decline is that of the long-spined sea urchin (*Diadema antillarum*). This once abundant herbivore has experienced significant reductions in population size in recent years following a massive die-off in the early 1980s. It is found throughout the Caribbean and Gulf of Mexico in calm waters near coral reefs, seagrass beds, mangroves, and sandy or rocky bottoms. While it has been observed at depths to 400 m, it is usually found at depths less than 50 m.

Prior to the 1980s, the long-spined sea urchin was one of the dominant urchin species on Caribbean coral reefs and a major algal consumer. A massive, disease-induced die-off occurred in 1983, which resulted in a 97% loss of mature adult populations in some areas. The consequent explosion of algae growth smothered reefs and limited larval coral settlement and growth. This die-off is the most severe mortality event documented for a marine species (Lessios 1995; Del Monte-Luna et al. 2007). Recovery has been slow and this species remains rare and functionally extinct throughout its range (Lessios 1995; Mumby et al. 2006).

Despite this documented decline, it is not federally or state protected and the IUCN has not yet assessed its status. The Florida Fish and Wildlife Conservation Commission lists this as a species of conservation concern due to its biological vulnerability, although it notes its population as stable (FFWCC 2011a).

Mollusks

The Gulf of Mexico is home to 2,455 species of mollusks, 259 (9.5%) of which have not been found anywhere else (Felder and Camp 2009). While freshwater mollusks are among the most imperiled organisms in North America, marine mollusks are thought to be more secure and few have gone extinct in modern times (Régnier et al. 2009). However, populations of several Gulf mollusk species are in decline, most notably the queen conch (*Strombus gigas*). Queen conch populations have collapsed throughout

the region due to overharvesting and poaching, declining by as much as 50–75% in some areas (NatureServe 2013). Despite bans on collection of this species, ongoing surveys have shown that recovery is slow and very limited (NatureServe 2013). This species is a candidate under the ESA and is considered critically imperiled at the national level by NatureServe. It is protected under CITES and considered a species of conservation need by the Florida Fish and Wildlife Conservation Commission (FFWCC 2011a).

Other marine mollusks, such as oysters, are commercially important and federally managed. Oysters are ecosystem engineers, producing reef habitats for entire ecosystems of other plant and animal species (Beck et al. 2011; Brown et al. 2011). They are prey for various marine invertebrate, fish, and bird species. Reefs formed by oysters are highly complex and provide stable habitat for a variety of organisms in areas that would otherwise be soft-bottom or vegetative beds. They are keystone species in many estuaries.

Oyster beds are found in intertidal estuarine or marine habitats throughout the Gulf of Mexico, which supports one of the healthiest and most productive remaining native oyster harvests in the world (Beck et al. 2011; Brown et al. 2011). These reefs provide high quality habitat for aquatic life, benefit water quality, and protect shorelines (Brown et al. 2011). A prominent reef-forming oyster, the eastern oyster (*Crassostrea virginica*), creates important habitat in nearshore, subtidal areas in the Gulf. Filtration capacity of eastern oysters in the Gulf of Mexico and northern Atlantic coast has decreased greatly in recent years due to lowered oyster density, likely from overharvesting (zu Ermgassen et al. 2013). Loss of filtration services can have enormous impacts. Anderson et al. (2011) estimated the loss of filtering capacity due to reduced numbers of bivalves to be the equivalent of approximately 11 million Olympic-sized swimming pools per day over the five-year period 2000–2004. The continued careful management of oyster reefs in the Gulf is of critical ecological and economic importance and these reefs may represent the last opportunity to achieve large-scale oyster reef restoration (Beck et al. 2011).

Globally, oyster reefs are the single most impacted marine habitat (85% loss) due to overharvest, disease, sedimentation, pollution, non-native species, and changing salinities (Kirby 2004; Mackenzie 2007; Beck et al. 2009; Beck et al. 2011; Brown et al. 2011). Dredging is the main method of commercial harvesting for oysters, a method that can cause great damage to the oyster reef habitat and the seabed upon which the reef was formed (see review by Mercaldo-Allen and Goldberg 2011). Oyster reef degradation and loss may result in the loss of vital ecological services, including foraging and nursery habitat for economically important finfish and commercially important coastal invertebrate fisheries (Lenihan and Peterson 1998; Eggleston et al. 1999; NMFS 2013b; Brown 2012). Oyster bed losses also impact water filtration and removal of excess nutrients (Dame et al. 1984; Coen et al. 2007; Cerco and Noel 2007) and reduce the benefits to coastal land protection as there are fewer beds to counter wave energy and storm surges (Piazza et al. 2005; Beck et al. 2009). These community declines are likely to continue in the future with changing ocean conditions due to pollution, global climate change, ocean acidification, and other human-induced stressors. Despite these identified threats, the conservation status of many oyster species is currently unknown. The IUCN has completed a preliminary assessment of all reef-building oysters, but the results may not be published until late 2014 (B. A. Polidoro, pers. comm.).

Many of the smaller and deeper water mollusk species remain poorly documented (Felder and Camp 2009) and greater survey efforts are needed to understand the ecology and life history of these species. The IUCN has plans to assess the status of some complete clades of gastropod and bivalve mollusks (Polidoro et al. 2008), including oysters (B. A. Polidoro, pers. comm.). Assessments of all 632 species of cone snails in the family Conidae were recently completed (Peters et al. 2013). Two species from the west coast of Florida, *Conus stearnsii* and *C. anabathrum*, have been assessed as vulnerable. However, many more species of cone snails that occur in the Gulf of Mexico lack basic biological and population data, making assessments of species status difficult.

Cone snails are threatened by habitat loss, especially in regions suffering from marine pollution, sedimentation, coastal development or destructive fishing practices such as dredging (Collen et al. 2012;



Populations of the queen conch (*Strombus gigas*) have declined across the Gulf of Mexico due to overharvesting and poaching. (Photograph: NOAA Photo Library.)

Peters et al. 2013). Species that have large or attractive shells, occur in shallow water, are endemic, or have a restricted geographical range are at particular risk (Collen et al. 2012). The Florida cone snail (*C. anabathrum*) prefers sand bars or muddy sand substrates and is found in the Caribbean and Gulf of Mexico at depths up to 120 m (Petuch 2013a). Along the western Florida coastline it is only common near Marco Island and in Tampa Bay. *Conus stearnsii* is endemic to Florida and occurs from Apalachicola to Marco Island (Petuch 2013b). Given the restricted ranges of these species, populations could easily be extirpated by coastal development and over collecting, and more information is needed about their population levels, habitat requirements, and threats (Petuch 2013a, b).

Intertidal mollusk species are especially at risk from oil spills (O'Sullivan and Jacques 1998). Filter feeders such as oysters can take in contaminants from the surrounding water and grazers may encounter oil in sediments or on the surfaces of rocks and other grazing areas (O'Sullivan and Jacques 1998). Some bivalves accumulate PAHs and other chemicals in the water in their tissues, making them unsafe for consumption. For example, suspension-feeding clams and mussels concentrate hydrocarbons and only slowly metabolize them, which can lead to chronically elevated tissue contamination (Peterson et al. 2003b). Oil on surfaces can also physically impair the ability of bivalves to attach to substrates (Earth Gauge 2010) or can completely encrust gastropods (Suchanek 1993). Gastropods may experience immediate mortality or decreased recruitment for up to two years after a spill (Garrity and Levings 1990).

