

What can selection experiments teach us about fisheries-induced evolution?

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Abstract

There is evidence that fisheries are altering the phenotypic composition of fish populations, often in ways that may reduce the value of fish stocks for the exploiters. Despite the increasing number of theoretical and field studies, there is still debate whether these changes are genetic, can be reversed, and are occurring rapidly enough to be considered in fisheries management. We review the contribution that selection experiments have already had in the study of the evolutionary effect of fisheries, identify issues that still require more study, and outline future directions to do so. Selection experiments have already been crucial in showing that harvesting can lead to phenotypic and genetic evolution over relatively short time frames. Furthermore, the experiments have shown the changes involve many other traits than those under direct selection, and that these changes tend to have population-level consequences, including decreasing fisheries yield. However, experiments focused on fisheries-induced evolution that fulfil all our desiderata are still lacking. Future studies should have more controlled and realistic set-ups and assess genetic changes in maturation and growth—traits most often reported to change—in order to be more relevant to exploited populations in the wild.

KEYWORDS: fisheries-induced evolution- genetic change - fishing selectivity - phenotypic change - selection experiments.

INTRODUCTION

Fishing is an inherently selective process, most commonly targeting large, more valuable individuals (Law, 2000). There is now a steadily increasing body of evidence suggesting that fisheries are driving phenotypic changes in fish and that these changes have a genetic component (reviewed by Law, 2000; Dieckmann & Heino, 2007; Jørgensen *et al.*, 2007; Law, 2007; Sharpe & Hendry, 2009; Devine *et al.*, 2012). Timing of maturation and growth are the main traits that have been observed to change (Law, 2000). However, there are many other traits (behaviour, morphology, sex ratio, etc.) that are directly affected by fishing (Miller, 1957; Heino & Godø, 2002; Enberg *et al.*, 2012). In addition, fishing can be indirectly selective on further traits that are correlated with those under direct selection, such as fecundity, egg survival, mating strategy, metabolic rate, etc.

A selective pressure imposed on a genetically variable population causes evolutionary change. Breeding programs in aquaculture clearly show evolvability of relevant traits in fish (Pottinger & Carrick, 1999; Fjalestad, Moen & Gomez-Raya, 2003; Gjedrem, Robinson & Rye, 2012). However, selective fishing can lead to population-level changes in characteristics such as growth and maturation without involving evolutionary change through density-dependent feedbacks that trigger phenotypical plastic responses or by reducing population's mean age, and thereby size.

Discussions whether the changes created by intensive fishing are due to “mere” phenotypic plasticity or also due to genetic adaptation are ongoing (Browman, Law & Marshall, 2008; Jørgensen *et al.*, 2008b; Kuparinen & Merilä, 2008; Andersen & Brander, 2009). Efforts on disentangling phenotypic and genetic changes have focused on maturation schedules, as maturation is the main trait observed to change due to fishing (Law, 2007). There are probably two reasons for this: many models suggest that maturation is particularly prone to undergo harvest-induced evolution

(Dunlop, Heino & Dieckmann, 2009; Enberg *et al.*, 2009; Audzijonyte *et al.*, 2013; but see Andersen & Brander, 2009), and maturation is the only trait for which statistically accounting for a major source of plasticity is straightforward using so-called maturation reaction norms (Stearns & Koella, 1986), in particular the probabilistic maturation reaction norms (PMRNs; Heino, Dieckmann & Godø, 2002). However, PMRNs cannot account for all phenotypic plasticity (Dieckmann & Heino, 2007; Kraak, 2007; Uusi-Heikkilä *et al.*, 2011; Diaz Pauli & Heino, 2013), and thereby cannot conclusively show whether evolution has taken place.

To unequivocally show that the documented phenotypic changes represent fisheries-induced evolution (FIE), (1) a genetic basis of the changes should be demonstrated (Kuparinen & Merilä, 2007) and (2) fishing should be identified as a driver of the changes (Heino & Dieckmann, 2008). In principle, the first condition is easily met. However, despite the rapid development of genetic techniques that now allow analysing large materials at low cost (Nielsen *et al.*, 2009; Hansen *et al.*, 2012), the genetic basis of traits associated with phenotypic changes in fish is still poorly known, and evidence for genetic change that could be linked to phenotypic differences in exploited populations is still very scarce (Jakobsdóttir *et al.*, 2011). Disentangling phenotypic and genetic consequences is also possible with comparative studies of populations of recent common origin but different harvest regime, but opportunities for carrying out such studies in fish stocks are limited (see Haugen & Vøllestad, 2001, for a rare exception). The second condition—that fishing is a driver of change—is usually not challenged, although it perhaps should be. Observational field studies are fundamentally handicapped in differentiating the effects of single factors (Heino & Dieckmann, 2008; Rosenbaum, 1995). However, comparative studies can facilitate credibility of fishing as a driver (Sharpe & Hendry, 2009; Devine *et al.*, 2012; Audzijonyte *et al.*, 2013), as do estimation of selection differentials caused by fishing

(Law & Rowell, 1993; Arlinghaus, Matsumura & Dieckmann, 2009; Kendall & Quinn, 2012).

Selection experiments are well-suited to understand both the nature and drivers of changes seen in harvested populations. With this review we present the contributions that selection experiments have made to the study of FIE. We argue that selection experiments specifically aimed at studying size-dependent selection may fill important gaps in our understanding of FIE.

Related reviews have already been carried out: Fuller, Baer & Travis (2005) presented importance of selection experiments for understanding evolutionary processes in general, whereas Conover & Bauman (2009) and Reznick & Ghalambor (2005) presented how experiments have increased our understanding of FIE. Our review differs from these earlier reviews in two important aspects. First, we focus on studies that were specifically carried out to understand FIE; we do not cover the classic experiments carried out to understand rapid life-history evolution in fish in general (e.g., Moav, Hulata & Wohlfarth, 1975; Wohlfarth, Moav & Hulata, 1975; Reznick & Endler, 1982; Reznick & Bryga, 1987). Second, our approach is analytic and critical, rather than descriptive: we assess the strengths and weaknesses of the experimental set-ups used, and evaluate the success or failure that selection experiments have had in clarifying the issues where the understanding of FIE is least complete.

We have identified seven key issues in understanding FIE: 1) clarify the role of size-selective mortality (or other harvesting-specific mortality) on direct phenotypic changes, 2) study how other traits are indirectly affected by selective fishing, 3) determine whether there are genetic changes associated with the phenotypic ones, 4) answer whether rapid evolution of maturation is possible due to size-selective fishing, 5) determine whether the rate of change is fast enough to have management implications, 6) test whether the change can be reversed, and 7) establish whether

these changes may affect the profitability of the fishery. The present review is organized around these seven points.

Our discussion on the strengths and weaknesses of experimental set-ups of the studies is focused on two criteria: 1) how the experiment was designed to unequivocally conclude that selection is the source of change (i.e., how well-designed the experiment is), and 2) how the study can be related to the study of fisheries-induced evolution in the wild (i.e., whether the experimental design is realistic enough to be related to more general processes). Furthermore, we discuss the potential of and the need for further selection studies to improve our knowledge on evolutionary processes and on fisheries-induced evolution in particular.

SELECTION EXPERIMENTS

DEFINITION

Selection experiments study evolution in action, in a controlled and replicated manner, in contrast to observational studies made in the wild (Garland, 2003; Fuller *et al.*, 2005). They allow observing phenotypic and genetic change in populations and communities that are caused by experimentally imposed selective pressures. As under experimental conditions other factors can be controlled or their impact can be reduced to noise, such changes may be indisputably attributed to the selection imposed (Garland, 2003; Fuller *et al.*, 2005).

