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Implications of fisheries-induced evolution for population recovery: Refocusing the science and refining its communication

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Abstract

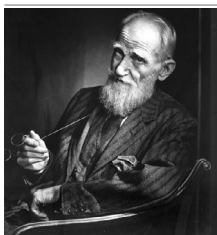The argument that sufficiently high fishing mortality (selective or not) can effect genetic change in fished populations has gained considerable traction since the late 1970s. The intervening decades have provided compelling experimental and model-based evidence that fisheries-induced evolution (FIE) can cause genetic changes in life history, behaviour and body shape, given sufficiently high trait heritability, selection intensity and time. Fisheries-induced evolution research has also identified or inferred negative implications to population recovery and sustainable yield, prompting calls for evolutionarily enlightened management to reduce the probability of FIE and mitigate its risks. Sufficient time has now elapsed to evaluate whether predicted negative consequences to recovery have been empirically realized. We find that many FIE-implicated populations have recovered rapidly to management-based targets following cessation of overfishing. We conclude that FIE is generally of minor importance to recovery when compared with overfishing, magnitude of depletion and natural mortality. By posing a series of questions and responses, we illustrate how science advice pertaining to human-induced evolution in fishes can be strengthened. We suggest that FIE research be refocused and its communication refined to: (a) better integrate FIE within existing stock-assessment modelling frameworks; (b) pose questions of greater relevance at the science:policy interface; and (c) concentrate research on questions pertaining to the subset of depleted populations for which the implications of FIE are likely to be magnified because of their synergistic interactions with other correlates of recovery and yield.

KEYWORDS
fishery rebuilding, genetic change, natural mortality, policy, stock decline

Ghoti papers

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Etymology of Ghoti

George Bernard Shaw (1856-1950), polymath, playwright, Nobel prize winner, and the most prolific letter writer in history, was an advocate of English spelling reform. He was reportedly fond of pointing out its absurdities by proving that 'fish' could be spelt 'ghoti'. That is: 'gh' as in 'rough', 'o' as in 'women' and 'ti' as in palatial.

1 | INTRODUCTION

The hypothesis that predators can generate evolutionary change in their prey has a long and rich history (Abrams, 1990, 2000; Endler, 1986; Michod, 1979). Although Darwin (1859) touched on the subject of how natural selection might diversify geographical races of predators, the fundamental question of how predator-prey interactions might result in a co-evolutionary arms race was not fully considered until the 1940s (Abrams, 2000). In the context of fisheries, this research did not have a sustained, applied focus until the late 1970s/early 1980s. Handford, Bell, and Reimchen (1977) published the first empirically defensible examination of whether fishing could generate genetic change in exploited populations, studying a gill-net fishery for lake whitefish (*Coregonus clupeaformis*, Salmonidae) in Alberta, Canada. This was followed by Ricker's (1981) similarly motivated contribution to Pacific salmon (*Oncorhynchus* spp., Salmonidae).

The field of fisheries-induced evolution (FIE) grew measurably and significantly in the late 1980s and early 1990s, precipitated by the pioneering work of Richard Law and colleagues (e.g. Edley & Law, 1988; Law & Grey, 1989; Law & Rowell, 1993), ultimately leading to an edited volume of 17 papers that explored the causes and consequences of harvest-induced evolution, especially by fishing (Stokes et al., 1993). By the early 2000s, the development of probabilistic maturation reaction norms (PMRNs) by Heino, Dieckmann, and Godø (2002) opened up the possibility that genetically based phenotypic shifts in life-history traits could be detected by a method thought to disentangle growth-related phenotypic plasticity from genetic change (Heino, Pauli, & Dieckmann, 2015).

The potential utility of PMRNs contributed to a breadth of research (population modelling, mathematical simulations, genetics/genomics, selection experiments/studies) manifest by a substantive increase in the number of peer-reviewed publications on FIE. Over the past decade, however, the number of publications on FIE has remained stable with 20–25 papers being detected by the ISI Web of Science annually. This stability suggests that the field of FIE research is not expanding and has perhaps attained some form of intellectual stasis.

The stasis is somewhat surprising, given numerous calls for fishery managers to apply the knowledge gained from FIE research to establish evolutionarily enlightened management strategies (e.g. Enberg, Jørgensen, Dunlop, Heino, & Dieckmann, 2009; Hutchings, 2009; Jørgensen et al., 2007; Laugen et al., 2014; Mollet, Poos, Dieckmann, & Rijnsdorp, 2016). These calls have been motivated by negative implications of FIE predicted or inferred by laboratory and model simulation studies, most of which can be grouped into two categories: (a) impairment of population recovery within single-species (Dunlop, Eikeset, & Stenseth, 2015; Hutchings, 2005; Walsh, Munch, Chiba, & Conover, 2006) and multi-species (Audzijonyte, Kuparinen, Gorton, & Fulton, 2013) contexts, partly because of truncation in age and(or) size-structure (Venturelli et al., 2010; Venturelli, Shuter, & Murphy, 2009) or reductions in age and size at maturity (e.g. Hutchings, 2005); and (b) reduction in some aspect of fishery "performance," usually yield (Conover & Munch, 2002; Law & Grey, 1989; Ratner & Lande, 2001).

The purpose of this perspective is neither to review FIE, for which there have been several efforts (e.g. Dieckmann & Heino, 2007; Heino et al., 2015; Hutchings & Fraser, 2008; Kuparinen & Festa-Bianchet, 2017; Kuparinen & Merilä, 2007), nor to debate its existence, for which the logical basis would seem unassailable, given the evidence for evolutionary change resulting from predator-prey interactions (Abrams, 2000; Burak, Monk, & Schmitz, 2018). Rather, we take advantage of the fact that sufficient time has elapsed to evaluate whether predicted or inferred negative consequences to population recovery associated with FIE have been empirically realized.

