

# 13 Effects of Fishing on Long-Lived Marine Organisms

Selina S. Heppell, Scott A. Heppell, Andrew J. Read,  
and Larry B. Crowder

North America once had a rich array of megafauna that included 31 genera of large and long-lived mammals such as mastodons, horses, and saber-toothed tigers. But around 12,000 years ago, these organisms disappeared. What led to the demise of this fascinating fauna? Although it is still the subject of some debate, a prevailing hypothesis is that these organisms were rendered extinct as technology invaded the continent and moved from west to east (Frison 1998; Martin 1973), either carried directly by humans as they spread through the continent or as the technology passed through existing populations. Even with modest technologies, hunters were able to hunt or modify the habitats of these large organisms to force their extinction. Although humans have been seafaring for thousands of years, our impact on marine megafauna has lagged relative to our effect in the terrestrial realm. In the most recent review of documented human-induced marine extinctions (Carlton et al. 1999), only eight vertebrates and four invertebrates are listed. The status of many other marine organisms is uncertain, although many populations appear to be in decline (Myers and Worm 2003) and it seems likely that the current estimate of recent extinctions in the sea is low. What is most striking, however, is that hunting and other anthropogenic effects account for most of these extinctions in the marine environment (Carlton et al. 1999; Norse 1993). Nine of 13 marine animals con-

sidered in jeopardy by Norse (1993) are overexploited, and a substantial number of currently threatened or endangered marine animals are subject to direct exploitation or bycatch (Crowder and Murawski 1998).

One characteristic of many extinct or endangered marine animals is that they are relatively large, long-lived organisms. Hunters in the sea often focused first on large organisms and hunted them intensively. Steller's sea cow (*Hydrodamalis gigas*), a massive sirenian first discovered by Europeans in 1741, reached lengths exceeding 8 m and weights of over 5 tons. Abundant, slow moving, and unafraid of humans, Steller's sea cows were hunted intensively for their meat and driven to extinction by 1768. Similarly, great auks (*Alca impennis*) were not only large but also flightless, making them easy prey for hunters who collected eggs and killed the birds for feathers and meat. Like the slow-moving, long-lived terrestrial mammals of the Pleistocene, these species suffered as a result of improved hunting efficiency and the exploitation of new habitat by humans.

Direct exploitation has resulted in the decline of a number of long-lived fishes, including pelagic sharks (primarily lamnid and carcharhinid species), swordfish (*Xiphias gladius*), groupers (Serranidae), rockfishes (Scorpaenidae), and sturgeon (Acipenseridae) (Baum et al. 2003; Musick 1999a and papers that follow; Musick et al. 2000a). In many cases, these species are still

the subject of underregulated, targeted fisheries despite rapid declines in abundance. A number of long-lived marine invertebrates also face heavy exploitation pressure, including elkhorn coral (*Acropora palmata*), geoduck (*Panopea generosa*), abalone (*Haliotis* spp.), giant clams (*Tridacna* spp.), and sea urchins (Echinoidea) (Carlton et al. 1999; Norse 1993). They are also impacted by habitat alterations and invasive species (Carlton et al. 1999; Carlton and Ruiz, Chapter 8) and in some places have become so sparse that they have difficulty spawning successfully, despite the potential for high reproductive output (Leviton and McGovern, Chapter 4).

Indirect exploitation of many long-lived marine organisms, including cetaceans and sea turtles, has caused dramatic population declines when these organisms appear as bycatch in fisheries that are directed at other species (Crowder and Murawski 1998; Dayton et al. 1995; Hall et al. 2000). Approximately 20 percent of the world's seabird species are considered to be at risk of global extinction (Collar et al. 1994; Russell 1999), many due to overexploitation through bycatch. These charismatic species are large and highly visible and have captured the public's attention. In some areas of the world, these species are legally protected to enhance their chances for recovery. Other, less charismatic, long-lived species are also in serious decline due to bycatch, including many elasmobranchs (sharks, skates, and rays) and long-lived bony fishes (Musick et al. 2000a, b). Common skates (*Raja batis*) were declared locally extinct in the Irish Sea in 1981; several other long-lived skates have suffered precipitous declines (Casey and Myers 1998; Walker and Hislop 1998), primarily due to bycatch in trawl fisheries (Carlton et al. 1999). Because most fisheries bycatch is poorly regulated and monitored, impacts to populations might not be noticed or mitigated until populations crash (Crouse 1999).

In addition to public concern generated by a fascination with certain long-lived marine species, some species are also "strong interactors" (sensu Paine 1980) that play a disproportionate role in the structure and function of marine food webs. Other species operate

as "keystone species" that have large per capita effects on marine food webs. A well-known example is the sea otter (*Enhydra lutris*) and its effect on the kelp forest ecosystem in the North Pacific (Estes 1995). In this system, sea otters suppress grazing sea urchins (*Strongylocentrotus* spp.), allowing kelp forests to expand, which subsequently provides a habitat for juvenile rockfishes (*Sebastes* spp.) and other long-lived organisms. When humans hunt otters, urchin populations explode, driving down kelp biomass and reducing protection for juvenile fishes.

Large body size is often correlated with long life. Until humans developed the ability to hunt and fish at sea, large adult body size conferred reduced risk of predation (Peterson and Wroblewski 1984). There are few natural predators in the sea that can attack large fishes, turtles, or marine mammals; notable, but rare, exceptions include killer whales (*Orcinus orca*) and large predatory sharks (which are themselves long-lived marine species). Because adults of large-bodied species had a high probability of living from one year to the next, they could mate and reproduce multiple times, thereby compensating for uncertainty in juvenile survival. But humans have drastically impacted selection for this trait; because we tend to select larger organisms, we have increased the mortality rates for just those stages that must experience high survival for populations to persist. For this reason, few long-lived species can sustain high fishing mortality rates (Musick 1999a). Also, size-selective fishing can also strongly skew sex ratios in animals with sexual differentiation in adult body size (Coleman et al. 1999, 2000). Careful management is needed to assure sustainable fishing and conservation of long-lived marine species.