Garland (2003) classified selection experiments in four different categories: *artificial selection*, *laboratory culling*, *laboratory natural selection*, and *introduction experiments*. We do not, however, see compelling reasons to restrict ‘laboratory culling experiments’ and ‘laboratory natural selection experiments’ to laboratory settings. Moreover, for the current purposes, the classification can be further

simplified to just two categories: natural selection experiments and artificial selection experiments.

Natural selection experiments and artificial selection experiments differ in the extent the experimenter controls the selection. In artificial selection experiments (culling and artificial selection experiments *sensu* Garland, 2003), the experimenter is the direct agent of selection controlling the nature, strength and consistency of selection, by determining the number and type of breeders in each generation. Examples of artificial selection experiments include those of selection for certain traits (e.g., fast larval development, laterality and activity) in fruitflies, fish and mice, just to cite a few (e.g., Zwaan, Bijlsma & Hoekstra, 1995; Bisazza *et al.*, 2007; Meek *et al.*, 2009). In natural selection experiments (Garland's natural selection and introduction experiments), the strength and consistency is not directly controlled (the breeders are not directly selected), but different selective forces can be imposed by controlling certain factors in the environment (Garland, 2003; Fuller *et al.*, 2005). These selective forces can be naturally imposed, as in the particular case of introduction experiments, or experimentally imposed, which usually requires a laboratory setting or a controlled field setting, e.g. field enclosures. Introduction experiments of guppies are a good example of natural selection experiments (Reznick & Bryga, 1987).

In addition to classic, manipulative experiments with controlled treatments, we also include mensurative experiments where the "treatments" are based on pre-existing variability in space or time (Hurlbert, 1984). This variability could be either naturally-occurring (e.g., lakes differing in water quality) or human-induced (e.g., lakes differing in fishing pressure). Mensurative experiments are usually observational field studies and are natural selection experiments rather than artificial selection experiments.

EXPERIMENTS CONSIDERED

Here we review selection experiments that have specifically studied fisheries-induced evolution, and how these experiments have enhanced our understanding of this phenomenon. We do not consider selection experiments not focused on the study of FIE, even though results of some of those can be applied to understand FIE; many of such experiments have been reviewed elsewhere (Reznick & Ghalambor, 2005; Conover & Baumann, 2009). Neither are non-evolutionary experiments that addressed the effect of size-selectivity on population dynamics, rather than its effects on phenotypic and genetic composition, considered (e.g., Silliman & Gutsell, 1958; Schröder, Persson & de Roos, 2009). We could identify three artificial selection experiments and six natural selection experiments fulfilling our selection criteria. Of the six natural selection experiments, three took advantage of existing lake populations, while the other three were performed under laboratory conditions. The studies and their key characteristics are summarized in Table 1; a more detailed description of the experiments is presented as supplementary material.

CONTRIBUTIONS OF SELECTION EXPERIMENTS TO UNDERSTANDING OF FISHERIES-INDUCED EVOLUTION

Our presentation of selection experiments is organized around the seven core questions outlined in the introduction. Here we elaborate on these questions and review the answers that the experiments offer, before summarising the emerging insights.

1. DOES SELECTIVE FISHING LEAD TO PHENOTYPIC CHANGES?

Most commonly fishing is selectively removing large individuals from the population (Law, 2000). Not surprisingly, most empirical studies focus on phenotypic changes in

size. However, fishing can be directly or indirectly selective towards behaviour, growth rate, maturation, fecundity, etc. (Miller, 1957; Heino & Godø, 2002; Enberg *et al.*, 2012), and it is important to understand these broader impacts.

Lessons from experiments

Three mensurative field experiments (*sensu* Hurlbert, 1984) have studied the phenotypic effects. Drake *et al.* (1997) showed differences in bluegill male reproductive strategies from high or low fishing pressure. In low fishing lakes, parenting males were older and bigger and there were fewer cuckolders compared to males from the lakes with high fishing pressure that were smaller and younger at maturation and had slower growth at older ages. Grayling from the five populations studied by Haugen & Vøllestad (2001) differed in their early growth rate, time to swim-up (i.e., when larvae change from living in substrate to living the water column and rely in exogenous feeding), larval survival (Haugen, 2000b), age at maturity, adult survival and growth rate (Haugen, 2000a). Haugen & Vøllestad (2001) concluded that the most likely cause of the between-lake differences in adult traits is the different fishing regimes that those populations experienced, while differences in juvenile traits may be due to differences in spawning habitats. The study by Carlson, Edeline and collaborators (Carlson *et al.*, 2007; Edeline *et al.*, 2007) is one of the first that considered the interaction between harvesting and natural selection and the effect of these on individual size and reproductive investment. They showed natural selection on growth changed over time, either favouring fast growth (antagonistic with fishery selection), or slow growth (synergistic with fishing; Edeline *et al.*, 2007).

Phenotypic effects have also been studied in manipulative experiments. Silliman (1975) showed how growth rate in length was reduced in harvested populations (where large individual were removed) for males but not females, compared to

unharvested control populations (Silliman, 1975). Edley & Law's (1988) *Daphnia magna* populations with positive size-dependent harvesting produced lower yield that decreased over time. In addition, this type of harvest resulted in populations dominated by slow-growing clones that reproduced at smaller size relative to harvest with negative size-selection (Edley & Law, 1988). Kasperski & Kozlowski (1993) showed that reduced adult life expectancy in harvested guppy populations lead to a reduced size at maturity in males and females, compared to the control populations. Philipp, Cooke and collaborators performed artificial selection experiments to study angling effects on physiology and behaviour of largemouth bass, *Micropterus salmoides* (Cooke *et al.*, 2007; Philipp *et al.*, 2009; Redpath *et al.*, 2009). Their study showed that angling was selective on a "vulnerability trait" (captures/recaptures by angling effort) and it was possible to create two distinct lineages (high and low vulnerability to angling). Conover & Munch's (2002) study on Atlantic silversides concluded that the populations subjected to negative size selective harvest presented faster growth, compared to populations where larger individuals were harvested (Conover & Munch, 2002). van Wijk *et al.*'s (2013) study on guppies showed that size-selective mortality in males lead to changes in length, and age and size at maturation on males.

On the one hand, the more controlled set-up in the artificial selection experiments enables to unequivocally attribute the selective force as the driver of the changes, as was the case with the studies by Philipp *et al.* (2009), Conover and Munch (2002), and van Wijk *et al.* (2013). On the other hand, natural selection experiments allow for ecological feedbacks, which can play a role in the changes observed. Thus, natural selection experiments require extra caution in determining whether the selection is directly the cause for the differences in the traits measured, or through the different ecological feedbacks that the selection produced.

The studies by Drake *et al.* (1997), Edeline *et al.* (2007) and Haugen and Vøllestad (2001) are mensurative studies that took advantage of pre-existing variation in space (Drake *et al.*; Haugen & Vøllestad) or time (Edeline *et al.*), without controlling the selection pressures. Thus, their potential to study harvest-induced change depends on how well other factors were controlled for. They all took into account many environmental factors (lake area, depth, nutrients, prey abundance, etc.), but other important factors that were not considered could always confound the results. The studies performed separately by Silliman, Edley and Law, and Kasperski and Kozłowski are manipulative (*sensu* Hurlbert, 1984) natural selection experiments where the selective pressure on life history traits was controlled. The experimental set up allows controlling for confounding factors better than in the case of mensurative studies. However, only Edley and Law's study was an appropriate natural selection experiment to conclude that size-selective culling led to changes in size at maturation. Silliman's experiment had no replication and his founder populations were small and of mixed origin. Thus, the changes in growth may have resulted from fluctuations in the dynamics of a population that had not yet reached equilibrium or from founder and other random effects. Kasperski and Kozłowski's study on the other hand had replication and single-origin populations. The observed reduction of size at maturity may be attributable to size-selective harvest; however the small starting populations should be born in mind.

