

processes from the study of contemporary populations, this is likely not to be the case for nongenetic mechanisms. In this respect, the research avenues proposed by Cobben and van Oers [2] and their recommendation to look first at current range expansions are illuminating. We suggest that research efforts would be best focussed on long-distance colonisations and expansions in contiguous habitats (e.g., lessepsian migrations, range shifts promoted by the ongoing climate change, island invasions), as they mirror in several respects historical range dynamics and thus might prove invaluable for the mechanistic understanding advocated by Cobben and van Oers. A combination of these and other research directions promises to shed light on the contributions of nongenetic mechanisms of inheritance to historical biogeographical processes, despite the issues of signal erosion.

The huge opportunities opened up by the genomic era have already provided us with a number of technologies suitable for unravelling both the genomic architecture of personality traits across the whole animal kingdom and their role in the moulding of biogeographical patterns. Here we renew our invitation to follow this road. We accept, of course, that we will not obtain a complete picture of the importance of animal personality in this regard until heritable nongenetic contributions have been fully revealed, which will require considerable research effort. However, such challenges are unavoidable in evolutionary investigations. Despite their inherent incompleteness, we retrieved – and continue to retrieve – enormous insights into evolutionary processes from studying the fossil record, as well as from early genetic markers. In studying the link between personality and biogeography, genomic insights will surely come first, while insights regarding nongenetic inheritance will soon follow.

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Spotlight When Should Harvest Evolution Matter to Population Dynamics?

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The potential for evolution to influence fishery sustainability remains a controversial topic. We highlight new modeling research from Dunlop *et al.* that explores when and how

fisheries-induced evolution matters for population dynamics, while also emphasizing transient dynamics in population growth and life history-dependent responses that influence population stability and resiliency.

Commercial fishing has impacted many fish stocks to the point that some have collapsed. Such impacts include changes in life history traits, for example, maturation and growth, and are thought to influence population dynamics and thus productivity [1]. While these assertions are universally accepted, the cause of life history change in harvested populations remains controversial. Some investigators argue that the trait changes are strongly influenced by evolution [2], whereas others argue ecology (e.g., density-dependent growth) is much more important [3].

A new modeling study by Dunlop *et al.* [4] informs this debate through an eco-evolutionary model linking genetic processes to stock productivity. The authors conclude that fisheries-induced evolution (FIE) is important for population dynamics only some of the time – a result they link to fishing intensity and life history characteristics (Box 1). We here explore some of the nuances of their results and discuss their implications.

Fishery-Induced Evolution (FIE) Is Shaped by Harvest Rate and Life History Speed

The model of Dunlop and colleagues [4] suggests that FIE has the strongest effect on population growth when the harvest rate is high. The authors also show that a high harvest rate triggers changes in r that follow a transient dynamic. The population growth rate initially decreases as the largest individuals are removed via harvest, but later recovers when density is sufficiently reduced to trigger overcompensation, that is, density-dependent growth (Figure 1, left side). FIE enters the picture by altering the pace of change in r ; FIE slows the initial reduction and

Box 1. Take-Home Messages

1. The Dunlop *et al.* eco-evolutionary model suggests that population growth rate (r) is shaped by fisheries-induced evolution (FIE), but only when fishing mortality is sufficiently high.
2. During harvesting, changes in r show a transient dynamic, starting with a reduction when the largest individuals are harvested, followed by a recovery due to density-dependent growth (overcompensation). FIE slows the initial reduction and accelerates the subsequent recovery.
3. Fishing moratoria result in a reverse transient dynamic. r first increases as larger fish are protected from harvest and then decreases as the population approaches the carrying capacity.
4. FIE is life history-dependent; species with slow life histories evolve an earlier age at maturity that reduces the risk of collapse during fishing but also induces a genetic legacy that impairs recovery during moratoria. The reduced impact of FIE in species with fast life histories reduces the genetic legacy that hampers recovery during moratoria, but increases the risk of collapse at high harvest rates.

