and by the 1960s the fishery was strongly impacted, especially in the mid-Atlantic states. Overfishing has resulted in the scarcity of fish older than 5 years, which greatly impacts recruitment, since large fish have disproportionate production of gametes. This species is a planktivore and may have been an ecologically significant consumer before population numbers collapsed. Body size has declined greatly, and mid-Atlantic populations are at a low state. Menhaden also may be the last major prey species available to larger carnivorous fish. Overall, the ecosystem services performed by this species—keeping phytoplankton in check and providing food to top predators—may be worth more than its value as fertilizer. Fishing restrictions have allowed some recovery in northeastern U.S. waters.

Causes and Cures of Stock Reduction

- **Stock reduction can result from random variation as well as from environmental change; fishing would be superimposed on the effects of these factors and appears to cause greater fluctuations than when fishing is absent.**

Fishery managers are concerned with the causes of the great fluctuations in fish populations. Such fluctuations are commonplace in estuarine, shelf, and open-ocean fisheries. One of the most spectacular changes ever recorded illustrates the difficulties in understanding the population changes. In the 1920s and 1930s, the Pacific sardine was landed year after year in the thousands of tons, yet the population declined sharply in the 1940s. After this decline, the anchovy increased greatly in abundance (**Figure 21.13**). A relaxation of fishing pressure did not result in a major recovery of sardines. Competition between the two species, changes in water temperature, and other factors have all been implicated in the switch of dominance, but no factor has been convincingly identified. A similar case can be made for various fish stocks of the North Sea, including herring, cod, and mackerel. Fishing, climate, increased zooplanktonic food for larvae, and pollution have all been suggested as factors, but the one clear fact is the presence of strong fluctuations in population size.

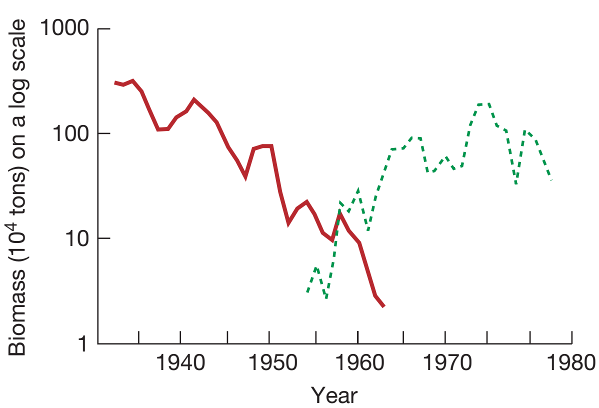


FIG. 21.13 Increase of the anchovy (dashed curve), following the decline of the Pacific sardine (solid curve), off the coast of California.

Fish populations consist of many age classes that grow and reproduce simultaneously. Most species, with the exception of some, such as Pacific salmon, spawn more than once, usually on an annual basis. The individual factors that collectively affect each year class may have a profound effect on population size. Variation in recruitment, for example, may have a great effect on the subsequent age structure. If a given year class is extraordinarily successful, it will appear as a major peak in the size structure of the population and will contribute many more young than will other year classes. Strong fluctuation in recruitment will cause great perturbations in the age structure of subsequent years in the population. Year classes can often be traced through several years as a size peak (as was shown in **Figure 21.6**).

Random fluctuations in recruitment and mortality may be a major background variation in fish populations. Perhaps such fluctuations have specific causes, but these causes may be so complex and varied that they cannot be identified individually, and their effects may be indistinguishable from random variation. Such complex and random fluctuations alone may bring the population down to a very low level. Under such circumstances, the additional imposition of fishing mortality would be quite dangerous for the stock.

Does fishing exacerbate natural population fluctuations? One might expect this to happen, especially when fishing truncates off the larger fish, whose capacity to provide large numbers of young might compensate for failures in success of the new year classes. It was possible to measure this by the use of a long-term data set from the California Cooperative Oceanic Fisheries Investigations, which allowed the comparison of exploited and nonexploited stocks of fishes living in similar environmental conditions. Fished populations clearly were more variable than nonfished populations (Hsieh et al., 2006), which suggests that fishing can cause major instabilities that might lead to local extinctions.

- **Fish stocks characterized by long generation times, small clutches of eggs, and fewer spawnings over time are the most vulnerable to overfishing.**

It is rather easy to see that some fish stocks are potentially much more vulnerable than others, owing to their life-history characteristics. Clearly, fish species with short generation time (which, for our purposes, is the time from birth to age of reproduction), multiple spawnings during adult life, and many offspring produced per female will have a greater chance of rebounding from low population levels. Species with long generation times, few spawnings, and small clutch size may be very vulnerable to combinations of environmental change and fishing pressure. Shark species are clearly vulnerable, as they typically produce very few pups and have typically long generation times, relative to bony fish species (**Table 21.1**). Most species feed at the tops of food chains, and, therefore, relatively small populations can be supported relative to members of lower food chain levels. These general characteristics have resulted in surprisingly rapid declines in shark populations and other top predators such as bluefin tuna.

TABLE 21.1 Life Characteristics of Some Sharks, in Comparison to Atlantic Cod

	WHITE SHARK (*Carcharodon carcharias*)	SANDBAR (*Carcharhinus plumbeus*)	SCALLOPED HAMMERHEAD (*Sphyma lewini*)	SPINY DOGFISH (*Squalus acanthias*)	ATLANTIC COD (*Gadus morhua*)
Age to maturity (y)	M, 9–10; F, 12–14	M, 13–16	M, 4–10; F, 4–15	M, 6–14; F, 10–12	M, 2–4
Litter size	2–10 pups	8–13 pups	12–40 pups	2–14 pups	2–11 million eggs
Reproductive frequency	Biennial (?)	Biennial	?	Biennial	Annual

M, male; F, female.
Source: Data from Klimley, 1999.

■ **Fishing technology, boat range, and even fishing policy have initiated or accelerated the decline of many stocks.**

Although it may be controversial to predict massive calamity for the fisheries of the United States or the world, there is no doubt that many specific fisheries have suffered greatly from human fishing pressure. In many instances, overfishing has led to drastic depletions of stocks, and fisheries have been closed down as a result. In Great South Bay, New York, a rich fishery of the quahog clam *Mercenaria mercenaria* was overexploited by thousands of clammers who worked the bay with small boats and hand tongs. Owing to this, the landings decreased markedly over the last few decades, and the largest company ceased to fish for clams in 1999. In North America, many fish stocks are now at very low levels, especially on the Atlantic coast. In Newfoundland, cod fishing has essentially ceased, and stocks of bottom-associated fish off New England and Nova Scotia are dangerously low. This pattern has been common in fisheries from the estuaries to the blue ocean. In the past few years, some recovery has been observed in cod on the Nova Scotia continental shelf.

While we have to be cognizant of the difficulties of using landings to estimate population sizes, overfishing can often be identified as a decrease in catch per unit effort. As the stock is overfished, more boats may be deployed, but the fish caught per boat per day decreases. One of the major problems in predicting declines in fisheries is the great increase in fishing effort that occurs in order for a commercial fishery to maintain a given amount of take. Increasing fishing effort over time may result in a continuing stable take, despite an actual underlying decline of stock size. Eventually, no matter how much the effort increases, the take will collapse. This type of decline was found in the Atlantic cod fishery in eastern Canada (Mullon et al., 2005).

One of the most compelling pieces of evidence for depletion of stocks from fishing is the trend of fish landings after World Wars I and II. During both world wars, fishing was understandably reduced. But after each war, the catch increased tremendously. This suggested that the war periods allowed enough time for the fish stocks to recover in numbers.

Overfishing has arisen from the use of long-ranging ships and technological advances that permit efficient catching and preservation. A song captures the old way: "Haul in the nets, same old fisherman, never catches more than he knows he can sell in a day." This pattern ended as large motor-driven trawlers began to ply the seas. After World War II, trawlers threw their nets over the stern. Later the fleets developed the capacity to freeze the fishes at sea, rather than bringing them back on crushed ice. In the years since 1950, a general trend from short-ranging to long-ranging fishing expeditions developed. Off the shores of North America, for example, Japanese and Soviet trawlers represented a dominant part of fishing and certainly took more fish than the small inshore fishing boats that once dominated the coast. Offshore fishing by foreign vessels was concentrated near the highly productive waters just seaward of the continental shelf.

Ironically, protection of U.S. fisheries from foreign exploitation at first did not help at all. In 1976, the passage of the federal U.S. Fishery Conservation and Management Act (also known as the Magnuson-Stevens Act) restricted foreign fishing to the outside of a perimeter greater than 200 miles from U.S. coastlines and established a series of eight regional fishing commissions to help in regulation of domestic fishing. This legislation protected continental shelf fishing grounds from foreign exploitation, and continental shelf species such as haddock began to recover. But no significant limits were imposed on domestic fishers, even as the catches were clearly declining in the 1980s. Some attention was paid to protection of spawning grounds and some size limits were imposed, but the overall effect of management failed to curtail overfishing. The size and number of U.S. fishing boats increased dramatically, and the stocks declined precipitously, to the point that no region of the contiguous lower 48 United States was in good condition, even if some fisheries were on the rise somewhat. In 1994, for example, salmon fishing was curtailed in the Pacific Northwest, and fishing on the Georges Bank of New England was essentially stopped for a few years by federal proclamation in the 1990s. Haddock had declined to very low numbers, but the temporary closure has been followed by a small degree of recovery since 2000. Stocks of yellowtail flounder declined precipitously since the 1970s, but fishing restrictions and recent strong recruitment has resulted in significant recovery (Stone et al., 2004) (**Figure 21.14**).

