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GHOTI

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Does fishing dismantle fish culture and ecosystem structure? Questions about the implications of social learning among fish and fishers

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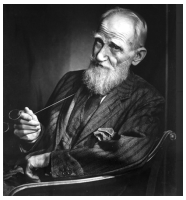
Abstract

Scientific awareness of social learning, especially among vertebrates, has expanded rapidly in recent decades. That literature suggests that social learning may be a second adaptive mechanism that interacts with and refines genetic adaptation. For an individual fish, learning from others reduces the costs of acquiring experience-based behaviours and minimizes the hazards that arise from imperfect knowledge of local regularities. For a group of fish, social learning facilitates the evolution of time and place behaviours that work in its locality. It spreads those behaviours within the group and to subsequent generations. Thus, social learning enables persistent adaptation at a finer scale than might be possible through genetic processes alone. Strong evidence of genetic differentiation at less than a panmictic scale and persistent local depletions suggests regular, fine-scale system structure. Social learning may play an important role in creating and maintaining this finer-scale structure. Fishers' learned adaptations to the market and natural system usually lead them to target larger/older fish and fish aggregations at familiar times and places. However, older fish are likely to be the principal repository of the time-and-place experience required for local growth, survival, and reproduction, while social aggregations are important schools in which younger fish acquire the experience of older fish. Consequently, if adaptation through social learning is important among fish, there is reason to be concerned that heavy fishing of social learners reduces their abundance, as usually assumed, and impairs the inheritance of the socially learned experience required for persistent local adaptation.

KEYWORDS
adaptation, evolution, fish knowledge, local population, selective harvesting



Ghoti papers

Ghoti aims to serve as a forum for stimulating and pertinent ideas. Ghoti publishes succinct commentary and opinion that addresses important areas in fish and fisheries science. Ghoti contributions will be innovative and have a perspective that may lead to fresh and productive insight of concepts, issues and research agendas. All Ghoti contributions will be selected by the editors and peer reviewed.

Etymology of Ghoti

George Bernard Shaw (1856–1950), polymath, playwright, Nobel prize winner, and the most prolific letter writer in history, was an advocate of English spelling reform. He was reportedly fond of pointing out its absurdities by proving that 'fish' could be spelt 'ghoti'. That is: 'gh' as in 'rough', 'o' as in 'women' and 'ti' as in palatial.

1 | INTRODUCTION

One hundred and fifty years ago, Spencer Baird, the first U.S. Commissioner of Fisheries, wrote, "It should … be understood that the exhaustion of a local fishery is not like dipping water out of a bucket, where the vacancy is immediately filled from the surrounding body; but it is more like taking lard out of a keg, where there is a space left that does not become occupied by anything else." (Baird, 1873).

Baird's statement highlights the problem of persistent local depletion in a way that resonates strongly with the widespread and long-lasting depletions of coastal stocks common today. Further, it is consistent with the growing and robust evidence of genetic differences among populations that might otherwise be assumed to be panmictic. Finally, Baird suggests but does not propose a mechanism that isolates local fish populations, preventing or slowing 'filling-in' by other fish of the same species, despite extensive larval drift and few restrictions on adult mobility.

Twenty-three years later, Baldwin (1896) proposed a dual evolutionary process in which learning selects and maintains well-adapted local behaviours until they become intrinsic. Much more recent work, consistent with modern genetics, is summarized by Whiten (2021) and Brakes et al. (2019). This work argues that there is strong evidence that social learning is a second evolutionary mechanism that operates at a fine scale and fast pace among many social vertebrates. Learning is seen as a mechanism allowing animals to adapt to rapidly changing local circumstances. Social processes spread learning within a group and pass it from generation to generation. The result is persistent, diverse, and fine-scale population and ecological structure that complements the broader temporal and spatial adaptations made possible by genetic evolution.

Moreover, genetics and social learning may interact in mutually reinforcing ways. Whiten (2021) notes, "cultural differences may exert selection pressures on functional genes … selection may favor organic adaptations that support culture…. [and] may drive the incipient phases of speciation." To the extent that this mutuality operates, it suggests social learning among fish may make an unappreciated contribution to long-term population and ecosystem structure.

