

CHAPTER 21

Fisheries and Food from the Sea

We can get a glimpse of prehistoric fishing practices by examining the reports of anthropologists and explorers who have observed aboriginal societies. When Europeans first encountered them, the aborigines of Australia were using bark boats, from which they threw snail-shell hooks attached to a line fashioned from beaten bark. When a fish was pulled in close to the canoe, it was speared and brought onboard. Native Americans of Pacific coastal Canada dropped lures to the bottom and bobbed them to the surface. The fishes followed the lures and were speared. These natives also used baited hooks, crab traps, and comblike devices with small bone spears to impale fishes.

It is an interesting question as to whether prehistoric natives overfished areas or whether their practices were sustainable. We can't assess motives, but studies of oyster fishing in native America and aboriginal Australia were apparently sustainable and did not drive the fishery to local extinction (see discussion of oyster reefs in Chapter 16). But in the twelfth century, a new type of trawl was so efficient that King Edward II banned its use in the Thames River. Technology has been the main source of rapid overexploitation in the past century. Open-ocean fisheries were essentially limitless until the development of power-driven vessels and gear, aided by modern remote sensing technology. The worldwide search for edible protein has further compounded the problem, and fish landings have doubled every 10 years in recent decades. Fishes are not only consumed directly by people, but are also used as meal for fowl and pigs, and for pet food (which, ironically, is then used as a favored bait for shrimp fishing in the Puget Sound region). These practices have led to many shortages and international disputes.

The Fishery Stock and Its Variability

Fish populations are renewable resources.

Fishery populations are a renewable resource; nutrients and energy are fueling their regrowth even as we exploit them. This concept of renewable resources serves as the entire basis of fishery management. In some fisheries, even modest fishing depletes the stock much more rapidly than it can be renewed. Such overexploitation can lead to cycles of near extinction of the fishery population, followed by eventual recovery if the fishery is managed. This is the case with many marine mammal populations that have been hunted nearly to extinction. The California sea otter, Enhydra lutris, for example, was hunted until only a few populations survived, in the Aleutian Islands and in a few isolated spots on the west coast of North America. The otters were prized for their skins. Hunting has been banned for decades, and population growth, migration, and restocking have resulted in a dramatic recovery of the population.

Stocks and Markers

Fishery species are divided into stocks. Various tags and markers can be used to monitor them.

Monitoring is a key to understanding of the trajectory of fisheries. For over a hundred years, many scientific organizations and governmental agencies have been learning about the life histories of important fishery species and have been attempting to monitor the populations and devise management schemes. This began in 1902 with the establishment of the International Council for the Exploration of the Sea, to address fishery problems in the North Sea.

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In Chapter 7, we discussed fish migration, which may occur between spawning, nursery, and adult feeding grounds. A fishery species may have a broad geographic range, but, for management purposes, we divide the total range into populations, or stocks. Each stock is controlled by separate oceanographic and ecological factors and has nearly complete reproductive separation from all others. This usually involves separation of the spawning grounds, but it may also involve separation of nursery and feeding areas. Tags are commonly inserted into fishes to follow their movements but also to delineate stocks (Figure 21.1). This allows the recording of time and location of release and capture. Some tags are visible outside the fish, but completely internal tags can be inserted with little mortality. We can detect them by means of magnetic inserts or even by small radio transmitters that are induced by a scanning device. Radio tagging and acoustic reflection can also be used. Tags that communicate with a global positioning system have been used in marine air breathers such as sea turtles, but fish often swim too far beneath the surface for detection, so the tags are designed to disattach and float to the surface, giving a location.

Biochemical and molecular markers of various types can also be used to diagnose differences among fish stocks that have become genetically isolated.

