Changes in ranges of large ocean fish

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he report by Worm and Tittensor in PNAS (1) is a superb example of using a macroecological approach to address an important question that could not be answered in any other way. In the late 1980s, Brian Maurer and I wrote two papers that laid the foundations for what has become macroecology (2, 3). Nothing in science is ever really new, and our papers and subsequent books borrowed liberally from earlier studies. We applied a statistical mechanics approach to ecological systems, and coined the term macroecology to emphasize two senses of "macro." The first was an emphasis on large scales of space and time in which ecology intersects with biogeography and paleobiology. The second was an emphasis on compiling and analyzing large databases, and on drawing inferences from patterns in the statistical distributions of large numbers of equivalent "ecological particles" such as individuals within populations or species within communities. We saw macroecology not so much as an alternative to the mostly small-scale experimental ecology that was in vogue at the time, but as a complementary approach that could be used to address questions at scales at which manipulative experiments are not feasible. It was timely, and macroecology has since taken off (4-7), in large part because of its application to investigate trends, correlates, causes, and consequences of global environmental change.

The past few years have seen increasingly dire reports of overharvest of ocean fisheries and collapse of marine ecosystems (8-10). Much of the attention has been on benthic fish and coastal ecosystems, in which the changes have been well documented because these systems are relatively easy to study (11–14). Of increasing concern and some debate, however, is the status of the large pelagic predators: tunas, swordfish, marlins, and sharks (15-17). These magnificent fish are highly prized for the table and heavily fished. However, their very biology makes it difficult to quantify population trends and human impacts. They occur at low densities and range widely over great expanses of

open ocean (18). Data on abundance and distribution are difficult to obtain, and come largely from reported catches.

Enter Worm and Tittensor (1), who used the spotty catch data to quantify changes in the geographic ranges of 13 species of tunas and billfish from 1960 to 2000. The authors acknowledge the potential pitfalls of using heterogeneous data from catches, but they were able to take advantage of the statistical power of macroecology. They compiled data on presence or absence in geographic grid locations and plotted the results on global maps to document convincing patterns of change: significant range contractions in nine species, significant expansions in two others, and no detectable changes in two species.

From a basic science perspective, two aspects of the results are especially interesting. First, these highly mobile pelagic fish, which seem to have few "hard" range boundaries except for coastlines, have experienced substantial shifts in geographic ranges rather than just increasing or decreasing in abundance throughout their ranges. This highlights a very general relationship between abundance (i.e., average local population density) and geographic distribution (i.e., area of geographic range) among pelagic marine species that was previously documented in terrestrial and freshwater organisms (19, 20). Second, the two species that expanded their ranges are of relatively small body size. This repeats another pattern seen in terrestrial environmentstermed "mesopredator release"-whereby small to medium-sized mammalian carnivores, such as raccoons, skunks, foxes, and coyotes, have increased after humans drastically reduced populations of large predators, such as wolves and mountain lions (21, 22).

Of at least equal importance, however, are the implications of Worm and Tittensor's study (1) for marine conservation and fisheries management. The authors are commendably cautious in reporting their results and addressing their implications. The documented range contractions are certainly consistent with overharvesting. Billfish, tunas, and sharks should be especially vulnerable to overfishing. Because of their large body size, they are commercially valuable, have "slow" life histories, and require long times for depleted stocks to recover (23, 24). In addition to fishing pressure, however, it will be important to consider other possible causes for the range shifts, such as changes in ocean conditions (e.g., temperature, acidification) and species interactions (e.g., competition among predators, availability of prey). Regardless of the cause, the changes in geographic ranges have serious implications. Most of the contractions were around the edges of the historic distributions, suggesting that these areas are less suitable environments for the species. This, together with the fact that populations have been extirpated from substantial areas, means that even if sound management policies and catch regulations are implemented, recovery of stocks may take longer than if abundances had simply declined.

More generally, this study by Worm and Tittensor (1) provides yet another example of how humans are transforming the earth on a truly global scale. Regardless of whether the documented range shifts in tunas and billfish are caused by direct impacts of fishing or by more indirect abiotic and biotic factors, there can be little doubt that they are ultimately caused by humans. The oceans, with their vast expanse and immense volume, might naively be expected to be buffered from human impacts, but some of the largest and most serious environmental changes are occurring in the deep blue waters far from land (8, 9, 25, 26). The near-exponential increases in population and resource use of our own species are straining the finite ecological capacity of our planet.

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