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Authors

Selden, Rebecca L
Warner, Robert R
Gaines, Steven D

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Ontogenetic shifts in predator diet drive tradeoffs between fisheries yield and strength of predator-prey interactions

Rebecca L. Selden[a,*], Robert R. Warner[a], Steven D. Gaines[b]

[a] Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, Santa Barbara, CA, 93106, United States
[b] Bren School of Environmental Science and Management, University of California, Santa Barbara, Santa Barbara, CA, 93106, United States

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ABSTRACT

In some marine ecosystems, overharvesting marine predators has triggered major changes in trophic structure and ecosystem function. However, harvest levels that are deemed sustainable for one species may still lead to unexpected impacts elsewhere in the ecosystem. For example, by imposing an additional source of mortality, even sustainable harvesting can lead to a reduction in the number of large individuals within a population, and this truncation in size structure is typically more severe when the largest, most valuable size classes are targeted. Often small and large individuals within a species differ in important ways, including in what they consume, so a loss in predator-prey interactions could occur even without changes in overall predator biomass. Here we explore whether a truncation in predator size structure alone can reduce or functionally eliminate linkages between predator and prey. For this outcome to occur, a predator's diet must change as it grows in size. We examined evidence for changes in diets with size among predators in three large marine ecosystems, and used a size-structured population dynamics model to evaluate the extent to which otherwise sustainable fishing results in disproportionate reductions in predation. Modelling suggests that diet shifts occurring late in life history (diet mid-point > 45% of the maximum size) led to losses in predation that were more severe than would have been expected from losses in predator biomass. Further, the form of the fishery selectivity was less important than the degree of reduction in biomass within each size class relative to the timing of diet shifts. Empirical diet information demonstrates that piscivores vary widely in their onset to piscivory, and this may buffer the potential impacts of truncation in size structure. However, over half of the piscivores had diet shifts toward specific fish taxa at sizes at or above that which would lead to disproportionate reductions in prey consumption. Information about when and how diets change with predator size could identify ecosystems where harvest may lead to unexpected losses in predator-prey interactions.

1. Introduction

Human exploitation has resulted in dramatic alterations in the food webs in which targeted species are embedded in many ecosystems. Top predators are often targeted preferentially due to their large body size and high value, resulting in disproportionate reductions in their biomass relative to other components of the food web. Exploitation has resulted in 50–70% reductions of predator biomass in some pelagic ecosystems (Hampton et al., 2005), while demersal predators have been reduced by an even greater extent in others (Christensen et al., 2003). In some cases, exploitation has even led to local predator extinction (Estes et al., 2011). Such predator depletions have caused ripple effects to cascade through food webs across a diversity of marine ecosystems (Breen and Mann, 1976; Daskalov et al., 2007; Dulvy et al., 2004; Estes and Duggins, 1995; Frank et al., 2005; Ling et al., 2009; Myers et al., 2007; Shears and Babcock, 2003; Steneck et al., 2002; Tegner and Dayton, 2000).

In some cases, disruption of food webs due to fishing predators has resulted in increases in pest species that adversely affect other fisheries through competition (Kideys et al., 2005; Robinson et al., 2014) or predation (Myers et al., 2007). Alternatively, where prey are commercially valuable, strategic depletion of predators by harvesting may benefit fisheries for the prey (Yodzis, 2001), though subsequent harvesting of prey populations can lead to additional regime shifts (Daskalov et al., 2007). Given the widespread, and potentially irreversible ecosystem consequences of depleting predators, it is critical to predict the conditions under which harvesting will disrupt predator-prey interactions, whether the goal is to benefit from prey production or avoid adverse ecosystem outcomes.

Scientists from across the conservation and fisheries spectrum have

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[*] Corresponding author. Current address: Department of Ecology, Evolution, and Natural Resources, Rutgers University, 14 College Farm Rd, New Brunswick, NJ 08901, United States.
E-mail address: becca.selden@rutgers.edu (R.L. Selden).

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suggested that sustainably managing stocks from a single-species perspective often will achieve many of the goals of ecosystem-based management (Froese et al., 2008; Hilborn, 2011) and reduce the impacts of fishing on marine ecosystems. For example, Froese et al. (2016, 2008) recently argued that setting the minimum size limit for a fishery at the size at which cohort biomass is maximized (L_{opt}) can increase sustainability of fisheries and ensure that species better fulfill their ecological roles. While more selectively targeting the largest individuals often increases the fisheries yield of a predator species (Beverton, 1992; Froese et al., 2008) and reduces the risk of overfishing even at high fishing mortality rates (Froese et al., 2016), the ecosystem-level consequences of these actions are not clear. Assuming constant recruitment, yield is theoretically maximized if the entire cohort is captured at the length L_{opt} (Holt, 1958). Even when not pursued at this extreme, such a fishing strategy can result in substantial reductions in the number of large individuals in a population. Since larger predators not only eat more prey, but they can also eat larger, better defended, and more mobile prey, small and large predators within a species can differ more in their diet than separate species (Rudolf and Lafferty, 2011). In aquatic food webs, changes in diet with size are the norm rather than the exception, particularly among fish that are piscivorous as adults (Werner and Gilliam, 1984), or that specialize on hard-shelled prey (Wainwright, 1991). As a result, loss of the largest predators may result in the virtual elimination of linkages between predator and prey, and may lead to a loss in prey regulation. Such an outcome was observed in the Scotian Shelf, where truncation in predator size structure led to a 300% increase in prey biomass, even while predator biomass remained constant (Shackell et al., 2010). To avoid (or facilitate) such an outcome, it is critical that managers anticipate the conditions under which truncations in predator body size will impact prey consumption in ways that could not have been predicted from reductions in predator biomass alone.

In this study we use a simulation model to evaluate how ontogenetic changes in predator diet with size alter the tradeoff between fisheries yield and prey consumption for various harvest strategies. We then examine evidence for variability in ontogenetic changes in diets among predators in three large marine ecosystems. This approach reveals the conditions under which the strength of predator-prey interactions will be reduced to a greater extent than would have been predicted from changes in predator biomass alone, and highlights key predator-prey linkages where ontogenetic shifts may be important to consider in an ecosystem approach to fisheries management.

2. Materials and methods

2.1. Population dynamics model with varying fishery selectivity

To evaluate how variation in the timing of ontogenetic shifts in diet alter the impacts of fishing on the functional role of predators, we constructed a deterministic age- and size-structured population dynamics model (c.f. Cope and Punt, 2009), with life history-traits modeled after a generic cod-like predator. The equations describing the model, the parameter values used, and sensitivity analyses are provided in Appendix A. In this model, size-specific mortality is the sum of natural mortality and the product of fishing mortality and selectivity. In this way, we can independently vary the relative intensity of harvest as well as the relative probability of capture as a function of size. These two components affect total predator biomass and the biomass distribution across predator sizes (Fig. B.1 in Supplementary materials).