Natural selection or random processes change the genetic composition of stocks after they have been separated for a time. The cod is an example of a species divided into a number of geographically isolated populations that can be

diagnosed by a number of biochemical genetic markers. Hemoglobin and transferrin genotypes were first used to diagnose different cod stocks in the North Atlantic. Other markers, including enzyme polymorphisms (genetically distinct variants of enzymes), morphology, and unique parasites can be used to distinguish among stocks. In recent years, DNA sequences and markers have been used to delineate stocks.¹ For example, mitochondrial DNA can be fragmented by different types of restriction enzymes, each of which breaks up the DNA at specific points. Such enzyme digestion produces a series of length variants that can be identified by their migration on a stained gel. Different populations tend to exhibit different length variants, and therefore DNA markers are useful in stock identification (Figure 21.2). More directly, DNA sequencing can be used to find sequence variants at highly variable genetic loci. At a number of genetic loci, genetic variants are diverse enough that they vary in content between populations and can thus be used to distinguish among stocks. Microsatellites are genetic loci where short sequences of nucleotides are extensively repeated. They are quite variable in populations, and the number of certain repeats may vary between species, among populations, or even between individuals. Consequently, they can be used as effective markers at several levels of organization. They have proven valuable, for example, in distinguishing among migrating Pacific salmon stocks from different river systems and



FIG. 21.1 A striped bass, *Morone saxatilis*, tagged ventrally with an internal tag. (Courtesy of John Waldman)



FIG. 21.2 Identification of stocks of the striped bass *Morone saxatilis* by use of DNA markers. An agarose gel, in which restriction enzyme–digested fragments of mitochondrial DNA (labeled with radioactive carbon) have been separated by size, is shown. (Fragments migrate in the direction of the arrow at left, within lanes marked by letters.) Marked fragments in lanes B, G, H, I, and J exhibit a mitochondrial genotype that is seen only in striped bass from the Gulf of Mexico coast, whereas marked fragments in lanes A, C, D, E, F, and K display a mitochondrial DNA genotype diagnostic of striped bass of Atlantic coast ancestry. (Courtesy of Isaac Wirgin)

¹ See bonus chapter, "Molecular Tool for Marine Biology," online.

investigating their mixing in the open ocean. It has been possible to cross-check DNA markers with data from tags (Beacham and Wood, 1999). The student should be aware that the use of genetic markers to delineate fisheries stocks is not straightforward (Palsbøll et al., 2007).

Stocks may be isolated from each other on the basis of use of the same drainage but at different times.

Stocks may differ in geographic occurrence, but they may also use the same geographic space (e.g., river drainage) at different times and thus still be isolated from each other. In the pink salmon, spawning occurs in streams and adult feeding occurs in the adjacent ocean, but there are oddand even-year populations in the same streams, which are reproductively independent. DNA markers can be used to delineate stocks and help to identify streams that deserve special protection or restoration.

Stock identification can have important societal implications.

Delineations of stocks according to ecology are often not the main motivations of fishery biologists. Fishermen often have a proprietary interest in their own local fishes, but the fishes also may range over broad areas. For example, many Native American tribes have rights, negotiated by treaty, to specific stocks of Pacific salmon. This requires the ability to distinguish among salmon stocks. To negotiate border disputes between Canadian and U.S. fishers, for example, it is useful to have an accurate means of distinguishing among local stocks and to be able to identify the geographic extents of spawning and feeding grounds. Even when armed with such information, fishery experts may still be frustrated in their efforts to reach an agreement because fishes often swim across international borders during migrations.

Fishing Techniques and Their Effects

Finfishes are mainly caught by (1) hooking fishes individually, (2) entangling fishes in stationary nets, or (3) catching fishes in hauled nets or traps.

