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Merilä, Juha

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# Human-induced evolution of salmon by means of unnatural selection

Juha Merilä<sup>a,b,1</sup> 

By modifying environmental conditions, human activities are generating novel selection pressures, which pose challenges to wildlife (1–3). When faced with novel selection pressures, organismal populations can respond to this through evolutionary adaptation, modifying their phenotype through plastic changes, or evading these new pressures by migrating to more beneficial environments (4). Otherwise, they will face loss of fitness and eventually, even extirpation. Although alteration of natural environments by humans has been long recognized as a potential source of novel and strong selection pressures, demonstrating human-induced evolution has proven to be challenging (4–6). In PNAS, Jensen et al. (7) provide intriguing evidence for rapid human-induced evolution in body size of Atlantic salmon (*Salmo salar*) within just 25 y.

Atlantic salmon (Fig. 1A) are mighty creatures; individual fish from large rivers can occasionally grow to weigh over 37 kg (80 pounds). However, the average size of salmon

shows great variance both within and among different river systems. Much of this variation can be attributed to variation in the time the salmon spend at sea—the later they mature and run into rivers to breed, the larger they

Author affiliations: <sup>a</sup>Area of Ecology & Biodiversity, School of Biological Sciences, The University of Hong Kong, Hong Kong Special Administrative Region; and <sup>b</sup>Research Programme in Organismal and Evolutionary Biology, Faculty of Biological and Environmental Sciences, University of Helsinki, FI-00014 Helsinki, Finland

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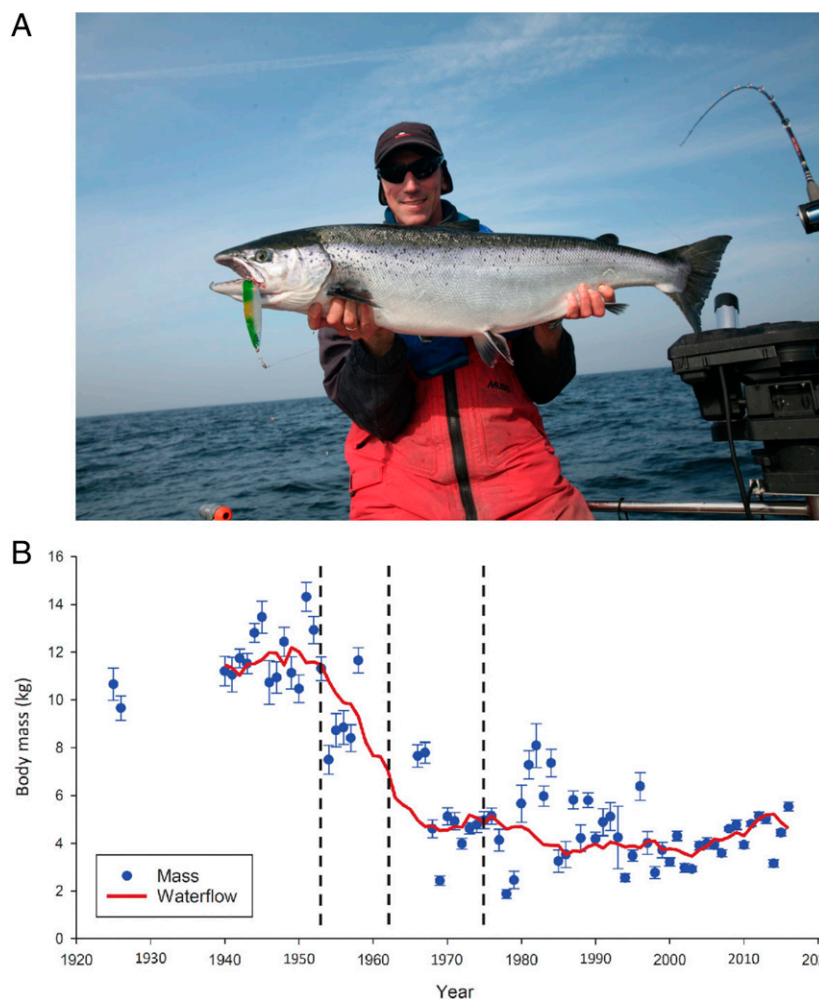
The author declares no competing interest.

