PERSPECTIVE

The emerging synthesis of evolution with ecology in fisheries science

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Abstract: Fisheries science is currently being transformed through a true integration of ecological and evolutionary perspectives. Many questions are emerging from the recognition that human-induced evolutionary change can elicit ecological change on short time scales, in some cases equal to or exceeding the changes brought on by classical ecological effects. For instance, to what extent does evolutionary change associated with size-selective harvesting, supplementation, captive breeding, aquaculture escapees, and related fisheries activities directly or indirectly affect species demography (persistence, productivity, or recovery), community structure, and ecosystem functioning? Under what conditions do feedbacks between evolution and ecology matter most for managing fisheries activities? Do such feedbacks generate predictable outcomes, and are they reversible? Although as yet, little consensus has been reached on the answers to these questions, it is clear that a synthesis of evolutionary and ecological perspectives holds great promise for improving and generating more biologically realistic modeling, monitoring, rebuilding, and management of fish populations, fish species, and aquatic ecosystems.

Résumé : Une transformation est en cours dans les sciences halieutiques associée à l'intégration véritable des perspectives écologique et évolutionnaire. La reconnaissance du fait que les changements évolutionnaires induits par l'homme peuvent entraîner, en peu de temps, des changements écologiques équivalents ou plus importants que les changements découlant d'effets écologiques classiques soulève de nombreuses questions. Par exemple, quelle est l'ampleur de l'incidence, directe ou indirecte, des changements évolutionnaires associés à la récolte selon la taille, à la supplémentation, à l'élevage en captivité, aux poissons échappés d'installations d'aquaculture et aux activités reliées à la pêche sur la démographie (persistance, productivité, récupération) des espèces, la structure des communautés et les fonctions des écosystèmes? Dans quelles conditions l'importance des rétroactions entre évolution et écologie est-elle la plus grande en ce qui concerne la gestion des activités de pêche? Ces rétroactions entraînent-elles des situations prévisibles et sont-elles réversibles? S'il n'existe pas encore de réel consensus sur les réponses à ces questions, il est clair que la production et l'amélioration de modèles plus réalistes sur le plan biologique, ainsi que la surveillance, la reconstitution et la gestion des populations et espèces de poissons et des écosystèmes aquatiques ne peuvent que bénéficier d'une synthèse des perspectives évolutionnaire et écologique. [Traduit par la Rédaction]

Introduction

Traditional fisheries science champions ecological principles to maximize sustainable yields, set fisheries mortality reference points, minimize population loss, and retain ecosystem services (Beverton and Holt 1957; Hilborn and Walters 1992; Worm et al. 2006). With advancing harvesting technologies, many fisheries worldwide are experiencing overexploitation and an alteration of aquatic ecosystems (Pauly et al. 1998; Worm et al. 2006). Fish hatcheries have sprung up to supplement declining wild stocks (Naish et al. 2007). Temporary moratoria or no-take reserves are being established to help fish stocks replenish (Hutchings and Myers 1994; Halpern 2003). Aquaculture is expanding to increase fish production (Naylor et al. 2000), and fishing pressure is now directed at previously nontargeted species at lower trophic levels (Pauly et al. 1998).

Along the way, unanticipated anomalies are accumulating as management targets for population recovery and productivity go unfulfilled. Halted exploitation does not necessarily lead to recovery of large body size and biomass in many populations, even where habitat loss had not occurred (Hutchings and Reynolds 2004; Swain 2011; Swain et al. 2011). Supplementation of declining populations with hatchery fish frequently does not demographically boost wild populations (Waples et al. 2007). Introductions of exploited species to vacant habitats only rarely generate the anticipated and desired new fisheries (Federenko and Shepherd 1986). Moreover, continued declines of wild populations strongly correlate with the increasing, geographically proximate production of their aquaculture counterparts, the very activity intended to offset fishing pressure on remaining wild fish (COSEWIC 2006; Ford and Myers 2008).

Certainly, such anomalies could be explained by a number of factors. Yet they cannot be easily understood without recognition that phenotypic and genetic variation within fish populations matters for ecology and that rapid, often human-induced evolutionary changes to phenotypes can have undesirable effects. Given increasing global change, it is a critical insight that rapid evolutionary change within species can elicit ecological change at higher levels of organization, sometimes equal to or exceeding that brought on by classic ecological effects (Fussmann et al. 2007; Bolnick et al. 2011; Palkovacs et al. 2012).

This paper reveals the emerging synthesis of evolution with ecology in fisheries science. It specifically shows that a greater infusion of evolutionary perspectives will help to achieve sustainable fisheries practices through improved and more biologically realistic modeling, monitoring, and management of populations, species, and aquatic ecosystems. By their very nature, fisheries activities can generate rapid changes to population abundance, density, and (or) mortality from harvesting, stocking, or aquaculture escapes. During such periods, evolutionary dynamics might strongly influence ecological dynamics and vice versa (Ellner et al. 2011).

The idea that merging evolutionary with ecological perspectives will aid fisheries management is not new. There have been repeated calls for such a synthesis (e.g., Law and Grey 1989;

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Browman 2000, and essays therein). But a flurry of empirical and modelling research activity in this area has occurred within the past 5–10 years, meriting a fuller perspective.

I first discuss the importance of phenotypic variation in fishes and the breadth of phenotypic change being elicited by fisheries and other human activities that can impact fishes. I then explore several critical questions regarding the ecological consequences of such evolutionary change. Does phenotypic change affect fish population growth rate, recovery, and (or) persistence? Does phenotypic change affect a species' productivity (yield)? Also, does phenotypic change affect community structure and ecosystem functioning? Addressing these questions reveals that feedbacks likely readily form between evolution and ecology. I therefore briefly consider under which circumstances such feedbacks might be of most conservation concern and whether or not these generate predictable outcomes across species and ecosystems. Throughout, I also consider the general implications of evolutionary perspectives for the sustainability of fisheries activities. These implications (*i*) bolster recent suggestions that evolutionary perspectives are of importance for achieving traditional, ecologically based management goals (e.g., Hutchings 2009; Hendry et al. 2011) but also (*ii*) raise questions about the meaning of sustainability.

The importance of phenotypic and genetic variation to fisheries

Phenotypic trait variation has long been recognized in fishes, including variation in morphology, size, age, colouration, behaviour, physiology, and phenological traits such as timing of migration and spawning (e.g., Ricker 1972; Iles and Sinclair 1982). Such variation is of prominent interest for evolutionary theory because it provides the raw material for natural selection. While ecological theory has long recognized that different age classes and sexes can have important ecological influences, substantial phenotypic variation exists within these classes. This variation is not accounted for in most current ecological models, including models quantifying population growth (Bolnick et al. 2011). Recent works, however, primarily on plants, have shown that such variation can have dramatic effects on population growth, population productivity, community stability, and ecosystem functioning (Reusch et al. 2005; Bailey et al. 2009).