In light of this work, we conjecture that social learning is a second system of adaptation that probably affects many ecologically and commercially important fish species. Social learning operates at a relatively fine spatial and temporal scale. It complements the broad-scale adaptations made possible by genetic evolution, thereby permitting rapid adaptation to the peculiarities of local places. Together the two systems of adaptation generate a diverse, multiscale, and complex system. Unfortunately, the usual methods of fishing and regulation tend to erode the circumstances required for social learning and local adaptation. Fishing tends to target older fish that hold the memory of infrequent local events, for example, migration, and the social aggregations in which learning occurs. Regulation does not restrain and may encourage these targeting patterns. Thus, our concern is that the loss of the social learning part of this dual system of adaptation may seriously impair the structure and dynamics of the entire natural system.

2 | SOCIAL LEARNING AMONG FISH

Brown (2023) and Brown and Laland (2011) thoroughly review the evidence for social learning among laboratory fish. As they summarize, fish of many smaller species are easily maintained in laboratories and readily subject to controlled experiments. The principal findings of these experiments are that fish are quick to learn. They readily form groups and, in a group, learn even faster than alone. They detect predators and prey quicker when in a group. They appear to recognize other individuals and prefer persistent relationships with familiar individuals. They are able to repeat learned behaviours after long absences from the applicable circumstances. Finally, they accomplish the intergenerational transfer of learned behaviours, that is, culture, by simply executing learned behaviours in the presence of new generations. In short, in laboratory settings, the fish studied exhibit cognitive, communication, and social capabilities that allow them to learn from one another in ways comparable to other non-human social vertebrates. These laboratory studies do not conclude that social learning is universal among fish, but they do suggest it is well within their capabilities and likely to be adaptively beneficial.

The idea that social learning is common among wild fish is mainly inferential. The theoretical and empirical studies of Baldwin (1896), Brakes et al. (2019), and Whiten (2021) argue that genetics and social learning can work together. Thus, observing a multi-generational, locally unique behaviour at less than a panmictic scale is a likely indicator of a local selection process. Recent work and observations of social learning among other vertebrates and laboratory experiments with social learning among fish strongly suggest social learning is involved in much of that selection.

Conspicuous and rigorous evidence of finer scale structure in fish can be found in the many studies of incipient speciation or genetic differentiation. There is extensive genetic evidence of persistent sub-panmictic population structure for important commercial species such as gadoids, herring-like pelagics, tunas and salmons, see the extensive citations in Bradbury et al. (2013), Breistein et al. (2022), Clucas et al. (2019), Conover et al. (2006), Grabowski et al. (2011), Hauser and Carvalho (2008), Reiss et al. (2009), Riccioni et al. (2010), and Ruzzante et al. (2000). These studies do not mention social learning; however, they all emphasize that the genetic evidence they present is glaringly inconsistent with the usual broad-scale spatial assumptions of fisheries management.

A second large body of suggestive evidence can be found in the widespread, persistent depletion of local stocks, echoing Baird's complaint. As Pauly et al. (1998 and elsewhere) have persistently pointed out, the age structure of almost every depleted stock was severely truncated before depletion, lending credence to the idea that the loss of collective experience among fish is closely associated with depletion. Much of the evidence for local depletions comes from verbal description since the quantitative methods of management agencies focus on a broader scale that obscures local depletion. However, there are a number of studies that rigorously complement causal observation, for example, Ames (2004), Bradbury et al. (2013), Caddy and Cochrane (2001), Ciannelli et al. (2013), Conover et al. (2006), Jackson et al. (2001), McKenzie (2010), Petitgas et al. (2010), and Ruzzante et al. (2000).

We consider the evidence of widespread genetic differentiation and local scale depletions to be consistent with but not proof of the idea of a second, finer-scale adaptation system. Consequently, we are primarily curious about how social learning among fish might affect the interactions between fish and fishers, leading to the emergence of similar results in many places and times.

3 | FISHING AND SOCIAL LEARNING

3.1 | The mechanisms that store and retrieve adaptive knowledge among social learners

Maurer (1999) poses the overfishing problem in its most general form: "Complex systems that are capable of information storage and retrieval ... should maintain complex structure." Given the apparent widespread loss of population and ecological structure due to fishing, the obvious question is, 'how might fishing affect the information essential for the continuing adaptation of fish?' Here we highlight what we think are the likely considerations.