By examining empirical trajectories for previously over-exploited, FIE-implicated populations, we find that FIE may be of minor importance to recovery relative to other known correlates such as overfishing, magnitude of depletion and natural mortality. We conclude that failure to evaluate the risks of FIE relative to those caused by other factors underscores one of the weaknesses in how science advice on FIE and its consequences have been communicated to decision-makers. After exploring the correlates of recovery of marine fish stocks for which FIE has been implicated, we pose a series of questions and responses that might serve to better frame and strengthen science advice pertaining to human-induced evolutionary change in fishes.

2 | CONSEQUENCES OF FIE FOR POPULATION RECOVERY: AN EMPIRICAL PERSPECTIVE
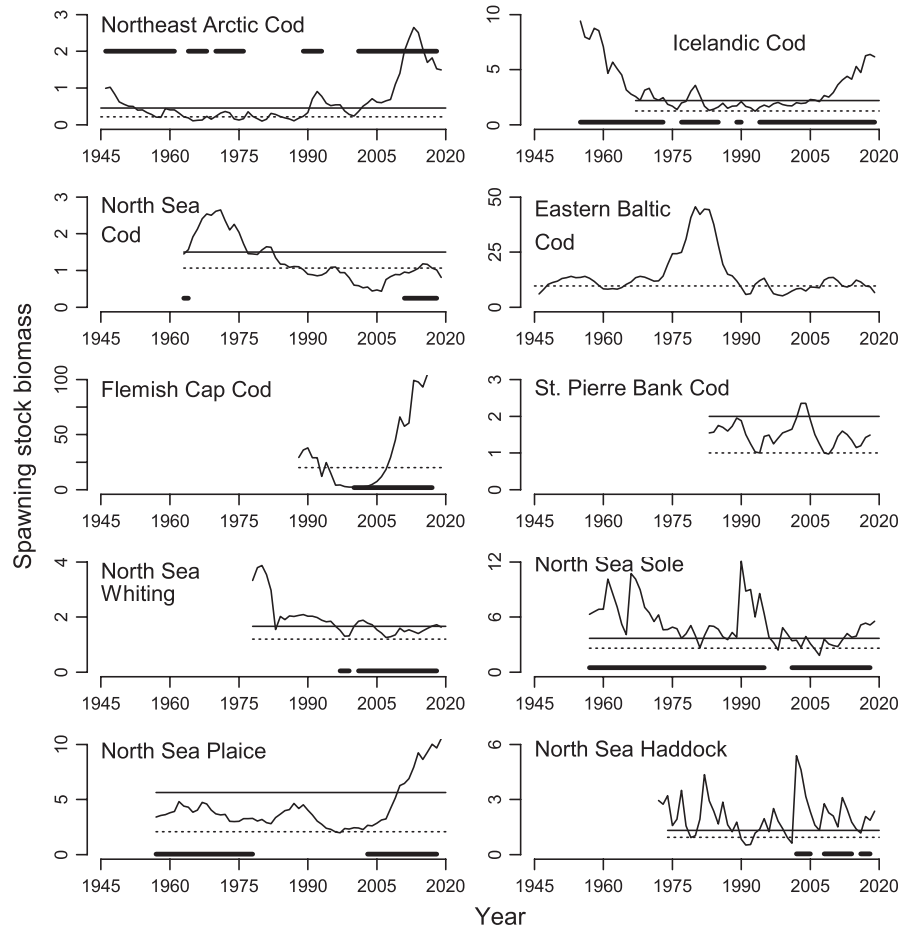
2.1 | Can FIE-implicated populations respond rapidly to reduced fishing mortality?

Fisheries-induced evolution is viewed to be problematic primarily because of its predicted negative impact on catch and(or) recovery/resilience, compounded by the concern that FIE might be slow to reverse. These predictions have a sound theoretical basis, supported by multiple, excellent laboratory and model simulation studies (see reviews by Kuparinen and Merilä (2007), Hutchings and Fraser (2008), and Heino et al. (2015)). But sound theory, experimental selection studies and mathematically defensible models alone are unlikely to influence decision-makers. Managers and policymakers, in addition to fishery scientists and stakeholders in the fishing industry (e.g. fishers, non-governmental organizations, seafood processors), will be poorly motivated to act if empirical evidence suggests that FIE cannot be shown to have, or to have had, demonstrably negative impacts on wild population recovery or resilience.

Predictions concerning FIE-induced changes in sustainable yield can be difficult to verify in natural populations because of the challenge in detecting empirical changes in the biomass associated with maximum sustainable yield (i.e. B_{msy}). Hypothesized impacts of FIE on population recovery, however, can be examined, given the

FIGURE 1 Trends in spawning stock biomass (*SSB*) of recovered stocks for which fisheries-induced evolution has been implicated. Thin horizontal lines identify the target (solid) and limit (dashed) biomass reference points. Thick solid lines identify years in which overfishing did not occur (note that overfishing cannot be assessed for Eastern Baltic and St. Pierre Bank cod stocks). Units of *SSB*: Northeast Arctic Cod and North Sea Plaice ($\times 10^6$ tonnes); Icelandic Cod, North Sea Cod, North Sea Whiting, North Sea Sole and North Sea Haddock ($\times 10^5$ tonnes); Flemish Cap Cod ($\times 10^3$ tonnes); St. Pierre Bank Cod (a relative measure, based on fishery-independent survey data)

existence of multiple fish stocks that have and have not recovered following mitigation of overfishing (Hutchings & Kuparinen, 2017).

Heino et al.'s (2015) review of FIE included 18 populations of marine fishes for which FIE had been implicated by the authors of the original studies. These stocks are distributed in the Northeast Atlantic (assessed by the International Council for the Exploration of the Sea or ICES) and the Northwest Atlantic (assessed by Canada's Department of Fisheries and Oceans (DFO) or the Northwest Atlantic Fisheries Organization).