## Conservation Efforts and Policy

By the early 1970s it was apparent that many populations of long-lived marine vertebrates had been systematically overexploited. For example, it was clear that populations of blue and humpback whales (*Balaenoptera musculus* and *Megaptera novaeangliae*, re-

spectively) in the Antarctic had been decimated and that hunting of other whales needed to be reduced dramatically (Chapman et al. 1964). This recognition helped change societal attitudes toward whales and other marine animals and set the stage for an era of environmental protection and conservation. Cornerstone pieces of environmental legislation in the United States were passed during this period, including the National Environmental Policy Act (NEPA, 1970), Marine Mammal Protection Act (MMPA, 1972), Endangered Species Act (ESA, 1973) and Magnuson Fishery Conservation and Management Act (FCMA, 1976). This unprecedented suite of legislative initiatives reflected the transition from an era marked by unregulated consumptive exploitation to one characterized by environmental management, regulation, and protection (see Lavigne et al. 1999). Underpinning this transition was a growing recognition of the nonconsumptive value of wildlife and discussion of ethical considerations of the ways in which we interact with animals.

Today, many long-lived marine organisms are afforded special status in North America (Dallmeyer, Chapter 24). This is recognized explicitly by legislation such as the MMPA, which prohibits killing or harassing marine mammals, with few exceptions. Societal attitudes toward other species, including sea turtles and seabirds, also favor protection despite a lack of specific legislation. It is difficult to envision resumption of sea turtle exploitation in the United States, for example, even if populations should recover sufficiently to sustain it. Societal attitudes toward other taxa are less certain. Large sharks, in particular, are extremely vulnerable to overexploitation, and while there are conservation measures in place for some species, they are not yet among those afforded special protection (Musick et al. 2000b). Finally, other less charismatic long-lived species, such as sturgeons, groupers, and abalones, are routinely overexploited in commercial fisheries and not generally afforded nonconsumptive value.

Although our focus is primarily North American, international management of long-lived marine ver-

tebrates has also undergone a sea change in recent decades. Early international treaties, such as the 1946 International Convention for the Regulation of Whaling, were concerned primarily with regulation and allocation of take. More recent agreements, such as the UN General Assembly Resolutions on high-seas drift nets, are directed toward prevention of intentional and unintentional overexploitation. The World Conservation Union (IUCN) has recently increased its attention to marine species, and a committee is currently forming a "Red List" of conservation status for marine fishes (IUCN 1997; Musick 1999b). The criteria for this list include life history considerations such as longevity and population rates of change. International conservation efforts are, of course, complicated by differences in the value systems and economic conditions of individual nations. Regulation of trade in fishery products has played an increasingly important role in structuring recent international conservation efforts. Several attempts by the United States to impose trade sanctions on nations not complying with US conservation initiatives have been thwarted by rulings of panels of the World Trade Organization (WTO) and the General Agreement of Tariffs and Trade (GATT; Gosliner 1999). It remains to be seen how regulation of trade will affect conservation efforts in the international arena over the long term.

### **Life History Characteristics of Long-Lived Marine Species**

Although long-lived marine species include a diverse array of classes and life histories, they share several common characteristics. For conservation and management, the most important traits include low natural adult mortality,<sup>1</sup> relatively large body size, and relatively low annual recruitment to the adult stock (Garrod and Knights 1979). There is a strong correlation between adult lifespan and age at first breeding for fishes, mammals, birds, reptiles, and some invertebrates (Beverton 1992; Charnov 1993; Roff 1984; Winemiller and Rose 1992), thus most long-lived ma-

rine species also have delayed maturity. Finally, many species migrate long distances and breed in aggregations that are predictable in time and space (Musick 1999a). This makes them prime targets for fisheries.

Long adult lifespan and delayed maturity are often labeled as  $K$ -selected traits (Pianka 1970). Species that are  $r$ -selected take advantage of new opportunities in their environment by maximizing population growth ( $r$ ) through high fecundity, rapid development, and a large investment in reproduction that leads to short adult lifespan. In contrast,  $K$ -selected species have evolved traits that maximize fitness when resources are scarce but relatively constant, as they would be at population carrying capacity ( $K$ ). Fewer offspring and extended parental care, large body size, and iteroparity (the production of offspring over many years) are examples of traits that benefit genotypes under these conditions. Whereas some organisms, such as house sparrows (*Passer domesticus*) and albatrosses (Diomedidae), can be easily categorized as  $r$ - or  $K$ -selected, it is an inadequate classification scheme for many long-lived marine organisms that share characteristics of both (Garrod and Knights 1979; Winemiller and Rose 1992). For example, a white abalone (*Haliotis sorenseni*) has delayed maturity, large body size (relative to other gastropods), and long lifespan, but spawns millions of eggs each year (Hobday et al. 2000). The tiny larvae, like the fine airborne seeds of weedy plants, may settle and survive only if environmental conditions are favorable. Winemiller and Rose (1992) have proposed that this is a third major life history strategy, called a periodic or "bet-hedging" strategy. To avoid confusion, we have not used the  $r$ -/ $K$ -selection paradigm in this chapter, but instead contrast long-lived marine species with short-lived ones and compare their reproductive strategies.

Long lifespan often results in a relatively large standing adult biomass (Francis 1986; Garrod and Knights 1979; Leaman and Beamish 1984). Recruitment of newly mature individuals is low relative to the number and biomass of older adults, with the exception of occasional very strong year-classes for those

species with highly variable reproductive success. After innumerable years of population buildup, when a long-lived species is initially exploited, the biomass of adults might appear limitless. This often leads to overcapitalization by the new fishery (Francis 1986). Low recruitment to the adult population can result in sudden population collapse (e.g., orange roughy, *Hoplostethus atlanticus*; Clark and Tracey 1994). Delayed maturity or disrupted spawning behavior can further exacerbate overexploitation, resulting in very slow recovery times for the stock, or, in extreme cases, permanent loss of aggregations (Coleman et al. 2000; Huntsman and Schaaf 1994).

Many long-lived marine species have wide distributions but aggregate during key phases of the life history (e.g., reproduction and nesting in sea turtles, spawning aggregations in groupers), enhancing their vulnerability to fishing (Musick 1999a; Roff 1988; Sadovy 2001). Generally, breeding aggregations are temporally and spatially consistent from year to year, and intense fishing pressure at these sites can result in unsustainable mortality rates, loss of mature adults before they are able to reproduce, and disruption of reproductive behaviors. These effects could lead to *density depensation* (the Allee effect), where per capita reproductive success is reduced at low population densities (Levitan and McGovern, Chapter 4). Species that have apparently suffered from density depensation include some large cetaceans, groupers, and a few other fishes and invertebrates (Fowler and Baker 1990; Hobday et al. 2000; Huntsman et al. 1999; Myers et al. 1995; Tegner et al. 1996).

