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Toward Darwinian fisheries management

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Toward Darwinian Fisheries Management

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Introduction

When Charles Darwin made his argument that life was evolving he began by showing the potency of artificial selection to modify domesticated species, and how quickly animal breeders were able to create new varieties — he cited examples of talented farmers who created new races of livestock within their own lifetime (Darwin 1859). That fishing could act similarly was, to our knowledge, first mentioned in the scientific literature in 1902, when Cloudsley Rutter wrote: "A large fish is worth more on the markets than a small fish; but so are large cattle worth more on the market than small cattle, yet a stock-raiser would never think of selling his fine cattle and keeping only the runts to breed from. (…) The salmon will certainly deteriorate in size if the medium and larger sizes are taken for the markets and only the smaller with a few of the medium allowed to breed" (Rutter 1902). Thereafter, it took almost a century before these patterns were clearly identified in data, sparked by Ricker's (1981) study of declining sizes of Pacific salmon *Oncorhynchus* spp. returning to spawn; patterns he could not explain by any concurrent environmental trend but that were consistent with evolutionary change driven by the size-selective fishery.

Fisheries-induced evolution has experienced a surge in publications over the last decade (for reviews see Jørgensen et al. 2007; Kuparinen and Merilä 2007; Allendorf et al. 2008; Hutchings and Fraser 2008). Many of the purported findings have been lively debated. Some contentious issues have been the relative role and importance of evolution when there have been simultaneous ecological changes (Browman et al. 2008; Jørgensen et al. 2008b), limitations to field evidence for evolving life-history traits because of strong physiological and environmental influences (Dieckmann and Heino 2007; Marshall and Browman 2007; Heino et al. 2008; Swain et al. 2008), whether the strong selection applied in experiments can shed light on evolutionary processes in the wild (Hilborn 2006, 2007a; Conover and Munch 2007; Brown et al. 2008), and whether observed phenotypic change can be attributed to evolution when no parallel changes in gene frequencies have been reported (Jørgensen et al. 2008b; Kuparinen and Merilä 2008; Merilä 2009). At the core of these controversies is accounting for environmental influences that act on wild fish stocks, because environmental trends also have a potential to cause directed phenotypic changes over time.

Many of the traits expected to change due to fisheries-induced evolution could have large consequences for individual reproductive output, recruitment, population dynamics, and fisheries yield (Law and Grey 1989; Heino 1998; Walsh et al. 2006; Jørgensen et al. 2007). In parallel with finding out exactly how much total phenotypic change is due to environmental change and how much is due to evolution, it is pertinent that one constructively begins asking the question: Given that fisheries-induced evolution is taking place at decadal time-scales, how might it be necessary to adjust fisheries management to mitigate any potential negative effects of such evolutionary change? This is by no means a trivial academic exercise, as one needs to quantify how anthropogenic selection pressures influence harvested resources and their ecosystems, how this interplays with natural selection, and how ecological feedbacks and other environmental processes may confound the picture or alter the outcome.

To discuss evolutionary dimensions of fisheries management in the wider context of fisheries science, a symposium was organized at the 2008 American Fisheries Society Annual Meeting in Ottawa, Canada. Four keynote speakers were invited to spark the debate: Ulf Dieckmann summarized theoretical tools and achievements, David Conover reviewed the role of experiments, Mikko Heino discussed strengths and weaknesses of the evidence that can be derived from wild stocks, and Jeffrey Hutchings drew implications for practical fisheries management. Within these topics discussed by the keynote speakers, other researchers presented their work, and it is from this symposium that this special issue derives.

Acknowledging that current fisheries science is just embarking on such a daunting task, we have chosen the name *Toward Darwinian Fisheries Management* for this special issue. For this name we are indebted to David Conover (2000), who, in a theme section edited by Howard Browman (2000), called for Darwinan fishery science by the inclusion of evolutionary methods and considerations in the standard fisheries toolbox. He concluded that "ultimately the success of fishery management may be judged not by the catch achieved in any given year or decade, but by whether it was sustained across future generations." Adopting this aim, the current issue of *Evolutionary Applications* spans across new empirical investigations of fisheries-induced evolution in wild populations and controlled experiments, developments of theoretical and experimental methodology to strengthen the interpretation of field data, and applications of models to answer life-history questions and for testing management alternatives. The broad scope of these papers reflects that successful Darwinian management needs to recruit efforts all the way from the research vessels and laboratories of basic science to the hectic schedules of fisheries managers, and will ultimately rely on an active dialogue with stakeholders in the fishing industry and the public at large (Jørgensen et al. 2007).

