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The nature of fisheries- and farming-induced evolution

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Abstract

Humans have a penchant for unintentionally selecting against that which they desire most. In fishes, unprecedented reductions in abundance have been associated with unprecedented changes in harvesting and aquaculture technologies. Fishing, the predominant cause of fish-population collapses, is increasingly believed to generate evolutionary changes to characters of import to individual fitness, population persistence and levels of sustainable yield. Human-induced genetic change to wild populations can also result from interactions with their domesticated counterparts. Our examination of fisheries- and farming-induced evolution includes factors that may influence the magnitude, rate and reversibility of genetic responses, the potential for shifts in reaction norms and reduced plasticity, loss of genetic variability, outbreeding depression and their demographic consequences to wild fishes. We also suggest management initiatives to mitigate the effects of fisheries- and farming-induced evolution. Ultimately, the question of *whether* fishing or fish farming *can* cause evolutionary change is moot. The key issue is whether such change is likely to have negative conservation- or socio-economic consequences. Although the study of human-induced evolution on fishes should continue to include estimates of the magnitude and rate of selection, there is a critical need for research that addresses short- and long-term demographic consequences to population persistence, plasticity, recovery and productivity.

Keywords: cod, correlational selection, exploitation, fisheries-induced evolution, fitness, hybridization, local adaptation, outbreeding depression, salmon, selective harvesting

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Introduction

Many species of fishes are considered natural resources to be exploited for human consumption and profit. Put another way, fishes are evolving natural resources. Exploitation of these evolving resources (Stokes *et al*. 1993) alters the adaptive landscape of fished populations and, in so doing, has the potential to affect their phenotypic and genotypic variability in predictable and unpredictable ways. The same is true when captive-bred fishes, raised in aquaculture farms or hatchery facilities, interbreed with their wild counterparts following their intentional or unintentional release into the wild.

The potential for fishing to cause evolutionary change is not appreciably different from other forms of predator-induced mortality (e.g. Law 1979; Reznick *et al*. 1990), given its propensity for effecting differential mortality among genotypes. Indeed, the mortality wrought by humans on fishes almost certainly exceeds that of most natural predator-prey relationships, rendering the potential for exploitation to effect evolutionary change all the greater. Although the existence of phenotypic selection in nature was first hypothesized in the mid-19th Century (Darwin & Wallace 1858), many fisheries scientists and resource managers have been either reluctant to acknowledge the potential for fishing to elicit genetic changes (Stokes & Law 2000) or doubtful as to whether such changes are truly harmful. The latter point is a fundamentally important one because it raises questions as to whether human-induced evolution brought about by fishing or by fish farming is likely to significantly affect population attributes such as maximum sustainable yields, population resistance to natural environmental stochasticity, or probability of recovery following collapse.

Here, we examine the empirical basis for the hypotheses that direct and indirect influences of fishing and fish farming can yield evolutionary change in wild fish populations.

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From the perspective of fisheries-induced evolution, much of this work focuses on changes in life-history traits concomitant with high levels of size-selective fishing mortality. From the fish-farming perspective, the most conclusive evidence for evolutionary change stems primarily from fitness comparisons of farmed and wild fishes in nature and from studies of the consequences of interbreeding (the introgression of farmed genes into wild populations) on the survival, growth and life history of farmed–wild hybrids.

There are several conclusions that emerge from our study. First, in contrast to the work on farmed fishes, there is no unequivocal empirical evidence of genetic change resulting from fishing. However, the strength of the logical premise for, and the widespread indirect evidence of, fisheries-induced selection is sufficient to render moot the question of whether exploitation can bring about evolutionary change. Second, although the magnitude and rate of direct and correlational selection may be difficult to estimate, these parameters are required to predict the consequences of fisheries- and farming-induced evolution and to identify means by which these consequences can be mitigated. Third, the genetic consequences of fishing and fish-farming to reaction norms remain largely unexplored, despite general acceptance of the premise that plasticity can be adaptive. Fourth, and arguably most importantly, is the need to quantify the demographic consequences of human-induced evolution to the persistence, recovery and productivity of wild fish populations.

Causes and consequences of fisheries-induced evolution

The potential for fishing to generate evolution: changes in life-history traits

Fishing mortality is rarely random with respect to heritable, fitness-related traits (Ricker 1981), a fact that led Rijnsdorp (1993) to characterize fisheries as large-scale, uncontrolled experiments on life-history evolution. Indeed, having been documented repeatedly in exploited populations (Trippel 1995; Hutchings & Baum 2005), it is incontestable that fishing can lead to significant changes in characteristics such as age and size at maturity (Dieckmann & Heino 2007).

The difficulty (as in virtually all studies of fisheries-induced evolution) lies in disentangling phenotypically plastic responses attributable to changes in density (and the environment) from genetic responses attributable to selection. Earlier age at maturity, for example, provides one of the best examples of phenotypic change associated with fishing (Policansky 1993). As density declines, relaxed competition for food and space should lead to individuals growing at an increased rate. Fishes generally respond to increased growth by maturing earlier in life (Wootton 1998; Hutchings 2002; Roff 2003). Thus, fishing could lead to earlier maturity solely as a consequence of density- or environmentally driven changes to individual growth (Trippel 1995). Alternatively, by selecting against individuals whose genes predispose them to breed at older ages and larger sizes, fishing might favour genotypes that mature at relatively young ages or at small body sizes, or that grow at comparatively slow rates (Stokes & Law 2000; Law 2007; Swain *et al*. 2007). As Hilborn (2006) noted, when fishing pressure is high, fishes commonly grow faster as a result of reduced density. That is why it is of interest, from an evolutionary perspective, to examine those populations for which reductions in age and size at maturity are not associated with increased growth (Trippel 1995; Hutchings 2005).

Long-term changes in life-history traits have been interpreted as genetic responses to the size selectivity of fishing gear in a number of fishes (Table 1). Although most studies have focused on commercially exploited species, there are clearly parallels between recreational and commercial fishing in terms of their ability to impose differential mortality against particular genotypes (see Cooke & Cowx 2006). Interestingly, recreational fisheries may provide insight into an element of commercial fisheries that can be difficult to study — the evolutionary consequences of spatial differences in nonrandom harvesting. For example, because of the small scale at which they are usually conducted, recreational fisheries may increase the probability of fishing-induced genetic responses in behaviour. Many anadromous salmonids exhibit genetically based differences in return-migration timing (e.g. Quinn *et al*. 2000). These early and late runs may represent different components of the genetic diversity within populations and are likely to be adaptive. Fishing mortality which persistently and selectively targets only part of such a run-time distribution (e.g. Consuegra *et al*. 2005; Quinn *et al*. 2007) could elicit an evolutionary response, potentially leading to a reduction in genetic variability and a reduced capacity to respond to environmental change. In addition, aggregations of fishes may not be distributed randomly with respect to genotype at different life-history phases which may result in reduced genetic diversity if harvesting pressures are not distributed randomly within populations (e.g. Fraser *et al.* 2005, 2006).

However, notwithstanding the logical premise of the hypothesis that exploitation can generate evolutionary change in harvested populations, coupled with convincing evidence of such change in terrestrial mammals subjected to hunting (Coltman *et al*. 2003; see also Proaktor *et al*. 2007), we acknowledge that there is no unequivocal empirical evidence of genetic change resulting from fishing. But, given the strength of the indirect evidence of fisheries-induced selection (Table 1) and the potentially negative consequences of such selection on recovery, persistence and sustainable harvesting (see below), the potential for fishing to effect evolutionary change should not be dismissed outright.