A classic example of how phenotypic differentiation can enhance a fish species' productivity comes from sockeye salmon (*Oncorhynchus nerka*) in Bristol Bay, Alaska. Hundreds of phenotypically and genetically distinct populations contribute annually to that fishery's harvest (Hilborn et al. 2003). Using a series of simulations and data on catch and life history, Schindler et al. (2010) estimated that compared with a hypothetical conglomerate of Bristol Bay populations that behaves as a single, homogeneous population, the phenotypically rich, real-world diversity of populations led to a 2.2 times lower variability in annual returns and a 10-fold reduction in fishery closures. In other words, population diversity provides a "portfolio effect" (sensu Tilman 1996), wherein the complementary and (or) independent dynamics among populations that play similar ecological roles generate more temporary stable ecosystem services.

This example leads us to consider perhaps the longest-standing evolutionary principle in fisheries management that recognizes phenotypic variation: the stock concept. Like Bristol Bay sockeye, virtually all exploited fishes are composed of phenotypically and genetically distinct populations that are spatially and (or) temporally isolated from one another to varying degrees. Arguably, a main underpinning of the stock concept is that natural selection plays a predominant role in the phenotypic diversification with fish species by readily driving local adaptation (Taylor 1991; Conover et al. 2006). Support for this comes from several lines of evidence: (*i*) local individuals often outperform foreign ones in the local environment (Fraser et al. 2011); (*ii*) similar phenotypes have

routinely evolved independently across isolated fish populations, whether for migration timing (Waples et al. 2004), alternative life histories (Docker and Heath 2003), or trophic specializations (Gislason et al. 1999); and (*iii*) the failure of many restoration programs could be partly attributed to inadequate adaptive "matching" of translocated populations to new environments (Taylor 1991).

Management strategies aimed to minimize the loss of local adaptations within fishes in the short and long term are well-founded as the Bristol Bay sockeye example illustrated. Indeed, for conservation, local adaptations provide a clear example of direct value but also "option value". Humans might have little use for the local adaptation of population *X* today, but it might save the species, a fishery, or the aquaculture industry in the unforeseeable future; "to keep every cog and wheel is the first precaution of intelligent tinkering" (Leopold 1953).

A detailed examination of how phenotypic variation is determined in fishes is beyond the scope of this perspective, as it can involve genetic, epigenetic, plastic, or other nongenetic effects, or a combination thereof (see Naish and Hard 2008; Hendry et al. 2011). Research on fishes is indeed at the forefront of fully discerning such variation (Angers et al. 2010; Renaut et al. 2010; Jones et al. 2012) or tracking changes in such variation using molecular approaches (Jakobsdóttir et al. 2011; Hansen et al. 2012). What governs phenotypic variation is, nevertheless, critical for assessing and predicting responses to environmental or human-induced change. Overall, for several important reasons, many highlighted by Hendry et al. (2011), a consideration of the relationship between the genotype and phenotype should not detract from the importance of phenotypes when considering the ways in which fisheries activities elicit evolutionary change. First, selection acts directly on phenotypes with potential, indirect changes to the genotype. Second, phenotypic changes can elicit changes in population, community, and ecosystem dynamics. Third, phenotypes often have both genetic and nongenetic influences, which are difficult to disentangle using a strictly genotypic approach. Finally, genotypic "pathways" to adaptation **often** involve the effects of many genes of small to modest effect (see Jones et al. 2012 and Miller et al. 2012 for exceptions in fishes). So only a screening of very large numbers of genes will be sufficient to gauge **many** fish population responses to environmental change.

Phenotypic change and fisheries-related activities

Evidence is mounting that fishes can exhibit rapid and pronounced phenotypic responses to human-induced selective pressures imposed by a host of activities directly or indirectly associated with fisheries (Table 1). These changes extend to all aspects of phenotype (Table 1). Let us consider a few notable examples. Numerous studies have documented changes consistent with an evolutionary response to commercial or recreational fishing (e.g., Edeline et al. 2007; Biro and Post 2008; Philipp et al. 2009; but see Pukk et al. 2013) and captive breeding or hatchery supplementation (Araki et al. 2007; Christie et al. 2012; Milot et al. 2013). Phenotypic changes brought on by these activities can vary dramatically between males and females as well (Hutchings and Rowe 2008; Ford et al. 2012).

Evidence also exists that catch-and-release angling of large body-sized fish, an activity aimed at improving fisheries yields, might affect mating and reproductive success if the proportion of the adult population captured is large and if releases are conducted improperly (Richard et al. 2013). And then there is aquaculture, which through domestication and large-scale production, can lead to phenotypic or genetic change and multigenerational maladaptation in wild fish when large numbers of domesticates escape into nature and interbreeding ensues (McGinnity et al. 2003; Fraser et al. 2010*a*, 2010*b*).

Overall, it is clear that phenotypic changes induced by human activities can have substantial effects on individual fitness and

Table 1. Selected examples illustrating the plethora of rapid phenotypic and (or) genetic changes induced in wild fishes by a variety of human activities associated directly or indirectly with fisheries.

Activity	Phenotype	Specific phenotypic change	Reference
Fishing	Life history	Smaller size at maturity	Barot et al. 2004
		Earlier age at maturity	Olsen et al. 2004
		Slower growth	Swain et al. 2007
		Increased reproductive investment	Rijnsdorp et al. 2005
	Phenology	Earlier run-timing	Quinn et al. 2007
	Behaviour	Reduced aggression, parental care	Sutter et al. 2012
	Maternal effects	Contracted age structure and reduced reproductive rates	Venturelli et al. 2009
Aquaculture	Life history	Faster growth in farmed–wild hybrids	McGinnity et al. 2003
	Behaviour	Reduced antipredator responses in farmed–wild hybrids	Houde et al. 2010
	Phenology	Slower embryo developmental rates in farmed–wild hybrids	Fraser et al. 2010a
	Morphology	Shifts in body, head and caudal peduncle dimensions in farmed–wild hybrids	Fraser et al. 2010b
	Maternal effects	Changes to yolk reserves and early juvenile body size in farmed–wild hybrids	Debes et al. 2013
	Physiology	Reduced tolerance to naturally acidic pH in some farmed–wild hybrids	Fraser et al. 2008
Hatchery supplementation and captive breeding	Behaviour	Increased aggression	Fritts et al. 2007
		Reduced predation avoidance	Berejikian et al. 1996
		Inferior reproductive behaviour and reduced reproductive success	Fleming and Gross 1993
	Maternal effects	Reduced egg size	Heath et al. 2003
	Phenology	Earlier run-timing in hatchery fish or hatchery–wild hybrids	Seamons et al. 2012
Forestry	Life history	Increased expression of precocial male life history tactics	Gross 1991
Invasive species	Life history	Smaller size at maturity, increased reproductive output	Sharpe et al. 2012
Industrial waste releases	Physiology	Increased resistance to toxic contaminants	Wirgin et al. 2011
Hydroelectric and (or) impoundment dams	Life history	Older age at smoltification–migration	Williams et al. 2008
		Stabilizing selection for middle-sized trout	Haugen et al. 2008
	Morphology	Decreased body depth, increased caudal area	Franssen et al. 2013

