Fisheries-induced evolution and selection on physiological traits

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Key points

- Fishing-induced evolution can occur when fishing non-randomly removes individuals from populations by being selective for traits with a heritable genetic basis.
- Numerous physiological traits are likely to be important in determining which fish are likely to be captured and which are not, acting at various stages throughout the capture process from habitat selection, to fishing gear encounter and avoidance, to potential escape.
- Passive fishing methods like traps and angling are more likely to select for traits related to feeding motivation, metabolism, and spontaneous activity, while more active gears like trawls are likely to selectively capture fish based on the capacity for aerobic and anaerobic swimming.
- Environmental factors such as temperature and hypoxia will play an important role in determining which traits are under selection by modulating trait variability and heritability, via gene-by-environment interactions.
- Knowledge of the physiological mechanisms of fisheries-induced evolution will be key for devising ways to reduce selectivity, and understanding the extent to which evolutionary effects of fishing may make populations less able to cope with other forms of environmental change.

Glossary

Active fishing gear Fishing gears that actively pursue or encircle fish; capture success depends heavily on avoidance and escape capacities of fish

Aerobic scope The capacity for an animal to increase its level of aerobic metabolism beyond that which is required for maintenance alone; it sets the capacity for oxygen-consuming physiological processes that an animal may perform at a given time. Aerobic scope is the difference between minimal and maximal oxygen consumption rate

Boldness A behavioral trait describing the tendency of individuals to engage in risk-prone activities, usually in a non-novel environment

Critical oxygen tension (Pcrit) The critical oxygen tension at which an animal's oxygen consumption rate becomes limited by the environment, i.e., by the partial pressure of dissolved O_2 in ambient water

Density-dependent evolutionary effects Changes in the selective advantage of traits due to changes in population density, or the capacity for evolutionary change in traits

Fisheries-induced evolution The outcome of fishing selection that will affect fish populations over generations when selected traits carry some heritable component, leading to the erosion of genetic and phenotypic diversity of target populations

Fishing selection The non-random removal by fishing of a subset of the target fish population, based on specific phenotypic attributes. Here defined as any selection occurring throughout the entire fishing process, from habitat-specific gear deployment to the moment a fish is landed, as well as sublethal effects on growth, survival, and reproduction occurring after fish escape or release after capture

Hypothalamic-Pituitary-Interrenal (HPI) axis A set of complex interactions and neuroendocrine feedbacks centered around the hypothalamus, pituitary gland, and internal glands in fish; key to the functioning of many organ systems and induction of the primary stress response and signaling via cortisol release; functionally analogous to the hypothalamic-pituitary-adrenal axis (HPA) in other vertebrates

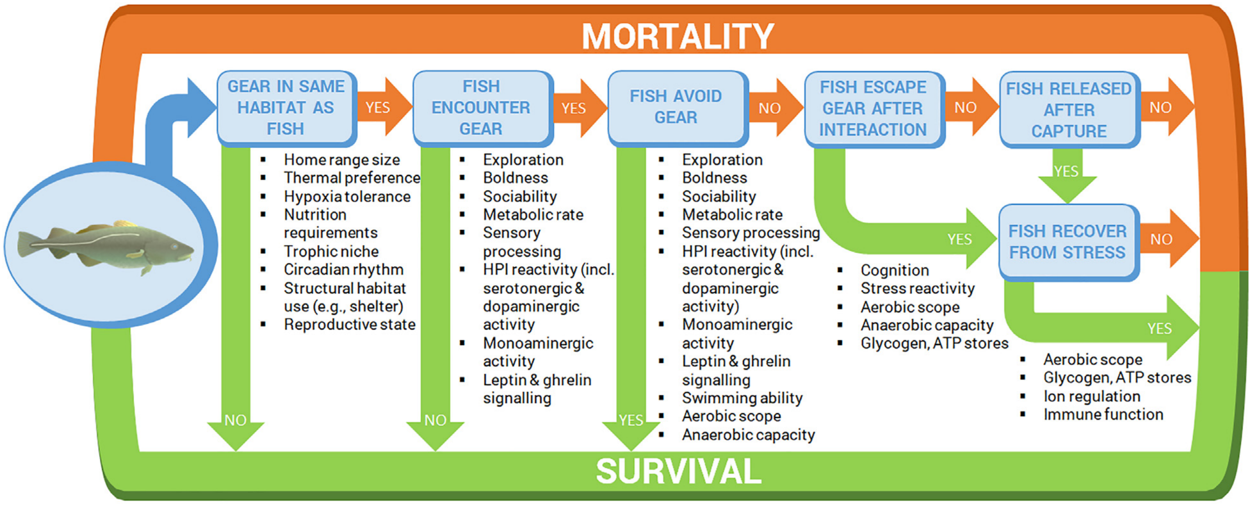
 https://doi.org/10.1016/B978-0-323-90801-6.00085-9

