Fisheries-Induced Evolution

Mikko Heino,[1,2,3] Beatriz Díaz Pauli,[1] and Ulf Dieckmann[3]

[1]Department of Biology and Hjort Centre for Marine Ecosystem Dynamics, University of Bergen, N-5020 Bergen, Norway; email: mikko.heino@uib.no

[2]Institute of Marine Research and Hjort Centre for Marine Ecosystem Dynamics, N-5817 Bergen, Norway

[3]Evolution and Ecology Program, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria

Keywords

applied evolution, behavior, life-history theory, phenotypic change, selection

Abstract

Increased mortality from fishing is expected to favor faster life histories, realized through earlier maturation, increased reproductive investment, and reduced postmaturation growth. There is also direct and indirect selection on behavioral traits. Molecular genetic methods have so far contributed minimally to understanding such fisheries-induced evolution (FIE), but a large body of literature studying evolution using phenotypic methods has suggested that FIE in life-history traits, in particular maturation traits, is commonplace in exploited fish populations. Although no phenotypic study in the wild can individually provide conclusive evidence for FIE, the observed common pattern suggests a common explanation, strengthening the case for FIE. This interpretation is supported by theoretical and experimental studies. Evidence for FIE of behavioral traits is limited from the wild, but strong from experimental studies. We suggest that such evolution is also common, but has so far been overlooked.

1. INTRODUCTION

Contemporary fisheries have been likened to a "large-scale experiment on life-history evolution" (e.g., Rijnsdorp 1993). All fishing is selective, and not only with respect to life-history traits. Fishing operations are deliberatively selective, often because of regulations enacted to protect small individuals, and more ubiquitously selective because fishermen target the types of fish that are most available or profitable to catch (Holland & Sutinen 1999, Salas et al. 2004, Andersen et al. 2012). Even fishing methods such as purse seining or dynamite fishing, which are unselective at the local scale, are selective at the population level because fish are not randomly distributed in space (Planque et al. 2011).

Whenever fishing is selective for characteristics that show genetic variability among individuals, fishing will lead to evolutionary change in the affected populations. This insight was first established—well before the genetic basis of inheritance became widely known—by Cloudsley Rutter, a Californian scientist who worked with Chinook salmon (*Oncorhynchus tshawytscha*) in the Sacramento River. Rutter (1902) remarked that the law prohibiting the use of nets to catch small male salmon returning to spawn countered common sense as "a stock-raiser would never think of selling his fine cattle and keeping only the runts to breed from" (p. 134). Yet, the fishery let the small salmon reach the spawning grounds, while catching the large ones. On this basis, Rutter predicted that "the salmon will certainly deteriorate in size" (p. 134). This would not surprise aquaculturists, who have demonstrated how various traits in a large number of species possess significant heritabilities and have responded to artificial selection (Friars & Smith 2010). For example, about 10 generations of selective breeding have increased the growth rate in Atlantic salmon (*Salmo salar*) threefold (Solberg et al. 2013).

Despite clear parallels with animal breeding—fisheries-induced selection is a form of artificial selection, albeit unintentional and uncontrolled—the idea of fishing as an evolutionary force has been slow to penetrate the fisheries-research community. Rutter passed away in 1903 (Roppel 2004) and his seminal remarks remained hidden in a long report, and were largely overlooked. Similarly, other early work attracted scant attention at the time it was published, including work on the effect of selection on growth by Cooper (1952), on fish behavior by Miller (1957), on a selection experiment by Silliman (1975), on gillnet selectivity with respect to multiple life-history traits by Handford et al. (1977), and on evolution of the age at maturation by Borisov (1978). This situation started to change only in the 1980s, perhaps partly in response to the blossoming of life-history theory (Roff 1992, Stearns 1992), and partly because life-history changes had been observed in many populations of harvested fish (reviewed in Trippel 1995). By the early 2000s, fisheries-induced evolution (FIE) had become a vigorous field of inquiry.

Several general reviews on FIE have already been presented, starting with the influential, but now partly outdated, review by Law (2000). Similarly, reviews by Kuparinen & Merilä (2007), Fenberg & Roy (2008), and Hutchings & Fraser (2008) predated many new developments. Although several recent reviews cover specific aspects of FIE—such as speed (Devine et al. 2012, Audzijonyte et al. 2013), growth rate (Enberg et al. 2012), theory and consequences (Heino et al. 2013), and experiments (Díaz Pauli & Heino 2014)—there is no recent general review covering the main developments of the field occurring during the past decade, a gap that this review aims to fill. After providing an overview of theoretical expectations, we summarize the empirical evidence for FIE, and conclude by discussing its implications. Although FIE is relevant for fisheries of finfish, elasmobranchs, and invertebrates alike, most of the empirical work has been based on finfish, which are the focus of this review.

2. THEORETICAL BACKGROUND

Theoretical expectations of fisheries-induced selection are fundamentally simple: it affects any trait that determines how individual fish are exposed to fishing. And to the extent that the affected traits possess any genetic variability, the resultant selection differentials become incorporated into a fish population's gene pool.

The salient theoretical questions are, therefore, more specific. What is the direction of fisheries-induced selection imposed by a given fishing regime on a given trait? How strong is such selection? What is the resultant pace of FIE? Can the direction of selection be reversed, or the pace of FIE be slowed, by using alternative fishing regimes? When must we expect fisheries-induced selection to be disruptive or the resultant evolutionary dynamics to be bistable? How are current heritabilities affected by past fisheries-induced selection?

Life-history traits are among the prime targets of fisheries-induced selection, prominently including traits regulating investments into growth, maturation, and reproduction (Heino & Godø 2002). Likewise, behavioral and morphological traits affecting exposure to fishing are likely to experience fisheries-induced selection; however, these targets have received less scientific scrutiny. In addressing the aforementioned questions, we therefore align with the literature's focus on life-history traits and, in particular, on maturation traits.

2.1. Fisheries-Induced Selection Pressures

Fisheries-induced selection may be direct or indirect. Fish evolving to grow more slowly to escape a fishing mortality that commences above a threshold body size (e.g., Conover & Munch 2002) respond to a direct selection pressure on growth. In contrast, fish evolving to grow more slowly because they invest more energy into early maturation (e.g., Olsen et al. 2004) respond to a selection pressure that is direct on maturation and indirect on growth. Also, any population-level covariance in the genetic variabilities of two traits can cause the selection pressure on one trait to be experienced by the other. It is, therefore, common that the effect of fisheries-induced selection on a trait implies such selection on many other traits. This is especially true for the wide ranges of traits affecting body size or exposure to fishing: Whenever fishing mortalities are size-selective or behavior-selective, all of these traits experience a complex array of selection pressures.

Importantly, selective fishing and fisheries-induced selection are by no means equivalent. As is sometimes overlooked, even a uniform rise in fishing mortality across all body sizes causes selection pressures on many traits. This is because such a rise devalues the importance of older ages in all life-history trade-offs. It then becomes less valuable, in fitness terms, for a fish to postpone reproduction, restrain current reproduction, or make antisenescence investments because the potential gains accrued through enhanced growth, survival, or future reproduction are erased when a fish ends its life in fishing gear. Consequently, faster life histories are favored.

Although nearly all changes in fishing mortality, be they selective or uniform, cause selection pressures, this is not true for what might be termed inescapable mortalities. The prime example is the elevated mortality of all newborn fish. Another example is an elevated uniform river mortality on anadromous semelparous fish. In either case, to the extent that no trait can affect the exposure to such mortality risks, all fish experience them equally; thus, no selection pressures result. The second example, however, underscores how special the circumstances must be to not cause any selection pressures: The elevated mortalities must be strictly uniform across all body sizes and behavioral traits, and fish must be perfectly semelparous, having no chance at all to spawn in a second season. Although such special situations do exist, at least approximately, they are rare.

Table 1 Selection pressures on iteroparous fish toward earlier or later maturation predicted to be caused by different patterns of fishing mortalities

Increased fishing mortality on	Induced selection pressures on maturation
All fish	↓
Small fish	↑, ↓, or ↕
Large fish	↓
Young fish	↓ or ↕
Old fish	↓
Immature fish	↓
Mature fish	↑

↓ indicates selection for earlier maturation; ↑ indicates selection for later maturation; and ↕ indicates evolutionary bistability. Table compiled as a collaboration between U.D. and Anna Gårdmark, Swedish University of Agricultural Sciences, Department of Aquatic Resources, Institute of Coastal Research, Öregrund, Sweden.

Theoretical models have suggested that fisheries-induced selection may sometimes be disruptive, in which case it might increase a stock's genetic variability (Landi et al. 2015). Fisheries-induced selection may also cause evolutionary bistability: The mean of a trait is then driven to alternative outcomes, depending on its initial value (Gårdmark & Dieckmann 2006).

Table 1 summarizes how fishing for iteroparous fish is expected to select for earlier or later maturation. For example, while fishing for mature fish causes delayed maturation, fishing for large fish causes earlier maturation—even though mature fish tend to be large and large fish tend to be mature. This shows the limitations of one-size-fits-all predictions of FIE. Accordingly, even qualitative insights into FIE are best derived from stock-specific models that account for the life-history details of the fished stock and for the selectivity patterns of its fishery. For quantitative predictions, such models are required.

2.2. Ecogenetic Models

Ecogenetic models integrate principles of life-history theory and quantitative genetics theory to account for a fish stock's life history, its fishing regime, and its genetic variability, resulting in a modeling framework that is especially suited to understanding, forecasting, and managing FIE (Dunlop et al. 2009). Such models benefit from the historically mutually exclusive advantages of two alternative quantitative approaches to predicting evolutionary dynamics based on the theories of quantitative genetics or adaptive dynamics: Models of quantitative genetics excel at predicting the time scales of evolutionary responses to selection pressures, and models of adaptive dynamics excel at accounting for realistic population structures and life-history details. Ecogenetic models simultaneously feature both advantages.

Building on the pioneering work by Law & Grey (1989), as well as on earlier model-based studies, such as those by Heino (1998), Ernande et al. (2004), and Hutchings (2005), ecogenetic models have been devised and calibrated for a variety of fish stocks and fishing regimes. The resultant insights range from the asymmetrically fast pace of FIE compared with the evolutionary reversal that occurs when fishing is relaxed (Dunlop et al. 2009), to the influence of FIE on stock recovery (Enberg et al. 2009), differences in selection pressures caused by different gear types (Jørgensen et al. 2009), and the economic implications of FIE (Eikeset et al. 2013, Zimmermann & Jørgensen 2015).

There have also been studies that retained the detailed descriptions of life histories, evolving traits, and selectivity patterns found in ecogenetic models, while focusing attention on predicting

selection pressures rather than the course of FIE (e.g., Arlinghaus et al. 2009, Matsumura et al. 2012). These models can be simpler, in so far as they do not require keeping track of genetic variabilities. Appropriately standardizing selection pressures turns out to be crucial for comparing these across species, stocks, and traits (Matsumura et al. 2012). On this basis, these studies have confirmed the general finding that the strongest selection pressures that fishing mortalities impose on life-history traits typically are those causing earlier maturation (Dunlop et al. 2009).

However, what models of fisheries-induced selection cannot describe is how a stock's heritabilities change through FIE. Although it is still common to consider ranges of heritabilities to be characteristic of types of traits (e.g., the heritabilities, h^2, of life-history traits are often assumed to lie between 0.2 and 0.3), the empirical and theoretical basis for this is slim. Empirical meta-analyses report much wider ranges (Friars & Smith 2010) and show that evolvabilities are more informative than heritabilities (Hansen et al. 2011). Theoretical studies have suggested that FIE may boost or erode heritabilities (Marty et al. 2015), so that observed heritabilities are strongly impacted by the past selection regimes of a stock. To capture any such effects, ecogenetic models are needed.

