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Ghosts of fisheries-induced depletions: do they haunt us still?

Jeffrey A. Hutchings^{1,2*} and Anna Kuparinen³

¹Department of Biology, Dalhousie University, Halifax, NS, Canada

²Centre for Ecological and Evolutionary Synthesis, Department of Biosciences, University of Oslo, Oslo, Norway

³Department of Environmental Sciences, University of Helsinki, Helsinki, Finland

*Corresponding author: tel: +1 902 494 2687; e-mail: jhutch@dal.ca

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The depletion of several North Atlantic gadoids in the 1980s and 1990s stimulated an unprecedented amount of research on the recovery of marine fish. Some of this work addressed long-standing questions of teleost population dynamics: (i) Does per capita population growth rate (r) always increase as abundance declines? (ii) Do teleost fish possess greater intrinsic recovery abilities (as reflected by r_{\max}) than terrestrial vertebrates? (iii) Does the magnitude of population reduction influence the probability of recovery? (iv) If fish evolve in response to fishing, changing average fitness and thus r_{\max} are the population-dynamic consequences likely to be negative, positive, or neutral? Challenging some long-standing perceptions and beliefs, recent meta-analyses and empirically based model simulations on marine teleost fish support theoretically based postulates that: (i) r_{\max} does not differ from that of terrestrial mammals; (ii) high fecundity has no influence on recovery potential; (iii) Allee effects can be manifest in some depleted populations; (iv) the greater the magnitude of population reduction, the greater the uncertainty of recovery; and (v) the consequences of fisheries-induced evolution for recovery need not always be negative. An emerging imperative of the work examined here is the need to more fully embrace and comprehensively examine the links that exist between fitness and per capita population growth, given that what happens at the level of the individual will have consequences for how populations respond to natural and anthropogenic environment change.

Keywords: Allee effect, fisheries-induced evolution, per capita population growth rate, rebuilding, recovery, uncertainty.

Introduction

Perception—the way in which something is regarded, understood, or interpreted—permeates science. Ideas and opinions, often but not always accompanied by empirical evidence, can have and have had tremendous influence in generating individual or group perspectives on how natural systems are structured, how they evolved, and how they are influenced by natural and human-induced perturbations. The influence of perception on scientists and science-based agencies, relative to the availability of evidence, can be particularly strong when natural systems are unduly stressed, or appear so. Under such circumstances, a lack of research can prevent a firm empirical grounding of scientific opinions and advice.

As in many areas of research, perception plays a prominent role in fisheries science and fisheries conservation biology. Hilborn (2006) indirectly drew attention to the influence of perception on these research fields, criticizing what he interpreted to be a trumping of objective empiricism by “faith-based” ideas. Hilborn's (2006)

comments echoed those made by Hutchings (2001a) who argued that perception, based on selective interpretations of life history theory and data, was unhelpfully influencing opinions on marine fish extinction probabilities.

It was the collapse of severely overexploited fish that predicated the influence of perception on the issues identified by Hutchings (2001a) and Hilborn (2006). Discussion of factors affecting the collapse and recovery of fish and fisheries began in earnest in the early 1990s (e.g. Ludwig *et al.*, 1993; Myers and Cadigan, 1993), a period concomitant with the greatest collapse of a gadoid, Canadian northern Atlantic cod, *Gadus morhua* (Hutchings and Myers, 1994). This was followed, in the mid-1990s, by intense discussions of the rate at which depleted stocks recover, spurred by the assessment of several depleted fish species as Vulnerable by the IUCN (International Union for Conservation of Nature; Hudson and Mace, 1996).

It was during this period (latter half of the 1990s and early 2000s) that perceptions concerning the recovery of marine fish were first

presented in a concerted manner. Collectively, these perceptions were interpreted to mean that marine fish have intrinsically greater recovery abilities than other vertebrates (e.g. Musick, 1999). As a consequence, criteria used to assess extinction risk in, say, terrestrial vertebrates, such as birds and mammals, were considered inappropriate for assessing extinction risk in marine fish [these arguments are discussed at length by several authors including Hutchings (2001a), Dulvy *et al.* (2003), and Reynolds *et al.* (2005)].

Individually, the perceptions were articulated, directly or indirectly, by several assertions or assumptions (Musick, 1999; Hutchings 2000a, b, 2001a, b; Powles *et al.*, 2000; Sadovy, 2001; Mace *et al.*, 2002; Reynolds *et al.*, 2005): (i) maximum per capita population growth rate (r_{\max}) is higher in marine teleosts than terrestrial taxa; (ii) the high fecundity of marine fish increases their recovery rate and reduces extinction probability; (iii) neither the predicted recovery rate nor the uncertainty associated with recovery is affected by weakening compensatory effects on r , one manifestation of which might be an Allee effect or depensation; and (iv) the probability of recovery is unaffected by the magnitude of population reduction.

Given the heightened interest in evaluating the recovery potential of gadoid fish (this issue), the time seems opportune to review these perceptions in the light of recent empirical analyses, including studies of the potential for fisheries-induced evolution (FIE) to affect per capita population growth rate (r).

Teleosts and terrestrial mammals do not differ in r_{\max}

It has been perceived that the r_{\max} of teleost fish exceeds that of other vertebrates, particularly terrestrial mammals (NMFS, 2001; FAO, 2002). Musick (1999), for example, asserted that “most fishes, particularly teleosts, are on the ‘ r ’ side of the r/K continuum [K refers to carrying capacity] and, thus, have naturally high production rates”. If r_{\max} was indeed greater, on average, in teleosts than it was in other vertebrates, then one would anticipate that their recovery would be faster once the threats to their recovery had been mitigated.

