Fish and Fisheries

WILEY

FISH and FISHERIES

ORIGINAL ARTICLE OPEN ACCESS

Overfishing Social Fish

James A. Wilson[1] | Jarl Giske[2] | Culum Brown[3]

[1]School of Marine Sciences, University of Maine, Orono, Maine, USA | [2]Department of Biological Sciences, University of Bergen, Bergen, Norway | [3]School of Natural Sciences, Macquarie University, Sydney, Australia

Correspondence: Jarl Giske (jarl.giske@uib.no)

Received: 18 October 2024 | **Revised:** 17 December 2024 | **Accepted:** 18 December 2024

Funding: The authors received no specific funding for this work.

Keywords: complex adaptive system | fisheries management | long-lived fish | myopic adaptation | patterns of overfishing | social learning

ABSTRACT

Social learning is common among vertebrates, including fish. Learning from others reduces the risk and costs of adaptation. In some longer-lived species, social learning can lead to the formation of persistent groups that pass learned adaptations from one generation to the next (culture). Variations in learned adaptations are subject to natural selection, leading to a second, fast-paced, fine-scale evolutionary process that complements genetics and enables adaptation to the peculiarities of local areas. Socially learned knowledge is stored mainly in the minds of older fish and subsequently inherited (learned) by younger fish. Consequently, the persistence of locally adapted groups of long-lived fish requires the inheritance of genetic and learned adaptations. Local populations of social learners are not often recognised nor conserved by fisheries managers. Fishing usually reduces the relative abundance of older fish far more than younger. We hypothesise that fishing may impair and eventually erase the learned local adaptations of long-lived fish, leading to the loss of local stocks of these species and significant ecosystem-wide changes. Fishing may shift abundance towards species not dependent on learned adaptations, i.e., invertebrates and short-lived fish. The hypothesis leads directly to the idea that conserving populations of long-lived social learners is likely best accomplished by protecting age and social structure or, more generally, the natural processes, such as social learning, that generate complexity in an adaptive ecosystem. Local area-based management is aligned with the local processes of social learners and can capture and learn about the effect of human activity at that scale.

1 | Introduction

In the four or five decades since the creation of exclusive economic zones, global marine fish landings have stabilised (FAO 2022) but with 'a gradual transition from long-lived, high trophic level, piscivorous bottom fish toward short-lived, low trophic level invertebrates and planktivorous pelagic fish' (Pauly et al. 1998). As Pauly and others (Frank et al. 2005; Howarth et al. 2013; Myers and Worm 2005; Steneck et al. 2011; Jackson et al. 2001; Worm et al. 2006; Shears and Babcock 2002; Synnes et al. 2023; Eriksson et al. 2024) point out, these patterns are symptomatic of a simplified and possibly unstable ecological structure. We also point out that these patterns suggest the recovery of long-lived, high trophic-level fish appears much slower than of other system components. Hauser and Carvalho (2008) present interesting and complementary evidence derived from molecular genetics suggesting that among fish, there is 'extensive differentiation and biocomplexity' with 'effective population sizes 2–6 orders of magnitude smaller than census sizes'. Using otolith chemistry, Kerr et al. (2024) come to similar conclusions, i.e., finer-scale population structures. Together, these studies suggest that the usually assumed structure and dynamics of fish populations and the outcomes of fishing differ significantly from conventional perceptions.

Like many of our colleagues, we have sifted through the evidence and the various theories about how fish and humans interact, hoping to find insight into these and other puzzling observations. A long list of candidates is reviewed by Howarth et al. (2013), Worm, Hilborn, and Baum (2009), Jackson et al. (2001) and others. Social learning among fish is an overlooked possibility that we believe should be on the shortlist. In extensive summaries, Whiten (2021) and Brakes et al. (2019) note that social learning, when one animal learns from another, is a second system of adaptation that complements genetics, enabling adaptation at a fine spatial and at a faster temporal scale. Social learning affects the diverse local niches fish develop, the size of self-reproducing populations and, generally, the diversity and complexity of the natural system. Older age and social learning are closely related. In a recent survey, Kopf et al. (2024) reviewed how older members benefit a population. The attribution of sentience among fish is not common in fisheries science, maybe because it is not thought to have a pervasive effect on the structure and dynamics of fish populations. In contrast, our interest here is in how consideration of social learning among longer-lived, typically higher trophic-level fish affects our understanding of the demographics and dynamics of these species and, consequently, our understanding of the impacts of fishing on individual populations and the rest of the ecosystem.

Social groups among animals, especially vertebrates, are common and well-known—a pack of wolves, a flock of birds, a pod of whales, a school of fish, etc. There is strong evidence that fish can be social learners and that the behaviours indicative of social learning appear common among fish (Brown and Laland 2003; Brown and Webster 2024). We find this significant because, as we explain below, the effects of fishing on populations of social learners appear to lead to outcomes broadly consistent with the worldwide shift towards invertebrates and short-lived fish identified by Pauly et al. (1998) and the finer-scale population structure that is apparent when using refined methods to identify effective populations as argued by Hauser and Carvalho (2008), Kerr et al. (2024) and others. Consequently, we conclude that understanding the demographic and behavioural effects of social learning among fish is essential to understanding the problem of overfishing.

For fish that learn, the peculiar variations in any local[1] area's physical and biological environment are the fodder for new, specific learned behaviours (Wilson and Giske 2023). Variations in topography, sediment types, macroalgae, water currents, prey, predators, competitors and other relevant aspects of a fish's local environment can lead to learned adaptations that benefit the individuals directly involved (Ginsburg and Jablonka 2019) and, in situations where social learning occurs, the other members of the group (Brown and Laland 2011) and, in some circumstances, subsequent generations (Laland and Evans 2017). The local scale and rapid pace of these peculiarities do not usually lead to genetic specialisation. However, social learning does allow for rapid and continuous adaptation to local variations and, as a result, gives rise to time and place behaviours unique to the different places the species inhabits.

Consideration of social learning suggests that the sustainability of local populations of social learners and local ecosystems depends on the inheritance of two bodies of adaptive knowledge—genetic and socially learned (Wilson and Giske 2023; Budaev et al. 2019). The inheritance of socially learned knowledge, i.e., culture (Boyd and Richerson 1985; Laland and Hoppitt 2013), tends to be significant to longer-lived species that can take advantage of longer-term regularities in a local area. Loss or impairment of this socially learned, locally appropriate adaptive knowledge is likely to affect the local stock directly. If this local outcome is repeated in many places, it may lead to substantial impacts elsewhere in the ecosystem. These likely effects of social learning and its possible loss lead us to an alternative interpretation of the mechanisms and outcomes of fishing. These ideas can be stated as a hypothesis (Figure 1):

> Long-lived social fish rely on social learning to adapt to the peculiarities of local areas, forming local sub-populations, or stocks, in the process. Socially learned knowledge important to local adaptation is stored mainly in the minds of older fish and subsequently inherited (learned) by younger fish. Fishing tends to preferentially remove older fish, impairing or erasing the learned adaptations of local populations of long-lived, social

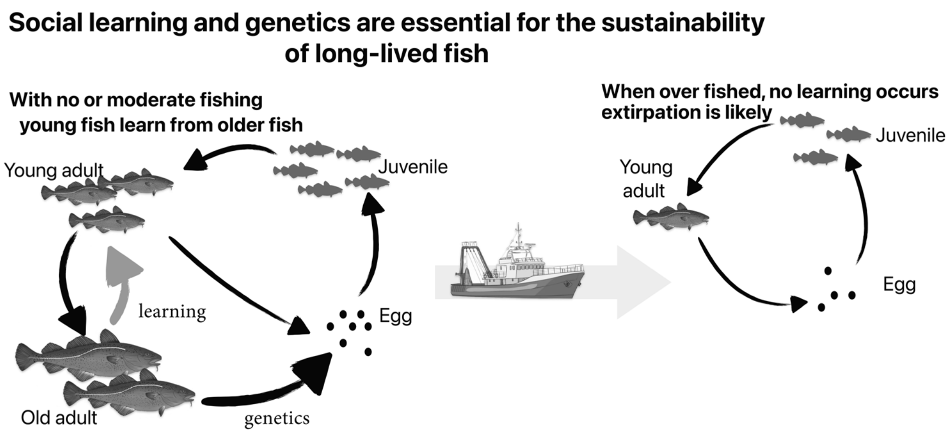

FIGURE 1 | Our social learning hypothesis. Local adaptation of long-lived fish requires genetic (black arrow) and learned (grey arrow) intergenerational knowledge. Fishing tends to remove older fish, the source of learned long-term adaptive knowledge. Extirpation is the eventual result. Artwork by Iylarose Willis.

species and inducing substantial disruptions in the adaptations of the local population's prey, predators, and competitors.