Recovery status can be assessed by comparing recent estimates of stock biomass, $B_{current}$, with their respective limit (B_{lim}) and target reference points (B_{target}). For the 18 FIE-implicated stocks in question, B_{MSY} has not been defined, necessitating the use of B_{target} proxies:

MSY $B_{trigger}$ (if not defined, then B_{pa}) for ICES stocks and $2B_{lim}$ for Northwest Atlantic stocks, as used by DFO for some stocks (www.dfo-mpo.gc.ca/csas-sccs/Publications/SAR-AS/2019/2019_009-eng.pdf). Since 2016, 10 of the 18 FIE-implicated stocks have exceeded B_{lim} (Figure 1; Table 1). Nine of these ten have defined targets and seven have recently exceeded B_{target}.

To evaluate the degree to which observed population trajectories might have been influenced by FIE, we compare observed rates of recovery with model predictions. Based on an analysis of 153

marine stocks, Neubauer, Jensen, Hutchings, and Baum (2013) concluded that recovery to B_{msy} (from $0.2B_{msy} < B < 0.5B_{msy}$) is generally achievable in 10 years by moderately productive ($r_{max} \sim 0.43$) stocks that experience an average fishing mortality (F) of $\sim 0.23F_{msy}$ for more than 30 years. Given that their estimate of an average, achievable recovery time of 10 yr did not incorporate evolution, we use this time frame as our expected recovery period in the absence of FIE.

To compare this with what might be anticipated in the presence of FIE, we consulted Dunlop et al. (2015) who modelled biomass trajectories of Atlantic cod (*Gadus morhua*, Gadidae) following 100 years of fishing, simulated in the presence and absence of FIE. Using the output of these simulations (their Figure 3), we collated annual estimates of r at the beginning of the recovery period, i.e., the initial year (t) in which $r > 0.01$ for populations that had not experienced FIE (r increased earlier and at a greater rate in non-FIE populations after fishing ceased). For the non-FIE populations, these simulation-based estimates were then used to calculate the increase in relative population size (N) from the initial year (N_0, set to 1 to standardize comparisons) for the first 10 years of recovery (sensu Neubauer et al., 2013), using the classic model $N_t = N_0 \times \exp(rt)$.

The relative population sizes achieved during the first 10 years of recovery (N_{10}) by non-FIE populations were 1.39, 2.69 and 5.78 at

F = 0.22, 0.51 and 1.02, respectively (Figure 2). By comparison, the FIE populations required 19, 29 and 31 years, respectively, to achieve the same N_{10}. Given that F = 0.22 is a very low fishing mortality for commercially exploited fishes, we focus on the outputs at F of 0.51 and 1.02. For these simulations, the recovery of FIE-implicated populations is, on average, 20 years longer than that required for non-FIE populations (Figure 2).

Given these estimated recovery time periods of 30 and 10 years for populations that did and did not experience FIE, we examined the ten FIE-implicated stocks (Heino et al., 2015) that had recently attained B_{lim}. Since the year in which F began a prolonged and sustained long-term decline (Table 2), 8 of the 10 stocks had achieved their targets, requiring an average of 5.4 ± 4.7 SD years (range: 1–12 years) to do so. Thus, we conclude that FIE had no meaningful influence on the recovery of these 8 stocks. Of the remaining two stocks, the steady decline in F for North Sea cod since 2001 was never sufficient to achieve an annual F less than F_{MSY}, meaning that the stock has been continually overfished (despite reaching B_{LIM} in 2016). The other stock—St. Pierre Bank cod—has no defined fishing mortality reference points, meaning that its overfishing status cannot be ascertained.

In terms of what the causal driver(s) might be for the current status of these stocks, it is instructive that recent increases in stock size were almost always concomitant with periods when overfishing was not occurring (Figure 1).

2.2 | Can the recovery trajectories of FIE-implicated populations be attributed to factors other than fishing?

The question of whether population decline influences recovery in marine fishes has a chequered history. Based on data from stock assessments and fisheries-independent surveys, Hutchings (2000, 2001) concluded that magnitude of depletion negatively affected recovery; the greater the magnitude of decline, the slower the rate of recovery, a finding corroborated by subsequent modelling (Neubauer et al., 2013). Using a variety of other approaches that have examined evidence for single-parameter shifts in stock–recruitment curves, some researchers have concluded that marine fish recovery is unlikely to be negatively affected by Allee effects or depensation (e.g. Hilborn, Hively, Jensen, & Branch, 2014; Liermann & Hilborn, 2001; Myers, Barrowman, Hutchings, & Rosenberg, 1995). These modelling approaches have been heavily criticized (e.g. Perälä & Kuparinen, 2017; Shelton & Healey, 1999) amidst empirical evidence that a reduction of F is not always a sufficient condition for recovery (Hutchings & Kuparinen, 2017) and that the population dynamics of some stocks at low size are consistent with the presence of Allee effects (Keith & Hutchings, 2012; Neuenhoff et al., 2019; Perälä & Kuparinen, 2017).

To examine the effects of decline on recovery potential, we compare the magnitude of depletion for FIE-implicated stocks that have and have not recovered above their limit reference point, i.e., $B_{current}$ relative to B_{lim}. Specifically, we compared spawning stock biomass in the year that the threat of overfishing (SSB_{threat}) was initially mitigated (i.e. when F began a prolonged and sustained decline) with the stock's maximum recorded SSB (SSB_{max}) (Figure 3, Table 2).

The ten FIE-implicated stocks that had recovered above B_{lim} include 6 Atlantic cod stocks (Northeast Arctic, Icelandic, North Sea, Eastern Baltic, Flemish Cap and St. Pierre Bank; unfortunately, estimates of F are not available for St. Pierre Bank cod) and four stocks of other species from the North Sea (whiting [*Merlangius merlangus*, Gadidae], sole [*Solea solea*, Soleidae], North Sea plaice [*Pleuronectes platessa*, Pleuronectidae] and haddock [*Melanogrammus aeglefinus*, Gadidae]). The non-recovered stocks included three of cod (Northern cod, Southern Grand Bank and Southern Gulf) and three of American plaice (*Hippoglossoides platessoides*, Pleuronectidae): Grand Bank, St. Pierre Bank, and Newfoundland and Labrador.

