

1 Fisheries-induced Evolution

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12 **Abstract**

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

23 **Table of Contents**

24 1. Introduction 2
25 2. Theoretical Background 4
26 2.1. Fisheries-induced Selection Pressures..... 4
27 2.2. Eco-genetic Models 6
28 3. Evidence 7
29 3.1. Genotypic versus Phenotypic Evidence 8
30 3.2. Experimental Evidence..... 9
31 3.3. Evidence from the Wild 11
32 3.3.1. Life-history Traits..... 11
33 3.3.2. Behavioral Traits 16
34 3.3.3. Caveats 17
35 4. Implications..... 18
36 5. Summary Points 19
37 Acknowledgements 20
38 Literature cited 20
39 Tables 31
40 Figure Captions 32
41

42 **1. INTRODUCTION**

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

50 Whenever fishing is selective for characteristics that show genetic variability among individuals,
51 fishing will lead to evolutionary change in the affected populations. This insight was first
52 established—well before the genetic basis of inheritance became widely known—by Cloudsley Rutter,

53 a Californian scientist who worked with Chinook salmon (*Oncorhynchus tshawytscha*) in the
54 Sacramento River. Rutter (1902) remarked that the law prohibiting the use of nets catching small male
55 salmon returning to spawn countered common sense as “a stock-raiser would never think of selling his
56 fine cattle and keeping only the runts to breed from”. Yet, the fishery let the small salmon reach the
57 spawning grounds, while catching the large ones. On this basis, Rutter predicted that “the salmon will
58 certainly deteriorate in size”. This would not surprise aquaculturists, who have demonstrated how
59 various traits in a large number of species possess significant heritabilities and have responded to
60 artificial selection (Friars & Smith 2010). For example, about ten generations of selective breeding has
61 increased the growth rate in Atlantic salmon (*Salmo salar*) threefold (Solberg et al. 2013).

62 Despite clear parallels with animal breeding—fisheries-induced selection is a form of artificial
63 selection, albeit unintentional and uncontrolled—the idea of fishing as an evolutionary force has been
64 slow to penetrate the fisheries research community. Rutter passed away already in 1903 (Roppel 2004)
65 and his seminal remarks remained hidden in a long report, and were largely overlooked. Similarly,
66 early work on selection on growth by Cooper (1952), on fish behavior by Miller (1957), on a selection
67 experiment by Silliman (1975), on gillnet selectivity with respect to multiple life-history traits by
68 Handford et al. (1977), and on evolution of the age at maturation by Borisov (1978) attracted scant
69 attention at their time. This situation started to change only in the 1980s, perhaps partly in response to
70 the blossoming of life-history theory (Roff 1992, Stearns 1992), and partly because life-history
71 changes were observed in many harvested fish populations (reviewed by Trippel 1995). By the early
72 2000s, fisheries-induced evolution (FIE) had become a vigorous field of inquiry.

73 Several general reviews on FIE have already been presented, starting with the influential, but now
74 partly outdated, review by Law (2000). Similarly, reviews by Kuparinen and Merilä (2007), Fenberg
75 and Roy (2008), and Hutchings and Fraser (2008) miss many new developments. While several recent
76 reviews cover specific aspects of FIE (speed: Devine et al. 2012, Audzijonyte et al. 2013; growth rates:
77 Enberg et al. 2012; theory and consequences: Heino et al. 2013; experiments: Díaz Pauli & Heino
78 2014), there is no recent general review covering the main developments of the field during the last

79 decade, a gap that this review aims to fill. After providing an overview of theoretical expectations, we
80 summarize the empirical evidence for FIE, and conclude with discussing its implications.

81 **2. THEORETICAL BACKGROUND**

82 Theoretical expectations on fisheries-induced selection are fundamentally simple: it affects any trait
83 affecting a fish's exposure to fishing. And to the extent the affected traits possess any genetic
84 variability, the resultant selection differentials become incorporated into a stock's gene pool.

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

91 Life-history traits are among the prime targets of fisheries-induced selection, prominently including
92 traits regulating investments into growth, maturation, and reproduction (Heino & Godø 2002).

93 Likewise, behavioral and morphological traits affecting exposure to fishing are likely to experience
94 fisheries-induced selection, even though these targets have received less scientific scrutiny so far. In
95 addressing the aforementioned questions, we therefore align with the literature's focus on life-history
96 traits, and on maturation traits in particular.

97 **2.1. Fisheries-induced Selection Pressures**

98 Fisheries-induced selection may be direct or indirect. Fish evolving to grow more slowly to escape a
99 fishing mortality that commences above a threshold body size (e.g., Conover & Munch 2002) respond
100 to a direct selection pressure on growth. In contrast, fish evolving to grow more slowly because they
101 invest more energy into early maturation (e.g., Olsen et al. 2004) respond to a selection pressure that is
102 direct on maturation and indirect on growth. Also any population-level covariance in the genetic
103 variabilities of two traits can cause the selection pressure on one trait to be experienced by the other. It

104 is therefore common that fisheries-induced selection on a trait implies such selection on many other
105 traits. This is especially true for the wide ranges of traits affecting body size and/or exposure to fishing:
106 whenever fishing mortalities are size-selective and/or behavior-selective, respectively, all these traits
107 experience a complex array of selection pressures.

