contained lower-molecular-mass hydrocarbons, and about half of the hydrocarbons released were methane gas, the remainder being crude oil (King et al., 2015). Thus, the oil was more biodegradable than the oil released in Alaska in 1989. A small minority of the oil was collected from the vicinity of the well. The wellhead was not capped until July 15, 2010, 84 days after the initial event. Toxic drilling muds were also released in the immediate vicinity of the wellhead.

Nearly 2 million gallons of dispersants were added to the water, a large fraction near the wellhead itself. By the beginning of May, the oil reached the Louisiana coast, and authorities used booms to attempt to prevent the oil from reaching shore. The booms were too small and generally failed, however, resulting in concentrated oil-polluted areas in Louisiana. Currents moved the oil to the east and spread as far as Florida, over a period of 3 months. The extent of oil movement and stretch of coastline affected was about 650 km, which was much smaller than the 2,500 km of coast affected during the 10-month spread of the 1979–1980 Ixtoc event in Mexico (**Figure 22.11**).

The coastal environments affected included a large stretch of salt marsh environment. Oil permeated marsh sediments, and a number of seabird and sea turtle nesting grounds were saturated. Marsh sediments impacted with oil killed marsh vegetation, making it likely that such areas will experience erosion in the coming years. Thousands of seabirds and other marine organisms were oiled and killed (see effects of oil on seabirds in next section). Nearly 600 marine mammals, mostly bottlenose dolphins, were found dead ashore, and a few died from an apparent bacterial infection, *Brucella*, that normally afflicts cattle. The longer-term effects for the dolphin are unknown but may involve compromising of the dolphin immune system. While a number of sea turtle eggs were relocated to beaches in Florida, it is likely that most of an entire year class of sea turtles was lost to the Gulf. Economic losses were also severe. About half of the bottlenose dolphins examined showed evidence of direct toxicity from the oil, including lung disease (Schwacke et al., 2014). Most Gulf fisheries off of Louisiana, Mississippi, Alabama, and the panhandle region of Florida were closed for months, although some began reopening in the fall.

Salt marshes in several areas of Louisiana suffered extensive oiling, which led to plant death and erosion. Seaward edges of marshes were oiled more and suffered erosion, which has caused marsh loss. Even 5 years later, storms erode sediments and wash buried oil onto marshes and shores in Louisiana. Such environments already have been lost at a great rate, so the Gulf oil spill represents a stress that mounts on other problems such as low oxygen concentrations and coastal habitat loss. Still, marsh areas where erosion was slight have been recolonized after 2 years by thick marsh grass (Silliman et al., 2012). Oil was found in a restricted set of marshes in Louisiana, but was not detected in most offshore sediments, except within a few kilometers of the well itself, where polycyclic aromatic hydrocarbons (PAHs) and barium concentrations were believed to be toxic to marine organisms.[2] Both macrobenthos and meiobenthos were severely affected within 3 km of the wellhead, but significant effects could also be detected in a larger area around the wellhead of approximately 150 km^2 (Montagna et al., 2013). Recovery may take several decades. In the short term, Alabama coastal juvenile fishes were not affected within important nursery eel grass beds, and some fish stocks are even larger because of the reduced fishery pressure from the fishing closures after the oil spill began (Fodrie and Heck, 2011). Zooplankton dropped during the first summer but returned to normal a year later. Still, there is early evidence that oil hydrocarbons have been incorporated into zooplankton, which might increase through higher levels of the food web. Longer-term effects or even broad areas of sea bottom that might have been affected in the early days after the blowout are essentially unknown, but after a year, widespread evidence shows that the seabed has dense populations of infaunal benthos and sediment bioturbation seems typical, indicating bottom health. An especially exciting part of the story is the question of breakdown of oil by bacteria and the contribution to recovery within the Gulf, which we discuss in **Hot Topics Box 22.1**.

