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Evolutionary changes in cognition due to fisheries mortality?

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Fish experiencing harvest mortality often evolve a fast life-history that prioritizes investment in current versus future reproduction, thereby potentially limiting energetic investment in the brain. Fisheries may also select for shy fish that are less willing to learn, or directly select fish with poor cognitive ability. The resulting evolutionary changes can alter the cognitive performance of individuals and affect fish populations and fisheries quality.

Fisheries-induced selection

Capture fisheries substantially increase mortality beyond natural levels. Over multiple generations, elevated harvest-induced mortality can promote evolution of a fast life-history [1]. Positively size-selected harvest, whereby large-sized individuals have a greater probability of being captured, is typical of most fisheries and can intensify evolution of a fast pace of life [1,2]. A faster life history means that fish attain sexual maturation earlier and often at a smaller body size, investing more energy into reproduction, which reduces postmaturation growth and longevity [1]. Such adaptations are generally characterized by a shift in energy allocation away from somatic growth to early reproduction, thereby betting on current versus future reproduction [1].

Most research on fisheries-induced evolution (FIE) has focused on life-history traits, such as maturation, and the related morphological trait body length [1]. Recently, fisheries-induced adaptive changes in behavioral traits have gained attention [1–3]. A fast life history can be associated with elevated boldness and foraging activity, which allows the fish genetically predisposed to early reproduction to acquire enough resources for growing gonads and engaging in reproductive behaviors [2]. However, if positive size-selective harvest is pronounced, or harvest selection directly operates on behavioral traits that affect encounters with fishing gear, such as activity and boldness, increased shyness can also be adaptive, despite the evolution of a fast life history [2]. Both mechanisms (alteration of energy allocation and changes in behavioral traits) can affect the cognitive performance of fish. Here, we present a novel hypothesis by which fisheries could impact the evolution of fish cognition, and derive implications for future research.

Mechanisms that can cause changes in cognition due to fisheries mortality

We hypothesize that fisheries mortality may cause changes in cognition through at least two mechanisms: one direct energy-expenditure pathway that affects the ability to express cognition, and a behavior-mediated indirect pathway that affects the opportunities for, or willingness of, the animals to learn. Other mechanisms are plausible, such as direct selection on brain regions involved in fitness that can alter cognitive functions, or direct selection on cognitive traits (e.g., ability to avoid fishing gear [4]).

Energy-expenditure pathway

When life history has evolved to be fast in response to harvest mortality, there is typically more investment of energy in the development and maintenance of reproductive structures and processes [1]. However, because energy input and food processing are limited, energy allocation to either reproductive, somatic, or other energy-intensive tissues are in conflict with each other. Similar to energy investments in growth and reproduction, investments in neuronal tissues in the brain are energy hungry [5]. Thus, increased allocation of energy to reproduction can limit the energy available for investments in neuronal tissues, resulting in a smaller brain relative to that expected from the allometric relationship between the brain and body size of an individual, which can be associated with a lower count and density of neuronal and non-neuronal cells [6,7]. Given that cognitive abilities in animals are largely attributed to neural processing in the brain, smaller size-corrected brains with fewer neurons can lead to reduced cognitive ability [6], thereby altering cognitive behavioral types and affecting learning and memory (Figure 1). Energetic trade-offs between the brain and other tissues may, depending on the evolutionary context, also produce different outcomes than expected (e.g., [8]), and this may increase cognitive performance in response to predation (Figure 2).

Behavioral pathway

Harvest selection can also alter fish personality traits, defined as consistent among-individual differences in behaviors, such as boldness, exploration, activity, aggression, or sociability [2,3]. These traits may be related to cognitive behavioral styles [9]. Under a plausible scenario in which intensive and positively size-selective harvest favors the evolution of shy behaviors [2,3], cognitive performance may be affected through alteration of willingness and motivation to acquire new information (Figure 1). Fish that are shy and less explorative and reactive in nature may demonstrate slow cognitive phenotypes and, consequently, may not only learn about rewards more slowly, encounter rewards later, and generally make slower decisions, but also sample the local environment more intensively [9]. Slower learning and decision-making speed can, in turn, impact foraging because the fish might take longer to make exploratory decisions and find food [9]. Yet, a more detailed sampling effort by slow learners may help them to update their information more accurately, especially when the environment