The question of whether r_{\max} is greater in teleosts than terrestrial mammals was recently examined for 47 species of teleosts, 82 chondrichthyans (e.g. sharks, rays), 54 terrestrial mammals, and 16 marine mammals (Hutchings *et al.*, 2012). Estimates of r_{\max} were obtained by following established methods, such as those described by Goodman (1987) and Myers *et al.* (1997). In teleosts, for example, r_{\max} was estimated from the Euler–Lotka equation in which survival to age at first reproduction (l_{α}), adult survival (p), and annual fecundity (b) were assumed to be constant at low population size from maturity ($t = \alpha$) until age at senescence ($t = \omega$), such that

$$l_{\alpha} b \sum_{t=\alpha}^{\omega} e^{(-r_{\max} t)} p^{(t-\alpha)} = 1.$$

Ricker stock–recruitment functions were used to estimate l_{α} at low population size, following Myers *et al.* (1997, 1999). For chondrichthyans and mammals, r_{\max} was also estimated from the Euler–Lotka equation, but using data on age at maturity, fecundity, and natural mortality obtained from the literature [see Myers *et al.* (1997) and Hutchings *et al.* (2012) for full details].

This taxonomic comparison reported that the r_{\max} for teleosts [median of 0.432 with a bootstrapped confidence interval (CI) of 0.354–0.531] was less, though not significantly so, than that for terrestrial mammals [median of 0.706 (CI: 0.270–1.286); Figure 1]. Similarities in r_{\max} are evident among select commercially important marine teleosts and well-known terrestrial mammals: Atlantic

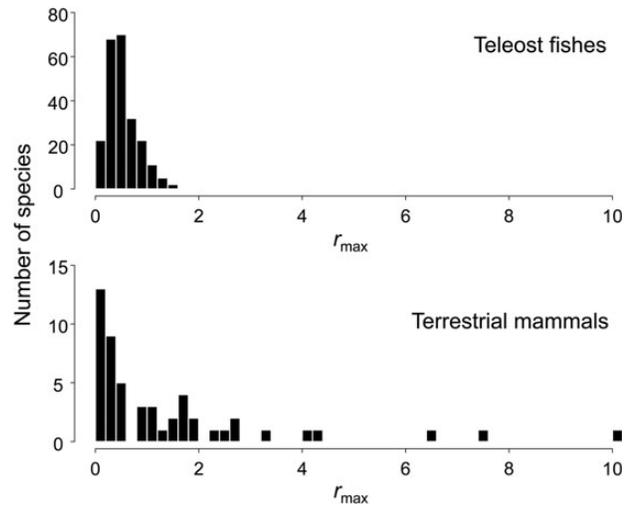


Figure 1. Estimates of maximum per capita population growth rate (r_{\max}) for 47 species of teleosts and 54 species of mammals. See Hutchings *et al.* (2012) for more details.

cod (range: 0.17–1.15); *Pleuronectes platessa* (0.33–0.71); sole, *Solea solea* (0.21–0.86); white-tailed deer, *Odocoileus virginianus* (1.02); bobcat, *Lynx rufus* (0.91); mule deer, *Odocoileus hemionus* (0.88); black bear, *Ursus americanus* (0.23).

Although not differing from each other, the r_{\max} estimates of teleosts and terrestrial mammals did exceed those estimated for chondrichthyans [0.256 (CI: 0.207–0.298)] and marine mammals [0.073 (CI: 0.030–0.095)]. The primary life history correlate of r_{\max} in teleosts was age at maturity, a result consistent with theoretical expectations (Cole, 1954; Roff, 2002); any influence of body size was equivocal (Hutchings *et al.*, 2012).

High fecundity does not influence recovery potential

There is a long-standing perception (perhaps better described as a “belief”) that high fecundity renders marine fish more resistant to depletion and allows them to recover faster than other vertebrates. It is a perception that can be dated to the 1880s, at the very least (Smith, 1994; Hutchings, 2000b). The perception continues today, manifest by recent studies in which the number of offspring is presumed to be positively linked to r_{\max} (e.g. Patrick *et al.*, 2010; Prugh *et al.*, 2010).

The effect that this perception has had on fisheries science is remarkable, despite an absence of empirical or indeed theoretical support (e.g. Cole, 1954; Brander, 1981; Hutchings, 2000b; Sadovy, 2001). When evaluating the appropriateness of criteria used by CITES (Convention on International Trade in Endangered Species) to identify endangered and threatened commercially exploited marine fish, FAO (2000) concluded: “Greater potential fecundity... would tend to make aquatic species more resilient [*sic*] to depletion and result in a lower risk of extinction”. Based on spawner-per-recruit analyses of marine European and North American stocks, NMFS (2001) concluded that cod has the “greatest resilience to fishing” because of its high fecundity. Reports having considerable influence in shaping policy on endangered and threatened fish in the American Fisheries Society (Musick, 1999) and the US National Marine Fisheries Service (DeMaster *et al.*, 2004) also include the presumption that high fecundity confers low extinction risk and high recovery potential.

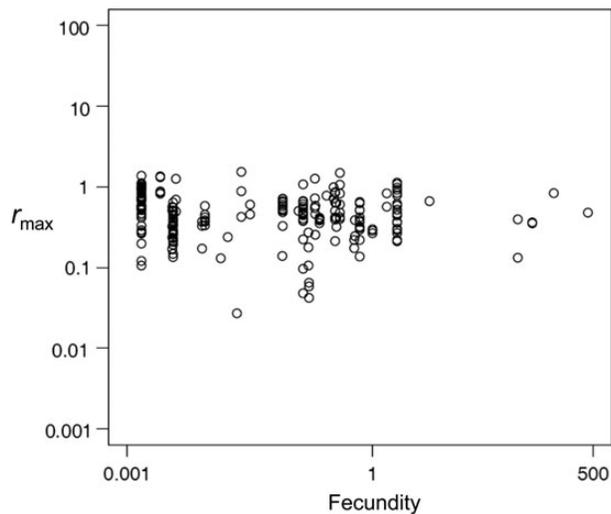


Figure 2. Relationship between maximum per capita population growth rate (r_{\max}) and fecundity for 233 populations of teleosts. See Hutchings *et al.* (2012) for more details.

