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Fisheries-induced Evolution

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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 types of fish that are most available or profitable to catch (Andersen et al. 2012, Holland & Sutinen 1999, Salas et al. 2004). 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". 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". 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 ten generations of selective breeding has 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) attracted scant attention at their time. 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 by 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 (speed: Audzijonyte et al. 2013, Devine et al. 2012, experiments: Díaz Pauli & Heino 2014, growth rate: Enberg et al. 2012, theory and consequences: Heino et al. 2013), 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 with 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 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 and/or exposure to fishing: whenever fishing mortalities are size-selective and/or behavior-selective, respectively, all these traits experience a complex array of selection pressures.

Importantly though, 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 tradeoffs. It then becomes less valuable, in fitness terms, for a fish to postpone reproduction, restrain current reproduction, or make anti-senescence investments, because the potential gains in terms of enhanced growth, survival, and/or future reproduction are erased when a fish ends its life in a fishing gear. Consequently, faster life histories are favored.

While 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 an elevated mortality on 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 mortalities, all fish experience them alike; thus, no selection pressures result. The second example, however, already 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 chances at all to spawn in a second season. While such special situations do exist, at least approximately, they indeed are rare.

Theoretical models suggest that fisheries-induced selection may sometimes be disruptive, in which case they 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 iteroparous fish is expected to select for earlier or later maturation. For example, while fishing more mature fish causes delayed maturation, fishing more 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 strictly needed.

2.2.Eco-genetic Models

Eco-genetic 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 modelling framework that is especially suited for 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, respectively, on the theories of quantitative genetics and adaptive dynamics. While models of quantitative genetics excel at predicting the time scales of evolutionary responses to selection pressures, models of adaptive dynamics excel at accounting for realistic population structures and life-history detail. Eco-genetic models simultaneously feature both advantages.

Building on the pioneering work by Law & Gray (1989), as well as on earlier model-based studies, such as those by Heino (1998), Ernande et al. (2004), and Hutchings (2005), eco-genetic models have been devised and calibrated for a variety of fish stocks and fishing regimes. Resultant insights range from the asymmetrically fast pace of FIE compared to the evolutionary reversal 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 are also studies that retain the detailed descriptions of life histories, evolving traits, and selectivity patterns found in eco-genetic 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 confirm the general finding that the strongest selection pressures 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. 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 suggest that FIE may boost or erode heritabilities (Marty et al. 2015), so that observed heritabilities are strongly impacted by a stock's past selection regimes. To capture any such effects, eco-genetic 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: that (*a*) the observed change is evolutionary and thus genetic, and that (*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 through observation of wild populations (section 3.3). Observational studies in the wild can never conclusively prove that fishing is a driver, since causal interpretations generally require replication and controls. Strengthening the case that fishing is indeed among the drivers is thus only possible through two approaches: comparative studies (Devine et al. 2012, Sharpe & Hendry 2009) and careful analysis 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 modelling (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, is a matter of considerable debate.

3.1. Genotypic versus Phenotypic Evidence

Adaptive change can be examined studying phenotypic traits or molecular markers, but both approaches present challenges. Monitoring phenotypes allows studying demographically important traits (e.g., growth or maturation), but disentangling adaptive change from phenotypic plasticity is challenging. Monitoring molecular markers could enable unambiguous identification of genetic changes associated with FIE, excluding alternative explanations such as phenotypic plasticity and population replacement (Hemmer-Hansen et al. 2014). 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 (Browman et al. 2008, Jørgensen et al. 2008, Kuparinen & Merilä 2008, Marshall & Browman 2007, Merilä 2009). While 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 study shifts in gene frequencies in response to environmental change in general (Hansen et al. 2012) and fishing in particular. Genetic differences due to selection, rather than population replacement, were 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 shallower than in deeper 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 seemed 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 on males (van Wijk et al. 2013).