Sponges

Sponges include over 8,500 species worldwide (Van Soest et al. 2012) and are one of the most species-rich and abundant groups of marine benthic organisms found on hard substrates (Felder and Camp 2009). Their biomass may well exceed that of any other benthic organisms (Felder and Camp 2009). Sponges are bottom-dwelling animals that are largely sessile (except for their larval stages) and are

common throughout the Gulf of Mexico at all depths. They are particularly associated with coral reefs, seagrass beds, and mangroves (Collen et al. 2012).

Sponges reproduce both sexually and asexually. Water flow through the sponge provides food and oxygen, and removes wastes. They provide habitat for a wide variety of animals including shrimp, crabs, spiny lobsters, barnacles, worms, brittle stars, sea cucumbers, and other sponges. Estimated numbers of species is difficult due to taxonomic problems, but within the Gulf of Mexico there are at least 339 species, of which more than 30% (109 species) are endemic (Felder and Camp 2009). Endemism in sponges can be high given the limited swimming capabilities of their larvae and their occasional asexual reproduction (Van Soest et al. 2012). Some species are commercially harvested off the Gulf coast of Florida, including the sheepswool sponge (*Hippiospongia lachne*) and yellow sponge (*Cleona celata*) (Stevely and Sweat 2008).

Despite the importance of sponges to the marine ecosystem, they are underrepresented in the literature. The study of sponges has picked up greatly over the last half century with advancements in diving equipment, but knowledge of the distribution and abundance of reef-forming sponges throughout the Gulf of Mexico is still incomplete (Felder and Camp 2009). Brooke and Schroeder (2007) point to the urgent need for studies in this group, although they note that identification of the many species involved is an extensive undertaking.

Little research on oil effects to sponges has been conducted to date. Because sponges depend on sinking surface plankton and particulates for food, oil spills and the subsequent death or fouling of surface plankton can have profound effects on these organisms by altering the food web (Boland et al. 2010) or by physically impeding their feeding mechanisms. Light deprivation due to oil on the water surface can also affect species such as red and orange encrusting sponges that depend in part on symbiotic photosynthesis for energy (Boland et al. 2010).



Barrel sponges (*Xestospongia* sp.) on Sonnier Bank in the northern Gulf of Mexico. (Photograph: NOAA Photo Library.)

Sensitive Marine Communities

Deep-Sea Coral Communities

Deep-sea coral communities are distributed throughout the world's oceans (Rogers 2004) and are widely recognized as biodiversity hotspots supporting substantial fish populations (Bongiorni et al. 2010; Prouty et al. 2011). Unlike shallow-water corals, deep-sea corals are azooxanthellate (they lack photosynthetic symbionts) and ahermatypic (they do not form reefs). They require a hard substrate on which to attach and are often found on parts of the continental slope or on summits or seamounts with strong currents. These currents are vital for food supply; the dispersal of eggs, larvae, and sperm; waste removal; and sediment removal from coral surfaces (Rogers 2004). As their name implies, these corals are often found in cold, dark areas of the deep seas at depths of 50 m to greater than 1,000 m. Although they do not form reefs in the same sense as shallow-water corals, they can still form lush assemblages over large areas, functioning quite similarly to shallow water reefs.

Deepwater coral assemblages are globally threatened. The largest threat is destructive fishing practices, especially trawling and other bottom-tending fishing gear (Rogers 2004; Schroeder et al. 2005; Brooke and Schroeder 2007), which can have profound effects on mature reefs that may have taken thousands of years to accumulate. Deep-sea corals are fragile and easily broken, and because they grow very slowly may never recover (Rogers 2004). Additional threats to these corals include energy and mineral exploration and development, submarine cable and/or pipeline deployment, climate change and ocean acidification, coral harvesting, marine debris, and invasive species (Schroeder et al. 2005).

Because of their great depths and often inaccessible locations these communities remain poorly studied and largely unknown (Brooke et al. 2013). Deep-sea habitats are beyond the range of regular SCUBA dives and it is only relatively recently that technological advances have paved the way for deep-sea inventories. Researchers continue to find new species with each dive suggesting that there is still much learn about deep-sea biodiversity and species distribution (Bongiorni et al. 2010).

In the United States, the National Oceanic and Atmospheric Administration (NOAA) manages deep-sea corals under the National Marine Sanctuaries Act (NMSA). This authorizes NOAA to identify and protect nationally significant habitats and resources throughout U.S. waters. Deep-sea corals and sponges are known to occur in nine of the nation's national marine sanctuaries or marine national monuments. The Gulf of Mexico harbors extensive deepwater coral communities in three primary sub-regions: the northern Gulf of Mexico, the west Florida shelf and slope, and the Florida Straits (Brooke and Schroeder 2007).

Intensive studies of deepwater corals in the Gulf of Mexico have only occurred in the last decade, although collections from trawls have been known since the 1950s (Boland et al. 2010). The largest known deepwater coral ecosystem in the Gulf is located on the Gulf's northern slope and the western Florida shelf, within 65 km of the Deepwater Horizon oil well (MCBI 2011). Some of the most extensive studies of coral communities in the Gulf are from the Flower Garden Banks National Marine Sanctuary (Brooke and Schroeder 2007). However, the total number, extent, and location of deepwater coral communities are largely unknown and our understanding of the ecology of these communities is limited (Brooke and Schroeder 2007).

Due to the many gaps in our knowledge regarding deep-sea ecosystems, it is not surprising that little research exists on the effects of oil pollution on these communities. However, the Deepwater Horizon oil spill has put deepwater corals at serious risk of direct degradation due to the deepwater origin of the disaster, the use of dispersants at the wellhead, and the resulting plumes of oil-based pollution floating and drifting with subsurface currents. The use of dispersants further compounds the problem

of subsurface plumes by creating small droplets that float in the water column. These droplets are encountered by organisms in the water column, potentially endangering a host of species. Because cold water corals are azooxanthellate, they depend on organic matter floating through the water column. Often, this organic matter is produced in surface water and sinks to the ocean floor. Enormous oil plumes from the Deepwater Horizon disaster occupy the water column between this food source and deepwater communities. Oil fouling and death of surface plankton could significantly impact the deep-reef food chain (Boland et al. 2010). In addition, toxic compounds may accumulate in deep-sea sediments. The slow growth rates of deepwater corals, coupled with uncertain reproduction, means damages to these animals may be difficult to impossible to recover from. Measurements of pollutants, descriptions of deep-sea communities, and in situ toxicity tests are urgently needed (Grassle 1991).

Stony corals (order Scleractinia)

The ivory tree coral (*Oculina varicosa*) has one of the most restricted geographic ranges of the deepwater corals (Rogers 2004). This species is unusual in that it can be either azooxanthellate or zooxanthellate, and can be found in a range of water depths from 2 to over 100 m (Reed 2002; Rogers 2004; CBD 2009). The largest known deepwater colonies of ivory tree coral are found in the Twin Ridges area of the Gulf of Mexico and in the Oculina Banks off the east-central coast of Florida (Barnette 2006; Brooke and Schroeder 2007). Deepwater colonies are taller and more fragile than their shallow-water counterparts (Brooke and Schroeder 2007). Deepwater ivory tree coral communities have been negatively impacted by destructive fishing practices off Florida's east coast and new interest in deepwater fisheries potentially poses a threat to this species in the Gulf of Mexico (Aronson et al. 2008j).