However, as others have noted (Hutchings, 2000b, 2001a, b; Sadovy, 2001; Dulvy *et al.*, 2003; Reynolds *et al.*, 2005), a key theoretical limitation to assuming that high fecundity is associated with high r_{\max} is that it treats one life history trait as having primacy above all others as a determinant of individual fitness. In addition, life history traits express trade-offs with each other, such that increases in the expression of one are associated with decreases in the expression of another (Roff, 2002). All else being equal, a female cannot increase her egg size without decreasing the number of eggs she produces (a trade-off curiously unacknowledged in most studies of the purported selective advantages to producing large eggs in marine fish; Hutchings, 1997). And within a fisheries context, Brander (1981) emphasized the point that “net survival to maturity rather than fecundity per se governs the response to exploitation”. In other words, the production of large numbers of eggs is simply one component of an overall life history strategy that results in the replacement of individuals within a population at equilibrium (Hutchings, 2000b).

The question of whether fecundity is related to r_{\max} was examined empirically for 199 vertebrate species (Hutchings *et al.*, 2012). Across five orders of magnitude, fecundity was found to be unrelated to r_{\max} in marine fish, irrespective of whether chondrichthyans were included in the analysis, either at the species level or at the population level (Figure 2). In addition to a lack of theoretical support for the supposition that fecundity is positively linked to r_{\max} (Cole, 1954; Roff, 2002) and, thus, rate of recovery, the perception is not supported by empirical analysis either.

Influence of population size on r

Among harvested species for which stock assessments exist, a recent meta-analysis concluded that exploitation rates have been sufficiently reduced to permit the rebuilding of depleted fisheries (Worm *et al.*, 2009). However, while a reduction in fishing mortality is clearly necessary for recovery, it has become evident that it is not always sufficient for recovery (Hutchings, 2001b; Murawski, 2010; Neubauer *et al.*, 2013). Indeed, the argument can be made that the question of whether a fish stock *will* recover is not particularly germane. Of greater interest and import are answers to the questions

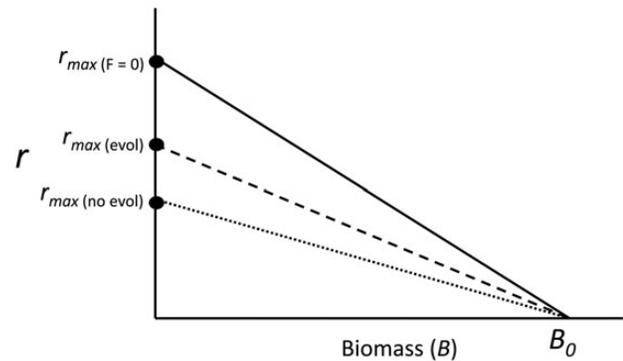


Figure 3. Classic models of density-dependent population dynamics incorporate the assumption that realized per capita population growth rate (r) declines linearly with increases in population abundance (typically represented in marine fish populations as biomass, B). Realized r declines from a high of r_{\max} at very low biomass to zero at carrying capacity, B_0 . In the absence of fishing mortality (i.e. $F = 0$; solid line), and for a population assumed to be at equilibrium and exhibiting its optimal life history under natural selection, r is higher for all levels of biomass than it is (i) under fishing in the absence of evolution (dotted line), attaining a maximum at r_{\max} (no evol), and (ii) in the presence of evolution (dashed line), attaining a maximum at r_{\max} (evol).

of the time-scale over which recovery is likely to occur and with what degree of certainty (Neubauer *et al.*, 2013; Kuparinen *et al.*, 2014).

These questions are inextricably linked to a basic assumption of fisheries science derived from classical models of density-dependent population regulation. In the simplest case, as population abundance (N) or biomass (B) declines, per capita population growth rate [i.e. r or $dN/(Ndt)$] is assumed to continually increase in a linear fashion until the maximum rate (r_{\max}) is obtained at the lowest levels of N (Figure 3). This leads to maximum population growth rate (dN/dt) and maximum sustainable yield, MSY, being achieved at half of carrying capacity, K or B_0 . Curvilinear, negative associations can result in MSY being achieved at $<0.5K$ (Hilborn and Stokes, 2010). More generally, the proportion of K at which maximum (dN/dt) is achieved appears to decline linearly with the value of r_{\max} per generation (Fowler, 1988).

The pattern of increasing r with declining abundance is termed “compensation” in the fisheries literature and “negative density-dependence” in the ecological literature. This pattern of change can be contrasted to situations in which r , at comparatively low levels of abundance, declines rather than increases with reductions in population size. This is termed “depensation” in the fisheries literature or “positive density-dependence” in the ecological literature, and is indicative of the presence of an Allee effect (Courchamp *et al.*, 2008; Hutchings, 2014).

The fisheries literature is circumspect in regard to the notion that Allee effects have been manifest, or could be manifest, in commercially exploited marine fish, a reflection perhaps of data limitations, statistical power, and (or) analytical approaches (Shelton and Healey, 1999; Liermann and Hilborn, 2001; Sugeno and Munch, 2013; Hutchings, 2014). There is evidence both for and against depensation in marine fish (Myers *et al.*, 1995; Liermann and Hilborn, 1997; Keith and Hutchings, 2012).

