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The strong connection between forage fish and their predators: A response to Hilborn et al. (2017)

We are pleased to see that in the years since the publication of our report, *Little Fish, Big Impact: A Report from the Lenfest Forage Fish Task Force* (Pikitch et al., 2012), researchers continue to study forage fish and to reach conclusions similar to ours. Hilborn et al. (2017) recommended, as we did, that forage fish management be tailored to individual species and ecosystems where possible. Hilborn et al. (2017), however, mischaracterized our work in several respects, presented selective analyses that are not widely representative of forage fish, and made claims not fully supported by their results.

In the interests of furthering science and the management of forage fish, we first briefly address the mischaracterizations, then discuss the selective analysis and unsupported conclusions that reduce the usefulness of the Hilborn et al. paper. We close by suggesting a path forward for forage fish management in light of the current state of the science.

1. Mischaracterizations of the Lenfest forage fish task force's work

The most important mischaracterization of our report by Hilborn et al. (2017) is their oversimplification of our approach and recommendations. Hilborn et al. often conflate our report with a single modeling approach, Ecopath with Ecosim (EwE), and present our recommendations as one-size-fits-all. For example, Hilborn et al. (2017) state “Pikitch et al. (2012) argued forcefully that their analysis provided general conclusions that should be broadly applied. However, relevant factors are missing from the analysis contained in their work...” This is simply not the case. Our recommendations are tailored to the level of uncertainty and data availability of each system, not broadly and uniformly applied. Furthermore, the statement above, and the subsequent focus on the shortcomings of EwE, ignores the multiple, independent lines of evidence we used in formulating our recommendations. In addition to modeling results, we relied upon evidence obtained during site visits, detailed case studies, analysis of the impacts of different harvest strategies in specific systems, and a comprehensive review of the literature. Our thorough and comprehensive approach considered all the relevant factors that Hilborn et al. (2017) claim we ignored.

Another mischaracterization by Hilborn et al. (2017) is that “None of the 11 EwE models used by Pikitch et al. considered the size or age structure of the forage fish (Essington and Plagányi, 2013) and in five cases the modeling was not conducted at the species level...” This is incorrect. Five of the 10 (not 11) EwE models we used in simulations considered age structure. These models received the highest score for “forage detail” in the separate study that Hilborn et al. (2017) cite in putative support of their statement, which was authored by two of us (Essington and Plagányi, 2013). Furthermore, all of our models included species-level forage fish groups. Some models aggregated a subset of the forage species, but this in no way supports the assertion that “modeling was not conducted at the species level.” Hilborn et al. (2017) also incorrectly presented the findings of Essington and Plagányi (2013) as a blanket rejection of the practice of model “recycling” (i.e., applying existing models to new questions or policy concerns). In fact, it is a guide on how to recycle models thoughtfully, which the Task Force did – for example by considering possible distorting effects of aggregating species groups.

2. Selective analyses and unsupported claims

In addition to mischaracterizing our report, Hilborn et al. based their general statements about forage fish on a small group of species that are not representative of forage fish as defined by Pikitch et al. (2012). They examined 11 prey species in their paper, and some analyses considered as few as 6 of these species. They focused only on U.S. species, excluding many of the world's largest and best-studied forage fish fisheries. The majority of forage fish species they selected (Pacific hake, chub mackerel, Atlantic mackerel, and three squids) do not meet the Pikitch et al. (2012) definition of “forage fish.” Given this difference, the results of the two studies are not comparable.

Hilborn et al. also ignored a large body of literature that contradicts their conclusions about predator dependencies on prey. For example, many empirical studies have demonstrated a strong connection between forage fish and the abundance of predators in southern Africa, Norway, Peru, and Antarctica (Roux et al., 2013; Erikstad et al., 2013; Crawford et al., 2011; Crawford and Jahncke, 1999). Others trace the link between forage abundance and breeding success, both through field data (e.g. Boersma and Rebstock, 2009) and global analysis of existing data (Cury et al., 2011; Hilborn et al. cite but dismiss this study). Cury et al. (2011) provide a comprehensive analysis, which demonstrates that marine birds require the long-term mean forage fish abundance, an evolutionary stable strategy. Hilborn et al. provide an incomplete and therefore potentially biased picture of predator-prey dependencies by emphasizing fishes in their selection of predator species.

