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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

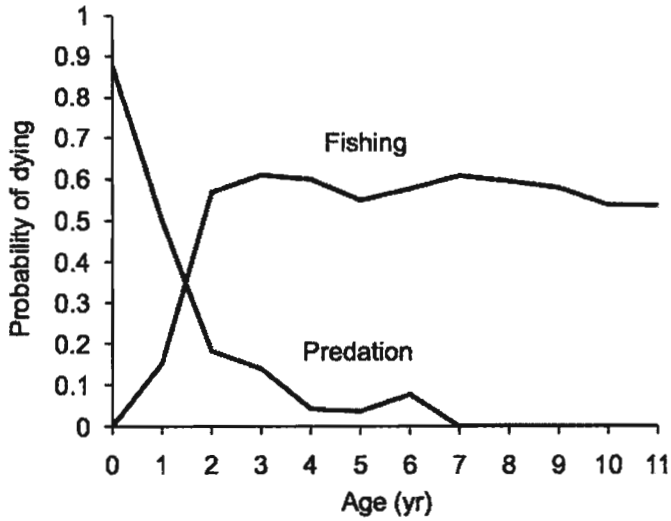


FIGURE 20.1 Estimated age-dependent profiles of annual mortality for North Sea cod (*Gadus morhua*) from predation and from fishing. The natural annual mortality originating from other causes is assumed to be around 5%. The probability that an individual of age 3 years survives until age 12 years is 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

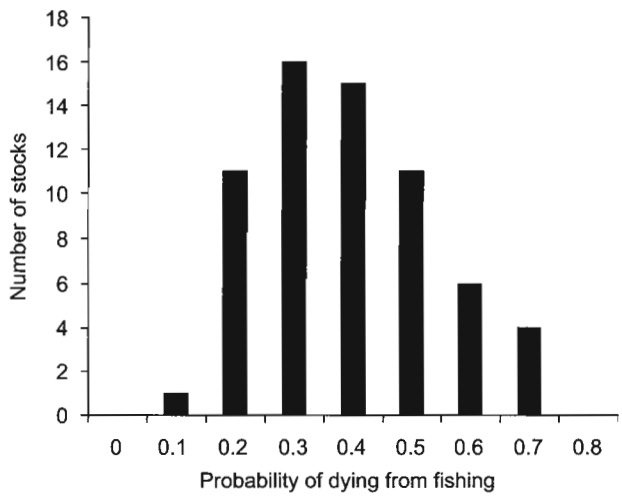


FIGURE 20.2 Estimated annual fishing mortality for 64 fish populations in the northeast Atlantic. On average, approximately 40% of individuals in the targeted age classes are removed each year. Natural mortality is typically believed to be around 20% on an annual basis. (Data from the International Council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

most obvious with respect to visible characteristics such as size; managers often impose such selectivity on populations to improve long-term harvest potential. For example, size limits are regularly used to protect a population's youngest individuals. Sometimes also maximum size limits are enforced to ensure that the largest and most fecund individuals are retained in a population, thus securing the successful recruitment of future generations. It must be appreciated, however, that any trait that lowers the likelihood of being harvested will be favored by selection, even when such selectivity is coincidental from the harvesters' perspective. In particular, such unintentional selection might influence a multitude of behavioral, morphological, and physiological traits such as escape behavior, burst swimming or running speed, risk aversion, and body morphology (Heino & Godø, 2002). Because of this multitude of target traits, some selectivity is largely inevitable. Even if unselective harvest were attempted, this would prove difficult to realize, because individuals are rarely randomly distributed with respect to their body size and many other characteristics.

Inheritance of Traits Affected by Harvesting

The exact genetic basis of traits affected by harvest-induced selection is usually unknown. In general, however, such traits will usually be influenced by many loci, each with small effect, so that genotypic variation among individuals is continuous. Inheritance of such quantitative traits can be described through the quantitative genetics framework (see, for example, Falconer & Mackay, 1996).

Because nongenetic factors affect phenotypic variability, the transmission of phenotypic traits from parents to offspring is almost never complete. The degree to which offspring phenotypes are correlated with, and thus can be predicted by, the corresponding midparental phenotypes is called *heritability*. Heritability is determined both by past selection history (which shapes genetic variability in the traits in question) and by current environmental conditions (which impinge on trait expression through developmental noise and phenotypic plasticity). In the first approximation, the speed of evolution is proportional to the strength of selection and to heritability. Although both of these factors are difficult to quantify accurately in the wild, all available evidence suggests that selection pressures associated with harvesting are often strong, and that the relevant traits have at least moderate heritability. With these ingredients, harvest-induced evolution can readily proceed.

Evidence for Harvest-Induced Evolution

The recent decade has seen increased acceptance of the fact that rapid contemporary evolution is commonplace (Hendry & Kinnison, 1999; Stockwell et al., 2003), with a growing number of such examples resulting from studies of harvest-induced evolution.

Most terrestrial examples concern hunting that is selective for sexual ornaments (Coltman et al., 2003; Harris et al., 2002; Jachmann et al., 1995). The idea is simple: If hunters preferentially shoot animals with the largest ornaments (like male horns or antlers), then an individual heavily investing in such ornaments is less likely ever to reap a payoff from its costly investments into these structures. Males with less developed ornaments will then gain a selective advantage, even if they would not gain many mating opportunities under more natural conditions. There are several models that confirm that this scenario could work, but much of the evidence remains suggestive (Box 20.1). An exception is provided by a study of bighorn sheep by Coltman and colleagues (2003) that we discuss in more detail later.

