

Chapter 4

Consequences for fisheries in a multi-stressor world

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Marine and freshwater fisheries are more important than ever for sustaining human populations but are also facing unprecedented threats from the combined effects of multiple environmental stressors. Here we review how the rapidly changing abiotic environment of fish may affect interactions between fish and fishers, at both the individual and population levels. Throughout, we highlight the role of physiological mechanisms underlying the sensitivity of fish to multiple stressors and their interactions with fishing gears. For each step in a typical capture sequence, we discuss how stressors can alter the behavioral and physiological mechanisms of capture and potential recovery after release

or escape. We also consider possible feedbacks among fishing practices, environmental stressors, and physiological response of fish, including the potential for harvest-associated selection and evolutionary effects. Fisheries can also induce changes to the biotic environment, including changes in population density, species interactions, and prey density, which can in turn alter the physiology of individual fish, entire ecosystems, and the fisheries themselves. We conclude by highlighting priority research areas required to advance our understanding of the effects of multiple stressors on fish physiology and behavior within the context of global fisheries.

1 Introduction

With the technological advances of fishing practices and gears, fishing has transitioned from hunter-gatherer subsistence fishing to a consumptive global commodity (Pitcher and Lam, 2015). Fish are still the primary protein source for 17% of the world's population and are among the most traded food commodities (FAO, 2019). Around the globe, a diversity of fishing practices exist, spanning from recreational hook and line fishing and small-scale artisanal fisheries to commercial fishing freezer vessels targeting inland and marine species from the coast to open ocean. Together, with the industrialization of commercial fishing (Finley, 2016) and the more recent diversification of recreational fishing practices (Cooke et al., 2021), nearly all fish species are directly targeted or indirectly impacted by some form of fishing practice (FAO, 2020).

Single stressors may not have considerable deleterious effects on fitness and survival of animals, but they may when occurring in combination with other stressors. Multi-stressor effects are well known in ecotoxicological research, where co-occurring pollutants can have synergistic effects, decoupling the effects of single chemical pollutants (Kimberly and Salice, 2015). For instance, Monteiro et al. (2020) show the additive effects of hypoxic conditions and mercury contamination, which often co-occur in neotropical freshwater ecosystems, causing the impairment of cardiac output of fish. The effect of multiple stressors, in order to better capture the environments animals are experiencing in the wild, are also increasingly studied in a broader ecological context (see for, e.g., Halfwerk and Slabbekoorn, 2015 for a multi-modal approach of sensory pollution; Fu et al., 2018; Hecky et al., 2010). In the context of fisheries, research shows that the outcome of a fish-fishing gear interaction is greatly impacted when interacting with other environmental stressors. For instance, while fish may be able to adjust to fluctuating temperature regimes, including temperatures temporarily exceeding their thermal optimum (Johansen et al., 2021), increased water temperatures can reduce swim performance, possibly increasing the risk of capture by fishing trawls (Hollins et al., 2018) or reducing recovery potential and chances of survival after discard from a vessel (Gale et al., 2013).

In addition to direct fishing or harvest, fish increasingly experience a multitude of other stressors that may interact with the physiological disturbance

caused during fishing, producing effects at various levels of biological organization (see other chapters in this book). To persist in a multi-stressor world, fish need to physiologically adjust and/or adapt to new habitat characteristics or shift to new habitats to meet their biological requirements and limit chronic stress that may affect fitness and survival. Despite a wide range of existing fishing gears and practices, all fishing gears exploit the natural behavior and performance of fish, such that changes in fish behavior via environmental effects on physiology, will affect the interactions between fish and fishing gears. Being predominantly ectothermic, teleost fish are particularly sensitive to changes in environmental temperature (Porter and Gates, 1969). Temperature changes near species' maximum or minimum tolerance thresholds can represent a major stressor causing impairment of cardiac and metabolic functions, increasingly the likelihood of mortality, or producing sublethal effects on physiological performance (Jensen et al., 2017). Environmental hypoxia is an increasing global concern in freshwater and marine habitats (Breitburg et al., 2018), and in fish can have numerous effects including alteration of cardiac function, oxygen delivery (Farrell and Richards, 2009), and spontaneous swimming activity (Schurmann and Steffensen, 1994; Metcalfe and Butler, 1984). Sensory and chemical pollution are additional stressors which can affect environmental cue perception (Halfwerk and Slabbekoorn, 2015), increasing stress in fish and more generally disrupting biological rhythms (Celi et al., 2016). Waterborne pharmaceutical residues of anxiolytic drugs can affect the functioning of the central nervous system of fish by reducing overall neurotransmission, which have shown to impact the migration propensity of Atlantic salmon in riverine systems (Hellström et al., 2016). Artificial light at night in urbanized waters affects biological rhythms such as sex steroids and gonadotropin production (Brüning et al., 2018), increases metabolism and disrupts natural circadian rhythms in fish (Pulgar et al., 2019). Changes to the physical environment of fish, such as water stratification, currents, and water flow will additionally affect the sensory reach of environmental cues by fish. Overall, not only may such multiple, co-occurring stressors amplify or compound the physiological stress caused in fish during fishing, but they may also affect the vulnerability of fish to various fishing practices at both the individual and population levels.