The Magnuson-Stevens Act has been amended several times with rules designed to establish sustainable fisheries. It was renewed in 2006 and required some more stringent controls and assessment of the health of fish stocks in U.S. waters. Important amendments in 2007 set catch limits for all federally managed fisheries and also established rights-based management approaches, which assigns shares of a

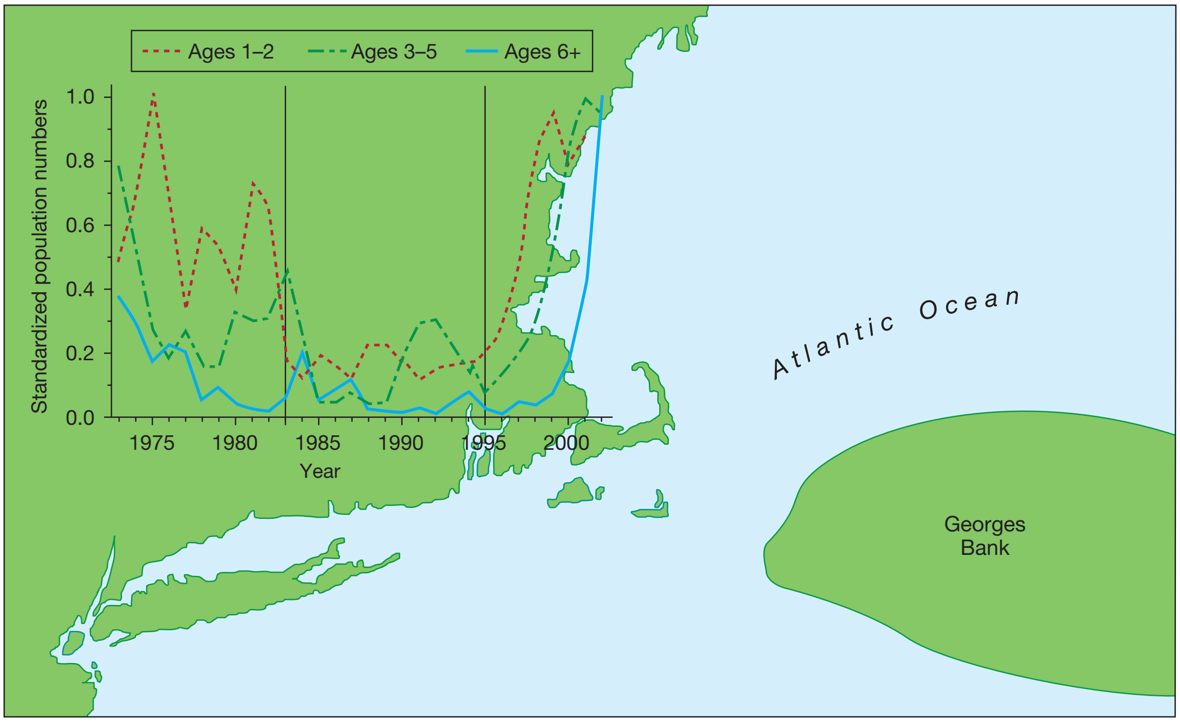


FIG. 21.14 Changes in abundance of yellowtail flounder *Limanda ferruginea*, showing a recovery after restrictions on fishing were imposed in the 1990s. (After Stone et al., 2004)

fishery to past fishery users (see below). As a result, the number of declared severely overfished fisheries in U.S. coastal zones has dropped from 92 to 29 over the period 2000–2015. Management in U.S. waters is finally showing some success.

The trend for coastal zone control of nations has spread throughout the world, and nearly all countries maintain **exclusive economic zones (EEZs)**, within which each country fishes intensively within a border of 200 miles from the coastline. Landings data show that this level of management has not reduced fishing impacts, however; quite the reverse has happened. Despite the difficulties of using landings to estimate fisheries, it is clear that fisheries worldwide, both in the coastal zone and on the high seas, have either reached a plateau or even reduced landings since the 1980s, over a broad range of finfisheries. These results have been accumulated by the Food and Agriculture Organization (FAO) of the United Nations (www.fao.org/fishery) and by the Fisheries Centre at the University of British Columbia (Watson et al., 2005) (www.seaaroundus.org).

- **Ice retreat caused by anthropogenic climate change is opening up new areas for overexploitation especially in subarctic areas such as the Barents Sea.**

As we discussed in Chapters 3 and 19, anthropogenic climate change is having especially strong effects in high latitudes of the Northern Hemisphere. This has caused retreat of sea ice in many areas especially the Arctic Ocean and parts of the Barents Sea in the North Atlantic region. Cod have exploded (**Figure 21.15**) as their food sources, capelin and krill, have also greatly increased in numbers. The Norwegian cod catch is shifting steadily toward northern Norway in the Barents Sea as sea ice retreats and waters warm. Agreements between the Russian and Norwegian governments have led to successful regulation of fishing effort on these newly expanded populations of cod and other fish species. Unfortunately, the cod explosion has also led to a greatly expanded bottom trawler fishing effort in the northern Barents Sea from other countries, which may have major negative impacts on the seabed and demersal fish populations. Total benthic biomass is vulnerable to bottom trawling. But epibenthic species—such as *Geodia* sponges, basket stars (*Gorgonocephalus*), sea pens (*Umbellula encrinus*), and sea cucumbers (*Cucumaria frondosa*) (Jørgensen et al., 2015)—are especially vulnerable. Norway has included the island of Svalbard in its exclusive economic zone of 200 km and has some ability to regulate the impending devastation by such intense trawler fishing. Cod fishers have also agreed to curtail, for now, fishing in areas newly opened by the retreat of sea ice. Many major retail purveyors of fish have recently signed an international agreement, stimulated by the efforts of the Greenpeace organization, to refuse to sell cod taken by bottom trawlers in these waters, which may slow down the expansion of bottom-trawling fisheries into this newly opened area where high-latitude sea ice is retreating owing to climate change.

- **Jellyfish blooms around the world may be the combined result of overfishing, climate change, and pollution.**

The consequences of overfishing can be predicted through an understanding of the role of the missing fish in the food web. This has been one approach in understanding the removal of large sharks from the top of food webs and the

FIG. 21.15 A bottom trawl net of cod being loaded onto a fishing ship near Svalbard, Norway, July 2016. Black steel otter boards that hold the net open as the trawling net moves along the sea bed are visible. (Photograph by Carl Safina)

resulting trophic cascade effects. But many other responses are more complex. First, fish are usually removed by fishers from food webs at several trophic levels. Second, other factors such as ocean warming and pollution must be factored in. An extreme example of this is the invasion of the ctenophore *Mnemiopsis leidyi* into the overfished Black Sea. This species entered a sort of ecological vacuum and its population exploded, causing a large degree of mortality on native fish eggs.

Similar complexities have accompanied the widespread increases of scyphozoan jellyfish populations around the world. For example, jellyfish of various species have increased dramatically in recent decades in the Gulf of Mexico and in the extremely productive Bering Sea near Alaska. In the Mediterranean, very large fluctuations of the jellyfish *Pelagia noctiluca* have been known for many decades, and high population densities are associated with higher sea temperatures and atmospheric pressure. Jellyfish abundance is also known to strongly correlate with climatic fluctuations such as the North Atlantic Oscillation (NAO). In Chesapeake Bay, jellyfish do well when the NAO index is low, which corresponds locally to higher water temperatures and slightly higher salinities. In coastal waters worldwide, the moon jellyfish *Aurelia aurita* has become much more abundant in recent decades. Such increases must impact marine food webs, since jellyfish are efficient predators on zooplankton.

The reasons for such explosions are not so clear, but many fisheries biologists have argued that overfishing has removed planktivorous fishes and jellyfish have replaced them. But jellyfish blooms also are generally correlated with warm temperatures and oscillate in numbers that correspond to climatic oscillations. Abundances may be controlled by regional climate oscillations, and the general global warming of the surface ocean may also contribute strongly to the increases. Finally, pollution may be altering coastal ecosystems to favor jellyfish, but the exact mechanism has not been determined with certainty. Right now, we have only correlations. Ocean warming may also be responsible for shifting the geographic ranges of jellyfish species to higher latitudes (Mills, 2001; Purcell, 2005).

Cures for Overfishing?

CLOSURES AND QUOTAS

■ **Temporary closures and fishing limits allow some fisheries to be sustainable.**

If overfishing occurs, the question is what actions will help. Most fishing nations have laws in place that set limits to the **length of season** and **size of catch** for different fisheries. These limits are often set in the context of strong political pressure to have no limits at all or not to impose very strict limits on the size of the catch. In the United

States, legislation in recent years has prescribed the means to regulate fisheries to be sustainable. Of course, we have discussed a number of cases in which such limits have not forestalled major fishery collapses—or even complete reorganizations of ecosystems. Imposition of limits often occurs only after a major disaster occurs and fish are so scarce that they cannot be recovered economically. Such was the case of the haddock on Georges Bank, where legislation and closures occurred only after major collapses in the 1960s (from foreign fleets) and the 1980s (from U.S. domestic fleets). Many shellfish resources, such as the eastern oyster *Crassostrea virginica* in Chesapeake Bay and the northern quahog in Great South Bay, Long Island, New York, have been fished down to a near-hopeless state, so limits are sometimes too late. On the other hand, several northern Pacific U.S. fisheries, such as the Pacific halibut *Hippoglossus stenolepis* and several species of salmon, have been successfully managed. Pacific halibut in Alaska is divided up in shares, which reduces overfishing, and there are strict limits to catch and bycatch.

■ **Catch shares, or individual transferable quotas, might produce a sustainable fishery.**

To sustain a fishery is quite difficult, given the strong natural fluctuations of natural populations against which additional fishing pressure must be regulated. As we have mentioned, merely excluding some groups from fishing does not usually solve the problem, as other groups fill in the void. Fishing furthermore is becoming more and more sophisticated, with satellite navigation, sonar detection, and other technologies aiding exploitation.