Another stony coral species, *Lophelia pertusa*, is the dominant azooxanthellate deepwater scleractinian coral in the Gulf of Mexico (Schroeder 2007). Assemblages of this species are fragile, slow growing, and long lived (Schroeder et al. 2005; Schroeder 2007), and can be found at depths from 40 m to 2,170 m (Lessard-Pilon et al. 2010). *Lophelia pertusa* can form dense aggregations on cold seep-associated carbonates that provide habitat to diverse and abundant communities of fauna, including many types of corals and cnidarians, crustaceans, fishes, and polychaete worms (Schroeder et al. 2005; Lessard-Pilon et al. 2010). Cordes et al. (2008) were the first to describe the communities associated with *L. pertusa* in the northern Gulf of Mexico. They documented 68 taxa that were closely associated, including three species with specific relationships with this coral: a polychaete in the genus *Eunice*, a corallivorous gastropod in the genus *Coralliophila*, and a decapod crustacean in the genus *Stenopus*. The researchers also compared species assemblages in these deepwater corals with assemblages of nearby vestimentiferan tubeworm aggregations and found that they showed a low degree of overlap and fairly distinct community structures. Lessard-Pilon et al. (2010) found elevated species diversity in communities associated with *L. pertusa*.

Oil and gas exploration and extraction are the primary threats to *L. pertusa* in the deep Gulf of Mexico, yet because of these fossil fuel interests, colonies of this species in the northern Gulf of Mexico are among the best studied. The most extensive colonies are located in the Viosca Knoll 826 block of the Minerals Management service (Brooke and Schroeder 2007), an area approximately 65 km from the Deepwater Horizon blowout. *Lophelia* reefs also occur in DeSoto Canyon off Alabama (Reed et al. 2006) and Green Canyon off Louisiana (Schroeder et al. 2005; Brooke and Schroeder 2007). These areas are unique and as such are worthy of protection from potential anthropogenic impacts (Brooke and Schroeder 2007). While the full extent of the Deepwater Horizon disaster will probably not be known for many years, deposition of toxic sediments could cause extensive coral mortality from both smothering and a reduction in oxygen content. *Lophelia pertusa* reefs are slow growing and their recruitment rates are unknown, and it is possible that damaged reefs may take many years to recover.



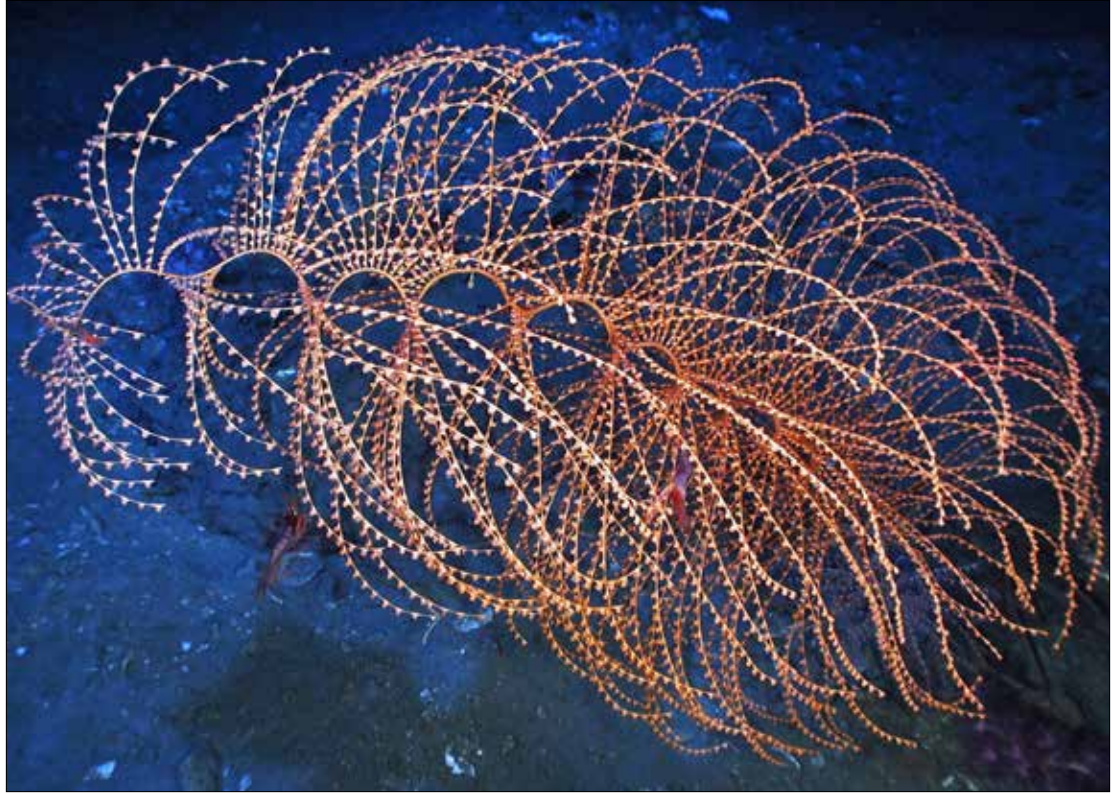
Assemblages of *Lophelia pertusa* are fragile, slow growing, and long lived, and provide habitat to diverse and abundant communities of fauna, including basket stars and fishes. (Photograph: NOAA Photo Library.)

Black corals (order Antipatharia)

Black corals can be locally common in the Gulf, particularly in the northern region and in the Florida Straits (Brooke and Schroeder 2007). No comprehensive faunal investigations have been undertaken but at least 20 species have been documented in the region, half of which are known from the Flower Garden Banks (Brooke and Schroeder 2007; Prouty et al. 2011). Most species live at depths of 20 to 500 m. Deepwater antipatharians are slow-growing, with estimated radial growth rates of 0.0145 mm per year, far slower than those recorded from warm and temperate shallow-water antipatharians (Williams et al. 2006). *Leiopathes* sp. is especially slow growing and in the Gulf of Mexico represents the slowest growing deep-sea coral known (Prouty et al. 2011; reviewed in Wagner et al. 2012). Radiocarbon analyses of deep-sea black corals in the Gulf indicate that these animals have been growing continuously for at least the last two millennia (Prouty et al. 2011).

Direct observations of black corals have been rare and little is known about the specific diet or feeding behavior of most species. However, the field observations that have occurred suggest that black corals are suspension feeders (Wagner et al. 2012). Antipatharians can be important habitat engineers to the benefit of a number of other marine organisms, including annelids, echinoderms, mollusks, sponges, and cnidarians, several of which are adapted to live exclusively on black corals (Wagner et al. 2012).

Given the longevity of many of these species, overexploitation of black corals could lead to local extinctions. Additional research is needed to determine how similar black coral communities are to their better known shallow-water counterparts. Information is also lacking on biogeographic ranges, reproduction, growth rates, and associated fauna (Wagner et al. 2012). The effects of oil spills on these communities are also relatively unknown, although their proximity to the Deepwater Horizon oil spill may cause harm to these populations, as has been observed by White et al. (2012). The recovery of deep-sea corals, and black corals in particular, would take decades—possibly centuries—based on their slow growth and the extreme age of many of these individuals (Prouty et al. 2011).



Gorgonian soft corals (also called sea fans) are a highly diverse and important part of deepwater communities. This *Iridigorgia pourtalesii* is providing shelter for shrimp, seen as pink-colored shapes. (Photograph: NOAA Photo Library, Aquapix and Expedition to the Deep Slope 2007.)