3. EVIDENCE

Theory makes a strong case for fishing being a potent driver of evolutionary changes in exploited populations. A conclusive empirical demonstration that FIE has occurred in a particular population and trait would require proving two logically independent conditions: (*a*) The observed change is evolutionary and thus genetic, and (*b*) it has been caused, at least partly, by fishing rather than by other selective forces alone (Dieckmann & Heino 2007).

Evidence for exploitation-induced evolution is conceptually easy to obtain through controlled experiments (Section 3.2) but much harder to obtain by observing wild populations (Section 3.3). Observational studies in the wild can never conclusively prove that fishing is the driver because causal interpretations generally require replication and controls. Strengthening the case that fishing is indeed among the drivers is thus possible only through two approaches: comparative studies (Sharpe & Hendry 2009, Devine et al. 2012) and careful analyses of the roles of other drivers (i.e., environmental factors). The latter can be achieved using process-based models parameterized for specific case studies (e.g., Wright et al. 2014) or through pattern-oriented statistical modeling (e.g., Neuheimer & Grønkjær 2012). Nevertheless, the role of fishing as a driver of selection often goes unchallenged. In contrast, the use of phenotypic data to reveal evolutionary (and thus genetic) change, as discussed below (Section 3.1), is a matter of considerable debate.

3.1. Genotypic Versus Phenotypic Evidence

Adaptive change can be examined by studying phenotypic traits or molecular markers, but both approaches present challenges. Monitoring phenotypes allows demographically important traits (e.g., growth or maturation) to be studied, but disentangling adaptive change from phenotypic plasticity is challenging. Monitoring molecular markers could enable unambiguous identification of genetic changes associated with FIE and exclude alternative explanations, such as phenotypic plasticity and population replacement (Hemmer-Hansen et al. 2014), but this has proven far from trivial. Field studies supporting FIE in the wild (Section 3.3) have been criticized for not reporting changes in gene frequencies together with phenotypic changes in maturation (Marshall & Browman 2007, Browman et al. 2008, Jørgensen et al. 2008, Kuparinen & Merilä 2008, Merilä 2009). Although this point is easy to make, in practice it is difficult to link variation in molecular markers to the phenotypic variation associated with fishing (Hansen et al. 2012).

Despite technological advances facilitating the compilation of genome-wide molecular data (Hemmer-Hansen et al. 2014), few studies have successfully applied them to examine shifts in gene frequencies in response to environmental changes in general (Hansen et al. 2012) and fishing, in particular. Genetic differences due to selection, rather than population replacement, have been found in populations of Atlantic cod (*Gadus morhua*) from Iceland and Canada (Jakobsdóttir et al. 2011, Therkildsen et al. 2013). In Iceland, the changes were associated with differential fishing mortality, which was higher in shallow waters compared to deep waters, in agreement with different observed allele frequencies (Jakobsdóttir et al. 2011). However, fishing pressure is just one of the factors differing between shallow and deep waters. Shifts at loci in Canadian cod seem to be correlated with temporal trends in temperature and midpoints of probabilistic maturation reaction norms. However, these temporal correlations were based on small sample sizes, and more data are needed to corroborate these results (Therkildsen et al. 2013). In an experiment on guppies (*Poecilia reticulata*), differences in candidate genes associated with body length were found in association with contrasting size selection in males (van Wijk et al. 2013).

The difficulty of monitoring FIE at the level of molecular markers lies in being able to identify the genetic basis of specific traits of interest and link them to fishing pressure (Vasemägi & Primmer 2005, Hemmer-Hansen et al. 2014). To overcome this challenge, population genomics and quantitative genetics need to be combined, but performing quantitative genetic tests in natural populations of marine fishes remains difficult (Hemmer-Hansen et al. 2014). Consequently, molecular genetic approaches are complementing, not replacing, phenotypic approaches to studying FIE.

3.2. Experimental Evidence

Field observations and comparative studies aided by common-garden experiments can provide evidence of divergent adaptation in the wild (Conover & Baumann 2009, Díaz Pauli & Heino 2014). However, cases are rare that feature wild replicate populations suitable for experiments (but see Haugen & Vøllestad 2001). Therefore, we suggest that selection experiments are instead best suited to mimicking changes observed in harvested populations and understanding their nature and drivers. The main advantage of selection experiments is that genetic and phenotypic changes can both be observed and unequivocally attributed to the experimentally imposed selection pressure. Moreover, selection experiments enable attention to be concentrated on traits of interest for fisheries. The prime examples are maturation traits, which are particularly susceptible to FIE (Dunlop et al. 2009, Audzijonyte et al. 2013) and have been observed to change in response to fishing pressure after accounting for major sources of plasticity (Law 2007, Heino & Dieckmann 2008). Selection experiments also allow assessment of the rate at which changes happen, their reversibility, and their effects on population productivity and fishery profitability, which are major issues for resource management.

Most experimental studies performed, independent of their model species, can be categorized as (*a*) studies using semelparous species (or iteroparous species forced into semelparity, both referred to as semelparous species in this review) and (*b*) studies using iteroparous species. The choice of model species reflects the trade-off between the feasibilities of running large experiments and the ability to link the results to real fisheries, but the difference in results is not negligible. Experiments using both types of model species seem to reach similar conclusions about the effects of size selection on life-history traits. The removal of large individuals from a population leads to evolution of reduced body size in both semelparous species (Conover & Munch 2002, van Wijk et al. 2013) and iteroparous species (Edley & Law 1988, Haugen & Vøllestad 2001; B. Díaz Pauli & M. Heino, manuscript in preparation). It also leads to maturation at smaller body sizes in both

semelparous species (van Wijk et al. 2013) and iteroparous species (Edley & Law 1988; B. Díaz Pauli & M. Heino, manuscript in preparation).

However, conclusions concerning the effect of size selection on population productivity and fishery profitability are diametrically opposite when results from experiments using semelparous species are compared with those using iteroparous species. The removal of large silversides (*Menidia menidia*, a semelparous species) led to a markedly lower total biomass yield relative to the removal of small individuals after four generations of size-selective harvest (Conover & Munch 2002). In contrast, the removal of large-sized daphnids (an iteroparous species) led to a higher biomass yield after nine generations of selection (Edley & Law 1988, Díaz Pauli & Heino 2014). The absolute biomass yield decreased to lower levels in populations in which small individuals were culled than in populations in which large individuals were culled (Edley & Law 1988, Díaz Pauli & Heino 2014). Also, the decrease in biomass yield relative to initial conditions was steeper in populations in which small individuals were culled (Díaz Pauli & Heino 2014). Similar results were found for guppies in a selection experiment allowing for their iteroparous life history: After four generations of selection, the removal of large guppies resulted in a higher biomass yield compared with the removal of small guppies (B. Díaz Pauli & M. Heino, manuscript in preparation). Thus, considering species with semelparous or iteroparous life histories leads to contrasting conclusions regarding the effect of fishing on biomass yield: Removing large individuals from iteroparous species results in a higher biomass yield than removing small individuals, whereas this relation is reversed for semelparous species (**Figure 1**).

Experiments also allow fisheries-induced selection pressures to be studied that would be difficult to observe in the wild. In addition to being size-selective, fishing can be directly selective on behavior (Law 2000, Heino & Godø 2002, Enberg et al. 2012). Experiments have shown that different fishing methods tend to remove fish with particular behavioral traits. Passive fishing gear (e.g., traps, gillnets, and longlines) selectively catch more bold individuals, but active gear (e.g., trawls) seem to catch more shy individuals (Biro & Post 2008, Klefoth et al. 2012, Díaz Pauli et al.
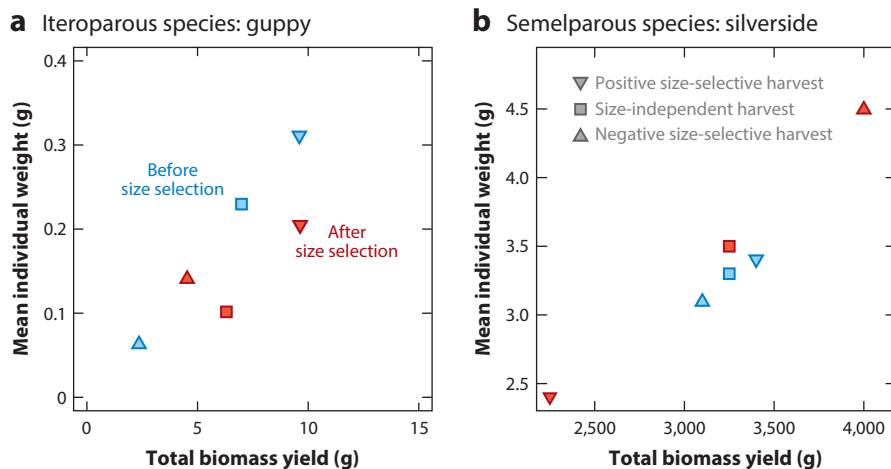

Figure 1

Comparison of the total biomass yield obtained from selection experiments with (*a*) guppies (*Poecilia reticulata*), an iteroparous species (B. Díaz Pauli & M. Heino, manuscript in preparation), and (*b*) silversides (*Menidia menidia*), a semelparous species with terminal harvest (data extracted from figure 1 in Conover & Munch 2002). Both selection experiments lasted for approximately four generations.

2015). This experimental evidence is in accordance with evidence from the wild (Section 3.3; B. Díaz Pauli & A. Sih, manuscript in preparation).

When fishing exerts selection pressure on a given trait, it can lead to changes in other life-history traits, behavioral traits, and physiological traits because sets of traits usually coevolve (Réale et al. 2010). Selection experiments are well suited to studying such correlated traits. For example, the selection experiment by Philipp et al. (2009) on vulnerability to angling in largemouth bass (*Micropterus salmoides*) showed that individuals that were more vulnerable to fishing were better at nest guarding (Cooke et al. 2007) and had higher metabolic rates. Walsh et al. (2006) showed that the removal of large silversides also selected for lower consumption rates and lower fecundities.

3.3. Evidence from the Wild

Evidence for FIE in wild, exploited populations is still almost entirely based on using phenotypic data to infer genetic change. Genetic changes in selected loci have been reported in populations of Atlantic cod (Jakobsdóttir et al. 2011, Therkildsen et al. 2013), but it remains difficult to link these changes to phenotypic traits under selection and to specific agents of selection. This section therefore summarizes the evidence for the evolution of phenotypic traits. A central challenge is to disentangle evolutionary changes from those that are phenotypically plastic or implied by demographic changes (Ricker 1981, Policansky 1993, Rijnsdorp 1993, Heino & Dieckmann 2008).

3.3.1. Life-history traits. Life-history traits are by far the most-studied class of traits, partly because the underlying theory is well developed, but probably mostly because of the availability of data. Many programs monitoring marine fish resources started in the late 1970s when coastal states obtained ownership to resources within their newly enacted exclusive economic zones. Time-series data from these programs are now more than three decades long, and typically include data on individual age, size, and sex, and sometimes gonad size, allowing estimation of parameters related to growth, maturation, and reproduction. Some monitoring programs started much earlier. This puts oceanic fish in a special position as a test bed for life-history theory: Nothing comparable exists for terrestrial systems.