The difficulty of monitoring FIE at the level of molecular markers lies in identifying the genetic basis of specific traits of interest and linking it to fishing pressure (Hemmer-Hansen et al. 2014, Vasemägi & Primmer 2005). 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 study FIE.

3.2.Experimental Evidence

Field observation 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 appropriate wild replicate populations suitable for experiments (but see Haugen & Vøllestad 2001). We therefore suggest that selection experiments, instead, are best suited to mimic changes observed in harvested populations and understand 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 concentrating attention on traits of interest for fisheries. Prime examples are maturation traits, which are particularly susceptible to FIE (Audzijonyte et al. 2013, Dunlop et al. 2009) and have been observed to change in response to fishing pressure after accounting for major sources of plasticity (Heino & Dieckmann 2008, Law 2007). Selection experiments also allow assessing the rate at which changes happen, their reversibility, and their effect on population productivity and fishery profitability, which are major issues for resource management.

Most experimental studies performed to date, independently of their model species, can be categorized into (1) studies using semelparous species (or iteroparous species forced into semelparity, both referred as semelparous species below) and (2) studies using iteroparous species. The choice of model species reflects the trade-off between the feasibilities of running large experiments and linking the results to real fisheries, but the difference in results is not trivial. Experiments with both types of model species seem to reach similar conclusions about size-selection on life-history traits. Removal of large individuals from a populations leads to evolution of reduced body size in both semelparous (Conover & Munch 2002, van Wijk et al. 2013) and iteroparous species (Edley & Law 1988, Haugen & Vøllestad 2001, B. Díaz Pauli & M. Heino, in prep.). It also leads to maturation at smaller body sizes in both iteroparous (Edley & Law 1988, B. Díaz Pauli & M. Heino, in prep.) and semelparous species (van Wijk et al. 2013).

However, conclusions concerning the effect of size-selection on population productivity and fishery profitability are diametrically opposite in experiments using iteroparous or semelparous species. Removal of large silversides (*Menidia menidia*, a semelparous species) led to markedly lower total biomass yield after four generations of size-selective harvest, relative to the removal of small individuals (Conover & Munch 2002). In contrast, removal of large-sized daphnids led to higher biomass yield after nine generations of selection (Díaz Pauli & Heino 2014, Edley & Law 1988). 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 (Díaz Pauli & Heino 2014, Edley & Law 1988). 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 their iteroparous life history: after four generations of

selection, the removal of large guppies resulted in higher biomass yield compared to the removal of small guppies (B. Díaz Pauli & M. Heino, in prep.). 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 higher biomass yield than removing small individuals, whereas this relation is reversed for semelparous species (**Figure 1**).

Experiments also allow studying fisheries-induced selection pressures that are difficult to observe in the wild. In addition to being size-selective, fishing can be directly selective on behavior (Enberg et al. 2012, Heino & Godø 2002, Law 2000). Experiments show that different fishing methods tend to remove fish with particular behavioral traits. Passive gears (traps, gillnets, long-lines) selectively catch bold individuals, while active gears (e.g., trawls) seem to catch more shy individuals (Biro & Post 2008, Díaz Pauli et al. 2015, Klefoth et al. 2012). This experimental evidence is in accordance with evidence from the wild (section 3.3; B. Díaz Pauli & A. Sih, in prep.).

Fishing exerting selection pressure on a given trait can lead to changes in other life-history traits, behavioral traits, and physiological traits, as sets of traits are usually coevolved (Réale et al. 2010). Selection experiments are well suited to study 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 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 rate and fecundity.

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 is therefore summarizing 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 (Heino & Dieckmann 2008, Policansky 1993, Ricker 1981, Rijnsdorp 1993).

