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The consequences of fishing-induced changes in predator body size for top-down control of prey populations

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Summary

The cascading consequences of overharvesting top marine predators are becoming increasingly clear. While most of the ecosystem effects of fishing have been attributed to a decline in predator abundance, a largely unexplored mechanism for explaining these trophic cascades is the reduction in predator body size due to fishing. Because body size often determines what and how much a predator eats, the loss of large individuals may eliminate the capacity for predators to regulate prey populations. We developed a size-structured predator-prey model to identify the life history characteristics of predators that make predator-prey interactions most vulnerable to disruption by fishing. When ontogenetic shifts in diet occurred, fishing caused the greatest reductions in prey consumption for prey eaten late in the life history. We applied this model to California kelp forest ecosystems where predation by sheephead, *Semicossyphus pulcher*, on sea urchins, *Strongylocentrotus* spp., begins at adulthood. In field populations where large sheephead are absent, urchin mortality rates are lower, particularly for the largest urchins. Reductions in body size due to fishing sheephead may lead to a reduction in the ability of these predators to control urchin densities, increasing the likelihood of kelp forests being converted to urchin barrens.

Introduction

While most of the cascading effects of fishing on ecosystems have been attributed to a reduction in predator abundance, a largely unexplored mechanism is the reduction in predator body size due to fishing. Exploitation results in the disproportionate reduction of the largest individuals in a population, and recent evidence from the north Atlantic suggests these reductions in predator body size may reduce the capacity of the predator population to limit prey populations. Though aggregate predator biomass remained constant during this time frame, a 60% decline in predator body mass on the Scotian Shelf from 1970-2000 was associated with a 300% increase in prey biomass (Shackell et al. 2010). A reduction in predator body size may result in releases in prey populations in two ways: (1) larger predators consume more prey biomass per capita than small predators, so removing the largest individuals would result in lower prey consumption; and (2) most aquatic organisms undergo ontogenetic niche shifts in prey size or species, so removing the largest individuals may remove all predation by that predator on particular prey species or size classes. Traditional food web models developed to investigate the ecosystem effects of fishing, such as Ecopath, often neglect these ontogenetic niche shifts by aggregating diet information to the species level. We examined the extent to which ontogenetic changes in diet alter our predictions about the effects of fishing on predator-prey interactions in a simulation model, and tested the model empirically in California kelp forests in which predation by sheephead on sea urchins depends on size.

Materials and Methods

Fishing was simulated on a theoretical predator population with life history parameters similar to that for Pacific cod, *Gadus macrocephalus*. The predator population entered the fishery at its optimal length, based on its natural mortality, von Bertalanffy growth coefficient, and length-weight relationship (Hordyk et al. 2014), and fished at a level which reduced the spawning stock biomass to 40% of the unfished level, which is defined as fishing at maximum sustainable yield (MSY). We examined the effects of fishing on prey consumption based on four hypothetical scenarios of predator diet shifts with body size: (1) no change in diet, (2) ontogenetic shift in prey size, (3) ontogenetic shift in prey species, and (4) ontogenetic shifts in both prey size and species. For all scenarios, total prey consumption increased with predator body mass, and the prey size classes consumed were normally distributed around the mean prey size for each predator size class. Prey consumption was calculated from the biomass in each predator size class and a size-specific daily ration estimated for Pacific cod. This prey consumption was distributed over the prey size classes consumed by each predator assuming either no change or an increase in mean prey size with predator body size. The prey consumption was also assigned to one of three prey species assuming a generalist predator that consumed each prey throughout life history, or a sequential specialist on each of the three species. The reduction in prey consumption due to fishing was compared for each predator diet scenario.

The predictions of the model were tested empirically in California kelp forests. Sheephead exhibit ontogenetic niche shifts in both prey species and size, shifting from bivalves to urchins and consuming larger urchins as they grow. Predation rates on tethered urchins were compared at two sites in the Channel Islands where sheephead densities were similar but size structure varied.

Results and Discussion

Fishing a generalist predator that consumed the same prey sizes and species throughout its life history resulted in a reduction in consumption to 56% of the unfished level. For predators that increase prey size as they grow, predation on the largest prey size classes was disproportionately reduced relative to small prey. For predators that undergo shifts in the prey species consumed, prey eaten early in the life history were largely unaffected by fishing, and the magnitude was over-estimated by assuming a generalist predator that consumed each prey throughout its life history. In contrast, predation on prey eaten late in the life history was reduced by a much greater extent to 31% of the unfished level, and this was under-estimated by assuming a generalist predator. When the predator changed both prey size and species, the largest of prey eaten late in life history was affected most strongly. The results of this model suggest that specifying ontogenetic niche shifts is critical for accurately predicting the effects of fishing using food web models.

Based on the results of the general model, we predicted that populations in which large sheephead were absent would result in lower mortality rates for urchins and reductions in mortality should be greatest for largest urchins. These predictions were upheld in the field with lower urchin mortality at the site without large sheephead. Predation was approximately 50% lower on the smallest urchins and 66% lower on the largest urchins. Fishing-induced changes in size may limit the capacity for sheephead populations to control urchin outbreaks. Because the conversion of kelp forests to urchin barrens results in losses of ecosystem services, it will be important to incorporate sheephead size structure into metrics of kelp forest resilience.

Quantifying the degree of difference in diet between juvenile and adult populations could be used to flag potential predator-prey interactions that will be most disrupted by fishing. If ontogenetic changes in diet occur, changes in predator size structure associated with fishing, even at levels deemed sustainable from a single-species perspective, can still result in almost complete removal of the capacity for predator populations to regulate prey eaten late in their life history. As a result, for these types of predators, it will be important to include predator size structure when evaluating ecosystem health as managers move towards more ecosystem-based approaches to management.

References

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