Conclusions

Numerous experiments have shown that fishing can cause a wide range of phenotypic changes in experimental populations. Selective fishing can lead to populations with reduced individual size, lower growth, and earlier maturation, as well as individuals less likely to be captured. These changes can have important ramifications on yield and thus for the future of the fishery. Artificial selection experiments are the best at

unequivocally attributing the selective force as the driver of the changes. However, such experiments do not allow for a realistic setting where ecological feedbacks can interact with and alter the effect of fishing. Results from natural selection experiments can be applied more generally due to their higher realism, but their complex set-up makes them more difficult to control and interpret.

2. DOES SIZE-SELECTIVE FISHING ALTER OTHER TRAITS CORRELATED WITH THE SELECTED TRAIT?

Experimental studies allow observing a wider array of potentially evolving traits than observational field studies. Furthermore, when several traits are measured from a single individual, the experimenter can also estimate correlations between traits, something that is usually beyond the scope of observational field studies (but see Mollet *et al.*, 2010).

Lessons from experiments

In the largemouth bass studies by Philipp, Cooke and collaborators (Cooke *et al.*, 2007, Philipp *et al.*, 2009), vulnerability to angling was also related to differences in physiological, behavioural (Cooke *et al.*, 2007; Nannini *et al.*, 2011; Sutter *et al.*, 2012) and life-history traits (Redpath *et al.*, 2009; Sutter *et al.*, 2012). High-vulnerability individuals showed higher resting heart rate and cardiac output during the resting period, which is associated with higher metabolic rate, and this in turn with higher aggression and dominance (Cooke *et al.*, 2007; Sutter *et al.*, 2012). In addition, high-vulnerability individuals presented superior parental care (more time guarding and oxygenating the nest; Cooke *et al.*, 2007; Sutter *et al.*, 2012), higher mating success (number of eggs in nest placed by females; Sutter *et al.*, 2012) and higher reproductive fitness (number of sired offspring; Sutter *et al.*, 2012), compared to low-vulnerability individuals. Moreover, high and low-vulnerability individuals differed in

growth rate and gonadosomatic index (Redpath *et al.*, 2009), in metabolic capacity (Redpath *et al.*, 2010) and in foraging behaviour (number of attacks to prey, capture efficiency, etc.; Nannini *et al.*, 2011).

The differently selected lineages of Conover & Munch (2002) did not only differ in size and growth rate, but also in fecundity, egg size and larval growth. Later on also differences in egg volume, larval viability, larval size at hatching, consumption rate, swimming performance and antipredator behaviour were assessed (Walsh *et al.*, 2006). The populations subjected to the removal of small individuals presented higher spawner biomass, larger egg size and faster larval growth and thus, higher larval viability, compared to populations where larger individuals were harvested (Conover & Munch, 2002; Walsh *et al.*, 2006). In addition, the populations in different treatments differed in physiological and behavioural traits, with the positively size-selected individuals expressing lower food consumption rate, fecundity and boldness, among other traits (Walsh *et al.*, 2006). Low food consumption and fecundity result in low survival and fitness (Walsh *et al.*, 2006; but see Billerbeck, Lankford & Conover, 2001).

Grayling from the Norwegian populations differed in age and size at maturity and growth rate due to differences in adult survival caused by fishing (Haugen, 2000a). In addition differences in egg size, fecundity and gonadosomatic index were also found and were correlated with fishing pressure (Haugen & Vøllestad, 2001). As mentioned before the differences in juvenile traits did not seem to be related to size-selective fishing.

Conclusions

The studies summarized above show that the effect of fishing pressure is more complex than just removing certain size classes; it affects other traits in sometimes-

unexpected ways. The correlated changes observed in the experiments mentioned above due to selective harvest, such as reduced fecundity, reduced gonadosomatic index, reduced feeding rate, reduced willingness to forage and reduced parental care, may ultimately reduce a population's resilience (Walsh *et al.*, 2006). It was previously thought that fishing reduces competition and thus increases food availability and productivity, but the studies discussed above show that fishing can influence traits related to converting available energy into population growth, therefore reducing the recovery capacity of populations (Walsh *et al.*, 2006; Conover *et al.*, 2009; Sutter *et al.*, 2012).

3. ARE THE OBSERVED CHANGES PHENOTYPIC OR GENETIC?

In order to prove that fisheries-induced evolution has occurred, it is necessary to prove that the changes have a genetic basis. Suitably designed experiments have power to disentangle phenotypic and genetic changes, without the use of molecular genetic analyses. Because parental environment or condition may affect offspring traits (i.e., trans-generational plasticity; Uller, 2008), the gold standard today is that only differences that persist to second generation under common-garden conditions are considered as likely genetic (Falconer & Mackay, 1996; Urban 2008; for examples see, Reznick & Bryga, 1987; Dam, 2012; Pascoal *et al.*, 2012). In the present review, we mainly refer to maternal-environmental effects, i.e. the influence of the mothers' environment on her offspring (Mousseau & Fox, 1998; referred to as 'maternal effects' in the review), rather than the broader definition (which covers epigenetic inheritance, transmission of organelles, nutrients, hormones or paternally modified environment, etc.; Badyaev & Uller, 2009, but see Wolf & Wade, 2009, for a narrower definition).

Below we will only consider those studies where genetic changes have been explicitly considered either through molecular methods or common-garden experiments. We thus exclude the studies by Drake *et al.* (1997), Carlson *et al.* (2007) and Edeline *et al.* (2007) that were ambiguous in this respect.

Lessons from experiments

Silliman (1975) concluded that the difference in growth rate between his control and harvested populations was due to genetic changes. However, we consider this conclusion as very uncertain. Silliman assessed genetic change by extracting 46 individuals from each population and rearing them outside the selection aquaria, with ad lib feeding for two months. Males from the selectively harvested aquarium presented slower growth than control ones, while females did not differ. In addition to the concerns mentioned above about the experimental design (mixed-origin and lack of replication, making the results vulnerable to the effects linkage equilibrium and randomness; Conover & Baumann, 2009), we assert that the observed difference cannot be attributed to genetic changes with a high confidence because maternal effects were not accounted for.

Kasperski & Kozłowski (1993) did rear the offspring (F1 generation) of their experimental populations (five size-selected and five controls) in common-garden conditions until maturation. They concluded that the differences in maturation size observed in the harvested populations compared to the controls were due to phenotypic responses to the different environments because the differences were not maintained in the offspring when reared in common-garden conditions (Kasperski & Kozłowski, 1993), which controlled for environmental factors, but not for maternal effects. Thus, a 15 month-experiment (2–3 generations according to Kasperski & Kozłowski, 1993) in guppies in which selection intensity was approximately 2%

every four weeks (one large individual was removed each time from populations with an average size of 47 individuals) resulted in a phenotypic but not genetic decrease in size at maturation. It should be noted that even though female guppies may produce their first offspring when they are on average twelve weeks old (Auer, 2010), the generation time of a population where reproductive period is prolonged (iteroparity) is much longer than age at first reproduction. Thus, we believe that the numbers of generations in the populations of Kasperski & Kozlowski (1993) were probably less than the stated 2–3 generations.

Conover & Munch's (2002), Philipp, Cooke and collaborators' (Cooke *et al.*, 2007, Philipp *et al.*, 2009), and van Wijk *et al.*'s (2013) artificial selection experiments showed that genetic changes took place in their populations. In general, the set-up of artificial selection experiments is characterized by 1) environmental effects that are controlled for (i.e. between-population differences are minimized), 2) maternal effects and epigenetic effects that are diluted as the lines are maintained for several generations and 3) genetic drift which influence is minimized with replication and large population size. Therefore, the changes observed in the experimental populations are most likely genetic (Figure 1). Furthermore, van Wijk *et al.* (2013) used molecular genetic methods to show that genetic change had taken place.