3.3.1. Life-history Traits

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

Maturation. Maturation is the most studied life-history trait, for several reasons: maturation is a key life-history trait (Roff 1992, Stearns 1992), data are relatively abundant, maturation changes have obvious impacts on a stock's productivity, and large changes towards 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 the body size required for maturation earlier in their life (Jørgensen 1990, Law 2000, Trippel 1995). Moreover, at the population level, an earlier average age at maturation is also observed as a direct demographic response to fishing, because the average age in a population declines with increasing mortality (Dieckmann & Heino 2007, Heino & Dieckmann 2008, Policansky 1993, Ricker 1981). 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 available 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.

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 of 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 (Díaz Pauli & Heino 2013, Salinas & Munch 2014, Uusi-Heikkilä et al. 2011). Nevertheless, the PMRN approach has become the standard method for analyzing phenotypic 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 other demersal marine species show mostly positive findings. Only three studies have looked at pelagic marine species, suggesting 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 come from short-lived species that naturally experience high mortality and exhibit early maturation (e.g., Norway pout, sardine, and capelin; 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 others come from populations that are selectively harvested at spawning grounds only (Norwegian spring spawning herring; Engelhard & Heino 2004) or are semelparous and subject to terminal harvest (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 are associated with short time series that may have lacked statistical power. On the other hand, 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 were intensively exploited (northern cod, Olsen et al. 2004). Taken together, **Figure 2** suggests that FIE in maturation is common but not ubiquitous.

Reproduction. Theory predicts that fishing favors increased 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 migrations 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 change 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 (Baulier 2009, Wright et al. 2011, Yoneda & Wright 2004). One of the freshwater studies shows a positive result (Thomas et al. 2009), while another does not (Nusslé et al. 2009). Whether this mixed picture reflects the difficulty of measuring reproductive investment or systematically lower selection pressures on, or evolvabilities of, reproductive investment remains an open question.

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 (Cooper 1952, Handford et al. 1977, Miller 1957, Rutter 1902, Silliman 1975, 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 fisheries-independent factors (e.g., temperature) and 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).

Methods for disentangling environmental effects from fisheries-induced selection include multiple regressions. 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 such a key factor as "resource availability" is difficult to quantify. Physical variables like 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. While data storage tags now enable gathering such data, they have not yet been used at the scale necessary for drawing inferences about evolutionary changes.

An improvement of this strategy is to include fisheries-induced selection pressure as an explanatory variable, as first shown by Swain et al. (2007) for southern Gulf of St. Lawrence cod. By modelling the change in body length as a function of the selection differential induced by fishing and two environmental variables (temperature and density), they 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 by Swain et al. 2008).

A comparison of 73 fish populations world-wide found no correlation between changes in size-at-age and the intensity of fishing, and on this basis concluded that there is little evidence for FIE (Hilborn & Minte-Vera 2008). However, this study did not control for environmental effects, despite noting that 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 be towards slower growth, 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 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 (Pardoe et al. 2009, Swain et al. 2008) changes in growth are attributed to changes in maturation. Studies on freshwater or anadromous species have covered 13 species, mostly salmonids. These studies, when suggesting FIE of growth, are generally not attributing it to increased reproductive allocation, while investing 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 very cautious in attributing changes in size-at-age to

FIE (which was an unorthodox idea at the time), reaching a strongly positive conclusion only for one species, pink salmon (*O. gorbuscha*), and a more conditional positive conclusion for coho salmon (*O. kisutch*). These conclusions held up after Ricker extended the time series by 16 years (Ricker 1995). 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 (Bigler et al. 1996, Healey 1986). Nevertheless, there has been no rigorous attempt to estimate the relative strengths of various factors contributing to the size trends in Pacific salmon, and to date there is no consensus regarding just how good the evidence for an FIE component in these size trends is.

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 data availability. 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 (*Oncorhynchus 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 observing behaviors that were unthinkable just a few decades ago. Methods include active fisheries acoustics (sonars and echo sounders, 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 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 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 also 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. Olsen et al. (2012), using acoustic tagging of Atlantic cod in their natural habitat, 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 (Ariyomo et al. 2013, Chervet et al. 2011, Philipp et al. 2009), these studies suggest that such traits evolve in response to fishing just like life-history traits—so far, we simply have been unable to document these changes happening.