Metabolic rate Energy throughput required by an animal to perform all physiological tasks, including those required for maintenance, activity, digestion, and biosynthesis. Often referred to using specific definitions, for example only including the energetic requirements of maintenance (i.e., standard metabolic rate) or maintenance plus spontaneous activity (i.e., routine metabolic rate)
Passive fishing gear Fishing gears that are relatively stationary and depend on fish to voluntarily interact with the gear; capture success depends on active behaviors of fish associated with spontaneous activity and motivation to inspect and ingest a bait, attack a lure, enter a trap, or approach a gill net.
Phenotypic plasticity The environmentally-induced expression of multiple possible phenotypes based on a single genotype; depending on the trait, and timing and duration of the change, changes can be reversible or permanent
Sociability A behavioral trait describing the tendency of individuals to associate with conspecifics, excluding associations due to aggression
Trait repeatability A measure of how consistently individuals express potentially plastic traits. Functionally defined as the proportion of trait variation within a population that is attributable to differences among individuals, as opposed to variation that occurs within individuals

Abstract

Fishing selectively removes individuals from populations when phenotypic traits make certain individuals more desirable or vulnerable to capture. When this fishing-associated selectivity occurs due to traits with a heritable, genetic basis, fisheries-induced selection can occur. Evolutionary changes in body size and life-history characteristics due to fishing have received the most research attention, but at every stage of the fish capture process, physiological mechanisms may also play a role in determining which fish within a species are captured and which are not. Environmental variables, including temperature, hypoxia, food availability, and population density, may all influence which traits are under selection due to fishing and to what extent, largely due to the effects of plasticity and gene-by-environment interactions. Increased understanding of the relevance of physiology in modulating the evolutionary effects of fishing will be key in devising solutions for reducing selectivity and preserving genetic diversity for adaptive capacity in the face of environmental change.

Teaching slide



Introduction

The exploitation of wild fish populations by humans is a worldwide phenomenon, with recreational or commercial fishing occurring in nearly every aquatic habitat on earth. A large proportion of the global human population depends on fish as a source of protein, and the commercial and recreational fishing sectors contribute enormously to local economies. Human fishers have proven to be incredibly effective predators, with overfishing often being cited as a factor contributing to population declines in wild fish populations. To understand the true extent of the effects of fishing, however, we must also consider the fish that are not captured. Similar to natural predators, human fishing often non-randomly removes fish from populations in a selective manner, though the nature of this selection may differ. A key question to consider with respect to fishing, therefore, is why are some individuals within a population captured by fishing while others are not? Are there differences in the traits expressed by fish that avoid capture as compared to those that are removed from the population? If fishing-associated selection is related to traits that have a heritable genetic basis, evolutionary effects can occur in a process termed fisheries-induced evolution (FIE).

The potential for fishing to act as a selective force has been recognized for nearly a century, but has gained increasing research attention over the last two to three decades. The majority of this research has focused on the consequences of size-selective fishing (Heino et al., 2015). For numerous reasons, including legal requirements, fisher preferences, and the physical mechanisms by which fishing gears operate, there is often a tendency for fishing to remove larger-sized individuals. This represents a major difference from selective pressures caused by natural predators in aquatic ecosystems, whereby larger fish are usually less vulnerable to predation and therefore tend to have the highest reproductive success. In contrast, the removal of the largest individuals from a population by fishing may have numerous effects on population demography, with selective pressure for fish to mature earlier, and at smaller sizes, because those that devote more energy to reproduction as opposed to growth will be those that tend to survive and reproduce, and therefore have the highest fitness in a fished population. Accordingly, the occurrence of smaller mature fish in wild, exploited populations has frequently been observed.