Table 1 Examples of fish species for which commercial or recreational fishing has been hypothesized to have effected a selection response in one or more traits

Species	Hypothesized selection response	Reference
Northern pike (*Esox lucius*)	Increased fecundity	Law (1979)
Lake whitefish (*Coregonus clupeaformis*)	Smaller body size; slower growth	Handford *et al.* 1977)
Atlantic salmon (*Salmo salar*)	Smaller size at maturity	Bielak & Power (1986); Consuegra *et al.* (2005); Quinn *et al.* (2006)
Pink salmon (*Oncorhynchus gorbuscha*)	Smaller size at maturity	Ricker (1981)
Chinook salmon (*O. tshawytscha*)	Smaller size at maturity	Ricker (1981)
Sockeye salmon (*O. nerka*)	Earlier run-timing	Quinn *et al.* (2007)
	Smaller girth	Hamon *et al.* (2000)
European grayling (*Thymallus thymallus*)	Earlier age at maturity	Haugen (2000); Haugen & Vøllestad (2000)
Atlantic cod (*Gadus morhua*)	Earlier age at maturity	Hutchings (1999, 2005); Heino *et al.* (2002); Barot *et al.* (2004); Olsen *et al.* (2004, 2005)
	Smaller size at maturity	Barot *et al.* (2004); Hutchings (2005)
	Smaller body size	Law & Rowell (1993)
	Slower growth	Sinclair *et al.* (2002); Swain *et al.* (2007)
Smallmouth bass (*Micropterus dolomieui*)	Earlier age at maturity	Dunlop *et al.* (2005)
Orange roughy (*Hoplostethus atlanticus*)	Increased fecundity	Koslow *et al.* (1995)
European plaice (*Pleuronectes platessa*)	Earlier age at maturity	Rijnsdorp (1993); Grift *et al.* (2003)
	Increased reproductive investment	Rijnsdorp *et al.* (2005)
American plaice (*Hippoglossoides platessoides*)	Earlier age at maturity	Barot *et al.* (2005)

Selection responses to fishing

The magnitude of evolutionary change in any trait can be estimated from knowledge of the additive genetic variance or heritability of the trait and the average value of the trait before and after selection. Specifically, the genetic response to selection over generation i (ΔG_i) can be approximated as

$$\Delta G_i = h^2 S_i,$$

where h^2 represents the heritability of the trait in question and S represents the selection differential, i.e. the difference in the mean value of the trait before and after the selection episode (Falconer 1981).

Remarkably few attempts have been made to estimate selection differentials caused by fishing (Stokes & Law 2000; Law 2007). Law & Rowell (1993) estimated selection differentials on body size for Atlantic cod (*Gadus morhua*) in the North Sea. Under levels of exploitation that prevailed in the 1980s, they estimated a selection differential of –1 cm, meaning that individuals within a year-class (i.e. cohort) that survived fishing were, on average, 1 cm shorter than they would have been in the absence of fishing. Rijnsdorp (1993) estimated that almost half of the 5.8 cm reduction in size at maturity of heavily exploited European plaice (*Pleuronectes platessa*) from 1910 to 1985 could not be explained by changes in density or temperature. Ricker (1981) hypothesized that a 34% reduction in the body weight of pink salmon (*Oncorhynchus gorbuscha*) (all of which mature at two years) since the 1950s might be attributable to fisheries-induced selection. McAllister *et al.* (1992) concluded that this reduction could be explained as a genetic response if h^2 ranged between 0.18 and 0.25, which are heritabilities for body weight well within those reported for salmonid fish (Law 2000).

Perhaps the best estimates of S for an exploited fish population are those reported by Swain *et al.* (2007) for Atlantic cod from Canada's Southern Gulf of St. Lawrence. Controlling for the effects of density and temperature, they reported that the change in mean length of four-year-old cod between offspring cohorts and their parental cohorts was positively correlated with selection differentials experienced by parental cohorts between the age of four years and age at reproduction. From 1980 to 1997, the average S per cohort ranged between *c.* –1.5 and –3.5 cm for length at the age of four years, indicating that survival was higher among slower-growing fishes during this period.

Although selection differentials can be difficult to quantify, the potential consequences of fisheries-induced selection cannot be reliably modelled in the absence of such estimates. Some genetic changes may be relatively inconsequential to fitness whereas others (e.g. those hypothesized by Swain *et al.* 2007) may be of considerable import. There is also the question of whether traits genetically correlated with those directly affected by fishing also experience evolutionary change and whether other factors (such as sexual selection or altered predator-prey relationships) might alter the rate of evolutionary change generated by fishing.

Correlated responses to fisheries-induced evolution

Fishing has the potential to generate unanticipated responses to selection that may increase or impede the rate of evolutionary change effected by exploitation alone. The most direct means by which this can occur is by traits that genetically covary with those under direct selection (Law 1991; Walsh *et al*. 2006). Correlational selection may exacerbate fisheries-induced evolutionary change, a point underscored by Hard (2004) in his quantitative-genetic study of chinook salmon (*Oncorhynchus tshawytscha*), such that the overall selection response is greater than would be expected from analyses of single traits in isolation (Law 2007). Generally, time to reach sexual maturity is genetically correlated with larger body size in many organisms (Roff 2003; Kingsolver & Pfennig 2007). Under these circumstances, in a size-selective fishery, selection against either larger size at maturity or older age at maturity would be expected to generate a selection response in the other trait in the same direction. Such correlational selection might account, in part, for the substantive reductions in age at maturity that are frequently associated with reductions in size at maturity in fisheries that selectively harvest larger individuals.

The rate of fisheries-induced evolution might also be affected by how exploitation influences the mean and variance of traits under sexual selection. Although the question of whether fishing affects mating systems has received comparatively little attention (Rowe & Hutchings 2003), there is reason to believe that the relative magnitude of phenotypic selection generated by variation in mating or reproductive success (sexual selection) can be comparable to or greater than that attributable to variation in survival and/or fecundity (natural selection). Indeed, among diverse plant and animal taxa, Kingsolver *et al*. (2001) reported the median magnitude of sexual selection, as reflected by directional selection gradients, to be more than twice that of natural selection.

To date, when quantifying selection differentials in fished populations, an implicit assumption has been that reproductive success (or the probability with which surviving individuals will contribute genes to future generations) is independent of the trait in question. For example, one way of estimating S for a trait such as growth rate is to compare the mean size-at-age of individuals within a cohort after the selection event with the mean size of individuals from the same cohort at a much younger age before the effects of fishing have been experienced (e.g. Swain *et al*. 2007). If reproductive success is random with respect to size-at-age, then a comparison of the means before and after selection should yield a reasonably good approximation of S. However, if mating and/or reproductive success increases with size, for which there is evidence in commercially exploited marine fishes (e.g. Atlantic cod; Rowe *et al*. 2007), sexual selection for increased body size might counter or offset (to varying degrees) selection against larger size effected by fishing (Hutchings & Rowe 2006). One would predict, then, that maintenance of variability in body sizes, notably the maintenance of large individuals, might serve to reduce the rate of fisheries-induced selection for smaller body size.

De Roos *et al*. (2006) provide another example of how additional factors might alter the evolutionary response expected from fishing selection alone. Their work was based on a size-structured, consumer-resource model that incorporated information on life history, quantitative genetics, density-dependent growth and the allocation of energy between soma and gonads. They concluded that evolutionary trends to earlier maturity resulting from fisheries that target late-maturing individuals can be associated with step-wise, one-year shifts in age at first reproduction. De Roos *et al*. (2006) hypothesized that early maturation at small sizes and late maturation at large sizes may represent alternative evolutionarily and ecologically stable states. A key implication of their work is the high probability that, under some circumstances, genetic life-history changes driven by harvesting may not be readily reversible, a conclusion consistent with earlier research on the reversibility of fisheries-induced evolution (Law & Rowell 1993; Stokes & Law 2000).

Thus, correlational selection has the potential to accelerate or decelerate evolutionary responses predicted to occur by exploitation alone. Although relatively unexplored (but see Walsh *et al*. 2006), this field of research has the potential to significantly influence our perceptions of the magnitude, rate and consequences of fisheries-induced evolution.

Selective changes in reaction norms and phenotypic plasticity

The ability of populations to persist in the face of natural, albeit stochastic, environmental change depends on the spatial correspondence between the scale of the perturbation and the scale of adaptation. The former depends on the level of phenotypic plasticity expressed within a population, whereas the latter is reflected by genetic differences in plasticity at the population level.