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

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

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

128 **Table 1** summarizes how fishing iteroparous fish is expected to select for earlier or later maturation.
129 For example, while fishing more mature fish causes delayed maturation, fishing more large fish causes

130 earlier maturation—even though mature fish tend to be large and large fish tend to be mature. This
131 shows the limitations of one-size-fits-all predictions of FIE. Accordingly, even qualitative insights into
132 FIE are best derived from stock-specific models that account for the life-history details of the fished
133 stock and for the selectivity patterns of its fishery. For quantitative predictions, such models are
134 strictly needed.

135 **2.2.Eco-genetic Models**

136 Eco-genetic models integrate principles of life-history theory and quantitative genetics theory to
137 account for a fish stock's life history, its fishing regime, and its genetic variability—resulting in a
138 modelling framework that is especially suited for understanding, forecasting, and managing FIE
139 (Dunlop et al. 2009). Such models benefit from the—historically, mutually exclusive—advantages of
140 two alternative quantitative approaches to predicting evolutionary dynamics based, respectively, on
141 the theories of quantitative genetics and adaptive dynamics. While models of quantitative genetics
142 excel at predicting the time scales of evolutionary responses to selection pressures, models of adaptive
143 dynamics excel at accounting for realistic population structures and life-history detail. Eco-genetic
144 models simultaneously feature both advantages.

145 Building on the pioneering work by Law & Gray (1989), as well as on earlier model-based studies,
146 such as those by Heino (1998), Ernande et al. (2004), and Hutchings (2005), eco-genetic models have
147 been devised and calibrated for a variety of fish stocks and fishing regimes. Resultant insights range
148 from the asymmetrically fast pace of FIE compared to the evolutionary reversal when fishing is
149 relaxed (Dunlop et al. 2009), to the influence of FIE on stock recovery (Enberg et al. 2009),
150 differences in selection pressures caused by different gear types (Jørgensen et al. 2009), and the
151 economic implications of FIE (Eikeset et al. 2013).

152 There are also studies that retain the detailed descriptions of life-histories, evolving traits, and
153 selectivity patterns found in eco-genetic models, while focusing attention on predicting selection
154 pressures, rather than the course of FIE (e.g., Arlinghaus et al. 2009, Matsumura et al. 2012). These
155 models can be simpler, in so far as they do not require keeping track of genetic variabilities.

156 Appropriately standardizing selection pressures turns out to be crucial for comparing these across
157 species, stocks, and traits (Matsumura et al. 2012). On this basis, these studies confirm the general
158 finding that the strongest selection pressures fishing mortalities impose on life-history traits typically
159 are those causing earlier maturation (Dunlop et al. 2009).

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

168 **3. EVIDENCE**

169 Theory makes a strong case for fishing being a potent driver of evolutionary changes in exploited
170 populations. A conclusive empirical demonstration that FIE has occurred in a particular population
171 and trait would require proving two logically independent conditions: that (1) the observed change is
172 evolutionary and thus genetic, and that (2) it has been caused, at least partly, by fishing, rather than by
173 other selective forces alone (Dieckmann & Heino 2007).

174 Evidence for exploitation-induced evolution is conceptually easy to obtain through controlled
175 experiments (section 3.2), but much harder through observation of wild populations (section 3.3).
176 Observational studies in the wild can never conclusively prove that fishing is a driver, since causal
177 interpretations always require replication and controls. Strengthening the case that fishing is indeed
178 among the drivers is thus only possible through two approaches: comparative studies (Sharpe &
179 Hendry 2009, Devine et al. 2012) and careful analysis of the roles of other drivers (i.e., environmental
180 factors). The latter can be achieved using process-based models parameterized for specific case studies
181 (e.g., Wright et al. 2014) or through pattern-oriented statistical modelling (e.g., Neuheimer &

182 Grønkjær 2012). Nevertheless, the role of fishing as a driver of selection often goes unchallenged. In
183 contrast, the use of phenotypic data to reveal evolutionary (and thus genetic) change, as discussed
184 below, is a matter of considerable debate.

185 **3.1.Genotypic versus Phenotypic Evidence**

186 Adaptive change can be examined studying phenotypic traits or molecular markers, but both
187 approaches present challenges. Monitoring phenotypes allows studying demographically important
188 traits (e.g., affecting growth or maturation), but disentangling adaptive change from phenotypic
189 plasticity is challenging. Monitoring molecular markers could enable unambiguous identification of
190 genetic changes associated with FIE, excluding alternative explanations such as phenotypic plasticity
191 and population replacement (Hemmer-Hansen et al. 2014). Field studies supporting FIE in the wild
192 (section 3.3) have been criticized for not reporting changes in gene frequencies together with
193 phenotypic changes in maturation (Marshall & Browman 2007, Browman et al. 2008, Jørgensen et al.
194 2008, Kuparinen & Merilä 2008, Merilä 2009). While this point is easy to make, in practice it is
195 difficult to link variation in molecular markers to the phenotypic variation associated with fishing
196 (Hansen et al. 2012).