Gorgonians (order Alcyonacea)

Gorgonians (also called sea fans) are classified within the octocorals, an extremely diverse group of soft corals that are an important component of many deepwater, hard-bottom communities. In the Gulf of Mexico alone there are at least 162 species of gorgonians (Lunden and Georgian 2013). Octocoral biology is not well understood, and conservation of these species hinges on more research. For example, the habitat-forming deep-sea endemic *Callogorgia americana delta* is known in the Mississippi Canyon and is associated with areas of increased seep activity (Brooke and Schroeder 2007; Quattrini et al. 2013), but little is known about its basic biology.

Recently, research has emerged linking the Deepwater Horizon oil spill with damage to deep-sea gorgonians and their ophiuroid associates (White et al. 2012). The team of researchers found a deep-water coral community 11 km southwest of the Macondo wellhead that exhibited clear signs of stress response and was covered in a brown flocculent material. This colony was located beneath a large oil plume that was documented emanating from the wellhead, and Macondo oil signatures were found in nearby sediments. These findings suggest that impacts from the oil spill may be much larger and widespread than initially expected.

Deep-Sea Cold Seeps

The deep shelf and slope regions of the northern Gulf of Mexico have been extensively mapped for oil and gas exploration, and cold seeps in this area are the best studied in the world (Fisher et al. 2007; Cordes et al. 2009). Still, relatively little is known about species interactions and shifts in community structure in these habitats, and information on the ecology for many organisms associated with these areas is lacking. Deep-sea, cold-seep communities are dominated by symbiont-associated bivalves and polychaetes. Cordes et al. (2010) sampled some of these communities and found 66 other taxa, 39 of which had not been previously reported in the Gulf of Mexico. Forty-three of these appeared to be restricted to depths of 1,000 m or more. Deep-sea benthic environments are hotspots of biodiversity (Quattrini et al. 2013), and these recent findings of a high proportion of new species emphasize the importance of conservation efforts for these patchy benthic communities. Additional research into threats to seep communities is needed. For instance, although the organisms associated with these seeps have a natural high tolerance for reduced oxygen concentrations and hydrocarbons, oil spill impacts may challenge the tolerance of these communities beyond their natural thresholds (Joye and MacDonald 2010).

In the Gulf of Mexico, three species of vestimentiferan worms are known, all from deep waters and all linked to cold hydrocarbon seeps (Felder and Camp 2009). Tube worms can have life spans in excess of 250 years. Studies of the impacts from the oil spill on this unique, long-lived species are needed.

Conclusion

Oil spills have affected, and will continue to affect, invertebrates and their habitats across the globe. There is no question that petroleum hydrocarbons and their degradation products have high acute and chronic toxicity to marine invertebrates, but because of the extreme diversity of marine invertebrates and the relative lack of research and conservation attention they receive, we still know little about the ultimate ecosystem-level impacts of these events. More and better baseline data is needed on existing populations of ocean organisms, including invertebrates, so that we can better understand how these important animals are being affected not only by oil spills but also by multiple additional impacts such as other types of pollution, over fishing, and climate change. A tremendous amount of scientific expertise is available globally to conduct these baseline studies—for example, IUCN specialist groups are working specifically to determine the extinction risk of many marine invertebrates—but funding sources are lacking.

In addition to expanding our baseline knowledge of marine invertebrates in nearshore, coral reef, open water, and deep sea habitats, more research must be focused specifically on marine invertebrates in the aftermath of oil spills to monitor both immediate and long-term impacts, as well as recovery. As has been stated repeatedly in this report, any investigations of marine invertebrates are generally confined to groups with direct economic value in oil-impacted areas, i.e., invertebrate fisheries, but multiple other types of invertebrates will be affected and many of these groups play critical roles in ocean and coastal food webs.

Spills occur when oil is transported, as well as during exploration and drilling activities, in spite of regulations intended to prevent such events. No amount of precautions can guarantee that a spill will never occur. Thus, if we are to protect marine wildlife, we must reduce our consumption of oil while following best practices to reduce the possibility and impact of oil spills. This includes developing recommendations on where it is relatively safe to drill and on technologies and practices that can be used to stop or minimize spills. Such recommendations are beyond the scope of this report, but the publications below are recommended reading for insights on how to prevent oil spills and lessen their impacts in the future.

Recommendations for Reducing the Presence and Impacts of Oil in Marine Environments

For information and recommendations on how to prevent oil spills:

- ⇒ Oil Spill Prevention and Response in the U.S. Arctic Ocean: Unexamined Risks, Unacceptable Consequences (Pew Environment Group)

http://www.pewtrusts.org/uploadedFiles/wwwpewtrustsorg/Reports/Protecting_ocean_life/PEW-1010_ARTIC_Report.pdf

- ⇒ Recommendations to Prevent Oil Spills Caused by Human Error (The Pacific States/British Columbia Oil Spill Task Force)

http://www.oilspilltaskforce.org/docs/project_reports/HumanFactorRec.pdf

- ⇒ How to Prevent Deepwater Spills (MIT Technology Review)
<http://www.technologyreview.com/news/419328/how-to-prevent-deepwater-spills/>
- ⇒ Environmental Management in Oil and Gas Exploration and Production (Joint E&P [Exploration & Production] Forum/UNEP [United Nations Environment Programme] Technical Publication)
<http://www.ogp.org.uk/pubs/254.pdf>
- ⇒ “Oil Spill Prevention: A Proactive Approach,” by S. A. Lentz & F. Felleman (2003 International Oil Spill Conference)
<http://ioscproceedings.org/doi/pdf/10.7901/2169-3358-2003-1-3>

For information and recommendations on how to reduce oil dependence:

- ⇒ Reducing Petroleum Consumption from Transportation (C. R. Knittel. 2012. *Journal of Economic Perspectives* 26: 93-118)
<http://pubs.aeaweb.org/doi/pdfplus/10.1257/jep.26.1.93>
- ⇒ Breaking the Habit: Eliminating Our Dependence on Oil from the Gulf of Mexico by 2020, the Persian Gulf by 2013, and All Other Nations by 2033 (Oceana)
<http://oceana.org/en/news-media/publications/reports/breaking-the-habit-eliminating-our-dependence-on-oil-from-the-gulf-of-mexico-by-2020-the-persian>

For information on preparedness, mitigation, and response:

- ⇒ Cutting-Edge Oil Spill Response Research (The Minerals Management Service)
<http://ioscproceedings.org/doi/pdf/10.7901/2169-3358-1999-1-1167>
- ⇒ Long-term Biological Damage: What is Known, and How Should That Influence Decisions on Response, Assessment, and Restoration? (National Oceanic and Atmospheric Administration)
<http://ioscproceedings.org/doi/pdf/10.7901/2169-3358-2001-1-399>

Appendix A

Gulf of Mexico Marine Invertebrates at Risk

The information given here shows the status of at-risk marine invertebrates in the Gulf of Mexico, as listed by the U.S. Endangered Species Act, the IUCN Red List, and NatureServe.