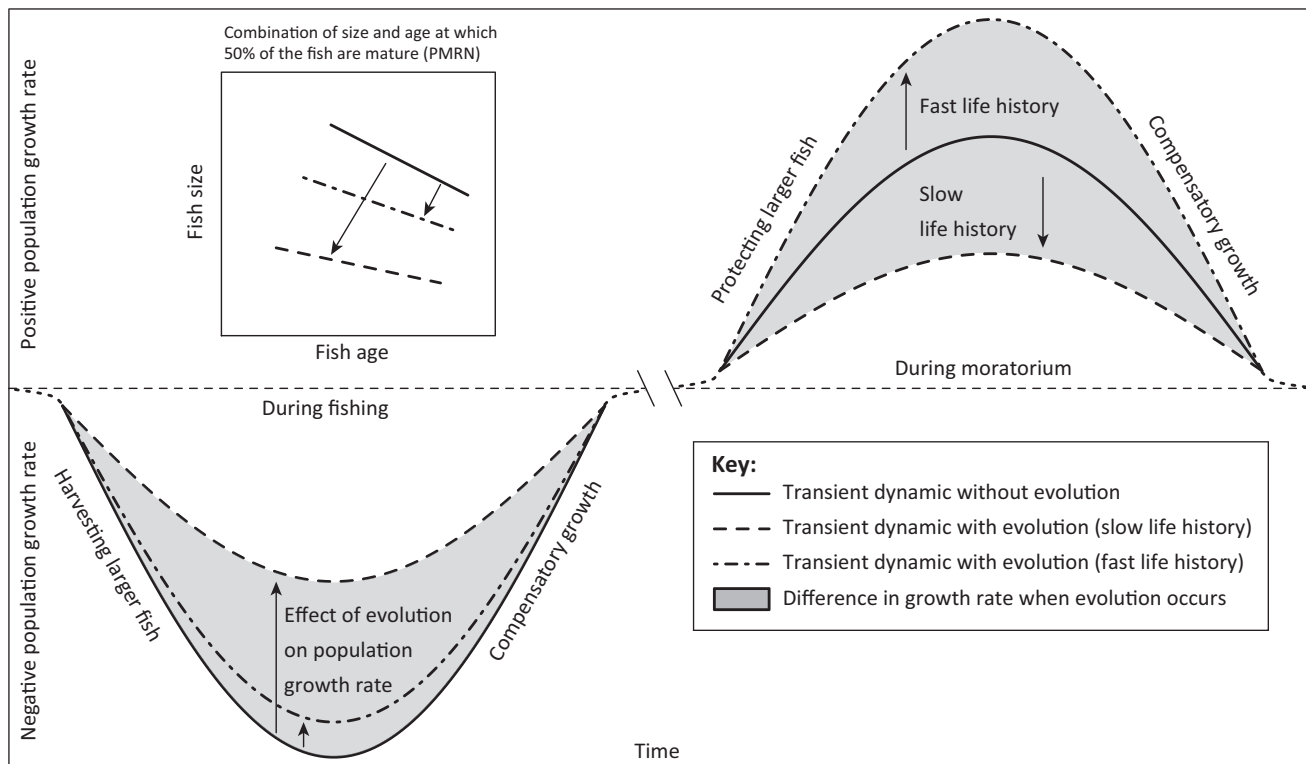
accelerates the subsequent recovery. By contrast, during a fishing moratorium, the transient dynamic is reversed; r first increases as the cessation of harvest protects the larger fish, but later decreases as fish density increases and the population

approaches the carrying capacity (Figure 1, right side).

In addition, high harvest rates cause evolution in a life history-dependent fashion. These effects were investigated through

model parameterization to match the life histories of three exploited species (Atlantic cod, lake whitefish, and yellow perch), representing a gradient of life history speeds from 'slow' (cod: late reproduction at a large size) to 'fast' (perch: early reproduction at a small size).

A first life history-dependent effect of FIE is that the transient dynamic caused by the onset of harvesting (r first decreases then increases – Box 1, point 2) is reduced for species with a slow life history (Figure 1, left side). FIE favors individuals that mature earlier and at smaller sizes, which increases the population growth rate and lessens the negative effects of removing the largest fish. By



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Figure 1. Transient Dynamic of Population Growth Rate (r) through Time. The unbroken line in the left side of the graph describes the transient dynamic of population growth rate (r) during intense fishing (i.e., harvest rate greater than 40%), with a negative and decreasing growth rate when the largest fish are harvested, followed by an increasing (but still negative) growth rate due to compensatory growth linked to density-dependent factors. The population growth rate eventually stabilizes when the population reaches carrying capacity. The unbroken line in the right side of the figure represents the reverse transient dynamic that occurs during a fishing moratorium with the same phenomenon reversed. The broken lines represent the trajectories of species with fast (broken-dot) versus slow (broken) life history speeds after evolution of the probabilistic maturation reaction norm (PMRN), which is represented in the box in the upper left part of the graph. The PMRN represents the combination of fish size and age at which 50% of individuals are mature (represented by the unbroken bar), that is, at a given age, larger fish are more likely to be mature than smaller ones. PMRN evolution is expected to trigger maturation at smaller sizes and younger ages.

contrast, species with a fast life history are already on the edge of what is physiologically possible in terms of maturation schedules, which limits their ability to evolve earlier maturity during harvest. For species with fast life histories, the transient dynamics are therefore strong and the probability of collapse increased (Box 1, point 4).

A second effect was that FIE in slow life history species caused a long-term impairment of population recovery following a moratorium. In particular, the reverse transient dynamic during the moratorium (r first increases then decreases – Box 1, point 3) was reduced for these species, partly because of the genetic legacy of FIE that favored early maturity under the previous period of harvest (Figure 1, right side). However, in fast life history species that did not evolve significantly during fishing, genetic variability was not depleted and the genes favoring high fecundity remained, which facilitated rapid recovery during moratoria.

Long-Term Costs of Fisheries-Induced Evolution

Overall, the new modeling study by Dunlop and colleagues suggests that population growth rate can be affected by evolution, particularly when harvest rate is high and life history speed is slow.

Their results might explain the discrepancy in response to size-selective fishing observed between species with different life histories [2]; or why some species with slow life histories that have experienced high harvest rates have shown slow recoveries even after several years of fishing moratoria [5]. Additional knock-on effects seem likely. For instance, decreased age at maturity under such conditions might lead to constrained age structure that could result in more variable population dynamics leading to destabilized fish stocks and increased risk of collapse [6].

Understanding how and when evolutionary change matters is a key management question because it influences management actions [7]. This is particularly true in a changing environment where predictions are poor and for which management policies should be flexible, well monitored, and robust to environmental and evolutionary uncertainty [8]. Size-selective fishing can impact many different traits, including individual growth, maturation, and behavior [2], suggesting that even small changes in these traits have the potential to alter not only population but also community and ecosystem processes [9]. The work by Dunlop *et al.* takes us one step closer to understanding the conditions under which fishery-induced

evolution will matter for population stability and sustainability, emphasizing the importance of harvest rate and life history speed, both of which should be incorporated into evolutionary impact assessments [10].

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