reproductive success. Most researchers would not dispute this now, irrespective of the degree to which the phenotypic changes are truly genetic. Whether the evolutionary change elicited translates into appreciable consequences for ecology is another matter. Recent papers recommend that more research be directed at investigating the consequences of human-induced evolutionary change to fish population growth, persistence, productivity, and recovery (Hutchings and Fraser 2008; Kinnison et al. 2008; Enberg et al. 2009) and to community structure and ecosystem functioning (Palkovacs 2011; Laugen et al. 2013). So what research has explicitly investigated these issues?

The ecological consequences of evolutionary change in fishes

How might phenotypic change affect population growth rate, recovery, and (or) persistence?

Fish geneticists have regularly emphasized that evolutionary changes to individual fitness and reproductive success may affect population demography, typically without quantitative demonstration. Fish ecologists, conversely, have tended to discount that evolutionary changes to individual fitness and reproductive success alter population demography, without incorporating such changes in ecological modelling. More balance between these perspectives is needed. To understand how phenotypic change induced by fisheries-related activities might affect population growth and persistence, consider some of the ways that natural or human-induced selection can affect population dynamics.

First, in the absence of density dependence, natural selection can affect population size independently of factors related to local density (Saccheri and Hanski 2006). For example, sockeye salmon spawning in shallow streams are often smaller and shallower in body depth than salmon spawning in deeper, larger streams, in part owing to selection induced by bear predation in shallow streams (Carlson et al. 2011). A population with a "smaller–shallow" morphology is better adapted to a shallow stream than a population having a "larger–deeper" morphology, so it would

likely have a correspondingly higher carrying capacity in a shallow stream based on having higher birth rates and lower death rates.

Second, even if the strength of selection is density dependent, it can still affect population size and regulation. Suppose a population is characterized by having two phenotypes. Each phenotype might be differentially sensitive to its own density (Sinervo et al. 2000) or its predator's density (Yoshida et al. 2003) depending on environmental conditions and the life stage. This results in the population size or growth rate being either higher or lower relative to if the population was phenotypically homogeneous. As a possible example in fishes, Trinidadian guppy (*Poecilia reticulata*) phenotypes from high-predation stream stretches suffer disproportionately reduced individual fitness and survival under higher local densities than phenotypes from low-predation stream stretches, which likely alters population regulation (Bassar et al. 2013).

Third, whether density dependence is operating, selection can indirectly alter population dynamics by affecting phenotypic traits (including those influenced by maternal effects) that subsequently affect natural mortality. Notably, life history theory predicts an increase in the survival costs to reproduction as age and size at maturity decline (Roff 2002). This has been hypothesized to account for increased natural mortality observed in certain cod stocks following intensive exploitation and concomitant size-at-age reductions (Jørgensen and Holt 2013; but see Swain et al. 2011). Similarly, high selective mortality from fisheries that favours early maturation might, as a by-product, lead to earlier or more rapid senescence, higher natural mortality in older individuals, and reduced abundance and (or) recruitment (though alternative predictions exist; Swain et al. 2011).

Finally, through correlated genetic responses between traits, selection on one trait can affect other traits linked to survival at the same or different life stage (Hard 2004; Sutter et al. 2012) and perhaps alter population recruitment (Johnson et al. 2011). For instance, Walsh et al. (2006) proffer a compelling case that

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harvest-induced evolution towards smaller adult size is correlated with earlier maturation as well as reduced egg size, fecundity, larval growth, and larval viability. The result, they suggest, is that populations are stripped of the "normal" correlated trait expression needed for dealing with environmental change when fishing is absent. Thus, even when fishing ceases and food availability increases, population persistence and recovery are not guaranteed, or recovery might be considerably delayed, because harvest selection has diminished the very traits needed to convert energy into population growth (Walsh et al. 2006).

Does phenotypic change affect population growth rate, recovery, and (or) persistence?

Few empirical data or modelling efforts on fishes still exist that either support or refute the effects of phenotypic and (or) genetic change on population growth rate, recovery, and (or) persistence (Table 2). Nevertheless, available works suggest that responses might be highly variable and dependent on the degree of environmental change or local adaptation and the "time point" at which individual population trajectories are assessed (e.g., whether increasing or declining). These few works are probably an under-representation of conditions in which short-term evolutionary change might elicit population-level ecological change in fishes.

Typically, studies compare scenarios in which ecological change is estimated with and without consideration of evolution. For example, Kinnison et al. (2008) used colonizing Chinook salmon (*Oncorhynchus tshawytscha*) to explore how, as populations diverged and adapted to new environments, evolutionary changes to vital rates (reproductive output and survival) might affect population growth relative to simply the effect of habitat quality alone (the role of ecology). Indeed, irrespective of the habitat quality in the new environment, individuals colonizing those environments initially will not be locally adapted. But adaptive evolution in subsequent generations following colonization could result in a demographic boost to the new, expanding population. The authors found that after only 26 generations, adaptation to new environments might have mitigated a modest 12% to 29% of the "population growth costs" associated with colonizing new, differing habitat, although habitat quality itself accounted for much of the variation in vital rates.

Similarly, Weese et al. (2011) used Trinidadian guppy populations occupying divergent habitats to explore the role that local individuals (adapted) versus foreign migrants (maladapted) might play in local population recovery following a habitat disturbance (flooding). They specifically estimated the demographic cost of selection against foreign migrants to local population recovery by comparing population sizes under two scenarios: (*i*) when selection acted on recruits of foreign migrants versus (*ii*) when recruits of foreign migrants and remaining local individuals were assumed to have equal survival. In two consecutive years, the authors found that population sizes were 45% and 47% lower when accounting for selection on foreign migrants than when local and foreign individuals were assumed to have equal fitness. Such differences might be muted in natural settings; migrants were experimentally transferred as a random sample from their population, whereas dispersal is often nonrandom and migrants tend to match their phenotypes to the environments they disperse to (see Edelaar and Bolnick 2012). Nonetheless, the results illustrated how maladaptation of migrant recruits can put a substantial constraint or delay on local population recovery.