Conover & Munch's (2002) experiment proved evolvability of length at age (through evolution of growth rate) under the controlled conditions of the lab. In addition, genetic correlations between adult length and egg size were found. Egg diameter was found as genetically correlated with adult length at harvest with a realized heritability of 0.0006, which was highly significant, i.e., selection in adult size led to small but significant genetic change in egg diameter (Munch, Walsh & Conover, 2005). However, while it is undeniable that evolution took place, it has been

suggested that due to the simple and unrealistic conditions of the experiment, their results cannot be applied to real fisheries (Hilborn, 2006; Brown *et al.*, 2008).

Philipp *et al.*'s (2009) study showed that angling could act as an evolutionary force towards a "vulnerability trait". However, the set-up was not as controlled as Conover & Munch's (2002), as the founder population was small (three pairs) and rearing both lineages together in a common pool may have introduced confounding factors. While rearing the lineages together for testing the vulnerability to angling was appropriate to reduce possible environmental differences in the test, it also introduced possible noise in the study of selection and genetic change. In principle, changing the individuals from one single-lineage-pond to a mixed-lineage-pond might affect how the individuals were interacting, thus confounding the effects of selection. However, later studies more unambiguously indicate that a genetic change took place: Sutter *et al.* (2012) showed that the selected lineages maintained their differences in angling vulnerability after two generations without selection.

Haugen & Vøllestad (2001) concluded that the differences in adult traits observed between lakes were most likely caused by the different fishing regimes. In addition, some of the phenotypic differences were also shown to be genetic, at least in three of the lakes (Lesjaskogsvatn, Hårrtjønn and Aursjøen), under common-garden conditions (Haugen & Vøllestad, 2000). Early life history traits (survival, growth and size during the period of first feeding) were assessed from first generation individuals reared in the laboratory. Traits remained different between populations and thus it was concluded that the differences had a genetic basis (Haugen & Vøllestad, 2000), although maternal effects could still play a role. However, the genetic basis of the differences was only studied for the juvenile traits and not for the adult ones, the latter being those more closely associated with selective fishing.

Edley & Law (1988) showed evidence for clonal evolution of maturation size. Removal of big individuals resulted in populations dominated by slow-growing clones that reproduced at smaller size relative to negative size-selection harvest. These differences were maintained when the size-dependent selection was halted and when sampled individuals from all populations were reared isolated under common conditions. Edley & Law's (1988) study was the first one to show genetic changes due to harvesting under experimental conditions. However, the life cycle of *Daphnia* differs profoundly from that of the commonly exploited fish, making it difficult to apply Edley and Law's (1988) results to fisheries-induced evolution.

Van Wijk *et al.* (2013) not only showed a genetic basis of the observed changes in male guppy length with their controlled artificial selection, but they also showed that the selected lines differed in allele frequencies of candidate genes. Four candidate genes associated with quantitative trait locus for length (linked to the Y chromosome) showed a response to size-selection on males (Van Wijk *et al.*, 2013), while variation in neutral microsatellites was not different between lines. This study is thus the first one to show a direct link between genetic and life-history change in selection experiments directly focused on FIE. It should, however, be noted that Van Wijk *et al.*'s (2013) experiment only considered size-selective mortality on males, a setting not representative of most fisheries. Indeed, their evidence for genetic changes was strongly linked to the male sex (Y) chromosome. Furthermore, the set-up with strong knife-edge selection and non-overlapping generations was no more representative of real fisheries than Conover and Munch's (2002) study.

Conclusions

Experiments have shown with high likelihood that life history and larval traits can undergo evolution when populations are subjected to harvesting. However,

experiments that have employed the necessary design to unambiguously achieve this are still few in number. Knowledge on whether the changes induced by fishing have a genetic basis is necessary in order to develop appropriate management plans. Thus, more selection experiments used to their full potential should be performed.

4. IS THE MATURATION SCHEDULE AFFECTED BY FISHING?

Most of the changes observed in the wild stocks are related to maturation schedules, and secondly with growth (Trippel, 1995; Law, 2000; Hutchings & Baum, 2005). In many of these examples the changes have been interpreted as fisheries-induced evolution (Jørgensen *et al.*, 2007). Most of the evidence comes from studies using one approach, the probabilistic maturation reaction norms. The capacity of this approach to disentangle phenotypic and genetic changes has been challenged, both on basis of fundamentals of reproductive physiology (Wright, 2007) and on basis of concrete experiments (Morita, Tsuboi & Nagasawa, 2009, Uusi-Heikkilä *et al.*, 2011, Diaz Pauli & Heino, 2013). Thus, selection experiments aimed at studying the effect of size selective fishing would help to clarify this matter, and even further, to test whether probabilistic maturation reaction norms are appropriate for disentangling genetic and plastic changes in maturation. Despite of this, few selection experiments have dealt with maturation schedules.

Lessons from experiments

Haugen (2000a) studied differences in age at 50% maturity among lake populations, and found individuals maturing at earlier ages in the lakes with higher fishing intensity. Even though divergence rates and evolutionary rates have been calculated for many life history traits in these lakes, those related to maturation schedules were based on phenotypic, not genetic data (Haugen & Vøllestad, 2001). Thus, this study was unable to conclusively show genetic changes in maturation schedules.

Until recently, Edley & Law's (1988) experiment with water fleas was the only selection experiment that studied the evolution of maturation schedules due to size selection. As mentioned in the section above, those populations in which large individuals were removed started reproducing at smaller size. With common-garden experiments, Edley & Law (1988) were able to show that the changes were genetic.

van Wijk *et al.* (2013) showed that the guppy lines differed in male age and size at maturation after three generations of size-selective mortality. Because there was only a minor change in growth (results not reported, but this can be inferred from their Fig. 1), underlying maturation tendency had evolved. This phenotypic change could be concluded to have a genetic basis, thanks to their controlled artificial selection experiment set-up. van Wijk *et al.* (2013) also performed a molecular genetic analysis, but the candidate genes that responded to selection were associated with individual size and not maturation.

van Wijk *et al.* (2013) joins Edley and Law's (1988) as the only evidence from selection experiments for evolution of maturation schedule in size-selected populations. Notice that Conover & Munch (2002) did not consider evolving maturation, despite the experiment being sometimes interpreted in that way (e.g., Morita *et al.*, 2005; Rankin & López-Sepulcre, 2005; Mollet, Kraak & Rijnsdorp, 2007; Quinn *et al.*, 2007). In their experiment maturation was triggered by photoperiod, and thus it was not allowed to evolve; changing size at maturation was a secondary consequence of changing juvenile growth.

Conclusions

Very few experimental studies have so far focused on maturation, and only two studies rigorously demonstrated harvest-induced evolution of maturation. There are more experimental studies considering fishing-induced changes in growth than in

maturation schedules, perhaps because growth is easier to measure in experiments than maturation. This is contrary to the field-based, observational evidence of harvesting-induced changes that are dominated by maturation. We believe that this is the main gap that should be filled in the study of FIE, and we encourage more studies that focus on how maturation schedules are affected by different types of fishing. However, the ability of probabilistic reaction norms to disentangle genetic and phenotypic changes has been assessed by Uusi-Heikkilä *et al.* (2011) and Diaz Pauli & Heino (2013), and several studies are currently being performed to study adaptation of maturation schedules in experimental populations.