Guide to Species Rankings				
<i>NatureServe global (NSG)</i>	G3: Vulnerable	G4: Apparently Secure	G5: Secure	Q: Taxonomic questions persist
<i>NatureServe state (NSS)</i>	S1: Critically Imperiled	S2: Imperiled		
<i>U.S. Endangered Species Act (ESA)</i>	LT: List Threatened	PE: Proposed Endangered	PT: Proposed Threatened	
<i>IUCN Red List</i>	CR: Critically Endangered	EN: Endangered	VU: Vulnerable	LC: Least Concern
<i>Florida Fish and Wildlife Conservation Commission (FFWCC)</i>	BV: Biologically Vulnerable	K: Keystone Species		

Scientific name	Common name	NSG	NSS	ESA	IUCN	FFWCC
Cnidarians (corals)						
<i>Acropora cervicornis</i>	Staghorn Coral	G3	S1 - FL	LT	CR	BV
<i>Acropora palmata</i>	Elkhorn Coral	G3	S1 - FL	LT	CR	BV
<i>Acropora prolifera</i>	Fused Staghorn Coral	G3Q	S1 - FL			BV
<i>Agaricia agaricites</i>	Lettuce Coral	G4	S2 - FL		LC	BV
<i>Agaricia lamarcki</i>	Lamarck's Sheet Coral			PT	VU	BV
<i>Colpophyllia natans</i>	Boulder Brain Coral	G3G4	S2 - FL		LC	BV, K
<i>Dendrogyra cylindrus</i>	Pillar Coral	G3	S1 - FL	PE	VU	BV
<i>Dichocoenia stokesii</i>	Elliptical Star Coral			PT	VU	BV
<i>Diploria clivosa</i>	Knobby Brain Coral	G4G5	S2 - FL		LC	BV
<i>Diploria labyrinthiformis</i>	Grooved Brain Coral	G4	S2 - FL		LC	BV, K

Scientific name	Common name	NSG	NSS	ESA	IUCN	FFWCC
Cnidarians (corals), continued						
<i>Diploria strigosa</i>	Symmetrical Brain Coral	G4	S2 - FL		LC	BV, K
<i>Eusmilia fastigiata</i>	Smooth Flower Coral	G3G4	S1 - FL		LC	BV
<i>Meandrina meandrites</i>	Maze Coral	G4	S2 - FL		LC	BV, K
<i>Montastraea annularis</i>	Boulder Star Coral	G5	S2 - FL	PE	EN	BV, K
<i>Montastraea cavernosa</i>	Great Star Coral	G5	S2 - FL		LC	BV, K
<i>Montastraea faveolata</i>	Mountainous Star Coral			PE	EN	BV, K
<i>Montastraea franksi</i>	Star Coral			PE	VU	
<i>Mussa angulosa</i>	Spiny Flower Coral	G3G4	S1 - FL		LC	BV
<i>Mycetophyllia ferox</i>	Rough Cactus Coral			PE	VU	BV
<i>Oculina varicosa</i>	Ivory Tree Coral				VU	BV
<i>Siderastrea siderea</i>	Massive Starlet Coral	G4	S2 - FL		LC	BV, K
Mollusks (gastropods)						
<i>Conus anabathrum</i>	Florida Cone Snail				VU	
<i>Lobatus gigas</i>	Queen Conch			CA		BV

Appendix B

Florida's Marine Invertebrate of Greatest Conservation Concern (Gulf of Mexico)

The tables in this appendix were compiled from:

Florida Fish and Wildlife Conservation Commission. 2011a. *Florida's Wildlife Legacy Initiative: Florida's State Wildlife Action Plan*. Tallahassee, Florida, USA.

Abbreviations

Fed. = Listed under U.S. Endangered Species Act

Fla. = Florida Fish and Wildlife Conservation Commission (FFWCC)

BV = Biologically vulnerable (FFWCC rank)

KS = Keystone (FFWCC rank)

TC = Taxa of concern (Despite limited information on these species, there is evidence or expert consensus of population declines, rarity, or limited habitat requirements.)

Scientific name	Common name	Trend	Fed.	Fla.	Rare	BV	KS	TC
Cnidarians (Corals, Anemones, and Sea Fans)								
<i>Acropora cervicornis</i>	Staghorn Coral	Declining	x	x		x		
<i>Acropora palmata</i>	Elkhorn Coral	Declining	x	x		x		
<i>Acropora prolifera</i>	Fused Staghorn Coral	Unknown				x		
<i>Agaricia agaricites</i>	Lettuce Coral	Declining				x		
<i>Agaricia fragilis</i>	Fragile Saucer Coral	Stable						x
<i>Agaricia lamarcki</i>	Sheet Coral	Declining				x		
<i>Bartholomea annulata</i>	Ringed Anemone	Unknown				x		
<i>Colpophyllia natans</i>	Boulder Brain Coral	Declining				x	x	
<i>Dendrogyra cylindrus</i>	Pillar Coral	Declining		x		x		
<i>Dichocoenia stokesi</i>	Pineapple Coral	Declining				x		
<i>Diploria clivosa</i>	Knobby Brain Coral	Stable				x		
<i>Diploria labyrinthiformis</i>	Grooved Brain Coral	Declining				x	x	
<i>Diploria strigosa</i>	Symmetrical Brain Coral	Declining				x	x	
<i>Discosoma neglecta</i>	Umbrella Mushroom	Unknown			x	x		
<i>Eusmilia fastigiata</i>	Smooth Flower Coral	Declining				x		
<i>Gorgonia flabellum</i>	Venus Sea Fan	Unknown						x
<i>Gorgonia ventalina</i>	Purple Sea Fan	Declining				x		

Scientific name	Common name	Trend	Fed.	Fla.	Rare	BV	KS	TC
Cnidarians (Corals, Anemones, and Sea Fans), continued								
<i>Isophyllastraea rigida</i>	Rough Star Coral	Stable						x
<i>Isophyllia sinuosa</i>	Sinuuous Cactus Coral	Stable						x
<i>Leptoseris cucullata</i>	Sunray Lettuce Coral	Declining					x	
<i>Madracis auretenra (mirabilis)</i>	Yellow Pencil Coral	Stable						x
<i>Madracis decactis</i>	Ten-rayed Star Coral	Stable						x
<i>Madracis formosa</i>	Eight-rayed Star Coral	Stable						x
<i>Madracis pharensis</i>	Encrusting Star Coral	Stable						x
<i>Manicina areolata</i>	Rose Coral	Stable						x
<i>Meandrina meandrites</i>	Maze Coral	Stable				x	x	
<i>Millepora alcicornis</i>	Encrusting Fire Coral	Declining						x
<i>Millepora complanata</i>	Bladed Fire Coral	Declining						x
<i>Montastraea annularis</i>	Column Star Coral	Declining				x	x	
<i>Montastraea cavernosa</i>	Great Star Coral	Declining				x	x	
<i>Montastraea faveolata</i>	Mountainous Star Coral	Unknown				x	x	
<i>Mussa angulosa</i>	Large Flower Coral	Stable				x		
<i>Mycetophyllia aliciae</i>	Knobby Cactus Coral	Declining					x	
<i>Mycetophyllia danaana</i>	Low-ridge Cactus Coral	Declining					x	
<i>Mycetophyllia ferox</i>	Rough Cactus Coral	Stable				x		
<i>Mycetophyllia lamarckiana</i>	Ridged Cactus Coral	Declining					x	
<i>Oculina robusta</i>	Robust Ivory Tree Coral	Stable						x
<i>Oculina varicosa</i>	Large Ivory Coral	Unknown				x		
<i>Phyllangia americana</i>	Hidden Cup Coral	Stable						x
<i>Phymanthus crucifer</i>	Bearded Anemone	Unknown				x		
<i>Porites branneri</i>	Blue Crust Coral	Stable				x		
<i>Porites porites</i>	Finger Coral	Declining						x
<i>Rhodactis osculifera</i>	Warty False Coral	Unknown			x	x		
<i>Scolymia cubensis</i>	Artichoke Coral	Stable						x
<i>Scolymia lacera</i>	Atlantic Mushroom Coral	Stable						x
<i>Siderastrea siderea</i>	Massive Starlet Coral	Declining				x	x	
<i>Solenastrea bournoni</i>	Smooth Star Coral	Stable						x
<i>Solenastrea hyades</i>	Knobby Star Coral	Stable						x
<i>Stichodactyla helianthus</i>	Sun Anemone	Unknown			x	x		
<i>Stylaster filigranus</i>	Friilly Lace Coral	Declining						x
<i>Tanacetipathes barbadensis</i>	Bottle Brush Black Coral	Unknown			x	x		
<i>Tanacetipathes tanacetum</i>	Bottle Brush Black Coral	Unknown						x
<i>Tanacetipathes thamnea</i>	Black Coral	Unknown						x