3.3.3. Caveats

Exploitation-induced evolution is fast compared to 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 effects of certain confounding factors and estimated selection differentials, or to link residual patterns to assumed patterns of selection. The strength of such inference depends on how well the non-evolutionary effects can be modelled. Achieving a good description of non-evolutionary effects is easier for maturation than for other traits. Since individual size-at-age is a proxy of the growth conditions an individual has encountered, studies using the PMRN approach are in a special position, because the data that are used to estimate the trait also carry information on the environment. This environmental proxy is evidently not perfect, but studies on other traits usually have to rely on even weaker proxies. By construction, any single observational field study is handicapped in demonstrating that phenotypic changes are evolutionary or that such changes are fisheries-induced when only phenotypic data are available.

While we must acknowledge that individual studies might have missed important drivers of phenotypic change—not just any drivers, but drivers that would cause similar patterns as 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 accomplish on its own.

4. IMPLICATIONS

Fisheries-induced evolution (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. While 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 may initially recover faster when exploitation is reduced (Enberg et al. 2009, Heino 1998, Kaitala & Getz 1995). This beneficial aspect of FIE is not guaranteed, though, and under special conditions adaptive evolution can even lead to extinction (so-called evolutionary suicide; 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). While this will only happen 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 turn 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 sustainable fisheries yields, at least in populations that are not seriously overfished (Eikeset et al. 2013, Heino 1998). Also the average body size of caught fish will decline (Heino 1998), usually implying a lower price per biomass unit (Zimmermann & Heino 2013). All these considerations lead to the recommendation that FIE best be

minimized. This recommendation was challenged by Andersen and 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 glance, but 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 time scales relevant for resource management, FIE is practically irreversible. Such a precautionary approach does not require a full overhaul of contemporary fisheries management. Rather, FIE should be assessed along with other determinants of sustainability, e.g., using the Evolutionary Impact Assessment (EvoIA) framework (Jørgensen et al. 2007, Laugen et al. 2014).

5. SUMMARY POINTS

- Theory predicts that most types of fishing favor evolution of faster life histories. This usually means earlier maturation, and may involve increased reproductive investment. At least post-maturation growth is also expected to decline.
- Fishing will exert selection pressures also 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).
- Theoretical studies suggest that reversing FIE through natural selection after fishing pressures are relaxed may be considerably slower than causing it.

- Empirical evidence for fisheries-induced evolution (FIE) is almost entirely based on phenotypic data, which suffices to infer evolutionary change under experimental conditions, but not from observational data collected in the wild.
- Empirical evidence for FIE in the wild is strongest for maturation, and the majority of case studies suggest evolution towards earlier reproduction. There is also some evidence for evolution towards slower growth and increased reproductive effort.
- Evidence of evolutionary changes in behavioral traits in wild fish is so far limited to phenology. Historic baseline data for other behavioral traits are missing, but experimental studies clearly show selection on behaviors and suggest that evolution in behavioral traits must have taken place.
- Empirical studies suggest that FIE can be fast, even compared to other examples of contemporary evolution. Concerns remain that phenotypic methods for studying FIE exaggerate its speed.
- FIE can make fish populations more robust to over-exploitation, but it can also reduce their resilience to natural fluctuations and undermine sustainable fisheries yields. There is a need to acknowledge and account for FIE when managing wild fish resources.

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

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	↑

↓: Selection for earlier maturation. ↑: Selection for later maturation. ↕: Evolutionary bistability. Table compiled in collaboration between U.D. and Anna Gårdmark, Swedish University of Agricultural Sciences, Department of Aquatic Resources, Institute of Coastal Research, Öregrund, Sweden.