HOT TOPICS IN MARINE BIOLOGY

Is the Gulf of Mexico Adapted to Oil? 22.1

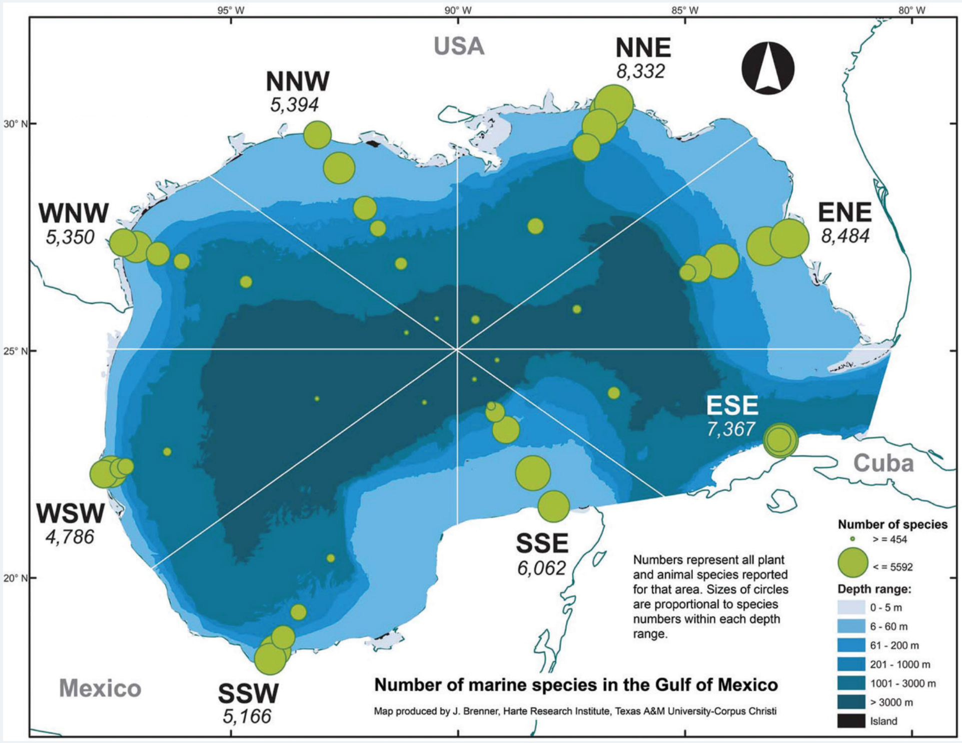
The Deepwater Horizon oil well blowout dumped about 200 million gallons of crude oil into one of most productive inland seas in the world. The Gulf of Mexico ecosystems are among the most diverse in the world, with over 15,000 species. Most of the known diversity is found in depths shallower than 60 m (**Box Figure 22.1**). These shallow areas have much more habitat diversity, which probably explains the increased species diversity. The shallower areas are therefore the most vulnerable with regard to diversity loss. Shoreline habitats harbor crucial seabird nesting areas and fish spawning grounds, which makes it likely that other major Gulf-wide ecosystem effects will be detected following a spill as large as the BP accident. Given the size of the Gulf, it seems unlikely that we will ever get a good estimate of the magnitude of larval, benthic invertebrate, and planktonic mortality caused by the release.

When the well was finally capped in July 2010, many expected the worst: a water body with oil that would persist for years, if not decades. So

[2] Barium in these sediments derive from oil drilling muds.

HOT TOPICS IN MARINE BIOLOGY

Is the Gulf of Mexico Adapted to Oil? *continued* 22.1



BOX FIG. 22.1 Number of marine species in the Gulf of Mexico as a function of depth. (Courtesy of Harte Research Institute)

it came as a surprise that the volume of oil in the Gulf of Mexico following the BP spill appeared to have been reduced to very low levels in only a matter of months! Some oil was trapped in booms along the shoreline and removed at the wellhead to tankers, but underwater plumes of oil were soon discovered, so not all of the oil was even at the surface to be scooped up or destroyed by surfactants, which were liberally sprayed on the surface from airplanes. Indeed, the National Oceanic and Atmospheric Administration can account for about 25 percent of the total oil as being recovered or burned, so most oil has entered the system in a variety of ways.

Where did the oil go? A previous oil well blowout in Mexico in 1979 resulted in the release of 140 million gallons of oil and, although longer-term data are largely anecdotal, short-term studies in the first 3 years showed that Texas shoreline habitats and biotas seemed to recover rapidly and persistent effects remained only in some isolated Mexican localities. Is there a pattern here?