One thing is clear however. If Allee effects are going to be manifest, it is unlikely that they will be measurable unless the reduction in population size is sufficiently high. How great a reduction is sufficient? That is a matter of some conjecture and more research on this topic is

clearly warranted. It has been suggested that an Allee effect is unlikely to be evident unless a population has declined by more than 90% relative to its maximum observed abundance (Fowler and Baker, 1991; Sæther *et al.*, 1996; Keith and Hutchings, 2012). When detailed fisheries stock assessments are not available, Hutchings (2014) suggested that Allee effects might be most likely to be expressed when SSB falls below 10% of the maximum observed value, SSB_{max} . And when biomass reference points have been identified, it has been suggested that an Allee-effect limit reference point might range between 0.20 and 0.26 of SSB_{msy} (Hutchings, 2014), the spawning-stock biomass at which MSY is predicted to be obtained [for comparison, Neubauer *et al.* (2013) defined a collapsed stock as one that had declined lower than $0.20B_{msy}$]. In the late 2000s, ~12% of marine fish stocks for which peer-reviewed stock assessments have been undertaken were lower than $0.20B_{msy}$, including several gadoids (Worm *et al.*, 2009; Hutchings *et al.*, 2010).

However, it needs to be stressed that the simple passing of an Allee-effect threshold or similar limit reference point need not imply that an Allee effect will be realized (Hutchings, 2014). The period that a stock remains at low levels is almost certainly of equal, if not considerably greater, importance. For example, although Northeast Arctic cod (currently at a historical high) fell below $0.10SSB_{max}$ twice (in 1965 and 1980) before its current extraordinary recovery, it remained below $0.10SSB_{max}$ for only 1 year on each occasion (www.ices.dk). Icelandic cod, another stock that has experienced impressive growth in recent years, is estimated to have never fallen below $0.10SSB_{max}$ (www.ices.dk).

In other words, it might well be that the passing of an Allee-effect threshold by a population for a short period, relative to that population's generation time, will in itself not be sufficient to generate a reduced rate of recovery (Brander, 2005; Hutchings, 2014). Rather, the longer a depleted stock remains at low abundance, the more likely it is that the environment around it will change in ways that are unfavourable to recovery. Among other things, this can result in an "emergent" Allee effect for the depleted stock resulting from changes in its interspecific interactions with prey (De Roos and Persson, 2002; Van Leeuwen *et al.*, 2008) or its predators (Hutchings and Rangeley, 2011; see also Swain, 2011).

Magnitude of population reduction and recovery

Based on an analysis of 90 marine fish stocks, Hutchings (2000a) concluded that there was remarkably little evidence of meaningful recovery following large reductions in population size. After later accounting for the influence of fishing mortality on recovery (Hutchings, 2001b), this result seemed to hold true, a finding consistent with the hypothesis that weakening compensation, or possibly Allee effects, can influence the probability of recovery of depleted stocks. Weakening compensation has been reported for some populations at moderately low levels of abundance (Keith and Hutchings, 2012).

One notable exception to the general pattern documented by Hutchings (2000a) was the finding that clupeiforms (e.g. clupeids, engraulids) appeared to be more likely to recover from depletion than other marine fish (see also Hilborn, 1997). Four explanations were proffered to explain this apparent increased resilience in clupeiforms (Hutchings, 2000a): (i) higher r_{max} , resulting from a generally younger age at maturity; (ii) reduced susceptibility to environmental stochasticity, as conferred by high r_{max} ; (iii) increased ability to "track" favourable fluctuations in primary and secondary productivity, resulting from the species' generally low trophic level; and (iv) higher probability that directed-fishery

closures will reduce fishing mortality to zero, resulting from the low incidence of clupeiform bycatch in non-clupeiform fisheries.

Mace (2004), took issue with Hutchings' (2000a) analysis, implying that it provided an inappropriately bleak depiction of marine fish recovery potential. In support of her assertion, she tabulated stocks thought to have exhibited substantial increases following reductions in fishing mortality. However, of the 28 marine fish stocks considered by Mace (2004), 7 were clupeiforms (e.g. herring, sardine), whose comparatively high resilience was not contested by Hutchings (2000a, 2001b), as noted above. Stock assessments do not exist for an additional six stocks, such that their current status relative to B_{msy} cannot be evaluated. Five of the remaining 15 stocks had not declined by more than $0.20SSB_{msy}$, the level suggested by Hutchings (2014) at which Allee effects might be expected to be manifest and identified as constituting "collapse" by Neubauer *et al.* (2013): US Atlantic silver hake, *Merluccius bilinearis*; US Atlantic summer flounder, *Paralichthys dentatus*; US Gulf of Mexico king mackerel, *Scomberomorus cavalla*; North Sea saithe, *Pollachias virens*; and Northwest Atlantic swordfish, *Xiphias gladius*. Of the remaining ten stocks considered by Mace (2004), seven are currently in an over-fished state, according to data available in the RAM Legacy stock assessment database (<http://depts.washington.edu/ramlegac/stocks/>). Based on the same database, the three remaining stocks in Mace's (2004) analysis (Georges Bank haddock, *Melanogrammus aeglefinus*; Gulf of Maine haddock; Georges Bank Acadian redfish, *Sebastes fasciatus*) have recovered and it indeed seems likely that they had declined as low as $0.2SSB_{msy}$. Taken as a whole, these examples of "recovery" provide tepid support, at best, for Mace's (2004) criticism (see also Murawski 2010).

Modelling the rate and uncertainty of recovery

Impressive recoveries, including those by gadoids (e.g. Northeast Arctic cod, Icelandic cod), have been documented. In contrast, a number of severely depleted populations have experienced slow or negligible recovery, despite severe reductions in fishing pressure. Among others, these include Northwest Atlantic stocks of cod (Hutchings and Rangeley, 2011), northern wolffish (*Anarhichas denticulatus*; COSEWIC, 2013a), spotted wolffish (*Anarhichas minor*; COSEWIC, 2013b), winter skate (*Leucoraja ocellata*; COSEWIC, 2005), cusk (*Brosme brosme*; COSEWIC, 2013c), porbeagle (*Lamna nasus*; COSEWIC, 2004), and white hake (*Urophycis tenuis*; Benoît *et al.*, 2011).