Although the methods may have improved slightly, the basic ways of catching fishes have not changed for centuries. Perhaps spearing is the one technique that has been essentially abandoned by all but aboriginal peoples. It is still quite useful for hunting fishes living on rock and coral reefs. Harpoons are used widely for whales and swordfish. Currently, (a) hooked lines, (b) stationary nets, and (c) hauled nets are the most popular techniques (Figure 21.3). Hook



FIG. 21.3 Some fishing techniques: (a) hook-and-line and longline fishing, (b) gill net fishing, and (c) purse seine and trawl netting. (From Cushing, 1988)

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and line may appear to be equally primitive, but variants are used extensively. Most popular are **longlines**, from which short leaders with hooks extend at regular intervals. Longlines can be thousands of meters in length. The line may be paid out and suspended by floats, or it may be trolled behind a boat. Trolling is a common means of fishing for albacore and some species of Pacific salmon.

Many different types of shoreline nets staked into the bottom have been developed that entrap fishes swimming in schools along the shoreline. Such nets are especially effective in trapping migratory fish that have strongly constrained routes, such as American shad, which move upriver to spawn. **Pound nets** often have some sort of leader wire that guides the fish into a blind-ended net. If currents are strong enough, there is no need for a long leader and the fish can be trapped directly. These net arrangements can also be suspended from rigid floating frames and are used to catch some species of salmon. **Fyke nets** are long nets that are usually staked to the bottom. They have leading wings that guide fishes moving with the current into the main bag, from which escape is difficult.

Gill nets have a specified mesh size, chosen to entrap the fishes by their gills, fins, and jaws as they attempt to swim through. These nets could be stationary, but also can be towed from one end through the water, while the other end is attached to a smaller stationary boat or is anchored to the bottom. From both shore and boat, a variety of finemesh nets are hauled to entrap large numbers of fishes. One of the laziest techniques is to drop a net stretched over a horizontal frame. The net is raised periodically. This is a common technique used in the Mediterranean to trap small fishes and squid. Many fishing peoples haul seine nets across beach areas, sometimes with the aid of fourwheel-drive trucks on the beach. The top of the net is attached to floats, and the bottom is weighted down. This method catches a large variety of fishes and was used to catch striped bass on the south shore of Long Island, New York. In other areas, a boat offshore hauls the net, which is fixed to the bottom at the beach. The boat gradually brings its end of the net toward the beach, and the fishes are entrapped in the closed portion.

Seine nets are also deployed entirely from boats. Purse seines are particularly effective. The end of the net is attached to a small boat, and the net is paid out as a larger boat moves away. The larger boat attempts to encircle a school of fishes with the net, and a rope acts like a purse string as the net is drawn aboard and closes about the fishes. This method is used for a variety of fish species, and is used from inshore waters to the blue ocean. Environmentalists have complained in recent years about the damage to porpoises, which are entrapped in purse seines with tuna. For reasons that are not well understood, schools of tuna congregate beneath groups of porpoises, and fishing boats, therefore, seek out the porpoises, which indicate that tuna are below. As the tuna net is hauled in, the porpoises are often trapped underwater and drown. Many fishing boats now employ divers to help save the porpoises, and there has been strong pressure to eliminate the fishing technique. Many large

fishing fleets in the Pacific have changed fishing practices to avoid trapping porpoises, which enjoy popular support among the public.

Many other nets that are employed are essentially bags towed by a harness of wire. **Bottom trawls** are especially efficient because the harness is attached to two or more panels, called otter boards, that spread the opening of the net efficiently. The bottoms of the boards are weighted in order to drag the net over the bottom. This technique is used widely to bring in bottom fishes such as plaice and flounder along with schools. In midwater, **pelagic trawls** are used in a similar way to net schools of fish. Modern remote-sensing techniques, such as multibeam sonar, permit oceangoing vessels to locate enormous otter trawl gear accurately at depths of hundreds of meters to target large schools of fish.

In recent years, extremely large open-ocean nets were employed to catch squid and other abundant nekton. Fishers from a number of nations used nets over 30 miles long. These nets kill off large numbers of squid and fish and threaten to wipe out a number of different species. A treaty was ratified to ban the nets, which went into effect in 1993.

Bottom-associated animals are trapped in baited mesh traps.