Phenotypic plasticity is the ability of a genotype to produce different phenotypes across an environmental gradient (Schlichting & Pigliucci 1998; Sultan & Stearns 2005). Plasticity can be heuristically and graphically described as a norm of reaction, a linear or nonlinear function that expresses how the phenotypic value of a trait for a given genotype changes with the environment (Fig. 1A). Reaction norms describe how individuals respond to environmental change. Within an evolutionary context, norms of reaction pertain to responses by genotypes, the units of study when Woltereck (1909) first coined the term *Reaktionsnorm*

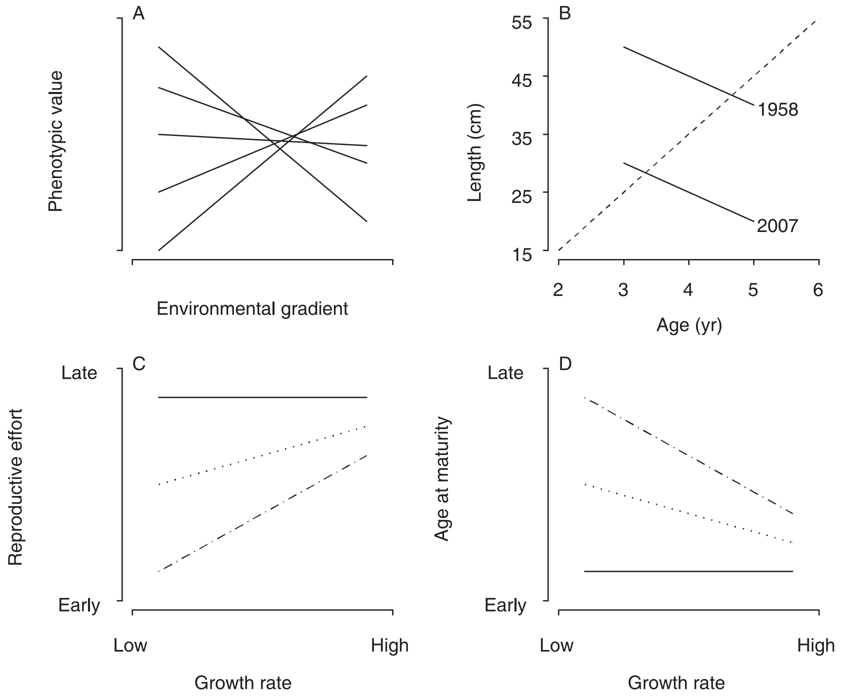

Fig. 1 Univariate plasticity and bivariate maturation norms of reaction and how they might change in response to fishing. (A) crossing plasticity reaction norms, indicative of genetic variation (V_G) in plasticity with V_G being greatest at the environmental extremes. (B) probabilistic maturation reaction norms (PMRNs; solid lines), representing the age and size at which 50% of a population reaches maturity, and a growth function (dashed line) which relates size to age. An individual growing at the average rate in 1958 would intercept the 50% maturation probability contour at about 4.6 year and 41 cm. In 2007, an individual growing at the same rate would mature at 3.3 year and at 28 cm. (C) hypothetical plasticity reaction norms for reproductive effort, as functions of environmentally induced growth rate, for a population subjected to low (dotted and dashed line), medium (dotted lines) and high (solid line) fishing pressure. (D) hypothetical plasticity reaction norms for age at maturity for a population subjected to low (dotted and dashed line), medium (dotted lines) and high (solid line) fishing pressure.

in his work on *Daphnia*. Within the context of understanding how genotypes, and ultimately populations, might respond adaptively to environmental change, reaction norms provide information about the magnitude of trait plasticity and the presence of genotype × environment interactions on the phenotypic expression of a given trait (de Jong 2005). Importantly, univariate reaction norms can also provide information on the extent to which the heritability of a trait changes with the environment (Stearns 1992), potentially providing insight into the rate at which the trait will respond to selection. For example, Fig. 1A depicts reaction norms for which the differences in phenotype among genotypes are greatest at the environmental extremes; if that genetic variation is additive, one would conclude that the heritability of the trait in question will be highest at the extremes of the environmental gradient. In contrast, heritability will be much lower near the centre of the environmental gradient, where the reaction norms converge, because of the similarity in phenotypic values among the different genotypes. Thus, the additive genetic variation of the trait in question, and the rate at which it will respond to selection, will vary with the environment.

For the purpose of our work, we refer to these classically defined (Woltereck 1909; Schmalhausen 1949; de Jong 2005) univariate reaction norms as plasticity reaction norms to distinguish them from bivariate maturation reaction norms. The latter, based on the work of Stearns and colleagues (e.g. Stearns 1983; Stearns & Koella 1986), usually describe associations between size and age at maturity. Probabilistic maturation reaction norms, or PMRNs (which estimate the probability that an individual that has reached a specific age and size matures at that age and size), have been employed as a means of detecting fisheries-induced evolution (e.g. Heino *et al*. 2002; Grift *et al*. 2003; Olsen *et al*. 2004; Barot *et al*. 2005). As noted by Dieckmann & Heino (2007) in their recent overview, PMRNs potentially control for the effects of phenotypic plasticity on life-history traits, such that temporal trends in PMRNs may be indicative of genetic changes in maturation schedules (e.g. Fig. 1B). One fundamental assumption inherent to this approach is that PMRNs are insensitive to environmentally induced changes to growth rate. Law (2007) has questioned the validity of this assumption, citing evidence that maturation reaction norms can be substantially influenced by the environment and that the rate of change documented for some maturation reaction norms is too high to be explained solely as a genetic response to selection (see also Morita & Fukuwaka 2006).

Reaction norms can differ among individuals and among populations. Much of this variability has been demonstrated to be heritable for a broad range of organisms (notably plants; studies on vertebrates are comparatively few), meaning that the shapes of reaction norms, and the ability of individuals to respond to environmental change, can respond to selection (Schlichting & Pigliucci 1998; de Jong & Bijma 2002; de Jong 2005; Sultan & Stearns 2005). In fishes, the most compelling evidence of selection responses in plasticity may be that observed for life-history reaction norms among populations of European grayling (*Thymallus thymallus*) over a period of 9–22 generations (Haugen 2000; Haugen & Vøllestad 2000). In marine fishes, Hutchings *et al*. (2007) recently provided evidence that reaction norms for growth and survival in Atlantic cod differ genetically amongst populations and may represent adaptive responses to their local environments.

Surprisingly, the question of whether fishing can change the shapes of plasticity reaction norms has received comparatively little attention, particularly in recent years. Reznick (1993) hypothesized that the primary effect may be to change the elevation (i.e. the intercept) of some reaction norms, assuming that fishing would select against individuals genetically predisposed to mature at large body sizes. Based on optimality modelling of brook trout (*Salvelinus fontinalis*) life histories, Hutchings (1993, 1997) predicted that exploitation might change the slope, in addition to the elevation, of reaction norms. As fishing mortality increases, selection would be predicted to favour a canalization of reaction norms (i.e. reaction norms for which the slope approaches zero), notably for age and reproductive effort at maturity, such that individuals would be increasingly favoured to reproduce as early in life as possible, and to expend the maximum amount of effort at that age, irrespective of growth rate (Fig. 1C, D).

These hypothesized changes in plasticity resulting from fishing are consistent with differences in life-history reaction norms observed in salmonid fish. Among three populations of grayling, individuals in the population that experience the greatest adult mortality (quite possibly as a result of recreational fishing) mature as early in life as possible, irrespective of their rate of growth (Haugen 2000). The same pattern is evident among three brook trout populations; higher overwinter mortality amongst adults appears to favour early maturity irrespective of growth rate (Hutchings 1996).

Reduced plasticity in age at maturity is predicted to occur when the probability of realizing the fitness benefits of delayed maturity (increased fecundity for females and increased access to mates for males) declines with increased adult mortality (Hutchings 1993, 1997; Haugen 2000). A flattening or canalization of reaction norms will presumably affect the variance in fitness. For example, assuming that plasticity provides genotypes with a means of buffering the effects of the environment, reduced plasticity can be expected to reduce the capacity of individuals to respond adaptively to environmental change (de Jong & Bijma 2002), leading to an increase in the long-run (intergenerational) variance of fitness. Random variability in population growth rate can have seriously destabilizing effects on population dynamics, even though the expected population size may increase with time (Lewontin & Cohen 1969; Roff 1974).