We evaluated the effect of fishing for two selectivity patterns. We first considered a fishery with logistic selectivity with an inflection point at $0.25(L_\infty)$ [hereafter "Early"]. This selectivity pattern corresponds to the historical fishery selectivity pattern for Atlantic Cod in 1982–1986 (NEFSC, 2012). We compared this to a fishery that selectively targeted the largest individuals by delaying harvest until L_{opt}, the size at which cohort biomass is maximized (Fig. B.1 in Supplementary materials) [hereafter "L_{opt}"]. The size at L_{opt} is defined by the natural mortality rate (M), the growth coefficient (k) and asymptotic size (L_∞) from the von Bertalanffy growth equation describing length at age (L_A): $L_A = L_\infty 1 - exp(-kA)$, and the length-weight scaling exponent (b in $W_A = aL_A{}^b$, where W_A is the weight at age; Froese et al., 2008; Hordyk et al., 2015), such that:

$$L_{opt} = L_\infty \frac{b}{\frac{M}{k} + b}. \tag{1}$$

For the L_{opt} fishery, selectivity was knife-edged at this value of L_{opt}.

Values for instantaneous rates of mortality (yr^{-1}) due to fishing (F) ranged from 0 (unfished) to 3. The F-values for the fully-selected size classes corresponding to maximum sustainable yield (F_{MSY}) were calculated for the length selectivity pattern of each fishery. F_{MSY} was defined as the level of fully-selected fishing mortality at which equilibrium yield was maximized for the selectivity pattern, assuming steady-state recruitment according to a Beverton-Holt stock recruitment relationship (see Appendix A for details). For the early selectivity fishery, F_{MSY} was 0.19 yr^{-1}, while that for the L_{opt} fishery was 1.79 yr^{-1}.

2.2. Simulating variation in ontogenetic diet shifts

Consumption of a focal prey species i by the predator population P_i is a function of the predator numbers at age N_A, weight at age W_A, total annual consumption per unit predator biomass C_A (see Appendix A for derivation), and the percentage of the diet of a predator of age A comprised of prey $i(\theta_{A,i})$ such that

$$P_i = \sum_A^\omega N_A W_A C_A \theta_{A,i} \tag{2}$$

We considered a diet function where 50% of the diet of the predator was comprised of the focal prey at a particular predator body size (πL_∞) following a logistic curve:

$$\theta_{A,i} = \frac{\phi}{\left(1 + \exp\left(-q\left(\frac{L_{A,i}}{L_\infty} - \pi\right)\right)\right)} \tag{3}$$

Based on this formulation, ϕ controls the maximum diet fraction for the focal prey, and q controls the rate of the change around the mid-point of the diet. For these diet scenarios we varied the slope at the mid-point from 2 to 10 in increments of 1, and varied π from 0 to 0.9 in 0.01 increments (Fig. 1). For the baseline case, we used $\phi = 1$, but we also

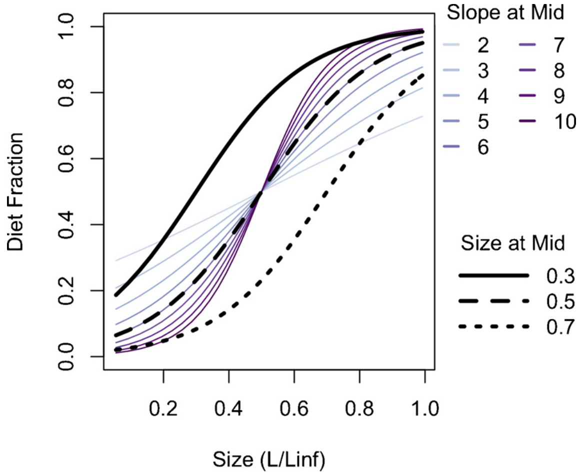

Fig. 1. Focal species diet proportion for a logistic diet pattern with size at the mid-point of the diet between 0 and 0.9 with a maximum diet fraction of 1 ($\phi = 1$). A subset of the logistic diets are depicted with the midpoint of the diet at 30% (solid), 50% (dashed), and 70% (dotted) of the maximum size and the range of slopes at the mid-point from shallow (light colors) to steep (dark colors).

consider the effects of maximum diet fractions of 25%, 50%, and 75%.

2.3. Tradeoff analysis

Because fishing at any level reduces predator biomass, there is an inherent tradeoff between fisheries catch and the magnitude of prey consumed by the remaining predator population. To quantify this tradeoff, we calculated the relative catch and predation achieved for each level of fishing mortality. Relative catch was defined as the catch relative to the maximum achieved under the L_{opt} fishing scenario. Relative predation was defined as the prey consumption relative to that of an unfished predator population. We examined relative catch and relative predation as a function of the range of F values, as well as at F_{MSY}. We evaluated the degree to which the form and intensity of the tradeoff between catch and prey consumption varied with fishery selectivity and the ontogenetic diet pattern.

We also examined the degree to which variation in timing of ontogenetic shifts would lead to losses in prey consumption greater than expected from reductions in predator biomass. To do this we compared predator biomass and the consumption of prey by the predator population when fished at MSY relative to that of an unfished predator population. We identify the timing of ontogenetic shifts in diet at which prey consumption on a focal prey is reduced to a greater degree than overall predator biomass.

2.4. Empirical diet analyses of ontogenetic shifts

Diet information was compiled for groundfish predators in the Eastern Bering Sea, Gulf of Alaska and Northeast U.S. Continental Shelf large marine ecosystems (LMEs) to evaluate the degree to which predator diets vary with body size. Diet information for all three LMEs was collected by the National Marine Fisheries Service on scientific trawl surveys. For the Gulf of Alaska (GOA), diet information was collected tri-annually since 1987, and bi-annually since 1999. Diet information from the Eastern Bering Sea (EBS) has been collected annually since 1981. Both Alaska diet datasets are available from the Resource Ecology and Ecosystem Modeling Program at the Alaska Fisheries Science Center (Aydin and Alaska Fisheries Science Center, 2015). For the Northeast U.S. Continental Shelf LME (NEUS), diet information has been analyzed annually since 1973 by the Food Web Dynamics Program of the Northeast Fisheries Science Center (http://www.nefsc.noaa.gov/femad/pbb/fwdp/databases.html). We restricted our analysis of stomach samples from NEUS to 1981–2015 due to a change in sampling methodology in 1981 (Smith and Link, 2010).