197 Despite technological advances facilitating the compilation of genome-wide molecular data (Hemmer-
198 Hansen et al. 2014), few studies have successfully applied them to study shifts in gene frequencies in
199 response to environmental change in general (Hansen et al. 2012) and fishing in particular. Genetic
200 differences due to selection, rather than population replacement, were found in populations of Atlantic
201 cod (*Gadus morhua*) from Iceland and Canada (Jakobsdóttir et al. 2011, Therkildsen et al. 2013). In
202 Iceland, the changes were associated with differential fishing mortality, which was higher in shallower
203 than in deeper waters, in agreement with different observed allele frequencies (Jakobsdóttir et al.
204 2011). However, fishing pressure is just one of the factors differing between shallow and deep waters.
205 Shifts at loci in Canadian cod seemed correlated with temporal trends in temperature and midpoints of
206 probabilistic maturation reaction norms (Therkildsen et al. 2013). However, these temporal
207 correlations were based on small sample sizes, and more data are needed to corroborate these results

208 (Therkildsen et al. 2013). In an experiment on guppies (*Poecilia reticulata*), differences in candidate
209 genes associated with body length were found in association with contrasting size selection on males
210 (van Wijk et al. 2013).

211 The difficulty of monitoring FIE at the level of molecular markers lies in identifying the genetic basis
212 of specific traits of interest and linking it to fishing pressure (Vasemägi & Primmer 2005, Hemmer-
213 Hansen et al. 2014). To overcome this challenge, population genomics and quantitative genetics need
214 to be combined, but performing quantitative genetic tests in natural populations of marine fishes
215 remains difficult (Hemmer-Hansen et al. 2014). Consequently, molecular genetic approaches are
216 complementing, not replacing, phenotypic approaches to study FIE.

217 **3.2. Experimental Evidence**

218 Field observation and comparative studies aided by common-garden experiments can provide
219 evidence of divergent adaptation in the wild (Conover & Baumann 2009, Díaz Pauli & Heino 2014).
220 However, cases are rare that feature appropriate wild replicate populations suitable for experiments
221 (but see Haugen & Vøllestad 2001). We therefore suggest that selection experiments, instead, are best
222 suited to mimic changes observed in harvested populations and understand their nature and drivers.
223 The main advantage of selection experiments is that genetic and phenotypic changes can both be
224 observed and unequivocally attributed to the experimentally imposed selection pressure. Moreover,
225 selection experiments enable concentrating attention on traits of interest for fisheries. Prime examples
226 are maturation traits, which are particularly susceptible to FIE (Dunlop et al. 2009, Audzijonyte et al.
227 2013) and have been observed to change in response to fishing pressure after accounting for major
228 sources of plasticity (Law 2007, Heino & Dieckmann 2008). Selection experiments also allow
229 assessing the rate at which changes happen, their reversibility, and their effect on population
230 productivity and fishery profitability, which are major issues for resource management.

231 Most experimental studies performed to date, independently of their model species, can be categorized
232 into (1) studies using semelparous species (or iteroparous species forced into semelparity, both
233 referred as semelparous species below) and (2) studies using iteroparous species. The choice of model

234 species reflects the trade-off between the feasibilities of running large experiments and linking the
235 results to real fisheries, but the difference in results is not trivial. Experiments with both types of
236 model species seem to reach similar conclusions about size-selection on life-history traits. Removal of
237 large individuals from a populations leads to evolution of reduced body size in both semelparous
238 species (Conover & Munch 2002, van Wijk et al. 2013) and iteroparous species (Edley & Law 1988,
239 Haugen & Vøllestad 2001, B. Díaz Pauli & M. Heino, unpublished). It also leads to maturation at
240 smaller body sizes in both iteroparous species (Edley & Law 1988, B. Díaz Pauli & M. Heino,
241 unpublished) and semelparous species (van Wijk et al. 2013).

242 However, conclusions concerning the effect of size-selection on population productivity and fishery
243 profitability are diametrically opposite in experiments using iteroparous or semelparous species.
244 Removal of large silversides (*Menidia menidia*, a semelparous species) led to markedly lower total
245 biomass yield after four generations of size-selective harvest, relative to the removal of small
246 individuals (Conover & Munch 2002). In contrast, removal of large-sized daphnids led to higher
247 biomass yield after nine generations of selection (Edley & Law 1988, Díaz Pauli & Heino 2014). The
248 absolute biomass yield decreased to lower levels in populations in which small individuals were culled
249 than in populations in which large individuals were culled (Edley & Law 1988, Díaz Pauli & Heino
250 2014). Also the decrease in biomass yield relative to initial conditions was steeper in populations in
251 which small individuals were culled (Díaz Pauli & Heino 2014). Similar results were found for
252 guppies in a selection experiment allowing their iteroparous life history. The removal of large guppies
253 resulted in higher biomass yield compared to the removal of small guppies, after four generations of
254 selection (B. Díaz Pauli & M. Heino, unpublished). Thus, considering species with semelparous or
255 iteroparous life histories leads to contrasting conclusions regarding the effect of fishing on biomass
256 yield: removing large individuals from iteroparous species results in higher biomass yield than
257 removing small individuals, whereas this relation is reversed for semelparous species (**Figure 1**).

258 Experiments also allow studying fisheries-induced selection pressures that are difficult to observe in
259 the wild. In addition to being size-selective, fishing can be directly selective on behavior (Law 2000,
260 Heino & Godø 2002, Enberg et al. 2012). Experiments show that different fishing methods tend to

261 remove fish with particular behavioral traits. Passive gears (traps, gillnets, long-lines) selectively catch
262 bold individuals, while active gears (e.g., trawls) seem to catch more shy individuals (Biro & Post
263 2008, Klefoth et al. 2012, Díaz Pauli et al. 2015). This experimental evidence is in accordance with
264 evidence from the wild (section 3.3; B. Díaz Pauli & A. Sih, unpublished).