Empirical field evidence

Most evidence suggesting fisheries-induced evolution is based on life-history traits. Indications of widespread changes in life-history traits of exploited fish started to become apparent in the 1970s. By the mid-1990s, it had become established that trends toward earlier maturation were commonplace (Beacham 1987; Smith 1994; Trippel 1995). Similarly, studies of fisheries-induced changes in growth got an early start through Handford's (1977) work on lake whitefish *Coregonus clupeaformis* and Ricker's (1981) seminal work on Pacific salmon, although the field then remained relatively dormant until David Conover and colleagues (e.g., Conover and Munch 2002) started to publish their experiments of harvest-induced growth evolution. That growth and maturation have been the focus of research is no coincidence. Regarding maturation, the observed broad-scale pattern matched theoretical expectations for life-history adaptations to increased mortality (Law and Grey 1989; Roff 1992), although assessing alternative or complementary explanations was an almost insurmountable problem that continues to be debated today. For growth, appealing verbal hypotheses were easy to formulate (starting from Rutter 1902) and were supported by Ricker's (1981) empirical findings, although a comprehensive theoretical understanding is still missing. A very practical reason that maturation and growth have received so much attention is the availability of time series data on commercial species, collected by research and management agencies, which have made it possible to compare phenotypic changes across time and between stocks.

The evolution toward earlier maturation when fishing inflicts elevated mortality is driven by reduced longevity - future reproduction becomes uncertain and, in stead of investing in growth to acquire a larger body size, evolution favors individuals that invest resources in offspring earlier in life. Most recent studies examining potential evolutionary trends in maturation have focused on probabilistic maturation reaction norms (Heino et al. 2002; reviewed in Dieckmann and Heino 2007; see also the online supplementary material to Jørgensen et al. 2007). Like any metric based on phenotypic data, probabilistic maturation reaction norms (PMRNs) have their strengths and weaknesses when it comes to inferring evolution of the underlying genotype (Dieckmann and Heino 2007; Marshall and Browman 2007). PMRNs target the process of maturation rather than the state of being mature. This allows the removal of much of the variation stemming from growth, which can significantly confound observed changes in the age and size at which individuals mature (Heino et al. 2002).

There is controversy and debate in the use of PMRNs to infer evolutionary change, mainly because the estimation of PMRNs relies on phenotypic data, which are influenced by changes in the environment (Marshall and Browman 2007). Recent PMRN studies have placed a stronger emphasis on quantifying environmental influences and other factors (e.g., Grift et al. 2003, 2007; Kraak 2007; Mollet et al. 2007). As long as adequate data exist, the reaction norm estimation can be extended by an extra dimension for each environmental variable, thus directly accounting for the effect of that environmental factor on the probability of becoming mature. Kraak (2007) did so for plaice *Pleuronectes platessa* by including the effect of temperature, and concluded that although temperature could explain some of the observed change, a residual trend still suggested evolution of the maturation schedule. Alternatively, one can add as a third dimension an individual state that better reflects more rapid environmental fluctuations: for example, condition factor responds to both temperature and changes in feeding conditions and is thus an obvious candidate. In plaice (Grift et al. 2007) and sole *Solea solea* (Mollet et al. 2007) changes in condition explained some of the temporal change in maturation, but even after accounting for this change there was still a remaining temporal trend in the PMRNs suggestive of maturation evolution. Even though environmental variables can be included in this way it remains a challenge to account for the full suite of variables that could potentially influence maturation. However, when assessing the evidence as a whole, the majority of studies have shown remarkable similarities in the direction of change in PMRNs (Heino and Dieckmann 2008).

When expected life span declines, future reproduction is traded off in favor of current reproduction. This is expected to be manifested, in addition to timing of maturation mentioned above, as increased reproductive investment. Higher fecundity at size as has been recorded in Atlantic cod *Gadus morhua* (Yoneda and Wright 2004), haddock *Melanogrammus aeglefinus* (Wright 2005), and plaice (Rijnsdorp et al. 2005). Because reproduction requires resources, growth could become reduced for the mature age classes. Laboratory studies have furthermore suggested that many related reproductive characters could also be affected by fisheries-induced evolution (Walsh et al. 2006).

Several studies report finding evidence of fisheries-induced evolution of growth (Handford et al. 1977; Ricker 1981; Swain et al. 2007, 2008; Edeline et al. 2007; Nusslé et al. 2009). The most conclusive evidence comes from Pacific salmon (Ricker 1981) and Atlantic cod (Swain et al. 2007, 2008), although there are potential variables not accounted for even in these innovative studies (see for example Bigler et al. 1996 on pink salmon *Oncorhynchus gorbuscha*, although that study used a more recent dataset, and Heino et al. 2008 for cod). Growth is a difficult trait to study for at least two reasons. First, fishing is predicted to cause evolution of either faster or slower growth depending on a variety of factors including size-selectivity of the fishery (Dunlop et al. 2009). Second, phenotypic changes in growth can develop quickly in response to changes in density, food availability, or temperature, and such phenotypic plasticity can mask underlying genetic changes that act over longer timescales (Dunlop et al. 2009). This could explain the varied trends in growth rates observed in exploited populations (Hilborn and Minte-Vera 2008).