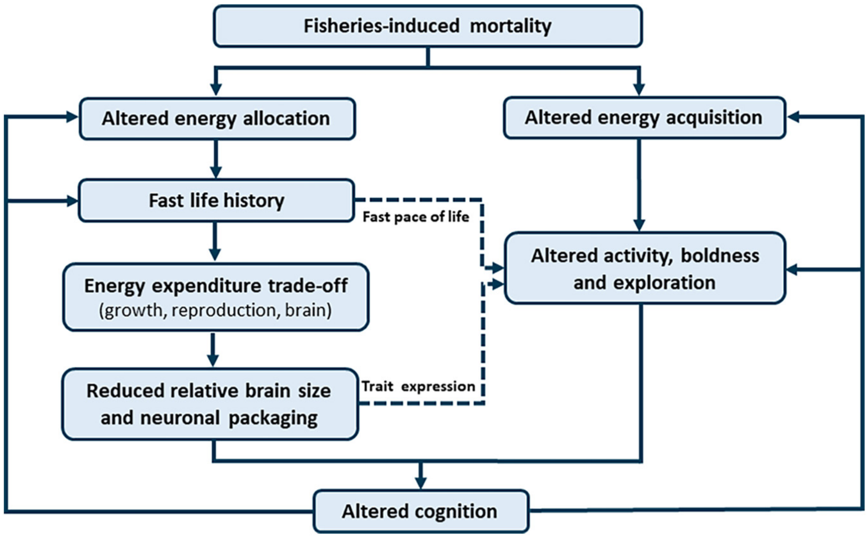

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Figure 1. Elevated fisheries-induced mortality can lead to changes in energy allocation and acquisition patterns. Changed energy allocation alters life history strategies. When reproduction is prioritized (fast life history), there will be a trade-off in energy investment between reproduction and other energy-expensive tissues in the body, such as the brain. This could lead to reduced relative brain size and neuronal packaging that can impact individual cognitive ability. Changes in energy acquisition can be caused by altered activity, and exploratory and risk-taking tendencies, which may, in turn, affect individual willingness to learn. Altered brain and cognition, through ecoevolutionary feedbacks, can have further impacts on behavioral, and life-history trait expression.

changes; this can accentuate cognitive flexibility [9]. In summary, altered behavioral tendencies as an adaptation to harvest mortality can alter individual cognitive behaviors in complex ways, either positively or negatively (Figure 1). However, it is possible that certain fishing gears, such as rod-and-reel used in recreational angling for predatory fish, can directly select on cognitive traits, such as the ability to recognize and avoid lures [4]. Removal of fish that are less able to learn about gear avoidance could leave behind individuals with elevated cognitive ability to avoid gears.

Experimental evidence for mortality-induced changes in the brain and cognition in fish

There are two lines of experimental evidence supporting the possibility of mortality-induced changes in the brain and cognition. The first example involves evolutionary changes in the brain in response to natural predation. Threespine stickleback (*Gasterosteus aculeatus*) experimentally exposed to trout as natural predators evolved significantly smaller brains [10]. A possible explanation for this finding is that the predators favored energy investment into specific behaviors (e.g., escape) and defensive structures that reduced predation risk at the expense of energy investments in the brain [10]. Another explanation could be that energy was reallocated away from the brain toward reproduction, thus limiting the energy available for brain development [10]. Reduced brain size is often associated with reduced cognitive abilities [6], but this greatly depends on the context in which cognition is measured [11] and demands further empirical confirmation.

The second example involves a multigeneration size-selective evolutionary harvesting experiment in zebrafish (*Danio rerio*), where fish evolved a fast life history in response to positive size selection. Large size-selective harvesting over five generations reduced collective learning and increased decision-making speed when fish were tested for memory in an associative task [12]. Probable explanations involve altered energy pathways associated with the evolution of a fast life history [12], or the correlated evolution of shy behavioral tendencies that affected cognition-related behaviors [13].