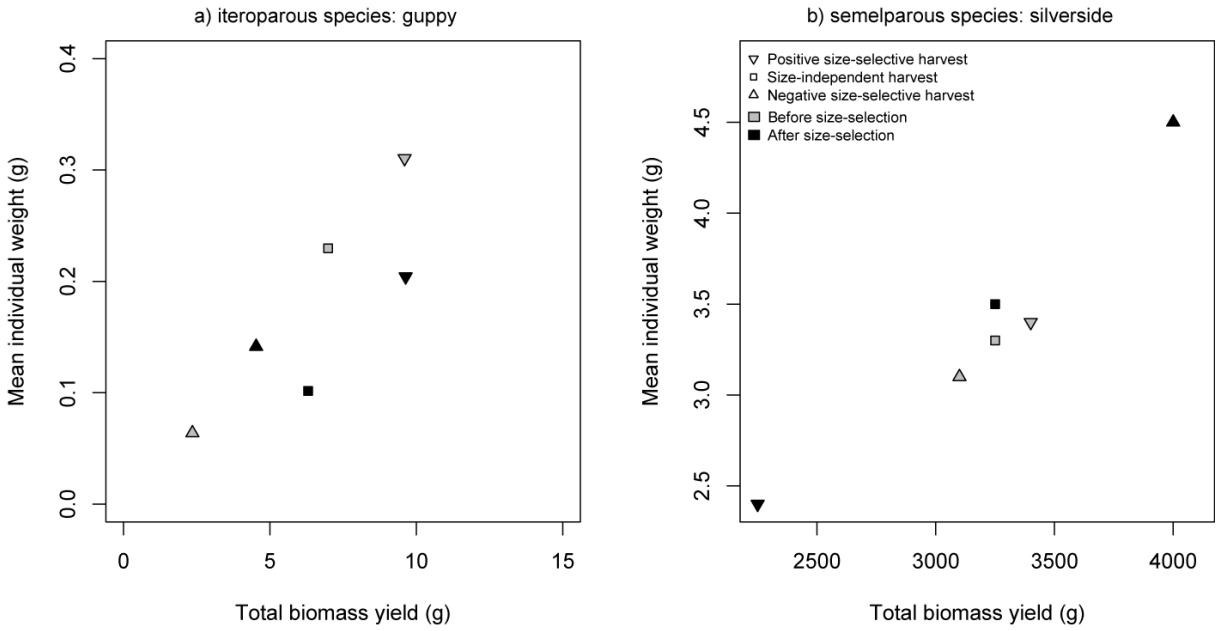

Figure 1. Comparison of the total biomass yield obtained from selection experiments with (a) guppies (*Poecilia reticulata*), an iteroparous species (B. Díaz Pauli & M. Heino, manuscript in preparation), and (b) silversides (*Menidia menidia*), a semelparous species with terminal harvest (data extracted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