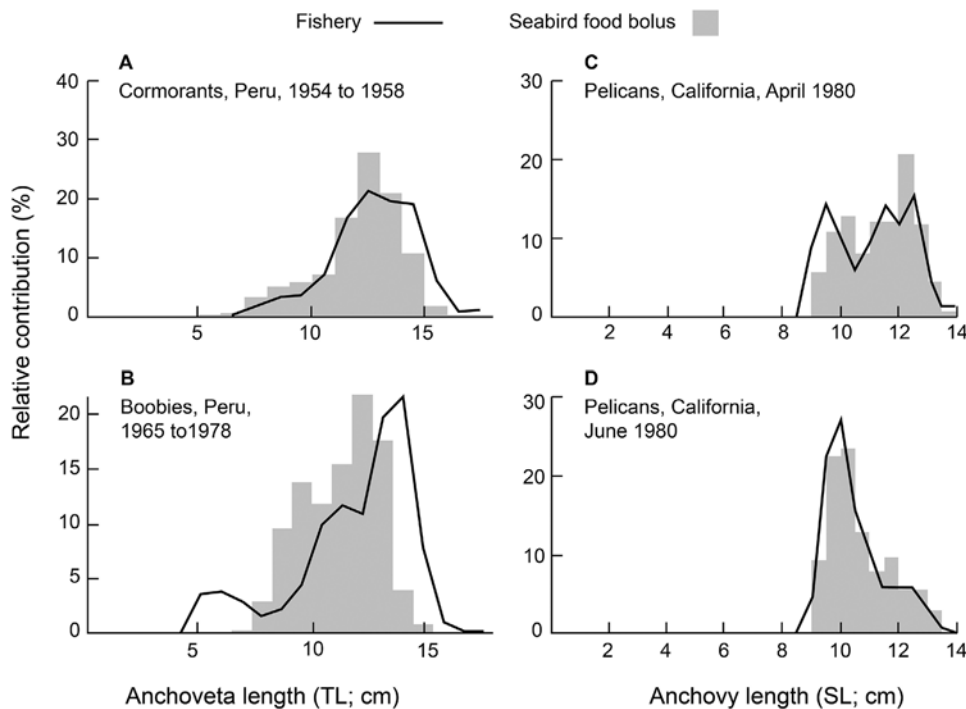


Fig. 1. Examples of the commonly observed overlap between the size of forage fish consumed by seabirds and the sizes caught by commercial fisheries (redrawn from Fig. 1–3 in Muck and Pauly, 1987). A: Overlap between the size of anchoveta (*Engraulis ringens*) ingested by Peruvian cormorants (*Phalacrocorax bougainvilli*) and the size of anchoveta caught in the Peruvian reduction fishery (based on Jordan, 1959); B: the same, for boobies (*Sula variegata*) (based H. Tovar, IMARPE, unpublished data and Fuentes, 1984); C and D: the same for Northern anchovy (*Engraulis mordax*), pelicans (*Pelecanus occidentalis californicus*) and a reduction fishery in California, in two different months. (based on data in Sunada et al., 1981)

In addition, Hilborn et al. (2017) made several methodological choices that reduced their ability to detect an impact on predators. One line of analysis looked at relationships between time series of predators and prey. Yet this work did not look at the broader food web context to investigate whether a strong relationship should be expected. For instance, Hilborn et al. (2017) included predator-prey combinations where the prey species made up as little as 20 percent of the predator’s diet. And they used estimated population levels generated by stock assessment models to identify correlations between predators and prey. The “data” from these models are not empirical measurements, but synthetic estimates predicated on model assumptions. These assumptions include holding constant the values of key demographic rates of predators that are likely to be sensitive to prey abundance.