Another scenario occurs when managers use antler size as a surrogate of age when enforcing a harvesting strategy that targets a certain-age interval. Unfortunately, however, in many species, such as white-tailed deer (*Odocoileus virginianus*), genetic variation in antler size at age implies that genotypes delaying the development of complex antlers can avoid the hunting pressure for longer (Strickland et al., 2001), resulting in an undesired hunting-induced selection pressure. In other cases, managers take a step toward animal breeding and encourage hunting of deer with simple antlers in an attempt to improve the quality of trophies in the long run. Either way, harvest-induced selection for antler characteristics is clearly present, whereas explicit empirical evidence remains suggestive.

There are also examples suggesting harvest-induced evolution in wild plants (Law & Salick, 2005; McGraw, 2001). Harvesting plants can be much like harvesting animals by being destructive and positively size selective. Selectivity may arise

BOX 20.1 Detecting Harvest-Induced Evolution

Demonstrating harvest-induced evolution with phenotypic field data is inherently difficult. Typically, one has to work with a time series showing a trend in a characteristic assumed to be under harvest-induced selection. There are a number of pitfalls that must be avoided before one can credibly attribute such change to harvest-induced evolution.

The first group of pitfalls arises from the need to prove that the observed phenotypic change really is evolutionary, and thus possesses a genetic basis. Changes in phenotypic distributions can simply result from the direct demographic effects of sustained selection. For example, if males with large antlers are always culled, then mean antler size must obviously end up being lower compared with a situation without culling, even if variation in antler size is not genetic. Similarly, whenever age at maturation is variable, increasing mortality results in a population with lower mean age, and thus also with lower age at maturation. Such demographic changes illustrate selection in action and are necessary for evolution to take place, but they alone are not sufficient evidence for evolution. The second source of nongenetic variability in phenotypic data is plasticity. Plastic changes result from the effect of environmental conditions on the translation from genotype to phenotype and may thus occur in response to just about any change in the environment. Also, harvesting may trigger plastic changes by resulting in lower population abundance and improved resource availability. After environmental conditions are restored, the corresponding plastic changes are expected to disappear within a generation or less.

There are only two ways to prove genetic change. The seemingly most appealing method is to use molecular genetic data. Two practical obstacles are immediately evident: lack of historic tissue samples and lack of identified genes determining the trait in question. The other method is to conduct common-garden experiments, which compare populations that supposedly differ genetically by exposing them to exactly the same environment; phenotypic differences remaining under such circumstances must have a genetic basis. This method is most useful for comparing extant populations of recent common ancestry. Species introductions have sometimes resulted in such seminatural experiments. By contrast, this method cannot be applied to comparing populations in time to corroborate the genetic basis of phenotypic trends, unless live samples of the ancestral population have been faithfully preserved.

If strict proof of genetic change is not possible, one has to try to make the best use of phenotypic data. One option is to capture plastic effects and genetic effects through multiple regression analysis. If plastic effects are not sufficient (and genetic effects are thus required) to explain observed phenotypic patterns, then the case for evolution is strengthened. Swain and colleagues (2007) provide a recent example of this approach. The second option is to use reaction norms. By definition, the estimation of reaction norms requires environmental variability to be observable. Maturation reaction norms typically include the age and size of individuals, and thus their growth rate as well, as explanatory variables and account for demographic effects, in addition to growth-related plasticity effects (Box 20.2). For both of these approaches, a fundamental limitation always remains: One can never exclude the possibility that some unaccounted environmental factor is triggering the phenotypic changes through a plastic response that is unknown or not considered. This possibility can be minimized through the careful analysis of potentially relevant environmental factors.

A second group of pitfalls arises from the need to prove that the observed phenotypic changes were caused by harvesting, and not by some other selective force. Unfortunately, a study based on historical data—without replication and controls—is the weakest

(continued)

possible setting for showing causal relationships. However, credibility of harvest-induced selection as the most likely causal factor may be increased in a number of ways. First, we can independently evaluate alternative hypotheses and determine whether harvest-induced evolution arises as the most credible hypothesis. Second, although replication in the strict sense is typically infeasible for important resource populations, populations subject to the same "treatment" (namely, increased harvest mortality) are plentiful. A large number of fish stocks from different species and geographic areas are showing similar changes in their maturation reaction norms in response to sustained and elevated harvest mortality (Table 20.1). This ubiquity of analogous trends is suggestive of a common explanation. Third, one can carefully construct a model, incorporating harvesting as well as other potential selective forces, to determine to what extent observed patterns are reproduced in the model. Such models are useful for assessing whether documented phenotypic change could result from selection-induced genetic change, for evaluating whether the speed of phenotypic changes is compatible with such an explanation, and for examining whether harvest-induced selection is among the main driving forces.

either because large plants are easier to spot or because they are more valuable (Mooney & McGraw, 2007). Also, nondestructive utilization of plants can elicit selection pressures, but these will be more subtle.