Diet information for each predator was pooled into 5 cm increments for the decades 1980–1989 (“1980s”), 1990–1999 (“1990s”), 2000–2009 (“2000s”) and 2010–2015 (“2010s”). These size bins were converted to sizes relative to the maximum by dividing by the 99th quantile of the observed length in the diet dataset across all years (L_{max}). The proportion of the diet composed of each prey item was calculated as the mean percent prey weight for predator size classes with more than 30 individual stomachs sampled per decade and divided by the total prey weight observed for that size class. Piscivore species were included in the analysis if at least 30% of the total percentage of the diet at large sizes ($> 75\%\, L_{max}$) was fish prey.

We first analyzed the timing of onset to piscivory in general, in which all fish prey were aggregated, such that fish identified to family or species as well as unidentified fish were grouped together. The second analysis examined diet shifts toward specific fish taxa. In the Eastern Bering Sea and Gulf of Alaska, walleye pollock represented 25–60% of all fish consumption when aggregating diets across predator size classes. We therefore focused on pollock as a focal fish prey for these regions. In the more diverse Northeast US LME, consumption of identified fish prey was principally divided among the families Ammodytidae (10% of overall fish consumption in the 1980s, ~1% thereafter), Clupeidae (10–30% of overall), Gadidae (13–28% of overall), and Scombridae (7–10% in the first three decades, 1% in the 2010s). The relative consumption within a fish family on specific prey taxa was calculated by summing the total prey weight of the specific taxa across all predators and predator size-classes and dividing by the total prey weight of fish in the family.

The fraction of diet represented by each focal prey taxa as a function of predator size was modeled for each decade using a beta regression in R (R Core Team, 2017) with the “betareg” package (Cribari-Neto and Zeileis, 2010). The coefficient from the model for predator size is reported as the “slope.” The predictions from the model were used to identify the maximum diet fraction, and the size at 50% of the maximum diet fraction.

2.5. Case study with Atlantic cod

To simulate the impact of truncation in size structure for prey consumption by Atlantic cod, we coupled the decadal trends in diet composition with observed cod size structure in the NEFSC fall trawl survey. We focused on clupeid consumption, as that was a dominant prey taxon for Atlantic cod since the 1980s, and a predator-prey interaction that has been disrupted in other ecosystems (Gårdmark et al., 2015). We compared the size structure in the 1970s (1970–1979) when relatively more large fish were present to that in the 1990s (1990–1999) when both number and size structure were reduced. While cod total abundance was about 4 times lower in the 1990s relative to the 1970s, we isolated the effect of the change in size structure alone by scaling the decade-specific proportions of individuals in a size class to achieve equal overall population numbers. Clupeid consumption was calculated from the population size structure using Eq. (2) in conjunction with observed clupeid diet fractions for cod in the 1980s, 1990s, 2000s, and 2010s. The contribution of *C. harengus* to the overall clupeid consumption by cod was calculated by summing the prey weight of *C. harengus* across all size classes in a decade and dividing by the total clupeid prey weight.

3. Results

3.1. Tradeoff between catch and prey consumption

Predation on focal prey declined as catch increased and predator biomass decreased (Fig. 2). The tradeoff between predation and catch was steeper for the early selectivity fishery (Fig. 2a) and for late prey, as measured by the size at the mid-point in diet (Fig. 2a–b). For a given level of prey consumption, catch was ~67% higher for the fishery that delayed harvest until L_{opt} (Fig. 2, Fig. B.2 in Supplementary materials). At maximum sustainable yield (MSY), overall predator biomass was similar between the two selectivity patterns (30% of unfished for the early selectivity fishery, and 36% of unfished for the L_{opt} fishery). However, this was achieved via more uniform reduction in biomass across size classes for the early selectivity fishery (Fig. B.1 in Supplementary materials), while that for L_{opt} was concentrated on sizes larger than L_{opt}. As a result, the early selectivity fishery had 3 times the biomass of fish larger than L_{opt} (Fig. B.1 in Supplementary materials), but both fished populations had small fractions of predators larger than L_{opt} relative to the unfished predator population (17% and 6% for the early and L_{opt} fisheries respectively).

3.2. Effect of timing and rate of change in ontogenetic diet patterns

The timing of ontogenetic diet patterns was a key driver of the impacts of fishing on prey consumption. As the degree to which prey were consumed disproportionately by large predators increased, the ratio of prey consumption by a predator population fished at MSY to an unfished predator population declined (Fig. 3). Averaged across all slopes, diet shifts occurring late in life history (mid-point of diet at 45% of the maximum predator size) led to losses in predation that were more

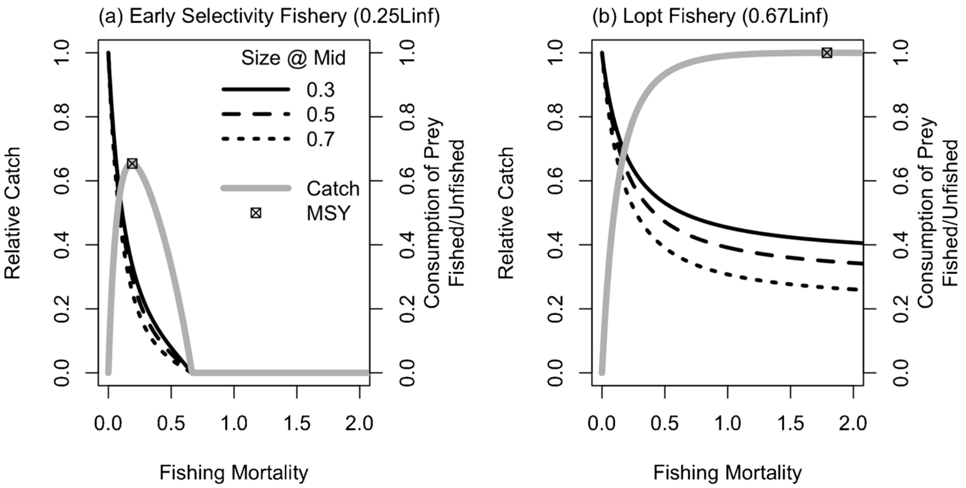

Fig. 2. Relative catch (bold gray line) as a function of fishing mortality for a predator population fished by an early selective fishery (a) or a fishery delaying harvest until *Lopt* (b). Thin lines depict the amount of prey consumed by the predator population relative to an unfished population as a function of fishing mortality on the predator. See Fig. 1 for details on the three diet scenarios depicted.

severe than would have been expected from losses in predator biomass. Predation ratios declined to a greater extent with later diet shifts for the fishery that delayed harvest until L_{opt} (Fig. 3b).