Traits other than those related to growth or maturation have been much less studied in wild populations, but could nonetheless evolve in response to fishing (Heino and Godø 2002;

Uusi-Heikkilä et al. 2008). Suitable data are often less detailed with smaller sample sizes, and techniques may need to be invented to examine these, often more elusive, traits. Given the multitude of coevolving traits relating to reproduction, offspring characteristics, and growth that have been observed to change in selection experiments (Walsh et al. 2006; Cooke et al. 2007), it is important to continue striving to study further traits. Although their quantification may be evasive, their impacts could be profound.

Contributions in this issue: PMRNs have been central to understanding maturation trends in harvested fish stocks, and the methods of estimating PMRNs have been extended to cases where data on maturation is less resolved and first-time spawners cannot be separated from repeat spawners (Barot et al. 2004). The detailed dataset on Atlantic cod analyzed by Pérez-Rodríguez (2009) presented a unique opportunity to compare the direct method of Heino et al. (2002) with the less data-intensive demographic method by Barot et al. (2004). Both methods produced similar results and their estimate of the PMRN fluctuated in parallel over time, which implies that analyses using these two methods are comparable. This has advantages for comparisons across numerous studies, for example the meta-analysis of phenotypic change by Sharpe and Hendry (2009). They observed trends toward younger ages and smaller sizes at maturation, and the rate of change for length at 50% maturity and the PMRN was significantly correlated with the intensity of fishing. Because this relationship arose in a comparison across species and systems, it strengthens the assertion that fishing intensity is one driver of the observed phenotypic trends. This analysis was similar to Darimont et al. (2009), who found that harvesting was a strong driver of phenotypic change. However, neither Sharpe and Hendry (2009) nor Darimont et al. (2009) could fully isolate the role of evolutionary change in contributing to the trends in trait phenotypes.

Several studies have suggested that differences in growth rate or behavior may be correlated with the vulnerability to fishing (Biro and Post 2008; Biro and Stamps 2008; Redpath et al. this issue). Growth rate and behavior may be difficult to quantify in the field or from routine surveys, but there is a possibility that such differences are correlated with physiological characteristics. Appreciating that such physiological indicators could be helpful when assessing the impact of fishing, Cooke et al. (2009) studied whether physiological traits (plasma ions and metabolites, cortisol, gill Na+/K+-ATPase, energetic status) were correlated with vulnerability to fishing in sockeye salmon *Oncorhynchus nerka*. They were, however, not able to detect any differences in the measured characteristics between the fish that were more vulnerable to fisheries and those that survived to the spawning grounds, possibly because of low statistical power. Logically, lack of evidence does not mean that fisheries-induced evolution is not taking place for these traits (nor, of course, does it mean that it is taking place).

Complementary evidence

Owing to the practical and fundamental difficulties in detecting genetic change — and drivers of such change — in the wild, complementary approaches have been invaluable in determining the scope for fisheries-induced evolution and the mechanisms involved. Both experiments and theoretical models have contributed to the body of evidence for fisheries-induced evolution and we discuss some of their contributions here.

Experiments

Experimental research has the great advantage that the environment can be controlled, implying that the genetic basis for observed trait changes can be quantified. In particular, the contribution of genetic variance to total phenotypic variance can be quantified experimentally, thus ascertaining whether there is sufficient genetic variation for a trait to evolve if it is selected upon, and if so, at what rate will evolution occur (see also Kuparinen and Merilä 2007; Allendorf et al. 2008). There are also richer opportunities for making measurements of multiple traits and correlations between them in the laboratory than in the field (e.g., Walsh et al. 2006). Moreover, experimental manipulations allow testing causes of genetic change, e.g., whether harvesting is capable of driving evolution in experimental populations.

Excellent experimental work on the role of predation, mortality, and fishing on life-history evolution has been done by David Conover and colleagues (e.g., Billerbeck et al. 2001; Lankford et al. 2001; Conover and Munch 2002; Walsh et al. 2006; Conover et al. 2009) and David Reznick and colleagues (e.g., Reznick et al. 1990, 1996; Reznick and Ghalambor 2005; Walsh and Reznick 2008). In particular, these experiments have demonstrated that 1) changes in mortality regime are capable of causing marked life-history evolution within just a few generations, and 2) mortality-induced evolution is manifested in a suite of individual traits, even though the most obvious changes observed are of life-history traits such as growth and maturation. Further work along the same lines, by these and other groups, will no doubt continue to influence and enlighten the field of fisheries-induced evolution in the future.