Concluding remarks: possible consequences of altered cognition and future research

Alteration of cognition in exploited fish can have consequences for social groups, populations, communities, ecosystems, and, ultimately, humans [1–3] (Figure 2). For example, cognitive changes could adversely impact collective learning and decision-making in fish groups [12] or reduce group cohesiveness, thereby elevating natural mortality [13]. At the population level, altered collective cognition could impact growth, recruitment, survival, and dispersal in complex ways (Figure 2). For instance, the ability to collectively accrue food resources and explore new patches may change [14], thereby affecting individual, and possibly population, growth. Population dispersal and migration to new locations when the environmental conditions change can also be altered due to altered spatial learning. Finally, because larger brains and higher cognitive ability in fish enable flexible use of food-web compartments at the community level [14], evolution of lowered cognition in response to harvesting may affect trophic interactions and food-web functioning, and, ultimately, fisheries yield. Alternative scenarios are plausible, for instance, when exposure to catch-and-release recreational fisheries or commercial longlining would leave behind cognitively better-performing individuals, which would lower catch rates through improved gear avoidance behavior [4].

Our proposal of harvest-induced adaptive changes in cognition must be considered a reasoned hypothesis, with initial

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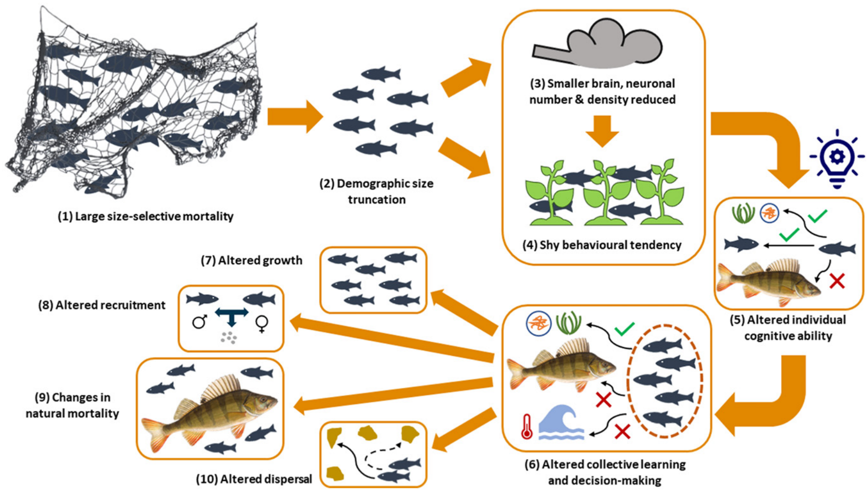

Figure 2. Possible consequences of harvest-induced changes in cognition. Clockwise from top left, (1) large size-selective mortality amounting to (2) demographic size truncation, and selection pressures on fitness-related traits that may lead to the development of (3) smaller brains with less dense neuronal packaging and (4) shy behavioral tendency. Together, these may lead to (5) altered abilities of individuals to find food, mates, and shelter, and avoid predators. Changed individual cognitive potential along with reduced social cohesion may result in (6) altered collective learning and consensus decision-making while foraging, avoiding predators, and responding to changing environments. (7) Individual growth and (8) recruitment in populations could be altered due to reduced resource acquisition potential and more choosiness in diets, mates, and patches or habitats. (9) Natural mortality might also change due to diminished body size and reduced attention to social cues, resulting in reduced transfer of information about potential threats. (10) Population dispersal could be affected due to decreased spatial and active learning potential. These possible outcomes need to be investigated further, and currently only represent reasoned hypotheses without substantial empirical support. Fishing net image in (1) sourced from imgbin.com. Perch image by Eric Otten/DAFV.

experimental support in small-bodied model fish. Whether similar patterns are also observed in wild fisheries, whether changes in cognition are evolutionary or merely occur within the realm of plasticity and development, and the degree to which environmental context determines fisheries selection of cognition and related traits [15], are open questions awaiting further empirical studies. Interdisciplinary research is required to examine the evolution of brain and cognition in wild fish in response to harvest-induced selection, and its possible consequences for populations, ecosystems, and fisheries.

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Declaration of interests

The authors declare no competing interests.

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