The rate of change in diet amplified the effect of diet timing on the degree to which predation was reduced (Fig. 3a–b). With steeper slopes, consumption was more knife-edged at the size at 50% of the maximum diet fraction. As a result, when prey were eaten early in life history, prey were consumed at high levels at small sizes and the fished predator population maintained predation at levels that were higher than would have been expected from the overall reduction in predator biomass. However, as the size at the mid-point of the diet increased, steeper slopes resulted in prey being consumed exclusively by the largest individuals. As such, predation was reduced to a greater extent than would have been expected as large individuals were reduced due to fishing. For the steepest slope, prey consumption was reduced to 25% of the unfished level for diet mid-points at 60% of the maximum size for both fishery types; subsequently the predation ratio declined more steeply for the L_{opt} fishery due to the disproportionate reduction in large fish with this selectivity pattern. The relationship between the timing of ontogenetic diet shifts and the predation at MSY relative to unfished was unaffected by the maximum diet fraction (Fig. 4), though higher maximum diet fractions led to higher absolute rates of prey consumption.

3.3. Empirical evidence for variation in ontogenetic shifts in diet

Piscivores across three large marine ecosystems displayed wide variation in the degree of specialization and the timing of onset in consuming late prey. Approximately 80% of the piscivores consumed fish as > 70% of their diet at some point in their life history (Table C.1 in Supplementary materials), and 65% of the piscivores consumed fish as > 70% of their diet at their largest sizes. Despite consuming fish as a similar proportion of their diets, piscivores varied widely in the size at which fish comprised 50% of their maximum diet fraction (Fig. 5, Table C.1 in Supplementary materials).

Within the Eastern Bering Sea and Gulf of Alaska, fish prey were dominated by walleye pollock, *Gadus chalcogrammus,* representing > 50% of the diet for 7 of the 9 Alaskan piscivores. Within the more diverse Northeast US LME, fish prey were divided among the families Ammodytidae (100% *Ammodytes* sp.), Clupeidae (> 50% *Clupea harengus* since the 1990s), Gadidae (> 50% *Merluccius bilinearis*), and Scombridae (> 93% *Scomber scombrus* since the 2000s), with comparatively lower diet fractions for each prey taxa. The majority of piscivores switched to one of these focal prey fish taxa at later sizes than their onset to piscivory in general (Table C.1 in Supplementary materials). More than half of the piscivores shifted toward these specific fish taxa with a mid-point of diet > 45% of maximum size—the threshold identified in the simulation modelling as that in which predation was reduced to a greater extent than would be predicted from biomass alone.

3.4. Case study with Atlantic cod

Atlantic cod (*Gadus morhua*) began eating fish early in its life history

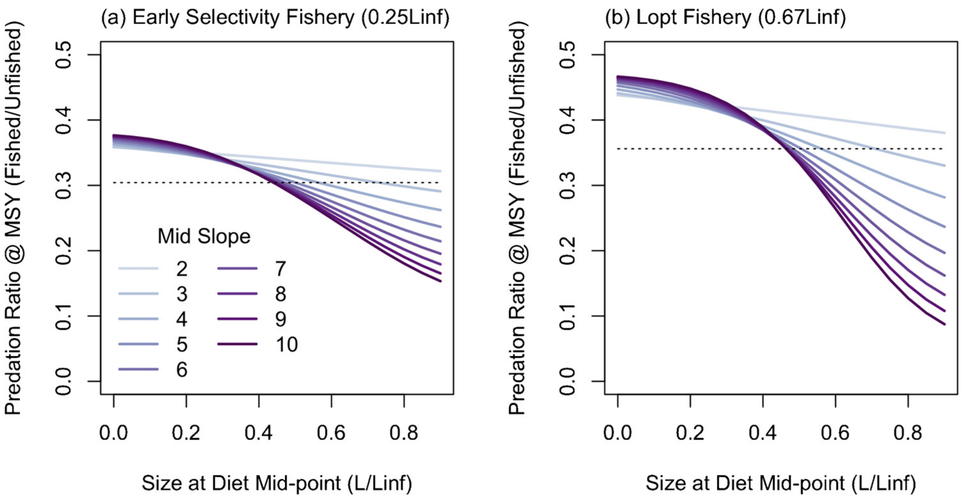

Fig. 3. Prey consumption of the predator population fished at maximum sustainable yield (MSY) for an early selective fishery (a) or a fishery delaying harvest until *Lopt* (b) relative to an unfished predator population as a function of the size at the mid-point of the diet. Colored lines represent slopes of the increase in diet fraction with predator size from shallow (light colors) to steep (dark colors). Horizontal dotted line represents the expectation from a reduction in overall predator biomass.