3.3.1.1. Maturation. Maturation is the most-studied life-history trait for several reasons: Maturation is a key determinant of life histories (Roff 1992, Stearns 1992), data are relatively abundant, maturation changes have obvious impacts on a stock's productivity, and large changes toward earlier maturation (as predicted by theory) have been documented for numerous fish populations (Trippel 1995). Earlier maturation, however, is also a well-known compensatory response to fishing: When fishing reduces population abundance, resource competition may be partly relaxed and the remaining fish can, thus, grow faster, attaining earlier in life the body size required for maturation (Jørgensen 1990, Trippel 1995, Law 2000). Moreover, at the population level, an earlier average age at maturation has also been observed as a direct demographic response to fishing because the average age in a population declines with increasing mortality (Ricker 1981, Policansky 1993, Dieckmann & Heino 2007, Heino & Dieckmann 2008). The possibility of exploitation-induced evolution was acknowledged during the 1990s, but most researchers concluded that evolutionary changes could not be satisfactorily demonstrated from the data, while phenotypically plastic (compensatory) and demographic responses appeared sufficient to explain the observed patterns (Jørgensen 1990, Smith 1994, Trippel 1995). A notable exception is the pioneering study by Adriaan Rijnsdorp (1993), who concluded that plaice (*Pleuronectes platessa*) in the North Sea had adapted to fishing by maturing earlier.

The introduction of the probabilistic maturation reaction norm (PMRN) approach (Heino et al. 2002) was an important methodological step that helped to move the field forward (as reviewed in Dieckmann & Heino 2007, Heino & Dieckmann 2008). Fundamentally, the strength of this approach stems from studying individual age and size simultaneously: Size-at-age is a proxy for growth, and the effects of many environmental variables on maturation are channeled through growth. The approach builds on the earlier, deterministic maturation reaction norm concept and the associated notion that such reaction norms can be used to disentangle growth-related phenotypic plasticity and genetic change (Stearns & Crandall 1984, Stearns & Koella 1986). Just how well this disentanglement works has been debated—see, e.g., the theme section edited by Marshall & Browman (2007)—with experiments showing some of its limitations (Uusi-Heikkilä et al. 2011, Díaz Pauli & Heino 2013, Salinas & Munch 2014). Nevertheless, the PMRN approach has become the standard method for analyzing phenotypic maturation data, and despite its shortcomings, has provided an important improvement over earlier approaches.

The PMRN approach has been used to analyze changes in maturation in a large number of fish populations and species (**Figure 2**). By far the most-studied species is Atlantic cod; all studies suggest that FIE in maturation has taken place. Also, studies of other demersal marine species have shown mostly positive findings. Only three studies have looked at pelagic marine species, and their findings suggested no, or only weak, evolutionary changes. For anadromous, freshwater, or estuarine species, the picture is mixed, with positive and negative findings similarly represented.

Many of the negative findings have come from studies of short-lived species that naturally experience high mortality and exhibit early maturation (e.g., capelin, sardine, and Norway pout; Baulier et al. 2012, Silva et al. 2013, Marty et al. 2014). Arguably, such species are already adapted to high mortality levels and may, therefore, have little scope for a further acceleration of their maturation. Some other negative findings have come from populations that are selectively harvested only at spawning grounds (e.g., Norwegian spring-spawning herring; Engelhard & Heino 2004) or are semelparous and subject to terminal harvest (e.g., capelin, Pacific salmon; Baulier et al. 2012, Kendall et al. 2014), settings that are known to exert less selection on maturation. A few other negative cases have been associated with short time series that may have lacked statistical power. However, some short time series have shown significant changes. These have been demonstrated in populations possessing relatively short generation times (e.g., eastern Baltic cod; Vainikka et al. 2009) or ones that have been intensively exploited (e.g., northern cod; Olsen et al. 2004). When these studies are taken together, **Figure 2** suggests that FIE in maturation is common but not ubiquitous.

3.3.1.2. Reproduction.
Evolutionary theory predicts that fishing favors increasing investments into reproduction after maturation. These investments can take many forms. An individual's investment into the production of its gametes can be relatively easy to quantify, but the same is not true for investments into secondary sexual characteristics or into behaviors related to reproduction (such as migration or courting).

A handful of studies have examined reproductive investment, relying on proxies such as weight-specific fecundity, relative gonad weight, and weight loss during the spawning period (**Supplemental Table 5**). Plaice is the most-studied species, with most proxies showing no changes or only changes that can be attributed to the environment (Rijnsdorp et al. 2005, van Walraven et al. 2010). Studies of other demersal fish have reported positive results, but typically not for all populations or for both sexes (Yoneda & Wright 2004, Baulier 2009, Wright et al. 2011). One freshwater study showed a positive result (Thomas et al. 2009), while another did not (Nusslé et al. 2009). Whether this mixed picture reflects the difficulty of measuring reproductive investment or
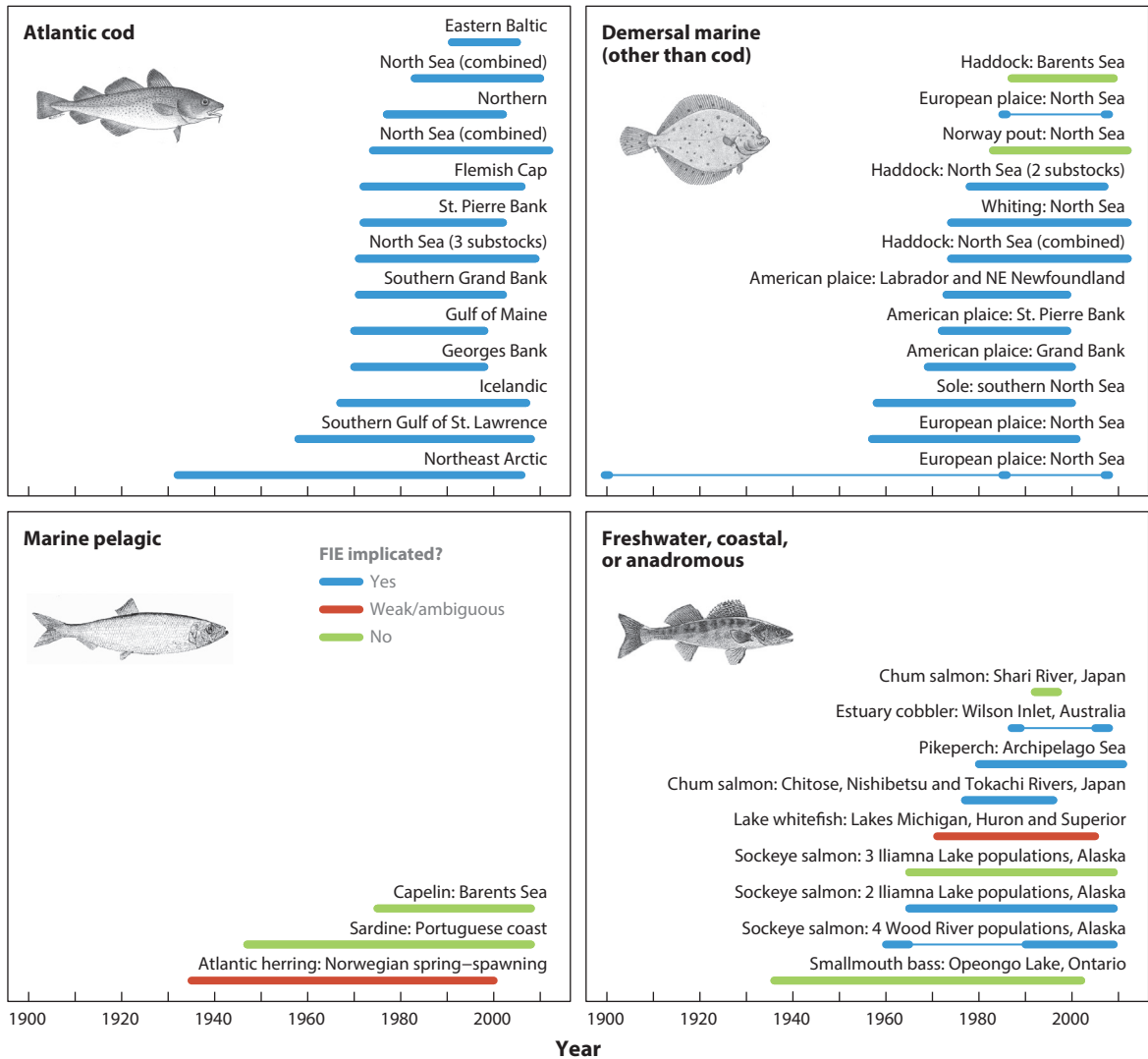
Figure 2

Studies in which probabilistic maturation reaction norms have been used to help interpret changes in maturation. Horizontal lines indicate whether fisheries-induced evolution (FIE) is implicated and the time periods of data, with thin lines indicating gaps. See **Supplemental Tables 1–4** for details and references (follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**). Fish images © Food and Agriculture Organization of the United Nations, 2015, FAO Species Fact Sheets (**http://www.fao.org/fishery/species/search/**). Reproduced with permission.

Supplemental Material

systematically lower selection pressures on, or evolvabilities of, reproductive investment remains an open question.

3.3.1.3. Growth. Most fishing methods are directly size-selective, and it was fisheries-induced selection on growth or size-at-age that first drew scientists' attention (Rutter 1902, Cooper 1952, Miller 1957, Silliman 1975, Handford et al. 1977, Spangler et al. 1977). However, it was recognized already early on that growth is readily influenced by the environment (Miller 1957, Spangler

et al. 1977), including both by fisheries-independent factors (e.g., temperature) and by fisheries-dependent factors (e.g., resource availability). Because of the difficulty of disentangling these effects from evolutionary changes in growth, obtaining strong evidence for FIE of growth has proven difficult in observational studies (Enberg et al. 2012).

One of the methods for disentangling environmental effects from fisheries-induced selection is multiple regression. In principle, if one constructs a statistical model that accounts for important environmental effects on growth in a biologically meaningful way, a residual trend is consistent with the action of a driver, such as fisheries-induced selection, that creates cumulative effects. However, this approach is typically hampered by a lack of data: Even a key factor such as resource availability is difficult to quantify. Physical variables such as temperature are straightforward to measure, but it is difficult to quantify an individual's ambient temperature at the locations where, and over the time intervals during which, its growth has occurred. Although data-storage tags now enable such data to be gathered, they have not yet been used at the scale necessary for drawing inferences about evolutionary changes.

An improvement in this strategy is to include fisheries-induced selection pressure as an explanatory variable, as was first shown by Swain et al. (2007) for cod in the southern Gulf of St. Lawrence. By modeling the change in body length as a function of the selection differential induced by fishing and of two environmental variables (temperature and density), the researchers were able to show that changes in body length over a two-decade period likely resulted from the joint action of all three factors, although the strength of this conclusion can be challenged (Heino et al. 2008; see reply in Swain et al. 2008).

A comparison of 73 fish populations worldwide found no correlation between changes in size-at-age and the intensity of fishing, and on this basis it was concluded that there is little evidence for FIE (Hilborn & Minte-Vera 2008). However, this study did not control for environmental effects, despite noting that the evolutionary and density-dependent effects of fishing likely counteract each other. It should also be remembered that FIE of growth is not always expected to move toward slower growth (Dunlop et al. 2009), complicating such meta-analyses.