Scientific name	Common name	Trend	Fed.	Fla.	Rare	BV	KS	TC
Crustaceans (lobsters and shrimp)								
<i>Enoplometopus antillensis</i>	Flaming Reef Lobster	Unknown						x
<i>Lysmata wurdemanni</i>	Peppermint Shrimp	Unknown						x
Echinoderms (sea stars, sea cucumbers, sea biscuits, and urchins)								
<i>Actinopyga agassizii</i>	Five-toothed Sea Cucumber	Unknown						x
<i>Asterinides folium</i>	Common Blunt Armed Sea Star	Unknown						x
<i>Asteroporpa annulata</i>	Basket Star	Unknown				x		
<i>Astropyga magnifica</i>	Magnificent Urchin	Unknown						x
<i>Clypeaster chesheri</i>	A Sea Biscuit	Unknown						x
<i>Clypeaster luetkeni</i>	A Sea Biscuit	Unknown						x
<i>Clypeaster rosaceus</i>	West Indian Sea Biscuit	Unknown			x	x		
<i>Clypeaster subdepressus</i>	A Sea Biscuit	Unknown			x			
<i>Copidaster lymani</i>	Mottled Red Sea Star	Unknown						x
<i>Diadema antillarum</i>	Long-spined Urchin	Stable				x		
<i>Echinaster echinophorus</i>	Thorny Sea Star	Unknown						x
<i>Euthyonidiella destichada</i>	A Sea Cucumber	Unknown						x
<i>Euthyonidiella trita</i>	A Sea Cucumber	Unknown						x
<i>Havelockia inermis</i>	A Sea Cucumber	Unknown						x
<i>Holothuria mexicana</i>	Donkey Dung Sea Cucumber	Unknown						x
<i>Holothuria occidentalis</i>	A Sea Cucumber	Unknown						x
<i>Holothuria parvula</i>	A Sea Cucumber	Unknown						x
<i>Holothuria rowei</i>	A Sea Cucumber	Unknown						x
<i>Luidia senegalensis</i>	Nine-armed Sea Star	Unknown						x
<i>Lytechinus williamsi</i>	Jewel Urchin	Unknown						x
<i>Oreaster reticulatus</i>	Cushion Star	Unknown				x		
<i>Poraniella echinulata</i>	Red Miniature Sea Star	Unknown						x
<i>Thyonidium seguroensis</i>	A Sea Cucumber	Unknown						x
Mollusks (octopus, snails, sea slugs, gastropods)								
<i>Amphioctopus burryi</i>	Brownstripe Octopus	Unknown						x
<i>Calliostoma adela</i>	Keys Topsnail	Unknown			x	x		
<i>Calliostoma javanicum</i>	Chocolate-lined Topsnail	Unknown						x
<i>Cassis flammea</i>	Flame Helmet	Unknown				x		
<i>Cassis madagascariensis</i>	Emperor Helmet	Unknown				x		
<i>Cassis tuberosa</i>	King Helmet	Unknown				x		
<i>Charonia tritonis variegata</i>	Atlantic Trumpet Triton	Declining				x		
<i>Cinctura lilium</i>	Banded Tulip	Unknown				x		
<i>Crassostrea virginica</i>	Eastern Oyster	Unknown						x

Scientific name	Common name	Trend	Fed.	Fla.	Rare	BV	KS	TC
Mollusks (octopus, snails, sea slugs, gastropods), continued								
<i>Cymatium femorale</i>	Angular Triton	Unknown						x
<i>Cyphoma mcgintyi</i>	Spotted Cyphoma	Unknown						x
<i>Dolabrifera dolabrifera</i>	Warty Seacat	Unknown						x
<i>Doriprismatica sedna</i>	Red-tipped Sea Goddess	Unknown						x
<i>Elysia clarki</i>	Lettuce Sea Slug	Unknown				x		
<i>Elysia crispata</i>	Lettuce Slug	Unknown				x		
<i>Lithopoma americanum</i>	American Starsnail	Unknown						x
<i>Lobatus gallus</i>	Roostertail Conch	Unknown						x
<i>Lobatus gigas</i>	Queen Conch	Unknown				x		
<i>Macrocypraea cervus</i>	Atlantic Deer Cowrie	Stable				x		
<i>Macrocypraea zebra</i>	Measled Cowrie	Unknown						x
<i>Octopus joubini</i>	Atlantic Pygmy Octopus	Unknown						x
<i>Panopea bitruncata</i>	Atlantic Geoduck	Unknown			x	x		
<i>Thuridilla picta</i>	Painted Elysia	Unknown						x

Abbreviations and Acronyms

cm – Centimeter

DH – Deepwater Horizon

EEZ – Exclusive Economic Zone

g – Gram

kg – Kilogram

km – Kilometer

L – Liter

lw – Lipid weight

m – Meter

mg – Milligram

mL – Milliliter

mm – Millimeter

MAH – Monocyclic Aromatic Hydrocarbon

MEA – Millennium Ecosystem Assessment

MCE – Mesophotic coral reef

ng – Nanogram

NOAA – National Oceanic and Atmospheric Administration

NRDA – Natural Resource Damage Assessment

NRC – National Research Council

PAH – Polycyclic Aromatic Hydrocarbon

ppm – Parts per million

Units and Conversions

The following conversion factors were used for the report. They were taken from the Society of Petroleum Engineers, Unit Conversion Factors (<http://www.spe.org/index.php>).

Barrels \times 42 = U.S. gallons

Liters \times 0.264 = U.S. gallons

Cubic meters \times 264.2 = U.S. gallons

Cubic feet \times 7.481 = U.S. gallons

Liters \times 0.0009 = metric tons

Metric tons \times 294 = U.S. gallons

U.S. gallons \times 0.0034 = metric tons

Note regarding conversions between gallons (or liters) and metric tons: Because the gallon (or liter) is a measure of volume and the metric ton is a measure of weight, for truly precise conversions, it is important to take into account that equal volumes of different types

of oil differ in their densities. The specific gravity (sp gr), or density in relation to pure water, is generally less than 1.0, i.e., oil is typically lighter than water.

Specific gravity of petroleum products varies from about 0.735 for gasoline to about 0.90 for heavy crude to 0.95 for Bunker C (No. 6 fuel). In some cases, especially with some the heaviest No. 6 fuels, oil has a specific gravity greater than 1.0; these oils can sink.

The volume of a particular weight of oil varies with temperature and atmospheric pressure. The conversion factor of 294 gallons per metric ton is derived from an average specific gravity of 0.83, which corresponds to an American Petroleum Institute (API) gravity of 39. Note that API gravity and specific gravity are inversely proportional as per the formulae below. The 294 gallons/metric ton conversion unit is also convenient because it happens that 294 gallons = 7 barrels.

$$\text{API} = (141.5/\text{sp gr}) - 131.5$$

$$\text{sp gr} = 141.5/(\text{API} + 131.5)$$

Glossary

Acute – Single exposure, or short-term exposure.