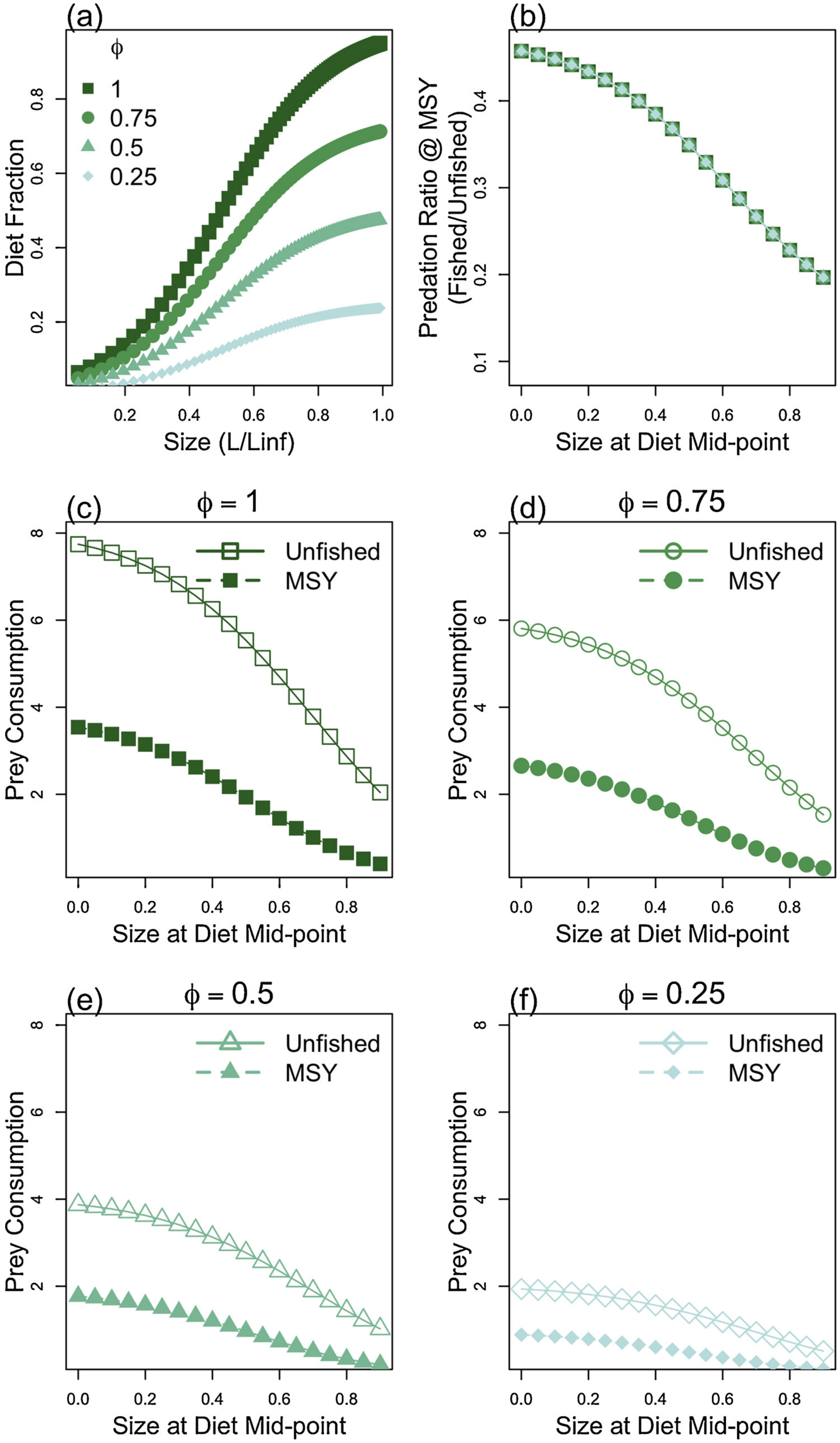

Fig. 4. The effect of differences in maximum diet fraction ϕ (a) on the ratio of prey consumption at MSY as a function of ontogenetic diet shifts (b). Effects of maximum diet fraction on absolute rates of consumption by fished and unfished predator populations (c–f).

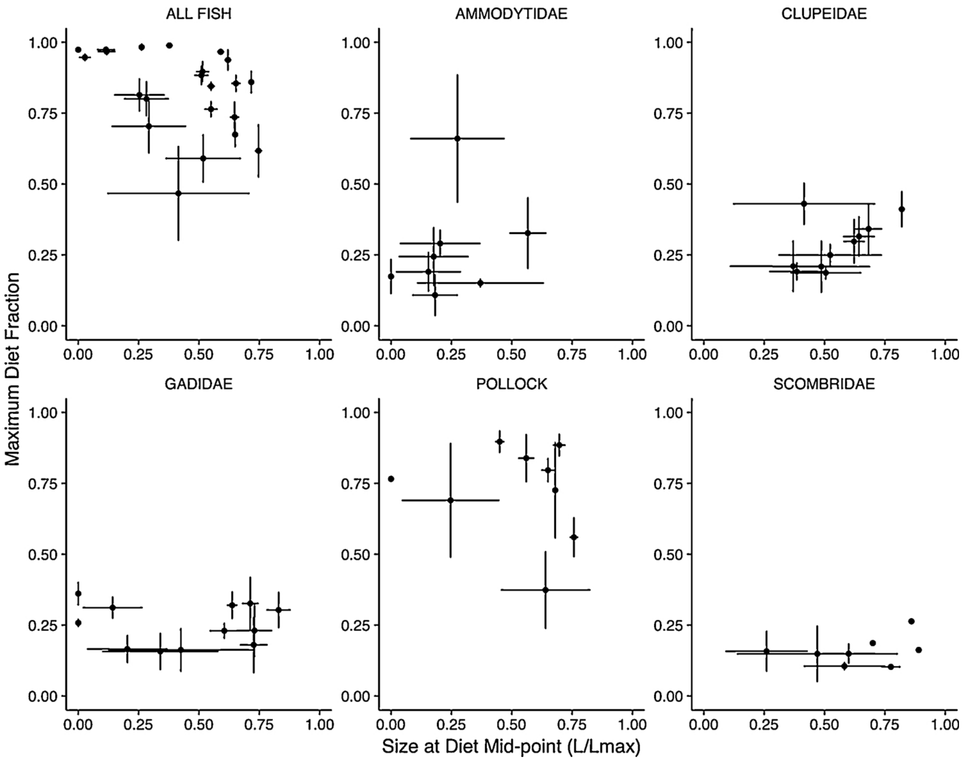

Fig. 5. Empirical ontogenetic diet patterns for each prey taxa: All fish (all three LMEs), Ammodytidae (NEUS), Clupeidae (NEUS), Gadidae (NEUS), Pollock (Eastern Bering Sea and Gulf of Alaska), and Scombridae (NEUS). Filled circles represent the size at the mid-point of the diet across the four decades of diet data. Error bars represent the standard error of the mean in both the maximum diet fraction and size at the diet mid-point.

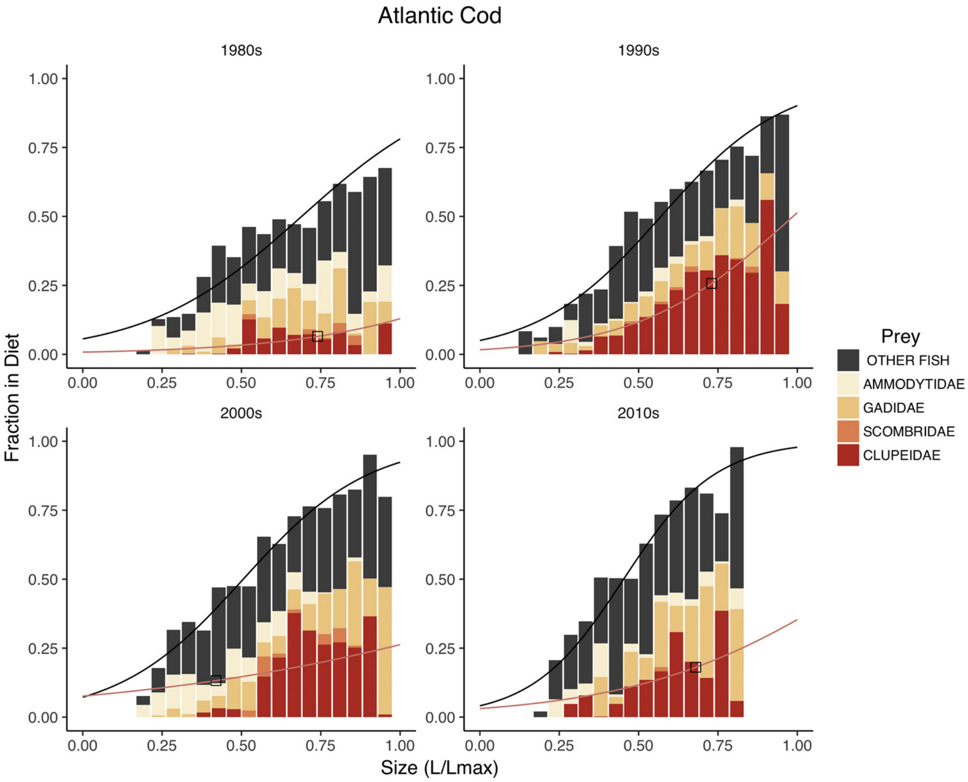

Fig. 6. Ontogenetic diet patterns for Atlantic cod in the 1980s (topleft), 1990s (topright), 2000s (bottomleft) and 2010s (bottomright). Solid black lines show the fit from a beta regression model for overall piscivory as a function of predator size while light red lines show that for clupeid prey. Open square is the size at the mid-point of the diet. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