265 Fishing exerting selection pressure on a given trait can lead to changes in other life-history traits,
266 behavioral traits, and physiological traits, as sets of traits are usually coevolved (Réale et al. 2010).
267 Selection experiments are well suited to study such correlated traits. For example, the selection
268 experiment by Philipp et al. (2009) on vulnerability to angling in largemouth bass (*Micropterus*
269 *salmoides*) showed that individuals more vulnerable to fishing were better at nest guarding (Cooke et
270 al. 2007) and had higher metabolic rates. Walsh et al. (2006) showed that the removal of large
271 silversides also selected for lower consumption rate and fecundity.

272 **3.3.Evidence from the Wild**

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

280 **3.3.1. Life-history Traits**

281 Life-history traits are by far the most studied trait class, partly because the underlying theory is well-
282 developed, but probably mostly because of the availability of data. Many monitoring programs on
283 marine fish resources started in the late 1970s when coastal states obtained ownership to resources
284 within their newly-enacted Exclusive Economic Zones. Time series from these programs are now
285 more than three decades long, and typically include individual data on age, size, and sex, and
286 sometimes gonad size, allowing estimation of parameters related to growth, maturation, and

287 reproduction. Some monitoring programs started even much earlier. This puts oceanic fish in a special
288 position as a test bed for life-history theory—nothing comparable exists for terrestrial systems.

289 *Maturation.* Maturation is the most studied life-history trait, for several reasons: maturation is a key
290 life-history trait (Roff 1992, Stearns 1992), data are relatively abundant, maturation changes have
291 obvious impacts on a stock's productivity, and large changes towards earlier maturation (as predicted
292 by theory) have been documented for numerous fish populations (Trippel 1995). Earlier maturation,
293 however, is also a well-known “compensatory response” to fishing: when fishing reduces population
294 abundance, resource competition may be partly relaxed and the remaining fish can thus grow faster,
295 attaining the body size required for maturation earlier in their life (Jørgensen 1990, Trippel 1995, Law
296 2000). Moreover, at the population level, an earlier average age at maturation is also observed as a
297 direct demographic response to fishing, because the average age in a population declines with
298 increasing mortality (Ricker 1981, Policansky 1993, Dieckmann & Heino 2007, Heino & Dieckmann
299 2008). The possibility of exploitation-induced evolution was acknowledged during the 1990s, but most
300 researchers concluded that evolutionary changes could not be satisfactorily demonstrated from the
301 available data, while phenotypically plastic (compensatory) and demographic responses appeared
302 sufficient to explain the observed patterns (Jørgensen 1990, Smith 1994, Trippel 1995). A notable
303 exception is the pioneering study by Adriaan Rijnsdorp (1993), who concluded that plaice
304 (*Pleuronectes platessa*) in the North Sea had adapted to fishing by maturing earlier.

305 Introduction of the probabilistic maturation reaction norm (PMRN) approach (Heino et al. 2002) was
306 an important methodological step that helped to move the field forward (as reviewed in Dieckmann &
307 Heino 2007, Heino & Dieckmann 2008). Fundamentally, the strength of this approach stems from
308 studying individual age and size simultaneously—size-at-age is a proxy of growth, and the effects of
309 many environmental variables on maturation are channeled through growth. The approach builds on
310 the earlier deterministic maturation reaction norm concept and the associated notion that such reaction
311 norms can be used to disentangle growth-related phenotypic plasticity and genetic change (Stearns &
312 Crandall 1984, Stearns & Koella 1986). Just how well this disentanglement works has been debated
313 (see, e.g., the theme section edited by Marshall & Browman 2007), with experiments showing some of

314 its limitations (Uusi-Heikkilä et al. 2011, Díaz Pauli & Heino 2013, Salinas & Munch 2014).
315 Nevertheless, the PMRN approach has become the standard method for analyzing phenotypic data,
316 and despite its shortcomings, has provided an important improvement over earlier approaches.

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

323 Many of the negative findings come from short-lived species that naturally experience high mortality
324 and exhibit early maturation (e.g., Norway pout, sardine, and capelin; Baulier et al. 2012, Silva et al.
325 2013, Marty et al. 2014). Arguably, such species are already adapted to high mortality levels and may
326 therefore have little scope for a further acceleration of their maturation. Some others come from
327 populations that are selectively harvested at spawning grounds only (Norwegian spring spawning
328 herring; Engelhard & Heino 2004) or are semelparous and subject to terminal harvest (capelin, Pacific
329 salmon; Baulier et al. 2012, Kendall et al. 2014), settings that are known to exert less selection on
330 maturation. A few other negative cases are associated with short time series that may have lacked
331 statistical power. On the other hand, some short time series have shown significant changes. These
332 have been demonstrated in populations possessing relatively short generation times (e.g., eastern
333 Baltic cod, Vainikka et al. 2009) or ones that were intensively exploited (northern cod, Olsen et al.
334 2004). Taken together, **Figure 2** suggests that FIE in maturation is common but not ubiquitous.

335 *Reproduction.* Theory predicts that fishing favors increased investment to reproduction after
336 maturation. This investment can take many forms. Investment to the production of gametes can be
337 relatively easy to quantify, but the same is not true for investment to secondary sexual characteristics
338 or behaviors related to reproduction (e.g., migrations, courting).