Social learning suggests significant non-genetic adaptation and leads naturally to a view of system organisation and dynamics that emphasises the role of 'information and adaptation' (Krakauer 2024). From this perspective, our hypothesis argues that the information, i.e., the knowledge, long-lived fish require for successful adaptation is genetic and socially learned; fishing impairs or removes the socially learned knowledge essential to that adaptation.

The sections of the paper that follow flesh out the reasoning that leads to our hypothesis. We begin (section 2) by explaining social learning among fish, emphasising the role of information and adaptation. We pay particular attention to the organisational and demographic consequences and the requirements for reproducing socially learned adaptations. We then (section 3) use the same social learning perspective to introduce the idea that the commercial fishing industry is an invasive population of very smart social learners. The interaction of fish and fishers—both social learners—generates distinct patterns of exploitation that appear to conform with the observations of Pauly et al. (1998), Hauser and Carvalho (2008) and others cited above. In the final sections of the paper, we briefly consider the out-of-the-ordinary scientific questions and the fisheries management implications raised by the consideration of social learning.

2 | Social Learning, Culture and Population Structure Among Long-Lived Fish

Not so long ago, fishes were often viewed as mindless automatons, pre-programmed to respond to environmental cues in predictable ways, as if their behaviour was ruled only and entirely by their genes. However, as more is learned about animal behaviour, that view is quickly fading. During the Cambrian explosion, early vertebrates emerged with the cognitive capacity for subjective experience (Feinberg and Mallatt 2013; Ginsburg and Jablonka 2010, 2019; Godfrey-Smith 2017) and episodic-like memory (Schultz 2024; Zacks, Ginsburg, and Jablonka 2022) that have enabled learning, planning and cooperation (Busia and Griggio 2020; Croft et al. 2006; Heathcote et al. 2017). Over the last several decades, research has revealed that fishes' cognitive capacity and behavioural flexibility are not overly different from most vertebrates (Brown, Laland, and Krause 2011; Bshary and Brown 2014; Budaev et al. 2024; Giske et al. 2025; Salena et al. 2021). Importantly, it has become apparent that while fish behaviour has essential genetic components, it is also quickly adaptable due to the capacity for learning. Learning allows animals to fine-tune their behaviour to adapt to changing local environments (Ginsburg and Jablonka 2019; Budaev et al. 2019).

Fishes can learn about their environment through individual experiences and interactions with others (Brown and Laland 2011; Brown 2023). Rather than wasting time and energy and incurring the risk of exploring its environment and a range of potential behavioural responses, a social learner can adopt the behaviour of others. The mechanisms by which this occurs are many and varied. They may be as simple as a conspecific drawing attention to a particular object or location (stimulus or local enhancement). They may also be complex, such as active teaching or goal emulation (Heyes 1994). This flexibility means social learning can inform behaviour in various contexts, including what to eat, where and when food can be found, how to recognise predators, who to mate with and which migratory pathways to use (Brown and Laland 2003).

Genetics gives individuals a hard-wired, persistent 'memory' of tested adaptations that worked in the past over broad spatial and temporal scales. In contrast, the memory of successful socially learned adaptations resides in the ephemeral minds and bodies of individuals. Learned memory content may vary considerably among individuals because individuals' memories are most likely derived from recent local experiences (including learning from others) and are likely to reflect their different experiences in a complex environment. As a consequence, for the group, the adaptive value of individuals' memories may only be realised through social cohesion that facilitates continuing local communication (Weinrich, Hoppitt, and Rendell 2013; Webster et al. 2013) and a collective decision process that resolves or minimises different experiences (Bottinelli et al. 2013). Consequently, natural selection also operates on the learned adaptive behaviours resulting from a group decision process. It refines that collective decision process, improving the adaptation of the cultural equivalent of the group's gene pool, thus benefitting its individual members. The very different mechanism of heritability of socially learned adaptive knowledge means fishing is likely to affect the processes essential for learned adaptation in ways that differ significantly from its effect on genetic adaptation.

From a demographic perspective, social cohesion means persistent associations emerge as local organisations or structures important to broader population structure. The groups that form this way can exploit niches and places that would otherwise be too costly for an individual to adopt. For social learners, the collective effect of the memories that arise with learning means that the reasonably regular seasonal or longer-term events that occur in a complex system and that an autonomous individual would find very costly to learn are effectively acquired at a low cost by large numbers of fish in a social setting (Clark and Mangel 1986). For example, herring appear to use the same spawning sites each year. It is difficult to imagine millions of autonomous individual fish independently learning those sites. Many niche and spatial opportunities that would not otherwise be possible are enabled. The once enormous biomass of large-bodied, long-lived predators suggests their refined niches were highly successful before fishing and that their loss due to fishing has substantially affected the rest of the system (Myers and Worm 2005; Jackson et al. 2001; Pauly et al. 1998; Hauser and Carvalho 2008).

2.1 | The Communication of Learned Adaptive Knowledge

It is helpful to distinguish two ways learned information is communicated because the organisational consequences are significant. Sharing information about highly particular, ephemeral local events can result in novel and short-lived collective behaviour. For example, a group of fish may make a beneficial discovery, e.g., a deadfall whale; when the benefits of such an event dissipate, the individual and collective memory of the dead whale has little value. Similarly, an individual benefits substantially when its predators are detected by other fish in its group. The particular knowledge of a prey attack at that time and place likely has little value afterwards. However, the benefits of the collective activity that generates these kinds of fleeting benefits create strong incentives to associate with others of the same species. Those same associations can quickly spread information that reflects knowledge of longer-term regularities. Usually, the intra-generational communication of valuable socially learned ephemeral knowledge is labelled *horizontal transmission* and may be common among invertebrates and vertebrates.

The transfer of socially learned knowledge from one to subsequent generations is termed *vertical transmission* (Laland and Hoppitt 2013). The vertical transmission of adaptive knowledge is most likely limited to longer-lived fish that might have the capacity to benefit from knowledge of longer-term events, such as appropriate spawning sites or complicated migration routes. Notably, the variations in adaptive experience among individuals (as noted above) and the transmission of this knowledge across generations enable the natural selection and evolution of learned adaptive behaviours and population organisation that are appropriate to longer-term, regular local phenomena (Aplin et al. 2015; Brakes et al. 2019; Boyd and Richerson 1985; Keith and Bull 2017; Whiten 2017, 2021).

Among long-lived fish, the intergenerational transfer of socially learned knowledge, i.e., culture, differs from the transfer of genetic information in two important ways. First, genetic information is passed from parents to offspring once in a lifetime; in contrast, the transfer of socially learned knowledge occurs continuously throughout an animal's life and can result from interactions with many unrelated individuals. It is entirely possible that younger fish may pass their experience to older fish. Consequently, social learning can spread well-adapted behaviours quickly over periods significantly shorter than a lifespan (Brown 2023). Second, it is usually assumed that larval drift and adult fish movement act to distribute genetic information over a potentially broad area. Consequently, if genetics is considered the only heritable body of knowledge, effective population size is defined accordingly. However, this common fisheries management view is challenged by the small-scale population structures identified by Hauser and Carvalho (2008) using molecular genetics and by Kerr et al. (2024) using otolith analysis.

In contrast with the standard view of large-scale populations, the inheritance of socially learned knowledge is limited by the restricted range of communication networks among fish. This restriction leads to persistent local associations among individuals and finer-scale population structure. Consequently, for longer-lived fish, the inheritance of genetic and socially learned adaptive behaviours via persistent social groups is, along with the inheritance of the adaptive knowledge in genes, essential for individual growth, adaptation, survival and population sustainability. Further, the scale of self-reproducing populations, i.e., those that pass on both genetic and learned adaptations, corresponds with the limited range of fish communications. Brakes et al. (2019) call these local population units cultural variants.