Contributions in this issue: Conover and Baumann (2009) review the role of experiments for the study of fisheries-induced evolution. After presenting past contributions, they also sketch avenues for future research.

Much of the work on fisheries selectivity has focused on size (e.g., Hamley 1975). Recently, an experimental approach went beyond size and focused on fish breeding lines selected for their vulnerability to angling (Philipp et al. 2009; Redpath et al. this issue). Analyzing fish from these selected lines, Redpath et al. (2009) observed a growth difference between high- and low-vulnerability fish, and delved into physiology to explain these differences. Although there were few clear trends from the factors they investigated, other work suggests that the differences in growth co-occur with differences in standard metabolic rate (Cooke et al. 2007). Higher metabolic rates in fish vulnerable to angling indicate physiological differences compared to those that are less vulnerable and would remain in the lake after an intense fishing season. In another recent experiment, Biro and Post (2008) used breeding lines that were selected for differences in growth, and showed how bold and fast-growing fish were more rapidly removed by fishing. Exploiting contrasts between strains of fish that can readily be interpreted in light of common fishing practices can broaden and deepen our understanding for the traits that fishing may affect, and expand the list of traits one should investigate further in wild stocks.

Theory

A different but complementary approach is theoretical modeling, which can test hypotheses quantitatively and has contributed potential mechanisms through which fisheries-induced evolution may lead to changes in harvested species (see Stokes et al. 1993 for many seminal contributions). Some of the earliest models specifically addressing fisheries-induced evolution were those by Lawrence Favro and colleagues (Favro et al. 1979, 1980, 1982). Their simulation models explicitly modeled inheritance of one or more loci genetically coding for growth, and predicted that selective fishing of brown trout *Salmo trutta* above a minimum size limit led to decreases in the numbers of large fish in the population. Most subsequent models have focused more on the evolution of maturation age or size and its consequences (e.g., Law and Grey 1989; Getz and Kaitala 1993; Hutchings 1993; Ernande et al. 2004; Baskett et al. 2005; de Roos et al. 2006). Many of the most recent models have expanded this further by focusing on the evolution of multiple traits (for example growth, PMRNs, and reproductive investment; Dunlop et al.

2009) and on less studied traits such as migration (Jørgensen et al. 2008a; Thériault et al. 2008; Miethe et al. 2009) and sex allocation in hermaphrodites (Sattar et al. 2006).

Evolutionary models of a general nature and not specifically about fishing have shown that mortality in general (from any source) has strong influences on life-history traits, and changes in mortality are therefore likely to cause adaptations (e.g., Gadgil and Bossert 1970; Schaffer 1974; Law 1979; Stearns and Crandall 1981; Charlesworth 1994). These models have formed much of the basis of life-history theory (Roff 1992; Stearns 1992), and are central also to understanding fisheries-induced evolution.

A variety of theoretical approaches have been applied specifically to study the evolutionary effects of fishing. The models range from simple and supposedly 'general' to complex and more system-specific models, with implications for the inferences that can be drawn. It is often advised to start simple, with the advantage that results are easy to interpret and may be generalizable; at least they form a first expectation against which more complex models and empirical findings can be compared. Some models of fisheries-induced evolution that have been kept simple and designed for their ability to generalize are, e.g., Gårdmark and Dieckmann (2006) and Andersen et al. (2007).

Going beyond simple models and digging into details may be necessary, particularly when the aim is model output of relevance for practical management where system-specific details matter (DeAngelis and Mooij 2003). In general, models that are used in the study of fisheries-induced evolution have added richness along one or more of three dimensions of model complexity. First, models may detail physiology and bioenergetics (e.g., de Roos et al. 2006; Jørgensen and Fiksen 2006) or behavior (e.g., Jørgensen et al. 2008a; Thériault et al. 2008) or more generally use specific ecological relationships for a given species or stock. The more specific the chosen biological relationships and parameter set becomes, the richer predictions can be made but for a narrower set of conditions. These models have been useful in detailing the role of individual state, and have shown how size distribution may affect intra-specific resource competition (de Roos et al. 2006) or how individual size and body condition may influence key life-history decisions (Jørgensen et al. 2008a). Second, models may include ecological feedbacks explicitly in order to allow richer interactions (e.g., Ernande et al. 2004; de Roos et al. 2006; Dunlop et al. 2009). The advantage is that density and frequency dependence, which are known to be important for individual growth and recruitment in fish, can be accounted for. Important results from these models include the degree to which phenotypic plasticity may affect observed phenotypic changes. The drawback with frequency-dependent models is that they are more difficult to parameterize and analyze. The third dimension of complexity is the level of genetic detail included. Requiring fewest assumptions about genetic detail are models of phenotypic adaptation, either in terms of optimization (e.g., Jørgensen and Fiksen 2006) or with frequency dependence added (Law and Grey 1989; Heino 1998; Ernande et al. 2004). These models obtain evolutionary insights by studying phenotypes in light of their fitness consequences, and they therefore rely on the set of assumptions embodied in the streetcar theory of evolution (Hammerstein 1996). Other models of harvest-induced evolution go beyond the phenotype by including genetic detail in the form of inheritance of quantitative traits, for example in quantitative genetics models (e.g., Ratner and Lande 2001; Baskett et al. 2005) or those modeling individual loci (Tenhumberg et al. 2004).