Thus, although the question has remained largely unexplored, we suggest that fisheries can generate selective changes to the shapes of plasticity reaction norms in addition to those hypothesized for maturation reaction norms, thus affecting the ability of populations to respond to, and persist in the face of, environmental change.

Demographic consequences of fishery-induced changes to life history

Changes to life-history traits are concomitant with prolonged periods of exploitation (Trippel 1995). Based on data collated for marine fishes from the northwest and northeast Atlantic, Hutchings & Baum (2005) reported a mean reduction in age at maturity of 21% over periods of decline that extended at least 15 years for each population, with several populations maturing at 30% lower ages than they had previously. Irrespective of whether these changes are phenotypic or genetic, they will have consequences to population growth rate (Law 1991; Myers *et al*. 1999) because of the various interrelationships and trade-offs that exist between fundamental components of fitness such as age, body size, fecundity, survival, offspring size, growth rate and longevity (Hutchings 2002; Roff 2003).

The potential demographic consequences of life-history change in a commercially exploited marine fish have been explored by Hutchings (1999, 2005) who used a stochastic, age-structured model to examine how reductions in age and size at maturity might affect the population growth rate of northwest Atlantic cod. These analyses focused on northern cod, the population ranging from southeastern Labrador to the northern Grand Bank off Newfoundland that had declined 99% between the early 1960s and the early 1990s (Hutchings & Myers 1994) and has since shown little or no recovery (Shelton *et al*. 2006). Between the mid 1950s and the early 1990s, age at 50% maturity is estimated to have declined from 6.5 to 7.0 years to approximately 5.0–5.5 years (Hutchings 2005). Hutchings (1999) suggested that reductions in northern cod age at maturity were most parsimoniously explained as genetic responses to fishing, a conclusion later supported by Olsen *et al*.'s (2004) study of PMRNs. The same argument has been proffered for reductions in age and size at maturity observed for Canada's Eastern Scotian Shelf cod (Hutchings 2005) and for reductions in growth rate among cod inhabiting the Southern Gulf of St. Lawrence (Sinclair *et al*. 2002; Swain *et al*. 2007).

Given the links between life-history traits and maximum population growth rate, it is surprising how little work has focused on the demographic consequences of fisheries-induced evolution. Based on the empirically supported premise (e.g. Beverton *et al*. 1994) that the probability of surviving reproduction declines with reductions in age and size at maturity, Hutchings (2005) reported that a shift in age at maturity from six to four years can reduce annual population growth in Atlantic cod by 25–30% and more than double the probability of negative population growth every generation. If the shifts in life history experienced by northwest Atlantic cod are partially attributable to genetic responses, then these changes, and their potentially negative demographic consequences, will almost certainly be slow to reverse (Law 2000).

Reversibility of fisheries-induced evolution

As with all types of genetic change, fisheries-induced evolution is potentially reversible. However, the probability that traits will revert to their former phenotypic values once the selection pressures associated with fishing have been removed (hereafter termed 'reversibility') is likely to be low in most cases (Law & Grey 1989; Law 2000).

Evolutionary change depends on a number of factors. In general, changes to the sign, magnitude and temporal constancy of genetic covariances among traits will influence the rate and type of selection response (Turelli 1988; Law 2000), following the cessation of fishing. The greater the amount of additive genetic variance in a trait, the greater the response to selection. But for fish populations that are at historically unprecedented low levels of abundance, reversibility may be hindered by an erosion of heritable genetic variation. Selection responses also depend on the magnitude of the selection differential. However, as Law (2000) noted, the potentially large selection differentials generated by fishing are unlikely to be matched by similarly large differentials in the absence of fishing, a prediction supported by an analysis on North Sea cod (Law & Rowell 1993). It may be much easier to select for early rather than delayed maturity (Law & Grey 1989). From a broader perspective, reversibility will almost certainly be negatively affected by changes to the adaptive landscape of the exploited species, resulting from factors such as evolutionary changes to life-history traits (Law & Grey 1989; Hutchings 2005), altered predator-prey relationships and other ecosystem-level changes (de Roos *et al*. 2006; Myers *et al*. 2007), and potential changes to the intensity and form of sexual selection (as discussed above).

One prediction common to all studies of fisheries-induced evolution is that genetic change effected by exploitation will be slow to reverse. However, there were until recently few empirical data against which this prediction could be evaluated. An exception may be the work by Swain *et al*. (2007) on Atlantic cod in the Southern Gulf of St. Lawrence. They concluded that the observed decline in size-at-age can be attributed to fisheries-induced selection against fast growth. Importantly, small size-at-age has persisted into the mid 2000s, despite a cessation of heavy fishing and favourable environmental conditions for growth over the past decade and a half. The persistence of small sizes is consistent with the hypothesis that selection differentials in the absence of fishing are unlikely to be as large as those generated by fishing (Law 2000). If reversibility is indeed as unlikely as the body of work to date would suggest, it behoves scientists to understand, and managers to try to mitigate, the predicted short- and long-term consequences of fisheries-induced evolution.

Causes and consequences of fish farming-induced evolution

The potential evolutionary changes that fish farming/aquaculture may induce in wild fish populations have received considerable attention in the primary and secondary literature over the past 15 years (e.g. Hindar *et al*. 1991, 2006; Hutchings 1991; Glebe 1998; Lacroix & Fleming 1998; Verspoor 1998; Naylor *et al*. 2005; Weir & Grant 2005; Bekkevold *et al*. 2006; Hansen & Windsor 2006). Our aim is to briefly review what is known of the causes of these changes, discuss and highlight key gaps in our understanding of their consequences, and raise some important and often contentious issues with respect to how to mitigate such effects. Although fish farming and hatchery supplementation (e.g. stocking practices) share a number of common concerns, we focus solely on evolutionary change associated with farming in our review. Relevant reviews relating to supplementation can be found in Waples (1991, 1999) and Reisenbachler & Rubin (1999) (see also Miller *et al*. 2004; Araki *et al*. 2007); Weir & Grant (2005) and Jonsson & Jonsson (2006) provide relevant reviews on competitive interactions between escaped farmed fishes and their wild counterparts.

Causes of evolutionary change in fish farming

Farmed fish broodstock is originally derived from wild populations and is maintained in controlled-rearing facilities over several generations. This is done for practical reasons to enable selective breeding of individuals for desirable traits such as rapid growth, delayed maturation and pathogen resistance (Gjoen & Bentsen 1997; Glebe 1998). Advertent changes in the genetic composition of these farmed populations from their wild ancestors are an inevitable result of such selective breeding (Table 2). By virtue of being raised in a controlled setting, farmed populations may also undergo inadvertent genetic changes because such environments relax natural selective pressures to which fishes are exposed in the wild (Table 2). For example, farmed fishes always have an abundant food supply, a lack of predators, and their diseases are readily treated, so genotypes normally at a disadvantage in the wild may not be in fish farms. Certain fishes may also, for behavioural reasons, be collected disproportionately for breeding in the next farmed generation (Bekkevold *et al*. 2006). Controlled-rearing environments can also indirectly favour certain genotypes that are disadvantageous in the wild through correlational selection. For example, more aggressive or bolder fishes often achieve more favourable growth in controlled-rearing environments due to their predictable food availability, but these same fishes also typically express lower propensity to avoid predators (Johnsson *et al*. 1996; Einum & Fleming 1997; Sundstrom *et al*. 2004).