2.2 | Myopia and Complexity

Understanding the agent-level mechanisms that lead to the emergence of cultural variants and other aspects of natural system dynamics is essential for understanding the human impacts on the system. In a complex system, each agent—fish or human—holds only a small part of the knowledge contributing to an orderly system (where we use the term 'orderly system' to mean a system with enough predictability to manifest the myopic expectations built into well-adapted behaviour). Every individual has a subset of the experiences of past generations incorporated in its genes. When learning occurs, an individual can draw on its experience (Budaev et al. 2024), and if the individual is a member of a species of social learners, it can also draw on the accumulated multi-generational experience of its social group. Thus, an individual's personal and socially acquired experience and the experience of its social group localise the individual's learned adaptive knowledge. This knowledge is myopic because the learned experience it draws upon is restricted to those evolved behaviours most likely to benefit its local survival and reproduction. We don't use the term myopic to mean very fine scale and restricted to a particular place. Instead, the term refers to a focus on only a small part of an extensive system, even if the focus has multiple scales, e.g., the geographic knowledge that might encompass seasonal migrations. We assume that when the individual's current circumstances align with its experience or knowledge, it will likely choose reasonably successful behaviour (Budaev et al. 2019; Giske et al. 2025). When its circumstances lie outside the realm of its acquired experience, as might happen in a disturbed environment or with fishing, we assume the likelihood of maladaptive behaviour increases (Giske et al. 2025).

Thus, adaptation, whether learned or genetic, generates current behaviours that reflect successful past behaviours and, for that reason, gives rise to a roughly predictable regularity in the timing, circumstances, and location of events in the system. This myopic knowledge governs the organisation and behaviour of individuals and, consequently, group and intergroup interactions. It is the basis for the complexity of the living portion of the natural system. From the perspective of our hypothesis, the conservation of the processes that generate this information is essential to the complexity of the natural system and critical to the sustainability of the system's evolved organisation.

Social learning suggests that non-linear population dynamics may be another source of complexity, at least for some exploited populations in some circumstances. Like many information phenomena, the growth and loss of culture among long-lived fish are likely to be non-linear (Holland 2012). Information sharing across generations is most valuable when it extends behaviours appropriate to longer-term regularities, such as when and where to migrate and spawn (Huse, Railsback, and

Fernö 2002; Rose 1993). If there were a uniform, clockwork-like environment, natural selection would likely lead to uniform behaviour and a genetically built-in consensus (Baldwin 1896; Morgan 1896; Osborn 1897). In the absence of physical change, the system would duplicate itself. In a variable environment, the behaviour of survivors is likely to be equally variable, reflecting their survival in different environmental circumstances. As a result, natural selection of well-adapted behaviours will require a longer history, i.e., more older fish, to sort out longer-term regularities. In a variable environment, if collective decisions involve any kind of consensus, the self-organisation of local culture will likely be a non-linear process (Holland 2012) that accelerates rapidly once a consensus develops around well-adapted behaviours—more individuals using the behaviours, leading to still more adopters, etc. The disassembly of culture due to fishing may work the same way but in reverse—less consensus, less individual benefit from group experience, and fewer individuals to pass on adaptive behaviours. Given the relatively fast pace of social learning, these non-linearities may produce surprisingly quick changes in population organisation. The few survivors of the local population that may be left after heavy fishing may not be able to muster the knowledge required to maintain the inherited local adaptation. Extirpation is the result. Genetic knowledge, in contrast, is entirely contained in each fish's DNA and may be recreated by only a few local survivors.

2.3 | The Fishing Relevant Demographic Effects of Social Learning

In long-lived fish, the population dynamics that emerge from social learning may differ significantly from those usually conceived in fisheries theory and practical management. These differences are significant because they change our understanding of how fishing affects the natural system.

We focus on four significant differences.

- First, the reproduction of genetic and learned knowledge is very different. A newly mature fish can pass its genes to the next generation, whereas all the events over its life can affect what is passed on to other individuals by social learning. Early in life, through numerous learning interactions, a socially learning individual acquires the experience of older fish as well as its own experiences. Later in life, it may contribute these experiences to younger fish. This lifelong process implies the need for a continuously cohesive local social unit whose senior members are the principal repository of the unique but continually changing body of knowledge required for local adaptation (Whiten 2021; Brakes et al. 2019).
- Second, when local population renewal requires the inheritance of genetic and socially learned adaptive knowledge, the scale of the communications that maintain coherent local social groups sets the scale of their renewal, not the broad scale usually assumed by managers who are generally thinking of broad-scaled genetic inheritance only.
- Third, each species will likely differ in its dependence on social learning and the adaptive memories held by older fish. Short-lived fish, such as anchoveta, living in a pelagic environment with behaviours closely aligned with physical processes, may benefit significantly from the horizontal transmission of learned information such as might occur when other fish signal that a predator is near. However, their knowledge of appropriate responses to changes in the physical environment is most likely incorporated in their genes, and their population range is appropriately large, i.e., the range over which the information in the genes is communicated. In contrast, the adaptations of long-lived predators, living and migrating between bio-diverse and highly variable environments, e.g., cod and other large-bodied piscivores, may depend significantly on the intergenerational transfer of inherited, socially learned information pertinent to finer-scale population structure and local adaptation.
- Fourth, among culture-dependent, long-lived social learners, the non-linearities of cultural disassembly and assembly (Holland 2012) may be responsible for a surprisingly sudden loss of local adaptive knowledge followed by extended periods without recovery (Hutchings and Myers 1994), during which the collective knowledge governing local adaptation is rebuilt. For example, in Eastern Maine the groundfishery collapsed in the early 1990s. An on-going hook survey of the area begun in 2010 and conducted by the Maine Center for Coastal Fisheries regularly catches juvenile cod and other demersals, but until this year, about 35 years since the collapse, the survey has not caught any adults. This year (2024), it caught one (Chen et al. 2013; E. Ames, pers. com).

In the next section of the paper, we extend the ideas of social learning to the commercial fishing industry, treating it as an invasive, highly adaptive population in a complex adaptive system.

3 | Commercial Fishing Considered as an Invasive Population of Social Learners

Consideration of social learning among fish leads naturally to the idea that commercial fishers might be conceived as a population of diverse, highly adaptive and fast-to-learn top predators. When thought of this way, the same information-centric analytical framework described above for social learning in fish, when applied to fishers, suggests a significantly different interpretation of the causes, patterns and consequences of overfishing.

Social learning among humans is much more consequential than among fish. Language, writing, communications and deliberate institutions for accumulating and spreading knowledge all contribute to social memory and its distribution (Arrow 1962; Ostrom 1990; Arthur 1992). Fishing benefits greatly from this broad social capacity. However, the complexity of the natural environment and the difficulty of observation means that the very fine-grained temporal and spatial knowledge fishers require to 'make a good set' at any moment is largely outside any body of collective knowledge. Small boat fishers working in complex environments are particularly versed in the knowledge of places whose scale is appropriate to the scale of their gear, e.g., the resolution of hook fishers' knowledge of particular places is often at a scale of a hundred metres or less. Their need to minimise the costs of acquiring this information leads to particular spatial and temporal patterns that are the basis for a different understanding of the patterns of fishing.

Fishing is all about search, i.e., acquiring and using environmental knowledge at multiple scales (Wilson 1990). Like fish, fishers cope with the complexity of a vast system by focusing on the regularities that occur in only a small part of the system. The breadth of fishers' confident knowledge is limited mainly to the restricted part of the system—the places, times, gear, other fishers and species—that they find familiar. Their knowledge is gained through direct experience, observing and talking with other fishers, self-testing hypotheses about the time and place fish might be caught and endless, but somewhat guarded, discussions about fishing and the market.

Significantly, fishers form groups that closely resemble the information-sharing groups formed by social learning fish. Williamson (1985) refers to these kinds of economic arrangements as 'clubs'; Acheson (1988), an anthropologist, prefers 'gangs'. Among smaller-scale independent fishers, these groups are informal, somewhat flexible associations of a small number of near equals (Acheson 1988; Wilson et al. 2013). Within a group, fishers acquire their knowledge of fish through their own experience and 'horizontal' communications with other group members. Transfers of knowledge about longer-term regularities in the local fishery, i.e., 'vertical' transmissions, occur through extended hands-on apprenticeships and extensive discussions within families and the community.