An interesting philosophy now being used in fisheries is **rights-based management**, in which traditional users of a fishery are declared to have use rights, which can be described as measurable commodities. By assigning these rights, one expects that fishers will adopt long-term sustainable policies, such as catch limits. One interesting approach to this type of management has been the **catch share**, or **individual transferable quota (ITQ) system**, in which a total catch is divided among a series of individual fishers who can sell their personal quotas to other fishers. This approach has been applied in New Zealand, British Columbia (Canada), Australia, Iceland, and Namibia, particularly to invertebrate fisheries, and it might give the economic flexibility needed in deployment of fishing boats and gear (Shotton, 2001). It has also been applied with success to Pacific halibut in Alaska and to ocean clams on the east coast of the United States. Currently, over 15 U.S. federally regulated fisheries are divided into catch shares. Some critics argue that the system is unfair, since it offers shares in a fishery to a group of participants at a specific time, and these participants can make a profit by selling shares to increasingly centralized large fishing corporations, which reduces competition. A recent analysis, however, shows that the approach works well in helping to avert crashes from overfishing (Costello et al., 2008). Participants with shareholder rights have a stake in obeying rules that lead to the sustainability of a fishery if the participants will benefit from the catch in the long run. This approach is believed to be behind a recent resurgence of a number of fisheries, especially along the Pacific coast of the United States. Regulation has also greatly reduced bycatch in Pacific groundfisheries.

ECOSYSTEM-BASED MANAGEMENT AND MARINE PROTECTED AREAS

■ **Ecosystem-based management may allow the environment of a fishery to sustain resource populations.**

We discussed ecosystem-based management in Chapter 20. This approach considers ecosystem interactions as the basis for fisheries management. In essence, the protection of an entire ecosystem is believed to maximize biological interactions that have sustained important fishery populations. For example, the diversity of the seabed would be considered because of the role of a variety of species of benthic organisms as food for finfishes. Thus, the damage caused by bottom trawling is not just the removal of fish but the collateral disturbance of the seabed. The negative effects of invasive species must also be considered. For example, a recent invasion of Georges Bank bottoms by an abundant sea squirt *Didemnum* sp. may have strong negative impacts on the availability of benthic invertebrates as food for benthic-feeding fishes. Consideration of the ecosystem as a whole allows a more accurate economic assessment of the ecosystem services provided by any given ecosystem. Marine protected areas can be established to maximize ecosystem functioning. Many have argued that ecosystem-based management should replace management practices based on individual fisheries alone (Crowder et al., 2008).

■ **The marine protected area concept can be adapted to fisheries management.**

In Chapter 20, we discussed the use of marine protected areas (MPAs) for the conservation of biodiversity. They can also be used for fisheries management. By designating a specific area for protection, one must assign a value to that area for fisheries management. These values include the following:

1. *Crucial habitat for refuge population.* A fishery species might be tightly dependent on a specific habitat. For example, in Chapter 18 we discussed deep-water coral mounds, which are important habitats for a number of species of fish valuable as fisheries. MPAs might allow the preserval of crucial habitat upon which a fishery population might depend. This refuge allows the population to be sustained because a minimal amount of habitat is not destroyed, allowing feeding or reproduction.
2. *Protection of an area where an important life-history stage must live.* An MPA might be erected to allow a resource species to spawn, or for juveniles to live, or for adults to feed. Thinking on this large scale, a network of habitat-related MPAs might have to be

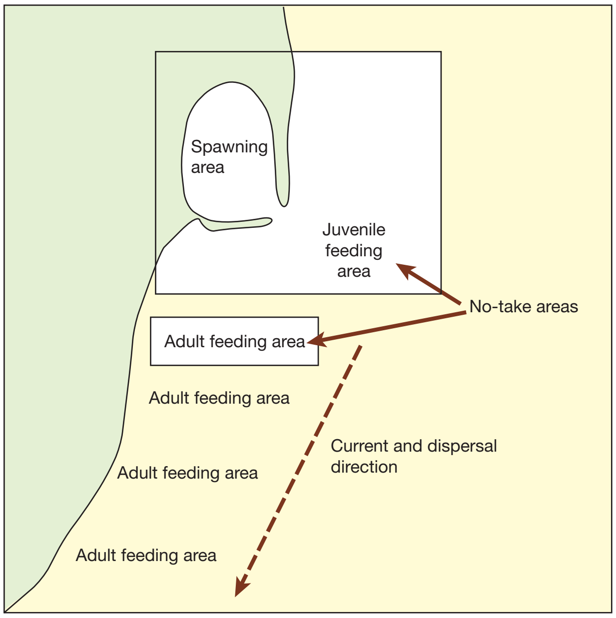


FIG. 21.16 Design of no-take areas in a hypothetical fishery. The spawning and juvenile feeding areas and one adult feeding ground are no-take zones, to allow a minimum population to complete a life cycle. Other areas might be fished, although quotas might be set on the amount of the take.

established to protect a minimal population. This network acknowledges that a metapopulation exists, and the nature of connectivity is important for life-history stages and movement of adults. Such a network would have to take proper habitat types into account, along with water currents for dispersal routes for eggs and larvae (**Figure 21.16**).

3. *Creation of a no-take sanctuary, which individuals might leave and be exploited outside.* If an MPA is large and safe from exploitation, one might expect that mobile species might survive well within the MPA and a **spillover effect** would result from their emigration from the MPA, where they could be fished outside. For example, the coral reefs of the Dry Tortugas National Park ecological reserve in Florida has proven to be a good place for fishing around the periphery of the preserve because individual fish emigrate from a now healthier population within the sanctuary that is closed to commercial fishing (Ault et al., 2013).
4. *Creation of a network of MPAs, among which larvae and adults can disperse.* Along a coast, a network of MPAs may be preferable, to maximize dispersal and successful recruitment as larvae and juveniles are carried by currents. A group of no-take MPAs have been recently established along the California coast. It is crucial to manage both the MPA areas and surrounding areas that are fished, because the establishment of no-take zones might just increase fishing pressure elsewhere, unless the whole ecosystem is managed.

Overexploitation of Whales: A Case History

■ **Whaling began as a shore-based fishery and then developed into an open-ocean fishery.**

Whaling is one of the most romanticized of human endeavors. In our folklore, a sinister and powerful monster appears suddenly on the horizon, and the brave men of the longboats move out after it, perhaps to their death. In the nineteenth century, American whaling ships ranged far and wide, from the coast of Greenland to the antipodes, searching for and killing the profitable beasts. In those days, the sperm whale was sought for its oil for lamps and candles, bones for household implements, and ambergris for perfume. Even today, the waxy substance spermaceti, from the head cavity of sperm whales, is used as a lubricant in outer space, because of its unique stability at low temperature. Other kinds of whale were boiled down for oil, and their flesh might be taken for food. "Whalebone," a bonelike material taken from baleen whales, was prized for women's corsets, buggy whips, and umbrellas.

At first, whalers worked from shore. Fishermen hunted the Biscayan (northern) right whale nearly to extinction as early as the seventeenth century, merely with harpoons thrown from skiffs that quickly returned to shore. On the south shore of Long Island, white settlers and natives harpooned whales from rowboats launched in the surf, and northern right whales were preferred because of their slow swimming speeds (they are baleen whales) and their tendency to keep close to shore. With the advent of large and swift sailing vessels in the early nineteenth century, voyages often lasted for several years, and larger open-ocean whales were hunted and processed at sea. Whales were sighted in the distance as water spouted through the blowhole ("Thar she blows!" was the cry of the spotter, when he saw a whale spouting), and men in longboats rowed out to harpoon the whales by hand. After the kill, the whales were tied along ships and were butchered and cooked on-board. If the killing was a dangerous outing, neither was it exactly safe to stand on the slippery, blubbery carcass and butcher the enormous animal.

We can only imagine the fantastic numbers of whales that the first Antarctic explorers must have encountered, for such numbers exist no more. At first, in the earliest part of the nineteenth century, whales migrating from the Antarctic were caught when they arrived in some of their breeding grounds, south of the Australian continent. The whales were hunted by convicts, who had been transported from England, and also by whalers who had traveled from North America. Shore stations were especially effective in reducing the numbers of the humpback whale, which bred in bays in Australia and New Zealand.

A number of technological advances set the stage for modern whaling in the Antarctic seas. In the 1860s a Norwegian sea captain invented the **cannon-powered harpoon**, and whaling crews began to pump air into carcasses to keep them afloat during butchering. Also, a technique of hunting was developed that was devastating in its efficiency. A series of smaller catcher ships searched out whales. When an individual whale had been harpooned and killed, it was delivered to a larger **factory ship**, equipped with a **stern slipway** for hauling in the whale. The whale was then cut up and processed on-board for oil. (That was the main product obtained from Antarctic whales until after World War II, when whalers began to save the meat for use in pet food and for human consumption.) Even the canning was done on-board the factory ship. This method was first fully developed in about 1925, when the first factory ship equipped with a stern slipway operated in the Antarctic Ocean.