In a dual adaptation system, the genetic and social mechanisms that store and retrieve adaptive knowledge are significantly different. The entire genetic code—DNA—is stored with each individual. Each element in the code is passed on to a descendant whether the parent used the code element or not. The code is distributed widely through reproduction and larval drift. It addresses adaptation to regularities found over a broad scale and (genetic) evolutionary time. The code also creates the capacity for learning and flexible behaviour. Significantly, the adaptive knowledge stored in DNA can only be lost through biological extinction, which is generally considered an unlikely outcome from fishing.

In contrast, the adaptive knowledge gained through social learning—cultural knowledge—is entirely absent at birth and gradually acquired from many sources. Individuals can only learn what they observe, and their observations are limited to the locations visited by their group. As a result, the learned, or adaptive, knowledge an individual can acquire and pass on is restricted to behaviours that occur during its lifetime in the local place(s) inhabited by its group. Thus, the geographical and temporal range from which cultural knowledge is sourced is far narrower than the range of genetic knowledge. It is equally important to note that the persistence of local culture is entirely dependent on the continuous intergenerational transfer of adaptive knowledge through social learning.

3.2 | Variations in the distribution of adaptive knowledge

The distribution of socially learned knowledge is probably much less uniform than genetic. It likely varies significantly between groups at different locations and within groups at the same location. Individuals' knowledge will vary at any location according to their experience and what they have learned from others. Very young fish, for example, have not had the time to gain much experience. Further, limited cognitive ability (Budaev et al., 2019) means fish are likely to learn different lessons from similar experiences, that is, copying errors are likely to be frequent.

Consequently, it would seem that a group is likely to develop a nearly uniform behavioural response to a particular kind of event only after repeated exposure. Thus, when learning opportunities occur often, for example, an hour and place where prey usually can be found, the resulting behaviours spread rapidly through the group.

In contrast, infrequent regular events, such as an annual spawning migration, create few learning opportunities. Young adults may get to the spawning ground or other seasonal locations because they live within a social group and simply follow the group; they may only gradually learn the way, possibly over several years. Presumably, older individuals have accumulated more experience with infrequent events (Chambers, 2021; Huse et al., 2010; MacCall et al., 2019; Petitgas et al., 2010; Rose, 1993) and are more likely to anticipate appropriate behaviours correctly. Thus, the culturally derived behaviours that adapt a group to infrequent but regular local events are likely to be acquired slowly and reside mainly in the memories of older fish.

3.3 | Collective decisions

In the immediate term, when schooling fish, even those composed entirely of naïve young, react to the presence of a predator, for example, they communicate very quickly, with little ambiguity and remarkable synchrony. According to Kao et al. (2014), information communication is close to optimal in these circumstances. The differences in the private information held by individuals are minor and of very short duration. This behaviour is more or less uniform over the range of the species and appears to have a genetic basis.

Another benefit of genetically driven group formation is that it puts fish close to one another and facilitates social learning. The knowledge that can be gained through social learning is, by definition, not held equally by all group members. It is knowledge that is experiential rather than genetic, reflecting group members' different private memories about particular local events. For example, memories of a feeding opportunity that occurs at a specific place on a certain phase of the moon or a seasonal migration are likely to be very different. Recent recruits may have little or no memory of such events. On the other hand, older fish are more likely to have encountered such events, have knowledge of the trade-offs involved, and have memories of the actions that worked in previous similar circumstances (Couzin, 2018; Kao et al., 2014; Krause et al., 2000).

Effective group decision-making regarding these quasi-regular events requires a collective mechanism that consistently focuses on those individuals with memories of successful past actions in similar instances. The literature on social learning calls this mechanism consensus (Couzin, 2018; Whiten, 2021). Consensus is a common form of decision-making that appears among many social animals, including fish, mammals, and birds. Experienced individuals generally drive consensus; their leadership spreads shared memories of behaviours that have worked in the past while simultaneously reducing the cognitive and informational demands of autonomous decision-making (Krause et al., 2000; Whiten, 2021). In a process like consensus, if any particular action is successful, the next time similar circumstances are encountered, the proportion of individuals sharing the memory of the previous successful response will be much larger, and group repetition of the behaviour will be more likely. In effect, so long as consensus can focus on experienced individuals, it is a conservative decision mechanism that preferentially repeats the behaviours of fish that survived or prospered when the group encountered similar circumstances in the past.