Case studies of single populations or species have had more success in finding evidence for FIE of growth. **Figure 3** summarizes studies in which FIE has been addressed. The selection of studies represents our best knowledge about relevant studies, but probably many studies have been missed, particularly when results were inconclusive or negative and not reported among the main results. There are seven studies of marine fish species that have all found positive evidence, but in all but two (Swain et al. 2008, Pardoe et al. 2009) changes in growth were attributed to changes in maturation. Studies on freshwater or anadromous species have covered 13 species, mostly salmonids. These studies, when suggesting FIE of growth, have generally not attributed it to increased reproductive allocation, and have invested less scrutiny than marine studies into trying to understand the role of changes in maturation.

Ricker's (1981) classic study of five species of Pacific salmon (*Oncorhynchus* spp.) in British Columbia is a notable exception: Ricker was cautious in attributing changes in size-at-age to FIE (which was an unorthodox idea at the time), reaching a strongly positive conclusion for only one species, pink salmon (*O. gorbuscha*), and a more conditional positive conclusion for only another species, coho salmon (*O. kisutch*). These conclusions held up after Ricker (1995) extended the time series by 16 years. Ricker's conclusions have not gone unchallenged, though, and other researchers have attributed greater importance to environmental drivers, particularly density-dependent effects, than Ricker did (Healey 1986, Bigler et al. 1996). Nevertheless, there has been no rigorous attempt to estimate the relative strengths of various factors contributing to size trends in Pacific salmon, and there is no consensus regarding just how good the evidence for an FIE component in these size trends is.
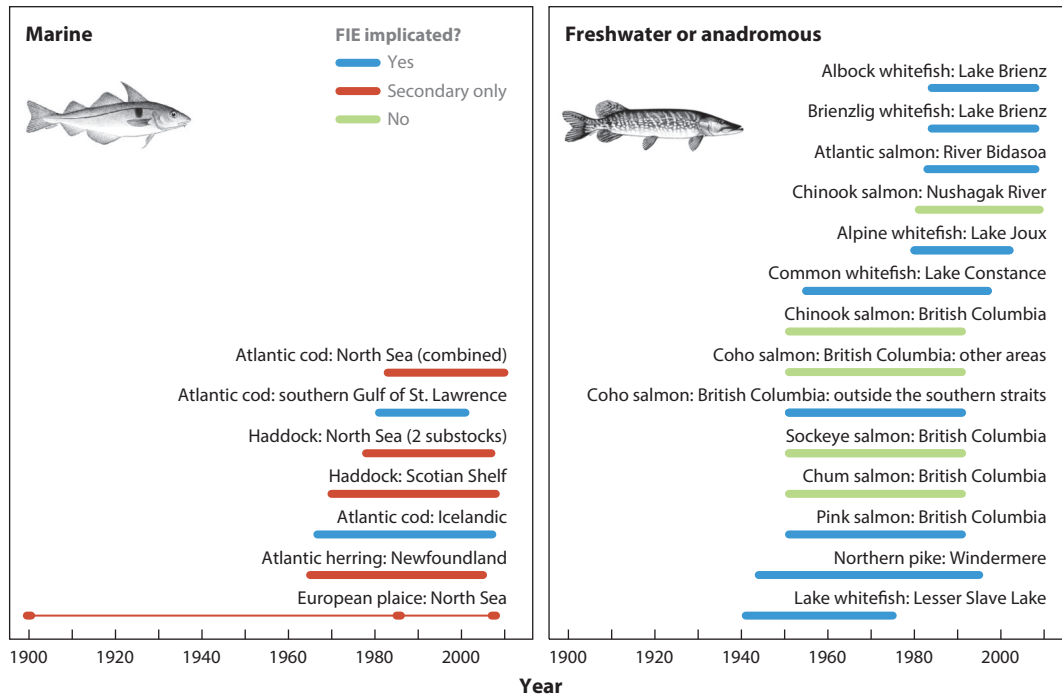
Figure 3

Studies in which fisheries-induced evolution (FIE) of growth has been addressed. Red bars indicate studies that documented evolutionary changes in the growth of adult fish but attributed these to changes in reproductive allocation. See **Supplemental Tables 6–7** for details and references. Fish images © Food and Agriculture Organization of the United Nations, 2015, FAO Species Fact Sheets (**http://www.fao.org/fishery/species/search/**). Reproduced with permission.

3.3.2. Behavioral traits. Evidence of FIE in behavioral traits in the wild remains scarce. Probably the single most important reason for this is the lack of data. The only behaviors that are routinely observed are related to the phenology of migrations in species such as salmon. Changes in run timing that seem partly to reflect different vulnerabilities of early- and late-running fish have been documented for Atlantic salmon (*Salmo salar*) in Ireland (Quinn et al. 2006) and, more conclusively, for sockeye salmon (*O. nerka*) in Alaska (Quinn et al. 2007). However, few fish species have such easily observed migrations, and run timing is just one of many behavioral traits that could be under selection. Rapidly improving technology is opening new possibilities for making behavioral observations that were unthinkable just a few decades ago. These methods include using active fisheries acoustics (sonar and echosounders; e.g., Handegard & Tjøstheim 2005), acoustic tracking (e.g., Langård et al. 2015), and data-storage tags (e.g., Le Bris et al. 2013). However, behavioral observations made using these methods tend to be one-off studies; only fisheries acoustics are widely used in routine monitoring, and then not for monitoring behavior but to determine spatial distribution and abundance. Past acoustic surveys represent a potential source of time series of behavioral data, but remain, to our knowledge, unutilized for this purpose.

It is much easier to find evidence that fishing selects for certain behaviors than that it results in FIE. Experimental studies documenting correlations between behavioral traits and vulnerability are already numerous (Section 3.2), but a few studies have also shown this in the wild. Using acoustic tagging of Atlantic cod in their natural habitat, Olsen et al. (2012) were able to show that

individuals with certain movement patterns were more likely to be fished than others. Wilson et al. (2011) showed that bluegill sunfish (*Lepomis macrochirus*) caught using a seine net differed from those caught by angling when tested in a lab for the boldness of their behavior. However, Kekäläinen et al. (2014) did not find such differences in perch (*Perca fluviatilis*) in a similar setting. Nevertheless, combined with the evidence that key behavioral traits possess heritable components (Philipp et al. 2009, Chervet et al. 2011, Ariyomo et al. 2013), these studies suggest that such traits evolve in response to fishing similar to life-history traits—so far, we simply have been unable to document these changes happening.

3.3.3. Caveats. Exploitation-induced evolution occurs quickly compared with other examples of contemporary evolution (Darimont et al. 2009), and it has been argued that the changes are too fast to be evolutionary (Andersen & Brander 2009). Empirically observed rates are also generally higher than rates in evolutionary models (Audzijonyte et al. 2013). The reasons for this discrepancy are not yet understood, but could be caused by unaccounted drivers of phenotypic change.

Using phenotypic field data to study evolution relies on a correlational approach to account for the effects of certain confounding factors and estimated selection differentials, or to link patterns of residuals to assumed patterns of selection. The strength of such inferences depends on how well the nonevolutionary effects can be modeled. Achieving a good description of nonevolutionary effects is easier for maturation than for other traits. Because individual size-at-age is a proxy for the growth conditions an individual has encountered, studies using the PMRN approach are in a unique position because the data that are used to estimate the trait also carry information about the environment. This environmental proxy is evidently not perfect, but studies of other traits usually have to rely on even weaker proxies. By its nature, any single observational field study relying only on phenotypic data is handicapped when trying to demonstrate that phenotypic changes are evolutionary or that such changes are fisheries-induced.

Although we must acknowledge that individual studies might have missed important drivers of phenotypic change—not just any drivers, but drivers that would cause patterns similar to those predicted for fisheries-induced selection—it seems unlikely that many independent studies suffer from the same bias. Therefore, the body of literature interpreting documented phenotypic patterns in terms of FIE jointly provides stronger evidence for FIE than any individual case study can possibly do on its own.

4. IMPLICATIONS

FIE is an intriguing example of contemporary anthropogenic evolution (Palumbi 2001). But it is much more than that: FIE affects the properties of fish populations, which in turn influence their dynamics and productivity, and ultimately, their utility for humankind (Jørgensen et al. 2007, Laugen et al. 2014). These effects can be undesirable, but as Rutter (1902) pointed out, not all FIE is undesirable.

FIE means that fish populations adapt to fishing. Although evolution is not driven by benefits to populations, adaptation to fishing nevertheless can benefit populations that are intensively fished: A population with a faster life history will generally tolerate more additional mortality before being driven to extinction, and it may initially recover faster when exploitation is reduced (Kaitala & Getz 1995, Heino 1998, Enberg et al. 2009). This beneficial aspect of FIE is not guaranteed, though, and under special conditions adaptive evolution can lead to extinction (so-called evolutionary suicide; e.g., Ernande et al. 2004).

FIE has also been characterized as "unnatural selection" (Allendorf & Hard 2009, Stenseth & Dunlop 2009). Indeed, adaptation to fishing often occurs at the cost of adaptation to a population's

natural environment (Heino et al. 2013). Although this will happen only when the net effect is positive at the individual level, evolution assesses this net effect myopically over the course of just a few generations. Adaptation to fishing may thus become costly in the long run, when environmental conditions change, exploitation is reduced, or rare environmental fluctuations probe a population's resilience. The situation is similar to domestication: It makes organisms better suited to the conditions established by humans, but less suited to the conditions in the wild.

A more immediate concern is that FIE is expected to reduce yields from sustainable fisheries, at least in populations that are not seriously overfished (Heino 1998, Eikeset et al. 2013). Also, the average body size of caught fish will decline (Heino 1998), usually implying a lower price per biomass unit (Zimmermann & Heino 2013). All of these considerations led to the recommendation that it is best to minimize FIE. This recommendation was challenged by Andersen & Brander (2009), who suggested that the rate of FIE is so low (0.1–0.6% per year in their model) that dealing with FIE is less urgent than reducing the direct detrimental effects of overfishing. This argument misses the point for two reasons. First, even low rates of change are important when they persist. An annual loss of 0.5% may sound insignificant at first, but it amounts to a loss of 10% in just 21 years. Such a loss is indeed significant, given that fish are an important source of nutrition for many people, and the human population is increasing. Second, dealing with the most urgent challenge (i.e., overfishing) is fundamentally compatible with curbing rates of unwanted FIE: Reducing exploitation addresses both challenges.

We explicitly encourage a precautionary approach for dealing with FIE. It would not be wise to wait until there is full certainty about the extent of FIE and its consequences: Not only is there a risk that the consequences are serious, but at the timescales relevant for resource management, FIE is practically irreversible. Such a precautionary approach does not require a full overhaul of contemporary management of fisheries. Rather, FIE should be assessed along with other determinants of sustainability, for example, by using the Evolutionary Impact Assessment framework (Jørgensen et al. 2007, Laugen et al. 2014).

SUMMARY POINTS

1. Life-history theory predicts that most types of fishing favor the evolution of faster life histories. This usually means earlier maturation, and may involve increased reproductive investment. Postmaturation growth is also expected to decline.

2. Fishing will also exert selection pressures on other traits, either directly (e.g., when fishing methods are directly selective on bold behaviors) or indirectly (e.g., when increased fishing mortality favors bold behaviors by devaluing survival).

3. Theoretical studies have suggested that after fishing pressures are relaxed, the reversal of FIE through natural selection may occur considerably more slowly than the changes associated with its development.

4. Empirical evidence for FIE is almost entirely based on phenotypic data, which suffices for inferring evolutionary change under experimental conditions but not from observational data collected in the wild.

5. Empirical evidence for FIE in the wild is strongest for maturation, and the majority of case studies suggest evolution moves toward earlier reproduction. There is also some evidence for evolution moving toward slower growth and increased reproductive effort.