Inadvertent genetic changes also arise in farmed populations because they are usually comprised of more limited numbers of breeders than many wild fish populations (Hansen *et al*. 2001; McGinnity *et al*. 2003). Such small populations have low effective population sizes (N_e), a characteristic governing the loss of genetic diversity attributable to the stochastic process of genetic drift (Frankham *et al*. 2002). Namely, genetic diversity is lost via drift more rapidly as N_e decreases. Small N_e populations also have a lower evolutionary potential and are more susceptible to inbreeding relative to large N_e populations (Frankham *et al*. 2002). Accordingly, farmed populations often (but not always) have reduced genetic diversity relative to their wild ancestors, at least at selectively neutral genetic markers (Weir & Grant 2005; Pampoulie *et al*. 2006; but see Wynne *et al*. 2007). This suggests that many farmed populations are less capable of responding to environmental changes such as exposure to new pathogens, changing temperatures or altered flow regimes. However, a particular farmed population may still possess genetic variants which are not found in other wild populations, if the variants existed in the ancestral wild population only (Verspoor 1998).

Consequences to wild fishes of farming-induced evolution

Farmed fishes recurrently escape from sea cages (Butler *et al*. 2005; Carr & Whoriskey 2006; Fiske *et al*. 2006). Thus, while the breeding performance of farmed fishes in the wild is sometimes lower than that of wild fishes (Fleming *et al*. 1996, 2000), farmed fishes can elicit evolutionary changes in wild populations if interbreeding between farmed fishes and their wild relatives occurs. These evolutionary changes can, in part, result from advertent/inadvertent genetic changes in farmed fishes attributable to selective breeding or genetic drift in controlled-rearing environments. The extent to which these changes are realized also depends on the degree to which the farmed fish's ancestral wild population experienced a different selective regime or contrasting evolutionary history relative to that of the wild populations with which the farmed-wild interbreeding is occurring (Fig. 2). In other words, even if *no* advertent or inadvertent selection occurred in farmed fishes, the mere transport and mass production of farmed fishes into different geographical regions (from which they were derived) sets the stage for the escape of potentially maladapted individuals that can interbreed with wild fish.

Of primary concern is that the smaller N_e characteristic of farmed fishes can result in the reduction of genetic variability in wild populations and a homogenizing effect when farmed–wild interbreeding occurs (Bekkevold *et al*. 2006; Hindar *et al*. 2006). Although low levels of farming in regions with very abundant wild fishes will probably

Table 2 Examples of fish species for which human-activities in aquaculture have been hypothesized to have effected evolutionary changes in one or more traits in farmed fishes, or in wild fishes through farmed–wild interbreeding

Species	Hypothesized or reported evolutionary change	Agent of evolutionary change	Reference
Farmed/controlled-rearing environment			
Atlantic salmon (*Salmo salar*)	Faster growth	Advertent selection	Gjoen & Bentsen (1997); Glebe (1998); Gjedrem (2000)
	Delayed age at maturity	Advertent selection	Gjoen & Bentsen (1997); Glebe (1998); Gjedrem (2000)
	Increased disease resistance	Advertent selection	Fjælestad *et al*. (1993); Gjoen & Bentsen (1997)
	Reduced incidence of male parr maturity	Advertent selection	Wild *et al*. (1994)
	Increased metabolic efficiency	Advertent selection	Roberge *et al*. (2006)
	Increased growth hormone production	Advertent selection	Fleming *et al*. (2002)

Table 2 *Continued*

Species	Hypothesized or reported evolutionary change	Agent of evolutionary change	Reference
Tilapia (*Oreochromis niloticus*)	Increased salinity tolerance	Advertent selection	Hena *et al*. (2005)
Channel catfish (*Ictalurus punctatus*)	Faster growth	Advertent selection	Rezk *et al*. (2003)
Atlantic salmon (*Salmo salar*)	Greater body depth in juvenile or adult morphology	Inadvertent selection	Fleming *et al*. (1994); Fleming & Einum (1997); von Cramon-Taubadel *et al*. (2005)
	Lower cortisol and glucose levels	Inadvertent selection	Poole *et al*. (2003)
	Lower genetic diversity	Founder effect, genetic drift and/or inbreeding	Danielsdottir *et al*. (1997); Norris *et al*. (1999)
	Shifts in gene expression profiles of unknown function	Inadvertent selection	Roberge *et al*. (2006)
	Genetic divergence	Founder effect, genetic drift and/or inbreeding	Danielsdottir *et al*. (1997); Norris *et al*. (1999)
Sea bream (*Sparus aurata*), Atlantic cod (*Gadus morhua*)	Genetic divergence	Founder effect, genetic drift and/or inbreeding	Alarcon *et al*. (2004); Pampoulie *et al*. (2006)
Pacific salmon (*Oncorhynchus* spp.)	Reduced survival, growth	Inbreeding	Kincaid (1983)
Pacific salmon (*Oncorhynchus* spp.)	Reduction in egg size and altered fecundity	Inadvertent selection	Heath *et al*. (2003)
Pacific salmon (*Oncorhynchus* spp.), Atlantic salmon (*Salmo salar*), brown trout (*S. trutta*)	Increased aggression, decreased predator avoidance, and/or risk-taking behaviour	Inadvertent selection	Johnsson *et al*. (1996); Einum & Fleming (1997); Fleming & Einum (1997); Rhodes & Quinn (1998); Sundstrom *et al*. (2003); Berekjikian (1995); Reisenbachler & Rubin (1999)
Pacific salmon (*Oncorhynchus* spp.)	Earlier spawning time	Inadvertent selection	Nichelson *et al*. (1986)
	Later embryonic developmental time	Inadvertent selection	Reviewed in Reisenbachler & Rubin (1999)
Farmed-wild interbreeding			
Atlantic salmon (*Salmo salar*)	Reduced lifetime fitness in F1 farmed–wild hybrids	Hybridization-outbreeding depression	McGinnity *et al*. (1997)
	Reduced lifetime fitness in F1/F2 farmed–wild hybrids	Multi-generational hybridization and outbreeding depression	McGinnity *et al*. (2003)
	Reduced survival to age 0+ in F1/F2 farmed–wild hybrids for one of two wild populations examined	Multi-generational hybridization and outbreeding depression	Fraser and Hutchings, unpublished
Rainbow trout (*Oncorhynchus mykiss*)	Reduced survival in second-generation backcross (F3) hybrids	Multi-generational hybridization and outbreeding depression	Tymchuk *et al*. (2007)
	Genetically based changes to growth rate in F1/F2/second-generation backcross (F3) farmed–wild hybrids	Multi-generational hybridization	Tymchuk & Devlin (2005); Tymchuk *et al*. (2007)
	Genetically based predator avoidance behaviour changes in F1/F2/second-generation backcross (F3) farmed-wild hybrids	Multi-generational hybridization	Tymchuk *et al*. (2007)
Coho salmon (*Oncorhynchus kisutch*)	Genetically based changes to growth rate in F1/F2 farmed–wild hybrids	Multi-generational hybridization	McClelland *et al*. (2005); Tymchuk *et al*. (2006)
Chinook salmon (*Oncorhynchus tshawytscha*)	Genetically based agonistic behaviour changes in F1 hatchery–wild hybrids	Hybridization	Wessel *et al*. (2006)