One difficulty in the study of FIE is to directly compare fished and unfished populations of the same species because there are numerous other confounding environmental variables that can affect trait expression. Moreover, evolutionary change can be difficult to observe in wild populations of large-bodied, slow-growing species. For these reasons, much of our empirical knowledge of FIE comes from laboratory studies on substitute model species (e.g., guppies, zebrafish) that have similar characteristics to the wild species of interest (Conover and Baumann, 2009; Diaz Pauli and Heino, 2014). From these studies, results suggest that repeated selection on body size may lead to correlated change in a number of other behavioral and morphological traits (Uusi-Heikkilä et al., 2015; Crespel et al., 2021a,b). It must be noted, however, that there are numerous challenges associated with choosing a suitable surrogate species for studies of FIE. Firstly, an ideal surrogate species will show similar behavior to species that are of broader fisheries interest. For example, European minnows have been used as a surrogate species when studying the behavior of benthic marine species around trawls and traps, because they show similar shoaling behavior and associations with the substrate. When studying reproductive consequences of selection and FIE, it is also important to consider how differences in the life histories or reproductive systems between the surrogate species and broader species of interest may differ. For instance, the overlapping generations of many marine species differs from the discrete, separate generations produced by surrogate species such as zebrafish in the laboratory, and live-bearing species such as guppies may display differing reproductive effects as compared to egg-laying or broadcast spawning species. In addition, the source population of the surrogate species must be considered: captive reared populations may have very low or unusually high genetic and phenotypic diversity for specific traits, depending on the degree of inbreeding that has previously occurred, the number of contributing broodstock, and the degree of mortality and artificial selection that has occurred during rearing. In contrast, obtaining fish from wild populations may be problematic because the capture process itself may bias the phenotypes that are ultimately used in the study, especially if only one capture method is used. Indeed, this can be a problem for all studies examining animals from wild populations and not only for those investigating FIE. For these reasons, the choice of surrogate species must be carefully considered when planning studies of fisheries selection and FIE, or ideally avoided by studying the actual species of interest.

Scientists have recently started to investigate the physiological mechanisms underlying expressed behaviors that render certain fish more susceptible to fishing mortality than others and have identified a number of physiological traits that may be under direct fishing-associated selection (Diaz Pauli and Sih, 2017; Hollins et al., 2018). Indeed, many fishing gears are designed to function in ways that directly exploit the natural behaviors of fishes, and especially those associated with their foraging and social-behaviors, two categories of behaviors that are also intimately linked with aspects of fish physiology including bioenergetics, endocrine signaling, and sensory systems. For example, individual fish that are more bold and willing to take risks while foraging may be more likely to inspect a baited hook or enter a trap. Furthermore, bolder individuals are often found to have a higher metabolic rate as compared to those that are more shy, meaning that they require more energy to survive and may therefore have a higher foraging motivation, putting them at greater risk. Given that both boldness and metabolic rate are known to show some degree of heritability, it is plausible that this mechanism may cause evolutionary change, with populations that have experienced heavy angling exploitation possibly containing more individuals that are very shy (Arlinghaus et al., 2017). Physiological traits may also directly determine which individual fish may be captured by active fishing gears. During trawling, for example, the net pursues fish and captures those that become physically exhausted and fall back into the net, thereby potentially capturing individuals with a reduced capacity for sustained swimming.

The specific traits under selection by fishing will depend on the gear type being used. Fishing gears can be broadly categorized as being either active or passive, although in reality this distinction is more of a continuum as opposed to binary (Hollins et al., 2018). Gears that are more active are those that are mobile and pursue or encircle fish, including trawls and seines. Passive gears are relatively immobile and rely on fish to voluntarily approach and engage with the gear, including gillnets, traps or pots and most forms of angling. In general, active gears may select on traits associated with threat detection or escape response, including sensory mechanisms and swimming ability. Alternatively, passive gears may be more likely to select on traits associated with risk-taking, exploration, and feeding motivation, including metabolic rate or endocrine systems controlling hunger. It should be noted, however, that while these are broad classifications that can be useful for deriving testable hypotheses and understanding general mechanisms,