with fish representing nearly 90% of its diet at the largest size classes. This level of piscivory was consistent across decades (Fig. 6). However, the relative composition of that piscivory varied over time. Clupeids increased in importance in the 1990s and were maintained as a large fraction of the diet through the 2000s and 2010s. *C. harengus* represented 53%, 84% and 84% of the Clupeid prey for *G. morhua* in the 1990s, 2000s and 2010s respectively. Clupeids consistently represented late prey with the average mid-point of the diet across the four decades at 64% of the maximum size (Table C.1 in Supplementary materials). The changes in cod size structure alone that have occurred over the last four decades within the Northeast U.S. LME are sufficient to reduce clupeid consumption by 20–30%, even without changes in cod numbers (Fig. 7).

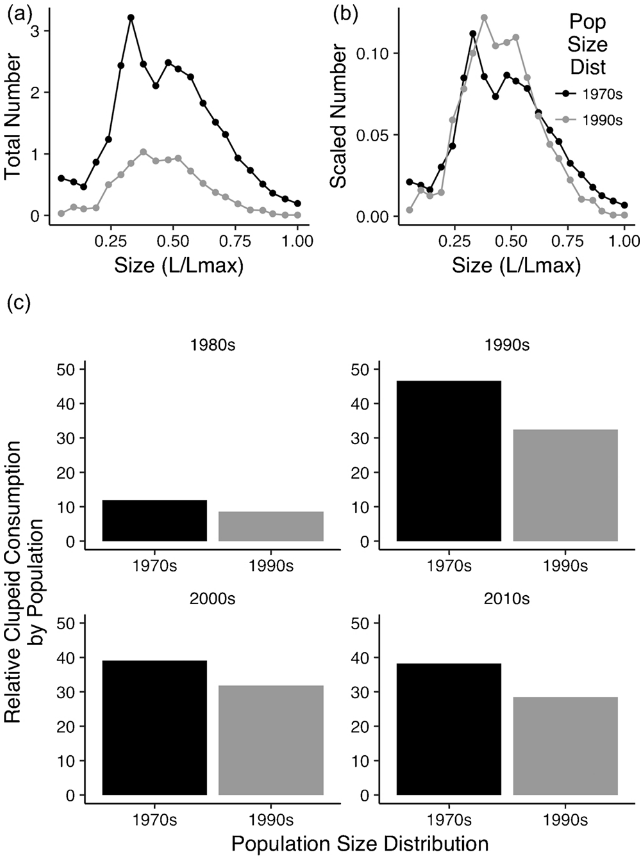

Fig. 7. Number in each predator size bin for the *Gadus morhua* population size structure in the 1970s (dark grey) and 1990s (light grey) (a). Scaled number in each size bin such that the populations had equal numbers of individuals (b). Relative clupeid consumption by the simulated population for each decadal diet pattern (c).

4. Discussion

While delaying harvest until L_{opt} had unequivocal benefits in terms of yield, the relative impacts on prey consumption depended on the timing of diet shifts for the focal prey relative to the fishery selectivity. For the early selectivity fishery, prey consumption was reduced more uniformly across ontogenetic shifts, because predator biomass was also reduced more uniformly. For the L_{opt} fishery that selectively targeted the largest predators, consumption was maintained at higher levels for early onset prey, and reduced to a greater extent for late onset prey. The form of fishery selectivity was less important than the degree of reduction in biomass within each predator size class relative to the timing of diet shifts. Both the early selectivity fishery with a low rate of fully selected fishing mortality and the L_{opt} selectivity fishery with a high rate of fully selected fishing mortality reduced the biomass of the largest predators to a small fraction of the unfished level. As such, consumption of focal prey eaten late in life history were reduced to a greater extent than early onset prey, though this reduction was more severe for the L_{opt} fishery which specifically targeted these large size classes.

For diet shifts where the mid-points of the diet occurred at 45% of the maximum size or larger, predation was reduced by a greater extent at maximum sustainable yield than overall predator biomass for both fishery selectivity patterns. More than half of the piscivores began consuming focal prey across three large marine ecosystems at these sizes. Since all but one of these late onset predators (arrowtooth flounder *Atheresthes stomias*) are currently targeted by fisheries, predator-prey interactions between these piscivores and these fish prey is likely weaker than would be expected from reductions in predator biomass alone.

The rate of reduction relative to the unfished population was unaffected by the maximum diet fraction. However, whether reductions in consumption due to fishing these predators affects prey population dynamics depends on the interaction of these diet fractions with the relative biomass of predators in each LME. Small maximum diet fractions for a particular taxa can still represent a large fraction of the predation mortality. In the more diverse NEUS, each fish taxa was consumed at lower overall percentages relative to the Alaskan ecosystems in which walleye pollock serves as the principal fish prey. For example, clupeids and scombrids represented 25% and 15% of the diet of spiny dogfish (Table C.1 in Supplementary materials), at maximum. However, the highly abundant spiny dogfish populations eat 54% of all herring consumed and 45% of all mackerel consumed annually, a rate exceeding overall fishery removals (Tyrrell et al., 2008).

Many predators exhibited strong variation in the relative composition of the fish consumed across decades. In particular, the increase in the relative importance of clupeids in the diet of piscivores in the Northeast US LME corresponded with an increase in herring abundance (Link and Garrison, 2002), suggesting prey switching may be common among these piscivores (Moustahfid et al., 2010). It is important to note that our model did not incorporate prey switching as a function of prey biomass changes. Prey switching to the most abundant prey may constrain the population release of prey due to fishing any single predator, if other predators remain in the ecosystem. However, it may be less important in dampening the effects of fishing where multiple predators are harvested simultaneously, as is the case in all three LMEs.