A variety of mobile animals, but principally large crustaceans such as crabs and lobsters, are taken from baited traps that are usually marked with surface buoys. Of necessity, these are generally coastal and estuarine fisheries. Traps often have inverted cones at the entrance, making it difficult for the animals to leave the trap. Unlike most net fisheries, trapping is associated with specific areas of bottom, and this has led to a variety of informal and formal divisions of fishing grounds among fishers.

Unintended catches are known as bycatch.

Another human-imposed source of fishing mortality is the incidental killing of undesirable species of fishes, known as **bycatch**. As mentioned earlier, dolphins are often trapped in nets during fishing for tuna in the Pacific. U.S. fishery legislation has required that fishing nets have **turtle exclusion devices (TEDs)** consisting of a screen or bars to prevent turtle entry and a trap door, which allows the escape of sea turtles that would otherwise drown in the nets. After some careful estimates of sea turtle mortality by fishery agencies and the realization that TEDs were not large enough for leatherback turtles, current widespread use of inshore and offshore trawlers has dramatically reduced turtle mortality at sea (Finkbeiner et al., 2011).

Large numbers of fishes of inappropriate species are caught and killed in the process of recovering gill nets. Floating longlines used in the central Pacific to catch swordfish may have strong impacts on some species of albatross that feed on fishes near the surfaces. In the northwest Atlantic, swordfish boat longlines catch a large number of blue sharks.

Fisheries biologists have come to realize that oceanographic patterns make bycatch almost inevitable. We have discussed patterns of upwelling and major current systems

that cause many species to migrate very long distances and to wind up in high-productivity zones and often in multispecies migration routes (see Chapter 10). Thus, longlines intended for one valuable resource species will likely catch other species attracted to the same high-productivity zone. In such areas in the North Pacific Ocean, longlines laid to catch tuna will likely catch sea turtles or albatrosses attracted to the large populations of forage fish that attract the tuna-and fishers-to the same regions. Peckham and colleagues (2007) describe a fascinating example: A pair of relatively small-scale gill net and longline fisheries near the open Pacific coast of Baja California caught as many endangered North Pacific loggerhead sea turtles, Caretta caretta, as the rest of the fisheries in the Pacific! These turtles nest in Japan, but juveniles move throughout a series of distant Pacific Ocean routes to find food. They were snagged by longlines deployed from small boats, but local fishers agreed to change from this fishing technique.

These considerations have led to a variety of techniques to avoid bycatch, many of which have been used in laws and rules set by fisheries agencies (Gilman, 2011; Moore et al., 2009):

Release devices. Turtle exclusion chambers allow sea turtles caught in nets to swim away and escape being trapped in nets.

Avoidance devices. Some nets have devices that make pinging noises, causing dolphins to swim away. We have already mentioned turtle exclusion devices.

Specialty hooks. Because the typical J-shaped hook can also catch turtles and species that are endangered, circular hooks have been adopted in some areas. These hooks efficiently catch fish, but sea turtles cannot easily be ensnared. Some hooks are designed to bend when seized by very large fish, such as Atlantic bluefin tuna, but will retain tuna species of smaller body mass that are acceptable for fishing.

Specialty trawl nets. Nets can reduce bycatch by adjusting net size and structure. For example, the Ruhle net allows haddock to rise as they enter the net and be caught. But Atlantic cod, which require protection, stay to the bottom. For this reason, the trawl net has large openings near the net bottom, allowing the cod to escape.

Timing of fishing and location. Setting of longlines at night is a powerful method of avoiding bycatch of seabirds such as albatrosses, who hunt visually and usually during the day. Undesirable bycatch of threatened species such as sharks and marine mammals can also be reduced by avoiding known hotspots of abundance for potential bycatch species.