In another situation, Bowlby and Gibson (2011) used extensive data to demographically model how adaptation to captivity in endangered Atlantic salmon (*Salmo salar*) might affect population size trajectories and extinction risk when supplementing wild populations with captive individuals. The modeling was based on three realistic values of generational fitness loss in captivity (15%, 30%, and 45%; see Fraser 2008) and two plausible heritabilities (0.1, 0.3; see Carlson and Seamons 2008). The authors observed an

intriguing conservation conundrum. Under most scenarios, continuous supplementation had a net benefit of augmenting population size in the first four to six generations, after which the fitness loss in captivity overwhelmed these initial benefits and led to population declines (particularly under the 30% and 45% scenarios), presumably because of a decrease in the average individual fitness (Fig. 1A). Hence, in the immediate short term, fitness losses induced in captivity through phenotypic and genetic change did not increase extinction risk, but at the cost of potentially delaying or preventing longer-term population recovery (Fig. 1A).

More recently, Kuparinen and Hutchings (2012) modelled the evolutionary–ecological dynamics of 300 years of recovery of an Atlantic cod (*Gadus morhua*) population following a 100-year period of harvesting. Modelling was conducted under alternative scenarios where life histories evolved or did not evolve through size-selective harvesting (during or after the fishing period). The authors found that per capita population growth rates did not differ between scenarios despite dramatic selective regimes and life history differences between them. This was because the different evolved life histories had cumulatively similar lifetime reproductive outputs because of the flatness of the genotypic fitness function predicted by the model. Limited wild population data on unaccounted processes that can generate non-flat fitness functions precluded their inclusion in the modelling. Additionally, whether or not such flat fitness functions are more or less common with certain life history attributes (e.g., greater versus lesser longevity) is an open question (J.A. Hutchings, personal communication). It therefore cannot be ruled out that fisheries-induced evolutionary effects on population growth might be stronger on cod in nature or in other species.

Human-induced habitat fragmentation is an additional, underappreciated route affecting fish population persistence, through what one could term "evolutionary stochasticity" to distinguish it from demographic, environmental, or genetic stochasticity. For example, across a series of fragmented stream brook trout (*Salvelinus fontinalis*) populations, habitat varied more among small than large populations, suggesting that selective regimes underpinning phenotypic differentiation become more variable at smaller population size (J.L.A. Wood and D.J. Fraser, unpublished data). An untested but plausible possibility then is that population responses to environmental change, and ultimately the probability of persistence, become more variable as habitat is fragmented and population sizes are reduced. Such "evolutionary stochasticity" could occur even if small populations are unaffected by demographic or environmentally stochastic events. While selection becomes less effective in small populations as genetic drift becomes more important, this would only be expected to affect the overall implication here in the very smallest populations (see Koskinen et al. 2002; Willi et al. 2006). In short, we know little about how the fragmentation process changes environmental selective regimes of fishes and what the consequences are to the evolution of mating systems, reproductive success, and population viability.

Lastly, a shorter generation length (*G*) is an inevitable consequence of selection towards the earlier maturation that is commonly induced by fisheries mortality and accentuated by selective harvest of older, larger individuals. Shorter *G* might have several implications for demography. It allows species to respond more quickly to selective pressures, whether these are deemed desirable or undesirable by humans. It may also mean species interact within their ecosystems differently (e.g., foraging). Conversely, as shorter *G* results in more generations elapsed per fixed time period, small populations with low *G* might more rapidly lose genetic diversity or experience inbreeding effects than those with large *G*.

Table 2. Estimated percentage shifts in classic ecological parameters in fish or other aquatic species when both ecological and evolutionary changes were incorporated (Evol+Ecol), relative to when evolutionary changes were ignored, at population (POP), community (COMM), and ecosystem (ECO) levels.

Level	Study	Species	Evolutionary change	Ecological parameter	Evol+Ecol	Reference
POP	E	Chinook salmon	Adaptation to a new environment	Population vital rates	12%–29% (4)	Kinnison et al. 2008
	E	Trinidadian guppy	Selection against immigrants	Population size	45%–47% (2)	Weese et al. 2011
	M	Atlantic salmon	Adaptation to captivity	Population size	40%–100% (6)[a]	Bowlby and Gibson 2011
	Ex	Freshwater rotifer (*Brachionus calyciflorus*)	Life history evolution (sexual versus asexual reproduction)	Population size	23%–28% (4)[b]	Data from Fussmann et al. 2003; re-analysis by Ellner et al. 2011
	M	Atlantic cod	Fisheries-induced reductions in age- and size-at-maturity	Population growth rate	6% (1)[c]	Kuparinen and Hutchings 2012
COMM	Ex	Alewife	Evolution of anadromous versus nonanadromous forms)	Invertebrate size, density, and abundance	85%–145% (5)[d]	Palkovacs and Post 2009
COMM–ECO	Ex	Trinidadian guppy	Indirect effects resulting from the evolution of high versus low predation phenotypes	Community and ecosystem parameters	18%–1000% (14, of which seven Evol+Ecol values exceeded 100%)[e]	Data from Bassar et al. 2010; re-analysis by Ellner et al. 2011
	Ex	Threespine stickleback (*Gasterosteus aculeatus*)	Evolution of limnetic versus benthic forms	6 measures of DOC, light transmission and chlorophyll *a*; 12 measures of species composition[g]	1.3%–3943% (18, of which eight Evol+Ecol values exceeded 100%)[f]	Harmon et al. 2009
ECO	E	Sockeye salmon	Selective (size-dependent) mortality by bears	Potential nutrient flux from salmon carcasses	0%–11% (10)	Carlson et al. 2011

Note: Evol+Ecol values are reported as ranges (numbers of estimates in parentheses) and can be either positive or negative. Study: E, experimental (in nature); Ex, experimental (laboratory or mesocosm); M, modeling.

[a]Based on predicted egg deposition under three fitness reduction scenarios, two heritabilities, and four to six generations of captive breeding.

[b]Based on four replicate predator–prey laboratory experiments.

[c]Calculated as the time difference to a population growth rate equilibrium following the cessation of fishing, between a scenario of no life history evolution versus evolution towards reduced age- and size-at-maturity.

[d]Approximated digitally from figures by comparing the effect size of alewife trait change (anadromous versus nonanadromous form) relative to the absence or presence of alewife.

[e]Approximated through converting values of Evol/(Evol+Ecol) from Ellner et al. (2011).

[f]Calculated digitally from figures for the "species pair" (benthic + limnetic) treatment relative to the "generalist treatment".

[g]Calculated for the "species pair" (benthic + limnetic) relative to "generalist treatment" for invertebrate species with nonzero values in both treatments.