The majority of examples of harvest-induced evolution deal with fish, and the bulk of them have focused on commercial fisheries. The fisheries-induced selection elicited by modern exploitation has thus been likened to a large-scale, uncontrolled experiment in life history theory (Rijnsdorp, 1993). As shown in Figure 20.2, the additional mortality imposed by industrial-scale fisheries can be very high. In typical fisheries, both immature and mature individuals above a certain size limit are harvested. Theoretical predictions on maturation evolution are then rather clear-cut: Evolution is expected to cause earlier maturation at smaller size (Ernande et al., 2004; Heino, 1998; Law & Grey, 1989). Experiments with fish agree with theoretical predictions (Reznick & Ghalambor, 2005). In addition, field studies corroborate these expectations: Trends toward earlier maturation are ubiquitous in commercially exploited fish stocks (Trippel, 1995). Furthermore, analyses utilizing maturation reaction norms (Box 20.2) have helped to conclude that these trends cannot be explained by mere demographic changes or by growth-related phenotypic plasticity (Table 20.1). Any single study based on phenotypic field observations will of course always be subject to alternative interpretations, so that the suggestion that observations are most parsimoniously interpreted in terms of fisheries-induced evolution may be challenged. However, when a large number of independent studies suggest the same pattern, the case for fisheries-induced evolution is significantly strengthened, especially when those studies are taxonomically and geographically diverse (Table 20.1).

In semelparous fish, Rutter's (1902) prediction that positively size-selective fishing favors slower growth seems theoretically robust and has been verified in experiments (Conover & Munch, 2002). Field evidence comes from Pacific salmon. Ricker (1981, 1995) concluded that evolution of slower growth was likely contributing to declining trends in size at maturation of pink salmon (*Oncorhynchus gorbuscha*) and coho salmon (*O. kisutch*). For iteroparous fish, the story is more complicated. Slower adult growth will result from earlier maturation, but evolution of juvenile growth is more complicated (D. Boukal et al., work in progress; E. Dunlop et al., work in progress). Empirical evidence is limited to one population of Atlantic cod (*Gadus morhua*), for which Swain and colleagues (2007) concluded that a genetic decline in juvenile growth had likely occurred.

Consequences of Harvest-Induced Evolution

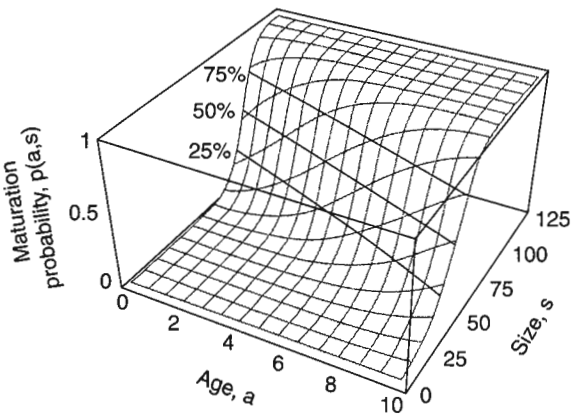
Is harvest-induced evolution beneficial? As we shall see next, there is no simple answer to this general question. There certainly exist conditions under which harvest-induced evolution makes resource populations more resilient to harvesting. This is

BOX 20.2 Fisheries-Induced Evolution and Maturation Reaction Norms

There is a ubiquitous trend toward earlier maturation in exploited fish stocks (Trippel, 1995). At first glance, this would seem to support unambiguously the hypothesis that fishing selects for earlier maturation (Beacham, 1987; Borisov, 1978; Law & Grey, 1989). However, because maturation is a very plastic trait, readily influenced by resource availability and other factors (Bernardo, 1993), it was believed for many years that mere plastic responses to the increased resources availability in fished-down stocks were sufficient to explain the observed maturation trends. This problem of disentangling plastic and genetic changes was essentially considered unsolvable in the field. However, as already pointed out by Rijnsdorp (1993), it is possible, through careful statistical analysis, to isolate certain plastic effects in maturation trends. In particular, probabilistic maturation reaction norms offer an elegant approach to identifying growth-related phenotypic plasticity in maturation based on commonly available data (reviewed in Dieckmann & Heino, 2007).

In general, a reaction norm is the profile of phenotypes that a genotype produces across a given range of environmental conditions. A reaction norm for age and size at maturation describes how variability in growth conditions, reflected by variations in size at age, influences maturation (Stearns & Koella, 1986). A probabilistic maturation reaction norm (Box Fig. 20.2) measures the *probability* with which an immature individual that has reached a certain age and size matures during a given time interval (Heino et al., 2002a). More important, this probability is conditional on having reached the considered combination of age and size—in other words, on surviving until, and growing to, this age and size. Through this definition, probabilistic maturation reaction norms allow considering the maturation process separately from survival and growth effects.

The introduction of probabilistic maturation reaction norms has opened the way for a large range of case studies (Table 20.1). Although only certain confounding effects are accounted for (such as those related to survival and to growth-related plasticity), the consistency of findings throughout these case studies strongly supports the hypothesis that fisheries-induced evolution toward earlier maturation is commonplace.



Box Fig 20.2 Schematic illustration of a probabilistic reaction norm for age and size at maturation. The reaction norm describes the probability for a juvenile individual to mature depending on its age and size. Often, only some probability contour lines projected on the age–size plane are shown, instead of the whole three-dimensional probability surface (compare with Fig. 20.4).