Bycatch has become so abundant in some fisheries that seabirds have become dependent on discarded fish. In the Baltic and North Seas, this dependence has produced an ironic linkage. Efforts to decrease bycatch may cause decreases in seabird populations. This is especially true in cases in which normal seabird habitat has been disrupted, making bycatch the only food that is available to some seabird species. When bycatch was reduced, the great skua *Stercorarius skua* shifted to preying on smaller shorebirds, potentially threatening some seabird communities (Votier et al., 2004).

Much of the world's catch consists of bycatch, used for fishmeal, and targeted pelagic fish taken specifically for fishmeal.

Fishmeal comprises the main marine protein and lipid sources used in animal feed (terrestrial and mariculture food). Some bycatch is set aside for fishmeal, but most fishmeal derives from targeted fisheries (e.g., anchovies), usually smaller pelagic fish such as anchovies, sardines, and capelin. Regulations are beginning to reduce the catch used for this purpose.

Bottom trawling may strongly alter the seabed.

Bottom trawling very strongly impacts living resources on the seabed (Thrush et al., 1998). In heavily fished areas, just about every square meter of bottom is dragged a few times a year. Many bottoms with gravel and a rich epifauna of bryozoans, hydroids, and echinoderms will be turned over, leaving a smoother soft-bottom interface with smaller softbottom invertebrates and much lower benthic diversity (Collie et al., 1997). In places where epifaunal communities are destroyed, the substitute is a mud bottom without the usual benthos (e.g., oysters, sponges, soft corals) that feeds on particles from the water column and deposits them on the sediment-water interface. Instead, the disturbed muddy bottom is easily resuspended, which returns to the water column organic-rich particles, which may be consumed by bacteria and reduce the oxygen content of the water. On the other hand, trawling of sandy bottoms seems to do less damage to the seabed, perhaps because infaunal burrowing organisms are more resilient to sediment overturn. The effects of such strong changes are obvious for the benthic communities, but the feedbacks on the resource species are poorly understood. If a bottom-feeding fish depends on smaller mobile prey, then it might suffer greatly for lack of a variegated cobbly bottom that shelters smaller fish and shrimp. On the other hand, some fish might find a bare bottom to be a more suitable habitat. It will be very important to understand the recovery time, which will help set trawling intensity quotas. On the Grand Banks off Newfoundland, eastern Canada, recovery time may be as long as a year (see Schwinghammer et al., 1998).

Life History and Stock Size

The life history of a fishery species and the size of the stock must be understood before sensible planning can be done regarding fishery management.

To make sensible decisions about fisheries management, the following must be known: (1) range of temperatures and salinities for maximum growth and survival, (2) location of spawning habitat, (3) location of migration routes, (4) location of feeding grounds, and (5) biological information that minimizes unintended mortality during fishing. To make proper management decisions, it is necessary to estimate the size of a stock. It is also desirable to know the abundance of the different year and size classes because only fishes of certain sizes are economically important. Certain age classes such as juveniles and reproductive individuals may be important to identify for conservation purposes.

In some cases, fish stocks are assessed by fishery agencies through a carefully designed sampling program that takes into account migration patterns and spatial distribution. Migration over wide geographic regions makes it very difficult to assess a stock size because one cannot easily design a sampling program that adequately follows a fish population over hundreds or thousands of kilometers. The spatial distribution is important because fishes are rarely distributed evenly but usually occur in distinct patches; they may also school. In such cases, small numbers of samples are liable either to miss the population altogether or to hit a dense patch accidentally. In either case, one cannot simply assume that the density estimated from a very few trawls adequately measures the population size. In many cases, we are ignorant of the mechanisms of clumping. For example, leatherback turtles have been found to occur in patches in the open ocean, which are loci of their jellyfish food, which is also very patchy in distribution (Houghton et al., 2006).