Recent modelling efforts, based on empirical data, predict that recovery can occur comparatively rapidly if meaningful action to reduce fishing mortality is taken immediately after stock depletion is detected. Neubauer *et al.* (2013) examined 153 instances in which stocks had declined to $<0.5B_{msy}$ (i.e. their definition of "depletion"). Using a Bayesian regression model based on stochastic population dynamics (and accounting for multiple potential correlates of recovery, including fishing mortality, life history, and exploitation history), they predicted the time required for recovery to B_{msy} to occur and compared these predictions with those forecast by a standard Graham–Schaefer model. They found that, in general, recovery following depletion is forecast to occur within 10 years but only if fishing mortality has been reduced rapidly once a decline in stock biomass below $0.5B_{msy}$ has been detected (Neubauer *et al.*, 2013). However, for stocks that had collapsed below $0.20B_{msy}$, recovery was predicted to be prolonged and highly uncertain. Neubauer *et al.* (2013) also noted that the debilitating effect of population reduction on recovery was exacerbated by low values of per capita population growth.

Another recent analysis reported that increased uncertainty in recovery is characteristic of an Allee effect. Kuparinen *et al.* (2014) used a density-dependent, individual-based model that incorporates demographic stochasticity to track changes in life history, survival, and r through time in cod. Following fishing-induced depletions to $0.05K$, they recorded the average time required, and corresponding variation, for the simulated populations to return to carrying capacity under scenarios of low to negligible, post-depletion fishing mortality and in the presence and absence (i.e. full compensatory dynamics) of an empirically based Allee effect for cod (Keith and Hutchings, 2012). Not only was the average time to recovery predicted to increase in the presence of an Allee effect, but so was the uncertainty of recovery, generated by higher probabilities of experiencing negative r (Kuparinen *et al.*, 2014). Their finding, and that reported by Neubauer *et al.* (2013) for collapsed stocks, suggests that projections of the uncertainty associated with recovery might be more important than, or at a minimum as important as, projections of the average rate of recovery.

It is noteworthy that the modelling work by Neubauer *et al.* (2013) and Kuparinen *et al.* (2014) focused on r rather than a proxy for r . Reliance on the latter can potentially contribute to misleading results, a caveat relevant to studies of Allee effects in marine fish. Most studies of depensation, for example, have used recruits per spawner (R/S) as a proxy for r (e.g. Myers *et al.*, 1995; Liermann and Hilborn 1997, 2001; Keith and Hutchings, 2012). However, while R/S can be a metric of r , it is not r . Per capita population growth rate is ultimately determined by individual age-specific rates of survival and fecundity (Roff, 2002; Hutchings, 2005).

Changes in R/S can reflect changes in offspring survival and (or) changes in age-specific fecundity, thus affecting r . However, changes in adult mortality can also influence r , and perhaps to greater degrees than changes in R/S (this is clearly a question that merits study). Mounting evidence indicates that natural mortality (M) of adults can increase as abundance declines in overfished populations (Benoît *et al.*, 2011; Swain, 2011; Audzijonyte *et al.*, 2013). These empirical data on survival raise the caveat that studies of depensation that focus only on R/S as a proxy for r can result in inappropriate conclusions about the presence/absence of Allee effects. That is, an increase in M with declines in abundance can potentially result in depensation, even if analyses of R/S suggest otherwise.

FIE and recovery

Since the early 1990s, there has been increased attention on the potential for fisheries to generate evolutionary change in exploited populations (Stokes *et al.*, 1993; Dieckmann and Heino, 2007; Hutchings and Fraser, 2008). Hypothesized genetic shifts are thought to be manifest primarily through declining age and size at maturity and reduced adult body size (Law and Grey, 1989; Heino and Godø, 2002; Kuparinen and Merilä, 2007). Considerable work on FIE has focused on disentangling genetic from phenotypically plastic changes in life history attributable to fishing (Dieckmann and Heino, 2007). In contrast, the consequences of FIE on individual fitness and recovery potential have remained less studied (Hutchings and Fraser, 2008; Conover *et al.*, 2009). It is increasingly accepted that the rate of selective change following FIE—often termed a “reversal” of FIE—is likely to be much slower than that of FIE itself (e.g. Law and Grey, 1989; Enberg *et al.*, 2009; Kuparinen and Hutchings, 2012), meaning that life history changes associated with FIE have the potential to affect population dynamics long after the cessation or reduction in fishing mortality.

Research on the impacts of FIE on population recovery, focused to date almost exclusively on Atlantic cod, has explored the degree to which slow or absent recovery might be attributable to life history changes associated with FIE (Olsen *et al.*, 2004; Swain *et al.*, 2007). Law and Grey (1989) concluded that recovery potential is likely to be very similar across a range of cod life histories. Hutchings (2005) concluded that r_{\max} can be negatively affected by reductions in age and size at maturity because of the increased costs of reproduction associated with earlier reproduction at smaller sizes (Jørgensen and Fiksen, 2010; Kuparinen *et al.*, 2012).

