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Evolution and Sustainability of Harvested Populations

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Sustainably harvested populations are characterized by a balance of births and deaths. If harvesting is too intensive, deaths exceed births and the harvested population declines. When this continues for too long, extinction becomes inevitable. For harvesting to be sustainable, harvesting mortality must thus be offset either by decreased natural mortality or by increased fecundity. Mechanisms underlying such compensation in nature are often not well known. Yet it is clear that the growth rate of most natural populations is reduced by density-dependent processes. Typically, when population densities become large, survival of newborn and juvenile individuals declines. Other common manifestations of density dependence are slower somatic growth and reduced fecundity in dense populations. When harvesting reduces population densities, pressures originating from density-dependent natural processes are thus relaxed. Accordingly, the key to ecologically sustainable harvesting is not to exceed the capacity of relaxed density dependence to compensate for the deaths caused by harvesting.

Even though achieving ecologically sustainable harvesting is by no means easy, it is important to realize that such short-term sustainability does not even suffice to guarantee sustainability in the long term. This is because harvesting may have evolutionary implications that gradually undermine the viability of the exploited population and/or the quality and quantity of the harvest. This occurs through selection-driven changes in demographically relevant adaptive traits. For example, large individuals often provide the most valuable targets to harvesters and thus experience the highest harvest-induced mortalities. In this way, harvesting may qualitatively change the mortality regime to which a population had adapted in the past (Fig. 20.1), and favor evolution of smaller adult body size. At the same time, large individuals, in addition to having the lowest natural mortality, often mate most successfully and have access to the widest range of resources. The loss of such individuals directly through harvesting, and indirectly through harvest-induced evolution, is thus likely to compromise a population's productivity and resilience.

In general, harvest-induced selection occurs whenever harvesting causes trait-specific differences in survival or fecundity. Evolution will then ensue, provided that selection is sufficiently consistent and persistent through time, and that the trait-specific differences possess a heritable basis. The history of successful animal and plant domestication and breeding is testimony to the heritable basis of a very large range of traits that might become exposed to harvest-induced selection. These include body size, growth rate, size and style of sexual ornaments, age and size at maturation, reproductive effort, and many aspects of behavior.

Indeed, mechanisms of harvest-induced evolution are in no way different from those that have been harnessed for millennia for the purpose

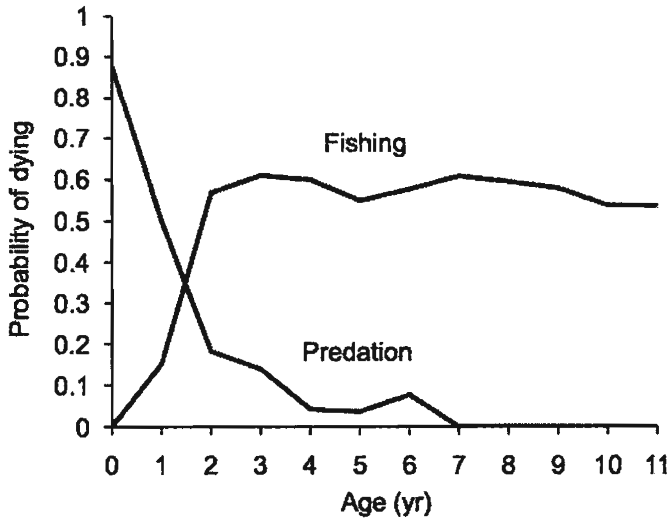

FIGURE 20.1 Estimated age-dependent profiles of annual mortality for North Sea cod (*Gadus morhua*) from predation and from fishing. The natural annual mortality originating from other causes is assumed to be around 5%. The probability that an individual of age 3 years survives until age 12 years is 0.02%. Without fishing mortality, that survival probability would be 47%. (Data from ICES [1997].)

of plant and animal breeding. The main difference is that, although harvest-induced evolution is usually unintentional and disadvantageous for the harvester, plant and animal breeders have actively promoted the breeding of individuals with desired characteristics to maintain or improve a stock's long-term quality. It is therefore not unexpected that a limited, and often merely intuitive, awareness of the evolutionary dimensions of harvesting has already existed for a long while. For example, foresters sometimes protect trees with straight trunks, based on the understanding that the subsequent inheritance of this characteristic will benefit future tree generations. Similarly, game managers may encourage the culling of individuals with only modest antlers, such that individuals with more rewarding antlers continue to arise in decent numbers.