6. Evidence of evolutionary changes in behavioral traits in wild fish has so far been limited to phenology. Historical baseline data for other behavioral traits are missing, but experimental studies have clearly shown the effect of selection on behaviors. This suggests that evolution in behavioral traits must have taken place.

7. Empirical studies suggest that FIE can occur quickly, even when compared with other examples of contemporary evolution. Concerns remain that phenotypic methods for studying FIE might exaggerate its speed.

8. FIE can make fish populations more robust to overexploitation, but it can also reduce their resilience to natural fluctuations and undermine the yields of sustainable fisheries. There is a need to acknowledge and account for FIE when managing fish resources in the wild.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

LITERATURE CITED

Allendorf FW, Hard JJ. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. *PNAS* 106(Suppl. 1):9987–94

Andersen BS, Ulrich C, Eigaard OR, Christensen A-S. 2012. Short-term choice behaviour in a mixed fishery: investigating métier selection in the Danish gillnet fishery. *ICES J. Mar. Sci.* 69(1):131–43

Andersen KH, Brander K. 2009. Expected rate of fisheries-induced evolution is slow. *PNAS* 106:11657–60

Ariyomo TO, Carter M, Watt PJ. 2013. Heritability of boldness and aggressiveness in the zebrafish. *Behav. Genet.* 43(2):161–67

Arlinghaus R, Matsumura S, Dieckmann U. 2009. Quantifying selection differentials caused by recreational fishing: development of modeling framework and application to reproductive investment in pike (*Esox lucius*). *Evol. Appl.* 2(3):335–55

Audzijonyte A, Kuparinen A, Fulton EA. 2013. How fast is fisheries-induced evolution? Quantitative analysis of modelling and empirical studies. *Evol. Appl.* 6(4):585–95

Baulier L. 2009. *Evolutionary and statistical modeling of life-time schedules of energy allocation in Atlantic herring and cod*. PhD Thesis, Univ. Bergen

Baulier L, Heino M, Gjøsæter H. 2012. Temporal stability of the maturation schedule of capelin (*Mallotus villosus* Müller) in the Barents Sea. *Aquat. Living Resour.* 25:151–61

Bigler BS, Welch DW, Helle JS. 1996. A review of size trends among North Pacific salmon (*Oncorhynchus* spp.). *Can. J. Fish. Aquat. Sci.* 53:455–65

Biro PA, Post JR. 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *PNAS* 105:2919–22

Borisov VM. 1978. The selective effect of fishing on the population structure of species with a long life cycle. *J. Ichthyol.* 18:896–904

Browman HI, Law R, Marshall CT. 2008. The role of fisheries-induced evolution. *Science* 320:47–50

Chervet N, Zöttl M, Schürch R, Taborsky M, Heg D. 2011. Repeatability and heritability of behavioural types in a social cichlid. *Int. J. Evol. Biol.* 2011:e321729

Conover DO, Baumann H. 2009. The role of experiments in understanding fishery-induced evolution. *Evol. Appl.* 2:276–90

Conover DO, Munch SB. 2002. Sustaining fisheries yields over evolutionary time scales. *Science* 297:94–96

Cooke SJ, Suski CD, Ostrand KG, Wahl DH, Philipp DP. 2007. Physiological and behavioral consequences of long-term artificial selection for vulnerability to recreational angling in a teleost fish. *Physiol. Biochem. Zool.* 80(5):480–90

Cooper EL. 1952. *Growth of brook trout* (Salvelinus fontinalis) *and brown trout* (Salmo trutta) *in the Pigeon River, Otsego County, Michigan*. Fish. Res. Rep. 1319, Dep. Nat. Resour., Fish. Div., Lansing, MI

Darimont CT, Carlson SM, Kinnison MT, Paquet PC, Reimchen TE, Wilmers CC. 2009. Human predators outpace other agents of trait change in the wild. *PNAS* 106:952–54

Devine JA, Wright PJ, Pardoe H, Heino M. 2012. Comparing rates of contemporary evolution in life-history traits for exploited fish stocks. *Can. J. Fish. Aquat. Sci.* 69(6):1105–20

Díaz Pauli B, Heino M. 2013. The importance of social dimension and maturation stage for the probabilistic maturation reaction norm in *Poecilia reticulata*. *J. Evol. Biol.* 26(10):2184–96

Díaz Pauli B, Heino M. 2014. What can selection experiments teach us about fisheries-induced evolution? *Biol. J. Linn. Soc.* 111:485–503

Díaz Pauli B, Wiech M, Heino M, Utne-Palm AC. 2015. Opposite selection on behavioural types by active and passive fishing gears in a simulated guppy *Poecilia reticulata* fishery. *J. Fish Biol.* 86:1030–45

Dieckmann U, Heino M. 2007. Probabilistic maturation reaction norms: their history, strengths, and limitations. *Mar. Ecol. Prog. Ser.* 335:253–69

Dunlop ES, Heino M, Dieckmann U. 2009. Eco-genetic modeling of contemporary life-history evolution. *Ecol. Appl.* 19:1815–34

Edley T, Law R. 1988. Evolution of life histories and yields in experimental populations of *Daphnia magna*. *Biol. J. Linn. Soc.* 34:309–26

Eikeset AM, Richter AP, Dunlop ES, Dieckmann U, Stenseth NC. 2013. Economic repercussions of fisheries-induced evolution. *PNAS* 110:12259–64

Enberg K, Jørgensen C, Dunlop ES, Heino M, Dieckmann U. 2009. Implications of fisheries-induced evolution for stock rebuilding and recovery. *Evol. Appl.* 2:394–414

Enberg K, Jørgensen C, Dunlop ES, Varpe Ø, Boukal DS, et al. 2012. Fishing-induced evolution of growth: concepts, mechanisms, and the empirical evidence. *Mar. Ecol.* 33:1–25

Engelhard GH, Heino M. 2004. Maturity changes in Norwegian spring-spawning herring *Clupea harengus*: compensatory or evolutionary responses? *Mar. Ecol. Prog. Ser.* 272:245–56

Ernande B, Dieckmann U, Heino M. 2004. Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. *Proc. R. Soc. B* 271:415–23

Fenberg PB, Roy K. 2008. Ecological and evolutionary consequences of size-selective harvesting: How much do we know? *Mol. Ecol.* 17:209–20

Friars GW, Smith PJ. 2010. *Heritability, correlation and selection response estimates of some traits in fish populations*. Tech. Rep., Atl. Salmon Fed., St. Andrews, N.B., Can.

Gårdmark A, Dieckmann U. 2006. Disparate maturation adaptations to size-dependent mortality. *Proc. R. Soc. B* 273:2185–92

Handegard NO, Tjøstheim D. 2005. When fish meet a trawling vessel: examining the behaviour of gadoids using a free-floating buoy and acoustic split-beam tracking. *Can. J. Fish. Aquat. Sci.* 62:2409–22

Handford P, Bell G, Reimchen T. 1977. A gillnet fishery considered as an experiment in artificial selection. *J. Fish. Res. Board Can.* 34:954–61

Hansen MM, Olivieri I, Waller DM, Nielsen EE, GeM Working Group. 2012. Monitoring adaptive genetic responses to environmental change. *Mol. Ecol.* 21(6):1311–29

Hansen TF, Pélabon C, Houle D. 2011. Heritability is not evolvability. *Evol. Biol.* 38(3):258–77

Haugen TO, Vøllestad LA. 2001. A century of life-history evolution in grayling. *Genetica* 112–113:475–91

Healey MC. 1986. Optimum size and age at maturity in Pacific salmon and effects of size-selective fisheries. In *Salmonid Age at Maturity*, ed. DJ Meerburg, pp. 39–52. Ottawa, Ont.: Dep. Fish. Oceans

Heino M. 1998. Management of evolving fish stocks. *Can. J. Fish. Aquat. Sci.* 55:1971–82

Heino M, Baulier L, Boukal DS, Dunlop ES, Eliassen S, et al. 2008. Evolution of growth in Gulf of St Lawrence cod? *Proc. R. Soc. B* 275:1111–12

Heino M, Baulier L, Boukal DS, Ernande B, Johnston FD, et al. 2013. Can fisheries-induced evolution shift reference points for fisheries management? *ICES J. Mar. Sci.* 70(4):707–21

Heino M, Dieckmann U. 2008. Detecting fisheries-induced life-history evolution: an overview of the reaction norm approach. *Bull. Mar. Sci.* 83:69–93

Heino M, Dieckmann U, Godø OR. 2002. Measuring probabilistic reaction norms for age and size at maturation. *Evolution* 56:669–78

Heino M, Godø OR. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. *Bull. Mar. Sci.* 70:639–56

Hemmer-Hansen J, Therkildsen NO, Pujolar JM. 2014. Population genomics of marine fishes: next-generation prospects and challenges. *Biol. Bull.* 227(2):117–32

Hilborn R, Minte-Vera CV. 2008. Fisheries-induced changes in growth rates in marine fisheries: Are they significant? *Bull. Mar. Sci.* 83:95–105

Holland DS, Sutinen JG. 1999. An empirical model of fleet dynamics in New England trawl fisheries. *Can. J. Fish. Aquat. Sci.* 56(2):253–64

Hutchings JA. 2005. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* 62:824–32

Hutchings JA, Fraser DJ. 2008. The nature of fisheries- and farming-induced evolution. *Mol. Ecol.* 17:294–313

Jakobsdóttir KB, Pardoe H, Magnússon Á, Björnsson H, Pampoulie C, et al. 2011. Historical changes in genotypic frequencies at the *Pantophysin* locus in Atlantic cod (*Gadus morhua*) in Icelandic waters: evidence of fisheries-induced selection? *Evol. Appl.* 4:562–73

Jørgensen C, Enberg K, Dunlop ES, Arlinghaus R, Boukal DS, et al. 2007. Managing evolving fish stocks. *Science* 318:1247–48

Jørgensen C, Enberg K, Dunlop ES, Arlinghaus R, Boukal DS, et al. 2008. The role of fisheries-induced evolution: response. *Science* 320:48–50

Jørgensen C, Ernande B, Fiksen Ø. 2009. Size-selective fishing gear and life history evolution in the Northeast Arctic cod. *Evol. Appl.* 2:356–70

Jørgensen T. 1990. Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). *J. Cons. Int. Explor. Mer* 46:235–48

Kaitala V, Getz WM. 1995. Population dynamics and harvesting of semelparous species with phenotypic and genotypic variability in reproductive age. *J. Math. Biol.* 33(5):521–56

Kekäläinen J, Podgorniak T, Puolakka T, Hyvärinen P, Vainikka A. 2014. Individually assessed boldness predicts *Perca fluviatilis* behaviour in shoals, but is not associated with the capture order or angling method. *J. Fish Biol.* 85(5):1603–16

Kendall NW, Dieckmann U, Heino M, Punt AE, Quinn TP. 2014. Evolution of age and length at maturation of Alaskan salmon under size-selective harvest. *Evol. Appl.* 7(2):313–22

Klefoth T, Skov C, Krause J, Arlinghaus R. 2012. The role of ecological context and predation risk-stimuli in revealing the true picture about the genetic basis of boldness evolution in fish. *Behav. Ecol. Sociobiol.* 66(4):547–59

Kuparinen A, Merilä J. 2007. Detecting and managing fisheries-induced evolution. *Trends Ecol. Evol.* 22:652–59

Kuparinen A, Merilä J. 2008. The role of fisheries-induced evolution. *Science* 320:47–48