At the time that the threat of overfishing was mitigated, the average size of the SSB_{threat} relative to SSB_{max} was significantly greater for stocks that have since recovered (0.24 SSB_{max} ± 0.05 SE) than for those that have not (0.08 SSB_{max} ± 0.04 SE) (t = 2.5968, df = 12.953, p = .022) (Figure 3, Table 2). For a larger sample of stocks, Hutchings (2015) concluded that 0.10 SSB_{max} constituted a "threshold" below which recovery of marine fishes was impaired.

Another empirically derived correlate of recovery is the natural mortality, M, corresponding to a population's life-history parameters, reflected by length at maturity (L_{mat}) and the von Bertalanffy growth coefficient (k) and asymptotic length (L_{inf} or length at "infinity"). Based on Charnov, Gislason, and Pope's (2013) report that natural mortality at maturity, M_α, can be estimated as ($L_{mat}/L_{inf})^{-1.5} \times k$, Hutchings and Kuparinen (2017) found that marine fish stocks that had recovered to targets set by national and international jurisdictional authorities had a significantly higher M_α than those that did not, a finding that they attributed to the positive association between M and r_{max}, a known correlate of recovery potential (e.g. Hutchings, Myers, García, Lucifora, & Kuparinen, 2012).

For the present analysis, although the average estimated maturity for FIE-implicated stocks that had recovered above B_{lim} (M_α = 0.57 ± 0.10 SE) did not differ from that for non-recovered stocks (M_α = 0.33 ± 0.06 SE) (t = 2.0732, df = 13.58, p = .058) (Figure 4, Table 2), the lack of statistical significance can probably be attributed to small sample sizes. The average M_α for recovered (0.57; n = 10) and non-recovered (0.33; n = 6) stocks documented here are similar to those reported elsewhere for recovered (0.60; n = 38) and non-recovered (0.38; n = 16) stocks (Hutchings & Kuparinen, 2017).

2.3 | To what extent does FIE negatively affect population recovery?

Based on our analyses of 18 FIE-implicated stocks, we find that: (a) 10 of 18 stocks recovered above B_{lim} after sustained, meaningful reductions in fishing mortality; (b) 7 of 9 stocks have exceeded their biomass targets; (c) non-recovered stocks ($B_{current}$ < B_{lim}) not currently subjected to overfishing experienced greater reductions in SSB (0.08 SSB_{max}) than recovered stocks (0.24 SSB_{max}); and (d) the estimated

TABLE 1 Status of marine fish stocks for which fisheries-induced evolution has been implicated. Current ($B_{current}$), limit (B_{lim}) and target spawning stock biomass (B_{target}) values were obtained from stock assessments[a-r]

Species	Stock	$B_{current}/B_{lim}$	$B_{current}/B_{target}$	$F_{current}/F_{msy}$	$F_{current}/F_{lim}$
Atlantic Cod (*Gadus morhua*)	Eastern Baltic (ICES subdivisions 24–32)[a]	1.01 (2017); currently 0.69	1.07 (2016); currently 0.61	F_{msy} undefined	F_{lim} undefined
	North Sea (ICES Subarea 4, Division 7.d, Subdiv. 20)[b]	1.09 (2016); currently < 1	0.54	2.03	1.17
	Northern Cod (NAFO Divisions 2J3KL)[c]	<0.50	B_{target} undefined	F_{msy} undefined	$F_{current}$ < 0.05; F_{lim} undefined
	Flemish Cap (NAFO Subdivision 3M)[d]	4.20	B_{target} undefined	F_{msy} undefined	0.5
	St. Pierre Bank (NAFO Subdivision 3Ps)[e]	1.49	0.74	F_{msy} undefined	<1 (?); F_{lim} undefined
	Southern Grand Bank (NAFO Divisions 3NO)[f]	0.31	B_{target} undefined	F_{msy} undefined	0.30
	Gulf of Maine (NAFO Division 5Y)[g]	0.10–0.15	0.06–0.08	1.23–1.27	F_{lim} undefined
	Georges Bank (NAFO Division 5Z)[h]	<1	Target undefined	F_{msy} undefined	F_{lim} undefined
	Icelandic (ICES Division 5.a)[i]	4.94	2.80	F_{msy} undefined	0.36
	Southern Gulf of St. Lawrence (NAFO Divisions 4TVn)[j]	0.17	Target undefined	F_{msy} undefined	$F_{current}$ = ~0.01; F_{lim} undefined
	Northeast Arctic (ICES subareas 1 and 2)[k]	6.80	3.25	1.05	0.57
Haddock (*Melanogrammus aeglefinus*)	North Sea (ICES Subarea 4, Division 6.a, Subdiv. 20)[l]	1.99	1.42	1.13	0.57
European Plaice (*Pleuronectes platessa*)	North Sea (ICES Subarea 4, Subdivision 20)[m]	4.67	1.71	0.89	0.36
Whiting (*Merlangius merlangus*)	North Sea (ICES Subarea 4, Division 7.d)[n]	1.44	1.04	1.16	0.43
American Plaice (*Hippoglossoides platessoides*)	Newfoundland & Labrador (NAFO Divisions 2J3K)[o]	Limit undefined	Target undefined	F_{msy} undefined	$F_{current}$ = 0.001; F_{lim} undefined
	St. Pierre Bank (NAFO Subdivision 3Ps)[p]	0.40–0.55	0.16–0.22	0.20	0.20
	Grand Bank (NAFO Divisions 3LNO)[q]	0.35	Target undefined	F_{msy} undefined	$F_{current}$ = 0.05; F_{lim} undefined
Sole (*Solea solea*)	North Sea (ICES Subarea 4)[r]	1.96	1.39	1.09	0.35

Note: The same sources were used to document current ($F_{current}$), limit (F_{lim}) and MSY (maximum sustainable yield) values for fishing mortality (F). See the text for an explanation of B_{target}.