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See companion article, “Large effect loci mediate rapid adaptation of salmon body size after river regulation,” [10.1073/pnas.2207634119](https://doi.org/10.1073/pnas.2207634119).

<sup>1</sup> Email: merila@hku.hk.

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**Fig. 1.** Mean body mass (kilograms) of Atlantic salmon (A) over time in River Eira as a function of water flow (B). The red line depicts the 10-y running average water flow, and the dashed vertical lines depict the timings of hydropower developments reducing water flow. (A) Image credit: J.M. (University of Helsinki, Helsinki, Finland). (B) Reproduced from ref. 7.

will be. Differences in average time spent foraging in the sea among different rivers translate to differences in average age and the size of salmon in different rivers. Salmon in the Norwegian River Eira were once among the largest salmon in the world, averaging 12 kg. However, the average size of salmon in this river plummeted to 5 kg by the mid-1970s and has stayed at this level until today (7).

The results of Jensen et al. (7) link the decline in body size of River Eira salmon to reduced water flow due to hydro-power developments. Following three consecutive water flow reductions in the 1950s, 1960s, and 1970s, the mean size of caught salmon was reduced to 74, 41, and 38% of the original mass, respectively. There is also a tight correlation between mean salmon body mass and water flow over time (Fig. 1B). Interestingly, about half of the observed size decline can be attributed to reduced age of spawners, with the other half being accounted for by size decline within age classes. Furthermore, since it is known that two major effect loci influence the number of years spent at sea before maturation, by interrogating allele frequency changes in these loci, Jensen et al. (7) were able to show a shift toward early maturation alleles in both loci. More importantly, the observed genetic changes were able to predict astonishing 84 and 81% of the mass changes between 1925 and 2016 in females and males, respectively. Collectively, these results give strong support for genetically based evolutionary change in salmon body mass associated with the human interventions in the flow regime of River Eira.

What makes the study by Jensen et al. (7) particularly convincing is that they were able to rule out some alternative possible explanations for the observed size decline, such as changes in fishing and stocking practices. They also used a complex quantitative genetics-based modeling approach to indicate that the observed dynamics of body size changes can be reproduced under reasonable assumptions and that the selective agent is tightly associated with the water flow regime. However, the million-dollar question the study does not give a straight answer to is what this selective agent is. Why should the reduced water flow favor small-sized salmon?

It is conceivable that large salmon might have struggled reaching breeding grounds in lowered water flow, giving the small-sized salmon an advantage to outreproduce the larger individuals. An alternative and nonmutually exclusive explanation would be that selection favoring small size indirectly selected for earlier maturation and reduced the mortality of the small-sized salmon in the sea, again providing them with a reproductive advantage over their larger conspecifics. The fact that the average size of salmon in another Norwegian river not subject to water flow reductions has not changed over the same time period (7) seems to suggest that the reasons for size decline in the River Eira are unlikely to be found from alterations of selection pressures at the high seas, where salmon from different rivers share the same feeding grounds.

Whatever the selective agent behind the observed body size decline, the study by Jensen et al. (7) provides compelling evidence that the size change is genetically based, driven by natural selection, and clearly associated with human interference with their environment. While concerns about undesirable consequences of human-induced genetic changes in natural fish populations were raised in 1950s (8), a lot of the early research on this topic failed to provide evidence that observed phenotypic shifts have a genetic basis and hence, represent evolutionary changes (6, 9). With this in mind, one of the major contributions of the work of Jensen et al. (7) is in providing hard evidence for human-induced evolutionary change. Furthermore, since the genetic analyses in their study were based on scale samples collected between 1925 and 2016, their results also underscore the value of preservation of historical tissue samples to gain insights into evolutionary processes (10–12).

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