It is desirable to use the same types of sampler in different studies because samplers vary in their ability to catch fish. In many cases, population estimates are made with different types of sampling gear, and different results are obtained. When this happens, we cannot be sure whether the difference is due to the gear employed or to actual differences in population size. For purposes of cross-checking, it would be desirable to employ different methods of assessing abundance in the same area at the same time, but this is rarely done. A good example of disparities in stock size estimates is the northern right whale dolphin, Lisodelphis borealis, which is often a victim of large drift nets (Mangel, 1993). Estimates from line transects yield far lower population size estimates than do estimates made from accidental catches in drift nets. These differences are crucial because they lead to very different conclusions about the degree of endangerment of this dolphin species in the Pacific Ocean.

Moreover, it is usually not possible to sample eggs, larvae, and adult fishes with the same type of sampling gear. Because each gear type has a different efficiency of catching fish (or eggs), and different life stages have differing spatial distributions, it is often impossible to compare estimates of abundance between very different life stages.

The size of a stock is mainly assessed by quantity of landings by fishers, which is principally a function of the population size, the spatial variability of the fish, and the amount of fishing effort.

Although fish surveys are done frequently by government agencies, most fishery data do not come from scientific surveys but from data on **landings** by fishing boats. For most important U.S. fisheries, federal and state agencies collect data presented by the fishermen. To some degree, inspectors may verify the data, principally through onboard checks during the fishing. By the end of a year, a fishery agency may know the total number and mass of fishes, and may have a breakdown by size and a record of the number of boats and the time each one spent fishing.

Although the quantity of landings is to some extent a function of population size, landings are difficult to interpret for one of the same reasons applicable to more systematic surveys: The spatial distribution is rarely even, and sampling therefore is biased away from the true density. Moreover, fishermen work in areas that customarily have the highest fish densities, but landings data may ignore other important areas, such as spawning and juvenile feeding grounds. There is also a complication generated by variations in the numbers of boats deployed, fishermen working, type of gear employed, and hours spent fishing. These four factors are collectively known as fishing effort. If effort increases, the catch will increase, but not necessarily because there are more fishes in the ocean. If the fishing effort doubles and the catch does not double, however, one may assume that the population is declining. All stock estimates must therefore take into account the catch per unit effort. A useful indirect measure of effort is fuel consumed to run the fishing boats involved in a fishery. Figure 21.4 shows the declining historical trend in catch per unit effort for the blue whale fishery.

Variation in fishing effort often masks the quantitative meaning of landings. If a group of fishers seek a certain catch per unit time, then they might increase effort over time to maintain the catch. Thus, the landings might be constant even if the actual population is declining. If landings decline over time, we might correctly interpret a corresponding decline in the actual population of fish. But fish might learn to avoid fishing boats, or fishing effort might decline over time. Both of these possibilities would give the false conclusion that the size of the stock is declining, when no such thing is occurring. Landings are of course also a function of management goals by government fisheries agencies, so a decline in landings may reflect rules rather than the actual sizes of fish populations.

Stock Health and Production

The health of a stock can be assayed by its production, which is explained in terms of growth of previous year classes and recruitment into the new year class.

Because a stock has been defined to be a population that is relatively isolated from others of the same species, one can try to evaluate the potential yield of a stock to a fisher. We are interested in the change in the potential yield, measured in pounds of fish per year, from the previous year. To make such an estimate, we have to have a general model for gains and losses in a stock of resource organisms (**Figure 21.5**), which includes recruitment, somatic growth, mortality, and reproduction.

The relationships among these factors can be expressed in an equation that relates them all to the change in population size:

$$\Delta W = W_{t-1} - MW_{t-1} + RW_{t-1} + GW_{t-1}$$

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FIG. 21.4 Catch per unit effort of the blue whale through the twentieth century.



FIG. 21.5 To produce a good fisheries model, we must account for all contributions to reproduction, growth, and mortality throughout the life cycle of the fishery resource species.

where ΔW is the change in mass of the total fish population over 1 year, W_{t-1} is the mass of the population at the same time in the previous year, M is a mortality fraction (varies from 0.0 to 1.0) giving the fraction of the mass of fish that was lost owing to death, R is the fraction by mass that is added from recruitment, and G is the fraction by mass that is added owing to growth of individuals that lived from the previous year to the present. We can neglect immigration and emigration because the stock has been defined to be independent of other populations.