Several authors have argued that traditional stock assessment methods are inappropriate for long-lived species. Management strategies based on fishing mortality rate might be inappropriate for long-lived groundfishes because the late age at recruitment and longevity of these species makes accurate assessment of  $F$  (the instantaneous rate of fishing mortality) nearly impossible (Leaman 1993; Musick et al. 2000a; Parker et al. 2000). The age distribution and status of the adult stock could be far more critical for assessing

population health than biomass (Chale-Matsau et al. 2001).

### Demographic Factors:

#### Reproduction and Age at Maturity

Long-lived marine mammals, seabirds, sea turtles, fishes, and invertebrates exhibit a wide range of life history strategies. While whales and albatrosses have a single offspring every two to five years, large groupers can spawn millions of eggs annually. A blue-fin tuna (*Thunnus thynnus*) could mature in eight or nine years but a loggerhead sea turtle (*Caretta caretta*) might not reproduce until it is 25 to 30 years old. Long-term population growth rates are primarily determined by fecundity, age at first reproduction, and survivorship (Caswell and Hastings 1980). To compare the demographic characteristics of different long-lived marine species, we plotted age at maturity in years versus fecundity in annual egg or offspring production (log-scale) for 35 populations that met our criteria for long lifespan (Figure 13.1). The species do not appear to be randomly distributed on the plot. Most marine mammals and birds are grouped in the low fecundity, early maturity quadrant. Some sharks and mammals, such as manatees (*Trichechus* spp.) and killer whales, have extremely low annual fecundity and late age at maturation; these species appear in the lower left quadrant of the graph. Although large sharks can have dozens of offspring per litter, they often do not breed every year. In the middle of the plot, sea turtles have relatively little variation in annual fecundity but vary widely in age at maturation. Other than turtles, there are few marine organisms with intermediate fecundity, between 10 and 10,000 eggs per year. Exceptions are lecithotrophic organisms, which produce large, well-developed larvae, such as whelks (Buccinidae), and certain deep-sea, cold-water fishes. Fishes and invertebrates on the right side of the plot are primarily those that disperse planktonic larvae, often by the millions. Sea urchins, tunas, groupers, Atlantic cod (*Gadus morhua*), and some flatfishes (Pleuronectiformes) all mature relatively early and can also

be batch spawners, reproducing several times in a year. Some fishes and invertebrates that delay reproduction, such as abalone, Pacific halibut (*Hippoglossus stenolepis*), rockfish, and sturgeon, might have fewer offspring per year because of larger egg size, ovoviparous reproduction, or infrequent spawning.

What selection pressures give rise to such a range of reproductive strategies and long adult lifespan? Most theorists agree that environmental uncertainty affecting offspring survival is a primary driver for extreme iteroparity. Marine mammals and seabirds have large offspring and extended parental care, which increases the probability that a given offspring will survive, but are generally restricted to one offspring per breeding attempt and often do not reproduce every year. Sharks and sea turtles do not have parental care but produce relatively large offspring that must survive for a decade or more before reproducing. Teleosts and invertebrates can produce millions of eggs each year, but survival in the plankton is extremely low and the probability of successful transport to nursery areas could be highly stochastic; in most years, none of a female's offspring will survive, thereby necessitating multiple spawnings over an extended lifespan to ensure reproductive success (Garrod and Knights 1979; Hobday et al. 2000; Murphy 1968; Sadovy 2001; Winemiller and Rose 1992).

Birds and mammals, unlike invertebrates, reptiles, and fishes, have determinate growth. Therefore the reproductive value of older females, measured as their contribution to population growth, can increase with age only due to experience or social status, as they generally cannot increase total offspring production with age. Invertebrates, reptiles, and fishes, on the other hand, generally exhibit an increase in fecundity and occasionally in offspring size with age because of indeterminate body growth, although growth after maturity can slow dramatically for some species (Beverton 1992). While fisheries models account for indeterminate growth with size–fecundity relationships, they generally fail to consider the impact that older females can have on population growth rates through

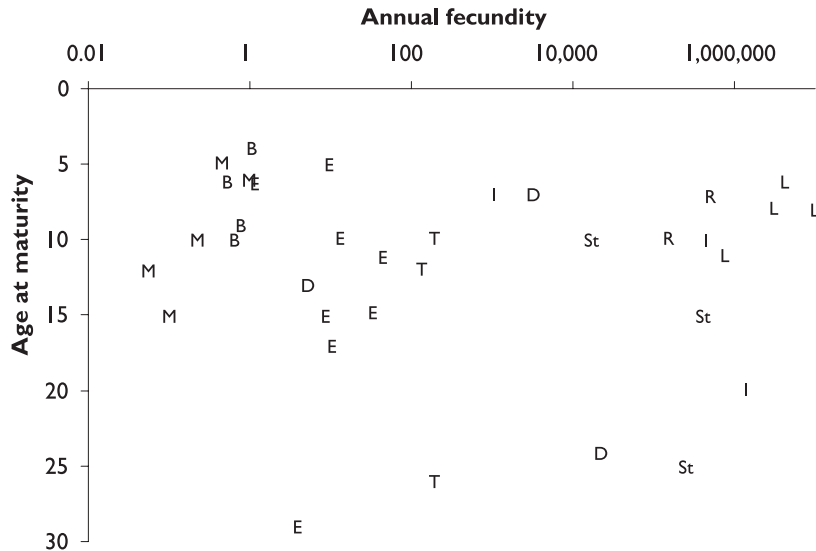


FIGURE 13.1. Age at maturity vs. annual fecundity for 35 long-lived marine organisms. Age at maturity is defined as the age at which 50 percent of females are mature, and fecundity is the mean number of eggs or progeny produced per average-sized female each year (note that many marine mammals, sharks, and sea turtles do not breed every year). A complete list of references used in this figure can be obtained by writing S.S. Heppell. Key: M = marine mammal, B = bird, E = elasmobranch (shark, ray, or skate), T = sea turtle, D = deep-water fish, I = invertebrate (common whelk, a gorgonian, and northern abalone), R = rockfish (Genus *Sebastes*), St = sturgeon, L = large teleost (bony fish, e.g., grouper, bluefin tuna, halibut).