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Fig. 1. Examples of how human-induced evolutionary change from various fisheries activities might affect population recovery and yield. (A) Trade-offs with supplementing depleted wild populations with captive-reared individuals. Under an ecological-only model, egg deposition of an endangered Atlantic salmon is predicted to increase steadily for several generations (one generation ≈ 4 years) following captive rearing and supplementation of juveniles. Under ecological–evolutionary models accounting for a realistic 15%–30% generational fitness loss arising from captive rearing, egg deposition increases steadily (though by not as much) and then declines following supplementation over several generations. (Reprinted and modified from Bowlby and Gibson (2011) with permission from The Ecological Society of America, copyright 2011, The Ecological Society of America.) (B) Lack of recovery in fisheries yield following fisheries-induced evolution. Shown is the abundance of Atlantic cod aged 4 and older in the Gulf of St. Lawrence, Canada, changes to the mean length at age 6 years following a multidecadal period of exploitation, and a lack of complete rebound in length at age 6 years or in species biomass after more than a decade of fishing (the dashed, vertical line is 1993, the year after which very little fishing occurred). (Reprinted and modified from Swain et al. (2007) with permission from The Royal Society, copyright 2007, The Royal Society.)
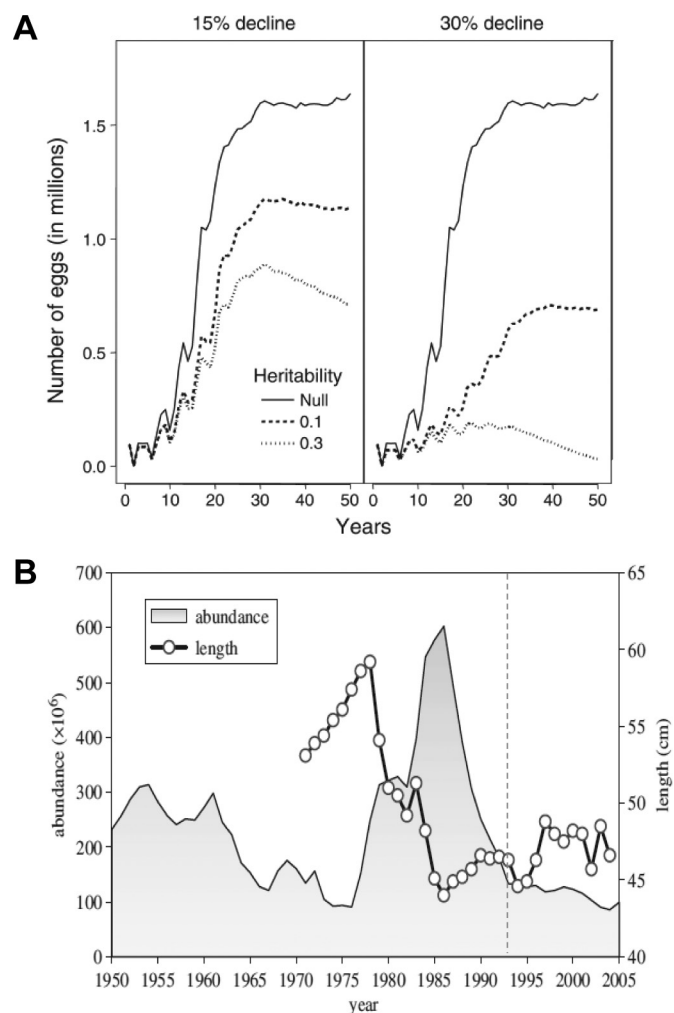
Does phenotypic change affect a species' productivity (yield)?

This question is inseparably linked to the previous one because whatever factors influence population growth might also affect species biomass to some degree. In Conover and Munch's (2002) well-known laboratory experiment on adult Atlantic silverside (*Menidia menidia*), six replicate populations derived from the same gene pool were reared under three treatments. Every generation for four generations, treatments were subjected to a harvest regime wherein 90% of the largest, smallest, and randomly sampled fish were removed. Consistent with the hypothesis that size-selective mortality and resulting evolutionary change could result in reduced productivity, treatments where the largest fish were removed showed the slowest growth rate and had the lowest yields after four generations. However, the work was criticized for not representing what happens in complex, natural ecosystems. First, it did not account for the shift toward faster growth that can occur in the remaining, nonharvested fish when fishing rates are high (Hilborn 2006), presumably because of reduced intraspecific competition. Second, meta-analyses have found equivocal support for a reduction in size-at-age being associated with fishing intensity (Hilborn and Minte-Vera 2008; Sharpe and Hendry 2009). Moreover, the mode and intensity of selection of commercial fishing gear is rarely as severe as in the silverside experiment (Hilborn and Minte-Vera 2008; Kendall and Quinn 2012). In fact, these might also change over time or be disruptive rather than directional, reducing the overall directional effects of size-selective harvesting (Kendall and Quinn 2012).

Experimental research on populations in nature with proper controls has not been conducted to formally test the "reduced productivity via genetic change" hypothesis. Yet temporal trends in size-at-age and abundance observed in some collapsed fish populations that have failed to recover after long-term cessation of fishing suggest this as a legitimate possibility (Hutchings and Reynolds 2004). In Gulf of St. Lawrence Atlantic cod (Fig. 1B), for instance, Swain et al. (2007) found a positive correlation between the change in mean length of 4-year-old cod offspring relative to their parents and the selection differentials experienced by parents from this age to spawning. Importantly, this relationship was observed after controlling for the effects of density- and temperature-dependent growth. Such presumably genetic changes to growth were hypothesized to account for the continued small size-at-age in the population and a lack of complete rebound in overall species biomass, despite good conditions for growth and very low fishing mortality for over a decade (Swain et al. 2007; Fig. 1B).

Another compelling argument that human-induced evolution might reduce fishery yields comes from activities affecting species with alternative life history tactics. Many salmonid populations, for instance, are composed of anadromous and nonanadromous individuals. Expression of either life history is associated with a threshold body size and influenced by both genetic and plastic effects (Theriault et al. 2008; Piché et al. 2008). The much larger migratory anadromous individuals are of primary interest for fisheries harvesting. The nonanadromous individuals are often too small to harvest at all. Human activities often directly select against anadromous individuals, favouring a shift towards an increased probability of expressing the nonanadromous life history. For example, fisheries harvesting in the ocean or spawning migration increases mortality of anadromous individuals (Theriault et al. 2008). Furthermore, dam construction, which prevents migration or makes it challenging, might either increase mortality or decrease reproductive success of anadromous fish. Both activities also indirectly favour the nonanadromous life history; the reduced population size of anadromous individuals decreases mating competition among nonanadromous individuals where the two exhibit alterative mating tactics (Gross 1991). Under such circumstances, **total population size** of the two life histories might actually remain stable or even increase as **total harvestable biomass** of the anadromous component decreases for some time.

