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When does fishing forage species affect their predators?

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ABSTRACT

This paper explores the impact of fishing low trophic level "forage" species on higher trophic level marine predators including other fish, birds and marine mammals. We show that existing analyses using trophic models have generally ignored a number of important factors including (1) the high level of natural variability of forage fish, (2) the weak relationship between forage fish spawning stock size and recruitment and the role of environmental productivity regimes, (3) the size distribution of forage fish, their predators and subsequent size selective predation (4) the changes in spatial distribution of the forage fish as it influences the reproductive success of predators. We show that taking account of these factors generally tends to make the impact of fishing forage fish on their predators less than estimated from trophic models. We also explore the empirical relationship between forage fish abundance and predator abundance for a range of U.S. fisheries and show that there is little evidence for a strong connection between forage fish abundance and the rate of change in the abundance of their predators. We suggest that any evaluation of harvest policies for forage fish needs to include these issues, and that models tailored for individual species and ecosystems are needed to guide fisheries management policy.

1. Introduction

There has been considerable interest in recent years on the impact of fishing low trophic level fishes, commonly called "forage fish", on the higher trophic level fishes, marine birds and marine mammals (Cury et al., 2011; Pikitch et al., 2012; Smith et al., 2011). For our purposes we consider forage fish to be the major small pelagic fishes and squid, but the juveniles of many species are also an important part of the diet of many predators. There is good evidence and theory to suggest that (1) fishing reduces the abundance of targeted fish stocks, and (2) reproductive success of predators is affected by the local density of their prey. The logic seems clear, lower fishing pressure results in more forage fish in the ocean, and thus better reproductive success and higher abundance of the higher trophic level predators. Pikitch et al. and Smith et al. used ecosystem models to quantitatively evaluate the impact of fishing forage fish on their predators, and both papers suggested that forage fish should be harvested at rates lower than would provide long term maximum yield of the forage fish.

Although it would therefore seem obvious that fishing forage fish would have a negative effect on the abundance of their predators, the empirical relationships between forage fish abundance and predator abundance, or population rates of change, have not been examined in a systematic way. There is evidence in the literature (Cury et al., 2011) showing changes in reproductive success in relation to local food abundance, but the assumed link between the changes in total population size of predators and the total forage fish abundance has not been evaluated against historical trends in abundance. Another way to explore the impact of fishing forage fish is to examine the population trends in a dependent predator. Given that most forage fish in the U.S. have been harvested more heavily in the past than they are at present, if predator populations increased under past fishing pressure on forage species, then fishing at those levels did not preclude the ability of the predators to increase. For many reasons, the predators of most concern should be those others that have been decreasing in abundance over recent decades.

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Most forage fish are well documented to undergo substantial fluctuations in abundance unrelated to fishing (Schwartzlose et al., 1999), a feature that is ignored in the ecosystem models used to evaluate ecological impacts of fishing which were mentioned above. This was recognized as a deficiency by the authors of the Pikitch et al. paper. "Major fluctuations in forage fish abundance have been observed and recorded for centuries. Forage fish can respond dramatically to shifts in oceanic conditions and may exhibit strong decadal-scale variability. Forage fish may be capable of responding quickly to favorable environmental conditions, but their populations cannot be expected to maintain a steady state and can plummet when conditions become unfavorable" (Pikitch et al., 2012, page 84).

Such fluctuations can range over three orders of magnitude. Vert-pre et al. (2013) showed that for about 50% of fish stocks, there were major changes in the productivity of the stocks unrelated to fish stock size. Given great natural variability in abundance of forage fish, a key question is how much does fishing impact abundance relative to the natural fluctuations?

The commonly accepted assumption that higher spawning stock sizes lead (in expectation) to higher recruitment (Myers and Barrowman, 1996; Myers et al., 1994) is implicit in EwE models that do not break taxonomic groups into size or age groups, and explicit in ATLANTIS models and EwE models that do break a group into stages. The assumption that increasing spawning stock size will lead to higher recruitment has been challenged first by Gilbert (1997) then by Szuwalski et al. (2014) who showed that most stocks do not exhibit a stock recruit relationship and of those that do, a large fraction of them have shifts in average recruitment over time. Myers et al. (1999) estimated that forage fish show clear relationships between spawning stock abundance and recruitment, but low spawning stock and low recruitment can be explained equally well by low recruitment generating low spawning stock (Szuwalski et al., 2014). If abundance of forage fish and their recruitment are primarily environmentally driven, then the impact of fishing on the food supply of higher trophic level predators is mainly through depletion of prey cohorts by fishing, not by reduced recruitment.