At the complex end of the scale and including multiple dimensions of complexity, several models have genetic detail, including mating and inheritance of quantitative traits, and ecological feedback (e.g., Dunlop et al. 2007, 2009; Thériault et al. 2008). These mainly individual-based models (often termed "eco-genetic models"), of which there are also several examples in this issue, are complex along the second and third dimension above (and could also be extended in the first dimension if desired). Based on fitness emerging through population dynamics, these models let ecological processes determine which characteristics are inherited while the traits in the population determine the outcome of the ecological relationships. This full integration of ecological and evolutionary dynamics has advantages when debating the degree to which ecological and genetic changes underlie observed phenotypic trends, but the model output is often complex, and efficient interpretation and communication of such models involve non-trivial challenges.

Contributions in this issue: The theoretical papers presented in this special issue span the entire range of model design, from more general models to highly detailed models describing specific species and ecological settings with numerous parameters. Hutchings (2009) used an age-structured model to investigate fitness consequences without optimizing life histories. With a relatively simple model, Hutchings illustrates a strong conceptual point: whether current reference points in fisheries management adequately reflect evolutionary concerns. Similar to Hutchings (2009), the models by Arlinghaus et al. (2009) and Jørgensen et al. (2009) do not model evolutionary trajectories over time but aim at predicting either initial responses to selection (Arlinghaus et al. this issue) or endpoints of selection (Jørgensen et al. this issue). The model by Arlinghaus et al. (2009) is a combination of a population projection matrix and a detailed sub-model of recreational fishers and their preferences. Focusing on graphical illustrations of likely immediate selection responses may be a powerful way to simplify the core message to fisheries managers and other decision makers. On the other hand, the model by Jørgensen et al. (2009) is based on methods of phenotype optimization that give indications of where evolution may eventually lead. The model addresses how optimal life histories are influenced by size-selective fishing gear. Optimization models have the drawback that they cannot quantify rates of evolution, nor separate evolutionary change from phenotypic plasticity. Still, knowing what is the optimal phenotype gives a valuable starting point for empirical comparisons, and in some cases individual processes and state-dependence can be more detailed, thus being an important intermediary step before turning to models where evolution and ecology are fully coupled.

Several individual-based models in this special issue include more complexity by modelling the quantitative inheritance of traits and ecological feedback (Dunlop et al. this issue; Enberg et al. this issue; Okamoto et al. this issue; Wang and Höök this issue). Although these models are centered on life-history traits relating to maturation and growth, there are interesting differences in how the genetics of the inherited traits and the life histories are modelled. The model by Wang and Höök (2009) differs from the other IBMs in that the length threshold for maturation is modelled as an independent quantitative trait for each age and sex. They observe that maturation length changes in response to fishing most for early ages, which is expected because in the modeled population these early ages are where selection acting on maturation is most prominent. In the remaining three IBMs in this issue, maturation is based on a PMRN (Heino et al. 2002) where the effect of age is linear and the slope and intercept of the PMRN evolve (Dunlop et al. this issue; Enberg et al. this issue; Okamoto et al. this issue). Because an evolutionary change in the slope or intercept may affect maturation length at all ages, this introduces correlations between the maturation probabilities at different ages.

A common difficulty when interpreting phenotypic change is the interplay between demography, phenotypic plasticity, and evolutionary trait change. Modelling a temporal fishing moratorium with a focus on stock recovery, Enberg et al. (2009) show how these processes have different timescales and different consequences. Demographic effects leave fingerprints within the first decade of the moratorium, phenotypic plasticity has effects that last a couple of decades, whereas recovery of the inherited traits may take centuries. The model also reiterates earlier findings that evolutionary recovery of a population’s original trait distribution if fishing were stopped is slow.

The diversity of theoretical approaches in this special issue illustrates well the many layers at which evolutionary insights are needed in order to piece together a comprehensive understanding of how management may respond to the potential for fisheries-induced evolution.

