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Predicting Eco-evolutionary Impacts of Fishing on Body Size and Trophic Role of Atlantic Cod

Holly K. Kindsvater[1] and Eric P. Palkovacs[2]

Fishing has caused changes in abundance and demography in exploited populations, in part due to rapid decreases in age and size at maturation. Few models address how direct effects of fishing on age- and size-structure compare to indirect effects on the trophic role of predators. Using Atlantic Cod as example, we model the possible consequences of fishing for trophic roles, contrasting purely demographic effects with those that also include adaptive responses to fishing. While fishing decreases cod abundance in both scenarios, mean trophic level decreases more when there is an adaptive response in maturation. Adaptation also resulted more small fish, which supported the persistence of larger fish, even with heavy fishing. These large fish have a high trophic position, increasing variation relative to the demography-only case. Our model provides a proof-of-concept that eco-evolutionary feedbacks can change the trophic role of fished populations, altering food web dynamics in harvested ecosystems.

HUMAN impacts have important implications for eco-evolutionary dynamics in wild populations (Palkovacs, 2011; Norberg et al., 2012; Palkovacs et al., 2012; Hendry et al., 2017). Fisheries are a primary example of human-driven influences on eco-evolutionary dynamics, along with changes in temperature, novel species interactions, and habitat alteration (Brady and Goedert, this volume, 2017; Fryxell and Palkovacs, this volume, 2017; Urban et al., this volume, 2017). Size-selective fishing has direct effects on the demographic characteristics of fish populations, removing the largest individuals and thereby truncating size distributions (Law, 2000). Fishing can also decrease the age of maturation, possibly by decreasing intraspecific competition or favoring delayed reproduction (Fraser, 2013; Opdal and Jørgensen, 2015; Eikeset et al., 2016). If the fecundity advantages of maturing later at a larger size are outweighed by the risk of dying before reproduction, maturation age and size are expected to decrease, leading to an accelerated life history (Reznick et al., 1990). Evidence from many exploited fish stocks—including Atlantic Cod, *Gadus morhua*—supports rapid decreases in age and size of maturation after fishing (Olsen et al., 2004; Ottersen et al., 2006; Jørgensen et al., 2007; Eikeset et al., 2016).

Despite much recent attention to the phenotypic effects of fishing on the target species, the effects of adaptive changes in body size on community- and ecosystem-level processes are less well studied (Palkovacs et al., 2012). Body size is related to trophic position in many fish lineages (Romanuk et al., 2011); the largest individuals in any population typically occupy the highest trophic level because fish prey selectivity is largely a function of gape width (Jennings et al., 2001). However, the potential for intraspecific changes in trophic position due to fishing have been largely overshadowed by the direct effect of fishing on mean trophic level in multispecies fisheries (e.g., Branch et al., 2010). Recently Audzijonyte et al. (2014) modeled the ecosystem effects of fishing of five target species, including both direct effects of biomass removal and phenotypic changes in body size of each species in response to fishing. Their model predicted a decrease in biomass at each trophic level and explored resultant changes in diet and predation risk of the focal species. Here we focus on predicting how adaptive trait change in a fished predator affects the distributions of body size as well as abundance, providing more details on changes in trophic level within a species. Specifically, we model the implications of fishing-induced changes to demography and maturation on the body size and trophic role of Atlantic Cod.

Several attributes of Atlantic Cod make it a good study species to explore eco-evolutionary linkages between fishing and trophic ecology. First, Atlantic Cod shows some of the strongest evidence to date for fishing-induced declines in maturation age and size (Olsen et al., 2004; Ottersen et al., 2006). These declines are seen across multiple stocks in both the Eastern and Western Atlantic (Heino et al., 2015). Second, the size of individual cod is tightly linked to its prey size and trophic position, with trophic position varying with body size from about 4.5 to greater than 6.0 (Jennings and van der Molen, 2015). Finally, accumulating evidence suggests cod is a key prey species in the Western Atlantic as well as a predator (Cook and Trijoulet, 2016). Cod abundance is linked to other species of commercial and ecological importance, including Atlantic Herring and shrimp (cod prey) and Grey Seals and Atlantic Mackerel (predators of adult and juvenile cod, respectively). Changes in Atlantic Cod abundance and trait distributions have the potential to alter key aspects of ecosystem function through trophic cascades (Frank et al., 2005; Shackell et al., 2010). Thus, the eco-evolutionary effects of size-selective fishing could go well beyond the demography and size-structure of Atlantic Cod populations, impacting predator-prey interactions and changing the marine food web.