Unlike fish (perhaps), information sharing among humans is subject to equity considerations. Among fishers and almost all informal groups exploiting a common resource (Ostrom 1990), unwritten rules tend to exclude individuals who do not contribute proportionate valuable knowledge or other services to the group (Acheson 1988; Ostrom 1990). Formal organisations, such as industrial fishing operations, require written contractual arrangements that replace the informality of small-boat fishing. However, the fundamental need to share equitably, or at least with reasonable certainty about the expected outcome, among human social groups is present regardless of scale. These information equity concerns reinforce the continuity of relationships and organisation.

The knowledge fishers acquire from and share with others about the location of fish tends to be about coarse-grained time and place patterns. For example, 'in the early spring, the fish tend to move up off the soft bottom into the gullies along the edge of the shelf'. Individual fishers remember particular places and times, of course. Nevertheless, when they leave port, they aim for the general areas where history and their most current information tell them fish might be. They don't attempt to predict the specific location of fish. In any but the most uniform environments, finding the exact location of fish at any moment is the result of a very local search. That search is heavily dependent on skill and experience, but even then, it is economical only due to the focus provided by broader-scale collective knowledge. In other words, fishers combine their essential myopia with a typical hierarchical search (Holland 2012). They begin by relying on broader scale, longer-term, slower-moving, collectively held and generally cheaper information. They conclude with the individual acquisition of faster-paced, much less predictable, finer-grained and more costly information. Fishers' attempts to minimise search costs appear to significantly influence the spatial and species patterns of exploitation in the system (Wilson et al. 2013, 2000).

The informal organisations of fishers and long-lived, predatory social fish share some interesting similarities. Both require shared information, both form persistent groups for this purpose, and both focus on a relatively restricted part of the system. In other words, acquiring adaptive knowledge is costly (Wilson et al. 2013) for fish and fishers, and the evolved solutions are similar. Both also face what is sometimes called 'the commons problem'.

Neither fish nor fishers are likely to be aware of broader-scale changes in the system brought about by their own and others' myopia until those changes work their way through the system and directly affect their current adaptation. Presumably, the persistence of relatively stable systems is due to evolved external restraints, not to self-restraint (Wilson and Wilson 2007). Thus, a natural system with myopic fish can be relatively stable in the sense that most species persist despite wide swings in abundance. Myopic fishers have the same capacity for unrestrained self-destruction, except their exceptional flexibility may extend their activity to many species and induce significant changes in the ecosystem. In the next to the last section of the paper, we comment on the kinds of external restraint that fishing in a complex system might require.

4 | Simplifying the Complexity of the System

Understanding a complex system requires some form of simplification, i.e., a strategy that allows one to conceive of the system without having to acquire the information that defines its 'infinite complexities'. Standard fisheries theory approaches (or avoids) complexity by focusing on single-species dynamics, ignoring the natural system's extensive interactions. We reach for simplicity by focusing on two patterns of commercial fishing (considering the industry as an invasive species) that remove essential organising information from the natural system. These patterns are relatively general and found in the interaction of fishing with almost all exploited species.

- The first is commercial fishing's strong tendency to truncate the age structure of local populations (Pauly et al. 1998) and, consequently, to weaken or eliminate those populations' socially learned adaptive local knowledge.
- The second is the economic incentives and social learning among fishers that spread the same loss of adaptive knowledge to multiple species at multiple places.

Simplifying the system from this perspective is helpful because it leads to a better understanding of the web of ecosystem effects emanating from the invasive effects of fishing.

The effects of a truncated age structure: Fishing has a strong tendency, with some exceptions,[2] to truncate the age structure of exploited populations. Bigger fish are often targeted because they bring a better price in the market. Still, even without that preference, the longer fish live, the more frequent their exposure to fishing. As a result, their relative abundance is reduced much more than that of younger fish or older fish in unfished populations. It follows that the impact of fishing on long-lived, culture-dependent populations is likely much more substantial than among short-lived fish and invertebrates that are not dependent on cultural adaptations.

In a culture-dependent population, as the proportion of older fish declines, the vertical transmission of experience to younger fish is diminished, social cohesion declines, and the adaptive capacity made possible by information sharing is weakened or lost. Accordingly, the circumstances of individual fish and groups are more likely to lie outside the realm of their personal or learned experience, and the likelihood of maladaptive actions increases. Infrequent existential annual events like spawning locations (Mason et al. 2024; Warner 1988) and migrations that are mainly dependent on the memory of older fish are likely to be most affected, e.g., herring (Huse, Railsback, and Fernö 2002) and cod (Rose 1993). As a population's age structure is compressed, the variability of its adaptive responses likely increases, and, eventually, with few or no older fish, a rapid, non-linear approach to extirpation is the probable result. Extirpation means the experience that constitutes a local adaptation may be permanently lost and irretrievable—the social learning equivalent of extinction.

When only one species in a local system is extirpated, it is reasonable to expect that acquiring the beneficial experience that constitutes a local adaptation may take time. If the extirpation in the local ecosystem extends across multiple interacting species, exponentially more time would seem likely. In contrast, fishing down local aggregations of short-lived fish and invertebrates—species that are not likely to depend on culture—is not likely to threaten the loss of their more broadly applicable (genetics only) adaptive knowledge. Thus, the pace of their renewal after depletion is not likely constrained by the need to coevolve a new adaptation with other species in the local area.

Spreading the effects of truncated age structure: As a local, harvested population declines, economic incentives generate a fundamental, profit-seeking dynamic that expands the impact of truncated age structure to other economically valuable local populations and different species in the system. To illustrate the dynamic, consider a broad area like the typical management zone; assume the area is a patchy conglomeration that contains multiple populations of many species of invertebrates and fish, some of which are locally adapted, long-lived social learners. Assume fishers share reasonably accurate but coarse-grained information about the timing, likely location and relative abundance of fishable aggregations. Also, assume fishers face significant search costs, i.e., travel time, energy and foregone local harvests. When fishing begins, fishers target valuable stocks and species close to home to reduce steaming costs and because they are likely to be familiar with the fine-scale behaviours of these stocks. As the abundance and revenues of nearby opportunities decline, some fishers realise the expected revenues from the greater abundance of more distant opportunities or other species will compensate for the greater risk, the costs of steaming and the costs of learning about a new target. Other fishers notice and, along with the initial explorer, shift their effort to different places and species (Synnes et al. 2023 and citations therein, Ames 2004; Sanchirico and Wilen 1999). As this process continues, the result at any moment might be called a 'bio-economic ideal free distribution' in which the relative profits (including discounts for risk) of fishing at each location and species are moving in the direction of equivalence. Despite individuals' attempts at secrecy, information about new opportunities tends to spread quickly. The resulting shift of effort to new stocks or species is likely to be a quick, non-linear process. 'All of a sudden, everyone is fishing on the lower bank.'

There is no equilibrium. The process continually reallocates fishing effort across fish stocks as the abundance of those stocks varies in response to fishing and natural causes. In general, costly search suggests that the effort assigned to each local stock varies in a way that is inversely proportional to risk, steaming and learning costs and directly proportional to revenue. Consequently, the amount of fishing on the various exploited stocks will likely differ by species and place. Because long-lived fish depend on culture, their response to fishing will likely differ dramatically from non-culture-dependent fish. The historical record tends to show the early reduction and eventual extirpation of convenient, i.e., nearby and inexpensive-to-fish, populations of long-lived social species (Ames 1997). Only remote and costly-to-fish subpopulations are likely to persist in the long run. Convenient aggregations of invertebrates and short-lived social learners—animals less dependent on culture—are likely to be affected in ways consistent with standard, genetics only, theory. Still, their abundance may deviate from what might be expected due to significant changes in their biotic environment, such as those that might occur with the removal of long-lived predators (Worm et al. 2006; Steneck et al. 2011). The populations of remote and non-marketable species are likely to be less disturbed, more abundant and contain a higher proportion of older individuals.

5 | Summarising Our Hypothesis About Fishing Social Fish in a Complex System

Social learning is a second method of adaptation that appears common among fish. It operates at a faster pace and finer scale than the broader scale genetics usually employed in fisheries management. Thus, social learning allows adaptation to unique, longer-term local regularities that might not be possible with genes alone. Among longer-lived fish, it may lead to the organisation of persistent, locally adapted stocks or cultural variants whose scale of renewal is finer than is usually assumed. Consequently, the persistence of local stocks of social learners requires the continuous inheritance of genetic and learned adaptative knowledge.