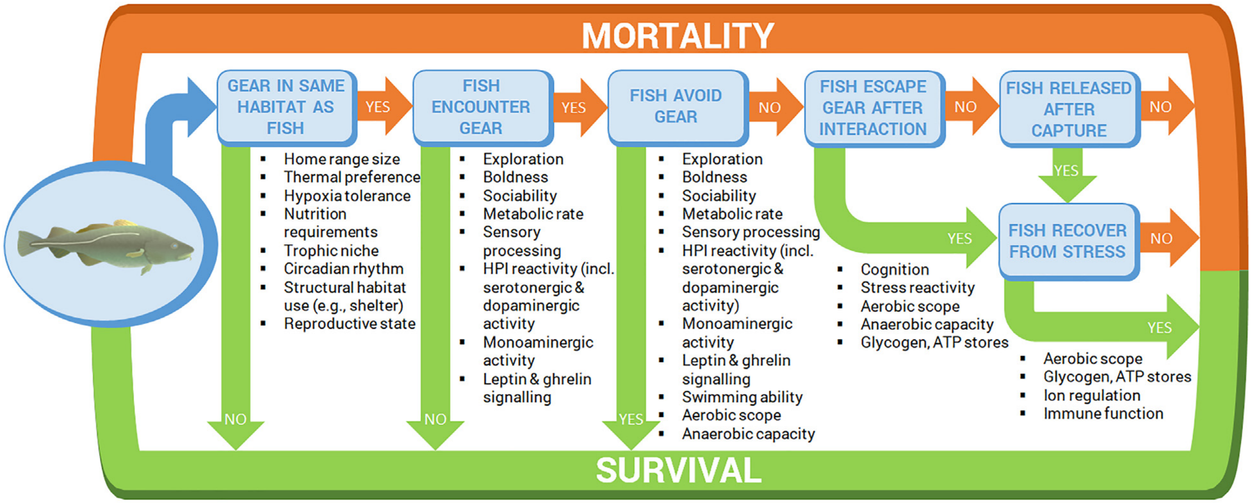


Fig. 1 Stages throughout the capture processing that lead to mortality or survival. At each stage, example traits are listed that may play a role in determining whether fish proceed to the next stage. The traits listed either directly or indirectly relate to physiology and exclude direct effects of body size on selective processes. ATP = adenosine triphosphate; HPI = hypothalamic-pituitary-interrenal axis.

there will be various degrees of overlap in trait selection between the vast array of fishing gears and techniques employed globally, despite gears being labeled as relatively active or passive in their functioning.

The role of physiological traits in FIE is only beginning to be uncovered, but increased knowledge of the physiological mechanisms of fisheries-associated selection will be valuable for understanding the basic processes underlying FIE, and devising potential solutions. This is particularly important given that changes in the genetic variation present within a population due to FIE could make wild populations less able to cope with additional environmental stressors, including those associated with climate change. A major challenge in the study of FIE is that the outcome of whether a fish is captured or not will be the culmination of numerous stages throughout the capture process, in which the fish needs to: (1) encounter a deployed fishing gear; (2) engage with the gear; and (3) be captured (Fig. 1). The traits under selection at one stage of this process may be very different from traits occurring at another stage, potentially amplifying or even counteracting selection occurring at other points within the capture sequence (Hollins et al., 2018). To date, there is virtually nothing known about how selection at each of these stages interact, but it is possible to review the typical sequence potentially leading to fish capture, and consider potential for selection on physiological traits at each step. Importantly, phenotypic plasticity caused by various environmental factors may alter trait magnitudes, variation and heritability, therefore altering the potential for selection at each stage of the capture sequence and associated evolutionary change caused by fishing (Villegas-Ríos et al., 2018).

Haabitat selection

Only fish that are within the sensory reach of a deployed fishing gear will be available to encounter and engage with fishing gear to eventually be captured. If specific physiological traits cause individuals to occupy those habitats—while other individuals within the species reside in unfished areas—the fished individuals will be at a selective disadvantage. Accordingly, any physiological traits that contribute to these differences in habitat use may be prone to evolutionary change.

Many fish species show intraspecific variation in habitat use that could generate among-individual differences in susceptibility to fishing. In Atlantic cod (*Gadus morhua*), for example, some individuals show daily vertical movements to shallow water where they are prone to capture, whereas others remain solely in deeper water and remain unavailable to fishing efforts (Olsen et al., 2012). Similarly, many species show among-individual variation in the tendency to utilize nearshore versus pelagic habitats (Kobler et al., 2009), or to associate with different substrate types that may cause differentiation in the degree of overlap with fishing efforts. The extent to which these differences in habitat use are related to physiological traits is largely unknown, but may be correlated with characteristics associated with thermal sensitivity, hypoxia tolerance, and requirements for energy and nutrition. Many water bodies, for example, show vertical stratification in temperature and oxygen availability, and so individuals with an increased tolerance for hypoxia (e.g., a lower P_{crit}) may be able to reside deeper within the water column and potentially avoid fishing.