3.4 | The persistence of groups

The advantages an individual gains from socially learned knowledge might also contribute to the persistence of locally adapted groups, reinforcing the group's coherence and its value to the individual. A high level of membership stability would appear to be critical for creating and maintaining local culture. If the flux of 'foreign' individuals into a group is too high, then locally irrelevant individual experiences will increase the ambiguity of feedback and reduce the possibilities for local adaptation through social learning. Off-setting the harmful effects of immigration, the circumstances leading to the reproduction of knowledge, that is, 'in situ' transmission, would appear to favor ongoing relationships (as shown by laboratory experiments cited in Brown, 2023). Furthermore, knowledge of valuable adaptive behaviours is only available to an individual who is present when the behaviours are employed. Thus, for social learners, there is likely to be an evolutionary incentive (coded in DNA) for individuals to stay with the group and for the cultural knowledge developed by the group to be localized and long-lasting.

If these incentives are particularly strong, local culture may isolate the biological reproduction of a group, facilitating the widely observed genetic differences within populations that might otherwise be considered panmictic (Whiten, 2021). Genetic studies of gadoids, herring-like pelagics, tunas and salmons (as cited above) all show local stocks that mix at certain times of the year and then, in other seasons, separate into persistent, genetically differentiated groups inhabiting different places. This kind of long-lasting social isolation would appear necessary for the evolution of a locally adapted genetic trait.

4 | THE VULNERABILITY OF SOCIAL LEARNING

From this perspective, social learning among fish contributes significantly to population and ecosystem structure, persistence, and, probably, continuing genetic evolution (Whiten, 2021). The most vulnerable aspect of this contribution is the storage and retrieval of the knowledge fish require for local adaptation. Social organization is necessary for the transmission of knowledge in the short term and across generations. Older fish appear to be the storehouse of the group's knowledge of life-history-critical but infrequent events and the source of much of the behavioural regularity and persistence of the group. For example, the memories of older fish would appear to play the same crucial hedging role as the extreme fecundity of BOFFFFs (big, old, fat, fecund, female fish, Hixon et al., 2014). That is, if there is a string of years in which biological or social recruitment fails, the knowledge held by older fish is crucial to maintaining the cultural adaptation of the group. This implies that if a group's collective memory is short-lived due to the loss of older individuals (or a sudden dominance of younger fish [Huse et al., 2010]), the intergenerational transfer and persistence of locally adapted knowledge might be easily corrupted or lost. In short, social learning would appear to be particularly vulnerable to the loss of older fish and the social circumstances that transfer their experience to new generations.

Furthermore, the restricted geographic scope of cultural knowledge might leave it vulnerable to external perturbances that are much more likely at a local rather than species-wide scale (De Luca et al., 2014; Huse et al., 2002; Petitgas et al., 2010). Fishing, of course, can be a significant local perturbance.

5 | HOW MIGHT FISHING IMPAIR SOCIAL LEARNING AND LOCAL ADAPTATION?

Fishers develop and refine behaviours based on their experience in the natural system and the market. They learn from one another and form groups (Acheson, 1984; Ostrom, 1990; Wilson, 1990; Wilson et al., 2007). Most importantly, humans learn and adapt far faster than fish, precluding co-evolution.

Fishers usually target easily caught, larger, valuable fish at convenient, familiar locations. They also target dense aggregations, for example, schools and migrating groups, simply because that is where fish are easiest to find and catch. At all times, they target high-value fish and minimize, as best they can, the diversity of their catch. For any target species, fishers focus on more valuable fish, for example, larger fish provide a higher meat yield than small fish and fish caught close to port are more valuable than fish caught at a distance. All other things equal, fishers, like fish, would prefer to operate at familiar places and times where experience tends to reduce their costs and increase their returns. These simple preferences lead to three forms of ecological disturbance that appear to be common to almost all fisheries. (1) Fishers target valuable market species in preference to others; (2) they tend to target larger fish and aggregations; and (3) they fish at familiar times and places.