Previous studies modeling the food web consequences of fishing-induced downsizing focused on changes in biomass, and less on the details of abundance and size distribution (Audzijonyte et al., 2013, 2014). Our research extends this idea to parse purely demographic effects of fishing on body size, abundance, and trophic position from those that also include adaptive trait changes. Through this approach, we can characterize the predicted eco-evolutionary links be-

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tween size-selective fishing, body size, and trophic ecology for a commercially and ecologically important fish species. We combine a deterministic population model with published stable-isotope based estimates of trophic position for Atlantic Cod across a spectrum of body sizes (Jennings and van der Molen, 2015). We predict the effects of fishing on the body size distribution of the population for two cases: 1) size-selective fishing causes a demographic shift in the population (demography-only), and 2) size-selective fishing causes a demographic shift and an evolutionary and/or plastic shift in maturation traits (demography plus trait change). Note that for the purposes of our analysis—where we are focused on the trophic consequences of overall phenotypic change—we do not distinguish between plastic and evolutionary changes in maturation. Both evolution and plasticity likely play a role in the phenotypic response of Atlantic Cod populations to fishing (Olsen et al., 2009; Eikeset et al., 2016). We then apply the empirically derived relationship between Atlantic Cod body size and trophic position (Jennings and van der Molen, 2015) to estimate how the trophic role of Atlantic Cod is expected to change.

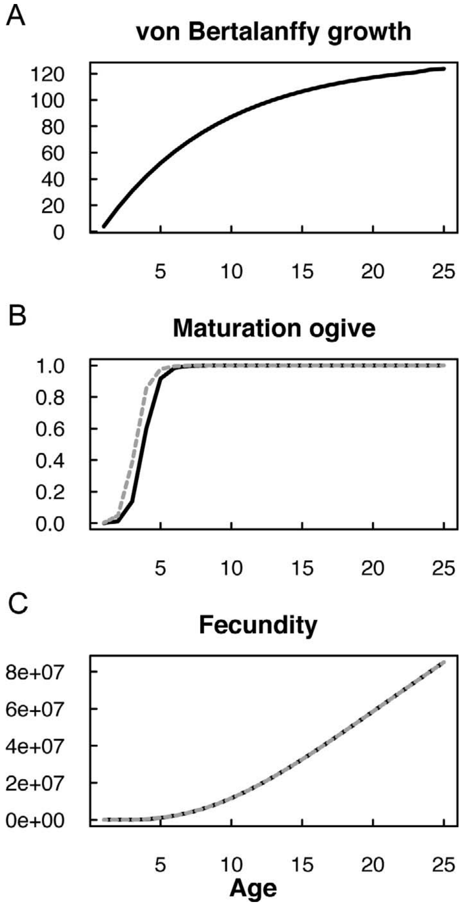

Fig. 1. Functions describing (A) somatic growth, (B) maturation, and (C) fecundity with age of our representative species, the Georges Bank stock of Atlantic Cod (*Gadus morhua*). A maturation ogive is the cumulative probability that an individual is mature. Black lines represent fixed relationships; dashed lines are plastic or evolutionary changes that occur with the advent of size-selective mortality. The decrease in size and age at maturation (dashed line, panel B) could be due to selection for earlier reproduction or due to lower relative size or density.

MATERIALS AND METHODS

We developed a deterministic model of a population with overlapping generations based on the life history of Atlantic Cod *Gadus morhua,* extending the model described in Kindsvater et al. (2016). In the Georges Bank stock, Atlantic Cod live up to 25 years and reach a maximum length of 130 cm (May et al., 1965). Cod are known to mature at differing rates throughout their range; in the Georges Bank, stock maturation has been observed in females as young as two years and as old as five years. We vary maturation rates below, but we assume throughout our analyses that all females are mature by the time they are 45 cm in length or five years of age.

We assume that age a and length L of each individual are described by the discrete-time version of von Bertalanffy growth function (Mangel, 2006), such that:

$$L(a+1) = L(a)e^{-k} + L_{\infty}(1-e^{-k}) \tag{1}$$

where L_{∞} is the maximum length of an average individual and k is the growth coefficient (Fig. 1A). We assume that individuals hatch at the same minimum size L(0); as our model simulates cod populations on annual time scales, variability in the size-at-hatch had no discernable effect on our results. Age-specific mass $W(a)$ can be related to length by $W(a) = cL(a)^{b}$, where b and c can be estimated from data. Parameters are given in Table 1.