For many of the predators considered here, prey taxa consumed late in life history consisted of fish that could potentially be harvested by fishers. Where prey and predator are harvested, coupling knowledge of the timing of predator diet shifts with readily available information on stock size structure can provide more accurate estimates of predation mortality on commercially valuable prey. Doing so can maximize ecosystem yield by avoiding foregone catch that would result from assuming higher levels of predation losses (White et al., 2012). In the case of the Alaska LMEs, the principal prey consumed by large predators was walleye pollock (*Gadus chalcogrammus)*—the target of the second largest single species fishery in the world by volume (Mueter et al., 2011). Results from a recently developed multispecies catch at age model that incorporates size-specific predator-prey interactions between pollock and two of its major predators in the Eastern Bering Sea shows that harvest of pollock is indeed higher when considering simultaneous fisheries on both predator and prey (Holsman et al., 2016). Without constraints on species-specific abundance, even higher aggregate yields are possible with multispecies models, but are often achieved via strategic simplification of ecological networks (White et al., 2012).

Where managed prey populations are already depleted, knowledge of ontogenetic shifts in predator diets can provide more accurate estimates of the indirect effect of fishing predators on prey recovery. Pacific cod *(Gadus macrocephalus*) is a late specialist on walleye pollock (Table C.1 in Supplementary materials), but in the Gulf of Alaska it first feeds on shrimp and later on tanner crab before finally feeding on pollock (Urban, 2012). Increased predation by Pacific cod in conjunction with a climate regime shift was suggested as a potential cause of the collapse of fisheries for both pink shrimp and tanner crab (Albers and Anderson, 1985). The current fisheries for Pacific cod selectively target individuals at or above its diet shift toward pollock (Barbeaux et al., 2016), resulting in reductions in its consumption of pollock, but little impact on its consumption of early diet items such as shrimp and crab. Ignoring such changes in Pacific cod diet with size may lead to overly optimistic predictions about the trajectories of recovery of these crustacean fisheries.

In the Northeast US LME, piscivores displayed wide variation in the size at onset of piscivory, with goosefish (*Lophius americanus*) and sea raven *(Hemitripterus americanus*) consuming fish at the smallest sizes surveyed, with others shifting to fish quite late in life history. The diversity of piscivores in this ecosystem and the variation in their ontogenetic diet patterns likely buffers overall piscivory in the ecosystem against the potential effects of truncation in size structure. Despite this variation in the timing of overall piscivory, the mid-point of clupeids in the diet was greater than 45% of the maximum size for two-thirds of the piscivores in NEUS. The clear outliers were the two early fish specialists (*Hemtripterus americanus* and *Lophius americanus*). The consistently late timing of clupeid consumption among piscivores in NEUS may make this predator-prey interaction more vulnerable than would have been expected from the relative greater diversity of piscivores in this ecosystem. Given that many of these piscivores have been exploited heavily in this ecosystem, truncations in size structure that may have resulted would likely result in larger reductions in consumption of clupeids than would have been expected from changes in predator biomass. We show that observed truncations in size structure in cod were sufficient to drive a potential reduction in 20–30% of the clupeids consumed, even without changes in cod abundance. In reality, for many predators in this ecosystem, truncations in size structure have been accompanied by reductions in abundance, thus fishing is likely to have even greater impact on these predator-prey interactions.

Where single piscivores or the piscivore assemblage regulate prey populations, reduction in consumption due to fishing may release those prey populations. In some cases, the now abundant forage fish may limit subsequent recovery of the piscivore population through direct predation or competition with juvenile predators (Gårdmark et al., 2015) as has been suggested for Atlantic cod on both sides of the Atlantic (Scotian Shelf (Bundy and Fanning, 2005), Gulf of St. Lawrence (Swain and Sinclair, 2000), North Sea (Fauchald, 2010), and the Baltic Sea (Casini et al., 2009)). Harvest of herring and other clupeids may minimize the potential for adverse impacts from prey population expansion. However, exploitation of top predators followed by harvest of prey may still be associated with undesirable ecosystem outcomes. This was true in the Black Sea where exploitation of clupeids following the depletion of fish predators favored the rise of jellyfish populations that adversely impacted other fisheries (Daskalov, 2002). Where regime shifts have occurred, knowledge of ontogenetic shifts in diet can identify where it is necessary to recover predator size structure in addition to predator biomass to restore ecosystem function.

Though our results suggest that late ontogenetic shifts are common among piscivores, late ontogenetic shifts also occur among predators that specialize on large hard-bodied invertebrates, such as crabs (Wainwright, 1988) urchins (Ling et al., 2009; Selden et al., 2017), and lobsters (Wahle et al., 2013). In temperate ecosystems, loss of the largest urchin predators has been linked to loss of top-down regulation on urchin populations (Ling et al., 2009; Selden et al., 2017) and subsequent regime shifts. For predators that specialize as adults on herbivorous echinoderms, it may be particularly important to consider the effects of fishing on predator size structure to maintain the resilience of macroalgal ecosystems.

More generally, knowledge of the timing of ontogenetic shifts in diet may be a valuable tool to assess the conditions under which it is desirable to set a management target for the proportion of large fish in the population. A Large Fish Indicator (LFI) that monitors the proportion of fish above a length threshold is currently being used as an “Ecological Quality Objective” in the North Sea (Greenstreet et al., 2010). In the Celtic Sea, fishing of large demersal predators has coincided with an increase in small fish biomass and a reduction in the LFI (Shephard et al., 2011). Recent modelling work suggests that the Large Fish Indicator principally reflects the proportion of large species (e.g., those with a large maximum length) in the community (Shephard et al., 2012), allowing managers to prioritize these species for often costly diet sampling programs. Linking information about the ontogenetic diet patterns of these large fish species with their relative abundance may allow an index of predation pressure to be calculated directly, providing a more mechanistic link between the LFI and ecosystem-based management metrics.

5. Conclusions

The tradeoff between fisheries catch and predator function depends strongly on the interaction between the fishery selectivity pattern and the changes in predator diet with size. In many cases, where harvesting is occurring too early for single-species objectives, win-win outcomes for fisheries and ecosystem function can be achieved by increasing the selectivity toward larger sizes (e.g., by altering trawl mesh sizes; Sala and Lucchetti, 2011). Where predator diets change little with size, or predation on a focal prey item occurs early in ontogeny, predation is maintained at the highest levels by delaying harvest until large sizes. However, where diet shifts toward a focal prey at large sizes, selectively harvesting the largest predators will lead to greater losses in predator function than would have been predicted from reductions in predator biomass. If this focal prey is also targeted by fisheries, total yield from both predator and prey fisheries will be maximized by fishing at L_{opt}. If this focal prey is a pest, in which prey release represents an undesirable outcome, alternative harvest strategies may be needed in order to maintain large predator size classes and the strength of predator-prey interactions.