Even in cases where fishing occurs across diverse habitat types within a region, selection may operate differently depending on the physiological traits of fish that occupy different habitats. In pumpkinseed sunfish (*Lepomis gibbosus*), for example, individuals differ in their stress responsiveness depending on whether they reside in nearshore versus open-water areas (Belanger et al., 2017). If these differences stem from genetic differentiation as opposed to being environmentally induced, then aspects of the primary stress response in these populations could show evolutionary change as a result of fishing-associated selection if fishing occurs in one habitat and not the other. Many fish species also show partial migration, where some members of a population will migrate at particular stages during their life history (e.g., reproduction), while others may remain resident in the same area throughout their lives (e.g., migrating to sea vs. remaining in freshwater). These divergent migration strategies are associated with a range of physiological traits such as growth, metabolism, immune responsiveness, and the endocrine system. Individuals exposed to fishing pressure in different subpopulations and habitats within a partially migrating population may therefore have different traits or trait values that confer a selective advantage in response to fishing in each environment.

Gear encounter and avoidance

Even if fish and fishing gears co-occur in the same general area, an individual needs to actually encounter and engage with the gear before it can be captured. Traits such as boldness and exploration vary among individuals within species, and may influence whether an individual will encounter and approach a deployed gear. For example, an individual that spends all its time hiding may be less likely to encounter a gill net or angler's lure than a fish that spends more time actively foraging. Indeed, populations of fish that have experienced intense fishing pressure may be comprised of more shy, less exploratory individuals, a so-called "timidity syndrome" (Arlinghaus et al., 2017). Sociability also varies among individuals within species, and in addition to facilitating increased rates of activity while group foraging, active fishing methods such as trawls and purse seines specifically target large shoals or aggregations of fish, thus increasing the chance that more social individuals will encounter these gears. There is also evidence that fish within species that are more social are also more vulnerable to capture by angling (Louison et al., 2018). Importantly, individual boldness, exploration, activity and sociability are all linked to traits associated with metabolic rate, aerobic capacity, and endocrine status. These physiological traits may also have direct links with encounter rate and capture vulnerability, as largemouth bass (*Micropterus salmoides*) and rainbow trout (*Oncorhynchus mykiss*) with a lower stress responsiveness (as indicated by the rise in blood cortisol after a standardized stressor) are more vulnerable to capture by angling (Louison et al., 2017; Koeck et al., 2019), possibly because they are more active or risk-prone in their behavior. In addition, largemouth bass that have been selected for high vulnerability to angling over successive generations have a higher aerobic scope (Redpath et al., 2010).

The effects of traits such as activity and exploration on fishing vulnerability are not binary, and can have a number of complex interactions with an individual's habitat and life-history to determine the overall frequency with which they may encounter deployed gears. Sea trout (*Salmo trutta*), for example, show repeatable variation in home range size and variable degrees of overlap with marine protected areas. Those that spent more time exploring and foraging outside of the reserve were more prone to fishing, suggesting that home range size and any associated traits could be under fisheries-associate selection (Thorbjørnsen et al., 2021). Fish can also show repeatable variation in circadian rhythms that may also affect their encounter rate with gears due to changes in activity and space use throughout the day. Theoretical models indicate that these differences in circadian activity may be under direct selection by fishing, possibly causing evolutionary change in circadian rhythms and underlying hormonal cues (Martorell-Barcelo et al., 2018). The effects of encounter-associated traits on overall vulnerability is also very likely to be modulated by the environment. Fish activity levels are influenced by factors such as temperature and hypoxia, but there may also be interactions between exploration tendency and environmental conditions. In the case of Atlantic cod, for instance, individuals with more reactive types (associated with increased activity of the hypothalamic—pituitary—adrenal (HPI) axis and shyness) decrease their home range size as temperatures increase while proactive individuals (possessing a generally low HPI reactivity and are which are generally more bold) tend to maintain or increase their range size during warming, the latter potentially increasing their vulnerability to mortality by fishing (Villegas-Ríos et al., 2018). Intra-specific consistent variation in proactive and reactive behavioral types are the expression of differences in the activation of the HPI axis, which controls the release of corticosteroids to the blood circulation and brain neurochemistry (Coppens et al., 2010), such as monoamine neurotransmitters. Chronic activation of the brain serotonergic system for instance causes behavioral inhibition of feeding, locomotion and aggression (Winberg and Thörnqvist, 2016), and the dopamine system plays a pivotal role in conditioned behavioral responses that affect risk-taking and avoidance behaviors (Höglund et al., 2005), which are all behavioral traits particularly targeted by passive gear fisheries. In rainbow trout for instance, intra-specific variation in stress responsiveness (as measured by serotonergic and dopaminergic brain activity and circulating plasma cortisol levels) was linked to differences in general behavioral activity and ultimately capture risk by angling (Koeck et al., 2018).