As will be discussed below, human-induced phenotypic change might not actually directly affect population productivity per se.

Fig. 2. Illustration of fisheries-induced trophic cascades under the "classic" ecological-only model versus an ecological–evolutionary one. In the classic trophic cascade, large piscivore depletion results in an increase of zooplantivorous prey, which in turn crop down the zooplankton biomass, resulting in an algal biomass increase. In the ecological–evolutionary cascade, the classic cascade is amplified at each trophic level because of phenotypic change initiated by fishing. In the example given, depletion of large piscivores results in phenotypic change (*i*) towards smaller body size and age-at-maturity in the piscivore and (*ii*) towards more competitive phenotypes in the zooplanktivorous prey. The latter is brought on by the relaxation of predator selective pressures and by the increase in prey density (solid black fish). This phenotypic change then amplifies the cropping down of zooplankton biomass, which thereby results in even greater increases in algal biomass. The increase in algal biomass is potentially further amplified by elevated nutrient availability provided by the remaining piscivores, which now have higher excretion rates due to their smaller size (see the main text). Following cessation of fishing, full recovery of piscivore size or biomass is not necessarily achieved or is delayed, due in part to natural selection on piscivore size being less intense than fisheries selection and perhaps bottom-up feedbacks. In reality, additional factors (both ecological and evolutionary) will generate an array of cascading effects, but the main point is that evolutionary changes can be substantial. Additional amplification of trophic cascades may arise if phenotypic change occurs in the zooplankton and algae as well.
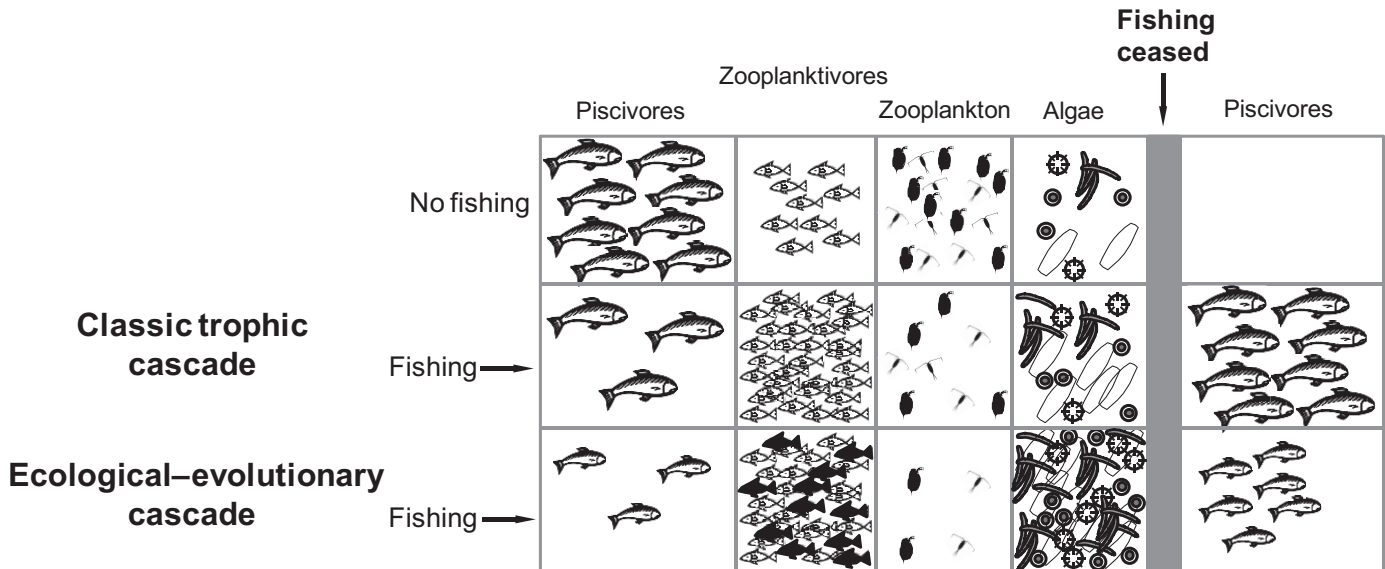
Rather, when we elicit phenotypic shifts within populations, we might trigger, directly or indirectly, feedbacks between evolution and ecology that can cascade through entire ecosystems (Palkovacs 2011; Walsh 2013). Such reshaping of the trophic cascades themselves in turn might diminish the harvestable populations of interest or generate other effects (Fig. 2).

Does phenotypic change elicit community structure and ecosystem change?

Human-induced phenotypic change related to fisheries activities can also diversely affect community structure and ecosystem function. Similar to the population level, the extent of ecological change at community or ecosystem levels is highly variable across different contexts (Table 2). Intriguingly, changes at the community and ecosystem level might often exceed those at the population level (Table 2). Perhaps community and ecosystem changes are more readily detectable; they reflect cumulative, indirect, and direct effects across different trophic levels. One can surmise that the most prominent effects will be manifested where one or a few impacted fish species play key roles in affecting species interactions and ecosystem processes; diverse fishes play these roles, including Pacific salmon (*Oncorhynchus* spp.), Atlantic cod, and certain freshwater species (e.g., flannelmouth characin, *Prochilodus mariae*), and so freshwater, marine, and estuarine ecosystems might all be affected (see Goeden 1982; Taylor et al. 2006; Palkovacs et al. 2012). One might also hypothesize that human-induced phenotypic change will have more pronounced effects in simpler communities and ecosystems than more complex ones. Known, direct, and indirect consequences include changes to food webs, trophic cascades, competitive interactions, nutrient cycling, and subsidies.

Size-selective harvesting is particularly likely to transform trophic interactions and food webs (Swain and Sinclair 2000; Walters and Kitchell 2001). Indeed, freshwater and marine fishes often occupy middle or upper trophic levels, so changes in their body size will result in altered trophic dynamics (Palkovacs 2011). A good example comes from the Western Scotian Shelf ecosystem in eastern Canada. Over 38 years, despite intensive harvesting contributing to a 60% reduction in body size of major predators in the system (e.g., Atlantic cod), overall predator biomass remained stable, but prey biomass increased by 300% (Shackell et al. 2010). Thus, population-level phenotypic changes can lead to trophic cascades and result in severe, direct alterations to trophic interactions.

Size-selective harvesting also has important, indirect effects; overexploitation of top predators can result in changes to predation selective regimes in their prey (Fig. 2). In this context, Palkovacs (2011) revealed the clear importance of feedbacks between ecology and evolution for fisheries science. Increases in prey densities following predator removal should result in evolution favouring phenotypes that confer competitive ability as opposed to antipredator responses (Palkovacs et al. 2009, 2011). In turn, these shifts can increase per capita effects of prey on their own resources, amplifying the trophic cascade brought on by the removal of predation (Fig. 2; Palkovacs et al. 2009, 2011; Walsh et al. 2012).