[a]http://ices.dk/sites/pub/Publication%20Reports/Advice/2019/2019/cod.27.24-32.pdf.

[b]ices.dk/sites/pub/Publication%20Reports/Advice/2018/2018/cod.27.47d20.pdf.

[c]publications.gc.ca/collections/collection_2018/mpo-dfo/fs70-6/Fs70-6-2018-038-eng.pdf.

[d]https://www.nafo.int/Portals/0/PDFs/sc/2019/scr19-026.pdf.

[e]www.dfo-mpo.gc.ca/csas-sccs/Publications/SAR-AS/2019/2019_009-eng.pdf.

[f]www.nafo.int/Portals/0/PDFs/sc/2018/scr18-028.pdf.

[g]www.nefsc.noaa.gov/publications/crd/crd1717/gulf_of_maine_cod.pdf.

[h]www.nefsc.noaa.gov/publications/crd/crd1717/georges_bank_cod.pdf.

[i]http://ices.dk/sites/pub/Publication%20Reports/Advice/2019/2019/cod.27.5a.pdf.

[j]http://www.dfo-mpo.gc.ca/csas-sccs/Publications/SAR-AS/2019/2019_021-eng.pdf.

[k]http://ices.dk/sites/pub/Publication%20Reports/Advice/2019/2019/cod.27.1-2.pdf.

[l]www.ices.dk/sites/pub/Publication%20Reports/Advice/2018/2018/had.27.46a20_replaced.pdf.

[m]ices.dk/sites/pub/Publication%20Reports/Advice/2018/2018/ple.27.420_replaced.pdf.

[n]ices.dk/sites/pub/Publication%20Reports/Advice/2018/2018/whg.27.47d_replaced.pdf.

[o]www.dfo-mpo.gc.ca/Library/343877.pdf.

[p]waves-vagues.dfo-mpo.gc.ca/Library/359938.pdf.

[q]www.nafo.int/Portals/0/PDFs/sc/2018/scr18-039.pdf.

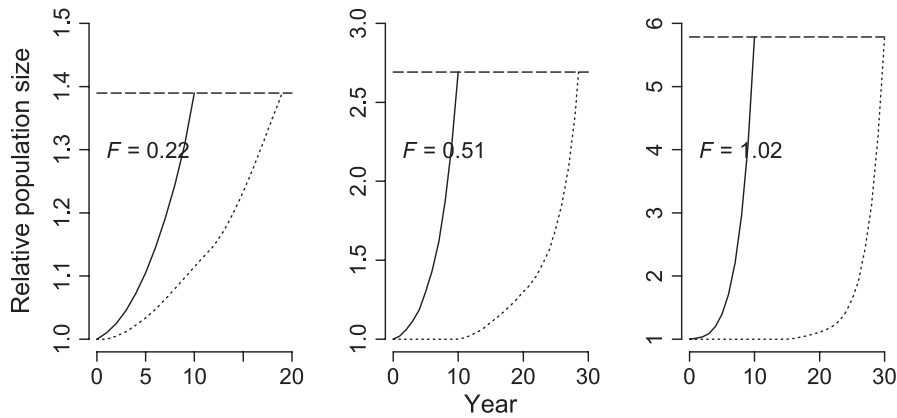[r]www.ices.dk/sites/pub/Publication%20Reports/Advice/2018/2018/sol.27.4.pdf.

FIGURE 2 Simulated population trajectories of Atlantic cod that did (dotted lines) and did not (solid lines) experience fisheries-induced evolution. Time represents the recovery period, following 100 years of fishing, at three levels of fishing mortality (*F*). Trajectories are based on annual, model-based estimates of *r* produced by Dunlop et al. (2015)

natural mortality of non-recovered stocks was 0.6 that of recovered stocks, the same ratio of *M* for non-recovered and recovered stocks reported elsewhere (Hutchings & Kuparinen, 2017).

Thus, it would seem that the stand-alone effects of FIE on recovery might often be minor relative to other variables known to affect recovery (Dunlop et al., 2015; Eikeset et al., 2016). This conclusion is not new. More than 40 years ago, Handford et al. (1977) cautioned that fisheries-induced "selection of this sort may only rarely be capable of determining the direction of change in population parameters, that is, that selection is only rarely capable of producing an effect larger than and opposed to that associated with density-dependent compensation." Kuparinen, Stenseth, and Hutchings (2014) illustrated how FIE can change density-dependent parameters and processes, revealing that the primary consequences of FIE are most likely to be manifest when population size is small.

But even if the relative contribution of FIE to phenotypic change is small, it may still have influence, as demonstrated by research that partitioned the sources of phenotypic change in the growth of horns in male bighorn sheep (*Ovis canadensis*, Bovidae), a species hypothesized to be subject to hunting-induced evolution (Douhard et al., 2017). An additional consideration is that there may be instances where FIE synergistically contributes to, or magnifies the effects of, other factors known to negatively affect recovery, such as high and prolonged *F*, excessively small population size (Kuparinen et al., 2014), low r_{max} (Neubauer et al., 2013) or short-term (<3 generations) increases in *M* (generated, e.g., by smaller size at maturity [Hutchings & Kuparinen, 2017] or altered predator-prey interactions [Audzijonyte et al., 2013; Neuenhoff et al., 2019]).

3 | COMMUNICATION OF FIE SCIENCE TO DECISION-MAKERS

3.1 | Humans as agents of evolutionary change in fishes

Humans are a dominant selective force, often causing more rapid phenotypic change in natural populations than other drivers (Alberti et al., 2017). Compelling examples include evolutionary changes in pathogen virulence (Melnyk, Wong, & Kassen, 2015; Perron, Inglis,

Pennings, & Cobey, 2015), behaviour (Sih, Ferrari, & Harris, 2011) and resistance to pollutants (Fraser, Cook, Eddington, Bentzen, & Hutchings, 2008; Ujvari et al., 2015).