The Deepwater Horizon well explosion occurred in April 2010, but by the following winter, officials from the U.S. Coast Guard and the National Oceanographic and Atmospheric Administration claimed that most of the oil was gone! This was a great surprise to the scientific community and to the public, who greeted the claim with a measure of appropriate skepticism. But some interesting facts about the oil distribution raised some questions. A December 2010 report from the Operational Science Advisory Team (OSAT), chartered by the U.S. Coast Guard, showed that oil was largely absent in Gulf sediments, with the exception of sites within a few kilometers of the Deepwater Horizon wellhead and some shoreline locations. Extensive sampling failed to find concentrations of oil that exceeded concentrations of oil or hydrocarbons that might endanger human health. Most important, any samples with oil did not bear the chemical signature of oil from Deepwater Horizon (Operational Science Advisory Team, 2010). As a result, federal agencies announced that more than three-quarters of the oil was gone by the fall of 2010, owing to cleanups and microbial breakdown. PAHs have been found in sediments within a few kilometers of the wellhead, but a recent report suggests that a year later, we have bottom sediments that are burrowed and show no strong evidence of oiled and anoxic sediments. Does this indicate a recovery? Still, a massive underwater plume of hydrocarbons over 35 km long and 1,000 m deep was reported in June. Are these plumes common, and will they disappear over time?

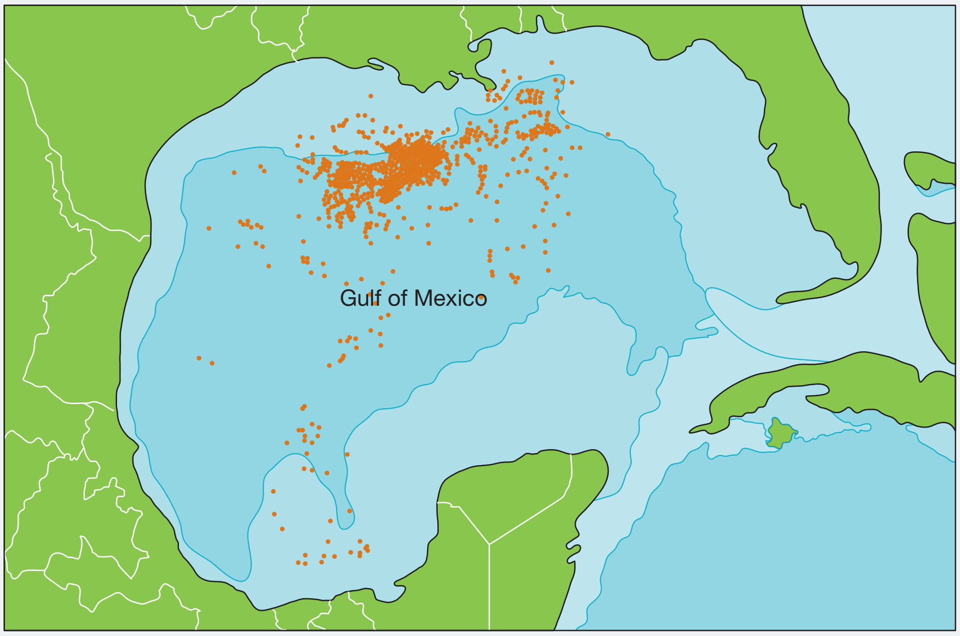
Keep in mind that hydrocarbons have been found in plankton and benthic organisms. Bottlenose dolphins show the effects of oil toxicity. Oil has affected corals but only at sites close to the wellhead. But we are seeing only short-term effects on bottom communities and offshore water column species and apparent recovery. Why? Is it just dilution of oil hydrocarbons?