TABLE 20.1 Overview of Case Studies in which Probabilistic Maturation Reaction Norms Have Been Used to Help Disentangle Demographic, Plastic, and Evolutionary Effects in Maturation

Species	Population or Stock	Period with Data	Evolutionary Trend in Maturation Reaction Norm?	Reference
Atlantic cod *Gadus morhua*	Northeast Arctic	1932–1998	Yes	Heino et al., 2002b
	Georges Bank	1970–1998	Yes	Barot et al., 2004
	Gulf of Maine	1970–1998	Yes	
	Northern (2J3KL)	1977/1981–2002	Yes	Olsen et al., 2004
	Southern Grand Bank (3NO)	1971–2002	Yes	Olsen et al., 2005
	St. Pierre Bank (3Ps)	1972–2002	Yes	
Haddock *Melanogrammus aeglefinus*	Georges Bank	1968–2002	Yes	L. O'Brien et al. (in preparation)
Plaice *Pleuronectes platessa*	North Sea	1957–2001	Yes	Grift et al., 2003, 2007
American plaice *Hippoglossoides platessoides*	Labrador–NE Newfoundland (2J3K)	1973–1999	Yes	Barot et al., 2005
	Grand Bank (3LNO)	1969–2000	Yes	
	St. Pierre Bank (3Ps)	1972–1999	Yes	
Sole *Solea solea*	Southern North Sea	1958–2000	Yes	Mollet et al., 2007
Atlantic herring *Clupea harengus*	Norwegian spring spawning	1935–2000	Yes, but weak	Engelhard & Heino, 2004
Grayling *Thymallus thymallus*	Lake Lesjaskogsvatnet, Norway	1903–2000 (ca. 15 years)	Yes	T. Haugen et al. (in preparation)
Smallmouth bass *Micropterus dolomieu*	Opeongo Lake, Ontario, Canada	1937–1990	No	Dunlop et al., 2005

With the exception of grayling and smallmouth bass, these fish stocks all are, or have been, subject to intensive commercial exploitation. All but one case study show a significant trend in maturation reaction norms, which means that changes in age at maturation cannot be explained by demographic changes or growth-related phenotypic plasticity alone. This suggests the existence of an evolutionary trend, even though this can never be shown conclusively with phenotypic field data.

positive both for the resource population and for those harvesting it. However, harvest-induced evolution also affects the utility of resource populations in other ways. In particular, our current understanding suggests that both the quality and the quantity of harvest are often likely to decline as a result of harvest-induced evolution.

Harvest-induced evolution is adaptation to harvesting, which sounds like a good thing to happen—at least from the perspective of the harvested populations. In concrete terms, adaptation to harvesting can often be envisaged as a resource population's evolving to avoid harvesting pressure. Individuals may become more difficult to find and catch, they may avoid expressing or developing characteristics that make them prime targets, or they may minimize the duration of those parts of their life cycle spent in stages particularly vulnerable to harvesting. For example, individuals could become more wary about human contraptions such as traps, nets, and hooks, or, if hunters preferentially kill animals with large ornaments, delay developing such ornaments. Thus, for a given population abundance and harvesting effort, the catch after harvest-induced evolution is expected to be lower than it was before.

Based on these considerations, one might expect that harvest-induced evolutionary changes always render resource populations more resilient against harvesting. However, there are several caveats to this simple conclusion. First, adaptation to harvesting usually implies that individuals become less well adapted to aspects of their "natural" environment. Evolution is a balancing act, so that sacrificing adaptedness to natural selection will pay off in evolutionary terms when harvesting pressures are high. However, environmental conditions will change over time. During a period of favorable climate, for example, natural selection may be relaxed, so that a population can evolve mostly in response to harvest-induced selection. After some harvest-induced evolution under favorable environmental conditions, such a population may become increasingly vulnerable to periods of unfavorable climate. This scenario is not as far-fetched as it may initially sound. Slow life histories with long reproductive life spans are often understood as adaptations to variable recruitment success. Fast life histories favored by harvesting may then do well most of the time, but are occasionally bound to receive severe "punishment" during periods of environmental adversity. If harvesting had already pushed such populations to the limit of their demographically sustainable exploitation, harvest-induced evolution in conjunction with adverse environmental periods may thus induce population declines, or even collapses.

A second caveat is that humans are very cunning predators. They will not simply sit and wait while their resource species are gradually escaping harvesting through harvest-induced evolution, but instead will adjust their harvesting practices and preferences. Human preferences and aspiration levels tend to be more relative rather than absolute. For example, everybody knows that fish were bigger and trophy antlers more common in the past, but beating decadal records (or at least one's neighbor) will already bring full satisfaction. Technological development has a similar effect. Given the same harvesting effort and resource abundance, more and more catch will be obtained as harvest technology progresses. Thus, the adaptive system of resources and their harvesters may not converge to equilibrium, but harvesters will continue to drive evolution of the resources further and further away from their "natural" state.

A third caveat results from an insidious aspect of evolution. Evolution, in general, is not driven by what is the best for a population as a whole, but by what best serves the selfish interests of individuals. It is therefore not guaranteed that evolution results in a population's abundance being maximized, and it is quite possible that this abundance declines as a result of the population's evolution (Mylius & Dieckmann, 1995). In the extreme, a population may undergo what is known as *evolutionary suicide*—meaning, through gradual adaptation, the population may evolve to a combination of adaptive traits for which it no longer is viable, suddenly crashing to extinction (for reviews see Dieckmann & Ferrière, 2004; Parvinen, 2005). Although no empirical examples of evolutionary suicide have been documented to date, it should be kept in mind that collapses or extinctions driven by selection pressures will often appear indistinguishable from ecologically driven extinctions, unless special care and attention is exercised in collecting and analyzing the relevant data. In theory at least, the potential for evolutionary suicide has been demonstrated for populations harvested based on fixed quotas (B. Ernande et al., work in progress). Adaptation to harvesting leads to the reduction of harvestable biomass, which, under fixed quota regimes, translates into elevated harvesting mortality. This

triggers a further evolutionary decline in the harvestable biomass and thus a further increase in harvesting mortality, and so forth. One could expect that this ecoevolutionary feedback process leads to steadily declining population biomasses, but this is not always the case. Instead, discontinuous transitions to extinction may occur suddenly and from rather large population sizes, without obvious prior warning signals.