Ecological changes brought on by size-selective harvesting likely extend beyond trophic interactions; fishes play important roles in nutrient cycling (Vanni 2002), and nutrient excretion rates might also increase enough to impact nutrient availability and primary production (Palkovacs et al. 2012). That is, smaller,

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earlier maturing fish have higher excretion rates and at lower nitrogen or phosphorus availability than larger fish (Hall et al. 2007; Palkovacs et al. 2009). The resulting (and as yet untested) prediction would be that at equal biomasses, exploited populations that have evolved smaller body sizes should excrete higher rates of nutrients than unexploited populations (Palkovacs et al. 2012).

Other phenotypic changes might also indirectly elicit community or ecosystem change, with impacts on fisheries. As discussed above, the regular establishment of dams disproportionately favours nonanadromy in species with anadromous and nonanadromous life histories, reducing the harvestable anadromous component. Those anadromous individuals would have also provided important marine-derived nutrient subsidies to freshwater environments, a loss that can alter primary productivity and energy flow in food webs (cf. Palkovacs et al. 2012; see Schindler et al. 2003). Shifts to nonanadromy under the same scenario are also thought to affect food web interactions through changes in trophic-related phenotypic traits. For example, a shift from anadromy to nonanadromy in planktivorous alewife (*Alosa pseudoharengus*) leads to community-level changes in zooplankton and resulting changes to phytoplankton abundance (Post et al. 2008). The overall ecological effects of this life history shift can be larger than those caused by the removal of alewife (Table 2). In essence then, human-driven phenotypic changes within a species can have ecological effects equal to those of human-induced extinctions (Palkovacs and Post 2009; Palkovacs et al. 2012).

Recurrent, intentional, or unintentional releases of millions and billions of hatchery-reared or aquaculture fishes are another widespread phenomenon, such that these individuals often far outnumber remaining wild conspecifics (Naish et al. 2007; Morris et al. 2008; Jensen et al. 2010). Their potential phenotypic and (or) genetic homogenizing effects on wild conspecifics have received extensive recent attention (McGinnity et al. 2003; Araki et al. 2007; Laikre et al. 2010). Most of these works, however, have not considered other possible ecological–evolutionary effects on communities and ecosystems of releasing large numbers of typically monocultured fishes in nature. Such homogenization of wild species might plausibly elicit new selective responses, with unknown ecological consequences that could diminish community stability, weaken portfolio effects of intraspecific biodiversity, alter predator functional responses, modify host–parasite dynamics, and (or) shift intraspecific or interspecific competition regimes.

Finally, phenotypic changes induced by climate change might also affect community structure and ecosystem function in ways that affect fisheries. For instance, the productivity of many fisheries is dependent on the seasonal timing of events associated with resource availability of prey species that are frequently keystone species. In Pacific salmon, plastic and evolutionary changes to breeding migration phenology due to climate warming might have concomitant impacts on the ecology and productivity of numerous species dependent on the seasonal availability of these species (Kovach et al. 2013).

Feedbacks between ecological and evolutionary change

We have known for a while that ecology affects the evolution of fish populations and species (e.g., Hendry and Stearns 2004 and references therein). It is increasingly accepted that evolution affects fish ecology (Hindar et al. 2006; Bassar et al. 2010). Preceding sections raise the possibility that fisheries-related activities might then elicit feedbacks between ecological and evolutionary change. Such feedbacks arise undoubtedly through many pathways and are perhaps most closely coupled under extreme human-induced environmental change. At the population level, for instance, as long as an ecological factor (abiotic or biotic) leads to an effect on individual fitness via a change in phenotype, that phenotype, if influenced in part by genes (as is usually the case), can alter population dynamics, which in turn can favour certain phenotypes over others, which can loop back to affect individual fitness. Similar feedback loops could be envisaged at community or ecosystem levels between competitively interacting species or between a harvested top-predator and its prey as discussed above.

Empirical demonstrations of ecological–evolutionary feedbacks require detailed multigenerational research and hence are, as yet, few. In aquatic organisms, Becks et al. (2012) used rotifer (predator) – alga (prey) mesocosms to show that cyclical changes in rotifer abundance resulted in fluctuating selection for a heritable defense trait in the alga (cell clumping). Predator population growth was affected more by prey evolution than by prey ecology (changes in abundance); the feedback was completed when changes to predator abundance subsequently generated further prey evolution. The authors also studied gene expression changes in the prey associated with the predator–prey cycle. Interestingly, similar defense phenotypes in consecutive cycles were produced by at least several different gene transcription pathways (Becks et al. 2012); such nonparallel genetic bases for the same phenotypes are also observed in many fishes (Elmer and Meyer 2011).

Only with additional research will we know the extent to which ecological–evolutionary feedbacks elicited by human activities yield predictable outcomes at various levels (population, community, ecosystem) and what their full consequences are for fishes. Nonetheless, by applying the precautionary principle and classical evolutionary (Travisano et al. 1995) and ecological theory (Paine et al. 1998), we can surmise that ecological–evolutionary feedbacks related to fisheries activities will generate some surprises. For example, reversal to a previously occupied state, such as large size-at-age following overexploitation, or "purging" of maladaptation due to interbreeding between wild and captive-bred fish, is anticipated to be slower in nature than the human activity eliciting the change in the first place (Fleming et al. 2000; Conover et al. 2009). This is because human activities can generate especially strong selective pressures relative to natural selective pressures (Law and Grey 1989; Darimont et al. 2009).

Reversal might also not happen at all; the stochastic nature of evolution cannot be dismissed. Even if broad environmental changes imposed on populations are similar (climate warming, overexploitation), we must not forget the importance of evolutionary history. Fish populations and communities rarely have the same "starting conditions" within their ecosystems. Phylogenetic constraints might influence the outcomes of fisheries-induced ecological–evolutionary feedbacks on different species and ecosystems, so the outcomes may not be convergent. These outcomes might also depend on the degree to which freshwater or marine ecosystem food web structure and function is bottom-up versus top-down controlled. Furthermore, they might depend on the extent to which asymmetries in interspecies interactions are generated (Thompson 1998) when different phenotypic changes are elicited (e.g., behavioural versus morphological versus life history). Similarly, the outcomes might depend on the nature of the human activity. Commercial netting and recreational hook-and-line fishing, for instance, do not necessarily target the same suite of traits associated with body size or, more generally, harvesting vulnerability (Sutter et al. 2012; Laugen et al. 2013). Different net gears also generate different selective responses (Hutchings 2009; Laugen et al. 2013). In short, in our search for a mechanistic understanding of feedbacks between evolution and ecology in fisheries science, it seems prudent to expect the unexpected.