3. Insufficient evidence to support the claims

We now address areas where Hilborn et al. (2017) provide insufficient evidence to support their broad generalizations. Hilborn et al. (2017) compare selectivity by the fishery with the actual sizes of prey eaten by predators to support their claim that “predators often take small forage fish that are unaffected by fishing.” However, a more appropriate evaluation would be to use the sizes of prey actually caught by the fishery, as selectivity is a measure of preference, not catch. Examination of their Fig. 3 suggests that predators target a wide range of prey sizes, and that one or more predators eat almost every size of prey. Furthermore, their Fig. 3 shows many instances where the preferred sizes in the fishery are quite similar to the average size in predator diets, and, for apex and many meso-predators, fishery selectivity and average size of prey eaten are very similar (e.g., Atlantic Bluefin tuna feeding on Atlantic menhaden; blacktooth and finetooth sharks feeding on Gulf menhaden; and harbor porpoise, Atlantic Bluefin tuna, harbor seal, spiny dogfish, and Atlantic cod feeding on Atlantic herring). Thus, Hilborn et al. (2017) do not provide sufficient evidence to support their assertion. Counter to their claim, and looking outside the limited sample they examined, one finds many examples where there is strong overlap between the sizes eaten by predators and the sizes taken by the fishery. Fig. 1 here (redrawn from Muck and Pauly, 1987) illustrates this point for species in the Peruvian and California Current ecosystems.

Hilborn et al. (2017) show (their Fig. 2) that the sensitivity of forage fish to fishing, particularly for the smallest size classes of forage fish, depends critically on whether spawning biomass affects average recruitment. Yet, for many of the populations Hilborn et al. (2017) analyzed, there is weak or inconclusive evidence for the hypothesis that spawning stock does not affect recruitment. For the 7 species examined (their Fig. 4), two indicate recruitment is best explained by a B-H stock-recruitment or hockey stick model (i.e. stock size more important), 3 species show regime shift as the most likely hypothesis, and for 2 species (Pacific hake and Gulf menhaden) the AIC scores are essentially identical across hypotheses (Hilborn et al. Table 2). Three of the species show a breakpoint for which recruitment is reduced below a given stock size, lending further evidence for the importance of stock size on recruitment.

The claim that “spatial distribution of forage species may be more important than their abundance” is not supported by any spatial analysis. Hilborn et al. consider spatial distribution “only qualitatively” and provide no citations or analysis to support the contention that it is more important than abundance. They highlight only the possibility that spatial distribution may trump abundance and not the equally plausible hypothesis that abundance may be more important than spatial distribution.

It should also be noted that a high level of environmentally driven fluctuation in forage fishes does not mean that fishing is unimportant (Shelton and Mangel, 2011). Essington et al. (2015) detected the fingerprint of fishing (in the troughs of population cycles) despite large fluctuations in recruitment and showed that fishing amplifies population collapses. This is particularly relevant for predators that are most sensitive to changes in prey availability. Pikitch (2015) discussed how the Essington et al. (2015) finding strengthens the case for minimum biomass thresholds for forage fish fisheries.

4. A path forward

We agree with Hilborn et al. that fisheries management should be tailored to individual species and ecosystems where possible. However, while Hilborn et al. advocate for a “case by case” analysis, they do not provide guidance for managers in the many circumstances where detailed information is lacking. In contrast, we (Pikitch et al., 2012) provide default recommendations for such situations based on a comprehensive account of forage fish and their ecosystems. Here, we reiterate our support for these recommendations and urge that they be used as an interim measure, in light of strong evidence that current management approaches are not designed to take into account the variability in forage fish stocks, their unusual life-history characteristics, and the role they play in the ecosystem.

In the five years since our report was released, research on forage fish and their role within ecosystems has grown. Recently, an integrated approach to assess the magnitude and consequences of fisheries-seabird resource competition has been proposed that will contribute to implementing best practices for moving towards ecosystem-based fisheries management (Sydeman et al., 2017). Given the importance of forage fish from ecological, economic, and social perspectives, we welcome further advances. We believe an approach that recognizes the strengths and weaknesses of various methods and seeks to use them in a complementary manner will be more effective than one that mischaracterizes and selectively interprets the work of others.

Declaration of interest

The authors declare that they have no competing interests.

Contributors

All authors have approved the final letter.

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