Although the three previous caveats explain why evolution cannot be relied on when trying to ensure an exploited population's persistence, it has to be borne in mind that, in addition, harvested populations are not only managed for their continual existence, but also for sustained harvest of good quantity and quality. Alas, theoretical studies suggest that the effects of harvest-induced evolution on harvest quantity and quality are largely negative (Heino, 1998; Law & Grey, 1989). Some of these predictions have already been confirmed empirically (Conover & Munch, 2002; Edley & Law, 1988): Yields may decrease, and the average size of harvested individuals may decline.

Populations adapted to harvesting may also have less capacity to rebound after harvesting pressures are relaxed. After a period of intense harvesting, the exploited population will have become increasingly adapted to harvesting, and thus less adapted to its natural environment. Genotypes best adapted to the natural environment will often have a higher potential rate of population growth than genotypes adapted to harvesting, so that the reduction in the frequency of the former at the expense of the latter will slow down recovery after harvesting is relaxed (K. Enberg et al., work in progress). For example, Hutchings (2005) has shown that maturation changes in northwest Atlantic cod stocks have likely led to a reduction in their potential rate of increase. This may be one factor contributing to the very modest rates of recovery these cod stocks are showing, despite a prolonged period of no or little fishing.

Independent from how harvest-induced evolution may change the resilience or value of a resource population, one can argue that maintaining the natural genotypic integrity of a resource population has an intrinsic value. For example, hunting elephants for ivory favors an increased frequency of tuskless female elephants (Jachmann et al., 1995). Most people would argue that elephants are best off as they are—with tusks—irrespective of whether tusks increase the commercial value or the natural viability of elephants.

We can conclude that harvest-induced evolution can improve the resilience of a harvested population (in the sense of being compared with the, usually only hypothetical, state of the same population subject to the same harvest regime but unchanged by harvest-induced evolution). From a strictly conservationist standpoint, this positive effect may dominate the overall picture, at least when considered to trade off favorably against concerns about preserving a population's ancestral genotypic composition. However, harvested populations are managed for utilitarian benefits. These benefits—sustained harvest and quality of harvest—are likely to deteriorate under harvest-induced evolution.

CASE STUDIES OF HARVEST-INDUCED EVOLUTION

Northeast Arctic Cod

Northeast Arctic cod is a stock of Atlantic cod (*G. morhua*) that uses the Barents Sea as its main feeding area. During the spawning season, mature cod migrate against the ocean currents to their spawning grounds off the northwest coast of Norway. Eggs and larvae are then taken by the currents back to the nursery and feeding areas in the Barents Sea, where juveniles remain until they mature. This separation of feeding and spawning grounds enables two fisheries, with evolutionary consequences of harvest that are strikingly different (Law & Grey, 1989). The feeder fishery is not selective with respect to maturity status of fish and will favor earlier maturation through the mechanisms explained earlier. The spawner fishery significantly affects only mature fish, and implies a selection pressure for delayed maturation. The latter serves as an example of how a population may evolve to become less exposed to harvesting. The centuries-long history of the spawner fishery may even have been responsible for the late maturation historically documented for this stock. The feeder fishery, in contrast, was only developed from the 1920s onward and became dominant after World War II. One must expect this reversal of the selective landscape to have strong evolutionary consequences—and this is exactly what data on age and size at first spawning are showing (Fig. 20.3). Estimated probabilistic maturation reaction norms (Box 20.2)