Longer-lived species refine their local adaptations through social learning, but refinement increases their vulnerability to fishing. Fishing disproportionately targets older, experienced fish, impairing the collective memory of culturally dependent species. As the group's collective experience declines, the communication of adaptive experience to younger fish becomes less regular and more haphazard. Socially learned knowledge of infrequent but existential events such as seasonal shifts in behaviour and annual migrations is the most likely to be lost (Chambers 2021; Huse, Railsback, and Fernö 2002; Rose 1993; Warner 1988, 1990). As adaptive knowledge is lost, the behaviour of the local population becomes more variable and the population less well-adapted and less abundant. Eventually, local adaptation breaks down, with extirpation the likely outcome.

Furthermore, fishers prefer to fish at times and places that minimise the costs and maximise the revenues of harvesting. As the abundance of economically convenient stocks declines, typical economic incentives distribute fishing effort in a way that tends to equalise longer-term profits across all fishable areas and species. The process allocates disproportionately more effort to convenient, well-known and cheaper-to-fish stocks. Among long-lived social learners, this leads to a cascade of extirpations (Baum and Worm 2009), starting with the lowest-cost-to-fish local populations, generally coastal and ending with costly-to-fish remote stocks. The loss of local stocks of social learners is the equivalent of removing some of the restraints that determine the impact of fishing on other non-learning species, likely leading to significant indirect effects, such as those that might occur with the removal of predators, as noted by several authors (Worm et al. 2006; Steneck et al. 2011; Howarth et al. 2013; Jackson et al. 2001). In short, fishing tends to remove the adaptive knowledge essential to the persistence of locally adapted populations of long-lived social learners, leaving a species distribution that is consistent with 'a gradual transition from long-lived, high trophic level, piscivorous bottom fish toward short-lived, low trophic level invertebrates and planktivorous pelagic fish' (Pauly et al. 1998).

Our hypothesis incorporates a perspective that departs from the usual conception and practice of fisheries management in three fundamental ways. The first concerns recruitment or the requirements for the sustainability of populations of long-lived, high trophic-level fish. Social learning among fish suggests that the reproduction of culture, i.e., of local adaptations, is a lifelong process dependent on a multi-age class social process in which younger, less experienced fish learn from older, more experienced individuals. The implication is that the sustainability of local populations of social learners may require a cohesive, multi-age social unit for the successful inheritance of learned adaptive knowledge (Wilson and Giske 2023; Budaev et al. 2019).

Second, when population renewal requires the socialisation of young fish, the scale of renewal likely corresponds with the range of social communications that support coherent social groups. Fish communicate over relatively short distances. Consequently, consideration of population renewal or sustainability at a broad scale and only with respect to genetic recruitment, as usually happens in standard fisheries management, ignores the inheritance of learned local adaptive knowledge and the fine-scale population structure relevant to the renewal of populations of long-lived social learners. If a local population's social structure is strong enough to generate reproductive isolation and is persistent, gene/culture interactions (Boyd and Richerson 1985) may explain the fine-scale population structure revealed by the molecular genetic approach presented by Hauser and Carvalho (2008), Kerr et al. (2024) and others.

The third departure from the usual conception concerns *social learning among fishers* (Wilson and Giske 2023). Fishers are great learners, but the spatial and species patterns of exploitation that result from their learning are rarely incorporated in fisheries theory and management. Here, we treat the commercial fishing industry as a population of highly adaptive, flexible and invasive social learners, effectively another component of a complex adaptive system. Approaching the dynamics of the fishing industry in this way suggests that the interactions between humans and the natural system are likely to have causes and patterns of overfishing and recovery that differ among social learners and other species and that are significantly different from those usually envisioned.

6 | Science Directions

We have hypothesised that sentience and learning among fish and fishers might lead to significant demographic effects among fish and distinct patterns of human intervention in the natural system. This perspective leads to questions that are significantly different from those that usually animate fisheries science and suggests an alternative agenda for fisheries. The list of questions below is motivated by a kind of self-scepticism, that is, questions we'd like to ask to fill in or test our knowledge of fisheries circumstances. We expect tests along these lines to find the logical implications of social learning consistent with real fisheries; however, we also know that questions like these are just as likely to lead to the refinement or (for some species) rejection of the ideas expressed in the elaboration of our hypothesis. These bullets cover questions about the population structure and dynamics of long-lived unfished social learners, questions about the response of populations of social learners to fishing and questions about the patterns of overfishing. While the questions are wide and open, they are meant to stimulate consideration of the kinds of scientific questions that arise when social learning is recognised. The bullets are not in any way meant to be a definitive list of important questions.

- How do social behaviours and group dynamics influence the population structure and dynamics of long-lived social learners?
- At what point in life does the vertical, intergenerational transmission of socially learned knowledge typically begin?
- Is social learning among short-lived fish and invertebrates limited to horizontal transfer?
- What role do gene-culture interactions play in shaping the fine-scale population structures of long-lived species?
- What are the consequences of truncating age structures and disrupting social groups for the recruitment and persistence of long-lived species?

- Do invertebrates and short-lived fish rebuild their populations faster than long-lived social learners in overfished circumstances?
- Can broader-scale population collapses emerge from the cumulative effects of local extirpations of long-lived fish? In the early 1990s there was a widespread collapse of cod stocks in the NW Atlantic? What was the cause of the near simultaneity?
- How do the patterns of collapse differ between social learners and other overfished species like invertebrates or short-lived fish?
- How do the behaviours and group dynamics of fishers influence fishing patterns, stock extirpations and the sustainability of fish populations?
- What role does fishers' knowledge and the implementation of area management play in promoting collective restraint and sustainable fishing practices?

A final broad question concerns the ability to model these kinds of questions. In most cases, questions like these will not be amenable to deterministic models. However, it is possible to combine environmental heterogeneity, age-class structure, some genetics and both individual and social learning with the use of individual-based modelling (Acerbi, Jacquet, and Tennie 2012; Acerbi and Tennie 2016; Budaev et al. 2024; Grimm and Railsback 2005; Railsback and Grimm 2011; Stillman et al. 2015; van der Post and Hogeweg 2009; van der Post, Ursem, and Hogeweg 2009). Such model studies can guide the empirical research that will also be needed.

7 | An Alternative Conservation Perspective

A social learning perspective emphasises the natural system's spatial, organisational and temporal complexity. It also suggests that quantitative manipulation of a complex system may be significantly more complicated and prone to unintended consequences than we imagine. The cornerstone of our hypothesis is the idea that the adaptive knowledge of long-lived fish is generated by both social learning and genetics. This knowledge plays a vital role in the evolved complexity of the system. Fishing tends to remove two critical components of complexity—the learned adaptive knowledge held by older fish and the continuing social structure necessary to retain and modify the adaptation of long-lived social learners. For these reasons, conservation efforts should aim to preserve the processes that maintain the information that generates complexity—socially learned knowledge and as usually assumed, the adaptive knowledge in fish's genes.

Standard management policies assume a genetics-only reproduction dynamic. They ignore the critical role of learned adaptations and have not conserved the diverse, patchy niches generated by the experience of long-lived fish. As a result, the restraints usually applied to fishing are designed to protect only the genetic part of the renewability equation and may be ineffective and often lead to perverse and unintended consequences. For example, (1) rules concerning the minimum size of capture are usually invoked to allow more newly mature fish to spawn with the expectation that more eggs will make adequate recruitment more likely. Unfortunately, when these rules are implemented with larger mesh nets, as they usually are, they make older fish more catchable and reinforce the tendency to truncate age structure with all the adverse effects that follow. (2) Quotas are intended to ensure adequate numbers of spawners. However, when a broad-scale quota is applied to social learners, fishing on local populations is not restrained in any meaningful way and, generally, leads to a focus of fishing effort on particular, economically advantageous stocks and a cascade of extirpations of local stocks. (3) Broad-scale licensing for pursuing one or a few species is consistent with the assumed scale and genetics-only recruitment processes envisioned by single-species theory. However, when applied to species of social learners or any species showing local self-reproducing aggregations or patchiness, it does not constrain and may accelerate the local-to-remote cascade of extirpations. Furthermore, (4) with the possible exception of closed areas, the current approach does not address ecosystem effects. It provides no reason to expect the kinds of results Pauly et al. (1998) and Hauser and Carvalho (2008) present. Finally, and perhaps most troublesome, (5) broad-scale licensing induces (almost requires) a mindset among fishers that is principally concerned with where to fish next after local abundance is reduced. In a management regime that allows fishers to roam, those who do not roam are not survivors. Larger mesh, quotas and roaming are a trifecta whose compounded unintended effects are likely to hasten the simplification of the complexity of the natural system.