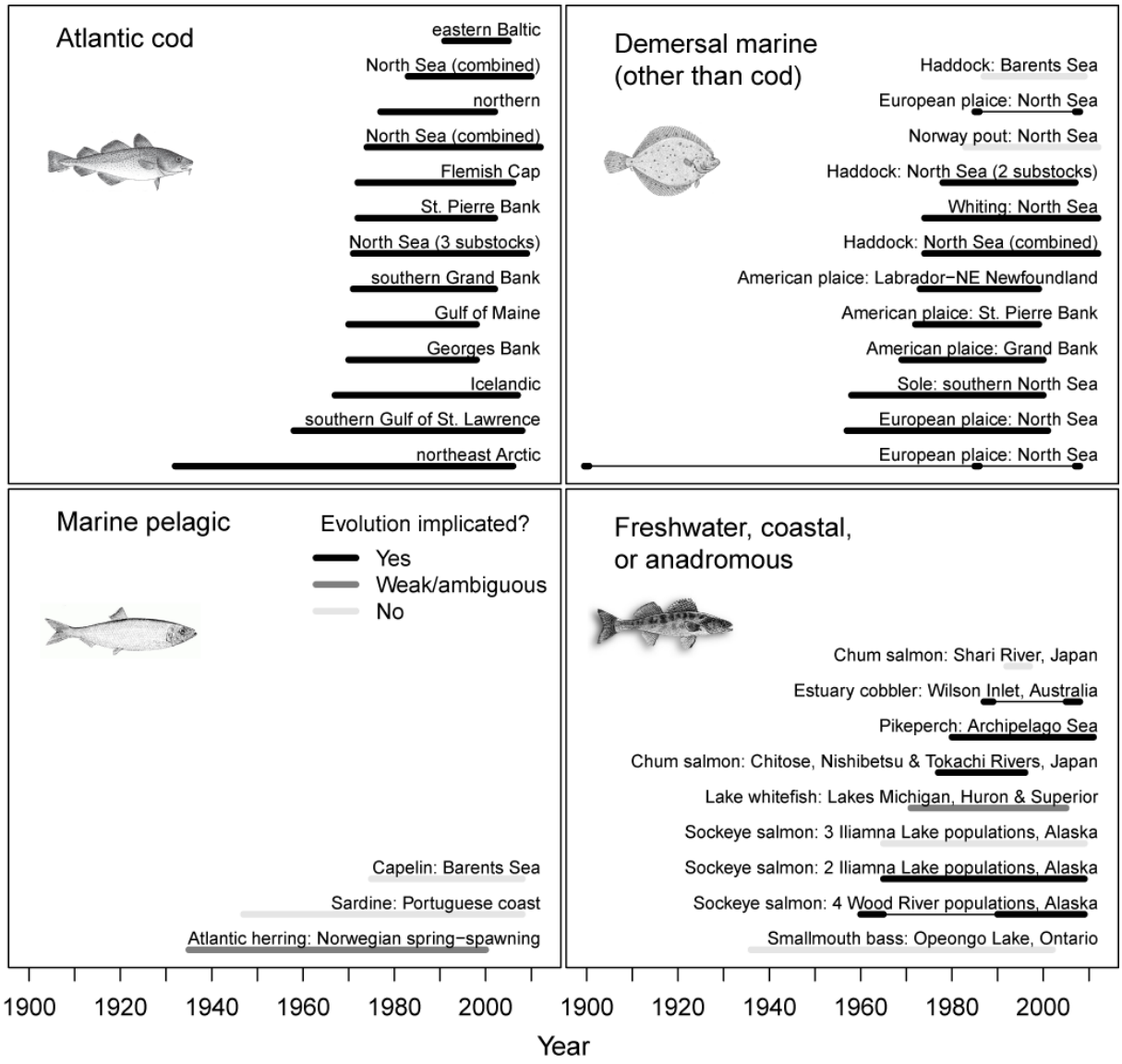

Figure 2. Studies in which probabilistic maturation reaction norms have been used to help interpret changes in maturation. Horizontal lines indicate whether fisheries-induced evolution is implicated and the time span of the data. See Supplemental Tables 1–4 for details and references.