5. WHAT IS THE RATE OF CHANGE, AND 6. IS IT REVERSIBLE?

For fisheries-induced evolution to be included in management plans, knowledge on the rate of fisheries-induced evolutionary change and its reversibility are critical. It is the quantitative rate of the change that is most important for practical purposes (Law, 2007). Conclusions about the rate of evolution range from fast and important (Jørgensen *et al.*, 2007; Darimont *et al.*, 2009; Sharpe & Hendry, 2009; Devine *et al.*, 2012) to probably moderate (Law, 2007) or so as to be unimportant (Andersen & Brander, 2009). Thus, there is a need to understand intensities of selection generated by fishing, heritabilities of the traits under selection, and whether the rates of change in traits predicted from this information are consistent with the changes observed. Heritabilities and selection differentials are useful as they provide a preliminary understanding of the absolute rate of evolution (Law, 2007), while rates in haldanes or darwins enable us to compare studies and to infer relative speed of evolution (Hendry & Kinnison, 1999; Sharpe & Hendry, 2009; Devine *et al.*, 2012). As the traits changing are important for fisheries, a related question is whether these changes can be reversed and how fast this can be done.

Philipp *et al.* (2009) estimated a cumulative selection differential of 0.07 (relative to 0.04 in the initial generation) in catch rate (captures per hour, individual and hectare) after three generations between selected lines; heritability in the vulnerability of being angled was $h^2=0.14$. These values were calculated taking into account the divergence response, not the change relative to the parental population. The population that was selected for low vulnerability to angling presented a reduction of 49% in the catch rate after three generations (Philipp *et al.*, 2009).

Haugen & Vøllestad (2001) studied the rates of divergence and evolution of both adult and juvenile life history traits in grayling. They studied divergence rates using synchronic data (i.e., comparing different populations at the same time period) of life history traits in five different populations in lakes in Norway. Rates of evolutionary change were estimated from allochronic data (time series of single populations) in a single lake. The evolutionary rates obtained were high (0.002–1.008 haldanes, 10–30,500 darwins) compared to other life-history studies on the same temporal scale (Haugen & Vøllestad, 2001; Hendry & Kinnison, 1999). However, they are only about twice as large as the average rate estimated for exploited fish (Darimont *et al.*, 2009). The allochronic data showed that constant reduction in age (–0.33 years in 10 years) and length (–18 mm in 10 years) at maturity had taken place and that selective fishing was the driver of those changes.

van Wijk *et al.* (2013) estimated both heritability and evolutionary rates for male length in their guppy selection experiment. Positively size-selected males were 6.5% shorter in standard length, while negatively size-selected males were 7.5% larger after three generations of selection. The estimated heritability was 0.20 and 0.27 for the positively and negatively size-selected lines, respectively. This resulted in an evolutionary rate for male length of 50,000–55,000 darwins and 0.3 haldanes (van

Wijk *et al.*, 2013). These values are two to ten times larger (after 7 and 13 generations, respectively) than the rates estimated for guppy male weight in natural habitats (Reznick *et al.*, 1997), and five times larger than the average rate estimated for changes in fish length due to fishing (Darimont *et al.*, 2009).

Conover & Munch (2002) controlled the selection pressure in their study, thus the response and the heritability of the selected trait could be easily estimated with the breeders' equation. The heritability for mean length on day 190 was $h^2=0.20$ and the cumulative selection differential was approximately ± 60 mm, depending on treatment. 90% size-selectivity intensity per generation produced a reduction of 25% in size at age over four generations in those populations where large individuals were harvested (Conover & Munch, 2002). However, this study used unrealistically high fishing pressure, thus the evolutionary change obtained cannot be readily compared with wild populations. Simulations based on this experiment showed that a more realistic fishing pressure would have resulted in an evolutionary change in size of 25% only after 15–50 generations (Brown *et al.*, 2008). Nevertheless, these simulations over longer time scales resulted in evolutionary change of magnitudes comparable to those estimated in the wild (Brown *et al.*, 2008).

The experiment of Conover & Munch (2002) was also taken one step further to assess the reversibility of the changes. During four more generations the populations experienced 90% harvest rate, but there was no selection for size, i.e. the removals were size-independent (Conover *et al.*, 2009). The initially positively size-selected populations started a slow recovery, and full recovery to initial values of mean length was projected to happen after about 12 generations. The negatively size-selected populations did not recover. Conover *et al.* (2009) suggested that the ultimate cause of the recovery is due to factors intrinsic to the population. In the positively size-selected populations there was selection pressure for size-dependent traits that increased

fitness and genetic correlations among traits during the time size selectivity was halted. This led the population to reverse to the original conditions. The negatively size-selected populations may have experienced stabilizing selection on size. Under the experimental conditions there were no factors that would lead to evolution of smaller size, so there was no recovery to initial conditions (Conover *et al.*, 2009).

Even though the positively size-selected line partially recovered the initial values of size and growth, not all the correlated traits followed the same trend after size-selective mortality was halted (Salinas *et al.*, 2012). Larval viability and growth efficiency under unlimited food availability showed full recovery, egg volume and size-at-hatch showed partial recovery, while food consumption, vertebral number and growth efficiency under limited food availability showed no recovery at all in positively size-harvested lines after 11 generations (Salinas *et al.*, 2012). During the recovery phase size-selection was halted, but there was still selection for increase fecundity; this resulted in traits related with fecundity and early survival to experience recovery in the positively size-selected lines (Salinas *et al.*, 2012).

Conclusions

Several studies have shown that fishing can cause significant changes in a few generations. However, standardised rates of change have only been estimated by two studies (Haugen & Vøllestad, 2001; van Wijk *et al.*, 2013), which is what is needed in order to compare the speed of evolution with other studies. It is necessary to set a reference point or to compare with other studies' evolutionary rates to determine whether the change takes place rapidly (for reviews of evolutionary rates, see Kinnison & Hendry, 2001; Darimont *et al.*, 2009; Devine *et al.*, 2012).

The selection studies presented here show that populations become adapted to fishing. Populations that are adapted to fishing are thought to be more resilient to fishing

pressure compared to those not well adapted. However, this may come to the cost of not being well adapted to natural conditions and to changing environments (Conover, 2000; Jørgensen *et al.*, 2008a; Heino, Rijnsdorp & Dieckmann, 2012). Experimental evidence for whether fishing-adapted populations are more resilient is lacking; only Walsh *et al.* (2006) looked at whether the characteristics of the fishing-adapted populations are suitable for a potential recovery. Furthermore, only one experiment so far has directly addressed the question of reversibility (Conover *et al.*, 2009; Salinas *et al.*, 2012), showing that rates of recovery, while not negligible, were slower than rates of adaptation to fishing in positively size-selected lines, and that the recovery of traits depends on the selective landscape remaining after size-selectivity is relaxed. While acknowledging that under laboratory conditions it is difficult to create a natural selection regime that would realistically drive recovery, these studies provide some support for the idea that we might be building up a Darwinian debt: for each year of selective fishing, it will take longer time for the inherited trait to recover to its original value (Dunlop *et al.*, 2009).

7. DO CHANGES IN THE POPULATION AFFECT THE PROFITABILITY OF THE FISHERY?

Selective fishing pressure results in changes in the composition of the population. These changes are initially demographic and phenotypic, but eventually can become genetic (Pigliucci, 2005; Tuomainen & Candolin, 2011). On the one hand, evolutionary changes caused by the fishery are positive from the fish point of view; fish become better adapted to the environment and thus produce the most progeny possible in such conditions (Heino *et al.*, 2012). On the other hand, those changes do not have to be positive from the fishery perspective; for instance, evolution to smaller size could mean more fish under the minimum legal body size, i.e. not attractive for fisheries and thus low yield and productivity for the fishery (Heino *et al.*, 2012).