The critical question is how to manage fisheries embedded in a natural system with 'infinite complexities' (Darwin 1859). Complex systems also exist outside the natural world, of course. Most human societies are organised in ways comparable with the complex hierarchical structure of natural systems (Holland 2012). Like natural systems, human systems are capable of infinite complexity. Over eons, humans have learned, regardless of political mode, to govern their own complexity through multilevel organisation. Responsibilities are divided according to scale, minimising the information required for governance at each level. Inter-scale problems are generally resolved through feedback and feedforward mechanisms focusing on interscale problems only, minimising cross-scale information costs. The reason for this close to universal organisation appears to be the essential need to reduce the costs of the information required at each level of governance (Krakauer 2024, 2011; Holland 2012).

Our social learning hypothesis is fundamentally an argument about how costly information affects the behaviour and the organisation of the natural system at different scales. For example, at a local scale, survival depends critically on the individual's ability to focus on a very restricted body of locally relevant information. The required inheritance of learned adaptive knowledge among long-lived social learners and the restricted communication abilities of fish lead to the localisation of populations of social learners. In contrast, the scale of populations of non-social learners corresponds with the broad scale at which genetic information is transferred. Thus, like other complex systems, the organisation of fisheries systems tends to be multiscale and favours a hierarchical organisation that minimises information costs (Ostrom 1990; Krakauer 2024; Holland 2012).

In light of the above, we assume effective fisheries management needs to be aimed at preserving the information processes that create complexity in the natural system and organised to minimise the information cost of governance. Our social learning hypothesis argues that the information problem in the natural system arises from two mechanisms or tendencies of fishing: first, the tendency to flatten the age structure of targeted populations, leading to the loss of learned adaptive knowledge in culture-dependent species. Second, there is a tendency for profit-seeking fishers to spread the loss of adaptive knowledge to other local stocks and species.

Addressing the *truncated age structure problem* is primarily a problem of learning how to maintain older fish in local populations of long-lived social learners. There has been a long awareness of the important reproductive contributions of big, old, fat, fecund, female fish—BOFFFFs (Hixon, Johnson, and Sogard 2014; Ahrens et al. 2020). Here we add the idea that both old females and old males contribute to the social reproduction of local stocks (Warner 1988, 1990). According to our hypothesis, successful rules intended to keep older fish in a population are likely to depend critically on the peculiarities of local conditions. In many single species fisheries 'slot rules' (a minimum and maximum size) are employed. The intended outcome of slot policies is thoroughly consistent with the maintenance of social learning processes. Nevertheless, we are sceptical about the ability of any existing gear to make the necessary selections in a fishery that catches multiple species, each of which would want its own slot. It may be that local prohibitions on the times and places of fishing may prove more selective and effective. Fish may move in or out of particular places at different times; they may segregate by age classes at some times and not others. They may engage in various kinds and times of migration. There are many possibilities, each one usually dependent on local circumstances. Understanding and adapting to these circumstances depends critically on knowledge of the local system and a governance system that can draw continuously on feedback about the local system and the effect of fishing. Human learning has to take place at the local scale. Local governance that aligns with the organisation of a local system is critical to the interpretation of feedback (Ostrom 1990). The practical problem at each locality will be understanding when and where to use different kinds of gear or time and place prohibitions, i.e., selection restraints. The development of a programme along these lines will have to be based on a robust collaborative effort bringing together scientists and fishers with locally relevant ecological knowledge. It will also have to involve the development of new gear with different selection properties. Furthermore, the required science will need to lean towards the behavioural and ecological aspects of the natural system rather than its large-scale population dynamics as described in the preceding section of the paper.

Preventing *the spread of adverse local consequences* most likely requires area-based governance. In these circumstances, each area is protected from intrusions of fishers from other areas, and, as a result, each fisher in each area can expect to share in the benefits of local conservation, but only if the typical race to get the fish—the commons dilemma—can be resolved. Local organisation means there is a relatively small number of fishers; their knowledge of each other and of the local system is likely to be similar, and the interests of this smaller number are more likely to be relatively homogeneous (Ostrom 1990; Wilson 2017). If higher-level management makes clear its intention to support local governance and efforts to end 'the race to fish', a major stumbling block to collective action and mutual restraint is removed (Ostrom 1990).

In these circumstances, before the commons dilemma has been resolved but after spatial restrictions are in place, an essential strategic question fishers ask themselves changes from 'When this place is fished out, where do I fish next?' to 'What might happen in this place next year with mutual restraint this year?' Fishers' self-interested economic incentives and the likely feasibility of solving the commons dilemma at the local level may incline fishers to collective action and leave them more likely to engage actively with scientists (Wilson 2006; Moller et al. 2004; Farr, Stoll, and Beitl 2018).

Finally, it is crucial to recognise that localising the commons does not isolate each local area. Fish move; various species move at different times to different places and are likely to cross any formal boundaries of local fish management. For example, coastal stocks may retreat to deeper waters in the winter, where they might mix with other local stocks. Many pelagic species migrate seasonally in patterns that take them across any conceivable set of local boundaries. Cross-boundary circumstances like these create a situation in which one group of local fishers may find it profitable to harvest fish another group has been trying to conserve. Suppose a migration crosses several local area boundaries. In that case, fishers at either end of the migration and those along the migration route might be tempted to operate an intercept fishery, but each one is also anxious that no other area does the same. In other words, localisation of governance can potentially convert a broad-scale, degenerate race for the fish into circumstances in which fishers from the affected local areas have strong incentives to engage in mutually beneficial restraint.

In short, our hypothesis argues that the conservation of a complex, multiscale natural system requires the preservation of the adaptive knowledge essential to system organisation. To understand the natural system and to engage in effective mutual restraint, human organisation must be roughly aligned with the multiscale organisation of the natural system.

Author Contributions

Conceptualisation: James A. Wilson, Jarl Giske and Culum Brown. Writing – original draft: James A. Wilson, Jarl Giske and Culum Brown. Final text: James A. Wilson, Jarl Giske and Culum Brown.

Acknowledgements

We thank Geir Huse, Michael Fogarty, Ted Ames, Robin Alden, Robert Steneck, Larry Mayer, Nancy Knowlton, Editor Gary Carvalho, and two anonymous reviewers for their thoughtful comments and perspectives, and Iylarose Willis for the artwork in Figure 1.

Data Availability Statement

The paper contains no data and builds on reading the literature we have cited.

Endnotes

[1] When we use the term 'local stock or sub-population', we refer to a socially formed subset of a larger population; we do not think of 'local' as a particular place or as a set of geographical circumstances. Over the course of a year, a socially cohesive local stock may be the exclusive representative of its species to occupy a particular area. At other times it may move to and share with other local populations different places such as an overwintering refuge. If social processes lead to reproductive isolation, genetics may also take on a local manifestation.

[2] An interesting counter example is the now defunct juvenile herring fishery in Atlantic Canada and New England. Initially, in the late 1800s and for the next 100 plus years, the fishery deliberately avoided the capture of older fish in order to focus on juveniles that could be canned and marketed, misleadingly, as canned sardines. The avoidance of adults was accomplished through time-and-place-based fishing that used weirs and stop seines in the shallow coves and inlets that juvenile herring, but not adults, retired to in the evening. Various pieces of legislation reinforced a ban on the nearshore use of purse seines that supplied adult and bait markets. The fishery for cannery sized fish existed for over a century but was quickly extinguished when with the appearance of new markets for adult fish in the 1970s and 80s and the subsequent relaxation of regulations led to the use of purse seines and mid-water trawls and the loss of older fish (Judd 1988).

References

Acerbi, A., P. O. Jacquet, and C. Tennie. 2012. "Behavioral Constraints and the Evolution of Faithful Social Learning." *Current Zoology* 58: 307–318.

Acerbi, A., and C. Tennie. 2016. "The Role of Redundant Information in Cultural Transmission and Cultural Stabilization." *Journal of Comparative Psychology* 130: 62–70.

Acheson, J. M. 1988. *Lobster Gangs of Maine*. Lebanon, NH: University Press of New England.