Modelling approaches that combine life history evolution with population dynamics have expanded the range of exploratory analyses of potential ecological feedbacks associated with FIE. This work generally concludes that populations are projected to recover to a lower equilibrium biomass than that which existed in the pre-fished state (Dunlop *et al.*, 2009; Enberg *et al.*, 2009; Kuparinen and Hutchings, 2012), despite potential increases in eggs- and recruits-per-spawner ratios concomitant with FIE (Enberg *et al.*, 2009). Using an individual-based model grounded in empirical data on Atlantic cod, Kuparinen and Hutchings (2012) concluded that per capita population growth rate itself can remain unaffected by FIE. Heino *et al.* (2013), based on a curious verbal argument, posited that r_{\max} increases after the initiation of FIE, although this would be surprising given that average fitness (for which r_{\max} is a direct proxy) in the presence of fishing is unlikely to be higher than average fitness in the absence of fishing (e.g. Law and Grey, 1989; Hutchings, 2005; Figure 3). Neubauer *et al.* (2013) presented circumstantial evidence that, as a consequence of FIE, r_{\max} can increase compared with the level to which it declined in the presence of fishing (i.e. represented by the dashed line in Figure 3). They presented results which suggest that the longer a population experiences moderate levels of overexploitation ($\sim 2.3 F_{\text{msy}}$), the faster its forecasted rate of recovery. Although additional work is required to address more comprehensively the potential consequences of harvested-induced evolution on population recovery, there are indications that, under some circumstances, the influence of FIE on r_{\max} might not be as detrimental as once thought.

Conclusions

Studies on the rate and uncertainty of recovery during the past two decades can be used to clarify and refine scientific advice on the potential fate of depleted marine fish to fishery managers, decision-makers, industry, and society. Work reviewed here suggests at least two areas in which scientific advice might be strengthened.

First, from a species-at-risk or sustainable-harvesting perspective, marine fish are unlikely to have a greater intrinsic ability to recover than other vertebrates. That said, one thing that might positively affect marine fish in this regard is the fact that habitat destruction is not typically considered a threat to, or a reason for the decline of, marine fish (excluding species that inhabit coastal waters and coral reefs; Dulvy *et al.*, 2003). Thus, the mitigation of threat (excessively high fishing mortality) can in theory be easier to effect than the mitigation of habitat destruction that constitutes a common threat to endangered terrestrial species (e.g., Venter *et al.*, 2006).

Second, it would seem that the extent to which a population is reduced by overfishing likely affects the rate and probability of recovery. Advice suggesting that the magnitude of abundance has no influence on the eventuality of recovery would not be consistent with empirical data available for a number of depleted populations, including many gadoids. However, this should not be interpreted to mean that all populations that experience massive reductions will

necessarily experience an Allee effect and (or) will be unable to recover. But appropriately nuanced advice, akin to the balanced conclusions reached by Neubauer *et al.* (2013) in their study of recovery correlates, would be helpful: (i) the greater the magnitude of population reduction, the slower the rate and the greater the uncertainty of recovery; and (ii) the longer it takes for fishing mortality to be meaningfully reduced once population depletion has been detected, the lower the chances that a fishery will be rebuilt in a timely manner.

As remarked upon elsewhere (e.g. Hutchings, 2000b; Enberg *et al.*, 2009), there is utility in more fully integrating studies of fisheries science and management with the basics of research in ecology and evolutionary biology. An emerging imperative of the work considered here is the need to more comprehensively examine the links that exist between fitness and r , given that what happens at the level of the individual will have consequences for how populations respond to natural and anthropogenic environment change.