Landi P, Hui C, Dieckmann U. 2015. Fisheries-induced disruptive selection. *J. Theor. Biol.* 365:204–16

Langård L, Skaret G, Jensen KH, Johannessen A, Slotte A, et al. 2015. Tracking individual herring within a semi-enclosed coastal marine ecosystem: 3-dimensional dynamics from pre- to post-spawning. *Mar. Ecol. Prog. Ser.* 518:267–79

Laugen AT, Engelhard GH, Whitlock R, Arlinghaus R, Dankel DJ, et al. 2014. Evolutionary impact assessment: accounting for evolutionary consequences of fishing in an ecosystem approach to fisheries management. *Fish Fish.* 15:65–96

Law R. 2000. Fishing, selection, and phenotypic evolution. *ICES J. Mar. Sci.* 57:659–68

Law R. 2007. Fisheries-induced evolution: present status and future directions. *Mar. Ecol. Prog. Ser.* 335:271–77

Law R, Grey DR. 1989. Evolution of yields from populations with age-specific cropping. *Evol. Ecol.* 3:343–59

Le Bris A, Fréchet A, Galbraith PS, Wroblewski JS. 2013. Evidence for alternative migratory behaviours in the northern Gulf of St Lawrence population of Atlantic cod (*Gadus morhua* L.). *ICES J. Mar. Sci.* 70(4):793–804

Marshall CT, Browman HI. 2007. Disentangling the causes of maturation trends in exploited fish populations. *Mar. Ecol. Prog. Ser.* 335:249–51

Marty L, Dieckmann U, Ernande B. 2015. Fisheries-induced neutral and adaptive evolution in exploited fish populations and consequences for their adaptive potential. *Evol. Appl.* 8(1):47–63

Marty L, Rochet M-J, Ernande B. 2014. Temporal trends in age and size at maturation of four North Sea gadid species: cod, haddock, whiting and Norway pout. *Mar. Ecol. Prog. Ser.* 497:179–97

Matsumura S, Arlinghaus R, Dieckmann U. 2012. Standardizing selection strengths to study selection in the wild: a critical comparison and suggestions for the future. *BioScience* 62(12):1039–54

Merilä J. 2009. It's the genotype, stupid! *J. Anim. Breed. Genet.* 126:1–2

Miller RB. 1957. Have the genetic patterns of fishes been altered by introductions or by selective fishing? *J. Fish. Res. Board Can.* 14:797–806

Neuheimer AB, Grønkjær P. 2012. Climate effects on size-at-age: Growth in warming waters compensates for earlier maturity in an exploited marine fish. *Glob. Chang. Biol.* 18(6):1812–22

Nusslé S, Bornand CN, Wedekind C. 2009. Fishery-induced selection on an Alpine whitefish: quantifying genetic and environmental effects on individual growth rate. *Evol. Appl.* 2:200–8

Olsen EM, Heino M, Lilly GR, Morgan MJ, Brattey J, et al. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428:932–35

Olsen EM, Heupel MR, Simpfendorfer CA, Moland E. 2012. Harvest selection on Atlantic cod behavioral traits: implications for spatial management. *Ecol. Evol.* 2:1549–62

Palumbi SR. 2001. Humans as the world's greatest evolutionary force. *Science* 293:1786–90

Pardoe H, Vainikka A, Thórdarson G, Marteinsdóttir G, Heino M. 2009. Temporal trends in probabilistic maturation reaction norms and growth of Atlantic cod (*Gadus morhua* L.) on the Icelandic shelf. *Can. J. Fish. Aquat. Sci.* 66:1719–33

Philipp DP, Cooke SJ, Claussen JE, Koppelman JB, Suski CD, Burkett DP. 2009. Selection for vulnerability to angling in largemouth bass. *Trans. Am. Fish. Soc.* 138:189–99

Planque B, Loots C, Petitgas P, Lindstrøm U, Vaz S. 2011. Understanding what controls the spatial distribution of fish populations using a multi-model approach. *Fish. Oceanogr.* 20(1):1–17

Policansky D. 1993. Fishing as a cause of evolution in fishes. In *The Exploitation of Evolving Resources*, ed. TK Stokes, JM McGlade, R Law, pp. 2–18. Berlin: Springer

Quinn TP, Hodgson S, Flynn L, Hilborn R, Rogers DE. 2007. Directional selection by fisheries and the timing of sockeye salmon (*Oncorhynchus nerka*) migrations. *Ecol. Appl.* 17:731–39

Quinn TP, McGinnity P, Cross TF. 2006. Long-term declines in body size and shifts in run timing of Atlantic salmon in Ireland. *J. Fish Biol.* 68:1713–30

Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio P-O. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philos. Trans. R. Soc. B* 365(1560):4051–63

Ricker WE. 1981. Changes in the average size and average age of Pacific salmon. *Can. J. Fish. Aquat. Sci.* 38:1636–56

Ricker WE. 1995. Trends in the average size of Pacific salmon in Canadian catches. *Can. Special Publ. Fish. Aquat. Sci.* 121:593–602

Rijnsdorp AD. 1993. Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. *Oecologia* 96:391–401

Rijnsdorp AD, Grift RE, Kraak SBM. 2005. Fisheries-induced adaptive change in reproductive investment in North Sea plaice (*Pleuronectes platessa*)? *Can. J. Fish. Aquat. Sci.* 62:833–43

Roff DA. 1992. *The Evolution of Life Histories: Theory and Analysis*. New York: Chapman & Hall

Roppel P. 2004. The steamer *Albatross* and early Pacific salmon, *Oncorhynchus* spp., research in Alaska. *Mar. Fish. Rev.* 66(3):21–31

Rutter C. 1902. Natural history of the Quinnat salmon: a report of investigations in the Sacramento River, 1886–1901. *Bull. U. S. Fish Comm.* 22:65–141

Salas S, Sumaila UR, Pitcher T. 2004. Short-term decisions of small-scale fishers selecting alternative target species: a choice model. *Can. J. Fish. Aquat. Sci.* 61(3):374–83

Salinas S, Munch SB. 2014. Phenotypic complexity: integrated responses of life-history characters to multiple environmental factors. *Evol. Ecol. Res.* 16:267–84

Sharpe DMT, Hendry AP. 2009. Life history change in commercially exploited fish stocks: an analysis of trends across studies. *Evol. Appl.* 2:260–75

Silliman RP. 1975. Selective and unselective exploitation of experimental populations of *Tilapia mossambica*. *Fish. Bull.* 73:495–507

Silva A, Faria S, Nunes C. 2013. Long-term changes in maturation of sardine, *Sardina pilchardus*, in Portuguese waters. *Sci. Mar.* 77(3):429–38

Smith PJ. 1994. *Genetic diversity of marine fisheries resources: possible impacts of fishing*. FAO Fish. Tech. Pap. 344, FAO, Rome

Solberg MF, Skaala Ø, Nilsen F, Glover KA. 2013. Does domestication cause changes in growth reaction norms? A study of farmed, wild and hybrid Atlantic salmon families exposed to environmental stress. *PLOS ONE* 8(1):e54469

Spangler GR, Payne NR, Thorpe JE, Byrne JM, Regier HA, Christie WJ. 1977. Responses of percids to exploitation. *J. Fish. Res. Board Can.* 34:1972–82

Stearns SC. 1992. *The Evolution of Life Histories*. Oxford, UK: Oxford Univ. Press

Stearns SC, Crandall RE. 1984. Plasticity for age and size at sexual maturity: a life-history response to unavoidable stress. In *Fish Reproduction: Strategies and Tactics*, ed. GW Potts, RJ Wootton, pp. 13–33. London: Academic

Stearns SC, Koella JC. 1986. The evolution of phenotypic plasticity in life-history traits: prediction of reaction norms for age and size at maturity. *Evolution* 40:893–913

Stenseth NC, Dunlop ES. 2009. Unnatural selection. *Nature* 457:803–4

Swain DP, Sinclair AF, Hanson JM. 2007. Evolutionary response to size-selective mortality in an exploited fish population. *Proc. R. Soc. B* 274:1015–22

Swain DP, Sinclair AF, Hanson JM. 2008. Evolution of growth in Gulf of St Lawrence cod: reply to Heino et al. *Proc. R. Soc. B* 275:1113–15

Therkildsen NO, Hemmer-Hansen J, Als TD, Swain DP, Morgan MJ, et al. 2013. Microevolution in time and space: SNP analysis of historical DNA reveals dynamic signatures of selection in Atlantic cod. *Mol. Ecol.* 22:2424–40

Thomas G, Quoß H, Hartmann J, Eckmann R. 2009. Human-induced changes in the reproductive traits of Lake Constance common whitefish (*Coregonus lavaretus*). *J. Evol. Biol.* 22:88–96

Trippel EA. 1995. Age at maturity as stress indicator in fisheries. *BioScience* 45:759–71

Uusi-Heikkilä S, Kuparinen A, Wolter C, Meinelt T, O'Toole AC, Arlinghaus R. 2011. Experimental assessment of the probabilistic maturation reaction norm: Condition matters. *Proc. R. Soc. B* 278:709–17

Vainikka A, Gårdmark A, Bland B, Hjelm J. 2009. Two- and three-dimensional maturation reaction norms for the eastern Baltic cod, *Gadus morhua*. *ICES J. Mar. Sci.* 66:248–57

Van Walraven L, Mollet FM, van Damme CJG, Rijnsdorp AD. 2010. Fisheries-induced evolution in growth, maturation and reproductive investment of the sexually dimorphic North Sea plaice (*Pleuronectes platessa* L.). *J. Sea Res.* 64:85–93

Van Wijk SJ, Taylor MI, Creer S, Dreyer C, Rodrigues FM, et al. 2013. Experimental harvesting of fish populations drives genetically based shifts in body size and maturation. *Front. Ecol. Environ.* 11:181–87

Vasemägi A, Primmer CR. 2005. Challenges for identifying functionally important genetic variation: the promise of combining complementary research strategies. *Mol. Ecol.* 14(12):3623–42

Walsh MR, Munch SB, Chiba S, Conover DO. 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. *Ecol. Lett.* 9:142–48

Wilson ADM, Binder TR, McGrath KP, Cooke SJ, Godin J-GJ, Kraft C. 2011. Capture technique and fish personality: Angling targets timid bluegill sunfish, *Lepomis macrochirus*. *Can. J. Fish. Aquat. Sci.* 68(5):749–57

Wright PJ, Gibb FM, Gibb IM, Millar CP. 2011. Reproductive investment in the North Sea haddock: temporal and spatial variation. *Mar. Ecol. Prog. Ser.* 432:149–60

Wright PJ, Palmer SCF, Marshall CT. 2014. Maturation shifts in a temperate marine fish population cannot be explained by simulated changes in temperature-dependent growth and maturity. *Mar. Biol.* 161(12):2781–90

Yoneda M, Wright PJ. 2004. Temporal and spatial variation in reproductive investment of Atlantic cod *Gadus morhua* in the northern North Sea and Scottish west coast. *Mar. Ecol. Prog. Ser.* 276:237–48

Zimmermann F, Heino M. 2013. Is size-dependent pricing prevalent in fisheries? The case of Norwegian demersal and pelagic fisheries. *ICES J. Mar. Sci.* 70(7):1389–95

Zimmermann F, Jørgensen C. 2015. Bioeconomic consequences of fishing-induced evolution: A model predicts limited impact on net present value. *Can. J. Fish. Aquat. Sci.* 72:612–24

Fisheries-induced Evolution

SUPPLEMENTAL TABLES 1–7

Mikko Heino,[1,2,3] Beatriz Díaz Pauli,[1] and Ulf Dieckmann[3]

[1]Department of Biology and Hjort Centre for Marine Ecosystem Dynamics, University of Bergen, Box 7803, N-5020 Bergen, Norway

[2]Institute of Marine Research and Hjort Centre for Marine Ecosystem Dynamics, Box 1870, N-5817 Bergen, Norway

[3]Evolution and Ecology Program, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria

Clarifications for the Supplemental Tables 1–7

Sex: F = females, M = males, C = both males and females combined

Data type: "Time series" = continuous time series with minor gaps, "X periods" = separate periods, "X populations" = separate populations from the same time

FIE implicated: "Yes" = the original authors concluded that fisheries-induced evolution (FIE) had likely occurred, "No" = the original authors concluded that explanations other than FIE were sufficient

Supplemental Table 1. PMRN studies of maturation trends or between-population differences in maturation associated with fishing in Atlantic cod.