Ahrens, R. H., M. S. Allen, C. Walters, and R. Arlinghaus. 2020. "Saving Large Fish Through Harvest Slots Outperforms the Classical Minimum-Length Limit When the Aim Is to Achieve Multiple Harvest and Catch-Related Fisheries Objectives." *Fish and Fisheries* 21: 483–510.

Ames, E. 2004. "Atlantic Cod Stock Structure in the Gulf of Maine." *Fisheries* 29: 10–28.

Ames, E. P. 1997. "Cod and Haddock Spawning Grounds of the Gulf of Maine From Grand Manan to Ipswich Bay." In *Implications of Localized Fishery Stocks*, edited by I. Hunt von Herbing, I. Kornfeld, M. Tupper, and J. Wilson. Ithaca, NY: PALS Publishing.

Aplin, L. M., D. R. Farine, J. Morand-Ferron, A. Cockburn, A. Thornton, and B. C. Sheldon. 2015. "Experimentally Induced Innovations Lead to Persistent Culture via Conformity in Wild Birds." *Nature* 518: 538–541.

Arrow, K. J. 1962. "The Economic Implications of Learning by Doing." *Review of Economic Studies* 29: 155–173.

Arthur, W. B. 1992. *On Learning and Adaptation in the Economy, Working Paper*. Santa Fe, NM: Santa Fe Institute.

Baldwin, J. M. 1896. "A New Factor in Evolution." *American Naturalist* 30: 441–451.

Baum, J. K., and B. Worm. 2009. "Cascading Top-Down Effects of Changing Oceanic Predator Abundances." *Journal of Animal Ecology* 78: 699–714.

Bottinelli, A., A. Perna, A. Ward, and D. Sumpter. 2013. "How Do Fish Use the Movement of Other Fish to Make Decisions? From Individual Movement to Collective Decision Making." In *Proceedings of the European Conference on Complex Systems 2012*, 591–606. Dordrecht, the Netherlands; Heidelberg Germany; New York London UK: Springer International Publishing.

Boyd, R., and P. J. Richerson. 1985. *Culture and the Evolutionary Process*. Chicago, IL: University of Chicago Press.

Brakes, P., S. R. Dall, L. M. Aplin, et al. 2019. "Animal Cultures Matter for Conservation." *Science* 363: 1032–1034.

Brown, C. 2023. "Fishes: From Social Learning to Culture." In *Oxford Handbook of Cultural Evolution*. Oxford, UK: Oxford University Press.

Brown, C., and K. Laland. 2011. "Social Learning in Fishes." In *Fish Cognition and Behavior*, edited by C. Brown, K. Laland, and J. Krause, 240–257. Cambridge, UK: Wiley-Blackwell.

Brown, C., and K. N. Laland. 2003. "Social Learning in Fishes: A Review." *Fish and Fisheries* 4, no. 3: 280–288.

Brown, C., K. N. Laland, and J. Krause. 2011. *Fish Cognition and Behavior*. Cambridge, UK: Wiley-Blackwell.

Brown, C., and M. Webster. 2024. "Fishy Culture in a Changing World." *Philosophical Transactions of the Royal Society*. https://doi.org/10.1098/rstb.2024.0130.

Bshary, R., and C. Brown. 2014. "Fish Cognition." *Current Biology* 24: R947–R950.

Budaev, S., M. L. Dumitru, K. Enberg, et al. 2024. "Premises for a Digital Twin of the Atlantic Salmon in Its World: Agency, Robustness, Subjectivity and Prediction." *Aquaculture, Fish and Fisheries* 4: e153.

Budaev, S., C. Jørgensen, M. Mangel, S. Eliassen, and J. Giske. 2019. "Decision-Making From the Animal Perspective: Bridging Ecology and Subjective Cognition." *Frontiers in Ecology and Evolution* 7: 164.

Busia, L., and M. Griggio. 2020. "The Dawn of Social Bonds: What Is the Role of Shared Experiences in Non-human Animals?" *Biology Letters* 16: 20200201.

Chambers, M. S. 2021. "Benefits to Migratory Fish Populations of Entrainment and Its Potential Role in Fisheries Collapse." *ICES Journal of Marine Science* 78, no. 1: 36–44.

Chen, Y., C. Zhang, L. Dawson, A. Dority, and P. Shepherd. 2013. *Eastern Gulf of Maine Sentinel Survey 2010–2013*. Stonington, ME: Maine Center for Coastal Fisheries.

Clark, C. W., and M. Mangel. 1986. "The Evolutionary Advantages of Group Foraging." *Theoretical Population Biology* 30: 45–75.

Croft, D. P., R. James, P. O. R. Thomas, et al. 2006. "Social Structure and Co-Operative Interactions in a Wild Population of Guppies (*Poecilia reticulata*)." *Behavioral Ecology and Sociobiology* 59: 644–650.

Darwin, C. 1859. *On the Origin of Species by Means of Natural Selection, or, The Preservation of Favoured Races in the Struggle for Life*. London, UK: John Murray.

Eriksson, B. K., U. Bergström, L. L. Govers, and J. S. Eklöf. 2024. "Trophic Cascades in Coastal Ecosystems." In *Treatise on Estuarine and Coastal Science Second Edition*, edited by D. Baird and M. Elliott, 5–49. Elsevier. https://doi.org/10.1016/B978-0-323-90798-9.00006-8.

FAO. 2022. *State of the World's Fisheries*. Rome, Italy: Food and Agriculture Organization of the United Nations.

Farr, E. R., J. S. Stoll, and C. M. Beitl. 2018. "Effects of Fisheries Management on Local Ecological Knowledge." *Ecology and Society* 23, no. 3: 15.

Feinberg, T. E., and J. Mallatt. 2013. "The Evolutionary and Genetic Origins of Consciousness in the Cambrian Period Over 500 Million Years Ago." *Frontiers in Psychology* 4: 667.

Frank, K. T., B. Petrie, J. S. Choi, and W. C. Leggett. 2005. "Trophic Cascades in a Formerly Cod-Dominated Ecosystem." *Science* 308: 1621–1623.

Ginsburg, S., and E. Jablonka. 2010. "The Evolution of Associative Learning: A Factor in the Cambrian Explosion." *Journal of Theoretical Biology* 266: 11–20.

Ginsburg, S., and E. Jablonka. 2019. *Evolution of the Sensitive Soul: Learning and the Origins of Consciousness*. Cambridge, MA: MIT Press.

Giske, J., S. Budaev, S. Eliassen, A. D. Higginson, C. Jørgensen, and M. Mangel. 2025. "Vertebrate Decision-Making Leads to the Interdependence of Behaviour and Wellbeing." *Animal Behaviour*.

Godfrey-Smith, P. 2017. "Animal Evolution and the Origins of Experience." In *How Biology Shapes Philosophy: New Foundations for Naturalism*, edited by D. Smith, 51–71. Cambridge, UK: Cambridge University Press.

Grimm, V., and S. Railsback. 2005. *Individual-Based Modeling and Ecology*. Princeton, NJ: Princeton University Press.

Hauser, L., and G. Carvalho. 2008. "Paradigm Shifts in Marine Fisheries Genetics: Ugly Hypotheses Slain by Beautiful Facts." *Fish and Fisheries* 9: 333–362.

Heathcote, R. J. P., S. K. Darden, D. W. Franks, I. W. Ramnarine, and D. P. Croft. 2017. "Fear of Predation Drives Stable and Differentiated Social Relationships in Guppies." *Scientific Reports* 7: 41679.

Heyes, C. M. 1994. "Social Learning in Animals: Categories and Mechanisms." *Biological Reviews* 69, no. 2: 207–231.

Hixon, M. A., D. W. Johnson, and S. M. Sogard. 2014. "BOFFFFs: On the Importance of Conserving Old-Growth Age Structure in Fishery Populations." *ICES Journal of Marine Science* 71: 2171–2185.

Holland, J. 2012. *Signals and Boundaries. Building Blocks for Complex Adaptive Systems*. Cambridge, MA: MIT Press.

Howarth, L. M., C. M. Roberts, R. H. Thurstan, and B. D. Stewart. 2013. "The Unintended Consequences of Simplifying the Sea: Making the Case for Complexity." *Fish and Fisheries* 15: 690–711.

Huse, G., S. Railsback, and A. Fernö. 2002. "Modelling Changes in Migration Pattern of Herring: Collective Behaviour and Numerical Domination." *Journal of Fish Biology* 60, no. 3: 571–582.