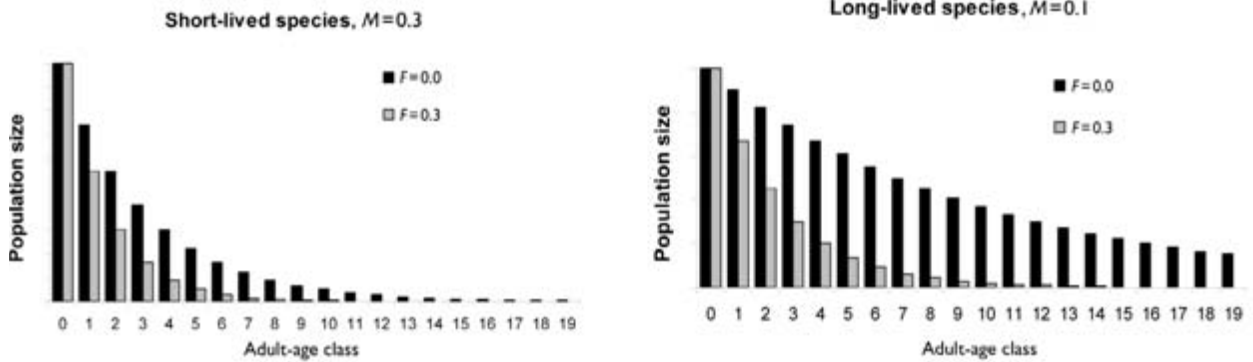
improved egg quality, social status, or timing of spawning (Chambers and Leggett 1996; Einum and Fleming 2001; Leaman 1991).

### Response to Exploitation: Effects of Fishing on Demographics

The adult population size of long-lived marine species tends to fluctuate less than those of short-lived species, and lifespan correlates with the frequency of strong year classes in some families (i.e., the longer the interval between strong year classes, the longer adult lifespan tends to be) (Leaman and Beamish 1984; Mann and Mills 1979; Spencer and Collie 1997). Multiple age classes of adults means that, in general, newly mature individuals make up a relatively small proportion of the adult population in long-lived species. As fishing mortality (on adults) is added to natural mortality, individuals are less likely to reach max-

imum age and the age distribution becomes truncated (Huntsman and Schaaf 1994; Kronlund and Yamanaka 2001; Leaman 1991). To illustrate this, we show the age distribution of a short-lived versus a long-lived species, assuming constant recruitment to the adult population and constant mortality (Figure 13.2a). When our two species are subject to lower adult survival through identical levels of fishing pressure ( $F$ , where annual survival  $S = e^{-(M+F)}$ ), there is a severe truncation of the age distribution in the long-lived species and the proportion of the population that are new recruits goes from 11 percent to 33 percent. Loss of older age classes could result in more than a loss of egg production; changes in offspring quality or adult behaviors mediated by older individuals, such as spawning and social interactions, might reduce reproduction in the remaining age classes (Coleman et al. 2000). Poor recruitment years could be

a.



b.

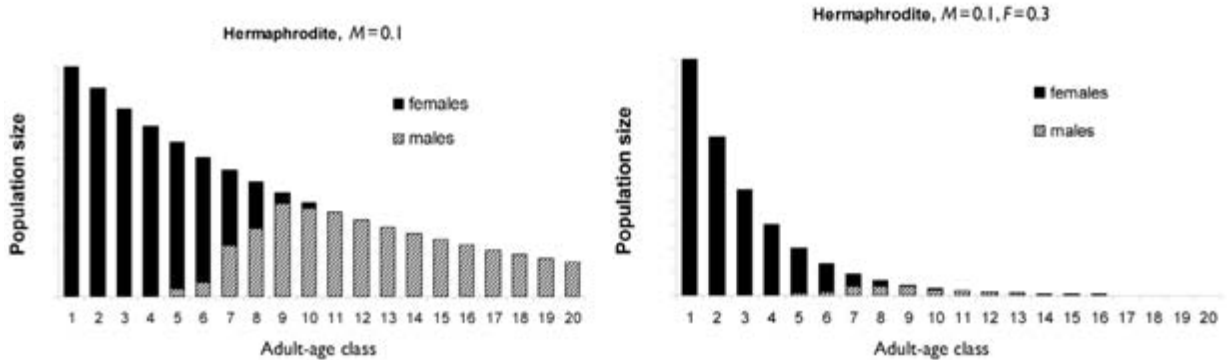


FIGURE 13.2. Changes in the age distribution of hypothetical short-lived and long-lived fish populations after the addition of fishing mortality ( $F$ ), where  $M$  is natural mortality and annual survival  $= e^{-(M+F)}$ . For this illustration, we assume constant recruitment and a stable age distribution. 13.2a: Truncation of the age distribution in a gonochoristic (two-sex) species. 13.2b: Truncation of the age distribution and proportion of males in a sequential hermaphrodite, such as grouper.

exacerbated or occur more frequently when females are not allowed to grow and survive for multiple spawning seasons (Diaz et al. 2000; Sadovy 2001). While any  $F$  level will result in a decline in abundance, depending on the relationships between stock size, age, and reproduction, even relatively low levels of  $F$  can result in population decline.

In addition to truncation of the age distribution, fishing mortality presents a special problem for fishes that change sex, such as the groupers (Coleman et al. 1999, 2000). The majority of groupers are sequential

hermaphrodites that are born female and then become male later in life (Shapiro 1987). Furthermore, unlike many species of coral reef fishes (e.g., bluehead wrasses *Thalassoma bifasciatum*; Warner and Swearer 1991), it appears that the rate and age of sex change in some groupers is either not plastic or cannot keep up with the loss of males in the population (McGovern et al. 1998). Thus, as the age distribution is truncated, fewer females survive long enough to become males and the sex ratio might be altered drastically (Figure 13.2b). In our hypothetical example, females start to

change sex at age 5 and all fish are male by age 11. Again assuming constant recruitment and mortality, the sex ratio prior to the addition of fishing mortality is 1.36 females to one male. When fishing mortality is added, the sex ratio jumps an order of magnitude to 13.2 females per male. Even if females respond to this change in sex ratio and start to change sex at age 4, the sex ratio only improves to 8.5 females per male. This change in sex ratio is due solely to the shortened lifespan caused by fishing mortality; males and females have the same annual survival rate. Measured skews in sex ratio for some grouper populations have been much worse, in part because recreational and commercial fisheries often target large males. This has resulted in higher mortality rates for males and an overestimate of their abundance in catch statistics. As an example, the sex ratio of gag grouper (*Mycteroperca microlepis*) has shifted dramatically over the last two decades, from approximately 6 females per male in the late 1970s to 30 females per male in the 1990s, concurrent with an increase in fishing pressure and decline in population size (Coleman et al. 1996; Hood and Schleider 1992). This sex ratio shift has been observed for other species of grouper as well (Beets and Friedlander 1992). While the short-term ramifications of such a shift in sex ratio are unknown, the long-term outlook is clear. As the sex ratio continues to shift and males become rarer, the population can become sperm-limited and reproductive failure can occur. This phenomenon is not considered in models designed for management of gonochoristic (two-sex) species. Huntsman and Schaaf (1994) demonstrated that for a simulated population of graysby (*Epinephelus cruentatus*), reproductive failure occurs at a much lower exploitation rate than for gonochoristic species. We don't know how skewing of the sex ratio might have contributed to the current grouper population declines because we don't know with how many females each male can spawn. But limited numbers of males can cause a disruption of spawning behavior and changes in hormone levels that would lead to density depensation in these fishes (Heppell and Sullivan, in revision).