Consequences and management

The consequences of fisheries-induced evolution are potentially far-reaching (Jørgensen et al. 2007), but have yet to be fully explored using data, experiments, and models. One expectation that is of particular concern is the asymmetry in evolutionary rates, where the rate of evolution during fishing is expected to be higher than the rate of evolutionary recovery when fishing is stopped (Stokes and Law 2000). This prediction, initially made by Law and Grey (1989) using a relatively simple model, has now received further support through experiments (Conover et al. 2009) and through more detailed models (Dunlop et al. 2009). For each year we fish, it may thus take more than one year of no fishing for the inherited traits to recover; this has been termed a 'Darwinian debt' because we harvest now in a manner that may entail costs for future generations (the term was coined by Ulf Dieckmann in an interview with the Financial Times, 28 August 2004). With due respect to the precautionary principle, this perspective alone is sufficient, in our opinion, for managers to be concerned about the evolutionary impacts of fishing.

Given what is known to date, there are two general recommendations worth reviewing for the manager who is concerned with mitigating unwanted fisheries-induced evolution. First, the most general advice is to fish less. Numerous models have shown that reduced harvest rates will reduce the rate and amount of evolution (Law and Grey 1989; Heino 1998; Ernande et al. 2004; Dunlop et al. 2009). This management option aligns with traditional fisheries management: a large proportion of fish stocks are over-fished, and by definition, could support larger catches if allowed to rebuild (FAO 2009). Second, size-selectivity can be altered through regulation, and using certain gears may reduce fisheries-induced evolution (Law and Rowell 1993; Conover and Munch 2002; Walsh et al. 2006; Law 2007). These recommendations do not stray far from traditional fisheries management, and may therefore be more likely to be adopted by managers and decision makers (Law 2007).

Management of major fisheries is ultimately conducted on a stock-by-stock basis, and specific recommendations will need to respect the details of each population, ecosystem, and society. Putting the general knowledge of fisheries-induced evolution into practice is not trivial, and the task of assessing whether fisheries-induced evolution has consequences that warrant action in a particular fish stock, and then finding the most cost-effective actions, may seem daunting. The framework of Evolutionary Impact Assessments (EvoIA: ICES 2007; Jørgensen et al. 2007) will hopefully help to guide such endeavours. An EvoIA emphasizes assessing what consequences fisheries-induced evolution has on utility of a fish stock. EvoIAs compare utility consequences of various management actions, including inaction, conducted in a dialogue between scientists, managers and stakeholders, and would ideally form a basis for informed management decisions toward sustainable harvest of our common living resources.

Contributions in this issue: It is positive to see that several of the papers in this special issue have adopted an applied and management-oriented approach. Central to fisheries management is the use of reference points to guide sustainable harvesting levels. In his case study of Atlantic cod, Hutchings (2009) suggests a new reference point, F_{evol}, defined as the fishing rate above which selection favors earlier maturity than currently observed. F_{evol} can thus be classified as a limit reference point that should not be exceeded, analogous to commonly estimated reference points such as F_{lim} (ICES 2008: the fishing rate that will eventually cause a stock collapse). In an optimization model, also for Atlantic cod, Jørgensen et al. (2009) observe that using gillnets may result in less life-history evolution compared to trawls or unselective gear, but only up to a threshold harvest rate. Beyond this harvest rate the optimal phenotypes mature early, and this harvest rate is thus another metric that could be interpreted as F_{evol}.

In addition to regulating fishing intensities or gear selectivity, fisheries can also be managed by creating protected areas where harvest is banned or limited. Several researchers have indeed suggested that marine protected areas or reserves (herein referred to as MPAs for simplicity) could be a promising management option for mitigating the evolutionary effects of fishing (Conover and Munch 2002; Law 2007) but it is only recently that models have begun to test this idea. Despite their different methodologies, the models developed thus far have all shown that MPAs can reduce the evolutionary effects of fishing (Baskett et al. 2005; Miethe et al. 2009; Dunlop et al. this issue). Dunlop et al. (2009) show that crucial to determining the effectiveness of MPAs in reducing fisheries-induced evolution is reserve placement: a reserve placed in a stock's feeding grounds is effective but a reserve placed in the spawning grounds can exacerbate the very evolutionary trends that one tries to avoid. What is less clear is whether by controlling fisheries-induced evolution, MPAs can actually improve fisheries yield, and what advantages MPAs might have over traditional management measures. For example, Dunlop et al. (2009) predict that only rarely does an MPA improve yield.

Several theoretical papers have suggested that evolution toward earlier maturation (among other possible traits) can be reduced by redirecting fishing effort away from feeding grounds and toward mature individuals (Law and Grey 1989; Heino 1998; Ernande et al. 2004; Dunlop et al. this issue). However, results presented by Jørgensen et al. (2009) suggest that this does not always hold when fishing is also directly size-selective. Even if the fishing only takes place at the spawning grounds, a sigmoid size-selectivity typical to trawls can create a size refuge for small fish, which may favour small spawners over large spawners, and thus set up selection toward earlier maturation.