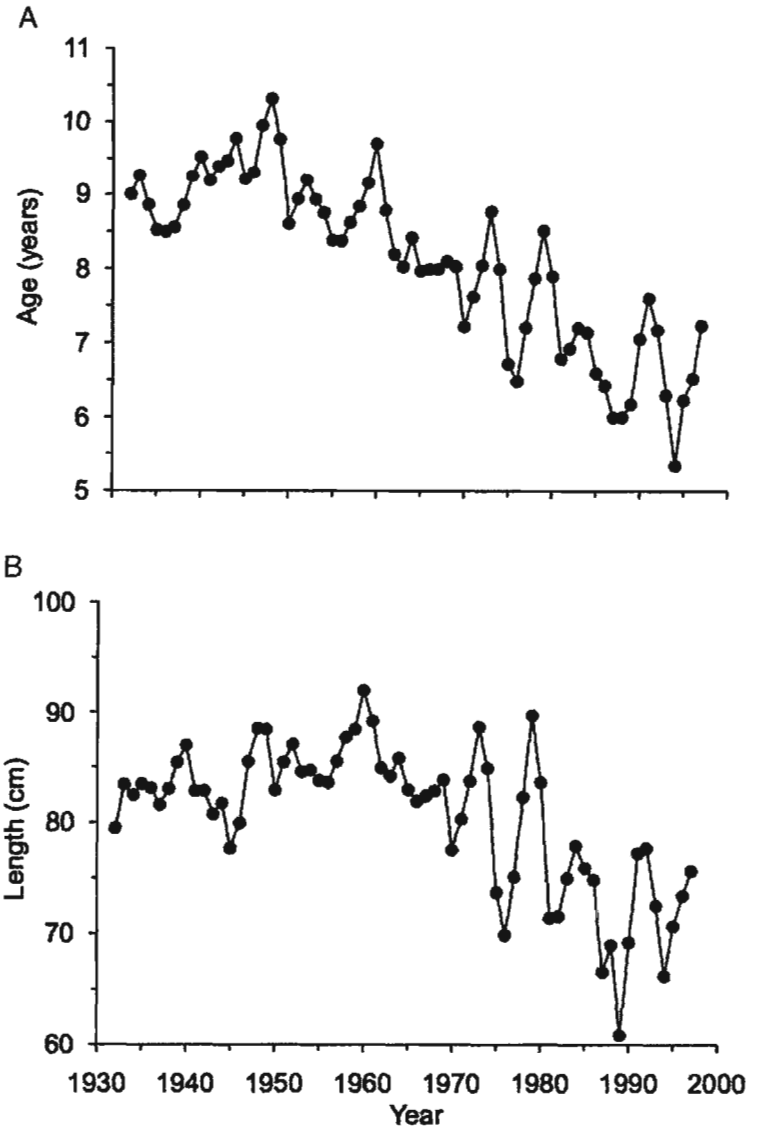


FIGURE 20.3 (A, B) Changes in mean age at maturation (A) and size at maturation (B) in Northeast Arctic cod (*Gadus morhua*). (From Heino et al. [2002b].)

suggest that the trend in maturation indeed has a large evolutionary component (Heino et al., 2002b).

Models indicate that this stock could not sustain current fishing pressures if it had retained the historical pattern of delayed maturation. However, there are also undesirable consequences of harvest-induced evolution. The average size of cod has dropped (small cod are less valuable per kilogram than large ones), and maximum sustainable yield may have decreased significantly (Heino, 1998; Law & Grey, 1989). Recruitment has probably been negatively affected because small, young female cod produce eggs of lower quality than large, old females (Ottersen et al., 2006). Furthermore, delayed maturation allowing for large adult body sizes is particularly important for a stock that undertakes a long, energetically demanding spawning migration (as relative migration cost declines with size) and inhabits a climatically extreme and variable environment. A period of poor feeding conditions hits

the smallest cod hardest, and therefore is especially dangerous for a stock in which the mean size of spawning adults has declined. Thus, although fisheries-induced evolution may have saved this stock from a harvest-induced collapse, this rescue comes at high costs. It might therefore have been better to avoid, or at least significantly redress, the fishing regime that has led to this evolutionary response in the first place. Harvest-induced evolution can thus be viewed as having obscured and delayed this realization.

What if managers were to attempt restoring the maturation schedule of Northeast Arctic cod? The current selection pressures would have to be reversed by switching back to the historical harvesting pattern. Unfortunately, there is a pronounced asymmetry in these selection pressures. Although the current harvesting pattern creates strong selection for early maturation, the historical harvesting pattern results in no more than mild selection for delayed maturation (Law & Grey, 1989). Our own analyses suggest that the evolutionary recovery of Northeast Arctic cod would thus take centuries.

This sobering estimate may even be deemed "optimistic," because resuming the historical harvesting pattern is hardly feasible. At the national level, within Norway, a challenge results from the fact that such drastic regulation would benefit only a certain segment of the fishing fleet (mostly small vessels operating in the spawning grounds), whereas another segment (big trawlers operating in the feeding grounds) would suffer. Cod fishing would also become increasingly seasonal, against the interests of consumers and the fishing industry. At the international level, the challenge is that the spawner fishery takes place deep in the Norwegian fishing zone, partly within the country's territorial waters. In such a setting, it is not obvious how access rights could be granted to other fishing nations such as Russia that would suffer most from much reduced fishing in the Barents Sea.

Northern Cod

The populations of Atlantic cod in the northwest Atlantic, off the coast of Canada and the northeastern United States, supported major fisheries for hundreds of years, but largely collapsed in the late 1980s and early 1990s. Many of these stocks have not yet recovered. Perhaps the most famous of these collapses was that of so-called *northern cod,* a stock complex off southern Labrador and eastern Newfoundland. Closure of the fisheries in the early 1990s has not brought the stock back, and its current abundance is estimated to be about 1% of that in the 1960s. Having once been the mainstay of Newfoundland's economy, the collapse and closure of the cod fisheries caused much economic and social hardship. Considerable effort has thus been invested in trying to understand why the stocks collapsed (and later on, why the recovery has remained pending for so long). It is now evident that excessive fishing pressure was the main cause of the collapse, whereas a period of unfavorable ocean climate made things even worse by contributing to triggering the collapse.

In contrast to Northeast Arctic cod, northern cod exhibits no clear separation of spawning and feeding grounds. Correspondingly, the northern cod fisheries have always targeted a mixture of immature and mature cod above some size threshold. The theoretical prediction under such a harvesting pressure is that the affected population will evolve toward earlier maturation. This prediction is supported by data on northern cod collected through research surveys: The age at which 50% of the females were mature dropped from about 6.5 years in the 1960s to about 6 years in the mid 1980s and to about 5 years in the mid 1990s (Morgan, 2000). Much of the drop occurred during a period of poor growth and body condition, which would instead have been expected to elicit the opposite phenotypic response had it been based on growth-related phenotypic plasticity. Probabilistic maturation reaction norms (Fig. 20.4) indeed suggest that that the observed changes in maturation were not merely phenotypically plastic, but also reflected genetic changes in maturation schedules (Olsen et al., 2004).

Did the change in maturation schedules affect the collapse? This is a question that is only now being investigated. Earlier maturation was favored by high mortality and might have increased the stock's capacity to sustain the harvesting. On the other hand, it is quite possible that earlier maturation at small size has been a costly strategy, in terms of lost resilience to poor feeding conditions. What appears to be clear is that the changed maturation schedule is not benefiting the stock's recovery potential. Hutchings (2005) estimated that an early-maturing population may suffer from a 25% to 30% reduction in its maximum annual population growth rate.