Species	Population or stock	Sex	Time span	Data type	FIE implicated?	Reference
Atlantic cod, *Gadus morhua*	Northeast Arctic	C	1932–2006	Time series	Yes	Heino et al. 2002, McAdam & Marshall 2014
	Eastern Baltic	F, M	1991–2005	Time series	Yes	Vainikka et al. 2009
	Georges Bank	F, M	1970–1998	Time series	Yes	Barot et al. 2004
	Gulf of Maine	F, M	1970–1998	Time series	Yes	Barot et al. 2004
	Northern (2J3KL)	F, M	1977/81–2002	Time series	Yes	Olsen et al. 2004, 2005
	Southern Grand Bank (3NO)	F, M	1971–2002	Time series	Yes	Olsen et al. 2004, 2005
	St. Pierre Bank (3Ps)	F, M	1972–2002	Time series	Yes	Olsen et al. 2004, 2005
	Southern Gulf of St. Lawrence	F, M	1958–2008	Time series	Yes	Swain 2011
	Flemish Cap (3M)	F	1972–2006	Time series	Yes	Pérez-Rodríguez et al. 2013
	Icelandic	F, M	1967–2007	Time series	Yes	Pardoe et al. 2009
	North Sea (3 substocks)	F, M	1971–2009	Time series	Yes	Wright et al. 2011b
	North Sea (combined)	F, M	1983–2010	Time series	Yes	Neuheimer & Grønkjær 2012
	North Sea (combined)	F, M	1974–2012	Time series	Yes	Marty et al. 2014

Supplemental Table 2. PMRN studies of maturation trends or between-population differences in maturation associated with fishing in marine bottom-living fish other than cod.

Species	Population or stock	Sex	Time span	Data type	FIE implicated?	Reference
Haddock, *Melanogrammus aeglefinus*	North Sea (2 substocks)	F, M	1978–2007	Time series	Yes	Wright et al. 2011a
	North Sea (combined)	F, M	1974–2012	Time series	Yes	Marty et al. 2014
	Barents Sea	F, M	1987–2009	Time series	No	Devine & Heino 2011
Whiting, *Merlangius merlangus*	North Sea	F, M	1974–2012	Time series	Yes	Marty et al. 2014
Norway pout, *Trisopterus esmarkii*	North Sea	F, M	1983–2012	Time series	No	Marty et al. 2014
European plaice, *Pleuronectes platessa*	North Sea	F	1957–2001	Time series	Yes	Grift et al. 2003, 2007
		F, M	1900–2008	3 periods	Yes	van Walraven et al. 2010
		M	1985–2008	2 periods	Yes	van Walraven et al. 2010
American plaice, *Hippoglossoides platessoides*	Labrador–NE Newfoundland (2J3K)	F, M	1973–1999	Time series	Yes	Barot et al. 2005
	Grand Bank (3LNO)	F, M	1969–2000	Time series	Yes	Barot et al. 2005
	St. Pierre Bank (3Ps)	F, M	1972–1999	Time series	Yes	Barot et al. 2005
Sole, *Solea solea*	Southern North Sea	F	1958–2000	Time series	Yes	Mollet et al. 2007

Supplemental Table 3. PMRN studies of maturation trends or between-population differences in maturation associated with fishing in pelagic marine fish.

Species	Population or stock	Sex	Time span	Data type	FIE implicated?	Reference
Atlantic herring, *Clupea harengus*	Norwegian spring-spawning	C	1935–2000	Time series	Yes, weak	Engelhard & Heino 2004
Sardine, *Sardina pilchardus*	Portuguese coast	C	1947–2008	Time series	No	Silva et al. 2013
Capelin, *Mallotus villosus*	Barents Sea	F, M	1975–2008	Time series	No	Baulier et al. 2012

Supplemental Table 4. PMRN studies of maturation trends or between-population differences in maturation associated with fishing in brackish water, freshwater, and anadromous fish.

Species	Population or stock	Sex	Time span	Data type	FIE implicated?	Reference
Pikeperch, *Sander lucioperca*	Archipelago Sea, northern Baltic Sea	F, M	1980–2011	Time series	Yes	Kokkonen et al. 2015
Estuary cobbler, *Cnidoglanis macrocephalus*	Wilson Inlet, Western Australia, Australia	F	1987–2008	2 periods	Yes	Chuwen et al. 2011
Chum salmon, *Oncorhynchus keta*	Shari River, Hokkaido, Japan	F, M	1992–1997	Time series	No[1]	Morita et al. 2005
	Chitose, Nishibetsu and Tokachi Rivers, Hokkaido, Japan	F	1977–1996	Time series	Yes	Fukuwaka & Morita 2008
Sockeye salmon, *Oncorhynchus nerka*	5 populations spawning in the Iliamna Lake system, Alaska, USA	F, M	1965–2009	Time series	Yes (2/5)	Kendall et al. 2014
	4 populations spawning in the Wood River system, Alaska, USA	F, M	1962–2009	2 periods	Yes (4/4)	Kendall et al. 2014
Lake whitefish, *Coregonus clupeaformis*	Lakes Michigan, Huron, and Superior, USA/Canada	F, M	1971–2005	4 populations	Ambiguous[2]	Wang et al. 2008
Smallmouth bass, *Micropterus dolomieu*	Opeongo Lake, Ontario, Canada	M	1936–2002	2 periods	No	Dunlop et al. 2005

[1] Empirically established PMRN from data in 1992–1997 was used to interpret changes over a 50-year period.

[2] Some spatial differences were concordant with the expectations from fisheries-induced evolution, but fishing is just one of the factors.

Supplemental Table 5. Studies on fisheries-induced evolution of reproductive investment. GSI = gonadosomatic index, ratio of gonad weight to body weight.

Species	Population or stock	Sex	Time span	Data type	FIE implicated?	Reference
Atlantic cod, *Gadus morhua*	North Sea (2 substocks)	F	1969–2003	2 periods	Yes, increased fecundity in 1 substock only	Yoneda & Wright 2004
	Northern (2J3KL)	F, M	1978–2013	Time series	Yes, increased GSI but for males only	Baulier 2009, L. Baulier, M. J. Morgan, G. Lilly, U. Dieckmann & M. Heino, unpublished
	Southern Grand Bank (3NO)	F, M	1978–2013	Time series	Yes, increased GSI but for males only	Baulier 2009, L. Baulier, M. J. Morgan, G. Lilly, U. Dieckmann & M. Heino, unpublished
	St. Pierre Bank (3Ps)	F, M	1978–2013	Time series	Yes, increased GSI but for males only	Baulier 2009, L. Baulier, M. J. Morgan, G. Lilly, U. Dieckmann & M. Heino, unpublished
Haddock, *Melanogrammus aeglefinus*	North Sea (2 substocks)	F, M	1978–2007	Time series	Yes, marginally increased fecundity	Wright et al. 2011a
European plaice, *Pleuronectes platessa*	North Sea (2 subareas)	F	1900–1985	2 periods	No (increase in fecundity attributed to the environment)[3]	Rijnsdorp 1991
	North Sea	F, M	1960–2002	Time series	No (increased	Rijnsdorp et al. 2005

---

[3] Rijnsdorp et al. (2005) interpreted the same data cautiously more positively in a context of a more comprehensive study on reproductive investment.

					weight loss during spawning attributed to the environment)	
	North Sea	F	1948–2002	3 periods	Yes, increased fecundity	Rijnsdorp et al. 2005
	North Sea	F, M	1985–2008	2 periods	No (no significant change in energetic investment)	van Walraven et al. 2010
Alpine whitefish, *Coregonus lavaretus*	Lake Joux, Switzerland	F	1980–2002	Time series	No (no significant change in fecundity)	Nusslé et al. 2009
Common whitefish, *Coregonus lavaretus*	Lake Constance, Germany/Switzerland/Austria	C	1963–1999	Time series	Yes, increased fecundity	Thomas et al. 2009

Supplemental Table 6. Studies on fisheries-induced evolution of growth in marine fish. If FIE has been implicated, we distinguish between "primary" response, where growth has evolved independently from changes in maturation or reproductive investment, and "secondary" response, where evolution of growth is indicated to have occurred as a consequence of earlier maturation or increased reproductive investment only.

Species	Population or stock	Sex	Time span	Data type	FIE implicated?	Reference
Atlantic cod, *Gadus morhua*	Southern Gulf of St. Lawrence	C	1981–2001	Time series	Yes, slower (primary)	Swain et al. 2007, 2008
	North Sea (combined)	F, M	1983–2010	Time series	Yes, slower (secondary)	Neuheimer & Grønkjær 2012
Haddock, *Melanogrammus aeglefinus*	Scotian Shelf	C	1970–2008	Time series	Yes, slower (secondary)	Neuheimer & Taggart 2010
	North Sea (2 substocks)	F, M	1978–2007	Time series	Yes, slower (secondary)	Wright et al. 2011a
European plaice, *Pleuronectes platessa*	North Sea	F, M	1900–2008	3 periods	Yes, slower (secondary)	van Walraven et al. 2010
Atlantic herring, *Clupea harengus*	Newfoundland	C	1965–2005	Time series	Yes, slower (secondary)	Wheeler et al. 2009

Supplemental Table 7. Studies on fisheries-induced evolution of growth in freshwater and anadromous fish. See Supplemental Table 5 for explanations.

Species	Population or stock	Sex	Time span	Data type	FIE implicated?	Reference
Northern pike, *Esox lucius*	Lake Windermere, UK	C	1944–1995	Time series	Yes, slower (maturation not considered[4])	Edeline et al. 2007
Lake whitefish, *Coregonus clupeaformis*	Lesser Slave Lake, Canada	C	1941–1975	Time series	Yes, slower (maturation not considered)	Handford et al. 1977
Common whitefish, *Coregonus lavaretus*	Lake Constance, Germany/Switzerland/Austria	C	1955–1997	Time series	Yes, slower (maturation not considered)	Thomas & Eckmann 2007
Alpine whitefish, *Coregonus lavaretus*	Lake Joux, Switzerland	C	1980–2002	Time series	Yes, slower (primary)	Nusslé et al. 2009
Brienzlig whitefish, *Coregonus albellus*	Lake Brienz, Switzerland	C	1984–2008	Time series	Yes, slower (primary)	Nusslé et al. 2011
Albock whitefish, *Coregonus fatioi*	Lake Brienz, Switzerland	C	1984–2008	Time series	Yes, slower (primary)	Nusslé et al. 2011
Atlantic salmon, *Salmo salar*	River Bidasoa, Spain	C	1983–2008	Time series	Yes, slower (maturation not considered)	Saura et al. 2010
Pink salmon, *Oncorhynchus gorbuscha*	British Columbia: multiple areas	C	1951–1991	Time series	Yes, slower (primary)	Ricker 1981, 1995
Chum salmon, *Oncorhynchus keta*	British Columbia: multiple areas	C	1951–1991	Time series	No	Ricker 1981, 1995

---

[4] Enberg et al. (2012) suggest that the decline in growth might have been caused by increased reproductive effort reported by Edeline et al. (2007).