Only three experiments have considered the effect of FIE on yield or catch rate. In general terms, the experiments showed that the removal of large individuals lead to lower yield, even though they were quite different in their set-up. Conover and Munch's study showed that removal of large individuals led to lower yield (biomass), spawning stock biomass, smaller individual size (Conover & Munch, 2002) and lower fecundity (Walsh *et al.*, 2006) in populations with discrete generations and fed ad-libitum. Edley & Law (1988) revealed that culling of large individuals in clonally-reproducing populations with overlapping generations and ecological feedbacks resulted in reduced catch (measured in numbers of individuals) over time, while culling of small individuals showed no such reduction. However, the biomass yield decreased in both selected lines; in absolute terms the decrease was steeper for populations where large individuals were culled (Figure 2a), but the decline of yield biomass relative to the initial conditions was stronger for populations that experienced culling of small individuals (Figure 2b). This happened because both culling regimes led to smaller mean size of harvested individuals, but this decrease was stronger in populations where small individuals were culled.

In addition, fishing alters the behavioural composition of the population; individuals that are better at parental care (Drake *et al.*, 1997; Sutter *et al.*, 2012) are being fished more, increasing the proportion of cuckolders. Given that vulnerability to fishing is heritable and can reduce catch rate in almost 50% in three generations (Philipp *et al.*, 2009), experiments now indicate that evolution toward fish that are more difficult to catch is possible—contrary to what Miller (1957) postulated half a century ago.

Conclusions

The only three experiments that considered the effect of FIE on yield show that selection towards large individuals or more vulnerable individuals produce lower yield, but also that the populations are less productive. However, the experiments have either used simplistic set-ups (Conover & Munch, 2002; Philipp *et al.*, 2009; Walsh *et al.*, 2006) or species (Edley & Law, 1988) that make it difficult to apply the results to real fisheries. We urge carrying out further experiments to better understand this important aspect of FIE.

Fishing selectivity is included in harvesting management plans to protect productivity of the fish stock and thus, the profitability of the fishery. However, selection experiments show that this selectivity leads to populations adapting to fishing, and this change may in turn reduce the productivity and the resilience of the population. Thus, it should be in the interest for fisheries managers to reduce such evolutionary effects of fishing.

Selection experiments also highlight another aspect of profitability. Experiments tend to suggest that fishing leads to smaller body size, at least post-maturation. Smaller individual sizes are often less valuable (Zimmermann & Heino, 2013) and even illegal catch when they lie under the minimum size limit. Smaller size is correlated with lower fecundity, reduced parental care and lower willingness to forage, which can result in lower productivity of the population. In addition, the removal of highly vulnerable fish can result in populations with higher gear avoidance abilities, which in turn would lead to lower probability of catching, and thus lower productivity and profitability.

In the previous section, we presented how selection experiments have contributed to the seven questions of concern in the study of FIE. In this section we summarize their contribution to FIE research according to their experimental design. The utility of selection experiments to elucidate FIE presumes both well-designed and realistic experimental set-ups. Thus, our discussion considers these two issues.

A well-designed selection experiment disentangles the effect of selection from other, confounding factors (environmental trends and feedbacks, maternal effects, drift, etc.). This is not an easy task, as this review shows for the particular case of FIE. In the present framework, the number of selection experiments performed is small, a mere nine experiments (some reported in multiple papers), but this number is nearly halved when only considering those studies with the “cleanest” experimental designs (viz. Conover & Munch, 2002; Edley & Law, 1988; Haugen & Vøllestad, 2001; Philipp *et al.*, 2009; van Wijk *et al.*, 2013).

In addition, we think that selection experiments designed such that their results can be applied to more general settings are crucial. This is what we called a more realistic design, where life histories similar to those of wild stocks are mimicked, and where ecological feedbacks and sexual selection are allowed (and accounted for, to fulfil the criteria of well-designed experiments); these can interact with and alter fishing-induced selection. After considering this criterion the number of studies is unfortunately reduced to zero. Conover & Munch’s (2002), van Wijk *et al.*’s (2013), and Philipp, Cooke and collaborators’ (Cooke *et al.*, 2007; Philipp *et al.*, 2009; Redpath *et al.*, 2009, 2010; Nannini *et al.*, 2011) studies only allow single reproductive events and discrete generations; i.e. the life history is constrained to be semelparous. For species or populations that are naturally iteroparous, this is a dramatic simplification. These simplifications ease the study of the mechanism of selection, but hamper comparisons with results obtained from wild populations

(Figure 1; Table 2). Edley & Law's (1988) work with *Daphnia* in principle fulfils the requirements presented here, but the use of tiny, clonally reproducing crustaceans limits the applicability of the results to exploited fish stocks in the wild. The studies by Haugen and Vøllestad (Haugen, 2000a, b; Haugen & Vøllestad, 2000, 2001) took fully advantage of the natural selection experimental design. They also took their analysis further by estimating genetic change and the rate of that change. However, only juvenile traits were assessed for genetic change; these traits were affected primarily by environmental factors and not fishing. The adult traits that were affected by fishing were not assessed under common-garden conditions. Thus, for the particular perspective of this review, we cannot consider Haugen & Vøllestad's (2001) study as fulfilling all our desiderata, despite being a well-designed and realistic experiment in many respects.

We must, of course, acknowledge that running an experiment that would pass all our criteria is very demanding. For example, the discrete-generation setup is much-used probably because it makes experiments easier to manage and for naturally iteroparous species, greatly reduces the generation time. We have also lamented the lack of studies focused on maturation, a key trait observed to change in the wild. A key challenge for experimental studies is that for many species, maturation is difficult to detect without sacrificing individuals. However, the most fundamental problem with experimental studies is creating conditions that resemble those in the wild. Natural selection experiments are a step into this direction, but unless carried out in the wild, involve only caricature representations of natural feedbacks due to resource availability, parasites, and predation (within the European Union, it is usually forbidden to run experiments with two or more interacting vertebrates). This also limits our ability to experimentally study population-level consequences of fishing.

The experiments have been based on a wide range of fish species that can be separated in two groups: small species with short life cycle suitable for tank experiments (guppy, silverside) and larger species that are targets of commercial and recreational fisheries and which tend to require larger enclosures or ponds (all the rest). Tilapia is an outlier in the latter group, and perhaps surprisingly, the only species that is used in aquaculture. Again, the choice of study species reflects the trade-off between the ease of running large experiments and linking the results to real fisheries.

FUTURE DIRECTIONS

Studying FIE is not easy, neither in the wild or experimentally. Both approaches have their strengths, and both are indispensable. We believe natural selection experiments are the most appropriate experiments to study fisheries-induced evolution. They enable one to study the effect of size selectivity on age- and size-structured populations under conditions allowing for iteroparous life history where trade-offs between current and future reproduction can unfold. Sexual selection can play its role in mating, as the experimenter does not choose the breeders. In addition, such experiments allow for density-dependent feedbacks and “natural” selection that might reduce the effects of fishing through compensatory effects, thus allowing more realistic selection pressures (Figure 1; Table 2). This all is making the experimental conditions more realistic and thus, more comparable to those experienced by exploited stocks, making the results more readily applicable. On the other side, results might become more complicated to interpret when some control on the experiment is sacrificed for realism.

To fulfil the criterion of being well-designed, such experimental set-ups should be accompanied with controlled selection pressures directed to a single trait, in order to

unequivocally attribute the observed changes to a single driver, and the estimation of the rate of change, to allow comparison with other studies. In addition, demonstrating phenotypic divergence between populations due to dissimilar selection pressures is not sufficient to conclude that fisheries-induced evolution has taken place; natural selection experiments should be complemented with common-garden experiments and/or genetic analyses.