339 A handful of studies have examined reproductive investment, relying on proxies such as weight-
340 specific fecundity, relative gonad weight, and weight loss during the spawning period (**Supplemental**
341 **Table 5**). Plaice is the most studied species, with most proxies showing no change or only changes
342 that can be attributed to the environment (Rijnsdorp et al. 2005, van Walraven et al. 2010). Studies
343 with other demersal fish have found positive results, but typically not for all populations or for both
344 sexes (Yoneda & Wright 2004, Baulier 2009, Wright et al. 2011). One of the freshwater studies shows
345 a positive result (Thomas et al. 2009), another not (Nusslé et al. 2009). Whether this mixed picture
346 reflects the difficulty of measuring reproductive investment or systematically lower selection pressures
347 on or evolvabilities of reproductive investment remains an open question.

348 *Growth*. Most fishing methods are size-selective, and it was fisheries-induced selection on growth or
349 size-at-age that first drew scientists' attention (Rutter 1902, Cooper 1952, Miller 1957, Silliman 1975,
350 Handford et al. 1977, Spangler et al. 1977). However, it was recognized already early on that growth is
351 readily influenced by the environment (Miller 1957, Spangler et al. 1977), including both fisheries-
352 independent factors (e.g., temperature) and fisheries-dependent factors (e.g., resource availability).
353 Because of the difficulty of disentangling these effects from evolutionary changes in growth, obtaining
354 strong evidence for FIE of growth has proven difficult in observational studies (Enberg et al. 2012).

355 Methods for disentangling environmental effects from fisheries-induced selection include multiple
356 regressions. In principle, if one constructs a statistical model that accounts for important
357 environmental effects on growth in a biologically meaningful way, a residual trend is consistent with
358 the action of a driver, such as fisheries-induced selection, that creates cumulative effects. However,
359 this approach is typically hampered by a lack of data: even such a key factor as “resource availability”
360 is difficult to quantify. Physical variables like temperature are straightforward to measure, but
361 quantifying an individual's ambient temperature at the locations where, and over the time intervals
362 during which, its growth has occurred is difficult. While data storage tags now enable gathering such
363 data, they have not yet been used at the scale necessary for drawing inferences about evolutionary
364 changes.

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

371 A comparison of 73 fish populations world-wide found no correlation between changes in size-at-age
372 and the intensity of fishing, and on this basis concluded that there is little evidence for FIE (Hilborn &
373 Minte-Vera 2008). However, this study did not control for environmental effects, despite noting that
374 evolutionary and density-dependent effects of fishing likely counteract each other. It should also be
375 remembered that FIE of growth is not always expected to be towards slower growth, complicating
376 such meta-analyses.

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

386 Ricker's (1981) classic study of five species of Pacific salmon (*Oncorhynchus* spp.) in British
387 Columbia is a notable exception—Ricker was very cautious in attributing changes in size-at-age to
388 FIE (which was an unorthodox idea at the time), reaching a strongly positive conclusion only for one
389 species, pink salmon (*O. gorbuscha*), and a more conditional positive conclusion for coho salmon (*O.*
390 *kisutch*). These conclusions held up after Ricker extended the time series by 16 years (Ricker 1995).

391 Ricker's conclusions have not gone unchallenged, though, and other researchers have attributed
392 greater importance to environmental drivers, particularly density-dependent effects, than Ricker did
393 (Healey 1986, Bigler et al. 1996). Nevertheless, there has been no rigorous attempt to estimate the
394 relative strengths of various factors contributing to the size trends in Pacific salmon, and to date there
395 is no consensus regarding just how good the evidence for an FIE component in these size trends is.

396 **3.3.2. Behavioral Traits**

397 Evidence of FIE in behavioral traits in the wild remains scarce. Probably the single most important
398 reason for this is data availability. The only behaviors that are routinely observed are related to the
399 phenology of migrations in species such as salmon. Changes in run timing that seem partly to reflect
400 different vulnerabilities of early- and late-running fish have been documented for Atlantic salmon
401 (*Salmo salar*) in Ireland (Quinn et al. 2006) and, more conclusively, for sockeye salmon
402 (*Oncorhynchus nerka*) in Alaska (Quinn et al. 2007). However, few fish species have such easily
403 observed migrations, and run timing is just one of many behavioral traits that could be under selection.
404 Rapidly improving technology is opening new possibilities that were unthinkable just a few decades
405 ago. Methods include active fisheries acoustics (sonars and echo sounders, e.g., Handegard &
406 Tjøstheim 2005), acoustic tracking (e.g., Langård et al. 2015), and data storage tags (e.g., Le Bris et al.
407 2013). However, behavioral observations using these methods tend to be one-off studies; only
408 fisheries acoustics are widely used in routine monitoring, and then not for monitoring behavior, but
409 spatial distribution and abundance. Past acoustic surveys represent a potential source of time series of
410 behavioral data, but remain, to our knowledge, unutilized for this purpose.

411 It is much easier to find evidence that fishing selects for certain behaviors than that it also results in
412 FIE. Experimental studies documenting correlations between behavioral traits and vulnerability are
413 already numerous (section 3.2), but a few studies have shown this also in the wild. Olsen et al. (2012),
414 using acoustic tagging of Atlantic cod in their natural habitat, were able to show that individuals with
415 certain movement patterns were more likely to be fished than others. Wilson et al. (2011) showed that
416 bluegill sunfish (*Lepomis macrochirus*) caught using a seine and those caught by angling differed
417 when tested in a lab for the boldness of their behavior. However, Kekäläinen et al. (2014) did not find

418 such differences in perch (*Perca fluviatilis*) in a similar setting. Nevertheless, combined with the
419 evidence that key behavioral traits possess heritable components (Philipp et al. 2009, Chervet et al.
420 2011, Ariyomo et al. 2013), these studies suggest that such traits evolve in response to fishing just like
421 life-history traits—so far, we simply have been unable to document these changes happening.