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References

- Audzijonyte, A., Kuparinen, A., Gorton, G., and Fulton, E. A. 2013. Ecological consequences of body size decline in harvested fish species: positive feedback loops in trophic interactions amplify human impact. *Biology Letters*, 9: 20121103.
- Benoît, H. P., Swain, D. P., Bowen, W. D., Breed, G. A., Hammill, M. O., and Harvey, V. 2011. Evaluating the potential for grey seal predation to explain elevated natural mortality in three fish species in the southern Gulf of St. Lawrence. 2008. *Marine Ecology Progress Series*, 442: 149–167.
- Brander, K. M. 1981. Disappearance of common skate *Raia baetis* from Irish Sea. *Nature*, 290: 48–49.
- Brander, K. M. 2005. Cod recruitment is strongly affected by climate when stock biomass is low. *ICES Journal of Marine Science*, 62: 339–343.
- Cole, L. C. 1954. The population consequences of life history phenomena. *Quarterly Review of Biology*, 29: 103–137.
- Conover, D. O., Munch, S. B., and Arnott, S. A. 2009. Reversal of evolutionary downsizing caused by selective harvest of large fish. *Proceedings of the Royal Society B*, 276: 2015–2020.
- COSEWIC. 2004. COSEWIC status and assessment report on the porbeagle, *Lamna nasus*, in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.
- COSEWIC. 2005. COSEWIC status and assessment report on the winter skate, *Leucoraja ocellata*, in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.
- COSEWIC. 2013a. COSEWIC status and assessment report on the northern wolffish, *Anarhichas denticulatus*, in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.
- COSEWIC. 2013b. COSEWIC status and assessment report on the spotted wolffish, *Anarhichas minor*, in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.
- COSEWIC. 2013c. COSEWIC status and assessment report on the cusk, *Brosme brosme*, in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.
- Courchamp, F., Berec, L., and Gascoigne, J. 2008. *Allee Effects in Ecology and Conservation*. Oxford University Press, Oxford.
- DeMaster, D., Angliss, R., Cochrane, J., Mace, P., Merrick, R., Miller, M., Rumsey, S., *et al.* 2004. Recommendations to NOAA Fisheries: ESA listing criteria by the Quantitative Working Group. Technical memorandum NMFS-F/SPO-67. National Oceanic and Atmospheric Administration, Washington.
- De Roos, A. M., and Persson, L. 2002. Size-dependent life-history traits promote catastrophic collapses of top predators. *Proceedings of the National Academy of Sciences of the United States of America*, 99: 12907–12912.
- Dieckmann, U., and Heino, M. 2007. Probabilistic maturation reaction norms: their history, strengths, and limitations. *Marine Ecology Progress Series*, 335: 253–269.
- Dulvy, N., Sadovy, Y., and Reynolds, J. D. 2003. Extinction vulnerability in marine populations. *Fish and Fisheries*, 4: 25–64.
- Dunlop, E. S., Heino, M., and Dieckmann, U. 2009. Ecogenetic modeling of contemporary life-history evolution. *Ecological Applications*, 19: 1815–1834.
- Enberg, K., Jørgensen, C., Dunlop, E. S., Heino, M., and Dieckmann, U. 2009. Implications of fisheries-induced evolution for stock rebuilding and recovery. *Evolutionary Applications*, 2: 394–414.
- FAO (Food and Agriculture Organization of the UN). 2000. An appraisal of the suitability of the CITES criteria for listing commercially-exploited aquatic species. *FAO Fisheries Circular*, 954, Rome.
- FAO (Food and Agriculture Organization of the UN). 2002. Report of the second technical consultation on the suitability of the CITES criteria for listing commercially-exploited aquatic species. *FAO Fisheries Report*, 667, Rome.
- Fowler, C. W. 1988. Population dynamics as related to rate of increase per generation. *Evolutionary Ecology*, 2: 197–204.
- Fowler, C. W., and Baker, J. D. 1991. A review of animal population dynamics at extremely reduced population levels. *Reports of the International Whaling Commission*, 41: 545–554.
- Goodman, D. 1987. The demography of chance extinction. *In Viable Populations for Conservation*, pp. 11–34. Ed. by M. E. Soulé. Cambridge University Press, Cambridge.
- Heino, M., Baulier, L., Boukal, D. S., Ernande, B., Johnston, F. D., Mollet, F. M., Pardoe, H., *et al.* 2013. Can fisheries-induced evolution shift reference points for fisheries management? *ICES Journal of Marine Science*, 70: 707–721.
- Heino, M., and Godø, O. R. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. *Bulletin of Marine Science*, 70: 639–656.
- Hilborn, R. 1997. The frequency and severity of fish stock declines and increases. *In Developing and Sustaining World Fisheries Resources*, pp. 36–38. Ed. by D. A. Hancock, D. C. Smith, A. Grant, and J. P. Beumer. CSIRO Publishing, Victoria.
- Hilborn, R. 2006. Faith-based fisheries. *Fisheries*, 31: 554–555.
- Hilborn, R., and Stokes, K. 2010. Defining overfished stocks: have we lost the plot? *Fisheries*, 35: 113–120.
- Hudson, E., and Mace, G. 1996. Marine fish and the IUCN Red List of threatened animals. Report of the workshop held in collaboration with World Wildlife Fund (WWF) and IUCN. Zoological Society, London.
- Hutchings, J. A. 1997. Life history responses to environmental variability in early life. *In Early Life History and Recruitment in Fish Populations*, pp. 139–168. Ed. by R. C. Chambers, and E. A. Trippel. Chapman and Hall, London.
- Hutchings, J. A. 2000a. Collapse and recovery of marine fishes. *Nature*, 406: 882–885.
- Hutchings, J. A. 2000b. Numerical assessment in the front seat, ecology and evolution in the back seat: time to change drivers in fisheries and aquatic sciences? *Marine Ecology Progress Series*, 208: 299–303.