Applying methods of population genomics and quantitative genetics (candidate genes, genome scan, QTL mapping, etc.) would allow identifying adaptive population divergence, however such techniques are still at their infancy in the study of FIE (but see Nielsen *et al.*, 2009; Jakobsdóttir *et al.*, 2011; van Wijk *et al.*, 2013). An important limitation is that relatively little is known about specific genes associated with the processes of growth and maturation, or with other traits of interest to FIE, even though the genomes of some commercially important species have been sequenced (e.g., eel, salmon and cod; Ng *et al.*, 2005; Star *et al.*, 2011; Henkel *et al.*, 2012). Thus, up to date most molecular studies on adaptive responses have focused on neutral loci or genes related to immune and temperature responses and circadian cycles (Hansen *et al.*, 2012). Until genetic studies can be fully harnessed to the study of FIE, unambiguous evidence of genetic changes can only be obtained in experimental conditions by rearing individuals from the diverging populations under common-garden conditions.

van Wijk *et al.*'s (2013) recent paper is the first one that directly aimed at studying differences in size due to size-selective mortality combining selection experiments and molecular methods. Their study seems to provide the evidence demanded for the case of FIE (Kuparinen & Merilä, 2008). However, artificial selection experiments might not yet differ much from genetic improvement in aquaculture (reviewed by Gui & Zhu, 2012). We believe that to improve the understanding on FIE selection

experiments should move towards more realistic settings, comparable to populations harvested in natural conditions.

Future natural selection experiments should be focused on studying how maturation schedules and growth are affected—which at the moment are the main concerns in FIE research—but not restricted to these, because we need to expand our knowledge of how other traits are affected. The consequences of FIE on yield are still poorly understood. In addition, we want to raise attention to the potential that these experiments have in helping to improve and test the different methods of population genomics (e.g. construct pedigrees that allows to study founder effect, loss of genetic variability and bottle necks; or identify and follow SNPs associated to certain phenotypes in small scale where results are easily interpretable) and applied statistics (e.g., the Probabilistic Maturation Reaction Norm, Heino *et al.*, 2002; the Animal Model approach, Wilson *et al.*, 2010).

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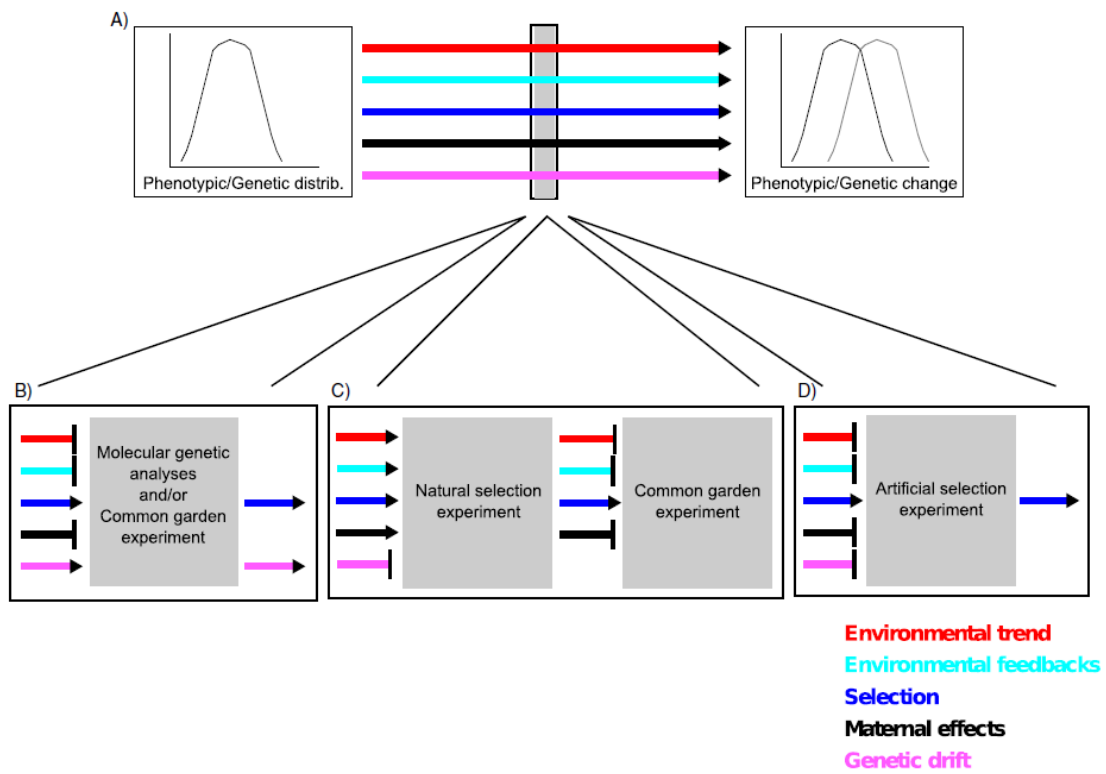


Figure 1. a) Schema of a shift (either genetic or phenotypic) in the distribution of a certain trait in a population. Coloured arrows represent the processes potentially contributing to that change. Grey box represents how different methods mentioned in this review allow disentangling genetic from phenotypic nature of the change by filtering (accounting for) the different arrows (processes). b) In natural conditions, the genetic evidence for change, but not the driver, can only be obtained through molecular genetic analyses and/or common-garden experiments. c) Natural selection experiments combined with common-garden experiments also give evidence for genetic change and driver of selection. d) Artificial selection experiments control all processes involved, showing evidence for genetic change and the driver of selection.

It is assumed that the experiments are performed with well-designed set-ups.

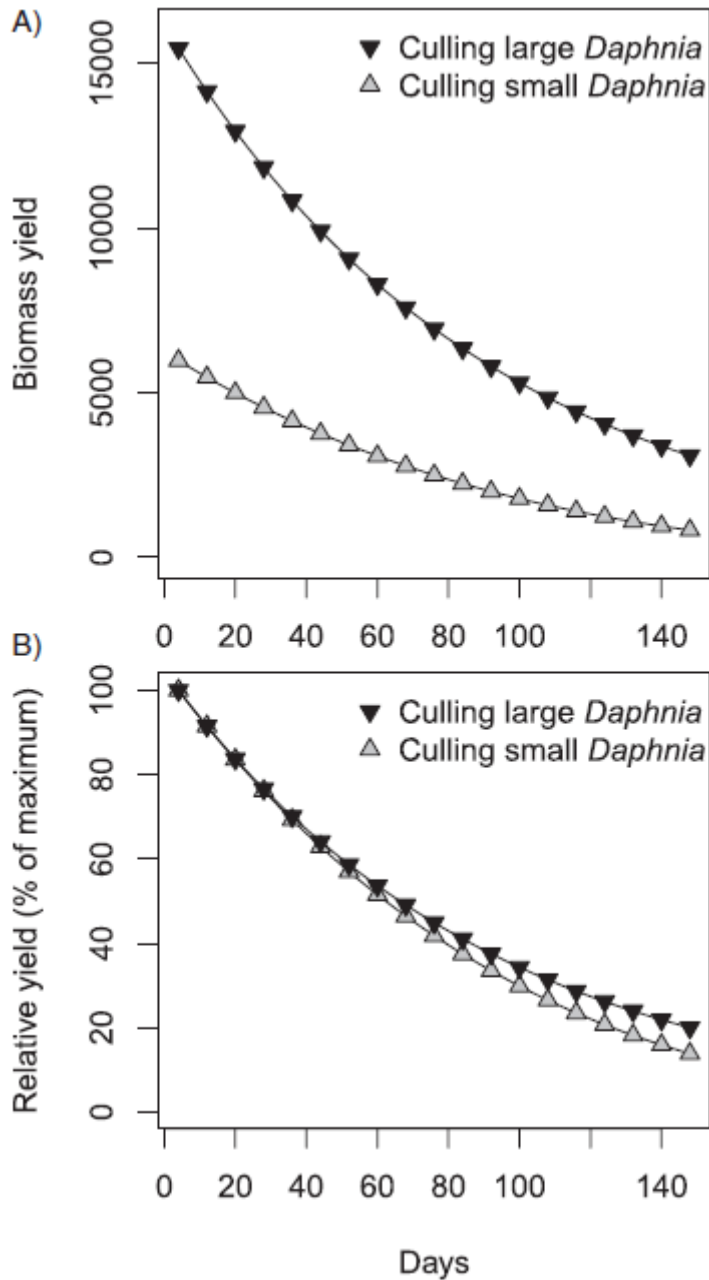


Figure 2. Trends over time in a) absolute biomass yield and b) relative to initial yield. The curves are derived from the results of Edley & Law's (1988) experiment on *Daphnia magna*. Grey triangles represent populations with culling of small individuals, while black inverted triangles represent populations where large individuals were culled. Biomass yield is expressed in arbitrary units based on Edley & Law's (1988) net mesh units.