- **Open-ocean fishing technology resulted in the decline of blue whale populations.**

The effectiveness of the catcher–factory ship system led to hunting for the blue whale, *Balaenoptera musculus*, in preference to the other species (fin and sei whales), owing to its large size (**Figure 21.17**). By the 1930s, blue whales were already declining. This decline continued until blue whales eventually reached very low numbers. A 1937 agreement set a minimum size limit on hunting blue whales and other species, and prohibited the killing of whales that had calves. A season was also set. No upper limit was placed on whaling in general, however, and the number of catcher ships increased, with no increase in the total blue whale catch. In other words, the total landings remained the same, but the catch per unit effort decreased. Subsequent international whaling conferences set limits on the number of catcher ships, whaling season, size, and number. A blue whale unit (BWU), established in 1944, set the following catch equalities: 1 blue whale = 2 fin whales = 2.5 humpback whales = 6 sei whales. Limits were set in terms of these blue whale units. This was not particularly good for the blue whale itself because whalers included in their limit as many blue whales as possible. The BWU was thought necessary to protect whales in general on the grounds that hunters would not be so impractical as to pass up any whale simply because it was not a blue whale. To do so would have wasted too much ship time.

The **International Whaling Commission (IWC)** was established in 1946. It had the advantage of forcing the representatives of whaling nations to continue to meet to establish quotas and fishing seasons. The charter of the commission permitted nations to ignore the limits, however. This laxity was a political necessity because whaling was a high-seas fishery in the Antarctic and therefore no nation's law regulated fishing. This led to accommodations that were political in nature, and the limits were set above a sustainable yield. The commission failed at first to set limits for each individual nation, although this was later done by means of negotiations outside the formal proceedings of the IWC. The early lack of individual country limits encouraged very intensive fishing effort. The quotas recommended by a scientific committee of the IWC were often ignored by the broader commission in favor of ones that could not even be met by the whalers.

Over time, the catcher ships continued to increase in number and size, and the blue whale stocks declined precipitously through the 1950s. Individual national limits were set in 1962, and fishing for blue whales was stopped in 1965, but blue whales had already ceased to be abundant enough to be taken in significant numbers. By the early 1960s, it had become impossible for the whaling nations to catch as many whales as allowed by the quotas adopted by the IWC. The fin whale also began to decrease greatly, and

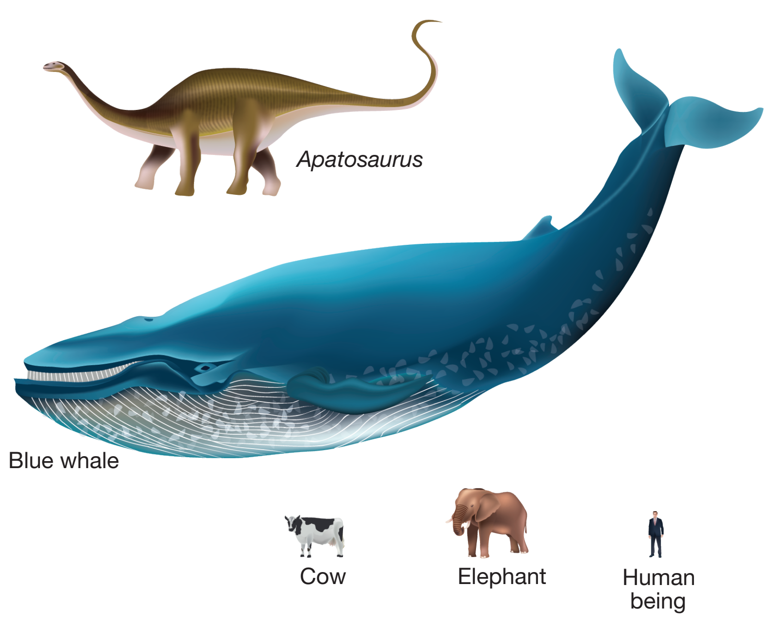


FIG. 21.17 The size of a 100-foot-long blue whale in relation to some other creatures.

fishing effort was shifted to sei whales, which were useful for their meat. Quotas were reduced, but not enough to permit the fin or blue whales to recover very well.

Many pointed out the dangerous position of the blue whale and fin whale stocks, and in 1986 an agreement was finally reached by the IWC that imposed a moratorium on whaling. Of the great whale species, five species are considered endangered, two are vulnerable to declines, and four are at low risk of extinction. The northern right whale is endangered and female survival has declined in recent decades, setting the small remaining population of this species on a course for extinction (Fujiwara and Caswell, 2001). Both Norway and Japan have objections to the moratorium, especially with regard to the minke whale. In 1994, the IWC established a sanctuary throughout much of the Antarctic Ocean, but Japan objected and continues "scientific" whaling, even within the sanctuary. Nevertheless, within the Antarctic minke whales have greatly increased and fin and sei whales are more abundant. In the eastern North Pacific, humpback and blue whales have increased in numbers owing to regional protections.

Other Types of Loss

- **Fish stocks can be affected by human degradation of water quality or fish habitats, or by killing of fish by means other than direct fishing.**

Although overfishing began to take its toll early in this century, other factors have combined to reduce fish stocks. In many bays and estuaries, the introduction of industrial wastes and sewage has degraded water quality substantially (see Chapter 22 for more details). As a consequence, many fisheries have collapsed, or have become contaminated and therefore unavailable for human consumption. In the most dramatic cases, pesticides have eliminated entire populations. For example, the manufacture and release of the insecticide Kepone into the James River of the Chesapeake Bay region collapsed the blue crab fishery for several years (Schimmel et al., 1979). Other toxic substances, such as heavy metals and various organic compounds, have contaminated fish and shellfish populations. Probably the major water-quality change, however, is in the lowering of dissolved oxygen content (see Chapter 22).

Human disturbance of either spawning grounds or migration routes is also a major cause of the decline of fish populations. In the Pacific Northwest region of North America, dams and deforestation have caused major reductions in salmon stocks (**Figure 21.18**). Dams interrupt the migration route, and juvenile salmon often swim through hydropower turbine intakes, causing extensive damage and mortality. Migrating juveniles often prefer the sluggish parts of lakes behind dams, and these areas are often filled with predators. The extensive clear-cutting of forests in areas such as British Columbia also has drastic effects because trees normally prevent erosion. Following a period of clear-cutting of trees, soil erosion increases greatly, and gravel spawning beds are often ruined by influxes of soft sediment. In many coastal areas, salt marshes have been filled in to allow coastal construction. The salt marsh creeks are nursery grounds for a variety of fishes, and many of these areas have been eliminated in the eastern United States. Damming of rivers has greatly impeded migration cycles of many species of sturgeon, whose populations have declined throughout the world's estuaries. Climate change may also disrupt migration routes, as shifts of temperature and currents cause changes in coupling of productivity hotspots and the occurrence of forage fish for major oceanic migrating predators (Hazen et al., 2012). A recent removal of the Elwha dams on the Olympic Peninsula of Washington State in 2011–2012 has been followed by increased salmon runs and the reintroduction of marine-derived nutrients into the freshwater system (Tonra et al., 2015).

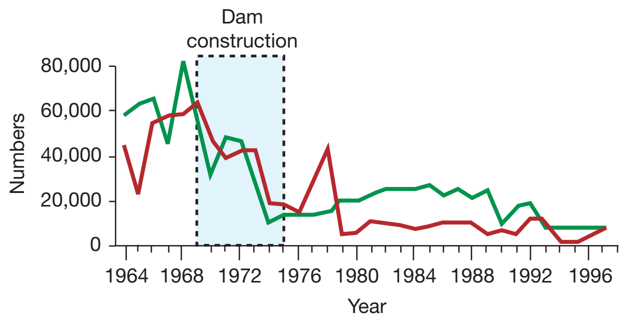


FIG. 21.18 Wild salmon counted on the upper Snake River, Washington: red line, spring–summer Chinook; green line, summer steelhead. (From the Idaho Department of Fish and Game)

Many activities cause reductions of fish populations. The intakes of power plants are often the site of extensive larval and adult fish mortality. Water is taken in to cool the turbines, and warm water is piped out into estuaries and coastal areas. The pump intake region entrains fishes and draws them through the intake pipes. When the larvae or adults approach the intake pipes, the sucking force may impinge them on the intakes, although a variety of diverting screens have been placed on intakes to prevent this.

- **Structural habitats are often endangered by human use. A multitiered strategy is essential for protection.**

Structural habitats often depend on the maintenance of a suitable substratum and the species that construct a biological landscape, such as corals in coral reefs or kelps in kelp forests. Coral reefs are an excellent example. They are endangered from many directions today, but tourist visits are especially worrisome. With tourists come organic pollution and direct disturbance of the reef through diving, boat anchor damage, taking of rare live marine specimens, and even hammering and blasting out coral colonies (Luttinger, 1997).

Temperate rocky reefs are an especially appropriate habitat for conservation, because many fish species use the reefs to breed and feed. They are also targets for sports and commercial fisherman and are therefore highly vulnerable to overfishing. In recent years, a system of protected rocky reefs has been established in California (see Gleason et al., 2013) and along the western coast of the Gulf of California.

By protecting a network of reefs, dispersal among reefs tends to increase the regional population.

Disease as a Major Danger to Coastal Fisheries

Coastal fisheries often consist of species with very high population densities, at least before they are overexploited. Disease is a major factor in fisheries decline and, in some cases in recent years, has proven to be a major challenge in fisheries management, especially in cases where overfishing has occurred. Although a great deal of attention has been paid to diseases of fishes and invertebrates (discussed shortly), we often know very little about diseases that affect natural populations.

In recent decades, bivalve mollusk populations have often been devastated by a variety of diseases that cannot be controlled to any extent. For example, the eastern oyster *Crassostrea virginica* has been infected by two common diseases that exert strong negative effects on populations. MSX is caused by an amoeboid parasite *Haplosporidium nelsoni*, whose complete life cycle is unknown but is believed to occur in some other unknown benthic species. It originated in the western Pacific and was first discovered by Harold Haskin in the late 1950s in Delaware Bay when it caused well over 95 percent mortality. Since that time it has spread throughout the East, including Chesapeake Bay and southern New England. Another oyster disease, Dermo, combines with MSX to be a major factor in the survival of natural oyster reefs. Ocean warming has facilitated the movement of this disease northward along the northeast U.S. coastline.