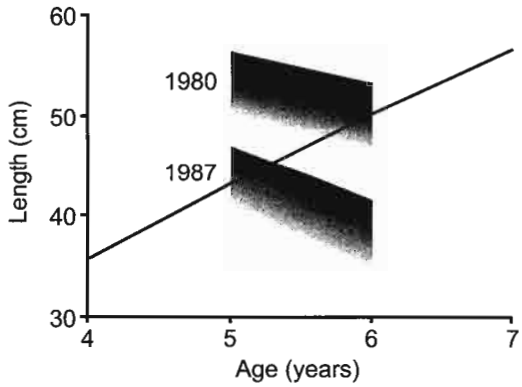


FIGURE 20.4 Probabilistic maturation reaction norms for female northern cod off southern Labrador born in 1980 and in 1987. Shaded rectangles show how the estimated maturation probability increases from 25% to 75% for the two considered ages. The solid line depicts the average growth trajectory. For the same growth trajectory, cod of the 1987 cohort reached a similar probability of maturing already 1 year earlier than cod of the 1980 cohort. (Data from Olsen and colleagues [2004].)

Irrespective on the possible effect of harvest-induced changes in maturation schedules on the collapse, these changes could have been used as an early warning signal. Drastic changes in maturation do not occur without strong selection pressures, and can thus serve as indicators that fishing mortality may affect a resource population more strongly than is advisable. In particular, Olsen and colleagues (2004) have shown that the changes in the maturation schedule of northern cod could have been detected up to a decade before the collapse of this stock became reality.

Mountain Sheep

Mountain sheep (*Ovis* spp.) in the Rocky Mountains are valuable targets of strictly regulated trophy hunting. Rams with big horns are the most sought-after targets for sport hunters, and harvesting is also legally limited to individuals fulfilling specific requirements for horn size. Consequently, rams with big horns are more likely to be shot at an early age. On the other hand, the mating success of rams increases with their dominance rank, age, and horn length. Thus, trophy hunting selects against those rams that naturally achieve the highest expected mating success.

Coltman and colleagues (2003) analyzed more than 30 years of data from a bighorn sheep (*O. canadensis*) population in Alberta, Canada. Not unexpectedly, horn length at a certain age shows a clear decline in this study population (Fig. 20.5). What is unique to this study is that Coltman and colleagues (2003) also had access to genetic data allowing pedigree reconstruction, which enabled them to show that horn size was highly heritable and that the observed decline in horn size was genetic.

Does declining horn size matter? One might be tempted to think that the absolute size of sexual ornaments is not that important: In male–male contests, it is the relative size differences that matter. As long as some variability in horn size persists, males should be able to establish their hierarchy just as before. Therefore, although undesirable from the trophy hunters' perspective, the documented decline in horn size might be rather inconsequential for the viability of the population.

Nonetheless, sexually selected traits do not exist in isolation from other traits. Indeed, Coltman and colleagues (2003) showed that there is a strong and positive genetic correlation between horn size and body weight. Consequently, selection for smaller horns will also select for smaller body size. Smaller body size could have direct negative effects

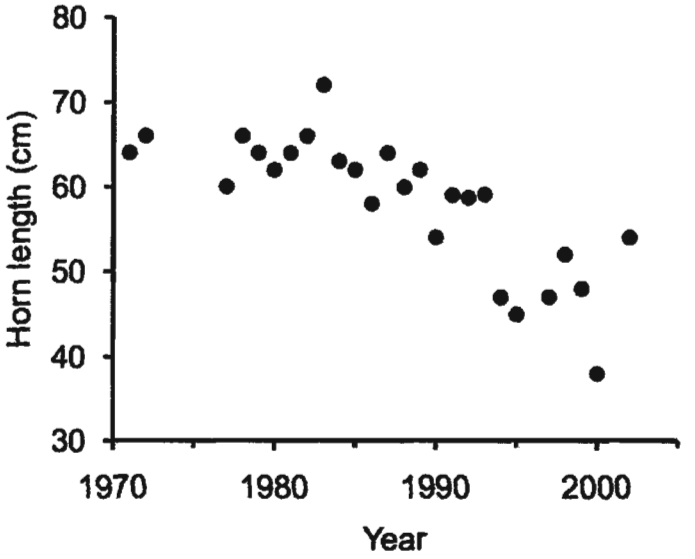


FIGURE 20.5 Average horn length in 4-year old rams of bighorn sheep. (Data from Coltman and colleagues [2003].)

on, for example, overwintering survival and parasite resistance (positive genetic correlation between parasite resistance and body size has been demonstrated in another sheep species). Thus, evolution driven by trophy hunting may indeed reduce the viability of the bighorn sheep population.

However, in thinhorn sheep (*O. dalli*) populations in Yukon Territory, Canada, horn growth seems to have remained essentially constant for the past 40 years (Loehr et al., 2007), despite selective harvest similar to that in bighorn sheep. Loehr and associates (2007) ascribe this to the positive correlation between natural mortality and horn growth: Size-selective harvest leads to higher mortality for rams with fast horn growth, but these rams would also face higher mortality without hunting. The correlation of horn size and horn growth with other traits related to fitness seems to vary significantly among different species. Such diversity impedes general conclusions, highlighting the need for wildlife managers to develop population-specific insights into the evolutionary implications of harvesting.