After a fish encounters a gear it faces a decision of whether to engage with the gear or avoid it. Interestingly, for some benthic freshwater species, various indices of space use within the environment (e.g., home range size, depth of occurrence) are related to gear encounter rate but show no relationship with how often individuals actually attack a bait during angling (Monk and Arlinghaus, 2017). This result suggests that fine scale decisions within the close vicinity of the gear are more important in determining overall vulnerability to capture. For other passive gears such as traps, many fish that encounter the trap will not actually enter it (Stoner, 2004), and the decision of whether to avoid or approach the trap may be related to stress responsiveness or cognitive appraisal of aversive stimuli (i.e., mechanisms involved in threat assessment and decision-making). Importantly, the overall motivation to approach a bait or lure is also likely to be influenced by internal state such as hunger and energy requirements, which are in turn modulated by hormonal signaling (e.g., circulating ghrelin, leptin, and insulin-like growth factor-1 (Igf-1)) and metabolic rate, or health status (e.g., parasitic load, disease). Changes in temperature or oxygen availability can alter hunger levels—an increase in feeding temperature below the thermal optimum may increase feeding motivation while hypoxia may constrain feeding as both factors affect the processes of digestion and nutrient absorption. As such, individual variation in traits related to thermal sensitivity and oxygenation may interact with these environmental factors to determine which individuals are most likely to approach a baited gear due to variation in hunger. Sociability also plays an important role in engagement with passive gears because more social individuals will follow others into traps (Thambithurai et al., 2018). Conversely, given that many gears cause aggregations of fish in their general vicinity (e.g., fish aggregation devices), those that are less social may be dissuaded from approaching the gear and thus avoid capture. In fishes, more social individuals have been found to have lower metabolic rates in some contexts (Killen et al., 2016), and sociability is also related to numerous endocrine factors, including components of the primary stress response. While the effects of social dynamics on capture vulnerability could result in selection on physiological traits related to sociability, plasticity in behaviors caused by social dynamics could also dilute the potential for selection on other traits at the individual level.

For active gears such as trawls, avoidance is also likely to be triggered by sensory stimuli originating from the trawl itself, and large degrees of variation have been observed in the directionality of startle responses displayed by fish in response to noises or visual cues from gears such as trawls. Some gear designs use visual or auditory stimuli as a means to discourage non-target species from encountering or entering the gear, but the extent to which these stimuli may generate selection on individual variation in sensory ability within species is unknown. An important distinction between passive and active gears is that active gears often exploit avoidance behaviors of fish in order to capture them. Trawls, for example, operate by herding fish as they attempt to avoid the oncoming net, then gradually containing them as they fatigue. Social dynamics play an important role in this process: some individuals appear to follow exhausted conspecifics backwards into the oncoming net, even if they themselves are not exhausted, potentially inducing selection on associated physiological traits.

Gear escape

Fish that become entrapped, entangled, enclosed, or hooked by gears can still avoid capture if they are able to escape. At this point, the fish is at the final stages of the capture sequence, and so traits related to escape ability could therefore supersede the effects of traits facilitating all other steps leading up to this point. For passive gears such as traps, escape may be related to exploration or traits associated with spatial awareness or cognition, allowing individuals to find the trap exit. While it has not been explicitly studied, it is possible that individuals that become more agitated or stressed by confinement may also be more motivated to search for an exit and escape, although it may be equally likely that erratic movements or struggling due to stress may make escape more difficult.