The interaction of climate change and a parasite is also a factor in strong declines of the blue crab *Callinectes sapidus* in the southeastern United States. For example, landings in the state of Georgia of blue crabs dropped over 75 percent from the 1950s to 2002. Infections of the dinoflagellate *Hematodinium perezi* have greatly increased locally and worldwide (Sheppard et al., 2003). The parasite invades the hemolymph and consumes the crab's blood pigment hemocyanin, which causes oxygen shortage. The infections are prevalent in summer, and the crabs do not have a sufficiently effective immune system to attack the dinoflagellate cells. The parasite does poorly in lower salinities, but the drought in the southeastern United States since 1997 has reduced freshwater flow and allowed the parasite to flourish in salinities over 28 psu, which are now common way up estuaries with low river flow (Lee and Frischer, 2004).

Mariculture

General Principles of Mariculture

- **In mariculture, the habitats of some natural populations can be simulated, changed for convenience of harvest, or enhanced to increase yields.**

Mariculture, often called aquaculture, is a loose term covering all techniques by which marine organisms are reared for most of their lives under controlled conditions in seawater directly in or connected to the sea. In the crudest form of mariculture, animals are transplanted to habitats that are optimal for growth (e.g., transplantation of hatchery-reared oysters to the seabed). In intermediate cases, organisms are reared throughout their life cycle, but much of the rearing is in open-ocean pens, and conditions are not controlled exactly (e.g., fish farming of salmon). In the most controlled case, the mariculturist controls the rearing environment completely and may attempt to provide completely defined foods (e.g., indoor aquarium hatcheries of striped bass). While the fishing take of wild fish has remained stable or is in decline worldwide, aquacultured fish and invertebrates continue to increase as an important part of total world consumption.

Successful mariculture requires the proper choice of a species for rearing. The following characteristics are desirable:

1. *Desirability as food.* The species should be already known as a desired food item or product.
2. *Uncomplicated reproduction.* The organism should be relatively easy to propagate, or young organisms should be easy to obtain.
3. *Hardiness.* The species should be resistant to handling and changes in environmental conditions.
4. *Disease resistance.* Diseases and parasites should be controllable, to minimize mortality.
5. *High growth rate per unit area.* The organisms should be able to grow rapidly in limited culture areas.
6. *Readily met food requirements.* Feeding the organisms should be easy and cheap. Animals that are high on the food chain are liable to require higher-cost protein foods.
7. *Readily met habitat requirements.* The physical habitat should be easy to duplicate in the mariculture system. There should be relatively low levels of aggressive behavior, and the organisms should be resistant to poisoning by waste products.
8. *Monoculture or polyculture.* It should be considered whether one species is to be grown alone (monoculture) or whether several species will grow most efficiently when placed in the same system (polyculture). For example, some mariculture habitats may be innately complex, and a polyculture, permitting several marketable species to grow in the assemblage of microhabitats, would be more efficient. Monocultures have the disadvantage of the rapid spread of disease that is especially efficient in attacking a single species.
9. *Marketability.* The chosen species should be easy to market, accessible to markets, and of a presentable growth form to consumers.
10. *Minimal ecological side effects.* The mariculture system should have few detrimental effects on the surrounding environment, such as release of cultured organisms into natural habitats.

■ **Mariculture may be uneconomical, especially because of some ecologically damaging side effects.**

When these requirements are considered, many species turn out to be uneconomical to culture. The New England lobster *Homarus americanus* is a highly prized food, but strong aggression among individuals requires that they be isolated, which increases the expense of rearing them. In contrast, the shrimp *Macrobrachium rosenbergii*, which thrives in both brackish and fresh water, proved ideal for culture in open ponds, as have marine shrimp species. Food is easy to prepare (brine shrimp eggs, fish flesh, etc.), survival is satisfactory, and the animals grow rapidly. Unfortunately, side effects of shrimp farming can be severe. Throughout the tropics, thousands of hectares of mangrove forests and marshes have been destroyed in order to establish shrimp farms. Under crowded conditions, a number of lethal viral diseases may spread and wipe out large shrimp mariculture facilities, which are often permanently abandoned (Kautsky et al., 2000).

In many species, mariculture-reared individuals are released purposefully into natural habitats. In some of these cases, mariculture produces juveniles that escape into coastal fisheries. The large number of Atlantic salmon farms has resulted in a great deal of inadvertent release, and wild salmon fisheries in rivers on both sides of the Atlantic have a considerable number of fish farm–bred salmon (Carr et al., 1997). Salmon raised in pens experience selection for traits that are not conducive to living in a wild environment, so there is a great deal of concern that crosses between farm-bred salmon and wild individuals will produce offspring of lower fitness in the open ocean. Parasites such as sea lice (a type of copepod) spread in fish farms, and planktonic early stages infect wild salmon.

Some Organisms Useful in Mariculture

■ **Mollusk mariculture systems enhance the availability of substratum and are located in areas of high phytoplankton supply.**

Mollusks, principally bivalves, have been among the most successful mariculture organisms. This has much to do with the rapid growth of some species, combined with the ability to place animals in areas of high phytoplanktonic food supply. All the major cultured species are suspension feeders. A number of species of oysters and mussels have been the mainstay of the industry throughout the world.

The culture of bivalves involves two main steps: (1) rearing of larvae through settlement and metamorphosis into juvenile animals, called spat or seed, and (2) rearing of adults, usually in rafts or attached to suspended poles or ropes. Spat can be collected in natural habitats, but they are often reared in hatcheries.

MUSSELS Mussel culture is best developed in France and became established quite by accident. Patrick Walton, an Irish sailor, was shipwrecked in the year 1235 on the Atlantic coast of France. To snare birds for food, he placed a net attached to poles on a mudflat. Instead of attracting birds, the poles were colonized by settling mussel larvae, which grew far more rapidly than those on the mudflat itself. Today, ropes are still placed near mussel beds, and larvae settle from the plankton on the ropes and grow to a size of 5–10 mm. The ropes are then wrapped in a spiral around poles stuck in the mud, and the mussels then grow rapidly. The bottom of the pole is sheathed in smooth plastic, to prevent predators from climbing the poles. The mussels are thinned out to allow maximum growth, and the harvest is taken about 1 year later.

A variant of this technique, practiced in Japan, Spain, Portugal, and Maine, is to use ropes suspended from rafts. There is some concern that deposition of mussel feces below rafts will cause anoxia on the bottom and negatively affect local marine communities. Mussels are also widely cultured throughout the Mediterranean, especially near estuaries where primary productivity is high.

OYSTERS The oyster is the most profitable bivalve employed in mariculture (**Figure 21.19**). Many different species have been used successfully in a wide variety of climates. Oyster culture is known to go back to the ancient Romans. In the past few decades, oyster culture has been expanded, owing to the high price of oysters and to the decline of many natural oyster beds because of overfishing, disease, and pollution.

Cultured oysters (members of the family Ostreidae) have planktotrophic larvae that swim in the water column for a few weeks. Culture therefore involves the settling and metamorphosis of larvae and the rearing of adults. Spat either are reared in hatcheries or are collected on hard substrata that are placed in natural oyster beds. Dead shells are a common substratum, but plastic, ceramic materials, and wood are also employed. Once spat have been collected, they are transferred to the adult growth area.

Oyster mariculture is complicated by abundant predators, disease, and the problem of maintenance of a natural oyster reef. Oysters can also be grown in cages, which protect them from predators but fail to deliver ecosystem services of increasing biodiversity, among others. The susceptibility of the world bivalve aquaculture industry to ocean acidification is discussed in **Hot Topics Box 21.2**.

OTHER BIVALVES A number of other bivalve species are cultured profitably with aquaculture methods. The common east coast and Gulf coast bivalves *Mercenaria mercenaria* and *M. campechiensis* are popular in Florida, both in the Indian River region on the Atlantic coast and the Cedar Key region of the Gulf coast, and now comprise a multimillion-dollar industry. Another growing industry in the Pacific Northwest focuses on the geoduck, *Panopea generosa*, whose large size (1 kg or more) and use in the sushi industry makes it a profitable species. Juveniles are planted in sediment with a surrounding PVC tube to protect against predators and are allowed to grow for 5–7 years before harvesting, usually in intertidal sites. A most interesting aquaculture industry is farming of the giant clams, a group of species belonging to the genera *Tridacna* and *Hippopus* and found in the