Table 1. Summary of the studies reviewed

| Study | Type of experiment | | Number of experimental | | Direct response and indirect correlated response | | Genetic or phenotypic changes | Rate of change | | | References |
|--|--------------------|------------------------------|------------------------|------------|--|---|-------------------------------|-----------------------|--|---------------------------|---|
| | Selection | Design | Units | Replicates | Life-history traits | Other | Phenotypic/ Genetic change | Number of generations | Heritability and selection differentials | Comparable rate of change | |
| Growth rate in Atlantic silversides | Artificial | Manipulative | 6 | 2 | Individual size Growth rate Fecundity Egg size Larval growth Egg volume Larval viability Larval size at hatching | Consumption rate, Swimming performance Antipredator behaviour | +/+ | 4 | + | - | Conover & Munch (2002); Munch <i>et al.</i> (2005); Walsh <i>et al.</i> (2006); Conover <i>et al.</i> (2009); Salinas <i>et al.</i> (2012) |
| Angling vulnerability in largemouth bass | Artificial | Manipulative | 1 | 1 | Growth rate Gonadosomatic index | Angling vulnerability Nest care behaviour Cardiac output Metabolic capacity Heart rate | +/- | 5 | + | - | Cooke <i>et al.</i> (2007); Philipp <i>et al.</i> (2009); Redpath <i>et al.</i> (2009); Redpath <i>et al.</i> (2010); Nannini <i>et al.</i> (2011); Sutter <i>et al.</i> (2012) |
| Reproductive strategy in bluegill | Natural | Mensurative | 6 | 1 | Growth | Male reproductive strategy: parental/cuckolder | +/- | ? | - | - | Drake <i>et al.</i> (1997) |
| Growth rate in pike of Windermere | Natural | Manipulative/ Mensurative | 1 | 1 | Individual size Growth Reproductive investment | | +/- | 2-5 | - | - | Edeline <i>et al.</i> (2007); Carlson <i>et al.</i> (2007) |
| Life history in daphnids | Natural | Manipulative | 6 | 3 | Individual size Growth Size at maturation | | +/+ | 5-9 | + | - | Edley & Law (1988) |
| Life history of grayling | Natural | Mensurative | 5 | 1 | Growth rate Adult survival Age at maturity | | +/+ | 9-22 | + | + | Haugen & Vøllestad (2001); Haugen (2000a); Haugen (2000b); Haugen & Vøllestad (2000) |
| Maturation in guppies | Natural | Manipulative | 10 | 5 | Individual size Size at maturation | | +/- | 2-3 | - | - | Kasperski & Kozłowski (1993) |
| Growth rate in tilapias | Natural | Manipulative | 1 | 1 | Individual size Growth rate | | +/- | 3-4 | - | - | Silliman (1975) |
| Size in guppies | Artificial | Manipulative | 5 | 2/1 | Individual size Size/age maturation | | +/+ | 3 | + | + | Van Wijk <i>et al.</i> (2013) |

Use of bold font indicates traits observed to change, whereas correlated traits are shown in normal font.

Table 2. Main characteristics of the two types of selection experiments with their advantages and disadvantages.

| Artificial selection experiment | | |
|--|---|--|
| Main characteristics | Advantages | Disadvantages |
| Experimentally imposed selection | | |
| Direct choice of the selected trait | + Simple & easy to perform | |
| Directly controlled selection (nature, strength, consistency) | + Straightforward results | – Lack of realism (no environ. feedback or natural sel.) |
| Controlled reproductive events | + Proximate and ultimate cause of change | – Not all traits allowed to evolve |
| Discrete generations (usually) | | |
| Natural selection experiment | | |
| Main characteristics | Advantages | Disadvantages |
| Indirectly imposed selection | | |
| No direct choice of selected trait | + Realism | |
| No direct control of selection | + Allow for compensatory response | – Requires extra test |
| No control on reproductive events | | – Unable to determine direct cause (proximate) of selection |
| Overlapping generations (usually) | + Ultimate cause of change | |
| Age and size structured populations | + All traits allowed to evolve | |

Table 3. Summary of the conclusions drawn for each of the seven issues of importance in the study of FIE. Numbers in parentheses refer to studies that fulfil the criterion; numbering (footnote) follows the same order as Table 1.

| Question | Conclusion | Number of studies | |
|---|--|---------------------------|-------------------------------------|
| | | dealing with the question | successfully answering the question |
| 1. Does selective fishing lead to phenotypic changes? | <ul style="list-style-type: none"> • Fishing can lead to phenotypic changes. • Artificial selection experiments are best at attributing fishing as the driver of change, at the cost of being less comparable to nature. | 9/9 (1–9) | 8/9 (1–9) |
| 2. Does size-selective fishing alter other traits correlated to the selected trait? | <ul style="list-style-type: none"> • The effect of fishing pressure is more complex than just removing certain size classes or traits. • Many different traits are indirectly affected by fishing. | 4/9 (1,2,5,9) | 4/4 (1,2,5,9) |
| 3. Are observed changes phenotypic or genetic? | <ul style="list-style-type: none"> • Fishing can lead to genetic change. • The number of experiments with appropriate design to answer this issue is scarce. | 6/9 (1,2,5–9) | 5/6 (1,2,5,9) |
| 4. Is the maturation schedule affected by fishing? | <ul style="list-style-type: none"> • Very few experimental studies focused on maturation. • Only two studied harvest-induced evolution of maturation. | 3/9 (6,7,9) | 2/3 (6,9) |
| 5. What is the rate of change? | <ul style="list-style-type: none"> • Several studies showed fishing can cause significant changes in a few generations. • Standardised rates of change have only been estimated by two studies. | 2/9 (6,9) | 2/2 (6,9) |
| 6. Is the change reversible? | <ul style="list-style-type: none"> • Recovery rates may be slower than rates of adaptation to fishing. • Only one study focused on reversibility of change. | 1/9 (1) | 1/1 (1) |
| 7. Do changes in the population affect the profitability of the fishery? | <ul style="list-style-type: none"> • Removal of large individuals leads to lower yield and less productive populations. • Removal of highly vulnerable individuals results in lower probability of catching. | 3/9 (1,2,6) | 3/3 (1,2,6) |

¹Conover & Munch (2002), Walsh *et al.*, (2006), Conover *et al.*, (2009); Salinas *et al.*, (2012); ²Cooke *et al.*, (2007), Philipp *et al.*, (2009), Sutter *et al.*, (2012); ³Drake *et al.*, (1997); ⁴Carlson *et al.*, (2007). Edeline *et al.*, (2007); ⁵Haugen & Vøllestad (2001); ⁶Edley & Law (1988); ⁷Kasperski & Kozlowski (1993); ⁸Silliman (1975); ⁹van Wijk *et al.* (2013)