In fishes, the strongest evidence that human activity can cause genetic change stems from advertent and inadvertent selection (Christie, Ford, & Blouin,2014; Fraser, 2008; Glover et al., 2017). Advertent selection is primarily a result of broodstock programmes that (a) prevent natural selection from operating on mating, reproduction and survival in early life, and (b) favour the spawning contributions of individuals deemed to have "desirable" characteristics. The former situation is characteristic of hatchery programmes in support of fish-stocking efforts to "enhance" recreational and commercial fisheries. The aquaculture industry more directly affects genetic composition by deliberately excluding fish that have traits considered disadvantageous from a commercial perspective (such as young age and small size at maturity, slow growth rate). Inadvertent selection can result from barriers (e.g. dams) to fish migration (Apgar, Pearse, & Palkovacs, 2017; Williams, Zabel, Waples, Hutchings, & Connor, 2008) and pollutants, such as acid rain (Fraser et al., 2008).

Based on the criterion of unequivocal empirical evidence of genetic change, the conclusion that human activity generates evolution in fishes is especially strong when hatcheries and aquaculture programmes are considered. The same cannot be said for FIE. Although laboratory selection experiments (e.g. Conover & Munch, 2002; Edley & Law, 1988; Uusi-Heikkilä, Savilammi, Leder, Arlinghaus, & Primmer, 2017; Uusi-Heikkilä et al., 2015) and theoretical modelling (e.g. Dunlop, Heino, & Dieckmann, 2009; Ernande, Dieckmann, & Heino, 2004; Stokes et al., 1993) make a strong case for the existence of FIE, there are considerably more reviews of FIE (more than ten; cf. Heino et al., 2015) than clear empirical examples of genetic change resulting from FIE in wild populations (some would argue none, although the data are compelling in some cases, such as Swain, Sinclair, and Hanson (2007) and Therkildsen et al. (2013), but see Heino et al., 2008)).

For clarity, and to reiterate what we stated earlier (section 1), we do not question the logical premise for the existence of FIE. It is sound. But when communicating with society and decision-makers, scientists are obliged to be clear that the evidentiary basis for fishing-induced genetic change in wild populations is not nearly

TABLE 2 Magnitude of stock decline (SSB_{threat}/SSB_{max}) and natural mortality at maturity (M_α) for marine fish stocks that have and have not recovered above the biomass limit reference point and for which fisheries-induced evolution has been implicated

Species	Stock	Year of SSB_{threat}	Years to recovery	SSB_{threat}/SSB_{max}	L_{inf}	k	L_{mat}	M_α
(a) Recovered at least once following reduction in fishing mortality								
Atlantic Cod	Eastern Baltic[a]	2001	7	0.17	111.1	0.12	34.2	0.70
	Northeast Arctic[b]	2000	2	0.23	134.0	0.11	77.0	0.25
	North Sea[b]	2001	14 (to B_{lim})	0.22	114.7	0.30	45.0	1.22
	Icelandic[b]	1994	11	0.17	149.0	0.12	70.0	0.37
	Flemish Cap[c]	2000	8	0.07	79.2	0.20	58.0	0.31
	St. Pierre Bank[d]	–	–	–	135.2	0.11	60.0	0.37
Haddock	North Sea[e,f]	2001	1	0.14	90.0	0.18	30.0	0.94
Plaice	North Sea[g]	1998	12	0.49	46.0	0.26	30.0	0.49
Whiting	North Sea[f]	2001	1	0.48	41.3	0.20	27.8	0.36
Sole	North Sea[f]	1998	1	0.23	38.0	0.40	27.0	0.67

Species	Stock	Year of SSB_{threat}	SSB_{threat}/SSB_{max}	L_{inf}	k	L_{mat}	M_α
(b) Not recovered							
Atlantic Cod	Northern Cod[b]	2002	0.01	118.0	0.15	50.5	0.54
	Southern Grand Bank[b,h,i]	1994	0.04	118.0	0.15	65.0	0.37
	Southern Gulf[b]	1993	0.28	68.0	0.22	42.5	0.45
American Plaice	Newfoundland and Labrador[j]	1994	0.06	54.0	0.09	30.5	0.21
	St. Pierre Bank[b]	2011	0.06	62.5	0.09	38.0	0.19
	Grand Bank[k]	1995	0.03	50.0	0.10	31.5	0.20

Note: SSB_{threat} is the spawning stock biomass (*SSB*) when *F* began a prolonged and sustained long-term decline. "Years to recovery" represents the number of years that elapsed between the year of SSB_{threat} and the year in which *SSB* attained the recovery target of B_{pa} or MSY $B_{trigger}$ (all European stocks, except B_{lim} for North Sea cod) or $2B_{lim}$ (Flemish Cap cod). SSB_{max} is the spawning stock size maximum. $M_\alpha = (L_{mat}/L_{inf})^{-1.5} \times k$, where L_{mat} is length at maturity, and L_{inf} and *k* are the von Bertalanffy asymptotic length and growth coefficient, respectively. Sources for *SSB* are those identified in Table 1.

[a]http://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/acom/2018/WKIDEBCA/WKIDEBCA_2018.pdf; Köster et al. (2017)

[b]Hutchings and Kuparinen (2017).

[c]Stanek (1967); www.nafo.int/Portals/0/PDFs/sc/2018/scr18-042.pdf.

[d]Chen and Mello (1999).

[e]Baudron, Needle, and Marshall (2011).

[f]fishbase.org.

[g]ICES (2017).

[h]www.nafo.int/Portals/0/PDFs/sc/2018/scr18-028.pdf.

[i]Trippel et al. (1997).

[j]Pitt (1967); www.dfo-mpo.gc.ca/Library/343877.pdf.

[k]González-Troncoso and Paz (2008); www.nafo.int/Portals/0/PDFs/sc/2018/scr18-039.pdf.

as strong or compelling as it is for human-induced evolution (HIE) resulting from hatchery and aquaculture programmes. The simple reason for this is that it is very difficult to demonstrate that a single factor (in this case, fishing; but it could also be climate change (Crozier & Hutchings, 2014)) can generate evolutionary change independently of other causal mechanisms, including plastic and environmental causes.