Adsorption – The process whereby one substance is attracted to and adheres to the surface of another substance without actually penetrating its internal structure.

Advection – Movement of a mass of fluid via bulk motion.

Aerobic – Biological processes requiring oxygen.

Alkanes – A class of hydrocarbons (compounds of hydrogen and carbon) that make up the primary part of the

saturate group of components in oil. They are characterized by branched and unbranched chains of carbon atoms with attached hydrogen atoms. Alkanes all have the general formula C_nH_{2n} , and contain no carbon-carbon double bonds, meaning they are “saturated” with hydrogen. Alkanes are also called paraffins and are a major constituent of natural gas and petroleum. Alkanes containing less than five carbon atoms per molecule are usually gases at room temperature (e.g., methane); those with 5 to 15 carbons are usually liquids, and straight chain alkanes with more than 15 carbons are solids. At low concentrations, alkanes with low carbon numbers may produce anesthesia and narcosis (stupor, slowed activity) and at high concentrations can cause cell damage and death in a variety of organism. Alkanes with a high number of carbon atoms are not generally toxic but have been shown to interfere with normal metabolic processes and communication in some species.

Alkenes – A class of straight or branched chain hydrocarbons similar to alkanes but characterized by the presence of carbon atoms united by double bonds. Alkenes are also called olefins and all have the general formula C_nH_{2n} . Alkenes containing two to four carbon atoms are gases at room temperature, while those containing five or more carbon atoms are usually liquids. Alkenes are not found in crude oils but are often formed in large quantities during the cracking of crude oils and are common in many refined petroleum products such as gasolines. These hydrocarbons are generally more toxic than alkanes but less toxic than aromatics.

Anaerobic – Biological process that does not require oxygen.

Aromatic hydrocarbons – Aromatic hydrocarbons are those which contain one (monocyclic, see “monocyclic aromatic hydrocarbon”) or more (polycyclic, see “polycyclic aromatic hydrocarbon”) benzene rings (the configuration of six carbon atoms in a ring). The name of the class comes from the fact that many of them have strong, pungent aromas. This is a class of hydrocarbon considered to be the most immediately toxic hydrocarbons found in oil and that are present in virtually all crude oils and petroleum products. Certain aromatics are considered long-term poisons and often produce carcinogenic effects. Aromatics are characterized by rings containing 6 carbon atoms. Most aromatics are derived from benzene, which is the simplest aromatic.

Ballast water – In order to maintain stability during transit along coasts and on the open ocean, ships fill their ballast tanks with water. Large ships often carry millions of gallons of ballast water. This water is taken from coastal port areas and transported with the ship to the next port of call where the water may be discharged or exchanged. Ballast water releases may contain oil and can be a source of oil discharges within the ocean.

Barrel – A unit of liquid (volumetric) measure for petroleum and petroleum products, equal to 35 imperial gallons, 42 U.S. gallons, or approximately 160 liters.

Benthos – The community of organisms which live on, in, or near the seabed, also known as the benthic zone.

Bioaccumulation (oil) – The incorporation of hydrocarbons in the tissue of a marine organism through the uptake of dissolved fractions of oil across the gills or skin or through direct ingestion of the pollutant that can affect its predators. If the pollutant is not broken down in the course of the organism’s metabolic processes, it can become increasingly concentrated up the food chain, see “biomagnification”.

Biodegradation (oil) – Under certain conditions, living microorganisms (primarily bacteria, but also yeasts, molds, and filamentous fungi) alter and/or metabolize various classes of compounds present in oil.

Biomagnification (oil) – Increase in concentration of a hydrocarbon from one link in a food chain to another.

Bioremediation (oil) – A technique used to remove oil residues in contaminated water or sediments by enhancing natural biodegradation by indigenous microorganisms through the application of nutrients (e.g., nitrogen and phosphorus) in the form of fertilizers, or by seeding new bacteria.

Bioturbation – Burrowing activities in benthic environments which may contribute to sediment turnover and increase oxygenation and nutrient availability in underlying sediments.

Byssal thread – Threads produced by bivalves (e.g., mussels) that allow attachment to substrate.

Chronic – Repeated exposures over time.

Cold seep – An area of the ocean floor where hydrogen sulfide, methane and other hydrocarbon-rich fluid seepage occurs through underlying rock and sediment and emerges on the ocean bottom.

Crude oil – A naturally occurring, unrefined petroleum product composed of hydrocarbon deposits. Crude oil

can be refined to produce usable products such as gasoline.

Dispersion (oil) – The breakup of oil on the surface of the water into droplets or fragments that spread and sink into the water column. This process allows dissolution, biodegradation, and sedimentation to occur.

Dispersant (oil) - Chemical agents such as surfactants, solvents, and other compounds that are used to reduce the effect of oil spills by changing the chemical and physical properties of the oil.

Dissolution (oil) – Occurs when soluble compounds of oil are dissolved in water.

Emulsification – Process whereby one liquid is dispersed into another liquid in the form of small droplets; occurs when two liquids become mixed and is increased by wave or storm action or chemical dispersants.

Emulsifier – A surface-active agent that positions itself at the oil–water or air–water interface and by reducing the surface tension promotes the formation and stabilization of an emulsion allowing oil to mix with water.

Emulsified oil (emulsion) – An oil–water mousse; a mixture of liquids that are normally immiscible.

Entrainment – Mixing by wind and water turbulence that moves oil into the water column.

Epifauna – Organisms that live primarily on the surface of sediment or substrate.

Exclusive Economic Zone (EEZ) – A sea zone in which a state has special rights over the exploration and use of marine resources, stretching from its coast out to 200 nautical miles.

Gonochoric – The state of having just one of two distinct sexes in any one individual organism.

Holoplankton – small marine invertebrates that spend their entire life cycle within the plankton community (e.g., krill, amphipods, and copepods)

Hydrocarbon – Organic chemical compounds composed only of the elements carbon and hydrogen. Hydrocarbons are the principal constituents of crude oils, natural gas, and refined petroleum products, and include four major classes of compounds (alkanes, alkenes, naphthenes, and aromatics) each with characteristic structural arrangements of hydrogen and carbon atoms, as well as different physical and chemical properties.

Hydrothermal vent – A fissure in the planet’s surface from which geothermally heated water is released.

Infauna (infaunal) – Species that burrow into or below the sediment-water interface.

LD₅₀ - Dose or concentration of a substance that induces mortality in 50% of the exposed test organisms; the lower the LD₅₀, the more toxic that substance.

Lipophilic – Fat-soluble.

Macrofauna – Benthic invertebrates which are larger than 500 mm.

Medusa (plural **medusae**) – Free-swimming body form (i.e., Cnidaria) that use pulsing movements of their bell- or umbrella-shaped bodies to travel through the water column.

Meiofauna – Benthic invertebrates which range in size from 50–500 mm (e.g., copepods and nematode worms).

Meroplankton – Small marine invertebrates that inhabit the plankton temporarily during immature phases (e.g., eggs and larvae of sea urchins, sea stars, crustaceans, mollusks, corals, marine worms).

Mesophotic (coral ecosystems) –Are ecosystems characterized by the low availability of light for photosynthesis and the presence of corals, sponges and algae as the dominant structural components; occurring from 30 m (100 ft) to greater than 100 m (330 ft) depth.

