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

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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 (onset > 25% 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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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
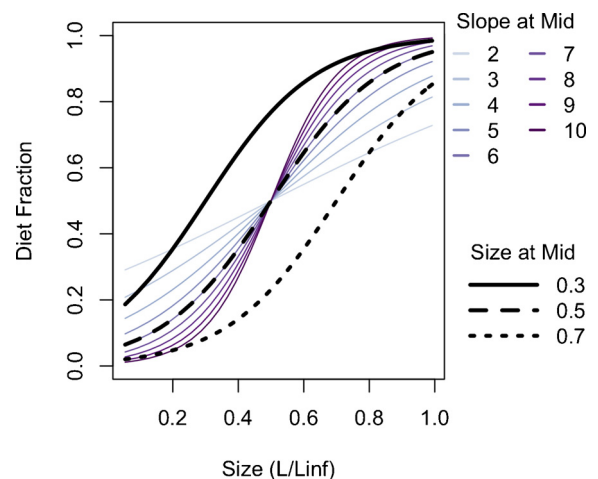

Fig. 1. Focal species diet proportion for a logistic diet pattern with size at the mid-point of the diet between 0 and 0.9 with a maximum diet fraction of 1 ($\phi = 1$). A subset of the logistic diets are depicted with the midpoint of the diet at 30% (solid), 50% (dashed), and 70% (dotted) of the maximum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