One possible clue to an important component of the apparent "recovery" can be found in the widespread natural seeps of hydrocarbons that are known throughout the Gulf of Mexico, amounting to a surprising 43 million gallons a year. Most of the known seeps are deeper than the 60 m depth boundary and are found in the central northern part of the Gulf,

continues

HOT TOPICS IN MARINE BIOLOGY

Is the Gulf of Mexico Adapted to Oil? *continued* 22.1



BOX FIG. 22.2 Distribution of known natural hydrocarbon seeps in the Gulf of Mexico. (Courtesy of Ian MacDonald, after Tunnell, 2011)

many near Louisiana and east Texas (**Box Figure 22.2**). In Chapter 18 we discussed the cold-water hydrocarbon seeps that support local hotspots of benthic diversity, resembling the faunas seen around mid-oceanic hot vents. Natural seeps of oil are very common in the Gulf, so we might expect that microbial organisms have appeared and evolved to break down and derive nutrition from the oil and especially methane gas, which can be broken down by specialized bacteria. If oil seepage suddenly increased, then oil-decomposing bacteria might reproduce rapidly and keep up with oil seepage. Keep in mind, however, that the oil spill added hydrocarbons at seven times the background seep rate from the Gulf, so bacteria may not be powerful enough to keep up with biodegradation.

A second important factor is water temperature: Microbial oil-decomposing activity might be faster in the Gulf than in the colder waters of Alaska, although we should note that the Deepwater Horizon well was about 1,500 m deep, where waters were only about 5°C. Still, currents may have spread the hydrocarbons to shallower and warmer waters. If microbial decomposition happened on the scale of the entire Deepwater Horizon blowout, then microbial breakdown may have produced a spectacular case of fairly rapid natural recovery from a stupendous human error, given the likely longer-term effects on shorebirds, perhaps future year classes of fish species, and the structural integrity of a number of marshes in Louisiana.

Do we have any evidence for such microbial action? Terry Hazen and a large group of colleagues (2010) investigated an undersea oil plume emanating from the area of the wellhead. This oil spill came at a time when next-generation sequencing methods allowed rapid molecular-based identification of bacterial groups specialized to degrade hydrocarbons. Reduced oxygen concentrations within the plume relative to outside of the plume indicated enhanced oil-degrading microbial activity. Confirmation of increased abundances of bacteria was found within the plume, especially genetic evidence for members of the Oceanospirales within the gamma-Proteobacteria, which are known to break down petroleum hydrocarbons. Molecular biologists could also use state-of-the-art methods of transcriptomics to study degrees of gene expression of the various bacterial groups associated with hydrocarbon degradation. High levels of gene expression of these bacteria was found for *n*-alkane and cycloalkane degradation, although activity for genes involved in breakdown of more resistant but abundant components (e.g., benzene, toluene, xylene) was low (Mason et al., 2012). Oil breakdown of some components was occurring faster than might be expected at the 5°C temperatures found near the bottom at the wellhead. Apparently, propane and ethane were the two main substrates used as energy sources by a very low diversity of bacterial species within the oil plumes (Valentine et al., 2010). Kessler and colleagues (2011) provided evidence that methanotrophic bacteria likely consumed all of the methane found in a large plume that stretched offshore of the Louisiana coast. Later, methane and aromatic hydrocarbons came to dominate the plume (Dubinsky et al., 2013). Hydrocarbons in crude oil were likely also broken down in large measure by bacterial groups (King et al., 2015).

The microbial community of Louisiana beaches also responded directly to the influx of oil, especially in the rapid expansion of bacterial species known to live on oils, as shown by a metagenomic analysis of beach sediment using 16S rRNA sequencing. Species capable of growing on oil as the sole carbon source also appeared. A transcriptomic analysis also demonstrated that expression of oil-degrading genes greatly expanded in beach microbial communities (Lamendella et al., 2014). Oil disappeared faster than in another oil spill studied in a colder and more pristine habitat. Again, the resilience of the Gulf seems notable.