422 **3.3.3. Caveats**

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

428 Using phenotypic data to study evolution relies on a correlational approach to account for effects of
429 certain confounding factors and estimated selection differentials, or to link residual patterns to
430 assumed patterns of selection. The strength of such inference depends on how well the non-
431 evolutionary effects can be modelled. Achieving a good description of non-evolutionary effects is
432 easier for maturation than for other traits. Since individual size-at-age is a proxy of the growth
433 conditions an individual has encountered, studies using the PMRN approach are in a special position,
434 because the data that are used to estimate the trait also carry information on the environment. This
435 environmental proxy is evidently not perfect, but studies on other traits usually have to rely on even
436 weaker proxies. By construction, no observational field study can conclusively demonstrate that
437 phenotypic changes are evolutionary or that such changes are fisheries-induced.

438 While we must acknowledge that individual studies might have missed important drivers of
439 phenotypic change—not just any drivers, but drivers that would cause similar patterns as predicted for
440 fisheries-induced selection—it would be unlikely that many independent studies were to suffer from
441 the same bias. Therefore, the body of literature interpreting documented phenotypic patterns in terms
442 of FIE jointly provide stronger evidence for FIE than any individual case study can possibly
443 accomplish on its own.

444 **4. IMPLICATIONS**

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

450 FIE means that fish populations adapt to fishing. While evolution is not driven by benefits to
451 populations, adaptation to fishing nevertheless can benefit populations that are intensively fished: a
452 population with a faster life history will generally tolerate more additional mortality before being
453 driven to extinction, and may initially recover faster when exploitation is reduced (Kaitala & Getz
454 1995, Heino 1998, Enberg et al. 2009). This beneficial aspect of FIE is not guaranteed, though, and
455 under special conditions adaptive evolution can even lead to extinction (so-called evolutionary suicide;
456 Ernande et al. 2004).

457 FIE has also been characterized as “unnatural selection” (Allendorf & Hard 2009, Stenseth & Dunlop
458 2009). Indeed, adaptation to fishing often occurs at the cost of adaptation to a population’s natural
459 environment (Heino et al. 2013). While this will only happen when the net effect is positive at the
460 individual level, evolution assesses this net effect myopically, over the course of just a few generations.
461 Adaptation to fishing may thus turn costly in the long run, when environmental conditions change,
462 exploitation is reduced, or rare environmental fluctuations probe a population’s resilience. The
463 situation is similar to domestication: it makes organisms better suited to the conditions established by
464 humans, but less suited to the conditions in the wild.

465 A more immediate concern is that FIE is expected to reduce sustainable fisheries yields, at least in
466 populations that are not seriously overfished (Heino 1998, Eikeset et al. 2013). Also the average body
467 size of caught fish will decline (Heino 1998), usually implying a lower price per biomass unit
468 (Zimmermann & Heino 2013). All these considerations lead to the recommendation that FIE best be
469 minimized. This recommendation was challenged by Andersen and Brander (2009), who suggested

470 that the rate of FIE is so low (0.1–0.6% per year in their particular model) that dealing with FIE is less
471 urgent than reducing the direct detrimental effects of overfishing. This argument misses the point, for
472 two reasons. First, even low rates of change are important when they persist. An annual loss of 0.5%
473 may sound insignificant at first glance, but amounts to a loss of 10% in just 21 years. Such a loss is
474 indeed significant, given that fish are an important source of nutrition for many people, and the human
475 population is increasing. Second, dealing with the most urgent challenge (i.e., overfishing) is
476 fundamentally compatible with curbing rates of unwanted FIE: reducing exploitation addresses both
477 challenges.

478 We explicitly encourage a precautionary approach for dealing with FIE. It would not be wise to wait
479 until there is full certainty about the extent of FIE and its consequences: not only is there a risk that the
480 consequences are serious, but at the time scales relevant for resource management, FIE is practically
481 irreversible. Such a precautionary approach does not require a full overhaul of contemporary fisheries
482 management. Rather, FIE should be assessed along with other determinants of sustainability, e.g.,
483 using the Evolutionary Impact Assessment (EvoIA) framework (Jørgensen et al. 2007, Laugen et al.
484 2014).

485 **5. SUMMARY POINTS**

- 486 • Theory predicts that most types of fishing favor evolution of faster life histories. This usually
487 means earlier maturation, and may involve increased reproductive investment. At least post-
488 maturation growth is also expected to decline.
- 489 • Fishing will exert selection pressures also on other traits, either directly (e.g., when fishing
490 methods are directly selective on bold behaviors) or indirectly (e.g., when increased fishing
491 mortality favors bold behaviors by devaluing survival).
- 492 • Theoretical studies suggest that reversing FIE through natural selection after fishing pressures
493 are relaxed may be considerably slower than causing it.

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

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772 **TABLES**

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.