Following convention, we model the probability that an individual is mature as a logistic function:

$$p_{mat}(a) = \frac{1}{1+e^{-q(L(a)-L_{mat})}} \tag{2}$$

where q determines the steepness of the function and L_{mat} is the length at which 50% of females are mature (Fig. 1B). For all analyses discussed below, we assumed the steepness of the maturation function (ogive) was similar before and after fishing (Fig. 1B); we varied the steepness of the ogive in sensitivity analyses. Finally, we assume that fecundity of mature females is proportional to their mass, such that age-specific fecundity $E(a) = p_{mat}(a)W(a)$ (Fig. 1C).

We initially assumed that maturation and fecundity functions are static; in subsequent versions of the model the maturation function shifts (dashed line, Fig. 1B), which also changes the age-specific fecundity function (dashed line, Fig. 1C). This shift could occur for multiple reasons. For example, maturation could be a plastic function of the mean length of individuals in the population $\bar{L}(t)$at a given time t. We model this dynamic size at maturation as $L_{mat}(t) = \bar{L}(t) + \Delta L$ (where ΔL modulates the magnitude of an individual's response to a change in relative size). Alternatively, this could represent the case where the trait L_{mat} decreases due to selection for a smaller, earlier size at maturation, as has been observed in Atlantic Cod (Olsen et al., 2005). In both the plastic and evolutionary interpretations, the change in maturation depends on the *average size of individuals* in the population, which changes over time and depends on the parameters determining growth, natural mortality, and fishing. In a second sensitivity analysis, we also considered a trade-off between maturation and survival. Rather than assuming a constant rate of natural mortality (as in the previous scenario), in this case, mature fish were approximately 2% less likely to survive each age than immature fish. This cost of reproduction accumulated over the lifespan of the mature fish.

Table 1. Model parameters and values.

Parameter	Interpretation	Value	Reference (if applicable)
t	Time (in years) in population simulation	600 (maximum)	–
$N(a,t)$	Number of females in each age class at time t	–	–
A_{max}	Maximum age a in years	25	May et al., 1965
L_∞	Asymptotic size (in cm) in the von Bertalanffy growth function	130	May et al., 1965
k	Growth coefficient in the von Bertalanffy growth function	0.12	May et al., 1965
$L(a)$	Length-at-age; L(1) is the initial size (in cm) at recruitment to the population model	4 (when $a = 1$)	–
L_{mat}	Length at which 50% of females mature	35	ICES, 2005
q	Shape parameter that determines the steepness of the maturation curve	0.2	–
$W(a)$	Body mass-at-age	–	–
c	Scale parameter relating body mass to length $L(a)$	$7\text{x}10^{-6}$	Wigley et al., 2003
b	Shape parameter relating body mass $W(a)$ to length at age $L(a)$	3	Wigley et al., 2003
$E(a)$	Fecundity-at-age, assumed to be a cubic function of mass	–	–
M	Natural mortality coefficient in the exponential survival function	0.2 (0.21 for mature fish in the sensitivity analysis)	O'Brien, 1999
F_{max}	Maximum fishing mortality coefficient	Varies from 0.1 to 0.9	–
$s(a)$	Selectivity of the fishing gear for each age or size $L(a)$	–	–
α	Parameter of the Beverton-Holt recruitment function; determines steepness of function near origin	0.5	ICES, 2005
β	Parameter of the Beverton-Holt recruitment function	1×10^{-8}	–
ΔL	Discounting parameter; modulates the length at maturation relative to average lengths of the population	5	–

We simulated the fates of each cohort in the population, as they move through each age a and time t. The population declines as a function of natural mortality M and fishing mortality $F(t)$, which can be constant or can depend on age or body length. The dynamics are:

$$N(a,t) = N(a-1,t-1)e^{-(M(a-1)+F(a-1,t-1))} \tag{3}$$

for $a > 0$. For $a = 0$, the number of recruits, $N(0,t)$, depends on the size of the larval pool P produced by spawning female biomass in the previous time t, modified by a density-dependent recruitment function (Beverton and Holt, 1957; Mangel, 2006):

$$N(0,t+1) = \frac{\alpha P(t)}{1+\beta P(t)} \tag{4}$$

In this function, α determines the steepness of the slope near the origin (in the absence of density dependence) and β the relative strength of density-dependent regulation. We estimated the parameters of Eq. 4 based on published stock recruitment curves for Atlantic Cod (ICES, 2005), but neither these parameters, nor our choice of recruitment function, have a qualitative effect on our results.

