benefit the discipline of history, which is often hindered by the lack of public awareness of the historical past.

There is considerable merit in adding historical perspectives to current environmental debates by drawing upon the centuries of accumulated historical and scientific knowledge to: (i) highlight historical precedents that demonstrate that acceptance of change by some in the community is slow; (ii) illustrate the intrinsic difficulties with the constant use of negative examples and 'doomsday' prophecies, which can undermine public support for environmental change; (iii) use historical precedents as a way of explaining similarities and differences with the current environmental debate to counteract unclear attitudes towards current problems; and (iv) encourage more and better critical thinking by scientists about societal response to environmental change, as well as bring in other thinking from outside scientific disciplines, to increase understanding by the public about scientific methods and findings.

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Letters

The overfishing debate: an eco-evolutionary perspective

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Are the oceans and freshwaters of the world being overfished? It seems a simple question and one which modern fisheries research should be poised to answer. However, an ongoing debate among fisheries biologists has largely ignored what is arguably one of the most important factors impacting the sustainability of fisheries and the health of freshwater and marine ecosystems: evolution.

Recently, the US National Oceanic and Atmospheric Administration has pointed to evidence that the USA is emerging from decades of overfishing onto a track of sustainability (http://www.legislative.noaa.gov/Testimony/Schwaab030811.pdf). Others have asserted that overfishing remains a serious problem in the USA and elsewhere around the world [1]. The debate about overfishing has surrounded a variety of social and ecological factors, including different definitions of overfishing (http://theseamonster.net/2011/05/forum-on-fish-food-and-people/). Largely missing from this debate is the recent observation that fisheries harvest is causing rapid evolutionary changes in harvested populations. The nascent field of eco-evolutionary dynamics focuses on understanding interactions between ecological and evolutionary processes occurring in contemporary time [2]. An eco-evolutionary perspective on overfishing is broadly informative because it explicitly recognizes that contemporary evolution is intertwined with population, community and ecosystem processes [3]; these are the same ecological processes that underlie prevailing definitions of overfishing.

The application of eco-evolutionary dynamics to the question of overfishing is important because fisheries harvest is currently driving the most rapid rates of evolution ever observed in wild populations [4]. Recent work suggests that this rapid evolution, which is a function of both harvest rate and harvest method (e.g. size-selectivity of fishing gear), can have important consequences for demographic sustainability, community structure and ecosystem function. Data from across 37 different commercial fish stocks reveals that by increasing extrinsic mortality rates, fishing commonly drives the evolution of reduced age and size at maturity [5]. Such evolutionary changes can have important ecological consequences for harvested populations. For example, typical trait changes associated with harvest can hinder demographic recovery. Thus, population models that ignore evolution can overestimate the rates at which populations will rebound following an end to fishing. In addition, the recovery of traits can take even longer than the recovery of population size, meaning that the legacy of overfishing can

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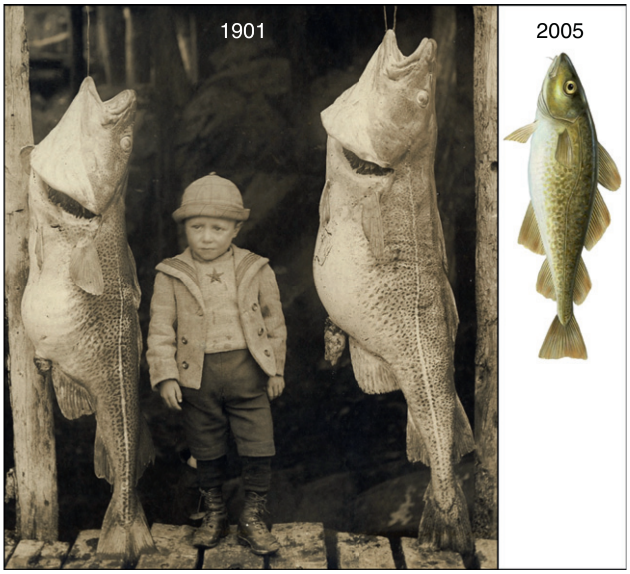

Figure 1. Substantial declines in body size have occurred in the heavily exploited stocks of Atlantic cod, *Gadus morhua*, off Newfoundland and Labrador, Canada. The photograph shows the size of cod harvested from these waters at the turn of the last century [10]. According to the plate, 'The larger fish measured 5 foot 5 inches (165.2 cm) and weighed 60 pounds (27.22 kg).' By contrast, average size for the oldest age class (17 years) captured in 2005 was 97.10 cm and 8.43 kg [11]. This change represents a 41% reduction in length and a 69% reduction in weight. The picture on the right-hand side is scaled to show the magnitude of this size shift. Although phenotypic plasticity and changes in population age structure reflect components of the overall size reduction, evolutionary contributions have been substantial [12]. Reproduced, with permission, from The Rooms Provincial Archives Division of Newfoundland and Labrador (http://www.therooms.ca/).

continue to depress harvestable biomass even after demographic sustainability has been achieved [6].

Evolutionary reductions in body size can impact community and ecosystem processes. Freshwater and marine food webs are highly size-structured. Therefore, changes in fish body size can alter trophic interactions. In one example, declines in the average body size, but not total biomass, of heavily harvested top predators on the Western Scotian Shelf between 1970 and 2008 caused trophic cascades, leading to greater biomass at lower trophic levels [7]. One of the most important predators in this region is the Atlantic cod, *Gadus morhua,* which has undergone marked fisheries-induced size reductions over the past century (Figure 1). In addition to altered trophic interactions, declines in fish size via mortality-related life-history evolution can lead to increased nutrient excretion rates, which can impact ecosystems via heightened nutrient availability and increased primary production [8].

Overfishing shapes the evolution of harvested populations directly, but ecological changes caused by overfishing can also impact evolution indirectly, via eco-evolutionary feedbacks [2]. For example, widespread population declines in overfished top predators can shift natural selection acting on prey species. When predators are present, selection favors prey traits that facilitate predator detection, avoidance, and escape. When predators are eliminated, prey densities commonly increase, favoring prey traits that enhance competitive ability. This evolutionary shift in prey (from an antipredator phenotype to a competitive phenotype) can, in turn, increase the *per capita* effects of prey on their resources, thereby amplifying the trophic cascade caused by top predator removal [9]. In this way, overfishing can set off cascades of eco-evolutionary effects that can ripple through ecosystems.

The study of eco-evolutionary dynamics has revealed that ecological and evolutionary processes are intertwined in contemporary time. Because overfishing drives both direct and indirect ecological and evolutionary changes in harvested ecosystems, understanding the full complexity of the overfishing problem will require an eco-evolutionary perspective. I encourage evolutionary ecologists and fisheries biologists to work together to apply emerging eco-evolutionary principles to fisheries management. Such collaboration can contribute toward achieving sustainable fisheries and healthy freshwater and marine ecosystems.

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