In addition to the assumption of a direct link between spawning stock and recruitment, the EwE models used to evaluate the impacts of fishing forage fish have a direct link between forage fish abundance, predator consumption and predator abundance implicit in the dynamics. However, few of these models have considered the life histories of the forage fish and their predators in enough detail to capture several key issues in the interaction between fishing on forage fish and impacts on dependent predators. None of the 11 EwE models used by Pikitch et al. considered the size or age structure of the forage fish (Essington and Plaganyi, 2013) and in five cases the modeling was not conducted at the species level, but instead grouped up to eight forage species, amongst which many may exhibit negative covariation in abundance. Indeed, two of the authors of the Pikitch et al. study subsequently questioned the use of "recycled" ecosystem models (i.e., those developed for other purposes) to understand the impacts of forage fish abundance on their predators; "We find that the depth and breadth with which predator species are represented are commonly insufficient for evaluating sensitivities of predator populations to forage fish depletion" (Essington and Plaganyi, 2013). All of the models used by Pikitch et al. were such recycled models.

A key factor determining reproductive success of many birds and marine mammals is the local density of prey within their foraging range of the breeding sites (Thaxter et al., 2012). So in addition to the variability induced by natural fluctuations in total abundance of the forage fish, the spatial availability can also vary, and two breeding colonies feeding on the same stock may see strikingly different food availability. Local density can either amplify natural variability in food supply, or the predators may be able to concentrate on high density locations even at low prey abundance, thus buffering them from the fluctuations in total abundance. Despite the importance of local forage abundance for central place foragers, there is little evidence relating abundance of forage species to the abundance of mobile predators. Jensen et al. (2012) cited several of the studies showing the importance of local abundance to central place foragers but also reviewed the empirical literature relating marine predatory fish abundance to abundance of their prey and found few clear links apart from a decline in cod productivity following the collapse of both herring and capelin in the Barents Sea (Hamre, 1994; Hjermann et al., 2004).

This brings us to another important factor in the life history of forage fish and their predators that is neglected in almost all of the EwE models. Some marine predators consume forage fish at sizes and ages before the fishery harvests them. This is most true for predatory fish and marine birds, where mouth gape sizes limit the maximum size of prey that can be eaten, and probably least true for marine mammals. As an example, Nelson et al. (2006) showed that the mean size of Atlantic menhaden (*Brevoortia tyrannus*) eaten by striped bass (*Morone saxatilis*) in Massachusetts was 8.4 cm but the mean size taken by the fishery was 28 cm. In the extreme, if the recruitment of forage fish is not affected by fishing, and the predators consume sizes smaller than taken by the fishery, then the fishery would have no impact on the food available to the predator. In other words, the fishery harvests only those individuals that have survived and grown large enough to escape most of their predators.

To summarize, the impact of fishing forage fish on dependent predators will depend on (1) the alternative prey available to the predators, (2) the impact of fishing on the recruitment of the forage fish, (3) natural variability in recruitment, (4) the relationship between abundance of the forage fish and what is actually available to the predators, (5) the overlap between sizes/ages eaten by the predators and those taken by the fishery, and (6) other factors that may limit the predator population abundance.

In this paper we explore these issues for a range of U.S. forage fish and their predators. First, we examine the relationship between forage fish abundance and predator population growth rates, then we evaluate the recruitment pattern for each forage species and evaluate the evidence regarding the relative importance of fishing and environmental influences on the recruitment. Thirdly, we compare the size/ages taken by predators to those taken by the fishery. We then model the changes in forage fish abundance as a function of different assumptions regarding the dependence of recruitment on fish stock size and environmental variability to generate scenarios of forage fish abundance as a function of fishing pressure. Finally we examine how much the abundance of forage fish in the target size range is affected by fishing.

2. Materials and methods

Eleven species of forage fish in the U.S. were selected for analysis, and for each of these species we conducted a literature review to identify: (1) what predators eat those species, (2) the importance of the forage fish species in the diet of the predator, and (3) the size range of each forage species found in the diet of the predator. The selected forage species were the Pacific sardine (*Sardinops sagax)*, Northern anchovy (*Engraulis mordax*), Market squid (*Doryteuthis opalescens*), Pacific hake (*Merluccius productus*), Pacific chub mackerel (*Scomber japonicus*), Atlantic herring (*Clupea harengus*), Atlantic menhaden, Atlantic mackerel (*Scomber scombrus*), Shortfin squid (*Illex illecebrosus*), Longfin inshore squid (*Doryteuthis pealeii*) and Gulf menhaden (*Brevoortia patronus*).