HOT TOPICS IN MARINE BIOLOGY

Is the Gulf of Mexico Adapted to Oil? *continued* 22.1

Because studies were undertaken within restricted areas, we do not know what happened on the large scale of the Gulf of Mexico, but we can formulate a hypothesis: Long-term leaks of short-chain hydrocarbons in the Gulf have resulted in evolutionary change that increased the responsiveness of bacteria to hydrocarbons. It is well known that bacteria exposed to petroleum tend to be more capable of breaking down petroleum over time (Leahy and Colwell, 1990). This response could be merely the result of an increase in gene expression as exposure to oil induces certain genes, or it might be the result of natural selection, in which certain bacterial genotypes are selected over others by virtue of their ability to obtain energy and reproduce by breaking down oil more efficiently. As it turns out, there are very few seeps near the Deepwater Horizon site, so it may be the case that natural selection for oil-decomposing bacteria might have occurred throughout the Gulf. At any one place, rare occurrences of the oil-decomposing genotypes would be selected from low to high abundance when oil appears. It is important to realize that there is no strong evidence currently to prove that bacterial breakdown was responsible for the disappearance of any submarine oil plume. But there is every reason to believe that hydrocarbon-degrading bacteria were present both in deep waters and in coastal marshes before the oil spill. Warm water temperatures also probably accelerated degradation rates. Hydrocarbon-degrading bacteria likely increased in abundance as the oil spill hit, and a form of succession resulted in replacements of bacterial groups by others as specific hydrocarbons became uncommon (Valentine et al., 2012; King et al., 2015). The growth and expansion of hydrocarbon-degrading bacteria likely has had its own disruption on the microbial ecology of Gulf habitats, and it is of great interest to know when a new postspill equilibrium will be reached.

Despite the notoriety of major tanker and offshore drilling accidents, much oil is probably spilled during delivery of oil to harbor terminals. Spills occur when valves malfunction and when workers attempt to pump more oil into a tank than it can hold. U.S. law requires a set of containment booms to surround any marine loading area, but not all countries have legislation like this. Because of the lack of such a precaution, an August 1999 release from open valves of the tanker *Laura D'Amato* in Sydney Harbor, Australia, resulted in a spill of as much as 300,000 liters of Saudi Arabian crude oil along the shores there. The spill oiled thousands of shorebirds but dispersed from the shoreline after a few days. Chronic releases are important in increasing the concentrations of toxic substances, such as polycyclic aromatic hydrocarbons, in marine sediments (see later).

COMPONENTS AND EFFECTS OF OIL

■ The effect of oil varies with chemical composition and the affected organisms.

Oils may have the following components:

1. *Paraffins.* Straight- or branched-chain alkanes that are stable, saturated compounds having the formula $C_nH_{2n}12$.
2. *Naphthenes.* Cycloparaffins that are saturated but whose chain ends are joined to form a ring structure.
3. *Aromatics.* Unsaturated cyclic compounds that are based on the benzene ring, with resonating double bonds, and six fewer hydrogen atoms per ring than the corresponding naphthene. Often toxic, aromatics have been implicated in cancers.
4. *Olefins.* Alkenes, or unsaturated noncyclic compounds with two or fewer hydrogen atoms for each carbon atom. Olefins have straight or branched chains; they are not found in crude oil.
5. *Light gases.* Hydrocarbons of very short carbon chains (1–4).

The effect of oil varies with oil chemistry and the organisms affected. Crude oil usually has less than 5 percent aromatics and is widely regarded as the least toxic. Refined oil such as fuel oil may have 40–50 percent aromatic compounds. The toxic compounds in oil are known to impair cell membrane function and may impair behavior in a wide variety of organisms. As mentioned earlier, reproduction can be impaired in invertebrates exposed to these substances. Survival and development of fish eggs and larvae are also affected negatively. Phytoplankton production can also be reduced.

■ Oil affects seabirds via direct toxic effects and by disrupting the mechanical structure of feathers.

Oil has an especially devastating effect on seabirds. Birds maintain a high and constant body temperature, and **feathers** act partially as insulation. The fluffy **down feathers** provide an air space for insulation, and the air is sealed in by **contour feathers**. The **barbules** interlock efficiently, and the hydrophobic surface of the contour feathers helps to keep water from collapsing the downy layer beneath (**Figure 22.12**). Unfortunately, oil readily coats the surface of the contour feathers and collapses their interlock. Seabirds that come into contact with oil, therefore, soon lose their insulation and are likely to die of hypothermia. The oil also impedes flight, and the birds often ingest toxic oil while preening. (Some birds such as puffins are attracted to oil, as if they expect food to be found on the surface.) Both the *Torrey Canyon* and *Amoco Cadiz* spills caused the majority of the affected Atlantic puffins and other diving birds to cease breeding. These are some of the reasons oil spills are usually followed by conservationists' frantic cleanup efforts, but historically these efforts have been in vain (**Figure 22.13**). However, more recent efforts to remove oil from seabirds have been more successful. A study of cleaning efforts of penguins following a 1994 oil spill in South Africa estimated that about 75 percent of the cleaned birds