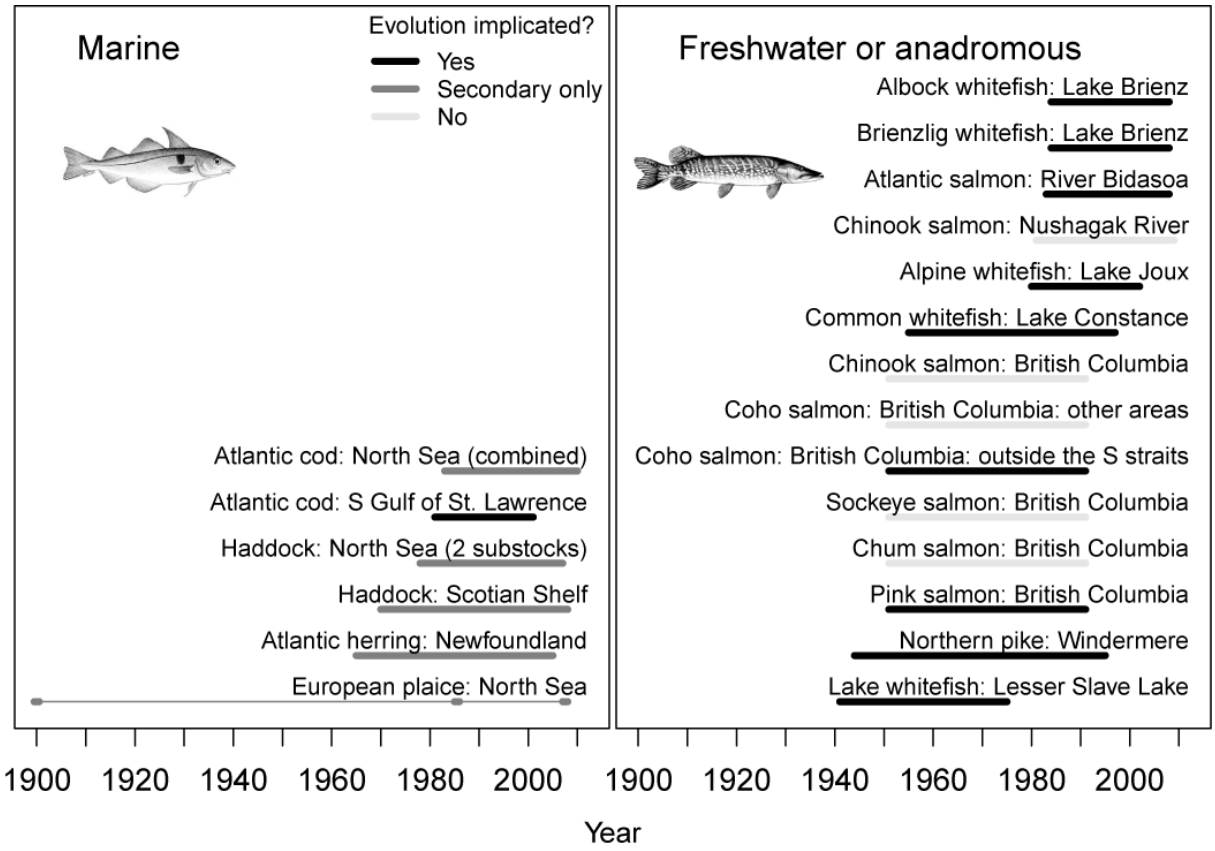

Figure 3. Studies in which fisheries-induced evolution of growth has been addressed. Dark gray bars indicate studies that documented evolutionary changes in the growth of adult fish but attributed these to changes in reproductive allocation. See Supplemental Tables 6–7 for details and references.

6. ONLINE-ONLY SUPPLEMENTAL TABLES 1–7

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6.1. Explanation of entries in Supplemental Tables 1–7

Column “Sex”: “F” = females, “M” = males, “C” = males and females combined

Column “Data type”: “Time series” = continuous time series with minor gaps, “*n* periods” = *n* separate time periods, “*m* populations” = *m* separate populations for the same time period

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 of 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 of 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 of 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 of 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] A PMRN empirically established from data during 1992–1997 was used to interpret changes over a 50-year period.

[2] Some spatial differences were concordant with expectations from FIE, but fishing was just one of the factors that differed among the populations.

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, increase in weight loss during spawning attributed to the environment	Rijnsdorp et al. 2005
	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

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

Supplemental Table 6. Studies on fisheries-induced evolution of growth in marine fish. If FIE has been implicated, we distinguish between a "primary" response, when growth has evolved independently from changes in maturation or reproductive investment, and a "secondary" response, when evolution of growth is understood 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
	Icelandic	F, M	1967–2007	Time series	Yes, slower (primary and secondary)	Pardoe et al. 2009
	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 6 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*	British Columbia, Canada:	C	1951–1991	Time series	Yes, slower	Ricker 1981, 1995

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

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

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