One phenomenon that is receiving increasing attention is the potential for parental effects, where a spawner's age, size, or experience may influence the quality of its offspring (e.g., (Venturelli et al. 2009). In an eco-genetic model of a species with paternal care, the smallmouth bass *Micropterus dolomieu*, Dunlop et al. (2007) found that including a survival advantage for the offspring of large males significantly reduced the magnitude of harvest-induced evolution. More recently, Wang and Höök (2009) included a maternal effect on offspring viability, and as a result their model predicted different maturation reaction norms for males and females, as has been observed in many cases (e.g., Barot et al. 2005; Olsen et al. 2005, 2009; Wang et al. 2008; Vainikka et al. 2009). In general, the factors that influence fitness may differ substantially between the sexes (Charnov 1982), for example if there is sexual selection or within-sex competition for access to mates. These and similar mechanisms have implications for a species' maturation schedule, and potentially how a population responds to fishing, e.g., to selective removal of large individuals (Hutchings and Rowe 2008a, 2008b; Urbach and Cotton 2008; Wang and Höök this issue).

To guide management actions, it can be helpful to visualize the selection imposed by a given harvest regime, for example when one wishes to compare alternative management measures. Arlinghaus et al. (2009) used an age-structured model to estimate selection differentials on reproductive investment generated by recreational fishing. The selection differentials on reproductive investment imposed by fishing were positive (indicating that fishing selected for higher reproductive investment) but could be considerably lowered with simple management measures such as increasing the minimum size limit. The type of approach of Arlinghaus et al. (2009) has potential to guide management because age-structured models are already commonly used by fisheries professionals to study non-evolving populations. Arlinghaus et al. (2009) also include an important component, overlooked in most studies of fisheries-induced evolution, that of feedback between the state of the resource and behavior of the fishers pursuing that resource.

It is also important to recognize that managers may have differences in the priority they place on reducing fisheries-induced evolution. Okamoto et al. (2009) take this practical approach in their eco-genetic model of brook trout *Salvelinus fontinalis*, in which they introduce a parameter that allows managers to weigh the importance of evolutionary change. Their model predicts that there are some harvesting scenarios (i.e., combinations of harvest rates and size-selectivity) that allow moderate to high yields while at the same time minimizing evolutionary change. This approach falls within the framework Hilborn (2007b) used to suggest the 'zone of new consensus', where one identifies system states that are desirable both to environmentalists and commercial fishers.

Future directions

As with any burgeoning field, there are several exciting avenues for future research on the topic of fisheries-induced evolution.

First, evolution and the environment together shape the traits of populations, with implications for ecosystems. The methodological toolbox that can partition these two drivers of change will no doubt be further developed. Also, finding and utilizing complementary data sets that better describe the physical and biological environment will help this endeavour.

Second, most studies have examined evolution of basic life-history traits such as growth and maturation, but many other traits, including behavior, could potentially evolve in response to fishing. Field observations, experiments, and models are all likely to contribute to the list of traits for which one might predict an evolutionary response to fishing; for example, Walsh et al. (2006) documented laboratory evolution of many traits that still need to be investigated in wild stocks.

Third, for the traits where evolution has been suggested or documented, we know little about the consequences of such change. When individual traits change, this affects population dynamics, ecological relationships, and may eventually set up selection gradients for evolutionary change in other traits or in other species. Both direct and second-order consequences of a changing trait may have implications for feedbacks between ecology and evolution, and detailing these inter-relationships will necessarily involve exciting research (for a relevant example of natural predation, see Palkovacs et al. 2009). An extension of this is the study of how the effects of fisheries-induced evolution go beyond single species to impact food webs and ecosystems; almost all research to date has focused on effects of fishing on the life-history traits of single species. Quantitative modelling is one promising avenue for deepening our understanding of these more complex feedbacks and impacts (e.g., Gårdmark et al. 2003; Matsuda and Abrams 2004).

Fourth, there are important gaps in the understanding of how natural and sexual selection shaped fish life histories in the first place. This makes it difficult to assess how fishing or other anthropogenic influences that act on top of natural selection may set up new selection gradients (Stenseth and Dunlop 2009). The science of fisheries-induced evolution is basically evolutionary ecology with an added twist, and a broad field-based and experimental approach is needed to provide the foundations for interpreting and predicting fisheries-induced evolutionary change. For example, current models only scratch the surface of what may influence evolution of fish, with the focus to date being on life-history traits.