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775 **FIGURE CAPTIONS**

776 **Figure 1.** Comparison of the total biomass yield obtained from selection experiments with (a) guppy
777 (*Poecilia reticulata*), an iteroparous species (B. Díaz Pauli & M. Heino, unpublished), and (b)
778 silverside (*Menidia menidia*), a semelparous species with terminal harvest (data from Figure 1 in
779 Conover & Munch 2002). Both selection experiments lasted approximately four generations.

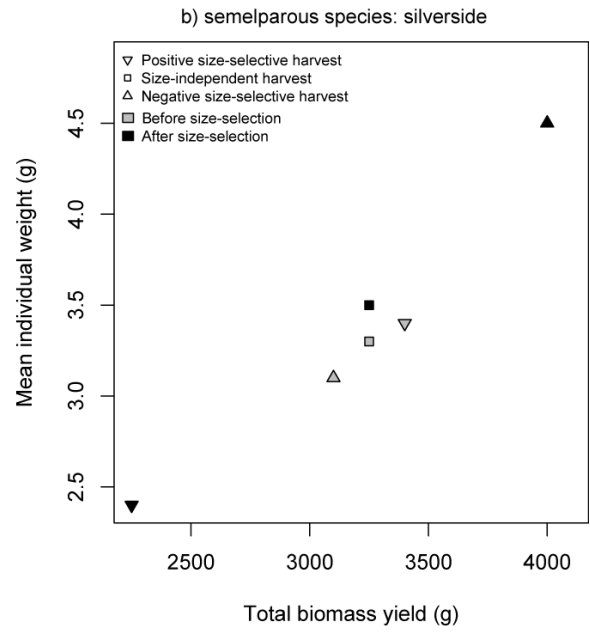
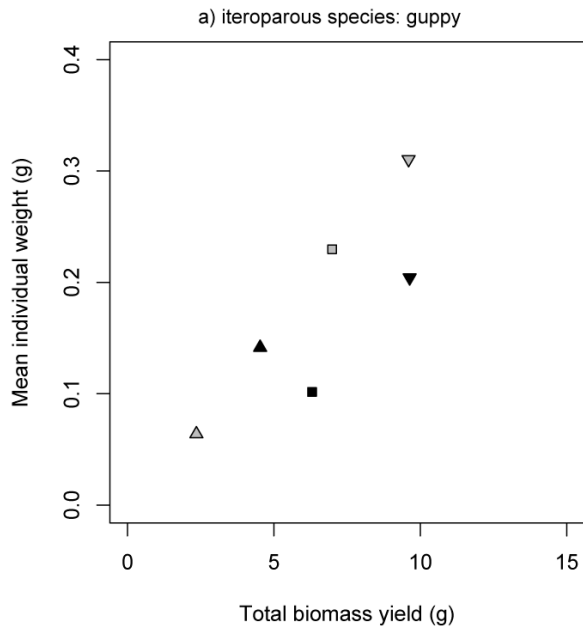
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781 **Figure 2.** Studies in which probabilistic maturation reaction norms have been used to help interpret
782 changes in maturation. Thick horizontal lines indicate the time span of data. See **Supplemental**
783 **Tables 1–4** for details and references. Fish images: © FAO Species Fact Sheets
784 (<http://www.fao.org/fishery/species/search/>).

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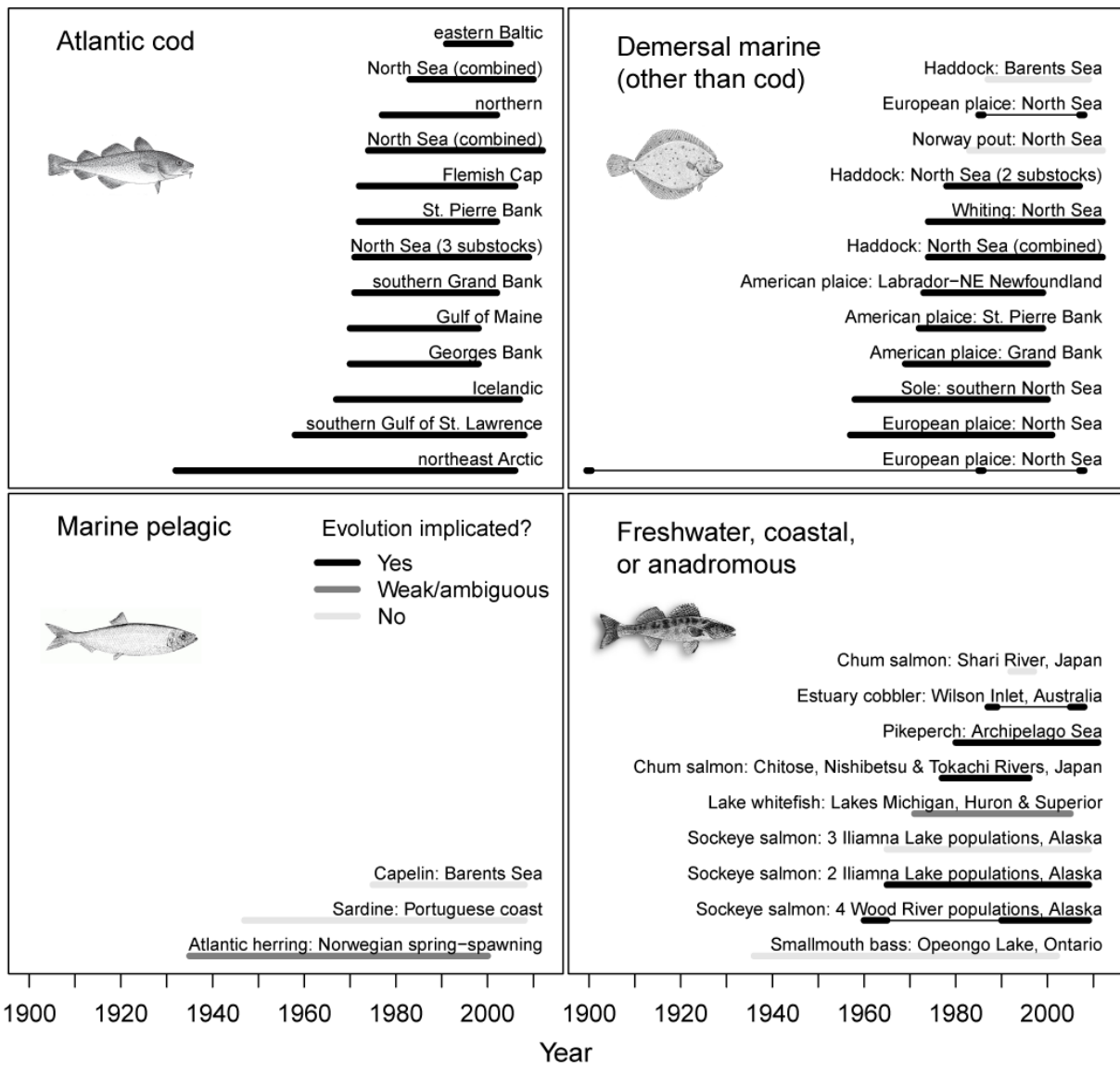
786 **Figure 3.** Studies in which fisheries-induced evolution of growth has been addressed. Dark grey bars
787 indicate studies that documented evolutionary changes in the growth of adult fish, but attributed these
788 to changes in reproductive allocation. See **Supplemental Tables 6–7** for details and references. Fish
789 images: © FAO Species Fact Sheets (<http://www.fao.org/fishery/species/search/>).