CONCLUDING REMARKS

Harvest-induced evolution has many facets. The hunting of mountain sheep is intentionally selective, whereas the historic fishing selectivity for Northeast Arctic cod was a by-product of spatial population structure. Harvest of northern cod was primarily size selective, although the evolutionary selection pressure mostly originated from the overall increase of mortality.

In all cases, significant evolutionary changes have taken place, although it is only for bighorn sheep that we can conclude with high certainty that changes were genetic; because of the lack of genetic sampling, evidence for fisheries-induced evolution is less direct. Despite this evidence of harvest-induced evolution, management in all three cases has been devoid of evolutionary awareness. This has come at a cost. The quality and quantity of Northeast Arctic cod catch has likely declined substantially, and without harvest-induced evolutionary responses, the stock might in fact have collapsed. The quality of bighorn sheep harvest has declined, and a decrease in the viability of the population is suspected. Also for northern cod, the quantity of potential harvest has likely declined, although it seems moot to agonize about such losses when a stock has collapsed and has yet to recover. And the role harvest-induced evolutionary changes have played in this tragedy still remains to be understood.

What could be done better? Lowering harvest pressure will almost certainly help to slow the pace of harvest-induced evolution. Further options depend on details that are specific to a

population and its harvesting regime. Shifting the bulk of harvesting of Northeast Arctic cod back to its spawning grounds would bring long-term benefits, but is hardly a realistic option because of social and political constraints. An analogous option is not available at all for northern cod, for which feeding and spawning grounds overlap; the remaining option here is to assess whether size limits could be set to minimize unwanted evolutionary impacts. The case of bighorn sheep would benefit from prioritizing management objectives. The size limit for hunting was increased in 1996 to a level that reduced harvest-induced selection as well as the harvest itself. If a supply of prime trophies were the first priority, managers could allow culling rams with small horns to give a selective advantage to rams with the potential to become top-class trophies. On the other hand, if the quantity of harvest is also deemed important, a less selective harvest might offer a good compromise.

FUTURE DIRECTIONS

Harvest-induced evolution poses an additional challenge to achieving sustainable harvesting: What appears to be ecologically sustainable may prove evolutionarily detrimental, which, in turn, may exert a negative feedback on ecological sustainability. A gradual awakening to this challenge has occurred only during the past two decades. We now have a fair understanding of harvest-induced selection pressures, and evidence is accumulating that certain harvest-induced changes are most parsimoniously interpreted as being of evolutionary nature. However, there still are many gaps in our knowledge of harvest-induced evolution that need to be addressed by future research:

- Empirical evidence of harvest-induced evolution is restricted to just a few types of traits (mostly maturation traits and sexually selected traits such as antlers and horns). Presumably this reflects more what types of trait are amenable to observation and analysis, rather than which traits are prone to evolve rapidly in response to harvesting.
- Similarly, the reported empirical evidence stems from just a few taxonomic groups (primarily fish and ungulates). Again, this is likely to reflect the availability of data, rather than the fact that these particular taxonomic groups are more vulnerable to harvest-induced evolution than others.
- The repercussions of selective harvesting based on sexually selected traits remains poorly understood. How do natural, harvest-induced, and sexual selection interact?
- Our understanding of the demographic consequences of harvest-induced evolution is still scant. Is evolutionary suicide a likely outcome? How do harvest-induced evolutionary changes affect the likelihood of population collapses and the potential for subsequent recoveries?
- Evolution always implies genetic change, but we still know little about the genetics of fitness-related traits in the wild. Observing evolution is mostly based on indirect evidence rather than on the direct identification of genetic change. We expect that the rapid development of molecular genetics will soon facilitate the direct detection of harvest-induced evolution. On the other hand, classic approaches to studying evolution based on phenotypic observations are far from being fully explored. For example, developing the quantitative genetics of complex traits such as maturation reaction norms will facilitate detecting and managing harvest-induced evolution in such traits.
- Although harvest-induced evolution may have beneficial effects on certain aspects of population resilience, the overall effect will often be deemed negative (1) because the beneficial effects on resilience may be weak or uncertain, (2) because a population's capacity for dealing with adverse environmental conditions may be compromised, and (3) because the quantity and quality of harvest are typically diminished. The obvious conclusion is that harvest-induced evolution should be managed. But are there better ways of managing harvest beyond the obvious recommendation of lowering overall harvest pressure? Are there ways to accelerate evolutionary recovery by carefully crafting the selectivity of harvesting?
- Learning to cope with harvest-induced evolution by trial and error is foolish. However, experimentation is seldom feasible, because resource populations are usually large and too valuable for risky trials, and evolution does not take place overnight. We therefore believe that modeling is an essential tool for developing the scientific basis of the evolutionarily sustainable management of harvested populations. Properly devised models—incorporating sufficient ecological and genetic

detail—will allow virtual experimentation, which will help to understand past evolutionary changes, predict the timescales on which harvest-induced evolution unfolds, and evaluate the expected effects of envisaged management measures.

SUGGESTIONS FOR FURTHER READING

Nelson and Soulé (1987) provide an early account of the evolutionary dimension of harvesting in aquatic systems; many of the points raised there remain topical to date. Stokes and colleagues (1993) and Smith (1994) summarize the state of the art at the beginning of the 1990s, whereas Dieckmann and Heino (2007) present an updated overview of fisheries-induced maturation evolution and Jørgensen and colleagues (2007) raise the issue of taking evolutionary perspectives aboard in fisheries management. Harris and associates (2002) offer a terrestrial perspective on the evolutionary consequences of hunting, and Dieckmann and coworkers (2008) give a comprehensive modern account of fisheries-induced evolution.

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