In this chapter we outline, based on examples of existing fisheries but also on knowledge of physiological processes gained from experimental work, how changes of the abiotic environment of fish may affect the interaction between fish and fishing gears interaction and ultimately shape the fisheries of our world. This includes how within-generational plasticity to environmental stressors may modulate vulnerability to fishing gears and the potential for selection by fishing practices. This chapter is constructed based on the consecutive steps of a fishing sequence, i.e., habitat selection, encounter, and interaction of fish and gear, and capture. For each step, we outline how environmental stressors modulate the corresponding behavioral and physiological

mechanisms involved in the fish-gear interaction. Additionally, we discuss possible feedback loops between fishing practices, environmental stressors, and physiological response of fish. Beyond the direct impact of fishing practices on population level mortality rates of a fish population, indirect effects and sublethal effects are numerous and can affect fish populations via mechanisms of selection, possibly producing transgenerational effects (Hollins et al., 2018) and constraining adaptation to climate variability (Morrongiello et al., 2019). While we focus on how abiotic stressors can shape fish-fisheries interactions, there are likely to be numerous cascading ecosystem-level effects. To this end, we discuss how modifications of species interactions and food webs in response to environmental conditions can affect fisheries, including interactions with the expansion of non-native species.

2 Habitat use and availability to fisheries

To be available to a fishery, fish must overlap in space and time with the gears being used to capture them. This will largely depend on the habitat that the fish occupy, either by active choice (e.g., choosing an area with a particular prey) or by avoidance of areas outside of their abiotic environmental preferences or limits (e.g., avoiding areas above a temperature threshold). At the narrowest spatiotemporal scale, fish make decisions on a moment-to-moment basis about which microhabitat they will occupy. Conversely, range shifts can occur at the scale of hundreds or thousands of kilometres over the course of years, decades, or centuries. The exact causes of this variance in habitat use is the focus of a great deal of research, and while in most cases these remain elusive, habitat use by fish and their subsequent availability to fisheries is likely to be influenced by a range of environmental factors that interact with fish physiology.

2.1 Habitat selection and microhabitat use

Within and among fish species, there is wide variation in space use associated with energy requirements, performance, and behavioral traits. For example, factors such as water velocity, food abundance, predation risk, water depth, temperature and oxygen availability may all affect microhabitat selection. This has been well-studied in stream-dwelling salmonids, for example, whereby individuals can face a trade-off between occupying faster flowing waters with increased drift feeding opportunities but with greater energetic costs while holding station, and lower flow areas where less energy is spent on swimming but where there is less prey availability (e.g., Fausch et al., 1997). Intrinsic variation in risk-taking tendency, spontaneous activity, and exploration will also influence space use of fish, and these behavioral traits can show context-dependent links with various aspects of physiology including metabolic rate, locomotor performance, and hormone status (although see

Baktoft et al., 2016). Individuals that are inactive or spend more time in shelter, for example, tend to be those with a lower metabolic rate and increased stress-responsiveness (Metcalf et al., 2016). In turn, these individuals may be less likely to encounter passive fishing methods such as traps or anglers because these depend on the fish to encounter and interact with the largely stationary gear (Hollins et al., 2018). As such, the associated fisheries-associated selection could possibly generate a “timidity syndrome” among the population of fish that remain uncaptured (Arlinghaus et al., 2017). Notably, however, the links between habitat use and vulnerability may be highly dependent on the type of gear being used. More active gear such as seines, for example, may be more likely to capture shy individuals or those in shelters, because they are less likely to escape the path of the net (Wilson et al., 2011).