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Appendix A. A.1 Population dynamics model

(A.1) A.1 Population dynamics model

The model was run with an age interval of 0.25 year for greater resolution of lengths. The stable age structure for this model with constant recruitment and no cannibalism is given by:

$$N_A = \begin{cases} R_F & A = 0 \\ N_{A-1}\exp(-(M + FS_{A-1})\gamma) & 0 < A < \omega \\ N_{A-1}\exp(-(M + FS_{A-1})\gamma)/[1 - \exp(-(M + FS_A)\gamma)] & A = \omega, \end{cases} \tag{A.1}$$

where N_A is the number of animals of age A, M is the age independent instantaneous rate of natural mortality (yr^{-1}), F is the instantaneous rate of fishing mortality (yr^{-1}) when selectivity is equal to 1, S_A is the selectivity of animals of age A in the fishery, γ is the age interval of 0.25 years, ω is the maximum longevity representing a “plus group” in which all fish that would have survived to another year are accumulated in this group, and R_F is the number of recruits based on a re-parameterized Beverton-Holt stock-recruit relationship (Cope and Punt, 2009) when fishing mortality equals F:

$$R_F = \frac{R_{F=0}[4h\widetilde{S_F} - \widetilde{S_{F=0}}(1-h)]}{\widetilde{S_F}(5h-1)}, \tag{A.2}$$

where $R_{F=0}$ is recruitment in the absence of fishing, h is the steepness of the stock-recruitment relationship (the fraction of $R_{F=0}$ when spawning biomass is reduced to 20% of the unfished spawning biomass), $\widetilde{S_F}$ is the spawning biomass-per-recruit when fully-selected fishing mortality equals F, and $\widetilde{S_{F=0}}$ is the spawning biomass per recruit in the absence of fishing.

$$\widetilde{S_F} = \sum\nolimits_{A=1}^{\omega} N_A^F W_A \delta_A, \tag{A.3}$$

where N_A^F is the number of individuals at age-per-recruit, δ_A is the fraction of animals of age A that are mature, W_A is the weight of an animal of age A based on the allometric growth model ($W = aL^b$) where length-at-age is assumed to follow the von Bertalanffy growth function (VBGF):

$$L_A = L_\infty 1 - exp(-k(A - A_0)), \tag{A.4}$$

where L_∞ is the asymptotic maximum length, k is the growth coefficient, and A_0 is the theoretical age at which fish length would be zero. L_{opt} is defined by the ratio of the natural mortality rate (M; yr^{-1}), the von Bertalanffy growth coefficient (k), and the length-weight scaling exponent (b) (Hordyk et al., 2015):

$$L_{opt} = L_\infty \frac{b}{\frac{M}{k} + b}. \tag{A.5}$$

The maturity function is defined as:

$$\delta_A = \{1 + \exp[-\log(19)(A - A_{mat})/\beta]\}^{-1}, \tag{A.6}$$

where A_{mat} is the age at 50% maturity and β is the difference between A_{mat} and the age at 95% maturity (Cope and Punt, 2009). β was set to $A_{mat}/4$ as per Cope and Punt (2009).

Yield was calculated using the Baranov catch equation:

$$Y = \sum\nolimits_{a=1}^{\omega} N_a W_a (1 - \exp{-(M + FS_A)\gamma}) \frac{FS_A}{M + FS_A} \tag{A.7}$$

Relative catch was defined as the yield relative to the maximum possible with the L_{opt} strategy.

(A.8) A.2 Age- and size-specific prey consumption

We used the resulting numbers at age N_A for the predator population simulated by the population dynamics model to estimate annual prey consumption by the predator population. Annual food consumption per unit biomass (C_A) was defined from weight at age W_A, and parameters from the von Bertalanffy growth curve (Essington et al., 2001):

$$C_A = (H/E){W_A}^{d-1}, \tag{A.8}$$

where d is the allometric slope of consumption (assumed to be 2/3 with von Bertalanffy growth), E is assimilation efficiency, assumed to be 0.65 (Holsman and Aydin, 2015), and $H = 3kW_\infty{}^{1-d}$, represents the assimilation constant, with W_∞ is the weight at the maximum length. As a result of this formulation, small predators consume more per unit biomass than large predators.

A.3 Life history parameters

The base choices for the parameters represent a generic predator in the cod and haddock family (Gadidae). The asymptotic size, L_∞, was set to a value of 100 cm, a common size for several species in the Gadidae family. The von Bertalanffy growth coefficient k was set to 0.16, the mean value for an $L_\infty = 100$ cm from a log–log regression of L_∞ on k for gadids on FishBase (Froese and Pauly, 2014). Natural mortality was assumed to follow the Beverton-Holt life history invariant where $M/k = 1.5$, yielding an $M = 0.24$ yr^{-1}. Based on these values, a length-weight scaling exponent equal to 3, and Eq. (A.5), $L_{opt} = 0.67\, L_\infty$. While the results were developed for a predator with a maximum size of 100 cm, the baseline results will apply to any fish with an $M/k = 1.5$, because this ratio, and not their absolute values, determines the distribution of biomass across sizes as a function of length relative to the maximum length in the unfished population (Hordyk et al., 2015). The steepness of the stock-recruitment relationship was set equal to 0.8, the median value for Gadidae in Myers et al. (1999), and the size at maturity was based on the median value for L_{mat}/L_{opt} in Prince et al. (2015).

The meta-analysis of Prince et al. (2015) showed that the ratio of the natural mortality rate (M) to the von Bertalanffy growth coefficient (k) can differ considerably from the Beverton-Holt life history “invariant” of $M/k = 1.5$. We explored the effects of different selectivity patterns on single species and ecosystem metrics for predators with $M/k = 1$ and $M/k = 3$, where $L_{opt} = 0.75L_\infty$ and $0.5\, L_\infty$, respectively. We also explored the effect of various assumptions about the steepness of the stock-recruitment relationship ($h = 0.65$, the 20th percentile for Gadidae in Myers et al. (1999)), and earlier maturity ($L_{mat}/L_{opt} = 0.65$, the 10th percentile in Prince et al. (2015) and 25th percentile for U.S. west coast groundfish in Cope and Punt (2009)).

Increasing the rate of natural mortality relative to maturity exacerbated the loss in prey consumption of the predator population fished at MSY relative to unfished (P*) for late ontogenetic shifts when delaying harvest to *Lopt* (Fig. B.3 in Supplementary materials). In contrast, earlier maturity and lower steepness had minimal impact on the relationship between the size at diet shift and the loss in predator function for this harvest strategy.

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.fishres.2018.03.021.

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