If we ignore the effect of density on vital rates, we

can use simple age- or stage-structured population models to estimate the impact of a reduction in annual survival on the annual population growth rate (e.g., Cortes 2002; Crouse et al. 1987; Moloney et al. 1994; Russell 1999; Sminkey and Musick 1996; Smith et al. 1998; Woodley and Read 1991). Elasticity analysis uses life tables and transition matrices to determine the proportional effects of changes in survival of different life stages to  $\lambda$  (Caswell 2000; Heppell et al. 2000). For example, an elasticity analysis of loggerhead sea turtles revealed that egg and hatchling survival contributes relatively little to overall population growth, while small proportional increases in juvenile or subadult annual survival has a major impact on population growth (Crouse et al. 1987; Crowder et al. 1994). This revelation bolstered management efforts to reduce incidental fishing mortality of subadult turtles in shrimp trawls. Because they have high adult annual survival rates, all long-lived species have very low fecundity elasticity and egg survival elasticity, particularly in species with delayed maturity (Heppell 1998; Heppell et al. 1999, 2000). Elasticity values are inversely correlated with parameter variance (Pfister 1998). Thus, while reproduction or larval survival can be extremely variable, these parameters have relatively little impact on long-term population growth in long-lived species. Adult and subadult survival might be far more critical for population viability.

The smaller contribution of offspring production relative to adult survival for population growth of long-lived species has important implications for management. While density dependence likely leads to increased survival or growth at low population levels, it primarily affects early life history stages. It is likely that the increase in egg production or larval survival needed to compensate for adult fishing mortality is unattainable for many long-lived species (Cortes 2002; Heppell et al. 1999). Even reductions in age at maturity might be insufficient to maintain populations when sensitive adult or subadult stages are subject to increased mortality levels. Smith et al. (1998) reviewed the "rebound potential" of 26 shark species and found that life history severely constrains the



maximum productivity of late-maturing species. Further analysis of species' life histories and response to density is needed to assess this problem more generally for other long-lived species.

Are long-lived species more susceptible to overexploitation than short-lived ones, and do they have a lower potential for recovery? Certainly there are many examples of short-lived species populations that have been severely reduced, and overfishing is common for species such as herring and anchovies. But fish species with delayed maturity are more likely to be at risk than species with early maturity (Musick 1999b; Parent and Schriml 1995), and larger species within fish families are more heavily impacted by exploitation on coral reefs (Jennings et al. 1999). Rockfishes (Leaman 1991) and elasmobranchs (Musick et al. 2000b; Sminkey and Musick 1996) show limited phenotypic plasticity in response to fishing mortality; while increased reproductive output, increased growth, or reduced age at maturity has been shown in many species, compensation is not as pronounced nor as responsive as would be expected for many shorter-lived species. In a comparison of two exploited shark species, Stevens (1999) found greater vulnerability to overfishing in the long-lived, late-maturing school shark (*Galeorhinus galeus*) than a shorter-lived species, the gummy shark (*Mustelus antarcticus*). Boreman (1997) compared the effects of fishing mortality on the lifetime egg production of sturgeon (Acipenseridae) and paddlefishes (*Polyodon spathula*) (long-lived, late-maturing species) with winter flounder (*Pseudopleuronectes americanus*), striped bass (*Morone saxatilis*), and bluefish (*Pomatomus saltatrix*). He found that the reduction in reproductive potential through fishing was far greater when maturation is delayed, a function of the age distribution truncation that occurs with even small increases in total mortality.

Longevity and delayed maturity are characteristics often associated with increased risk of overexploitation (Roberts and Hawkins 1999; Musick 1999a, 1999b). Estes (1979) argued that fishing long-lived marine mammals was akin to forcing a *K*-selected species to become an *r*-selected one. A more general

thesis is that exploitation, whether intentional or through bycatch, forces species that have evolved life history characteristics that include long lifespan to adjust to a short lifespan strategy (Law and Stokes, Chapter 14). Some species might be able to make this transition through density-dependent responses, such as reduced age at first reproduction, increased body size and fecundity, or higher reproductive success per female. But many species, including most of those on the left side of Figure 13.1, do not have the physiological or genetic capability to drastically alter their life histories. Regardless of lifespan or reproductive strategy, if fishing is such that excess mortality occurs before the age at first maturity then substantial declines in the population may occur (Butler et al. 2003).

### Management Options for Long-Lived Marine Species

Long-lived species have characteristics that make them appealing targets for fisheries and therefore vulnerable to depletion. With the implementation of certain management policies, however, these same characteristics might help prevent their extinction. These species generally have a large adult biomass that is spread over a wide geographic area and/or have life stages that occur in different habitats. This makes full exploitation by a single fishing method difficult. Some are adapted to withstand periods of low recruitment and are generally less susceptible to fluctuations caused by environmental variability. Mace and Sissenwine (1993) argue that large fishes with high fecundity are more resilient to overfishing than smaller fishes in the same family because of the cubic relationship between fish length and total egg production. On the other hand, long-lived species generally have low maximum population growth rates due to delayed maturity and rarity of successful recruitment years. Therefore fecundity itself might not confer resistance to overexploitation and full recovery—once a population is overexploited—might require decades regardless of maximum egg production potential (Dulvy et al 2003; Sadovy 2001). Because population

growth is lower than the economic discount rate, economic fishing benefits can be maximized by catching all of a population rather than fishing it sustainably (Clark 1973). Models that incorporate the maximum intrinsic rate of increase, such as the Schaefer surplus production model, show that maximum sustainable yield is less likely to be achieved in species with low  $r$ , such as sharks (McAllister et al. 2001). In some instances, overexploitation leads to rareness, which can increase the value of individuals in certain fisheries (Sadovy 2001); primary examples include the near-extinct white abalone, hawksbill sea turtles (*Eretmochelys imbricata*), and bluefin tuna. Management efforts that eliminate mortality, such as moratoria and area closures, are often needed to prevent local extinctions. While effective management will likely need to be species-specific and adaptive to changing environmental and economic trends, some of the life history characteristics of long-lived marine organisms could make certain management options more effective than others.