Sockeye salmon, *Oncorhynchus nerka*	British Columbia: multiple areas	C	1951–1991	Time series	No	Ricker 1981, 1995
Coho salmon, *Oncorhynchus kisutch*	British Columbia: areas outside of the Southern straits	C	1951–1991	Time series	Yes, slower (primary)	Ricker 1981, 1995
	British Columbia: lower Johnstone Strait and the Strait of Georgia	C	1951–1991	Time series	No	Ricker 1981, 1995
Chinook salmon, *Oncorhynchus tshawytscha*	British Columbia: multiple areas	C	1951–1991	Time series	No	Ricker 1981, 1995
	Nushagak River, Alaska	F, M	1981	Time series	No	Kendall & Quinn 2011

LITERATURE CITED

Barot S, Heino M, Morgan MJ, Dieckmann U. 2005. Maturation of Newfoundland American plaice (*Hippoglossoides platessoides*): long-term trends in maturation reaction norms despite low fishing mortality? *ICES J. Mar. Sci.* 62:56–64

Barot S, Heino M, O'Brien L, Dieckmann U. 2004. Long-term trend in the maturation reaction norm of two cod stocks. *Ecol. Appl.* 14:1257–71

Baulier L. 2009. *Evolutionary and statistical modeling of life-time schedules of energy allocation in Atlantic herring and cod*. PhD thesis. University of Bergen

Baulier L, Heino M, Gjøsæter H. 2012. Temporal stability of the maturation schedule of capelin (*Mallotus villosus* Müller) in the Barents Sea. *Aquat. Living Resour.* 25:151–61

Chuwen BM, Potter IC, Hall NG, Hoeksema SD, Laurenson LJB. 2011. Changes in catch rates and length and age at maturity, but not growth, of an estuarine plotosid (*Cnidoglanis macrocephalus*) after heavy fishing. *Fish. Bull.* 109:247–60

Devine JA, Heino M. 2011. Investigating the drivers of maturation dynamics in Barents Sea haddock (*Melanogrammus aeglefinus*). *Fish. Res.* 110(3):441–49

Dunlop ES, Shuter BJ, Ridgway MS. 2005. Isolating the influence of growth rate on maturation patterns in the smallmouth bass (*Micropterus dolomieu*). *Can. J. Fish. Aquat. Sci.* 62:844–53

Edeline E, Carlson SM, Stige LC, Winfield IJ, Fletcher JM, et al. 2007. Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection. *Proc. Natl. Acad. Sci.* 104:15799–804

Enberg K, Jørgensen C, Dunlop ES, Varpe Ø, Boukal DS, et al. 2012. Fishing-induced evolution of growth: concepts, mechanisms, and the empirical evidence. *Mar. Ecol.* 33:1–25

Engelhard GH, Heino M. 2004. Maturity changes in Norwegian spring-spawning herring *Clupea harengus*: compensatory or evolutionary responses? *Mar. Ecol. Prog. Ser.* 272:245–56

Fukuwaka M, Morita K. 2008. Increase in maturation size after the closure of a high seas gillnet fishery on hatchery-reared chum salmon *Oncorhynchus keta*. *Evol. Appl.* 1:376–87

Grift RE, Heino M, Rijnsdorp AD, Kraak SBM, Dieckmann U. 2007. Three-dimensional maturation reaction norms for North Sea plaice. *Mar. Ecol. Prog. Ser.* 334:213–24

Grift RE, Rijnsdorp AD, Barot S, Heino M, Dieckmann U. 2003. Fisheries-induced trends in reaction norms for maturation in North Sea plaice. *Mar. Ecol. Prog. Ser.* 257:247–57

Handford P, Bell G, Reimchen T. 1977. A gillnet fishery considered as an experiment in artificial selection. *J. Fish. Res. Board Can.* 34:954–61

Heino M, Dieckmann U, Godø OR. 2002. Reaction norm analysis of fisheries-induced adaptive change and the case of the Northeast Arctic cod. *CM 2002/Y:14*, ICES, Copenhagen

Kendall NW, Dieckmann U, Heino M, Punt AE, Quinn TP. 2014. Evolution of age and length at maturation of Alaskan salmon under size-selective harvest. *Evol. Appl.* 7(2):313–22

Kendall NW, Quinn TP. 2011. Length and age trends of chinook salmon in the Nushagak River, Alaska, related to commercial and recreational fishery selection and exploitation. *Trans. Am. Fish. Soc.* 140(3):611–22

Kokkonen E, Vainikka A, Heikinheimo O. 2015. Probabilistic maturation reaction norm trends reveal decreased size and age at maturation in an intensively harvested stock of pikeperch *Sander lucioperca*. *Fish. Res.*

Marty L, Rochet M-J, Ernande B. 2014. Temporal trends in age and size at maturation of four North Sea gadid species: cod, haddock, whiting and Norway pout. *Mar. Ecol. Prog. Ser.* 497:179–97

McAdam BJ, Marshall CT. 2014. Bayesian fitting of probabilistic maturation reaction norms to population-level data. *Fish. Res.* 159:105–13

Mollet FM, Kraak SBM, Rijnsdorp AD. 2007. Fisheries-induced evolutionary changes in maturation reaction norms in North Sea sole *Solea solea*. *Mar. Ecol. Prog. Ser.* 351:189–99

Morita K, Morita SH, Fukuwaka M, Matsuda H. 2005. Rule of age and size at maturity of chum salmon (*Oncorhynchus keta*): implications of recent trends among *Oncorhynchus* spp. *Can. J. Fish. Aquat. Sci.* 62:2752–59

Neuheimer AB, Grønkjær P. 2012. Climate effects on size-at-age: growth in warming waters compensates for earlier maturity in an exploited marine fish. *Glob. Change Biol.* 18(6):1812–22

Neuheimer AB, Taggart CT. 2010. Can changes in length-at-age and maturation timing in Scotian Shelf haddock (*Melanogrammus aeglefinus*) be explained by fishing? *Can. J. Fish. Aquat. Sci.* 67(5):854–65

Nusslé S, Bornand CN, Wedekind C. 2009. Fishery-induced selection on an Alpine whitefish: quantifying genetic and environmental effects on individual growth rate. *Evol. Appl.* 2:200–208

Nusslé S, Bréchon A, Wedekind C. 2011. Change in individual growth rate and its link to gill-net fishing in two sympatric whitefish species. *Evol. Ecol.* 25(3):681–93

Olsen EM, Heino M, Lilly GR, Morgan MJ, Brattey J, et al. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature.* 428:932–35

Olsen EM, Lilly GR, Heino M, Morgan MJ, Brattey J, Dieckmann U. 2005. Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* 62:811–23

Pardoe H, Vainikka A, Thórdarson G, Marteinsdóttir G, Heino M. 2009. Temporal trends in probabilistic maturation reaction norms and growth of Atlantic cod (*Gadus morhua* L.) on the Icelandic shelf. *Can. J. Fish. Aquat. Sci.* 66:1719–33

Pérez-Rodríguez A, Morgan J, Koen-Alonso M, Saborido-Rey F. 2013. Disentangling genetic change from phenotypic response in

reproductive parameters of Flemish Cap cod *Gadus morhua*. *Fish. Res.* 138(0):62–70

Ricker WE. 1981. Changes in the average size and average age of Pacific salmon. *Can. J. Fish. Aquat. Sci.* 38:1636–56

Ricker WE. 1995. Trends in the average size of Pacific salmon in Canadian catches. *Can. Spec. Publ. Fish. Aquat. Sci.* 121:593–602

Rijnsdorp AD. 1991. Changes in fecundity of female North Sea plaice (*Pleuronectes platessa* L.) between three periods since 1900. *ICES J. Mar. Sci.* 48(3):253–80

Rijnsdorp AD, Grift RE, Kraak SBM. 2005. Fisheries-induced adaptive change in reproductive investment in North Sea plaice (*Pleuronectes platessa*)? *Can. J. Fish. Aquat. Sci.* 62:833–43

Saura M, Morán P, Brotherstone S, Caballero A, Álvarez J, Villanueva B. 2010. Predictions of response to selection caused by angling in a wild population of Atlantic salmon (*Salmo salar*). *Freshw. Biol.* 55:923–30

Silva A, Faria S, Nunes C. 2013. Long-term changes in maturation of sardine, *Sardina pilchardus*, in Portuguese waters. *Sci. Mar.* 77(3):429–38

Swain DP. 2011. Life-history evolution and elevated natural mortality in a population of Atlantic cod (*Gadus morhua*). *Evol. Appl.* 4(1):18–29

Swain DP, Sinclair AF, Hanson JM. 2007. Evolutionary response to size-selective mortality in an exploited fish population. *Proc. R. Soc. B Biol. Sci.* 274:1015–22

Swain DP, Sinclair AF, Hanson JM. 2008. Evolution of growth in Gulf of St Lawrence cod: reply to Heino et al. *Proc. R. Soc. B Biol. Sci.* 275:1113–15

Thomas G, Eckmann R. 2007. The influence of eutrophication and population biomass on common whitefish (*Coregonus lavaretus*) growth — the Lake Constance example revisited. *Can. J. Fish. Aquat. Sci.* 64:402–10

Thomas G, Quoß H, Hartmann J, Eckmann R. 2009. Human-induced changes in the reproductive traits of Lake Constance common whitefish (*Coregonus lavaretus*). *J. Evol. Biol.* 22:88–96

Vainikka A, Gårdmark A, Bland B, Hjelm J. 2009. Two- and three-dimensional maturation reaction norms for the eastern Baltic cod, *Gadus morhua*. *ICES J. Mar. Sci.* 66:248–57

Van Walraven L, Mollet FM, van Damme CJG, Rijnsdorp AD. 2010. Fisheries-induced evolution in growth, maturation and reproductive investment of the sexually dimorphic North Sea plaice (*Pleuronectes platessa* L.). *J. Sea Res.* 64:85–93

Wang H-Y, Höök TO, Ebener MP, Mohr LC, Schneeberger PJ. 2008. Spatial
and temporal variation of maturation schedules of lake whitefish
(*Coregonus clupeaformis*) in the Great Lakes. *Can. J. Fish. Aquat. Sci.*
65:2157–69

Wheeler JP, Purchase CF, Macdonald PDM, Fill R, Jacks L, et al. 2009.
Temporal changes in maturation, mean length-at-age, and condition of
spring-spawning Atlantic herring (*Clupea harengus*) in Newfoundland
waters. *ICES J. Mar. Sci.* 66:1800–1807

Wright PJ, Gibb FM, Gibb IM, Millar CP. 2011a. Reproductive investment in
the North Sea haddock: temporal and spatial variation. *Mar. Ecol.
Prog. Ser.* 432:149–60

Wright PJ, Millar CP, Gibb FM. 2011b. Intrastock differences in maturation
schedules of Atlantic cod, *Gadus morhua*. *ICES J. Mar. Sci.*
68(9):1918–27

Yoneda M, Wright PJ. 2004. Temporal and spatial variation in reproductive
investment of Atlantic cod *Gadus morhua* in the northern North Sea
and Scottish west coast. *Mar. Ecol. Prog. Ser.* 276:237–48