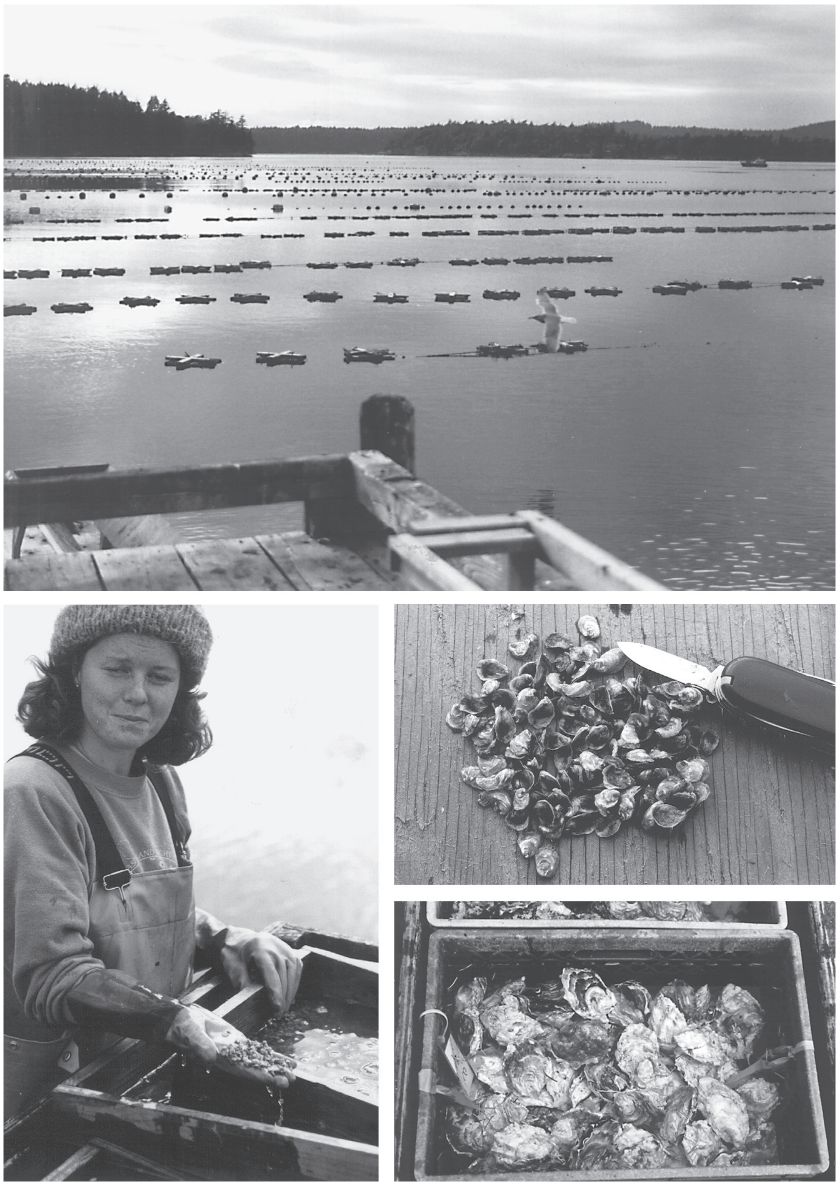


FIG. 21.19 Oysters (*Crassostrea gigas*) are cultured in racks suspended from floats in a tidally flushed bay (top) in San Juan Islands, Washington. Newly settled spat are sorted (lower left) to get the fastest-growing individuals (middle right), and these are raised in suspended plastic trays until ready for market (lower right). (Photographs by Jeffrey Levinton)

HOT TOPICS IN MARINE BIOLOGY

Shellfisheries: Which Will Fall to Ocean Acidification? 21.2

Since about 1750, approximately 337 billion metric tons of carbon have been released by the burning of fossil fuels and the manufacture of concrete. About 35.3 billion tons were released in 2013. The atmosphere's CO_2 concentration has increased from 278 parts per million in 1750, to over 400 today. As discussed in Chapter 3, the totality of this release has had profound effects on our climate, raising air and ocean temperatures in most parts of the earth, and will continue to do so. But another effect of CO_2 emissions also portends profound environmental changes. About 26 percent of all CO_2 emissions enters the ocean. In Chapter 3 we showed how this addition affects the acidity of the ocean, which will lead to areas that are undersaturated with respect to calcium carbonate skeletons—for example, the shells of bivalves, the skeletons of pteropods, and the skeletons of corals. The oceanographic community is now hard at work assessing the potential damage to marine

continues

HOT TOPICS IN MARINE BIOLOGY

Shellfisheries: Which Will Fall to Ocean Acidification? *continued* 21.2

species in the acidic ocean of the future. While pH has declined so far by a small amount on average throughout the global ocean, some marine communities are on the front lines of the threat of increasing ocean acidification.

Put simply, **upwelling systems** are at the head of the brigade of global threats from acidification. We can see this unfortunately already along the west coast of North America, where incidents of upwelling centers approaching the coast are not necessarily more frequent but appear to be more intense (Howes et al., 2015), which will exaggerate episodes of introduction of hypoxic and acidic water into the coastal zone, endangering calcifying organisms.

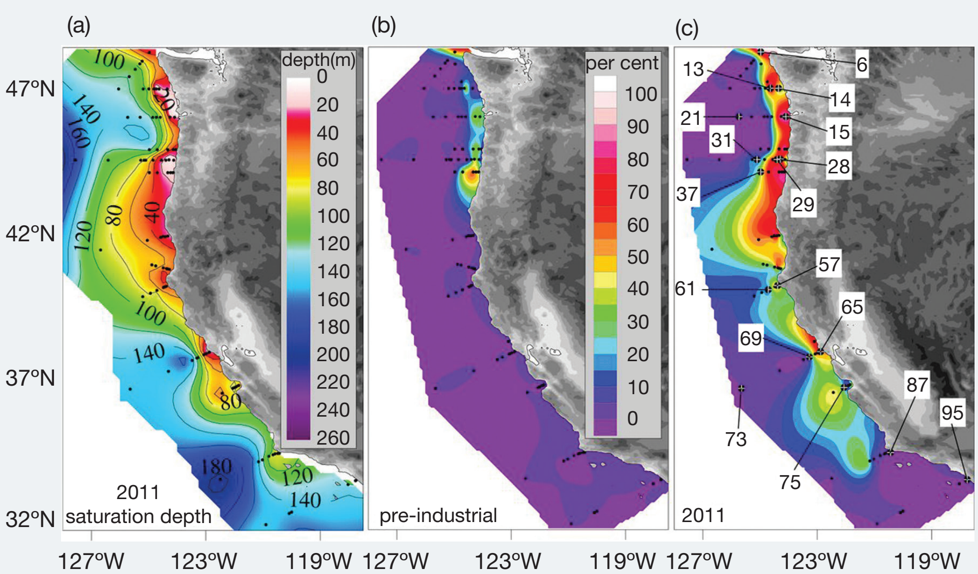
The process is fairly simple. A general zone of coastal upwelling exists along the west coast of North America from California to Alaska. The upwelling events occur every few years and may be far offshore or sometimes right over the relatively narrow continental shelf. In deep waters of upwelling systems, organic matter accumulates and oxygen levels are low because of microbial consumption of dissolved oxygen during decomposition processes. As the upwelling center approaches the coast, low-pH–low-oxygen water upwells to the surface.

The stress from upwelled water combines with an ever-increasing load of nutrients from the coastal zone, owing to inputs from populated centers and agricultural sources on the coast. The coastal input of nutrients, **eutrophication**, causes increased primary productivity, and decomposition of uneaten phytoplankton further reduces the oxygen concentration in the shallow coastal water column. Thus, we have a dual threat to calcifying organisms: acidification and low oxygen stress. But there is also an additional acidification stress in some areas, since bacteria decay uningested phytoplankton in the enriched coastal waters, producing even more CO_2 and potential acidification.

This dual stress especially has the potential to affect the larval stages of shellfish. Christopher Gobler and colleagues (2014) showed that the combination of low oxygen and high dissolved CO_2 produce both additive and interactive effects that reduce larval survival of east coast bivalves. In an east coast scallop *Argopecten irradians*, both low oxygen and low pH reduced larval survival but their combined effect was additive. But in the quahog *Mercenaria mercenaria*, early stage larvae were affected in the same way, but later stage larvae were not so affected by individual exposures to either low pH or low oxygen. In combination, however, there was some interactive effect that increased mortality. Unfortunately, it is not clear why effects are additive or interactive. Still, we can see that both low dissolved oxygen and low pH in combination are potentially harmful to larvae.

The occurrence of acidic, low-pH water is increasing along the west coast where intense upwelling is an important factor. A study by Booth and colleagues (2012) showed that episodes of intrusions by cold, low-oxygen and low-pH waters into the coastal zone have been increasing in frequency in central California. On the larger scale from California to Washington State waters, such upwelling events have very strong impact on pteropods, a major part of the zooplankton that produce shells made of aragonite. Upwelling events bring acidic water that is undersaturated with regard to aragonite, and the pteropods are frequently very damaged, with obvious evidence of shell corrosion (Bednaršek et al., 2014). Near-shore pteropods are far more damaged in frequency than those from offshore. The large California Current ecosystem has experienced a sixfold increase of undersaturated waters relative to preindustrial conditions (**Box Figure 21.4**).

Along with strong effects on the planktonic pteropods, bivalve shellfisheries in the Pacific Northwest have also been strongly impacted



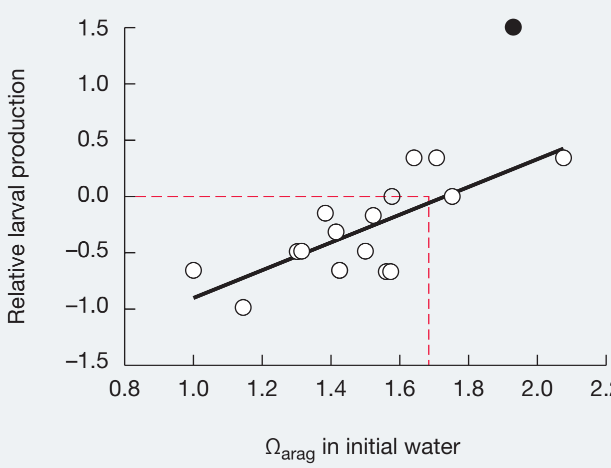
BOX FIG. 21.4 Conditions for aragonite deposition in shells off the west coast of the United States are now poor. (a) Depth of the aragonite saturation horizon. Below this depth, it should not be possible for a pteropod to make an aragonite shell. (b) Percent of the upper 100 m of the water column estimated to be undersaturated in pre-industrial times. (c) Percent of the upper 100 m of the water column estimated to be undersaturated in 2011 [same scale as in (b)]. Numbers refer to sampling localities for pteropods. (From Bednaršek et al., 2014)