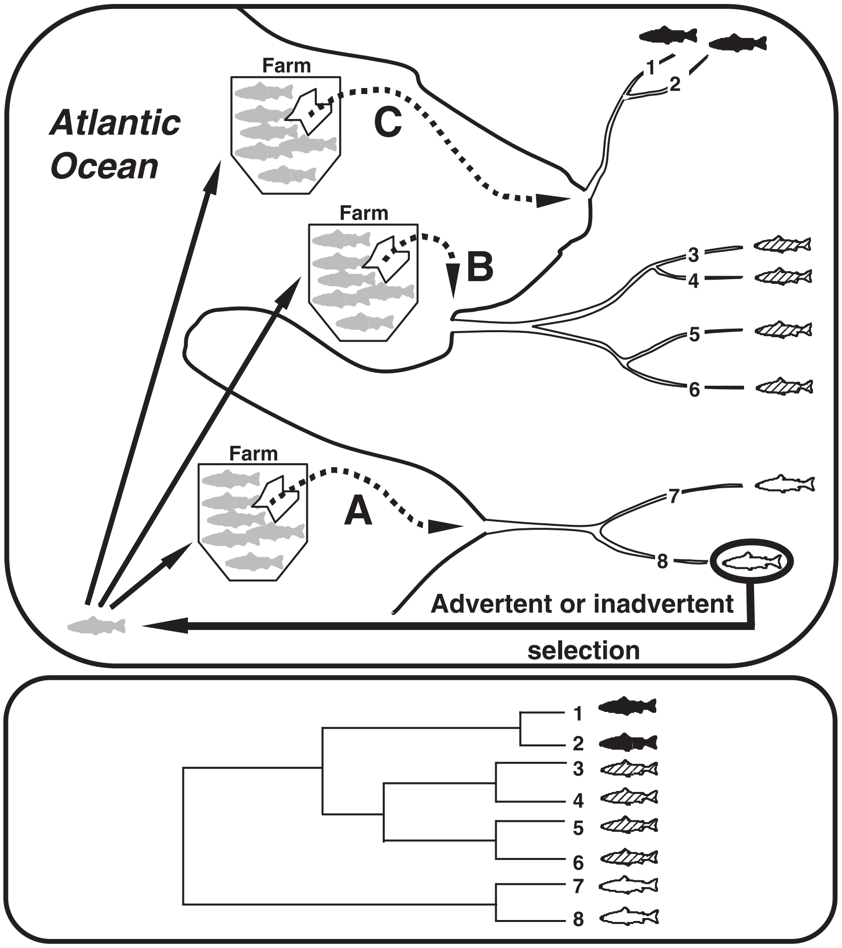

Fig. 2 Possible scenarios involving evolutionary changes to wild populations resulting from farmed–wild interbreeding following the escape of farmed fishes from sea cages. In the example presented here, three groups of genetically related, 'local' wild salmon populations (populations '1–2', '3–6' and '7–8') exist along a coastline within two main bays. The evolutionary divergence of the local population groups (depicted in the phylogenetic tree at bottom) is the product of selective processes for occupying different river environments, periods of historical isolation and/or the geographical distance separating river drainages. This evolutionary divergence is greatest between local wild population groups '1–2' vs. '7–8', with wild population group '3–6' being intermediate. A farmed strain is initiated from wild population '8' and undergoes evolutionary change through advertent and/or inadvertent selection during selective breeding. As is commonplace in aquaculture, the farmed strain is then transferred to sea cages at several different farms where it is mass-produced either in the same region or in regions different from those inhabited by its ancestral wild population ('8'). Periodically, accidental escapes of farmed salmon occur from sea cages ('A–C'), allowing them to enter rivers and potentially interbreed with wild salmon from the three different local wild population groups. For simplicity, the abundance of each wild population is assumed to be equal, and there is an equal probability of a farmed salmon escaping into each wild population. Owing to the genetic differences between the farmed strain and its ancestral wild population, as well as genetic differences between the ancestral wild population from which the farmed strain is derived and other wild populations, the rate at which farmed escapes will successfully interbreed with wild population groups will vary between 'A', 'B' and 'C', as will the outbreeding effects of farmed–wild interbreeding.

result in low levels of gene flow into wild populations, fish farming is normally intensive such that farmed fishes greatly outnumber their wild counterparts (Hansen & Windsor 2006). As a result, in addition to a reduction of genetic diversity, genetic homogenization is highly probable because farmed fishes escape recurrently and possess lower total genetic variation than all of the wild populations to which they escape (Norris *et al*. 1999; Naylor *et al*. 2005). This homogenization effect is potentially exacerbated in wild populations by farmed or farmed–wild hybrid males which attain sexual maturity at an earlier age through alternative reproductive tactics (Garant *et al*. 2003; Weir *et al*. 2005). If the rate of gene flow from escaped farmed fishes to wild fishes is sufficiently high, introgression of genetic material into wild populations might be facilitated and could lead to the extinction of the original wild genotypes (Fleming *et al*. 2000; McGinnity *et al*. 2003). Studies of interbreeding between artificially selected organisms and populations of their wild relatives in a variety of contexts suggest that such genetic assimilation could arise very quickly and may be facilitated by stressful environmental conditions and/or competitive interactions (Wolf *et al*. 2001; Ellstrand 2003; McGinnity *et al*. 2003; Campbell *et al*. 2006; Mercer *et al*. 2006, 2007).

A second concern is that farmed–wild interbreeding can lead to outbreeding depression, whereby the fitness of the offspring, or subsequent-generation offspring, is reduced (Edmands 2007; McClelland & Naish 2007). The overall result of farmed–wild outbreeding depression will be a reduction in fitness in the wild populations. Outbreeding depression can occur either through the disruption of intrinsic interactions between genes or disruption of extrinsic interactions between genes and the environment (reviewed by Edmands 2007). As a result, outbreeding depression in fishes can be manifested in a number of different ways, including, but not limited to: (i) reduced fertilization success; (ii) reduced embryonic survival through developmental incompatibilities; (iii) lower disease- or pathogen resistance; (iv) ineffective foraging ability; (v) reduced survival under the risk of predation; and/or (vi) reduced capacity to tolerate physiological stress (Gharrett *et al*. 1999; Hatfield & Schluter 1999; Gilk *et al*. 2004; Goldberg *et al*. 2005; McClelland & Naish 2007; Tymchuk *et al*. 2007). Studies to date have accordingly found that farmed–wild hybrids typically have lower fitness than pure wild fish, although this varies depending on the type of hybrid (Table 2: McGinnity *et al*. 2003; Tymchuk *et al*. 2007; DJ Fraser and JA Hutchings, unpublished). However, despite these data, it has been challenging to predict the consequences of evolutionary changes in wild fish populations resulting from farmed–wild interbreeding. We now briefly consider several reasons why this is the case.

Both adaptive divergence and historical isolation affect the outcome of farmed–wild interbreeding

Wild marine and freshwater fishes often exhibit varying degrees of phenotypic and genetic differentiation at varying spatial scales (Ruzzante *et al*. 1996, 2006; Waples *et al*. 2001; Bekkevold *et al*. 2005; Fraser & Bernatchez 2005a; Ostbye *et al*. 2005). These differences are in part a result of differential selective pressures but are also attributable to processes related to historical isolation (Taylor & McPhail 2000; Hendry *et al*. 2002; Waples *et al*. 2004; Fraser & Bernatchez 2005a, b; Rogers & Bernatchez 2006). Outbreeding depression in farmed–wild hybrids through the disruption of extrinsic interactions between genes and the environment would be expected primarily if differential selective pressures drive wild population differentiation. Conversely, outbreeding depression in farmed–wild hybrids through the disruption of intrinsic interactions between genes would be expected if the ancestral wild population of the farmed strain and the other wild populations had been historically isolated. Thus, depending on the relative roles of selection and historical isolation in population differentiation, interbreeding with escaped farmed fishes from even the same farmed strain will almost certainly have different outbreeding consequences, stemming from one or both of these mechanisms, for different wild populations (Fig. 2). These effects might vary from being undetectable to resulting in complete introgression (Hindar *et al*. 1991). Additionally, while theory predicts greater reductions in hybrid fitness with increasing population divergence from parental sources, this might range widely among fish species and perhaps even within species (Edmands 2002, 2007).

Unpredictability of interbreeding effects over multiple generations

Outbreeding depression is generally not manifested until the second (F2) or subsequent generations in which parental gene combinations are broken up by recombination (Edmands 2002, 2007). In fact, outbreeding effects in the first generation of interbreeding (hybridization; F1) are often decoupled from those in the F2 or subsequent generations due to the multitude of processes underlying the effects in each of these generations (some of which remain unknown; Edmands 1999, 2007; McClelland & Naish 2007). This unpredictability is confounded further by the fact that wild populations of many farmed fish species have experienced drastic declines, such that potentially superior fitness of offspring from outbred matings with farmed fishes in the F1 generation — due to the masking of inbreeding effects — could ultimately compromise management decisions if hybridization is not considered in later generations (F2 and beyond).