Of course, absence of compelling evidence need not constitute compelling evidence of absence. It will be surprising if ongoing advances in genomic techniques, such as RNA-seq, fail to shed light on FIE in the coming decade. We also wish to stress that our focus is on recovery of metrics of population size. We acknowledge that population recovery need not involve recovery of phenotypic or genetic variability that might have been reduced as a consequence of fishing.
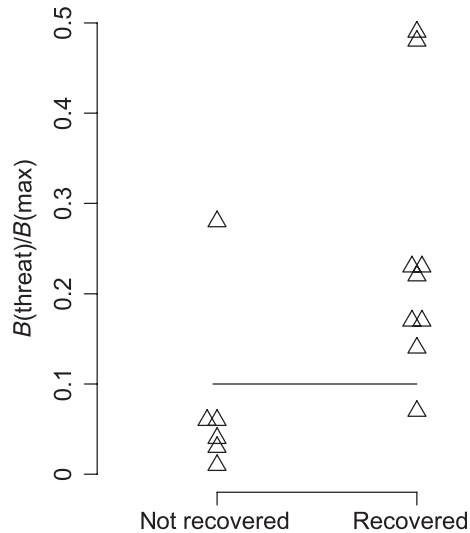
FIGURE 3 Spawning stock biomass in the year when *F* began a prolonged and sustained long-term decline (SSB_{threat}) relative to the maximum (SSB_{max}) for stocks that did and did not recover above B_{lim} and for which fisheries-induced evolution has been implicated

FIGURE 4 Estimated natural mortality at maturity for stocks that did and did not recover above B_{lim} and for which fisheries-induced evolution has been implicated

3.2 | Science advice on FIE: framing the issues for decision-makers

In terms of the communication of science, this duality in the strength of empirical evidence has positive and negative aspects from a FIE perspective. A scientifically strong and highly credible case can be made that humans are capable of creating biologically significant genetic change in fish populations. The case can also be credibly made that these genetic changes can be detrimental to population viability (Christie et al., 2014; McGinnity et al., 2003). This creates a solid basis for making the argument to decision-makers, and to the public, that human-induced genetic change exists in fishes and that fishing might be a driver of such change. The challenge is that scientists cannot credibly point to definitive examples of FIE in natural populations.

Independently of its evidentiary basis, it is not clear that researchers have effectively communicated science advice on FIE. When doing so, one should start not with what interests the scientist, but with what interests the parties to whom the scientist is communicating. In this regard, we envisage a set of questions (and corresponding responses) that fishery scientists, managers, policy-makers and perhaps politicians might pose to scientists within the context of FIE.

3.2.1 | What are the general and specific issues?

Responses to this question should be succinct and clear. The general issue is evolutionary change in fishes (or simply "genetic change," depending on jurisdictional sensibilities) resulting from human activity or HIE. The specific issue is evolutionary change caused by fishing, i.e., fishing-induced evolution (FIE).
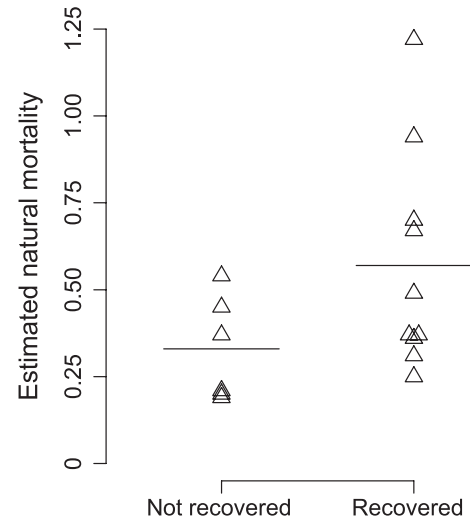
3.2.2 | Are there clear and unambiguous examples of these issues?

The most compelling scientific evidence that human activity generates evolution in fishes comes from research on domestication selection, which uncontestably results in genetic change in farmed and hatchery-reared individuals (Christie et al., 2014; Glover et al., 2017; Hutchings & Fraser, 2008), often over very few (1–3) generations (e.g. Christie, Marine, French, & Blouin, 2011; Debes & Hutchings, 2014). There is considerable evidence that fisheries-like selection in a laboratory setting can effect genetic change (e.g. Conover & Munch, 2002; Uusi-Heikkilä et al., 2017; Uusi-Heikkilä et al., 2015), but empirical evidence of such change in wild populations is, at best, not nearly as strong as it is for HIE resulting from hatcheries and aquaculture.

3.2.3 | What are the risks of human-induced evolutionary change (HIE)?

Risk reflects the probability that an issue will cause harm and the severity of that harm. Regarding HIE, abundant work indicates that the probability of interbreeding between (escaped) farmed and hatchery fish with their wild counterparts can be substantial (reviewed by Christie et al., 2014; Hutchings & Fraser, 2008; Glover et al., 2017). Considerable field and laboratory research (e.g. Christie et al., 2014; Fleming et al., 2000; McGinnity et al., 2003) supports the hypothesis that interbreeding between wild and farmed/hatchery fish reduces the viability of wild populations by reducing the fitness of individuals produced by (farmed/hatchery x wild) and (farmed/hatchery x farmed/hatchery) reproduction. Thus, the probability that HIE will cause harm is not negligible and might well be substantive in some cases. The severity of the harm will depend on factors such as the conservation status of the wild population, the generational frequency of

interbreeding, and the magnitude of genetic differentiation between wild and farmed/hatchery individuals (Glover et al., 2017; Hutchings, 1991; Hindar, Ryman, & Utter, 1991).

Regarding FIE, although studies have suggested or inferred negative implications to factors such as recovery and yield, there is little empirical evidence that it causes harm independently of other stressors, although it cannot be discounted that FIE might exacerbate harm caused by other factors.