## Fishing Regulation

### SIZE AND SLOT LIMITS

Minimum size limits for fished species, regulated through minimum net mesh size, escape rings in traps and pots, and manual release of undersized individuals, can prevent overfishing of potential recruits to the adult population. If set properly, a size limit can also ensure a minimum level of escapement for spawning, which allows young adults to reproduce at least once. But there are several potential disadvantages of minimum size limits for long-lived species. For some deep-water species, release mortality can be quite high due to acute barotrauma (expansion of the air-filled swim bladder during ascent), defeating the purpose of the size limit (Wilson and Burns 1996). Because of inherently slow growth rates, the number of times that an undersized individual comes into contact with and is handled by the gear could be quite high. While an individual encounter with fishing gear might confer only a small probability of mortality, multiple encounters over the lifespan of an individual could have

a cumulative effect on survival. As already discussed, long-lived species have evolved life histories that might require multiple reproductive attempts to produce successful offspring; minimum size limits do not prevent truncation of the age distribution and could even exacerbate it by focusing fishing pressure on older age classes.

Slot limits allow for a “window” between a minimum and maximum size. While not as common as minimum size limits, slot limits seek to protect populations from overfishing of juveniles while reducing the loss of older, mature adults. Slot limits are potentially more viable for long-lived species than minimum size limits but will not be effective if fishing mortality is too high in the slot, thereby preventing individuals from reaching the “safe” size-classes. Examples of slot limit application include sturgeon fisheries and the red drum (*Sciaenops ocellatus*) fishery in the Gulf of Mexico as well as the American lobster (*Homarus americanus*) fishery in the northeastern United States (primarily in Maine). But size limits in general are poor management options in the absence of other quota systems.

### QUOTA MANAGEMENT

One of the most common approaches to regulating exploitation is to estimate a fishing level that meets management objectives and then restrict catches to that level through a fixed quota. This is the basis for the concept of maximum sustainable yield (MSY), which underpins much of current fisheries management in North America. We do not have space to review here the conceptual problems with managing for MSY (see Larkin 1977), but note that in practice (and theory) it is difficult, if not impossible, to achieve. Nevertheless, it is possible to estimate more conservative fishing levels and to use these in a system of quota management. This is the approach taken by the International Whaling Commission (IWC) in its Revised Management Procedure (RMP) (Cooke 1995). The RMP is an algorithm designed to set stable catch limits from minimal data and was developed through extensive simulation modeling. The objectives of the

RMP are to protect depleted stocks and allow exploitation of other stocks, so that they are maintained at a set proportion (72 percent) of initial stock size. A similar approach is used in the United States to set allowable take limits for marine mammals under the MMPA (primarily in the form of commercial fishing bycatch). The limits, known as Potential Biological Removal (PBR) levels, are designed to allow stocks of marine mammals to be maintained above 50 percent of carrying capacity (Wade 1998). If anthropogenic mortality exceeds PBR for a given stock, a series of management measures are triggered. Both approaches are straightforward, robust to various biases, and make use of data that are readily available; either approach could be easily modified to accommodate other management objectives.

The primary problems with any quota management scheme are allocation and enforcement. Long-lived species are vulnerable in open access fisheries because of the low economic return from sustainable exploitation levels (Clark 1973). Even with fixed quotas in place, there is incentive for underreporting, misreporting, or high grading. This is exactly what happened during Soviet whaling expeditions to the Antarctic between 1951 and 1971, when over 3,000 protected right whales (*Eubalaena glacialis*) were taken and misreported as other species (Yablokov 1994). The IWC still has not agreed to a management scheme to implement the RMP, in large part due to problems associated with inspection and observation (Gambell 1999).

#### INDIVIDUAL TRANSFERABLE QUOTAS

Although individual transferable quotas (ITQs) deal only with allocation and are not strictly a conservation measure, ITQs can benefit long-lived species. Under an ITQ system, shareholders are allocated a percentage of the total quota. Shareholders can fish for their share throughout the year or can sell (transfer) their quota, contingent upon the regulations within the specific ITQ fishery and the perceived economic benefits of holding or selling individual quota (Clark et al. 1988). Because every participant in the

fishery is known, complete monitoring of the catch can be simplified and rapid feedback into population models can be incorporated (Clark et al. 1988). Detection of changes in population size estimates, age at maturity, and size at age can be used to indicate whether a fishery is being overexploited, which is extremely important for long-lived species where population recovery times can be extremely long. Under an ITQ system, the waste of resources associated with limited-duration “derby fisheries” can also be substantially reduced as fishermen bypass short-term catch in pursuit of higher-value product (Geen and Nayer 1988). In addition, each ITQ fisherman develops a vested interest in the long-term viability of the fishery. These fishermen should therefore be more prone to actively participate in management efforts and to identify cheaters in the system, although, as discussed in Hilborn and Walters (1992), this is not always the case. Socially, the major disadvantage to ITQ management is that it creates a system of “haves” and “have-nots” whereby new participants in the fishery are largely excluded until a share becomes available on the open market (Deweese 1989). Within the United States, very few ITQ systems are in operation at this time. Examples include the Pacific halibut and the wreckfish (*Polyprion americanus*) fisheries.

#### MARINE RESERVES AND TIME-AREA CLOSURES

Marine reserves (see Chapters 16–19), which are no-take zones set up to protect certain areas, ecosystems, and/or species, can have profound effects on the conservation of long-lived marine species. If established on the appropriate temporal and spatial scales, these protected areas can counter the effects of overfishing and discards by protecting multiple age classes in the reserve (Soh et al. 2001). Data from many reserve sites have shown increases in mean size and spawning potential of long-lived fishes within the reserve, although recruitment or “spillage” outside of reserves has been more difficult to ascertain (Mosquera et al. 2000; Roberts 1995; Russ and Alcala 1996). Short-term closure of certain areas to protect spawning aggregations or migrating stocks can ensure that adults

have an opportunity to spawn but might not provide adequate protection for the entire stock. This approach might be less effective for highly migratory species like the tunas and sharks.