Fifth, although much of the earlier work on fisheries-induced evolution was actually done on freshwater species (e.g., Silliman 1975; Handford et al. 1977; Favro et al. 1979), marine research on the topic has far outpaced freshwater research, perhaps because of the extensive time series available for commercially important marine stocks. Recreational fishing is a potentially important driver of evolutionary change in freshwater systems, and this field is now rapidly expanding (Biro and Post 2008; Nusslé et al. 2009; Philipp et al. 2009; Arlinghaus et al. this issue; Redpath et al. this issue). Commercial fishing can be an economically important industry in some freshwater systems, for example in the Great Lakes of North America, and studying its potential to induce evolutionary change has only just begun (Wang et al. 2008).

Last but not least, conclusive evidence that the observed phenotypic changes are evolutionary would require that they can be linked to underlying genetic changes. Documented molecular consequences of harvesting have hitherto been restricted to loss of alleles or heterozygosity (e.g., Smith et al. 1991; Jones et al. 2001; Hauser et al. 2002). With genomics rapidly expanding the molecular toolbox, one day it will be possible to link individual genotypes to phenotypes and further on to fisheries-induced selection. This task, however, is not trivial: a recent review of methods to build genotype-to-phenotype maps observed that "more than a decade into the genomic era, it remains easier to collect genomic data sets than to understand them" (Rockman 2008). It will be exciting to see the molecular revolution unfold within the field of fisheries-induced evolution, and especially how molecular evidence may support or change the conclusions that have been based on phenotypic data. As we are still years from being able to build genotype-to-phenotype maps for the study of fisheries-induced evolution, it would not be prudent to use lack of conclusive molecular evidence as an excuse for inaction.

The current challenges to fisheries management (reviewed in e.g. Clark 2006) suggest that broader perspectives may be needed, both biologically and when it comes to involving stakeholders and the public. Evolutionary impact assessment (EvoIA) has been suggested as a framework in which the ecosystem approach to fisheries management and the potential for evolutionary change can be treated together when designing management actions (Jørgensen et al. 2007). While there is probably no stock where the knowledge is yet complete enough for a full-fledged EvoIA, it is important to consider how humans influence ecosystems as a whole and how those changes impact society. The science of fisheries-induced evolution illustrates how a proper description of the biological consequences of evolution requires that ecology, evolution, and the interplay between them, is understood. At the same time, it is also clear that fisheries-induced evolution may alter a stock's, and the ecosystems', utility to society and the solution to these challenges will require input from multiple perspectives, including from stakeholders and the public.

Conclusions

In each case study of fisheries-induced evolution, the role of evolution versus the environment in driving phenotypic change can be debated, probably endlessly. These debates are sound and necessary. Only by carefully considering all factors can we be sure to rule out those factors that are less important and keep focus on the important drivers of change. The evolutionary fingerprint of fishing is sometimes non-existent, at other times it may just be difficult to demonstrate. Because the whole organism with all its traits may evolve, this undertaking is stronger the more biological sub-disciplines take part in interpreting field evidence and by suggesting hypotheses and mechanisms that may explain the observed temporal patterns. However, we argue that taken together, the field evidence for fisheries-induced evolution is compelling — phenotypes are changing over time in ways that are yet unexplained solely by concurrent environmental trends (see recent reviews by Jørgensen et al. 2007; Kuparinen and Merilä 2007; Allendorf et al. 2008; Hutchings and Fraser 2008). Across several harvested species, across lakes and oceans that comprise unconnected ecosystems, and in regions with different climatic influence, observed phenotypic change is consistently in the direction expected to be favored by evolution when mortality increases. For all the stocks combined, the most parsimonious conclusion is therefore that fishing causes adaptations in harvested populations. This does not logically imply that fisheries-induced evolution has been unequivocally demonstrated in each stock that has been investigated, not even when a residual unexplained trend has been documented. Nor does it mean that the environment hasn't played a role in shaping observed phenotypic change.

The evidence for fisheries-induced evolution also goes beyond what has been documented in wild stocks — it draws upon many approaches (experimental, empirical, theoretical), integrates several fields of knowledge (genetics, statistics, evolutionary ecology, life-history theory, fisheries science, aquaculture), and has made considerable strides in attempting to account for the role of the environment in contributing to phenotypic change.

We are also of the opinion that the substantial body of research published thus far makes a strong case for including fisheries-induced evolution in management considerations. Some potential management measures exist to deal with this challenge. It is therefore an encouraging sign that the International Council for the Exploration of the Sea (ICES), the major provider of fisheries management advice in Europe, has established a working group to explore the management implications of fisheries-induced evolution (ICES 2007). This kind of initiative should help to ensure an important dialogue between scientists in universities and governmental research institutions, fisheries managers, and policy makers.

As the papers reviewed here and those appearing in this special issue have shown, considerable progress has been made in the understanding of fisheries-induced evolution since Cloudsley Rutter (1902) first mentioned the topic in the scientific literature. Continued debate of the tools and methods in use and of the interpretation of findings is important so that the field keeps moving forward based on science that is solid and constructive.

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