We simulated the population without fishing mortality for several generations so that it converged on a stable age distribution. We considered the stable age distribution in three scenarios: no fishing (the historical baseline), fishing but no response in maturation rates (a demographic response to fishing mortality), and an evolutionary or plastic response to fishing pressure in maturation rate.

In both fishing scenarios, we assume that fishing mortality was size-selective such that individuals had an increasing probability of being caught as they grew larger. Fishing mortality is therefore the product of fishing effort F_{max} and selectivity for each length, which we define as:

$$s(L(a)) = \frac{1}{1+e^{-0.2(L(a)-50)}} \tag{5}$$

Given the stable age distribution, we can calculate the numbers of individuals in each size interval of 15 cm. This allows us to compare how size structure differs with variation in mortality, with and without an evolutionary or plastic response to fishing mortality.

We relate size structure to trophic level by using the relationship between log body mass W and mean trophic level TL, estimated for Atlantic Cod with isotopic samples of 154 fish (Jennings and van der Molen, 2015):

$$TL = 4.3706 + 0.2255 * W \tag{6}$$

The linear model fit the data well ($R^2 = 0.2005$), allowing the conversion from size distribution to trophic level. This tells us how the demographic and evolutionary effects of fishing affect community-level processes.

RESULTS

Size-selective fishing had a predictable effect on the age structure of mature fish in our model (Fig. 2). When maturation was a fixed function of age (Fig. 2B), the number of mature fish in each age class decreased, i.e., there was a demographic response to fishing. By contrast, if maturation changed due to a plastic or evolutionary response to fishing mortality, the abundance of mature fish in younger age classes increased (Fig. 2C). In the sensitivity analysis of the

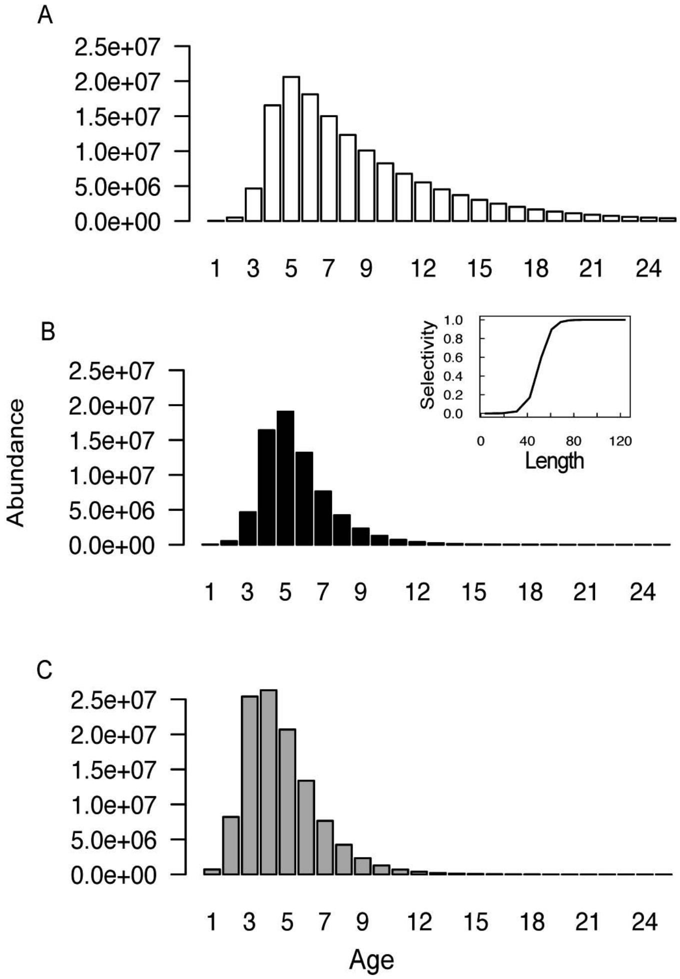

Fig. 2. (A) Age distribution of mature females in the unfished population. (B) Age distribution of mature females after size-selective fishing mortality. Note that growth, maturation, and fecundity functions are fixed functions of age and do not change with additional mortality (solid lines, Fig. 1B, C). Inset: Fishery selectivity (risk of fishing mortality) increases steeply with length. (C) Age distribution of mature females when maturation age decreases in response to size-selective fishing (dashed lines, Fig. 1B, C). Selectivity is identical to the inset in panel B.

maturation function, changing the ogive steepness did not change our results at low levels of fishing; when the population was overfished, a steeper maturation function slightly increased the number of high trophic level fish in the demography-only scenario because it meant there were more mature fish in the steady state. However, the ogive steepness did not affect our results in the scenario with a plastic or evolutionary response to trait change. Therefore, in the results discussed next, we assume the maturation ogive steepness is constant ($q = 0.2$).