Undertaking studies of multigenerational interbreeding between farmed and wild fishes is challenging. It is difficult to carry out multigenerational hybridization studies for many farmed fish species, owing to their usually lengthy generation times (e.g. several years), the large amount of space and resources required to maintain sufficient numbers of these species for experiments, and the challenges of conducting large-scale, farmed–wild experiments in natural environments. Not surprisingly, only two studies have directly considered the *direct* fitness consequences of interbreeding between farmed and wild fishes over multiple generations, and these were carried out with single wild populations (McGinnity *et al*. 2003; Tymchuk *et al*. 2007). In one of these studies, outbreeding depression in farmed–wild hybrids did not manifest itself until after two generations of backcrossing with wild fishes and even then only under particular environmental conditions (under risk of predation; Tymchuk *et al*. 2007). Evaluations of the differential effects of multigenerational interbreeding between escaped farm and wild fish populations of varying nature have not been addressed, and it is currently difficult to gauge the generational duration of outbreeding depression. Nevertheless, such evaluations are critical in evaluating the magnitude of evolutionary change that can occur from farming on species-wide scales.

Different features of farmed strains with respect to origin

Farmed strains originate from different geographical origins. For example, farmed Atlantic salmon used in aquaculture in Europe and eastern North America originate predominantly from their respective wild populations which themselves diverged at least 10 000–12 000 years ago (King *et al*. 2001). The fitness costs of possessing genes from farmed salmon will almost certainly depend on the geographical and/or ancestral affinity of the escaped farm fishes to the respective wild population (Hutchings 1991; Weir *et al*. 2004).

Duration in controlled-rearing environments differs among farmed strains

Farmed strains differ in the number of generations during which they have undergone selective breeding in controlled-rearing environments (e.g. European farmed Atlantic salmon strains have been established longer than North American strains). While some genetic changes in farmed strains may occur through parallel selective processes (Roberge *et al*. 2006), the degree to which such changes have been manifested, and thus the magnitude of their resulting consequences to wild populations, will depend on the intensity of selection in breeding programmes and on the number of generations that the farmed strains have been reared in captivity. Such characteristics usually differ among farmed strains (e.g. Glebe 1998; Verspoor 1998; McGinnity *et al*. 2003).

Reversibility of evolutionary change resulting from farmed–wild interbreeding

If natural selection in wild populations is strong enough, maladapted farmed traits could be eliminated and any negative effects of farmed–wild gene flow or outbreeding depression resulting from farmed–wild interbreeding might be overcome. Indeed, many fish populations exhibit remarkable rates of genetically based phenotypic change when exposed to new environments (reviewed by Stockwell *et al*. 2003), suggesting that the process of eliminating maladaptive farmed traits might be rapid as well. However, following escape (which frequently recurs within specific geographical areas), farmed fishes often significantly outnumber their wild counterparts (Naylor *et al*. 2005; Hansen & Windsor 2006). This implies that a cumulative reduction in fitness, rather than re-adaptation, is more likely to occur over the long term in many instances (Hindar *et al*. 1991; Hutchings 1991; Fleming *et al*. 2000; McGinnity *et al*. 2003; Naylor *et al*. 2005). In addition, what is perhaps not considered sufficiently is that even if re-adaptation does occur, the wild individuals may experience an initial drop in fitness, and possibly in population-growth rate, before selection removes farmed genes (see below). This can be expected to have particularly dramatic impacts on smaller populations given their increased sensitivity to demographic, environmental and genetic stochasticity.

Other unknown consequences of farmed–wild interbreeding

Effects on wild population growth rates

Although farmed–wild interbreeding can elicit evolutionary changes in wild populations that lead to fitness reductions in the wild, the degree to which these changes affect overall population growth rates or productivity is largely unknown. Under certain farmed-wild interbreeding scenarios (and over several generations), simulation studies suggest that (i) wild population size would be substantially reduced (Hutchings 1991) and that (ii) wild genotype composition would shift to include more farmed fishes or farmed-wild hybrids (Hindar *et al*. 2006). A primary reason for uncertainty concerning the effects of farmed-wild interbreeding on the population growth rate of wild fishes is that there is often a lack of reliable information on the numbers of and the frequency with which farmed fishes escape (Butler *et al*. 2005; Fiske *et al*. 2006). Vastly improved data of this nature are essential for assessing the overall risk that farmed-wild interbreeding poses to different wild fish populations. Considered at one extreme, there may be severe outbreeding depression between farmed fishes and a wild population that results in 100% mortality of farmed-wild offspring, but if the immigration rate of farmed fishes into the wild population is very low (e.g. 0.001, one farmed fish for every 999 wild fish), the effects of farmed-wild interbreeding will be negligible relative to other factors that affect the demography and genetics of wild fish populations. In many situations, however, escapes of farmed fishes are recurrent, wild populations are small (e.g. Fleming *et al*. 2000; McGinnity *et al*. 2003; Fiske *et al*. 2006), and fitness reductions attributable to farmed-wild interbreeding might significantly increase the probability of extinction for wild populations, even if the rate of introgression from farmed to wild fishes is low.

Could farmed-wild gene flow be beneficial to wild fishes?

A contentious possibility is that particular alleles bred into farmed fishes might actually be advantageous in the wild.

For instance, many aquaculture breeding programmes now aim to improve the resistance of farmed fishes to particular pathogens (Fjæalestad *et al*. 1993; Gjoen & Bentsen 1997; Kettunen *et al.* 2007) which might confer a fitness advantage to wild fishes if they are naturally exposed to the same pathogens. We are unaware of any empirical study on fishes that has examined such a possibility in the wild. However, in related studies of interbreeding between cultivated crops and their wild relatives, pest resistance, early flowering time and rapid growth in the crop appeared to confer a fitness advantage in the wild in certain situations, especially under more stressful environmental conditions (Snow *et al*. 1998; Mercer *et al*. 2007). Nevertheless, given the myriad of environmental conditions/features in which farmed–wild hybrid fishes will be at a disadvantage in the wild, it is likely that such potential benefits of farmed–wild gene flow will be outweighed by its costs in *many* natural situations, perhaps most notably in the long term.

Management strategies

Mitigating the evolutionary consequences of fishing

In the absence of differential mortality among phenotypes, selection against specific life histories will not be realized. Thus, resource managers and decision makers should seek to avoid the use of harvesting techniques likely to lead to strong directional selection against larger, older individuals. There should also be an emphasis on maintaining/rebuilding a breadth of variability in body sizes and age classes within exploited populations.

Put simply, the message to the fishing industry, resource managers and decision makers is, 'keep the big ones around'. The message is simple, intuitive, should often bear minimal economic costs, and echoes a primary recommendation articulated by other recent reviews (Birkeland & Dayton 2005; Law 2007). It also has the advantage that most fish harvesters would agree that it is highly desirable, if not critically necessary, to maintain large individuals in a population. Inshore Newfoundland fishermen, for example, have long recognized the importance of not fishing-down the 'mother fish', the largest of the females that bear the greatest numbers of eggs (Neis *et al*. 1999).

Protection of larger individuals could be achieved by a number of measures, including the establishment of (i) maximum harvestable size limits, (ii) marine reserves, or (iii) gear-related measures that would distribute fishing mortality more equitably among age- and size classes (see also Law 2007). Coupled with measures to reduce the ability of fisheries to effect directional selection is the need to maintain levels of fishing mortality across all ages and size classes at levels that would allow exploited populations to sustain increases in abundance (i.e. at fishing mortalities somewhat less than those at which maximum sustainable yields would be achieved). Managers could also take action to avoid selection against specific behavioural components of spawning populations, e.g. early vs. late runs of anadromous salmonids.

It could be argued that it is too late to take mitigative action. Given that many fishes have already been historically depleted and show unimpressive signs of recovery to ecologically meaningful levels (Hutchings 2000; Hutchings & Baum 2005), it could be argued that the genetic consequences (whatever they may be) of selective, fishing-induced mortality have already been realized and that little can be gained by taking strong management action now. However, we would argue that such a call for inaction would be neither prudent nor risk-averse. Depleted populations may benefit from the proposed management actions by reducing or eliminating directional selection intensities, allowing for the potential reversal of fishing-induced genetic changes to life-history traits. Newly exploited species would also benefit by the inclusion of specific management measures designed to minimize the probability of fishing-induced evolution as these new fisheries develop.