- Hutchings, J. A. 2001a. Conservation biology of marine fishes: perceptions and caveats regarding assignment of extinction risk. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 108–121.
- Hutchings, J. A. 2001b. Influence of population decline, fishing, and spawner variability on the recovery of marine fishes. *Journal of Fish Biology (Suppl. A)*, 59: 306–322.
- Hutchings, J. A. 2005. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 62: 824–832.
- Hutchings, J. A. 2014. Renaissance of a caveat: Allee effects in marine fish. *ICES Journal of Marine Science*, doi:10.1093/icesjms/fst179.
- Hutchings, J. A., and Fraser, D. J. 2008. The nature of fisheries- and farming-induced evolution. *Molecular Ecology*, 17: 294–313.
- Hutchings, J. A., Minto, C., Ricard, D., Baum, J. K., and Jensen, O. P. 2010. Trends in the abundance of marine fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, 67: 1205–1210.
- Hutchings, J. A., and Myers, R. A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences*, 51: 2126–2146.
- Hutchings, J. A., Myers, R. A., García, V. B., Lucifora, L. O., and Kuparinen, A. 2012. Life-history correlates of extinction risk and recovery potential. *Ecological Applications*, 22: 1061–1067.
- Hutchings, J. A., and Rangeley, R. W. 2011. Correlates of recovery for Canadian Atlantic cod. *Canadian Journal of Zoology*, 89: 386–400.
- Jørgensen, C., and Fiksen, Ø. 2010. Modelling fishing induced adaptations and consequences for natural mortality. *Canadian Journal of Fisheries and Aquatic Sciences*, 67: 1086–1097.
- Keith, D. M., and Hutchings, J. A. 2012. Population dynamics of marine fishes at low abundance. *Canadian Journal of Fisheries and Aquatic Sciences*, 69: 1150–1163.
- Kuparinen, A., Hardie, D. C., and Hutchings, J. A. 2012. Evolutionary and ecological feedbacks of the survival cost of reproduction. *Evolutionary Applications*, 5: 245–255.
- Kuparinen, A., and Hutchings, J. A. 2012. Consequences of fisheries-induced evolution for population productivity and recovery potential. *Proceedings of the Royal Society B*, 279: 2571–2579.
- Kuparinen, A., Keith, D. M., and Hutchings, J. A. 2014. Allee effect and the uncertainty of population recovery. *Conservation Biology*, doi:10.1111/cobi.12216.
- Kuparinen, A., and Merilä, J. 2007. Detecting and managing fisheries-induced evolution. *Trends in Ecology and Evolution*, 22: 652–659.
- Law, R., and Grey, D. R. 1989. Evolution of yields from populations with age-specific cropping. *Evolutionary Ecology*, 3: 343–359.
- Liermann, M., and Hilborn, R. 1997. Depensation in fish stocks: a hierarchical Bayesian meta-analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 54: 1976–1984.
- Liermann, M., and Hilborn, R. 2001. Depensation: evidence, models and implications. *Fish and Fisheries*, 2: 33–58.
- Ludwig, D., Hilborn, R., and Walters, C. 1993. Uncertainty, resource exploitation, and conservation: lessons from history. *Science*, 260: 17–36.
- Mace, P. 2004. In defence of fishery scientists, single-species models and other scapegoats: confronting the real problems. *Marine Ecology Progress Series*, 274: 263–291.
- Mace, P. M., Bruckner, A. W., Daves, N. K., Field, J. D., Hunter, J. R., Kohler, N. E., Kope, R. G., et al. 2002. NMFS/Interagency Working Group Evaluation of CITES Criteria and Guidelines. US Department of Commerce NOAA Technical Memorandum. NMFS-F/SPO-58.
- Murawski, S. A. 2010. Rebuilding depleted fish stocks: the good, the bad, and, mostly, the ugly. *ICES Journal of Marine Science*, 67: 1830–1840.
- Musick, J. A. 1999. Criteria to define extinction risk in marine fishes: the American Fisheries Society initiative. *Fisheries*, 24: 6–14.
- Myers, R. A., Barrowman, N. J., Hutchings, J. A., and Rosenberg, A. A. 1995. Population dynamics of exploited fish stocks at low population levels. *Science*, 269: 1106–1108.
- Myers, R. A., Bowen, K. G., and Barrowman, N. J. 1999. Maximum reproductive rate of fish at low population sizes. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 2404–2419.
- Myers, R. A., and Cadigan, N. G. 1993. Was an increase in natural mortality responsible for the collapse of northern cod? *Canadian Journal of Fisheries and Aquatic Sciences*, 52: 1274–1285.
- Myers, R. A., Mertz, G., and Fowlow, P. S. 1997. Maximum population growth rates and recovery times for Atlantic cod (*Gadus morhua*). *Fishery Bulletin*, 95: 762–772.
- Neubauer, P., Jensen, O. P., Hutchings, J. A., and Baum, J. K. 2013. Resilience and recovery of overexploited marine populations. *Science*, 340: 347–349.
- NMFS. 2001. Report of the NMFS CITES Criteria Working Group. Preliminary Draft 16 May 2001. NOAA, Woods Hole, MA.
- Olsen, M. E., Heino, M., Lilly, R. G., Morgam, M. J., Brattey, J., Ernande, B., and Dieckmann, U. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature*, 428: 932–935.
- Patrick, W. S., Spencer, P., Link, J., Cope, J., Field, J. J., Kobayashi, D., Lawson, P., et al. 2010. Using productivity and susceptibility indices to assess the vulnerability of United States fish stocks to over-fishing. *Fishery Bulletin*, 108: 305–322.
- Powles, H., Bradford, M. J., Bradford, R. G., Doubleday, W. G., Innes, S., and Levings, C. D. 2000. Assessing and protecting endangered marine species. *ICES Journal of Marine Science*, 57: 669–676.
- Prugh, L. R., Sinclair, A. R. E., Hodges, K. E., Jacob, A. L., and Wilcove, D. S. 2010. Reducing threats to species: threat reversibility and links to industry. *Conservation Letters*, 3: 267–276.
- Reynolds, J. D., Dulvy, N. K., Goodwin, N. B., and Hutchings, J. A. 2005. Biology of extinction risk in marine fishes. *Proceedings of the Royal Society B*, 272: 2337–2344.
- Roff, D. A. 2002. *Life History Evolution*. Sinauer, Sunderland, MA, USA.
- Sadovy, Y. 2001. The threat of fishing to highly fecund fishes. *Journal of Fish Biology (Suppl. A)*, 59: 90–108.
- Sæther, B.-E., Ringsby, T. H., and Roskaft, E. 1996. Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. *Oikos*, 77: 217–226.
- Shelton, P. A., and Healey, B. P. 1999. Should depensation be dismissed as a possible explanation for the lack of recovery of the northern cod (*Gadus morhua*) stock? *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 1521–1524.
- Smith, T. D. 1994. *Scaling Fisheries: the Science of Measuring the Effects of Fishing, 1855–1955*. Cambridge University Press, Cambridge, MA, USA.
- Stokes, T. K., McGlade, J. M., and Law, R. 1993. *The Exploitation of Evolving Resources*. Springer-Verlag, Berlin.
- Sugeno, M., and Munch, S. B. 2013. A semiparametric Bayesian method for detecting Allee effects. *Ecology*, 94: 1196–1204.
- Swain, D. P. 2011. Life-history evolution and elevated natural mortality in a population of Atlantic cod (*Gadus morhua*). *Evolutionary Applications*, 4: 18–29.
- Swain, D. P., Sinclair, A. F., and Hanson, J. M. 2007. Evolutionary response to size-selective mortality in an exploited fish population. *Proceedings of the Royal Society B*, 274: 1015–1022.
- Van Leeuwen, A., De Roos, A. M., and Persson, L. 2008. How cod shapes its world. *Journal of Sea Research*, 60: 89–104.
- Venter, O., Brodeur, N. N., Nemiroff, L., Belland, B., Dolinsek, I. J., and Grant, J. W. A. 2006. Threats to endangered species in Canada. *BioScience*, 56: 903–910.
- Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., Fogarty, M. J., et al. 2009. Rebuilding global fisheries. *Science*, 325: 578–585.