In the case of active gears such as trawls, scaled-down experimental simulations with surrogate species indicate that individuals with a higher maximum swim speed and, in particular, a higher capacity for anaerobic burst-type swimming, are more likely to avoid capture because they are better able to stay ahead of the oncoming net (Killen et al., 2015). This is supported by video footage from actual full-scale trawls, in which fish can be seen to fall back within trawl nets as they become exhausted from swimming, with those that remain swimming ahead of the net mouth often being able to escape. Together, these observations suggest a potential for selection on traits related to swimming performance being caused by this method of fishing. Escapes from active gears can also occur if fish are able to quickly burst at an angle away from the path of the trawl, to escape either above or below the mouth of the net, a form of behavior that would also require a high capacity for anaerobic swimming. Swimming while digesting food, or while responding to a stressor (e.g., elevated temperature, hypoxia), can also constrain the aerobic scope available for swimming, potentially influencing the spatial position of individuals within swimming groups. Individuals with an increased aerobic scope or capacity to cope with additional stressors may therefore also have a selective advantage in such cases. Even after being contained within a net, fish can escape by passing through the net mesh or via other exclusion devices that are designed to allow the escape of non-target species or size classes. These methods of escape are generally size-specific (e.g., different mesh sizes that allow smaller fish to escape) or directly exploit particular behaviors (e.g., position in the water column) to allow the escape of any unwanted fish before they can be brought to the surface. Aside from direct effects on size-selectivity, the link between these methods of facilitated escape and selection on physiological traits is unknown, but would be a useful avenue for additional research.

After escape from a fishing gear, individuals may have experienced physiological exhaustion or physical injury. Burst-type swimming or struggling will cause anaerobic metabolism, a depletion of glycogen stores, a buildup of lactate, ion imbalance, and an overall homeostatic disturbance (Falco et al., 2022). Throughout recovery from these effects, individuals may have a reduced ability or motivation to forage, or a decreased capacity to escape from predators (Ryer, 2004). Therefore, the ability to recover may increase the chances of post-release survival and be potentially under selection. There is some evidence that individuals with an increased aerobic scope may recover more quickly following bouts of anaerobic metabolism, but the direct relevance of this in the context of FIE is unknown.

Additional effects of the environment

Any selection that occurs due to fishing will happen within the context of environmental conditions that are constantly changing over various scales across space and time. In general, environments with high stochasticity (e.g., coastal ecosystems) will promote the evolution of populations with high genetic and phenotypic diversity, buffering them against environmental instability. If this diversity is eroded by intense and directed fishing selection, these populations would be at an increasing risk of local collapse. In addition, depending on the environment, the strength of selection may vary or different traits may be targeted by selection. In a food-limited environment, for example, levels of hunger may increase among fish, especially among those with an increased metabolic rate, causing them to be even more motivated to approach a baited trap or lure and thus strengthen selection on traits associated with metabolism and hunger. Conversely, phenotypic plasticity due to the environment can also reduce trait repeatability or among-individual variation, and so decrease the ability for selection to occur. For example, hypoxia or extreme temperatures can decrease and homogenize the capacity for swimming among all fish in a population, making it less likely for trawling to select on genetically-determined differences in swimming ability because the fishing effort is less able to be selective on phenotypes (Thambithurai et al., 2020; Hollins et al., 2021).

Broad-scale changes to ecosystems can also affect the nature of gene-by-environment interactions, changing the potential for selection, trait heritability, and rates of evolutionary change caused by fishing selection. The presence of invasive species, for example, can reduce growth rates in targeted populations in a manner that overwhelms and dampens any fishing-associated selection on size and correlated traits (Gobin et al., 2018). Fishing can also drastically reduce population sizes such that density-dependent changes in fish abundance alter competition, the use of resources, growth rates, and trait expression. While this is a direct result of overfishing, there can also be important gene-by-environment effects caused by such changes in population density that manifest to alter the outcomes of fishing selection. Reductions in population density may also alter the genes that contribute to specific phenotypes and the degree to which specific genes are targeted by fishing selection (Crespel et al., 2021).