HOT TOPICS IN MARINE BIOLOGY

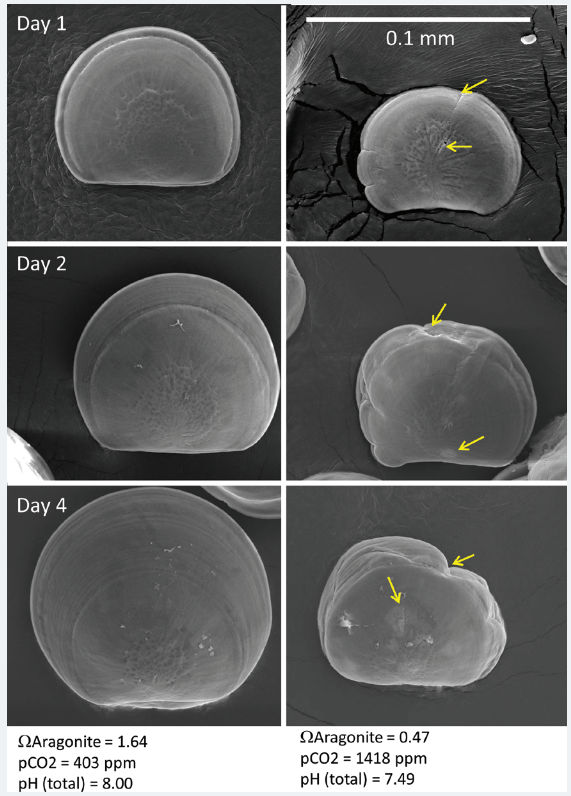
Shellfisheries: Which Will Fall to Ocean Acidification? *continued* 21.2

by these intrusions of upwelled acidic and hypoxic water. Since 2007, there have been widespread failures in hatcheries of Washington and Oregon. Most shellfish culture is of bivalves, specifically the Asian oyster *Crassostrea gigas*, the Mediterranean oyster *Mytilus galloprovincialis*, and the geoduck, *Panope generosa*. In 2009 the west coast shellfish industry earned about $270 million annually, so losses are quite worrisome. Barton and colleagues did careful studies on oyster larval growth at the Whiskey Creek, Netarts Bay, Oregon, hatchery where intrusions of upwelled water were common. In Chapter 3 we discussed the use of saturation state, or Ω, which best predicts when a mineral will be precipitated as a function of dissolved constituents. **Box Figure 21.5** shows a close positive relationship between Ω and oyster larval production rate. In another hatchery in Dabob Bay, Washington, researchers could sample from relatively saturated shallow waters and deeper, upwelled, more acidic waters and expose larvae to these different waters. Larval oyster shells of larvae placed in the deeper water samples (**Box Figure 21.6**) showed clear evidence of dissolution (Barton et al., 2015).

Upwelling events have been devastating to oyster hatcheries on the outer coasts of Washington and Oregon, but they are widespread in all coastal regions. A recent assessment (Ekstrom et al., 2015) shows that the dangers are widespread but are especially acute from the Pacific Northwest to Alaskan waters. The Alutiiq Pride Shellfish Hatchery in Seward, Alaska, is the only hatchery serving all of Alaska, with larvae of several species of bivalves, all of whose larvae are sensitive to acidification. The largest predictable changes from optimal to suboptimal values of Ω are seasonal, with extended suboptimal waters in fall and winter, when more CO_2 can dissolve into seawater, water-column respiration is elevated, and there is exposure to short-term runoff events (Evans et al., 2015). A survey of shellfish managers suggested that about half in the Pacific Northwest had experienced the effects of ocean acidification in their hatcheries (Mabardy et al., 2015).



BOX FIG. 21.5 Relative production of oyster larvae as a function of aragonite saturation state Ω. (From Barton et al., 2012)



BOX FIG. 21.6 Pacific oyster larvae from the same spawning source were placed in waters of Dabob Bay, Washington from a shallow (left column Ω = 1.64) water source (left column) and deeper water (Ω = 0.47) source (right column). Scanning-electron micrographs of shells show that defects develop in 1-, 2, and 4-day-old larval shells (yellow arrows). (Courtesy of George Waldbusser)

Is all hopeless? While the imminent and increasing threat of acidification is very worrisome, there are adaptive strategies used by shellfish hatchery managers that might ameliorate the threat to hatcheries, especially because older bivalves are more likely to survive transient acidification events than the larvae. Most important is monitoring, so that production of larvae and juveniles can be timed to avoid the most severe regional upwelling events. As in the case of Alaska we discussed, this may involve a seasonal adjustment to avoid the times of year when Ω is at danger levels. Some hatcheries have also used buffering strategies by adding sodium carbonate into the water, which increases the availability of carbonate ions for precipitation of calcium carbonate. In the future, shellfishery managers will have to maintain a partnership with scientists and continue to develop their own strategies to survive economically at the ever-worsening frontier of climate change.

Indo-Pacific. These species are grown for food, but also for aquarium specimens and for decorative shells. Clams are grown usually in cages to protect against predators such as crabs.

Seaweed Mariculture

■ **Mariculture of seaweeds may be useful in the production of products such as agglutinants, food, and organic matter suitable for methane production.**

Seaweeds are consumed widely as food and are used for a variety of products. The Japanese use a seaweed food (called nori) derived from the red seaweed *Porphyra* in sushi and other foods, and it has become popular in the United States and Canada. In recent years, seaweed has been identified as a "health food." Nori is richer in protein than rice and is more digestible. Seaweeds are also the source of a number of useful substances, including the agglutinant carrageenan, which is used in a number of food products. It has also been suggested that seaweed be grown and converted to fuels such as butanol.

Seaweed culture is well developed in Japan and China. Nori cultivation in Japan goes back to the seventeenth century and involves the collection of spores in nets or on branches of bamboo. The branches are then moved to an area suitable for rapid seaweed growth (e.g., a water body rich in dissolved nutrients such as an estuary). The thalli are harvested frequently and are cut and pressed into sheets for market. The best growth is in spring or early summer, when *Porphyra* grows in the form of a leafy thallus. In June the thalli begin to senesce and gametes are eventually formed, which unite to form a different type of spore. These are the source of a later life stage, the conchocoelis stage, which appears on oyster shells as a red film. This is the stage that produces the conchospores, a haploid stage that settles and germinates to form the leafy thallus that is eventually harvested. The discovery of the conchospore has been used to improve the efficiency of the hatchery rearing of nori. This has greatly increased the efficiency of culture because nori growers can immerse their nets in a tank filled with spores, thus eliminating the uncertainty of recruitment in the natural habitat.

In the eastern Pacific, kelp farming has become a major means of livelihood. The kelps *Macrocystis* and *Nereocystis* grow rapidly, sometimes as much as 15 cm a day. The kelps are harvested mainly for **alginates**, used in a number of foods. Harvesting usually involves boats that have a conveyor belt with cutter blades, which cut the stipes a few feet below the water surface. Kelp populations are enhanced by the culturing of the small gametophyte stage, which produces the sporophytes, whose early stages are cast from boats or applied directly by divers onto the bottom.

FISH FARMING

■ **Fish farming is a major means of rearing finfishes such as salmon.**

The principal advantage of fish farming is the management of a precise area to maximize the productivity and health of all life stages of the food organism. Fish farming has long been well developed in Southeast and east Asia. A variety of freshwater species are reared in ponds and streams. Multispecies culture has been developed in which several distinct microhabitats occur, such as quiet- and running-water habitats. **Salmon farming** is widespread in North America and in the British Isles, Norway, and Ireland. Hatcheries are used to rear fry, which are introduced as young fishes into pens suspended in shallow-water coastal areas. A variety of artificial foods enhance growth, and fishes are raised to market size in the pens. Although keeping the pens free of fouling organisms presents some problems, growth is excellent and the technique is spreading. Popular fish include marine salmonids, marine genetically male *Tilapia*, Branzino (the European marine sea bass *Dicentrarchus labrax*), and the perciform *Cobia*.

Fish farming conflicts with the objective of restoring wild fishes to their former natural levels, before overfishing and water withdrawal take their tolls. There is currently a great controversy over farmed fish, and many marine conservationists have objected to the great expansion of fish farms, which involve principally salmon and European sea bass in the Atlantic and Mediterranean. Escaped salmon are a major component of the populations of "wild salmon" rivers in Norway. Currently, many farms use ground fishmeal as food, which has a great indirect impact on inshore fisheries throughout the world. Another major concern are the diseases that might arise in farmed salmon, since the pens are kept in open water with few precautions taken to prevent release of pathogens. Farmed salmon in British Columbia, Canada, tend to have high occurrences of sea lice, a parasitic copepod that scrapes away at fish skin and causes major lesions, especially in the head area. These parasites are escaping and infecting juvenile wild salmon and causing significant mortality that may drive nearby populations of pink salmon *Oncorhynchus gorbuscha* to extinction (Krkosek et al., 2007). In Chile, a virus has caused a great deal of mortality in fish farms (Naylor et al., 2000).

USE OF GENETIC MANIPULATION

■ **Genetic manipulation proves useful in improving performance of organisms in mariculture systems.**

In agricultural systems, genetic approaches have long been used to enhance production, disease resistance, and general vigor. Such approaches are in their infancy in mariculture systems. At present, there are a large number of hatcheries for fishes and shellfish, and these can be the source of stocks for crossbreeding. The crossbreeding of stocks from different areas, combined with selection for desirable traits, can be used to select a population with high growth and survival characteristics. This approach is useful because one or more desirable traits may initially be fixed in one population and another set of desirable traits may be present in others. It is the combination of such traits that has been a source of vigorous stocks of agricultural plants and stock animals. Modern molecular techniques of gene transfer have also begun to be used to enhance growth of farmed salmon. In the past few years, Dennis Hedgecock has made great strides in producing extensive libraries of genetic markers and linkage maps for oysters (e.g., see Hubert and Hedgecock, 2004).