Evolution with ecology in practical management

As long as fisheries activities elicit only subtle environmental change, evolutionary change might not be a major problem for fisheries management, at least in the short term. But fisheries activities take, tinker, and transform in ways that fishes did not

naturally evolve to deal with over the millennia. Rapid episodes of environmental and demographic change are inevitable in many instances and will be undoubtedly compounded by global climate change. Evolutionary changes that influence ecological dynamics are here to stay. Key challenges include deciphering (*i*) when evolutionary changes generate undesirable, beneficial, or no ecological effects; (*ii*) the degree to which phenotypic and genetic variation within different fish species is malleable to change without compromising both evolutionary and ecological integrity; and (*iii*) whether the fine-tuning of feedbacks between evolution and ecology on short time scales is critical for community or ecosystem dynamics and stability.

Many strategies for managing evolutionary change are complementary to conventional, ecological management objectives, including maximizing yields, minimizing population losses, setting fisheries mortality reference points, reducing catch variability, retaining average catch size, and retaining ecosystem services. Managing evolutionary change therefore helps to ensure that the socio-economic and cultural benefits of fishes are accrued. Minimizing undesirable phenotypic changes induced by fisheries- or hatchery-induced selection are good examples (Fraser 2008; Laugen et al. 2013). So too is minimizing gene flow between farmed and wild fishes by minimizing farmed escapes into nature or limiting farming to regions without wild population strongholds (Naylor et al. 2005; Hutchings and Fraser 2008). In other cases, selection or gene flow could be increased to achieve similar goals. For instance, strongly directional selection for trait values optimal for the farm environment in theory makes farmed fishes completely maladapted to nature to prevent farmed–wild interbreeding (Hindar et al. 2006; Baskett and Waples 2013). Similarly, increasing gene flow in very small newly depleted fish populations can increase new genetic material to bolster recruitment and overcome inbreeding depression (Houde et al. 2011). Additionally, in species restoration programs where extirpation causes are unknown, hybridizing introduced populations provides natural selection with more options to generate self-sustaining populations (Krueger et al. 1981).

The reality, though, is that simple prescriptions and yardsticks will not be universally applicable because of complexities associated with the evolution and ecology of different fish species and communities and the nature or extent of different fisheries-related activities. Moreover, some strategies aimed at managing evolutionary change conflict with conventional objectives of fisheries management. For example, at least in the short term, protecting large fish to avoid undesirable reductions in size- and age-at-maturation can result in a loss of yield (Mollet 2010). In addition, some applied evolutionary perspectives themselves might conflict with one another. As discussed, conservation of population phenotypic differentiation resulting from local adaptation is a key long-term management goal (Schindler et al. 2010). Yet these frequent targets of conservation (populations with divergent phenotypes) are constantly evolving, and their distinctiveness can be altered rapidly with short-term, environmental or human-induced change (Williams et al. 2008). How to effectively balance long- and short-term goals associated with maintaining both inter- and intra-population variation warrants further discussion.

Much modeling into ecological–evolutionary dynamics of fish populations is emerging. This includes blending of quantitative genetic change and (or) selection differentials with size and (or) age structure demographic assessments towards improving (*i*) captive breeding (Bowlby and Gibson 2011); (*ii*) hatchery supplementation (Satake and Araki 2012; Baskett and Waples 2013); (*iii*) forecasts of spatial fishing allocation and effects of different fishing gear (Hutchings 2009; Jørgensen et al. 2009; Dunlop et al. 2009a); (*iv*) forecasts of the rate of fisheries-induced evolution and potential viability effects (Kuparinen and Hutchings 2012; Audzijonyte et al. 2013); (*v*) forecasts of the effects of escaped farmed fishes on wild conspecifics (Hindar et al. 2006; Huisman and Tufto 2012); (*vi*) marine reserve design (Dunlop et al. 2009b); (*vii*) the socio-economic costs of evolutionary change in fisheries (Enberg et al. 2009); and (*viii*) formalized evolutionary impact assessments in relation to harvesting (Laugen et al. 2013). Certainly, in addition to further empirical insights, more such modeling is needed, particularly for considering the direct and indirect effects of intraspecific phenotypic change to community and ecosystem dynamics.

In many situations, the benefits of achieving a closer approximation to biological reality afforded by incorporating evolution into ecological modeling should outweigh the costs of greater model complexity demands. It should also be expected that in some situations, a closer approximation to biological reality might mean that the explicitly acknowledged uncertainty increases. But among other things, evolutionary–ecological modeling has already taught us that limit or target reference points in fisheries can be biased, and increasingly biased over time, if assessments ignore evolutionary change (Hutchings 2009; Enberg et al. 2009). It has also shown us that lowering exploitation rates is the best way to reduce undesirable harvesting-induced evolution and associated ecological effects (Kuparinen et al. 2012), though in of itself, this might be insufficient for population recovery (Hutchings and Reynolds 2004).

In summary, combined ecological–evolutionary perspectives hold great promise to improve the monitoring, rebuilding, and management of fish populations, fish species, and aquatic ecosystems. Fisheries overexploitation results in more than just altered trophic cascades and mined down food webs. It, and the activities it directly or indirectly spawns (e.g., aquaculture, hatchery production), leads to evolutionary changes to life itself and a blurring of what is natural and unnatural. Some changes might be irreversible and as important in affecting human well-being as that most serious of irreversible processes — extinction. And so combined ecological–evolutionary thinking might even change human perceptions regarding what a sustainable fishery is and the full biological consequences of our activities.

Will future fisheries management take evolution more seriously?

Given the important implications of synthesizing evolutionary with ecological perspectives for fisheries management, why have most managers not taken evolutionary change more seriously? To be fair, concerns about evolutionary responses of fish populations have translated into direct management changes for some specific activities, such as hatchery–captive propagation strategies, but not for many others. Several nonmutually exclusive explanations could account for this. One is that evolutionary change might still be perceived as something occurring too gradually to be of relevance to management time scales. Evolutionary change may also be viewed as having little effect on yield, recruitment, or community or ecosystem dynamics. Furthermore, assessing and monitoring evolutionary change is not always straightforward, and its outcomes can be highly variable. To a lesser degree, justifying to the public any management decisions based on evolutionary change may be difficult if a considerable proportion of resource users do not believe in evolution.

Advancement of the integration of evolutionary with ecological perspectives will therefore demand (*i*) more published research demonstrating that evolutionary changes induced by fisheries activities have direct consequences (positive or negative) to yield, catch variability, and population recovery or persistence; (*ii*) a stronger prominence of such published work in major media; and (*iii*) the development of user-friendly approaches for incorporating ecological–evolutionary perspectives into risk assessments, stock assessments, and management decision-making.

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Acknowledgements

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