Mitigating evolutionary changes from farmed–wild interbreeding

The most obvious means of avoiding evolutionary changes induced by farming would be to develop land-based facilities that negate the possibility of interactions between farmed and wild fishes (RSC 2001; Naylor *et al*. 2005; Bekkevold *et al*. 2006). To do so would presumably be economically costly in the short term. However, to our knowledge, cost–benefit analyses for the development of land-based facilities have not yet factored in the long term economic and socio-cultural costs of losing or rehabilitating wild fish populations impacted by the farming industry.

Another perhaps more realistic means would be to develop improved technologies that reduce the probability of escape from sea cages (Hansen & Windsor 2006). However, given that fishes would still escape in appreciable numbers (by virtue of the mass production of farmed fish), other measures would be required to minimize farmed–wild interbreeding effects. First, sterility of farmed fishes might prevent genetic changes in wild populations resulting from farmed–wild interbreeding, although such procedures do have a number of potential disadvantages (Naylor *et al.* 2005) and the mating of sterile farm fishes with wild fishes could still reduce recruitment of wild populations. Second, farmed broodstock breeding programmes that incorporate large numbers of breeding individuals, or that breed individuals from various farms, might help to retain higher levels of genetic variability in farmed strains. This might reduce the rate of loss of genetic variability in wild populations through introgression with a genetically depauperate farmed strain. It may also reduce inbreeding within farmed strains and the susceptibility of farmed strains to pathogens or disease, which can directly affect farm yields and profitability. Nevertheless, potential trade-offs between inbreeding avoidance in farmed strains and reducing inadvertent selection in controlled-rearing environments need further consideration. For instance, recent work suggests that breaking up farmed strains into smaller subunits that are more prone to genetic drift might actually be a more effective way to conserve total genetic variation while limiting opportunities for inadvertent selection (reviewed by Frankham 2007). Third, reducing inadvertent selection in controlled-rearing environments could also be achieved by periodically adding wild fishes to farmed broodstock programmes, and this would help to avoid undesirable evolutionary changes in wild populations resulting from farmed–wild interbreeding (Ford 2002; Table 2). On the other hand, such an approach is unlikely to be attractive for aquaculture programmes that need to selectively breed their fishes to maintain economic viability (Bekkevold *et al*. 2006).

There are also trade-offs associated with using only farmed strains derived from local wild populations where the farming is taking place, as opposed to farming nonlocal fishes in regions where wild populations occur that differ from those used to derive the farmed strains (Box 1). Disadvantages of both options (Box 1) have raised the additional suggestion that the farming of fishes outside of their native range may be beneficial towards achieving an environmentally responsible aquaculture industry. Nevertheless, while many escape events are unlikely to lead to the colonization of novel environments, there is evidence to suggest that some escaped farmed species have established themselves outside their native ranges (e.g. Volpe *et al*. 2000; Soto *et al*. 2001). Some features of farming might also facilitate the invasiveness of farmed fishes (Ellstrand & Shierenbeck 2000; Ellstrand 2003).

It could be argued then that farming within native ranges might constitute the 'best approach to dealing with a bad situation'. Rather than risking the potential loss of multiple species and the alteration of ecosystems as a consequence of invasive species introductions effected by farmed fish escapees, it might be *less* risky overall to alter the genetic composition, individual fitness and maximum growth rate of *some* populations *within* the native range of the wild species.

To summarize, in the event that land-based facilities for aquaculture are not developed, there will be ongoing trade-offs associated with different options for mitigating the

Box 1 The pros and cons of utilizing local vs. nonlocal farmed strains

A challenge facing the mitigation of the evolutionary effects of fish farming is whether to use (i) local farmed strains derived from wild populations found in the same regions where farming takes place (e.g. 'A' in Fig. 2); or (ii) nonlocal strains derived from wild populations not found in the same regions where farming takes place (e.g. 'B' or 'C' in Fig. 2; see also Bekkevold *et al*. 2006). Arguments for using either local or nonlocal strains might proceed as follows:

- 'Local': local strains would be less divergent from nearby wild populations, so they would pose less severe outbreeding effects when farmed–wild interbreeding occurs than if nonlocal strains were used.
- 'Non-local': but in being less-divergent, local strains would have weaker differences in reproductive behaviour from wild populations, so they might be expected to successfully interbreed with wild fishes at a much higher rate than nonlocal strains. The fitness costs of farmed–wild interbreeding could therefore potentially affect more of the wild population over the short-term and occur more readily in subsequent generations.
- 'Local': nevertheless, reproductive behaviour in fishes is generally not fixed, and no farmed strain has been so thoroughly domesticated that it was unable to breed with wild relatives (Naylor *et al*. 2005). Thus, interbreeding would still occur with a nonlocal strain, and even if it did not initially affect as much of the wild population as a local strain, the fitness costs might actually be higher in the long term. For instance, new genetic variants in a more divergent, nonlocal strain could be introduced and/or be created through recombination down the generations in the wild population, and this might ultimately supplant the wild genotypes (e.g. Edmands & Timmerman 2003; Campbell *et al*. 2006; Johansen-Morris & Latta 2006).
- 'Non-local': perhaps, but in another context, implementing the use of nonlocal strains is more economically attractive since it would not require multiple breeding programmes associated with local population characteristics (i.e. one or a few chief farmed strains could be used ubiquitously).
- 'Local': perhaps, but the use of many local strains might maintain greater levels of genetic diversity in the species by reducing overall genetic homogenization, and thus be more likely to maintain viable wild populations and farmed strains in the long term.

consequences of evolutionary changes to wild fishes via farmed–wild interbreeding. Before any of these options are considered in a given situation, we suggest that all potential consequences resulting from such actions be weighed and that their discussion merits more open and serious debate.

Concluding thoughts

It is logically untenable to suggest that selective, intense and prolonged fishing mortality does not exact an evolutionary response to exploitation. Some form of genetic change attributable to fishing has almost certainly occurred in many fished populations, whether they have been over-exploited or not (Barot *et al*. 2005). However, while society needs to be fully informed of the possibility of evolutionary change, it is important that the potential consequences not be exaggerated. Thus, although the study of human-induced evolution on wild fishes should include estimates of the magnitude and rate of selection, we reinforce our assertion that there is a critical need for research that focuses on the short- and long-term demographic consequences of genetic change to population persistence, plasticity, recovery and productivity. Research to date suggests that the potential consequences, which might not be readily reversible (Law 2000; de Roos *et al*. 2006), include reduced productivity (Law & Grey 1989; Conover & Munch 2002), lower maximum sustainable yields (Ratner & Lande 2001; Conover & Munch 2002), and slower rates of population growth and lower probabilities of recovery (Hutchings 1999, 2005; Walsh *et al*. 2006).

Research on the evolutionary consequences of fish farming on wild fishes, primarily because of its greater experimental tractability, has provided strong evidence that interbreeding with escaped farmed fishes can have significantly negative consequences for the fitness of their wild counterparts (McGinnity *et al*. 2003). Again, however, we caution that it is both unwise and inappropriate to assume that the consequences of such genetic interactions will be uniform across all affected populations. Theoretical and experimental work suggest that the effects on wild populations will depend on a number of factors, including (i) the magnitude of genetic differences between wild and farmed fishes, (ii) the mechanisms underlying genetic differences between wild and farmed fish, (iii) the frequency of spawning intrusions by farmed fish, (iv) the numbers of farmed fishes relative to their spawning wild counterparts, and (v) the geographical distance between the farming activity and wild populations (Hindar *et al*. 1991, 2006; Hutchings 1991; Edmands & Timmerman 2003; Ellstrand 2003; Weir *et al*. 2004; Weir & Grant 2005; Mercer *et al*. 2006; Edmands 2007).

The consequences of anthropogenic evolution to wild fishes are difficult to predict, largely because the magnitude of genetic change resulting from fishing and fish farming almost certainly varies considerably among populations. Scientific uncertainty, of course, does not justify societal or governmental inaction. Rather, management strategies designed to minimize or negate the effects of human-induced evolution that we discuss would be interpreted as responsible, risk-averse and precautionary responses to the penchant that humans have for unintentionally selecting against that which they desire most.

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