Metric ton – A unit of mass and weight equal to 1000 kilograms. There are approximately 7 to 9 barrels (250 to 350 gallons) of oil per metric ton, depending on the specific gravity of the crude oil or petroleum product.

Molecular weight – Refers to the mass of a molecule. It is calculated as the sum of the mass of each constituent atom multiplied by the number of atoms of that element in the molecular formula.

Molt – The manner in which an animal casts off part of its body (often, but not always, an outer layer or covering), either at specific times of the year, or at specific points in its life cycle.

Monoaromatic compounds – See “Monocyclic Aromatic Hydrocarbons”

Monocyclic aromatic hydrocarbons (MAH) - Hydrocarbon molecules that may occur in varying proportions in crude oil and refined products and are composed of carbon and hydrogen atoms arranged in long chains and one single ring of atoms (e.g., benzene, toluene, ethylbenzene, xylenes).

Naphthenes – A class of cyclic aliphatic hydrocarbons obtained from petroleum with physical and chemical properties similar to alkanes but characterized by the presence of simple closed rings. Like alkanes, naphthenes are also saturated, meaning they contain no carbon-to-carbon double bonds, and have the general formula C_nH_{2n} . Also called cycloalkanes.

Narcosis – An effect induced by a compound that can result in toxic effects that result in the degradation of cell membranes, impairment of physiological mechanisms, decreased fitness in organisms or death depending on exposure.

Natural seep – See “oil seep”.

Oil seep (petroleum) – An area on the ocean floor where natural liquid or gaseous hydrocarbons escape to the earth’s atmosphere and surface, normally under low pressure or flow.

Oil/water separator – A device designed to separate gross amounts of oil and suspended solids from the wastewater effluents of oil refineries, petrochemical plants, chemical plants, natural gas processing plants, and other industrial sources.

Olefin – A group of unsaturated hydrocarbon compounds that contain fewer hydrocarbon atoms than the maximum possible. Olefins have at least one double carbon-to-carbon bond that displaces two hydrogen atoms. Significant amounts of olefins are found only in refined products (see also alkenes).

Paraffin – A waxy substance obtained from the distillation of crude oils and often contained in the crude oils. Paraffin is a complex mixture of alkanes with higher numbers of carbon that is resistant to water and water vapor and is chemically inert. The term is sometimes used to refer to alkanes as a class of compounds. (See also alkanes).

Parent compound/material – The original compound from which derivatives may be obtained.

Pelagic – A zone within the ocean that goes from the surface to almost the bottom; the “open sea”.

Petroleum – A naturally occurring liquid mixture of hydrocarbons and other liquid organic compounds that is present in certain rock strata and can be extracted and refined to produce fuels including gasoline, kerosene, and diesel oil. Petroleum is formed when large quantities of dead organisms, usually zooplankton and algae, are buried underneath sedimentary rock and undergo intense heat and pressure.

Photo-oxidation – Oxidation that is mediated by the energy from sunlight. Occurs when the sun’s action on an oil slick causes oxygen and carbon to combine to form new products that may be resins. The resins may be somewhat soluble and dissolve into the water, or they may cause water-in-oil emulsions to form. Some oils are more susceptible to photo-oxidation than others.

Phytoplankton – Microscopic photosynthetic organisms that inhabit the upper sunlit surfaces of water bodies; primary producers in aquatic ecosystems.

Plankton – Organisms that live suspended in the water column but generally are unable to counter water currents because of small size or insufficient mobility.

Planula (plural **planulae**) – A cnidarian larva that is elongated and radially symmetrical with anterior and posterior ends, which eventually attaches to a substrate upon which further growth occurs.

Polycyclic aromatic hydrocarbons (PAH) - Hydrocarbon molecules that may occur in varying proportions in crude oil and refined products and are composed of carbon and hydrogen atoms arranged in long chains and rings (multiple rings) (e.g., Benzo(a)pyrene, Benzoanthracene, Benzo(b)fluoranthene, Fluoranthene, Naphthalene).

Polyp – A life form in the phylum Cnidaria that is cylindrical in shape and elongated with an aboral end (the side or end that is furthest from the mouth) that is attached to substrate by a holdfast; while in colonies of polyps they are connected to other polyps. The oral end contains the mouth and is surrounded by a cirlet of tentacles.

Production facility – A facility which performs processing of production fluids from oil wells in order to separate out key components and prepare them for export.

Production platform (oil rig or offshore platform) – A large structure with facilities to drill wells, to extract and process oil and natural gas, and to temporarily store product until it can be brought to shore for refining and marketing. Depending on the circumstances, the platform may be fixed to the ocean floor, may consist of an artificial island, or may float.

Refined oil – A process where crude oil is refined into products such as petroleum naphtha, gasoline, diesel fuel, asphalt base, heating oil, kerosene, and liquefied petroleum gas.

Remediation – The act of reversing or stopping environmental damage (may be instituted naturally as in microbial oxidation (bioremediation) of oil or by the physical removal of a pollutant from the environment).

Saturate group – A group of hydrocarbon components found in oils that consist primarily of alkanes, which are compounds of hydrogen and carbon with the maximum number of hydrogen atoms around each carbon. The term saturated refers to the carbons that are “saturated” with hydrogen. The saturate group also refers to compounds made up of the same carbon hydrogen constituents but with the carbon atoms bonded to each other in rings or circles. Larger saturate compounds are often referred to as waxes. (See also Alkanes, hydrocarbons, paraffins, waxes).

Sessile – Non-motile; animals that are usually permanently attached to a solid substrate, such as a part of a plant or a rock, or on their own substrate such as corals and oysters.

Sheen – Common term used to describe a thin film of oil, usually less than 2µm thick on the water surface.

Slick – Term used to describe a film of oil resulting from a spill. (See also Sheen).

Stranding – Washing onto shore or becoming stuck in shallow water (e.g., dead or moribund marine animals or oil).

Sublethal – effect of exposure of a toxicant is detrimental to an organism, but below the level that directly causes death within a test period

Sublethal effect – Physical or behavioral effects on individuals that survive exposure to oil or are exposed to sublethal concentrations of oil.

Sublethal exposure (or dose) – Dose or concentration of a substance that does not cause significant mortality but may cause other detrimental effects.

Tar balls or mats – Compact, semisolid, or solid masses of highly weathered oil formed through the aggregation of viscous hydrocarbons with a high carbon number and debris in the water column. Tar balls are often washed up on shorelines where they tend to resist further weathering.

Trophic level – The trophic level of an organism is the position it occupies in a food chain.

Volatile organic compounds – Organic compounds with vapor pressure high enough to cause the compounds to evaporate at normal temperatures.

Water-in-oil emulsion – A type of emulsion in which droplets of water are dispersed throughout the oil. It is formed when water is mixed with relatively viscous oil by wave action. This type of emulsion is sometimes stable and may persist for months or years after a spill. Water-in-oil emulsions containing 50% to 80% water are most common, range in consistency from grease-like to solid, and a generally referred to as “chocolate mousse”.

Zooplankton – Small animals that are suspended within the water column and drift within marine, estuarine, and fresh water bodies. Invertebrate zooplankton in marine and estuarine waters include: jellyfish, tunicates, and crustaceans such as amphipods, krill, and copepods, and most larval forms of sea urchins, sea stars, crustaceans, and marine snails.

Zooxanthellae – Symbiotic photosynthetic microorganisms contained within shallow water corals; corals provide zooxanthellae with protection, nutrients, and exposure to sunlight, while zooxanthellae provide oxygen and supplemental energy to corals.

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