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 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

<table>
<thead>
<tr>
<th>Increased fishing mortality on</th>
<th>Induced selection pressures on maturation</th>
</tr>
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<tr>
<td>All fish</td>
<td>↓</td>
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<tr>
<td>Small fish</td>
<td>↑, ↓, or ⇓</td>
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<tr>
<td>Large fish</td>
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<tr>
<td>Young fish</td>
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<tr>
<td>Old fish</td>
<td>↓</td>
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<tr>
<td>Immature fish</td>
<td>↓</td>
</tr>
<tr>
<td>Mature fish</td>
<td>↑</td>
</tr>
</tbody>
</table>

↓ indicates selection for earlier maturation; ↑ indicates selection for later maturation; and ⇓ indicates evolutionary bistability. Table compiled as a collaboration between U.D. and Anna Gärdmark, 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 (Gärdmark & 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), to 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, $b^2$, 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](image_url)

**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-Helkkilä 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

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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 ex-
planatory 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.
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 (Jorgensen 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.

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Fisheries-induced Evolution

SUPPLEMENTAL TABLES 1–7

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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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Population or stock</th>
<th>Sex</th>
<th>Time span</th>
<th>Data type</th>
<th>FIE implicated?</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Southern Gulf of St. Lawrence</td>
<td>F, M</td>
<td>1958–2008</td>
<td>Time series</td>
<td>Yes</td>
<td>Swain 2011</td>
</tr>
<tr>
<td></td>
<td>North Sea (3 substocks)</td>
<td>F, M</td>
<td>1971–2009</td>
<td>Time series</td>
<td>Yes</td>
<td>Wright et al. 2011b</td>
</tr>
</tbody>
</table>
**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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Population or stock</th>
<th>Sex</th>
<th>Time span</th>
<th>Data type</th>
<th>FIE implicated?</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>1900–2008</td>
<td>3 periods</td>
<td>Yes</td>
<td>van Walraven et al. 2010</td>
</tr>
<tr>
<td></td>
<td></td>
<td>M</td>
<td>1985–2008</td>
<td>2 periods</td>
<td>Yes</td>
<td>van Walraven et al. 2010</td>
</tr>
</tbody>
</table>
### Supplemental Table 3. PMRN studies of maturation trends or between-population differences in maturation associated with fishing in pelagic marine fish.

<table>
<thead>
<tr>
<th>Species</th>
<th>Population or stock</th>
<th>Sex</th>
<th>Time span</th>
<th>Data type</th>
<th>FIE implicated?</th>
<th>Reference</th>
</tr>
</thead>
</table>
**Supplemental Table 4.** PMRN studies of maturation trends or between-population differences in maturation associated with fishing in brackish water, freshwater, and anadromous fish.

<table>
<thead>
<tr>
<th>Species</th>
<th>Population or stock</th>
<th>Sex</th>
<th>Time span</th>
<th>Data type</th>
<th>FIE implicated?</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Estuary cobbler, <em>Cnidoglanis macrocephalus</em></td>
<td>Wilson Inlet, Western Australia, Australia</td>
<td>F</td>
<td>1987–2008</td>
<td>2 periods</td>
<td>Yes</td>
<td>Chuwen et al. 2011</td>
</tr>
</tbody>
</table>

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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Population or stock</th>
<th>Sex</th>
<th>Time span</th>
<th>Data type</th>
<th>FIE implicated?</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atlantic cod, <em>Gadus morhua</em></td>
<td>North Sea (2 substocks)</td>
<td>F</td>
<td>1969–2003</td>
<td>2 periods</td>
<td>Yes, increased fecundity in 1 substock only</td>
<td>Yoneda &amp; Wright 2004</td>
</tr>
<tr>
<td>Haddock, <em>Melanogrammus aeglefinus</em></td>
<td>North Sea (2 substocks)</td>
<td>F, M</td>
<td>1978–2007</td>
<td>Time series</td>
<td>Yes, marginally increased fecundity</td>
<td>Wright et al. 2011a</td>
</tr>
<tr>
<td>European plaice, <em>Pleuronectes platessa</em></td>
<td>North Sea (2 subareas)</td>
<td>F</td>
<td>1900–1985</td>
<td>2 periods</td>
<td>No (increase in fecundity attributed to the environment)³</td>
<td>Rijnsdorp 1991</td>
</tr>
<tr>
<td></td>
<td>North Sea</td>
<td>F, M</td>
<td>1960–2002</td>
<td>Time series</td>
<td>No (increased</td>
<td>Rijnsdorp et al. 2005</td>
</tr>
</tbody>
</table>

³ Rijnsdorp et al. (2005) interpreted the same data cautiously more positively in a context of a more comprehensive study on reproductive investment.
<table>
<thead>
<tr>
<th>Location</th>
<th>Species</th>
<th>Year Range</th>
<th>Periods</th>
<th>Data Type</th>
<th>Result</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>North Sea</td>
<td>Fish</td>
<td>1948–2002</td>
<td>3 periods</td>
<td>Yes, increased fecundity</td>
<td>Rijnsdorp et al. 2005</td>
<td></td>
</tr>
<tr>
<td>North Sea</td>
<td>Fish, Males</td>
<td>1985–2008</td>
<td>2 periods</td>
<td>No (no significant change in energetic investment)</td>
<td>van Walraven et al. 2010</td>
<td></td>
</tr>
<tr>
<td>Common whitefish, <em>Coregonus lavaretus</em></td>
<td>Lake Constance, Germany/Switzerland/Austria</td>
<td>C</td>
<td>1963–1999</td>
<td>Yes, increased fecundity</td>
<td>Thomas et al. 2009</td>
<td></td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Population or stock</th>
<th>Sex</th>
<th>Time span</th>
<th>Data type</th>
<th>FIE implicated?</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>European plaice, <em>Pleuronectes platessa</em></td>
<td>North Sea</td>
<td>F, M</td>
<td>1900–2008</td>
<td>3 periods</td>
<td>Yes, slower (secondary)</td>
<td>van Walraven et al. 2010</td>
</tr>
</tbody>
</table>
### Supplemental Table 7. Studies on fisheries-induced evolution of growth in freshwater and anadromous fish. See Supplemental Table 5 for explanations.

<table>
<thead>
<tr>
<th>Species</th>
<th>Population or stock</th>
<th>Sex</th>
<th>Time span</th>
<th>Data type</th>
<th>FIE implicated?</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Common whitefish, <em>Coregonus lavaretus</em></td>
<td>Lake Constance, Germany/Switzerland/Austria</td>
<td>C</td>
<td>1955–1997</td>
<td>Time series</td>
<td>Yes, slower (maturation not considered)</td>
<td>Thomas &amp; Eckmann 2007</td>
</tr>
</tbody>
</table>

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).
**LITERATURE CITED**


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<table>
<thead>
<tr>
<th>Fish Species</th>
<th>Location</th>
<th>Sex</th>
<th>Time Period</th>
<th>Data Type</th>
<th>Maturation</th>
<th>Reference</th>
</tr>
</thead>
</table>


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