Marine reserves, or at a minimum time-area closures, might be the only solution to management of hermaphroditic species such as grouper (Coleman et al. 1999). Marine reserves can protect critical spawning aggregations and allow for all age classes to be present, a guard against highly skewed sex ratios (Beets and Friedlander 1999). But marine reserves cannot function in the absence of sustainable management of the remaining exploitable segment of the population (Allison et al. 1998). Furthermore, if not of appropriate size or in the absence of suitable habitat, marine reserves will not function as they are envisioned.

#### MORATORIA

The simplest and most drastic approach to reducing directed exploitation is to eliminate it altogether. This has occurred through special protection legislation, such as the case of marine mammals and sea turtles in the United States. Moratoria can also provide time for managers to develop more effective strategies, as is the case of the current moratorium on commercial whaling agreed to by the IWC in 1982 (Gambell 1999). This moratorium is described as a pause in whaling to allow development of the RMP and its associated implementation scheme. Moratoria have also been invoked for some rare and overexploited fishes, including the Goliath grouper (*Epinephelus itajara*) and Nassau grouper (*E. striatus*). But species-specific moratoria might not be effective for multispecies fisheries, such as those that target the snapper–grouper complex in the southeastern United States, the rockfish complex of the northeastern Pacific, or Atlantic demersal shark fisheries (Musick 1999a).

Moratoria can also be used to eliminate fisheries with bycatches that are incompatible with management objectives, such as the ban on high-seas drift net fisheries. In the United States, at least two fisheries have been closed due to unacceptably high bycatch levels of marine mammals: the Atlantic pelagic drift

net fishery for swordfish and the Atlantic pelagic pair trawl fishery for tuna. In both cases, however, conflicts over allocation of target species played a significant role in the decision to eliminate the fishery.

#### Gear Modification

##### ESCAPEMENT DEVICES

Trawl bycatch is a serious problem for many long-lived marine organisms. Trawl nets have been modified with escape doors and openings to allow sea turtles, large elasmobranchs, and juvenile fishes out of the trawl. The openings, called Turtle Excluder Devices (TEDs) and Bycatch Reduction Devices (BRDs), were developed by management agencies and fishermen to take advantage of behavioral differences between bycatch and target species, thereby reducing the loss of target species. For example, diamond-shaped holes in the tops of shrimp trawls encourage the escape of juvenile snapper and other species because fish tend to swim upward when stressed, while shrimp, the target species, tend to swim down and into the closed end of the net. Likewise, sea turtles in search of surface air can find their way through trap doors or openings in the trawl mesh. TEDs include metal grates, which catch other large organisms, such as sharks and rays, aiding their escape. Currently, TEDs are required on all shrimp trawls at all times of year in the United States and regulations are extending to other trawl fisheries. The implementation of TEDs in 1990 has contributed strongly to the ongoing recovery of the endangered Kemp's ridley sea turtle (*Lepidochelys kempi*) (Heppell et al. in press).

##### PINGERS

Pingers are acoustic alarms attached to static fishing gear to reduce the bycatch of marine mammals. The alarms produce high-frequency sounds that are audible to marine mammals but not to the target species, and were first designed to reduce the frequency of collisions between humpback whales and cod traps in Newfoundland. Cod fishermen in Newfoundland often lost an entire fishing season when a whale blundered into their trap and were eager to find some way

to warn whales that a trap was nearby. Experiments indicated that alarms reduced the probability of collisions between whales and cod traps (Lien et al. 1992). Since that time, pingers have been shown to be effective in other fisheries, most notably gill net fisheries that take dolphins and porpoises (Kraus et al. 1997) and seabirds (Melvin et al. 1999). Pingers are relatively attractive to fishermen because they do not require extensive modification of fishing practices or restriction of fishing effort. Drawbacks include the cost and maintenance of the pingers themselves. Perhaps more troubling, however, is the fact that we understand little about how pingers work or the potential for dolphins and porpoises to habituate to their presence over time. Continued monitoring will be required to determine whether these devices offer a long-term solution to the bycatch of marine mammals in gill net fisheries.

#### MODIFICATIONS OF LONGLINES AND TERMINAL TACKLE

Longline fisheries employ a long mainline from which are attached shorter lines, which terminate in a baited hook. The bycatch of pelagic longline fisheries includes sharks and other large pelagic fishes, sea turtles, marine mammals, and seabirds. Of particular concern is the bycatch of long-lived seabirds such as albatrosses, which are drowned after ingesting baited hooks as the longline is being set (Bergin 1997; Inchausti and Weimerskirch 2001). Several methods are being explored that could reduce the number of albatrosses killed, including the use of *tori* poles equipped with bird-scaring streamers to distract the birds, setting the longlines so that they sink more quickly, and setting at night, when the albatrosses are not feeding (Bergin 1997).

Modifications to terminal tackle can be used to increase the selectivity of the gear for target species and/or size classes and to decrease the mortality rates of released individuals. Hook design is a common target for gear modifications. Hook size (and therefore bait/attractant size as well) can have an impact on the size of individuals captured, while hook shape can be an equally important feature (Orsi et al. 1993). While

not a new design, circle hooks have gained popularity in recent years because the hook almost invariably sets in the lip or corner of the jaw instead of being swallowed. The resultant reduction in "gut-hooking" could increase an individual's chance for survival when released. This has particular applications to pelagic longlines, which set hundreds to thousands of hooks at a time, have extended gear soak times, and tend to capture nontarget, long-lived species such as seabirds, turtles, and marine mammals. In addition, because individuals are likely to encounter these gears multiple times over the course of their lives, reductions in per-incident mortality risk can have a large impact over the lifespan of the organism. An added advantage to the use of circle hooks is that gear recovery is easier because the hook is more accessible. This reduces the posthooking mortality when fishermen attempt to recover valuable gear from gut-hooked, nontarget species.

#### TUNA SEINE BACKDOWNS

The massive bycatch of pelagic dolphins in the eastern tropical Pacific yellowfin tuna (*Thunnus albacares*) fishery was one of the galvanizing issues leading to passage of the MMPA in 1972. For reasons that are still incompletely understood, yellowfin tuna and dolphins (*Stenella attenuata*) in the eastern tropical Pacific Ocean school together. Tuna fishermen take advantage of this association by locating schools of dolphins and setting purse seines around them to capture the tuna below. In the early days of this fishery, tuna and dolphins were both hauled aboard and the mammals discarded, resulting in the mortality of hundreds of thousands of dolphins each year (National Research Council 1992). In the late 1960s and following passage of the MMPA, tuna fishermen developed a series of techniques and gear modifications that drastically reduced dolphin mortality. These modifications include the backdown procedure, in which the entire purse seine is towed backward, allowing dolphins to escape over the submerged floatline. Throughout the tortured history of this issue, described in detail by Gosliner (1999), such modifications have proven par-

ticularly effective in reducing the number of dolphins killed; the majority of sets on dolphins now result in no mortality.