Such awareness, however, has largely been confined to terrestrial systems. An early exception was Californian fish biologist Cloudsley Rutter, who had the foresight to note already in 1902 that regulations encouraging the selective harvest of the largest salmon returning to spawn would inevitably lead to a deterioration in the salmons' body size, because only smaller salmon were thus allowed to breed. Despite this early warning, the management of capture fisheries has been remarkably unaffected by evolutionary thinking. This lack of attention is difficult to justify, especially when considering the socioeconomic importance of capture fisheries. Around the globe, harvesting of wild fish continues at an industrial scale, resulting in important sources of animal proteins for a significant proportion of humankind. By contrast, at least in industrialized countries, the capture of terrestrial animals is mostly of local importance, often providing recreational opportunities, rather than serving as a crucial source of nutrition.

For decades, the large-scale and economic importance of marine fisheries has motivated the continuous and detailed collection of data. This explains why our current understanding of the evolutionary dimensions of harvesting, based on quantitative observations in the field, has gained so much from the monitoring of marine fisheries. Although the resulting emphasis on marine populations is accurately reflected in this chapter, it must be understood that harvest-induced evolution concerns taxa irrespective of their biome.

It is this broader perspective that underlies the following overview of the evolutionary dimensions of harvesting.

CONCEPTS

Selection Pressures Caused by Harvesting

That genetic selection occurs when harvesting is selective is evident—and it should be understood that harvesting is virtually always selective. In contrast, it is less obvious, and thus often insufficiently appreciated, that even changes in overall mortality that are entirely unselective, affecting all individuals of a population uniformly, are powerful drivers of genetic selection. This is because increased overall mortality reduces longevity, so that the risks, and thus the costs, of all strategies involving waiting or saving are elevated. Prominent examples of such strategies are waiting to mature and saving acquired energy for the next season. Here mortality simply acts as a discounting factor of future benefits. Because harvesting may drastically increase this discounting factor (Fig. 20.2), it generally favors live-fast-and-die-young strategies.

For example, individuals may mature late, resulting in more time to achieve some characteristic such as large body size that increases their reproductive value *at the time of maturation*. Alternatively, they may mature early, resulting in a suboptimal reproductive value at maturation, but also in a shorter waiting time, and thus a higher probability of surviving to maturation and realizing that reproductive value. If there were no mortality, reproductive value at the time of maturation would alone determine the evolutionarily favorable option. However, mortality risk adds a penalty to delayed reproduction, and if mortality risk is very high, delayed reproduction is close to suicidal in evolutionary terms. Similarly, saving energy by reducing current reproductive effort in favor of current growth or future reproductive effort may pay if there is a future—but increased mortality quickly erodes these expected future benefits.

Although harvesting can drive evolution even when it is unselective, the evolutionary consequences of harvesting are often exacerbated by a harvest's selective nature. Such selectivity can be intentional or unintentional. Intentional selection is

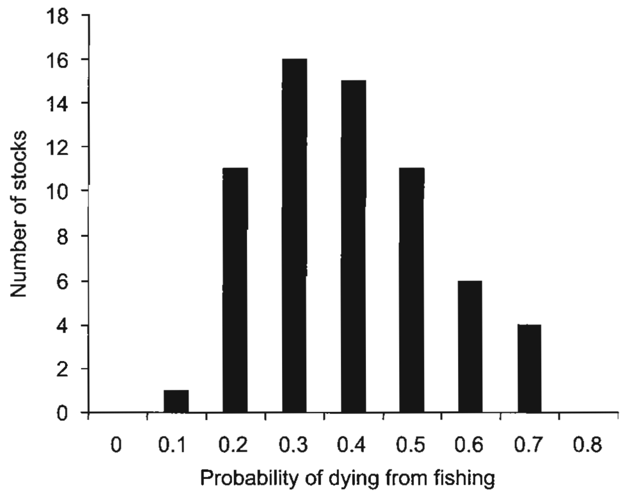

FIGURE 20.2 Estimated annual fishing mortality for 64 fish populations in the northeast Atlantic. On average, approximately 40% of individuals in the targeted age classes are removed each year. Natural mortality is typically believed to be around 20% on an annual basis. (Data from the International Council for the Exploration of the Sea [www.ices.dk].)