As expected, fishing reduced the average size of mature individuals (Fig. 3B). An adaptive response to fishing caused a notable increase in the numbers of fish in the smaller size classes (Fig. 3C). In the second sensitivity analysis, we considered a trade-off between reproduction and survival, whereby maturation incurred a cost (increased mortality). This trade-off reduced the survival of mature fish at each age, such that there were 20% fewer fish in the oldest age class (without fishing). This meant the population size was smaller overall.

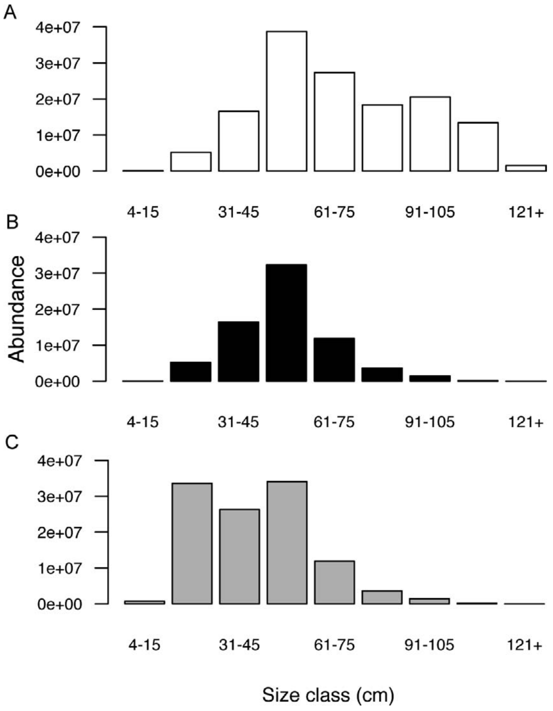

Fig. 3. Size structure of the three populations in Figure 2. (A) The unfished population, (B) size-structure after fishing if maturation probability does not change, (C) size-structure after fishing when maturation decreases as a response to size-selective mortality. In this example, fishing mortality $F_{max} = 0.4$.

We next quantified how these differences in age and size structure changed trophic level (Fig. 4). The range of predicted body sizes did not change dramatically under moderate fishing pressure in our model, although population variance was skewed towards younger, smaller individuals (Fig. 4). The weighted mean trophic level of the population decreased by 50–70% more when age and size at maturity decreased due to adaptive trait change (Fig. 5A). However, the abundance of these populations was always greater than control populations (i.e., equal fishing mortality but without any trait change), and there were up to three times as many large individuals in the population that experienced adaptation (Fig. 5B).

In the second sensitivity analysis, where reproduction was costly to survival, the mean trophic level of adults decreased slightly in the unfished population, because there were fewer older, larger fish. In this scenario, when maturation was a plastic response depending on relative body length, young mature fish were more abundant even without fishing because the cost of reproduction decreased the mean body size, driving earlier maturation. With adaptive trait change after fishing, the mean trophic level decreased further with the trade-off, because fish both matured earlier and had lower survival. The range—or scope—of the trophic level was not affected. As the population became overfished at higher fishing mortalities, the difference with and without a cost of reproduction disappeared (because there were no surviving large fish).

DISCUSSION

Based on the results of our model, size-selective fishing is predicted to truncate age structure and size structure, and also decrease the trophic position of Atlantic Cod. These effects depend on whether responses involve demographic changes only, or whether they also include adaptive changes

