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Commentary

Fishery selection across the millennia

Humans have been exploiting the Earth's resources for ages. Owing to tool limitations and risk of injury (including death), early human hunters targeted those individuals that were relatively easy to kill. On land, for instance, human hunters selectively targeted prey in poor condition, that is, the weak, sick, young and old. In the ocean, early humans selectively targeted accessible prey, that is, those found close to shore. Whether early fishing in the marine environment was also selective with regards to individual phenotypic traits (e.g. size) has been less clear, but new evidence suggests that it was.

This issue of *Proc. R. Soc. B* contains a paper comparing the characteristics of Baltic Sea cod harvested during the Neolithic period (4500 BP) to cod harvested in today's highly industrialized fishery (Limburg *et al.* 2008). This paper reports on the results of an interdisciplinary effort bringing together fisheries' scientists, ecologists and archaeologists to better understand the history of cod exploitation in the Baltic Sea. Such historical analyses are exceedingly rare but provide unique insights into the role of humans as agents of disturbance and selection, which would not be revealed from the analyses of modern data alone (e.g. Jackson *et al.* 2001).

Analysing otoliths (ear stones) and vertebrae collected from the historic and modern periods in the central Baltic Sea, Limburg *et al.* (2008) estimate both the age and size distribution of cod then and now. The historic otoliths were excavated from a single site (Ajvide) on the island of Gotland, Sweden; the modern otoliths were obtained from fishing areas near Gotland. Based on the archaeological findings of fish hooks and birch bark floats also recovered at the excavation sites, the Ajvide fishery consisted of a combination of hook-and-line (size-selective) and net fishing from shore (non-selective). By contrast, the modern fishery consists of gillnet and trawl fisheries, both of which are known to be highly size selective. Interestingly, only a narrow range of lengths were represented in the Neolithic samples relative to the modern samples (very small and very large cod were notably absent from their Neolithic samples; see also Olson *et al.* 2008), suggesting that the Neolithic cod fishery indeed was size biased.

Another difference between the two periods is the spatial location of fishing—the Neolithic fishery was confined to areas where the fish were accessible (nearshore environment), whereas the modern fishery occurs where harvestable biomass is the greatest (offshore environment). This difference is important because cod are known to move into deeper waters as they grow larger/older (Tomkiewicz *et al.* 1998). This implies that the Neolithic people at Ajvide did not have access to the largest cod, whereas the modern fishers do (figure 1). Despite this difference, cod caught at Ajvide in the Neolithic fishery were larger and older, on average, than the fish captured in the modern Baltic Sea cod fishery (Limburg *et al.* 2008). This suggests substantial changes in the size and age structure of Baltic Sea cod over this time period. The magnitude of the changes, however, does not appear to be as dramatic as reported for the Atlantic cod from the Gulf of Maine (Jackson *et al.* 2001).

Taken together, the results of Limburg *et al.* (2008) suggest differences between Neolithic and modern times in both the age/size structure of Baltic cod as well as the variation in the form of fishery selection (figure 1). What are the implications of a fishery that captured intermediate-sized fish during the Neolithic versus the one that captures the largest cod today? The Neolithic fishers were not removing the oldest and largest cod, whereas the modern fishers are. Body size is the main determinant of egg number in cod, such that females maturing at small sizes/young ages produce roughly 500 000 eggs, whereas females breeding at larger sizes/older ages produce several million eggs. Moreover, cod recruitment in the Baltic has been shown to be a function of better-quality eggs produced by old/large females (Vallin & Nissling 2000), suggesting that maintaining old/large females in the spawning stock is critically important for the sustainability of this stock. It is not surprising, therefore, that the rise of the industrialized and highly size-selective modern fishery in the Baltic triggered a rapid decline in numbers of Baltic cod, leading some to predict impending commercial extinction (Jonzén *et al.* 2001).

The importance of maintaining large and old cod in the spawning stock is not unique to the Baltic. For instance, in a recent essay, Law (2007) 'mounts a defence of [maintaining] large, old fish' in harvested populations. Providing support for Law's argument, recent work suggests that juvenescent (age-truncated) populations are susceptible to increased variability due to destabilized population dynamics (Anderson *et al.* 2008), an effect that might be irreversible if harvest-induced selection has occurred and genetic variation has been eroded (see Stenseth & Rouyer 2008). A precautionary management strategy designed to maintain the full range of phenotypic variations in the spawning stock—particularly the largest and oldest individuals—will minimize extensive fluctuations of harvested fish stocks and the potential for irreversible phenotypic changes, while maximizing long-term yield.

Limburg *et al.*'s (2008) analysis of changes to Baltic cod across the millennia provides historical knowledge of the Baltic Sea cod fishery, which should be considered by managers of this nearly extinct fishery as they work to restore this ecologically and economically valuable resource. While the study reported by Limburg *et al.* (2008) was confined to the Baltic, their results are presumably representative of other pre-industrialized coastal fisheries, that is, individuals in the nearshore

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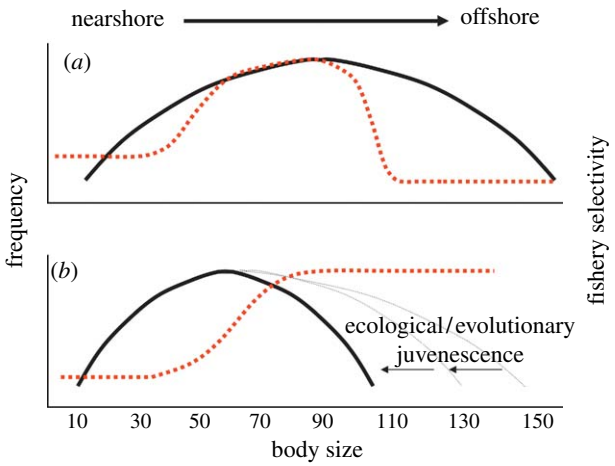

Figure 1. A conceptual plot illustrating the size distribution (black line, left *y*-axis) of Baltic Sea cod during (*a*) historic and (*b*) modern fisheries. Note that the range of sizes available for exploitation in the modern fishery is presumably narrower than in historic times due to age truncation ('juvenescence') of the stock from selective harvest. Such juvenescence is potentially irreversible if the changes in age/size structure reflect evolutionary effects. We have also plotted fishery selectivity as a function of body size (red line, right *y*-axis) during the two time periods. Note that the historic fishery targeted the relatively large individuals residing in the nearshore environment, but that individuals in the offshore environment were not vulnerable. By contrast, the modern fishery targets individuals in the offshore environment and so individuals in the nearshore environment are not exploited.

environment were likely more vulnerable to be captured than those found further offshore. An obvious extension is that species differed in their vulnerability to capture based on a nearshore to offshore gradient. Moreover, in spatially structured populations in which some component of the population used the nearshore environment relatively more than other components (e.g. juveniles, breeders), individuals would have differed in their vulnerability to be captured based on their phenotype. It seems that the depletion of fished species and fisheries-induced selection may both be as old as the practice of fishing itself.

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