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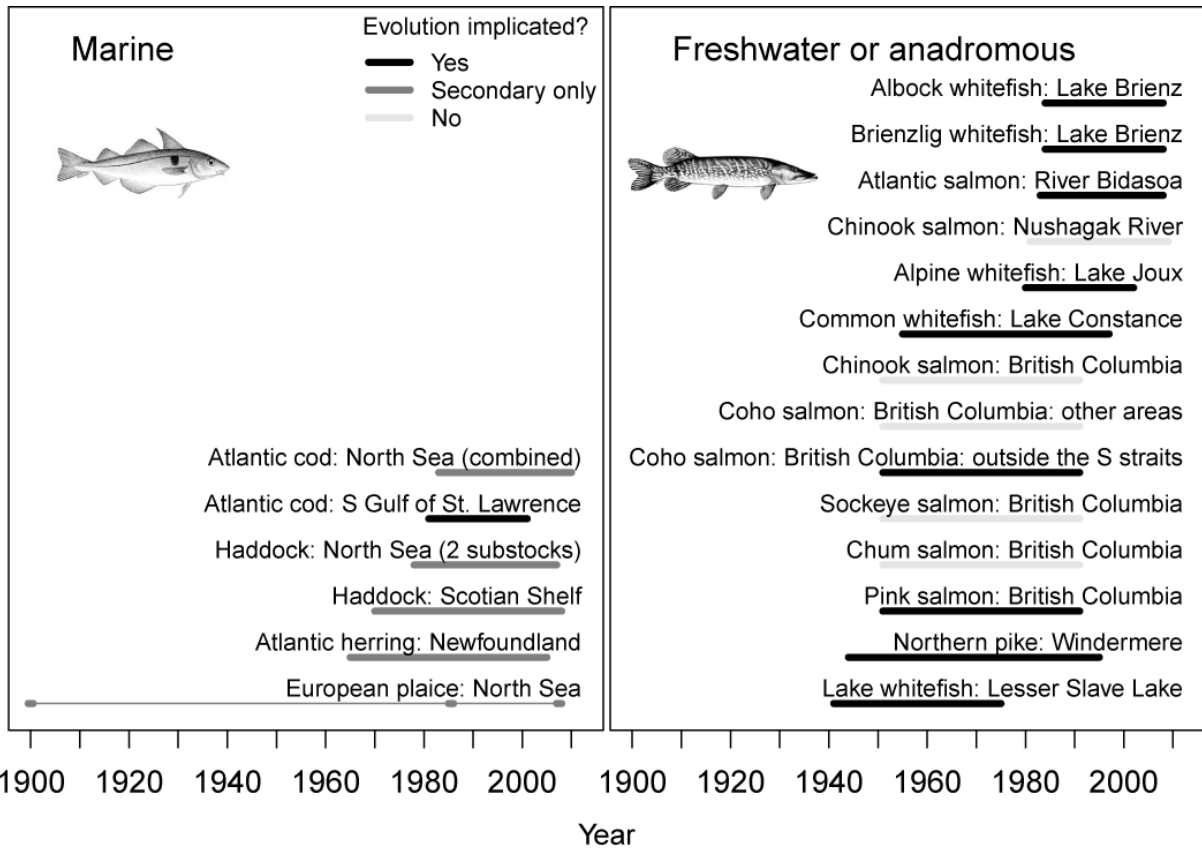
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792 Figure 1



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794 Figure 2



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796 Figure 3