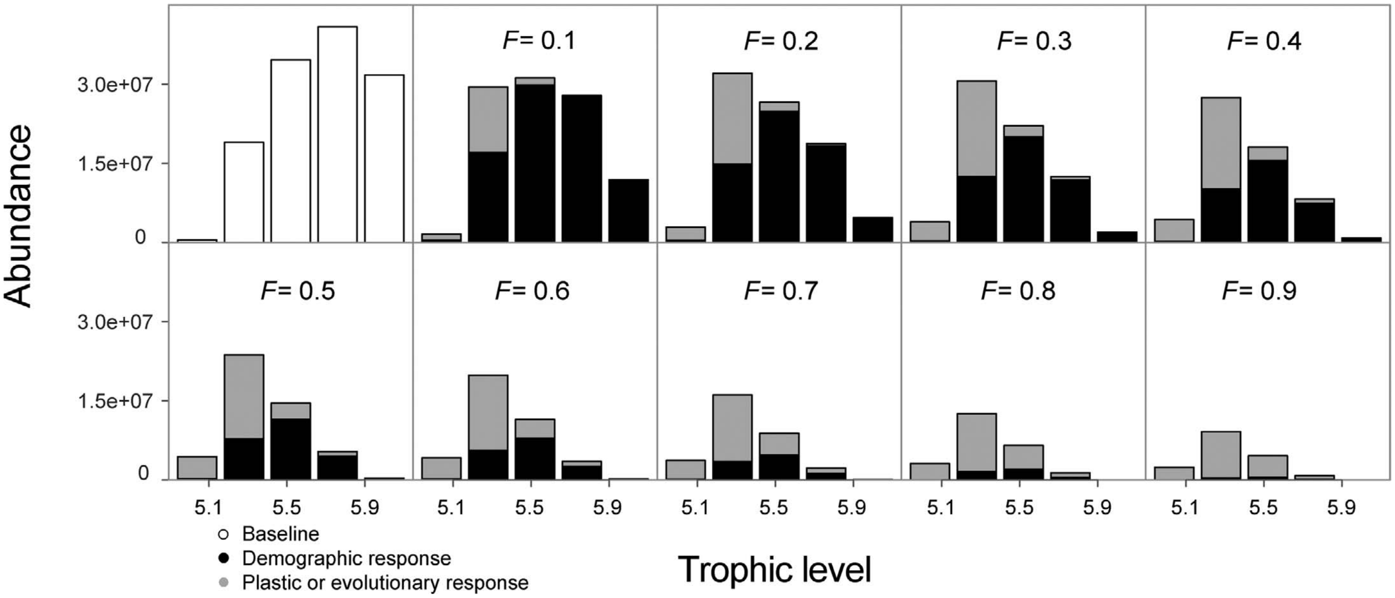

Fig. 4. Distributions of trophic level in the three scenarios: unfished baseline (white), demography-only with fixed age at maturation (black) and demography-plus-trait-change, with plastic or evolutionary change in age at maturation (gray). Note that gray bars are always equal to or greater than black bars in height.

in maturation age and size. In the latter case, adaptation is predicted to maintain the trophic scope of cod (Fig. 6). This suggests that the number of large, high trophic level fish in a harvested population is determined by the eco-evolutionary feedback from demography to adaptation, and then back to demography. The degree to which maturation schedules change in response to fishing pressure has profound implications for the prey communities at each trophic level.

Evidence from other studies suggests that such demographically eroded populations appear to suffer reduced resilience, recovering more slowly after fishing ceases (Hutchings, 2005; Walsh et al., 2006; Kuparinen and Hutchings, 2012; Salinas et al., 2012). Populations with truncated age- and size-structure have also been predicted to show increasingly variable dynamics, tracking the environment closely (Kuparinen et al., 2016). Reduced egg and larval abundance due to the loss of the largest, most fecund fish could drive this loss of stability, although the strength of the relationship between age diversity and recruitment has been questioned for gadoids (Hidalgo et al., 2014; Stige et al., 2017), which are among the best-studied marine fishes. In our model, age-structure does not directly affect recruitment or rebuilding capacity. However, our results highlight the specific role of eco-evolutionary dynamics on population age- and size-structure. In the demography-only case, the modal age and size of the fished population remains the same compared to the unfished population (Figs. 2, 3). In this case, the abundance of fish in older age and larger size classes