Hutchings, J. A., and R. A. Myers. 1994. "What Can Be Learned From the Collapse of a Renewable Resources: Atlantic Cod, *Gadus morhua*, of Newfoundland and Labrador." *Canadian Journal of Fisheries and Aquatic Sciences* 51, no. 21: 26–2146.

Jackson, J., W. H. Kirby, K. A. Berger, et al. 2001. "Overfishing and the Recent Collapse of Coastal Ecosystems." *Science* 293: 629–638.

Judd, R. 1988. "Grass-Roots Conservation in Eastern Coastal Maine: Monopoly and the Moral Economy of Weir Fishing, 1893-1911." *Environmental Review* 12: 80–103.

Keith, S. A., and J. W. Bull. 2017. "Animal Culture Impacts species' Capacity to Realise Climate-Driven Range Shifts." *Ecography* 40, no. 2: 296–304.

Kerr, L. A., Z. Whitener, S. Becker, et al. 2024. "Stock Identification of Sympatric Atlantic Cod Populations in the Gulf of Maine and Mixed Stock Fishery Analysis Using Otolith-Based Techniques." *Canadian Journal of Fisheries and Aquatic Sciences*. https://doi.org/10.1139/cjfas-2023-0159.

Kopf, R. K., S. Banks, L. J. N. Brent, et al. 2024. "Loss of Earth's Old Wise, and Large Animals." *Science*: eado2705. https://doi.org/10.1126/science.ado2705.

Krakauer, D. C. 2011. "Darwinian Demons, Evolutionary Complexity, and Information Maximization." *Chaos* 21: 037110. https://doi.org/10.1063/1.3643064.

Krakauer, D. C. 2024. *Complex World: An Introduction to the Foundations of Complexity Science*. Santa Fe, New Mexico: SFI Press.

Laland, K., and C. Evans. 2017. "Animal Social Learning, Culture, and Tradition." In *APA Handbook of Comparative Psychology: Perception, Learning, and Cognition*, edited by J. Call, G. M. Burghardt, I. M. Pepperberg, C. T. Snowdon, and T. Zentall, 441–460. Washington, DC: American Psychological Association.

Laland, K. N., and W. Hoppitt. 2013. *Social Learning: An Introduction to Mechanisms, Methods and Models*. Princeton, NJ: Princeton University Press.

Mason, E., T. Riecke, L. Bellquist, D. Pondella, and S. Semmens. 2024. "Recruitment Limitation Increases Suceptibility to Fishing-Induced Collapse in a Spawning Aggregation Fishery." *Marine Ecology Progress Series* 738: 203–224.

Moller, H., F. Berkes, P. O. Lyver, and M. Kislalioglu. 2004. "Combining Science and Traditional Ecological Knowledge: Monitoring Populations for Co-Management." *Ecology and Society* 9, no. 3: 2.

Morgan, C. L. 1896. *Habit and Instinct*. London: E. Arnold.

Myers, R. A., and B. Worm. 2005. "Extinction, Survival or Recovery of Large Predatory Fishes." *Philosophical Transactions of the Royal Society B* 360: 13–20.

Osborn, H. F. 1897. "Organic Selection." *Science* 4: 583–587.

Ostrom, E. 1990. *Governing the Commons, the Evolution of Institutions for Collective Action*. Cambridge, UK: Cambridge University Press.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres Jr. 1998. "Fishing Down the Food Web." *Science* 279: 860–863.

van der Post, D. J., and P. Hogeweg. 2009. "Cultural Inheritance and Diversification of Diet in Variable Environments." *Animal Behaviour* 78: 155–166.

van der Post, D. J., B. Ursem, and P. Hogeweg. 2009. "Resource Distributions Affect Social Learning on Multiple Timescales." *Behavioral Ecology and Sociobiology* 63: 1643–1658.

Railsback, S. F., and V. Grimm. 2011. *Agent-Based and Individual-Based Modeling: A Practical Introduction*. Princeton, NJ: Princeton University Press.

Rose, G. A. 1993. "Cod Spawning on a Migration Highway in the North-West Atlantic." *Nature* 366: 458–461.

Salena, M. G., A. J. Turko, A. Singh, et al. 2021. "Understanding Fish Cognition: A Review and Appraisal of Current Practices." *Animal Cognition* 24: 395–406.

Sanchirico, J., and J. Wilen. 1999. "Bioeconomics of Spatial Exploitation in a Patchy Environment." *Journal of Environmental Economics and Management* 37: 129–150.

Schultz, W. 2024. "A Dopamine Mechanism for Reward Maximization." *Proceedings of the National Academy of Sciences* 121: e2316658121.

Shears, N. T., and R. C. Babcock. 2002. "Marine Reserves Demonstrate Top-Down Control of Community Structure on Temperate Reefs." *Oecologia* 132: 131–142.

Steneck, R. S., T. P. Hughes, J. E. Cinner, and J. A. Wilson. 2011. "Creation of a Gilded Trap by the High Economic Value of the Maine Lobster Fishery." *Conservation Biology* 25: 904–912.

Stillman, R. A., S. F. Railsback, J. Giske, U. Berger, and V. Grimm. 2015. "Making Predictions in a Changing World: The Benefits of Individual-Based Ecology." *Bioscience* 65: 140–150.

Synnes, A.-E. W., E. M. Olsen, P. E. Jorde, H. Knutsen, and E. Moland. 2023. "Contrasting Management Regimes Indicative of Mesopredator Release in Temperate Coastal Fish Assemblages." *Ecology and Evolution* 13: 1–14.

Warner, R. R. 1988. "Traditionality of Mating-Site Preferences in a Coral Reef Fish." *Nature* 335: 719–721.

Warner, R. R. 1990. "Male Versus Female Influences on Mating-Site Determination in a Coral Reef Fish." *Animal Behaviour* 39: 540–548.

Webster, M. M., N. Atton, W. J. Hoppitt, and K. N. Laland. 2013. "Environmental Complexity Influences Association Network Structure and Network-Based Diffusion of Foraging Information in Fish Shoals." *American Naturalist* 181: 235–244.

Weinrich, M., W. Hoppitt, and L. Rendell. 2013. "Network-Based Diffusion Analysis Reveals Cultural Transmission of Lobtail Feeding in Humpback Whales." *Science* 340: 485–488.

Whiten, A. 2017. "A Second Inheritance System: The Extension of Biology Through Culture." *Interface Focus* 7, no. 5: 20160142.

Whiten, A. 2021. "The Burgeoning Reach of Animal Culture." *Science* 372: eabe6514.

Williamson, O. 1985. *Economic Institutions of Capitalism*. New York, NY: Free Press.

Wilson, D. S., and E. O. Wilson. 2007. "Rethinking the Theoretical Foundation of Sociobiology." *Quarterly Review of Biology* 82: 327–348.

Wilson, J. A. 1990. "Fishing for Knowledge." *Land Economics* 66: 12.

Wilson, J. A. 2006. "Matching Social and Ecological Systems in Complex Ocean Fisheries." *Ecology and Society* 11, no. 1: 9.

Wilson, J. A. 2017. "Learning, Adaptation, and the Complexity of Human and Natural Interactions in the Ocean." *Ecology and Society* 22, no. 2: 43.

Wilson, J. A., and J. Giske. 2023. "Does Fishing Dismantle Fish Culture and Ecosystem Structure? Questions About the Implications of Social Learning Among Fish and Fishers." *Fish and Fisheries* 24, no. 5: 889–895.

Wilson, J. A., J. Hill, M. Kersula, et al. 2013. "Costly Information and the Evolution of Self-Organization in a Small, Complex Economy." *Journal of Economic Behavior and Organization* 90: S76–S93.

Wilson, J. A., E. Ostrom, B. Low, and R. Costanza. 2000. "Scale Misperceptions: And the Spatial Dynamics of a Social-Ecological System." *Ecological Economics* 31: 243–257.

Worm, B., E. B. Barbier, N. Beaumont, et al. 2006. "Impacts of Biodiversity Loss on Ocean Ecosystem Services." *Science* 314: 787–790.

Worm, B., R. Hilborn, and J. Baum. 2009. "Rebuilding Global Fisheries." *Science* 325: 578–585.

Zacks, O., S. Ginsburg, and E. Jablonka. 2022. "The Futures of the Past. The Evolution of Imaginative Animals." *Journal of Consciousness Studies* 29: 29–61.