Fisheries management and FIE

While stressors on fish and aquatic ecosystems are numerous and in some instances synergistic, the harvest of populations remains relatively manageable in comparison to climatic or hydrological effects. Included within this is the capacity to manage fisheries in a way that minimizes or prevents fisheries-induced evolution, such that wild populations maintain their genetic diversity and resilience to climate related stressors. Fisheries management is a complex task, balancing diverse human needs against securing ecosystem services by limiting adverse ecological impacts. The current scientific consensus is that ecosystem-based fisheries management is the most viable approach for achieving this balance, by managing fisheries in a way that considers all components of an ecosystem and their interactions, rather than focusing management efforts on a single target population. For example, the concept of balanced harvesting proposes that size and species selectivity can be reduced by targeting trophic levels equally and in proportion to their productivity, preventing an imbalance that may cause ecosystem shifts while maintaining fishing yields. Similarly, for preventing unwanted demographic shifts and cascading ecosystem effects due to fisheries-induced evolution, several existing management strategies have been proposed.

When correctly implemented, spatially or temporally explicit fishing bans are one method by which the maintenance of phenotypic diversity may be achieved. These include the use of protected areas in which harvesting is prohibited, or harvest rotations, whereby fishing of specific populations or species is periodically halted but then shifted to another stock, alleviating fishing pressure during sensitive periods or allowing time for population recovery (Fernandez-Chacon et al., 2020). In addition to reducing overfishing, protected areas or periods can also act as sources of genetic diversity, potentially spilling over into neighboring regions or ecosystems that are not specifically managed. The spatial and temporal boundaries of these management techniques play a crucial role in determining their effectiveness, as ecological benefits of spillover effects may be limited if fishing closures are too small or too short-term relative to the movement patterns or life history traits of the species of interest. There are also additional risks that must be considered when it comes to fishing selection. For example, while protected areas may promote dispersal from within their boundaries, these fish may be especially prone to capture due to their inexperience with fishing and altered behavioral adjustment to previous threats, thus increasing the pool of vulnerable fish within a population (Januchowski-Hartley et al., 2013; Koeck et al., 2019), and possible phenotypic trait selection linked to stress responsiveness and cognitive processes. The optimal balance, in which fishing closures provide genetic diversity while maintaining the existence of this diversity when these populations are harvested is a focus of ongoing research. Undoubtedly, a key consideration is that fishing closures should be defined to encompass protection of suitable habitats for a diverse range of species, life stages and phenotypes.

The diversity of fishing practices targeting the same populations may also play a role in minimizing FIE. For example, using a mix of fishing gear types that select for different phenotypes may partially balance or dilute any selective effects. This is observed in some small-scale artisanal fisheries, which use a range of passive fishing gears within one ecosystem to achieve a more balanced harvest of species and phenotypes. Such artisanal fishing fleets are also more flexible in their execution and able to implement dynamic fisheries management strategies in response to changes in target populations or their environment. Fishing during periods in which trait plasticity causes homogenization of phenotypes may also be a way to minimize fishing selectivity. For example, trawling in the dark, while fish are in a sleep state or have reduced visual stimuli may reduce the selection on sensory processing or escape ability, or trawling during hypoxic conditions may reduce selection on swimming ability because all fish will be limited in the capacity to stay ahead of an oncoming trawl. Such strategies should be used with caution, however, because they may lead to synergistic effects between fishing and other sources of selection stemming from environmental stressors, including extreme weather events (Morrongiello et al., 2019). In such cases, dynamic fishing closures could be considered during extreme conditions, based on knowledge of physiological tolerances of targeted populations. Overall, the most fundamental management tools for preventing FIE may be implementing practices which prevent general overharvesting of populations (Kuparinen and Festa Bianchet, 2017) and which ensure the maintenance of essential fish habitats and connectivity among them by limiting habitat destructive practices.

Conclusion

Humans are effective predators and fishing can exert selective pressure on wild fish populations that may result in evolutionary change. While changes in the body size and life-histories of exploited fish populations have been observed, the non-random selective capture of fish with specific behavioral and physiological traits is only starting to be understood. The exact traits under selection will vary depending on the type of fishing gear being used and the manner it which it is employed, but in general passive gears are likely to select on traits associated with boldness, feeding requirements, exploration, and social behavior, while more active gears are likely to target traits associated with maximum capacity for aerobic or anaerobic swimming. Environmental conditions and interactions among stressors will also have a strong modulating effect on which traits are under selection and the strength of selection. Reducing the potential for FIE will be important for preserving within-species diversity, maximizing genetic variation, and ensuring wild populations can cope with fishing pressure and other forms of ongoing environmental change.

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