The outcome for the targeted fish is often reduced local abundance, truncated age structure (Pauly et al., 1998), and, for social learners, the 'exhaustion' of local groups (Ames, 2004; Sala et al., 2001). As emphasized above, truncated age structure and impaired social organization may lead to the loss of the group's collective memory of infrequent and life-history-critical seasonal events such as migration (see Berdahl et al., 2016; De Luca et al., 2014; Huse et al., 2002; MacCall et al., 2019 for observation and models of this effect). If fishing removes this knowledge, the advantages a group acquires through local adaptation dissolve. This is the social learning equivalent of extinction. Persistent local depletions suggest that the adaptive knowledge in DNA alone is not sufficient to support local populations even in places where they once existed as social entities. Hauser and Carvalho (2008), addressing only genetically supported lost local adaptations, note "locally adapted populations are unlikely to be replaced through immigration…"

5.1 | A proposition about social learning and overfishing

If fish are social learners and there is a dual system of adaptation, as argued in Whiten (2021), the effects of fishing are likely much different than usually imagined. Consider the following proposition about the interactions of fish and fishers:

> The local adaptations of fish that are social learners generate relatively regular patterns in time and place. Fishers learn these patterns. Fishers' knowledge is not precise (because the regularity of fish is not precise), but it is valuable information that informs and tends to localize their search. Market preferences lead fishers to target larger (older) fish of profitable, abundant species at familiar times and places.
>
> As fishing on a familiar local stock intensifies, the effects become apparent in the stock's declining numbers, reduced average size and age. These changes begin to impair the intergenerational transfer of socially learned, locally adapted fish behaviours, increasing the variability of the groups' time-and-place behaviour. Eventually, the abundance of older fish may be too low for consensus to demonstrate appropriate behaviours to younger fish, especially those associated with the infrequent life-history-critical aspects of their seasonal rounds. Young fish risk being at the wrong places at the wrong times, possibly leading to recruitment failure and the loss of the cultural knowledge that maintains local adaptation.
>
> As this happens to a local stock, fishers have increasingly strong incentives to move on to other local stocks or species. If they move to other social learners, the sequence leading to local 'exhaustion' may repeat. As more and more local cultures are affected in this way, the organization of the ecosystem is disrupted, for example, local stocks of an important prey species such as herring may be lost, leading to a cascade of effects (Ames, 2004; Petitgas et al., 2010).
>
> Normal regulatory controls that aim to keep spawning numbers sufficiently high tend to encourage fishing practices that actively dismantle social learning mechanisms. The principal regulatory tool, broad-scale quotas, tends to focus fishing on local groups of fish whose organization and time and place movements are still intact. Mesh size regulations typically make nets better able to catch large fish. On the other hand, common qualitative measures such as spawning closures and MPAs implicitly recognize culture.
>
> Thus, the human behaviour leading to persistent local depletion of fish is not simply 'catching too many fish' as imagined by the usual single species population model. It is also likely due to the loss of the cultural knowledge and social organization fish require for robust local adaptation. The long-term result may be a simplified ecosystem characterized by 'exhausted' local stocks of social learners, a cascade of significant changes among strongly interacting species, and the growing importance of species that do not engage in social learning, that is, species whose behavioural adaptations are not social and not affected by fishing except through extinction.

We conclude that a principal goal of fisheries management should be the conservation of the circumstances that enable social learning among fish.

6 | SUMMARY

Social learning is a system of adaptation that operates at a fine temporal and spatial scale. It complements the broad scale of genetic adaptation. Evidence of persistent local depletions and numerous instances of genetic differentiation at a sub panmictic scale is consistent with the idea that social learning may be common and significant among ecologically and commercially important fish. If social learning is indeed common, then there is good reason to suspect normal fishing and regulatory practices may dismantle the natural mechanisms fish require for social learning, leading to possibly severe consequences for population and ecosystem structure.

This view of the natural system will require rethinking our relationship with the ocean, especially the scale of the regulatory and scientific organization we will need to learn about and manage a natural system with two complementary systems of adaptation. We expect a dual adaptation perspective will generate many testable hypotheses that are simply not conceivable with a focus on genetic adaptation alone.

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DATA AVAILABILITY STATEMENT

The paper is a theoretical and purely verbal discussion based on data and results in the papers cited. There are thus no data sampled or stored for this paper.

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