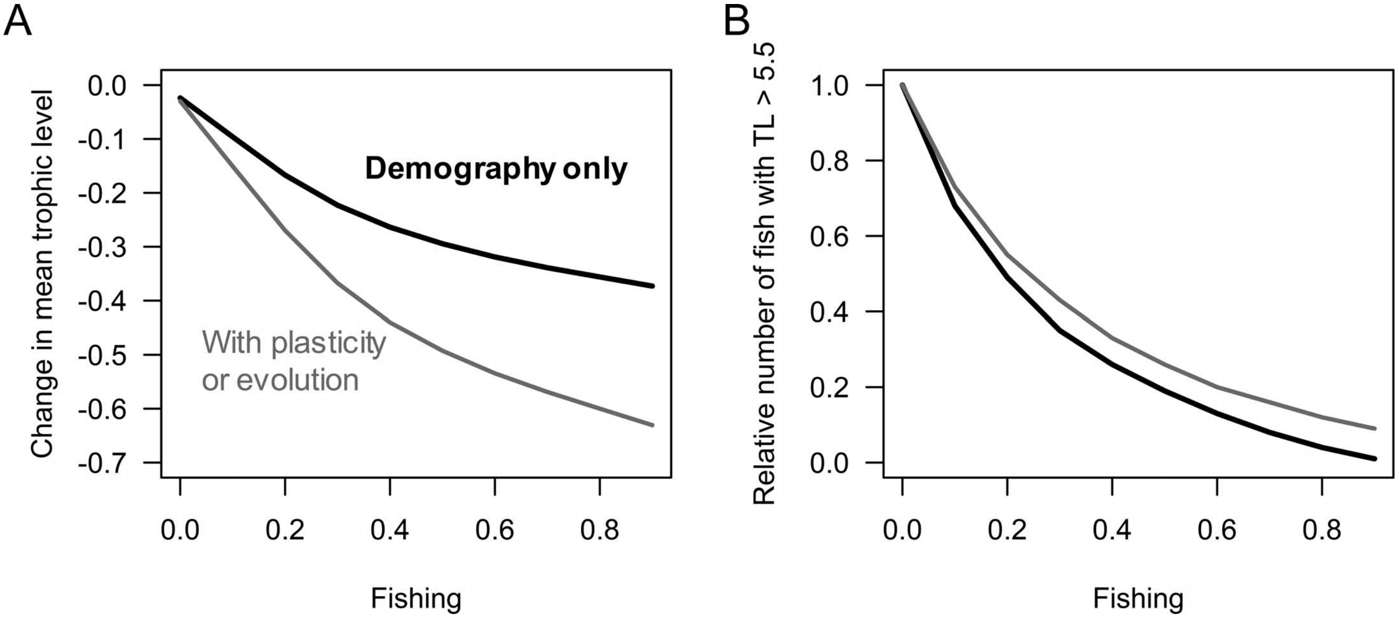

Fig. 5. (A) Change in mean trophic level and (B) the abundance of fish with trophic level greater than 5.5, relative to the unfished population, with size-selective fishing mortality in both scenarios. In both panels, black lines are demography only, gray lines are demography with adaptation.

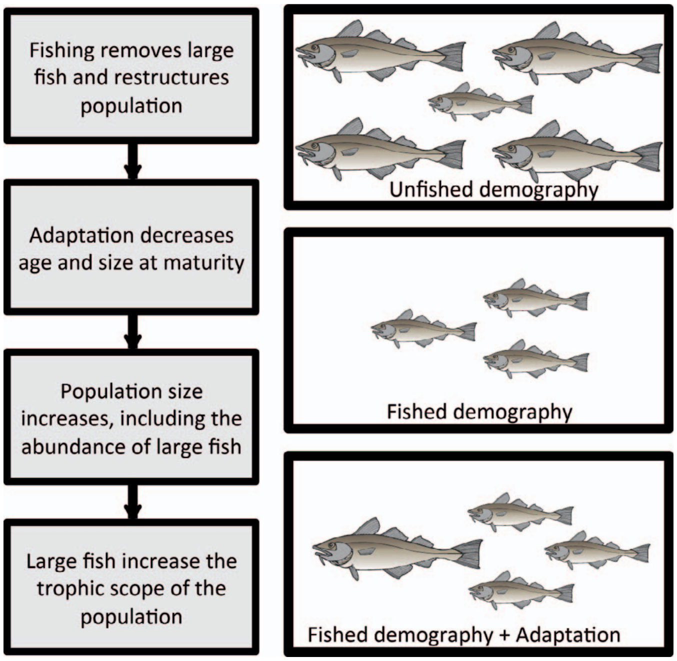

Fig. 6. Demography and adaptation are predicted to interact to shape the abundance, body size distribution, and trophic role of Atlantic Cod.

is reduced, while changes in younger age and smaller size classes are minimal. Relative to the demography-only case, the most notable effect of including adaptation in our model is to increase the abundance of fish in the young age and small size classes (Figs. 2, 3). But this shift has further impacts on size structure, as greater abundance at young ages leads to more fish surviving to reach the older, larger size classes. This effect is the eco-evolutionary feedback from demography to adaptation and then back to demography.