Drugs from the Sea: Marine Natural Products

- **Compounds that evolved for a variety of ecological functions—including chemical defense, poisoning prey, and antimicrobial functions—can be adapted for human use as drugs.**

Throughout this text we have mentioned a variety of compounds synthesized by marine organisms whose evolution is related to a variety of ecological functions. For example, many seaweeds have evolved a wide range of compounds ranging from sulfuric acids to polyphenolics, which deter grazers such as herbivorous snails and sea urchins. An amazing variety of conotoxins is synthesized by species of the venomous snail *Conus*, small peptides of about 50 amino acids that have deadly neurotoxic effects on prey. A wide range of organisms, from fungi to polychaetes, synthesize compounds that have strong antibacterial activity. These compounds have a wide range of chemistries and are synthesized in a broad range of biological processes. Many substances, especially toxics found in terrestrial plant leaves, were initially thought be just byproducts of other biosynthetic pathways and were given the misnomer of **secondary compounds**. We now appreciate that the astounding range of such substances has evolved for specific ecological functions, such as chemical defense.

Pharmacologists have discovered an important principle. **Natural products** with strong biological effects may be readily adapted as drugs with applications to human biology, agriculture, and veterinary science. In many cases, the compound's ecological function in the natural species may be adapted to a rather different pharmacological application. For example, the hormone prostaglandin A_2 is synthesized by the Caribbean marine gorgonian *Plexaura homomalla* as an antipredator deterrent, causing a vomiting response in predatory fish (discussed in Chapter 4). But prostaglandins are also active and functional in humans as locally acting cellular signals in a wide variety of functions. Though they were first extracted in quantity from the gorgonian, synthesized prostaglandins can be used in the induction of labor, treatment of ulcers, and many other applications.

- **Marine natural products are extracted from a wide variety of marine species and may be targeted at a number of specific functional human processes and diseases.**

A wide variety of chemical extraction techniques are now being employed to systematically extract many bioactive molecules from a large number of candidate marine species (for a complete discussion, see Haefner, 2003). Research in this area is extremely active, and literally thousands of new compounds are discovered and researched each year. We can give only a general idea as to the tremendous amount of progress made in several classes of marine compounds.

Ion-Channel Blockers

Species of the carnivorous snail *Conus* employ diverse peptides to poison prey. The general action of the peptides is targeted at **ion channels**, a large array of specialized proteins that allow active transport of ions such as Na and Ca across cell membranes. The diversity of peptide action is correlated with different mechanisms of targeting prey behavior and movement. Literally tens of thousands of conotoxin-like molecules have been synthesized and a number of patented drugs have been developed that target neurologically important Ca channels as pain killers, but do not have the addictive effects of commonly used painkillers such as morphine.

Enzyme Inhibitors

Marine natural products chemists have extracted a large variety of compounds that have strong effects on enzyme function. Many target protein kinases, which are crucial in cell signal transduction and cell division. Because these compounds affect fundamental cell-cycle processes, they are being developed into a wide variety of anticancer drugs in which regulation of cell division is crucial. For example, bryostatin (see Manning et al., 2005) was extracted from the common bryozoan *Bugula neritina*, although the exact ecological function of bryostatin in the bryozoan is obscure, and in fact derives from a bacterium resident in the bryozoan. Bryostatin activity results in the inhibition of protein serine/threonine kinases and has anticancer cell activity. Symbiotic bacteria in some sponges also have related types of activity and their products are being actively investigated as anticancer drugs, via inhibition of protein tyrosine kinases.

Apoptosis Stimulators

Ascidians are sessile and have no hard skeleton. As a result, many species have evolved a wide array of toxic compounds that deter mobile predators such as fishes. Some tropical species are rich in transition metals, and we discussed in Chapter 4 *Phallusia nigra*, which has high concentrations of vanadium and sulfuric acid. The bioactive compound aplidin has been extracted from the ascidian *Aplidium albicans*, found in the eastern North Atlantic and the Mediterranean. Aplidin stimulates the process of apoptosis, or programmed cell death. It is a very promising drug in the treatment of multiple myeloma tumor cells (Mitsiades et al., 2008).

- **The great diversity of sources of marine bioactive compounds suggests that conservation of biodiversity of species and diverse marine habitats in turn creates a diversity of sources of compounds for drug discovery.**

The previous section demonstrates an important principle. There is a surprising range of sources for new and medically important bioactive compounds. These compounds are diverse because of the existing ecological and taxonomic diversity of biochemical processes that have been discovered in marine organisms. In many cases, compounds have been isolated from single species or groups of closely related species, as in the case of the conotoxins extracted from cone snails. The genus *Conus* is widespread throughout the Indo-Pacific and Atlantic, but the peak of species and therefore biochemical diversity is within the Coral Triangle (see discussion of coral reefs in Chapter 17). Other important compounds come from bacteria that live as symbionts with host invertebrate species such as sponges. Therefore, drug discovery in this area depends on the conservation of mutualistic systems in the ocean. Finally, the complex predator-prey relationships in the ocean have led to the evolution of a broad array of antipredator toxins. This suggests that the conservation of natural and diverse marine food webs will have a direct relationship to our ability to investigate compounds arising from such interactions that might be important in drug discovery. It is therefore no exaggeration to state that marine conservation is crucial to the advancement of human health.

CHAPTER SUMMARY

- Fisheries are divided into stocks, usually geographically distinct populations. Tags, as well as biochemical and molecular markers, can help identify and monitor stocks that have become genetically isolated. Because stocks often transcend political borders, they can result in disputes.
- Sensible fishery management is based on an understanding of the life history of species and the size of the stock. Physical variables, spawning and feeding grounds, and migration routes are all important.
- The size of a stock is a function of population size, spatial variability, and the amount of fishing (fishing effort), including numbers of boats, fishing hours, and gear quality. The health of a stock can be assayed by its growth in the previous year and recruitment into production. Stock-recruitment models attempt to predict change in the stock as a function of the stock size in previous years. A popular model predicts that stock increase rate will decline as stock size becomes large, owing to resource limitation.
- Finfishes are caught mainly by hooking fishes individually, entangling them in nets, or catching them in nets or traps. Hooks are used mainly in longline arrays on the surface or at depth. Nets are commonly deployed as trawls, either near the surface or at the bottom, which is greatly disturbed. Unintended catches, or bycatch, are a major source of fish, sea turtle, and mammal mortality.
- In the maximum sustainable yield model, fishing may actually increase productivity, by reducing the effects of high fish density on reproduction and growth. However, this concept is not well supported by data. In recent decades, fishing for top carnivores has severely reduced populations at the apex of food chains and has increased abundance at lower trophic levels.
- Stock reduction results from random variation and environmental change. Overfishing accelerates the decline; stocks characterized by long generation times, small clutches of eggs, and fewer spawnings are the most vulnerable. Many countries have claimed exclusive economic zones of 200 miles from the coast, which allowed local overfishing. Temporary closures, transferable quotas, and fishing limits may allow some fisheries to be sustainable. Ecosystem-based management and marine protected areas are also important tools.
- Once shore based, whaling developed into an open-ocean fishery. New technologies around the turn of the twentieth century—including cannon-powered harpoons, factory ships, and stern slipways—accelerated the decline of whales. A whaling moratorium, molecular detection techniques, and public awareness have helped to arrest the declines of minke and humpback, but other species are still endangered.
- In mariculture, natural habitats are simulated or enhanced, to make harvesting of food fish more convenient or to increase yields. Mariculture systems for mollusks, especially bivalves, are located in areas of high phytoplankton supply, where red tides and other blooms can devastate fisheries. Mariculture of seaweeds aids in the production of agglutinants, food, and organic matter suitable for methane production.
- Fish farming is a major means of rearing finfishes such as salmon, but may produce fish with undesirable traits and spread of parasites. Genetic manipulation can improve the performance of mariculture systems.
- Marine natural products are diverse, probably mainly because of a diversity of evolution of ecological functions. Extraction of many of these compounds has proven useful in the development of drugs for a variety of human ailments.

REVIEW QUESTIONS

1. Why is stock identification so crucial in fisheries management?
2. How is the size of a fishery stock usually assessed?
3. What are three factors that might make animals in one fishery more vulnerable than others?
4. Draw a diagram illustrating an expected relationship between stock size and recruitment in the following reproductive season.
5. Why might the expected stock recruitment relationship you have diagrammed fail to develop?
6. What is the basis of the concept of maximum sustainable yield? Why has the effectiveness of this concept as a tool in fisheries management been criticized?
7. How did technology contribute to the decline of open-ocean whale stocks?

8. Why was the blue whale unit adopted? Why did it not represent a good management tool?
9. What characteristics are desirable in choosing a species useful for mariculture?
10. How might harmful algal blooms, discussed in Chapter 8, affect the economy of shellfish mariculture?
11. Why do you think many fishers are resistant to switching from fishing to mariculture?
12. What are some benefits and possible problems connected with fish farming?
13. Why might the culture of just one species of shrimp in crowded shrimp farms accelerate the effects of disease in shrimp population crashes?
14. How can it be that the total landings of a fishery can be constant year after year and then the fishery rapidly collapses?
15. A conservation committee decides to designate a group of subtidal reefs for marine protected areas. What is the value of protecting a group of reefs, as opposed to just the largest one?
16. What is the benefit of removing a dam on a major river connected to the ocean?
17. Suppose that you are given a research budget to find drugs that suppress cell growth to treat cancer. Devise a program of discovery of drugs derived from natural marine species.
18. Why are shellfish farms in special danger on the west coast of the United States?

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