Although we are interested in total mass of fish, fish population models must eventually be expressed in numbers, and it is essential to be able to know the age of the individuals that are surveyed and studied. In some cases, age can be identified by size. This is true in seasonal environments, where birth and rapid growth are often confined to short periods of the year when food is abundant. After several years, the population will consist of a series of **year-size classes**, which may be distinguishable by size (Figure 21.6). Growth slows in later years, and the variation in growth tends to blend the later age classes. Also, fishes growing at different rates may be mixed together in a feeding ground, and the age–size relationship may therefore be too complex to measure. Because of this, fishery biologists have resorted to other techniques. Both **otoliths** (small precipitated spheres used as part of a balancing organ) and scales have rings that record seasonal growth. Otoliths can be used to age larval fish to the day, which is quite important in the understanding of early life histories (Figure 21.7). For shellfish, growth rings can also be used, and cross sections of shells often give an accurate age and growth history.

Fishes and shellfish have the capacity to produce thousands to hundreds of thousands of eggs per female. When fertilized, these eggs produce the next generation of larvae and then early stage juveniles. A plankton net can bring in millions of fish eggs and thousands of yolk-sac larvae. As these **young-of-the-year** (0+ year class) feed and grow, one HUMAN IMPACT ON THE SEA



FIG. 21.6 Age classes of the lobster *Panulirus ornatus*. Curved line estimates age classes from the more discontinuous distribution of the histogram. Note the older age classes to the right, which are more indistinct. (Modified from King, 1994)



FIG. 21.7 A cross section of an otolith of the bluehead wrasse *Thalassoma bifasciatium* that settled from the plankton at a length of 13 mm. The daily growth record reveals the 41-day mark after hatching, when settlement on the bottom occurred (transition between closely spaced lines and relatively broad band). Otolith is about 300 μ m long. (Courtesy of Robert Cowan)

can trace a peak of body size as it increases with time. There is also considerable mortality in the year class as it ages. It is no coincidence that egg production per female is so prodigious. Most eggs and larvae are eaten, starve, or are lost to inappropriate habitats. Few survivors make it to adult age and size, to contribute the next generation.

A major objective of fisheries biology is to project population change into the future. The most common approach is to predict the size of the 0+ year class from the stock size in the previous year. The appearance of the 0+ year class comprises the recruits. A number of different **stockrecruitment models** have been proposed (see Needle, 2002, for an excellent introduction to the different stock recruitment models), but we shall focus here on one that relates reproductive success to population density.

If resources (e.g., food, space for spawning) are limiting, we might expect a relationship between the size of the stock and the recruitment as depicted in Figure 21.8. As the stock increases, the number of 0+ recruits in the next



FIG. 21.8 An expected relationship between the size of the stock and recruitment in the following year.

year should increase as well. But past a critical stock size, available food per adult may start to decrease to the point that eggs per female will decrease correspondingly. As the stock increases past this critical threshold, we expect a decline in recruits per reproductive female. Past the critical threshold, resources are limiting and production of recruits into the next year also declines. This reaction of population growth to high density is known as **compensation**. **Going Deeper Box 21.1** shows one ecological model that might explain compensation in terms of reduced resources per female as population size increases and resource per female decreases. This relationship of stock size to recruitment can be the basis of fishery management, as we discuss shortly.

In practice, often there is a poor correspondence between the size of the stock and the number of recruits surviving into the next year. Postreproductive processes in the first year of the 0+ year class will likely determine population size, but these processes (e.g., predation) may be independent of the parent stock and resource availability to that parent stock. Conditions change rapidly at sea! A simple example may illustrate why such a decoupling between stock size and recruitment of the next 0+ year class