#### ENHANCEMENT

Enhancement of marine stocks through hatcheries has been the subject of recent debate (*Bulletin of Marine Science* 1998 vol. 62[2]). The goal of such efforts is to rear larvae or juveniles to a size that reduces their susceptibility to natural predation, thereby increasing cohort size and ultimately aiding population recovery. Hatchery production of red drum, barramundi (*Lates calcarifer*), and Kemp's ridley sea turtles has shown that these long-lived species can be successfully reared in captivity and survive after release. But there is no evidence that enhancement through hatcheries has contributed to population growth rates for these species. Elasticity analysis (see earlier discussion) suggests that enhancement of early life history stages is unlikely to contribute substantially to population growth in long-lived organisms. More important, enhancement cannot compensate for mortality of more sensitive life stages, such as subadults and adults that are subject to fishing mortality (Heppell and Crowder 1998). However, it might be possible to use enhancement in conjunction with other management efforts to encourage stock recovery once the primary drivers of population collapse have been removed. Indirect enhancement, through the protection and restoration of nursery areas or other juvenile habitats to encourage surplus production, can have positive impacts on long-lived marine species (Winemiller and Rose 1992).

### Research and Policy Needs

#### Monitoring and Information Needs

Much of what we know about the effects of fisheries on long-lived marine organisms comes from information collected in fisheries observer programs (see Alverson et al. 1994). These programs are particularly useful in providing estimates of the mortality of bycatch species but are also critical for multispecies fish-

eries. Without independent, verifiable data collected by such programs, it is difficult to impossible to assess the ecological impacts of commercial fisheries (Pope et al. 2000). As noted by Crowder and Murawski (1998), monitoring programs should provide acceptable levels of accuracy and sampling precision. Such programs are expensive but necessary for effective management. Innovative measures, such as fishing industry-funded independent monitoring programs, are required to ensure we can assess the effects of fisheries on both target and nontarget species.

For some species, particularly those with complex life histories such as sea turtles, more work is required to determine what level of bycatch can be sustained without impeding population recovery (Hall et al. 2000). A scheme similar to the PBR would be particularly useful for fishermen and managers to determine the effects of current bycatch levels of sea turtles and to help guide future policy development.

#### Cooperative Management across Political Boundaries

Many long-lived species occur across political boundaries. This can seriously complicate management, conservation, and protection efforts, particularly when different belief and value systems exist between nations. Cetaceans, sea turtles, seabirds, and certain teleosts have migration routes that cover thousands of kilometers and cross multiple international boundaries, while other organisms exist primarily on the high seas in international waters. Pelagic dispersal of gametes and larvae means that source-sink dynamics could occur across political boundaries. International cooperation is necessary when one country wields control over source populations of economically or culturally important species (Stokke 2000). Cross-boundary management is not exclusive to the international scene. Management of salmonids in the Pacific Northwest of North America involves a complex network of local, state, regional, federal, tribal, and international management agencies and organizations, not all of which have complementary goals.

International organizations and treaties such as

the IWC, IUCN, Convention on International Trade in Endangered Species (CITES), and the International Commission for the Conservation of Atlantic Tunas (ICCAT) seek to manage and/or protect animals as they move across international boundaries. There are several difficulties with these treaties and agreements. Enforceability is problematic, particularly for high seas fisheries. Nations occasionally claim “exemptions” from applicable laws and agreements in order to meet the needs or desires of their populace. Disagreements over stock delineation and stock size estimates can lead to disputes and noncompliance. In spite of these and other difficulties, the primary advantage of these organizations, treaties, and agreements is that they provide an international forum for discussing issues pertinent to the conservation of long-lived marine species.

### **Harmonization of Legislation and Policy Initiatives**

Management regimes for commercial fisheries and protected species, such as sea turtles or marine mammals, often have conflicting objectives. For example, in the United States the original 1976 FCMA directs managers to maximize fishery yields (although this received less emphasis in the 1996 reauthorization), while at the same time the MMPA and ESA function to protect marine mammals and sea turtles taken as bycatch (Gerber et al. 1999). Ironically, the same agency is often responsible for managing fisheries and conserving protected species. When the FCMA was reauthorized in 1996, language was added to explicitly address overfishing, stock rebuilding, bycatch reduction, and essential habitat conservation. Such legislation provides a significant new opportunity to develop environmentally benign and economically efficient fishing strategies. To date, however, there have been few attempts to seize this opportunity and harmonize the objectives of fisheries management with the protection of nontarget species. Until this occurs, management of commercial fisheries will continue to exist as an inefficient patchwork of conflicting objectives.

## **Conclusions**

The vulnerability of marine organisms to extinction is difficult to quantify. Gerber and DeMaster (1999) advocate an approach that uses information on population size, variance in population size, and population growth rate for risk assessment. Other authors have suggested a need for new methods to assess status and risk for long-lived species that incorporate life history information and individual-based modeling (Jennings et al. 1999; Jennings 2000; Leaman 1993; Pope et al. 2000; Rose 2000). We have covered several life history traits of long-lived marine species that can have substantial impacts on population dynamics and subsequent conservation and management efforts: late age at maturity (most species), low fecundity (sharks, mammals), and low natural mortality limit resilience. Exploitation of hermaphrodites (groupers) can skew sex ratios in addition to reducing population size, leading to density depensation. Aggregation behavior (groupers, turtles, some sharks, tunas) concentrates mature adults and makes them targets for high levels of exploitation and vulnerable to specific perturbations. Large body size (bluefin tuna, some whales), leads to ease of detectability and also simplifies exploitation. High standing stocks of adults with low annual recruitment (Pacific rockfishes, orange roughy) make it difficult to identify changes in catch per unit effort (CPUE) until the population has experienced massive declines in total number. All of these traits need to be accounted for in risk assessment and the development of management and conservation plans in order to ensure the long-term sustainability of long-lived marine species.

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## Note

1. For our comparisons, we generally considered long-lived species to be those with an adult natural mortality rate of  $M \leq 0.1$ , corresponding to an annual survival rate greater than 90 percent per year and a lifespan on the order of 40 years (Hoenig 1983).

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