3.2.4 | How might the risks posed by HIE compare with other risk factors?

In the general sense, there is reason to conclude that risks to wild populations posed by HIE resulting from domestication selection and subsequent interbreeding can be considerable, a conclusion drawn by Canada's national science advisory body on species at risk (COSEWIC, 2010) and cited in recovery strategies for endangered Atlantic salmon (*Salmo salar*, Salmonidae) (Fisheries & Oceans Canada, 2010). For populations of conservation concern, the risks of interbreeding are likely comparable to those posed by other stressors (Christie et al., 2014; Glover et al., 2017; McGinnity et al., 2003), such as genetic/demographic/environmental stochasticity, industrial/urban development, overfishing and climate change. There is no evidence, however, that risks to wild populations or fishery yields extracted from them posed by FIE supersede or are comparable with those posed by factors such as overfishing or magnitude of population depletion.

3.2.5 | Do existing management plans sufficiently mitigate the potential risks posed by FIE?

Fisheries-induced evolution results primarily from excessively high levels of fishing mortality and secondarily from selective mortality against specific ages and(or) sizes. Most models predict that FIE has a low probability of occurring when fishing mortality is low. Thus, one can defensibly argue that management strategies intended to (a) ensure that F does not exceed F_{lim} (such as F_{msy}), (b) maintain stock biomass above B_{lim} and (c) facilitate stock growth to B_{msy} or higher will also effectively mitigate against risks posed by FIE. Although there may conceivably be circumstances where FIE occurs solely as a result of age/size-selective fishing in the absence of excessively high F, fishery management plans that have the above objectives, and that are effectively implemented, should be sufficient to mitigate the predicted risks associated with FIE.

3.2.6 | Would explicit accounting of FIE meaningfully increase the likelihood of realizing positive policy outcomes?

This might be the most important question asked by policymakers and politicians. Fishery management plans are (ideally) components of overarching jurisdictional fisheries policies. If a primary goal of such policies is to achieve sustainable fisheries and prevent overfishing (e.g. Canada's Sustainable Fisheries Framework, the EU's Common Fisheries Policy, the U.S. 's Magnuson-Stevens Fishery Conservation and Management Act), then these policies, and others that incorporate the precautionary approach, should be sufficient to prevent FIE, if appropriately implemented.

3.3 | Strengthen the management utility of model-based studies of FIE

Most predicted implications of FIE are based on model simulation outcomes, examples of which are cited above. Most of these simulations encompass time frames that can be, or will be perceived to be, inconsequential to decision-makers. It is not uncommon for researchers to model the outcomes of FIE over periods of one or more centuries. These efforts can, of course, be instructive in evaluating the potential outcomes of different magnitudes of FIE, particularly as a function of life history or fishing-gear selectivity. But it is highly questionable whether these same efforts will produce outcomes of importance to politicians and fishery managers, whose time horizons are typically less than a decade, or even to policymakers, whose time horizons often extend to the foreseeable future.

Amongst recent papers that have highlighted a need for evolutionarily enlightened fishery management strategies is the comprehensive effort by Mollet et al. (2016). Their primary goal was to undertake an evolutionary impact assessment of the North Sea plaice fishery; the *SSB* of North Sea plaice is currently greater than both B_{lim} and B_{target} (Table 1). Mollet et al. (2016) use an eco-genetic, individual-based model to compare fishery yields under different levels of F and different gear selectivity with and without an evolutionary response by the fished population. Their most dramatic finding was that an evolving plaice population fished by bottom trawl (as opposed to gill net) and subjected to $F = 0.5$ will yield a catch that is less than 5% of a non-evolving stock—after a period of more than 600 years (Mollet et al., 2016; their Figure 3a).

Predictions on changes in fishery catches several hundred years into the future will not be perceived to have merit to decision-makers. To be fair, Mollet et al. (2016; their Figure 3c) did examine the consequences of several scenarios of FIE over a period of 50 years but, notwithstanding the comparatively long time period, even after 50 years, the predicted proportional difference between their lowest and highest yield scenarios was only 1.09. By contrast, the proportional range in actual catches of North Sea plaice over the past 50 years (1968–2018) was 3.08 (http://ices.dk/sites/pub/Publication%20Reports/Advice/2019/2019/ple.27.420.pdf). Fishery managers might not be particularly motivated to explicitly account for FIE if the range in projected catches falls well within the range of observed catches.

4 | CONCLUSIONS

We conclude this perspective by offering the following suggestions for strengthening the science underlying FIE and the likelihood that FIE will be accounted for in management plans and strategies.

Researchers working on FIE need to better integrate their work within the modelling frameworks used by scientists who regularly advise decision-makers. Rather than creating a new modelling framework, quite possibly one that is far removed from those used by fisheries scientists, FIE modellers should examine how FIE can be effectively incorporated into existing stock-assessment methodologies.

Fisheries-induced evolution scientists should be far more strategic in the framing of research questions and supporting analyses to strengthen the utility of their research at the science:policy interface. This could be achieved by regularly asking the following questions of one's research: (a) Do existing policies or stock-assessment models sufficiently mitigate, or account for, the potentially negative implications of FIE? (b) Can FIE be minimized simply by controlling fishing mortality? (c) Would the incorporation of FIE substantially or meaningfully increase the likelihood of realizing positive policy outcomes?

The field of FIE-focused research would benefit by increased attention on the subset of populations for which the implications of FIE are likely to be magnified because of their interaction with other factors (such as depletion, excessively high fishing mortality, altered predator-prey interactions) known to affect recovery and(or) yield.

As noted earlier, the purpose of this perspective was not to question the logical basis for FIE but rather to draw attention to elements that might have contributed to what we perceive to be a stasis in the advancement and communication of knowledge as it relates to FIE. We find that some predicted and inferred negative implications of FIE have been difficult to verify empirically. The observation that FIE does not obviously affect population recovery in a negative manner contributes to a suite of challenges that face the communication of science advice pertaining to HIE in fishes.

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