Changes in population size structure have important consequences for the trophic role of Atlantic Cod. We compared the difference in the trophic structure of the population in the demography-only case relative to the adaptation case in order to clarify how eco-evolutionary dynamics, beyond simple demographic responses, could influence the trophic role of Atlantic Cod. The eco-evolutionary effects of adaptation on trophic level mean and variance are predicted to be greatest under heavy fishing pressure, when the populations are overfished (Fig. 4). This effect begins as a result of the increased abundance of fish in the small size classes. The mean trophic level is predicted to decrease substantially in this scenario (Fig. 5A). Yet this increased abundance of young individuals then allows some fish to survive to reach old age and large size, despite high mortality. The demography-adaptation-demography feedback serves to maintain variation in trophic position after fishing by increasing the number of large, high trophic level fish in the population (Fig. 5B). The elevated numbers of fish with a high trophic position increase the trophic scope of the population—the mean trophic position decreases rapidly but variation is maintained at a greater level than in the demography-only case (Fig. 5). Thus, the eco-evolutionary feedback extends beyond population size structure to also impact the trophic structure of the fished population. This novel insight could not have been attained without explicitly contrasting a demography-only scenario with a scenario that also includes adaptation.

For simplicity, we have ignored density- or frequency-dependent feedbacks. In reality, direct effects of fishing on abundance could allow for faster somatic growth (Lorenzen and Enberg, 2002). The relationship between growth, maturation, and fishing mortality is of primary importance. Whether plastic or evolutionary responses to fishing will compensate for demographic erosion depends on the fecundity-age relationship and the timing of maturation with respect to the size-selective gear (Hidalgo et al., 2014). Both of these aspects of the life history are intimately linked to somatic growth. Therefore, the assumptions about growth in our study—as in others—are a natural avenue of further research (Eikeset et al., 2016).

Our model results show that adaptive trait changes could dramatically modify the trophic role of Atlantic Cod. But what are the potential implications for predator-prey interactions and the dynamics of marine ecosystems? Recent food web models have linked fisheries-induced trait changes to potential changes in predator-prey interactions, food web dynamics, and ecosystem stability (Audzijonyte et al., 2013, 2014; Kuparinen et al., 2016). These studies show that fisheries-induced trait changes can alter predator-prey interactions in ways that can increase prey abundance and cascade across trophic levels. Our results add to this literature to show that, for mean trophic position in the population, adaptation compounds the demographic effects of fishing, causing an even greater reduction. However, eco-evolutionary feedbacks help maintain more individuals with high trophic position by increasing the number of fish at all sizes, despite fishing mortality. Thus, the trophic scope of the population is maintained to a greater extent by adaptation.

A few large fish may continue to exert some top-down control on the food web through direct predation. But large predatory fish, even if few in number, may also play a disproportionate role in the ecosystem through non-consumptive effects (Carpenter et al., 1987; Stallings, 2008). Sometimes termed trait-mediated indirect effects, non-consumptive effects occur when the presence of a predator alters prey behavior by reducing or shifting feeding behavior so as to avoid the predator (Lima and Dill, 1990). In many cases, non-consumptive effects may be stronger than consumptive effects for determining the strength of trophic cascades (Schmitz et al., 2004). Thus, the increased variance in Atlantic Cod trophic position promoted by adaptation may play a large role in maintaining ecosystem function if the presence of a few large fish induces a behavioral response in prey.

Our results predict that adaptive trait responses will substantially modify the ecological role of harvested populations of Atlantic Cod. Adaptation leads to a reduced mean but an increased variance in trophic position because there are many smaller fish, but also a few larger fish, in the population. This research provides a simple proof-of-concept that a combination of demographic shifts and adaptation in response to harvest could change the trophic role of Atlantic Cod. However, several caveats remain. For any population, the response to fishing will depend on the other selective forces acting on life history and population demography, which we have not captured in our model. For example, the relationship between population density and population growth is crucial, but may vary with geography or life stage.

Our theoretical predictions generate testable hypotheses for how demographic shifts and adaptation could interact to influence the population size structure and trophic structure of fished populations. The prediction that adaptation to fishing mortality could maintain variation in population size-structure has circumstantial empirical support to date. Selection for variability in maturation has been seen in Atlantic Salmon, due to the unique genetic architecture underlying this trait (Kuparinen and Hutchings, 2017). Directional selection on body size favored increased variability in size in experimental populations of zebrafish (Uusi-Heikkilä et al., 2016). In contrast, there is compelling evidence for a reduction in phenotypic variation in juvenile body size in a long-term study of fished populations Arctic cod (Olsen et al., 2009). The community-level implications of such phenotypic changes are only beginning to be appreciated. Eco-evolutionary feedbacks, such as that involving linked changes in demography, reproductive traits, and trophic position, may reshape harvested ecosystems in unexpected ways that deserve more detailed attention from ecologists and resource managers.

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