Factors such as temperature and hypoxia can have independent and combined effects on the metabolic rates and aerobic capacity of fish (Claireaux and Chabot, 2016; Claireaux et al., 2000) and it is likely that, via effects on behavior, these factors will affect habitat use and the potential to encounter deployed fishing gears. Temperature, for example, has strong effects on foraging activity and choice of depth of occurrence in Arctic char *Salvelinus alpinus*, likely affecting their ability to be targeted by specific gear types in relation to the prevailing environmental conditions (Guzzo et al., 2017). Importantly, however, the exact effects of these environmental factors on habitat use will depend greatly on the magnitude of the change in conditions in relation to the “baseline” conditions, and over what time scale (Evans, 1990). For example, if an increase in temperature increases spontaneous activity in fish, there may be an increasing their space use and the likelihood of encountering a fishing gear. With acclimation, however, metabolic compensation will occur and activity will partially return to the level that occurred at the cooler temperature (Evans, 1990). At extremely high temperatures beyond a species’ thermal optimum, such as that which can occur during heat waves (Mameri et al., 2020), activity may actually decrease if fish experience neuromuscular dysfunction or a diminished aerobic capacity for activity or digestion (and hence foraging). Hypoxia can have similarly variable effects on behavior: while mild hypoxia can decrease shelter use and exploration, especially for those with a high metabolic rate, severe hypoxia can suppress variation in activity among the majority of individuals and thus alter vulnerability to specific gear types at the population level (Killen et al., 2012).

Variation in depth preference among species or individuals will also influence their spatial overlap with fishing gears and can also be related to physiology. In warmer years, for example, some species will occupy greater depths with cooler water, or individuals with a general preference for cooler temperatures may consistently prefer deeper environments (Guzzo et al., 2017). In Atlantic cod *Gadus morhua*, the tendency for diel vertical migration is a repeatable trait, and individuals that make periodic migrations to

shallower depths are more likely to be captured by passive fishing gears as compared to those that stay in deeper water (Olsen et al., 2012). Targeted fishing on depth-associated phenotypes has been shown to cause changes in allele frequencies in exploited Atlantic cod populations (Árnason et al., 2009). Climate-associated hypoxia is also expected to restrict the depth of many pelagic species to more well-oxygenated surface layers. In blue sharks, for example, a shallower oxygen minimum zone associated with warmer has caused a decrease in dive depths, essentially compressing their vertical distribution in the water column, and increasing their catch rates by long-line fisheries (Vedor et al., 2021).

2.2 Range shifts

At broader spatiotemporal scales, interactions between the environment and fish physiology are already altering the habitable ranges of economically and ecologically valuable species. Overall, there is a general trend toward more poleward distributions of species or a shift to greater depths (Dulvy et al., 2008; Gaines et al., 2018). Although models that incorporate physiological mechanisms predict a continuation of these trends (Cheung et al., 2011), there is significant controversy regarding the exact physiological mechanisms underlying such shifts. The oxygen and capacity limited thermal tolerance (OCLTT) hypothesis, for example, has posited that constrained aerobic scope at temperatures beyond a thermal optimum should limit species' capacity for activity, growth, and reproduction, and therefore limit their geographical range (Pörtner and Knust, 2007; Pörtner et al., 2017). While this basic principle has been a component of attempts to model future ranges of fish species, the empirical evidence for these effects is mixed. For example, there are very few species for which adequate physiological data have been collected to effectively model changes in aerobic scope with temperature (Nati et al., 2016), and among those species that have been studied, many show no obvious optimum temperature for aerobic scope (Lefevre, 2016). Further attempts to model the geographical distribution of fish species have included interactions between temperature and oxygen availability to derive estimates of a metabolic index that generally coincides with the current distributions of species for which sufficient physiological data is available (Deutsch et al., 2015, 2020). While this work highlights that the physiology of fish species is likely critical in determining the geographical range of species in response to stressors, there remain many unknowns in this area. For example, even if current modeling approaches predict that a species could inhabit a given range given their responses to temperature, additional stressors including food or habitat availability may render an area unsuitable.

Ongoing and future changes in the range distribution of species will strongly impact fisheries. Commercial fishers may need to relocate fishing efforts to follow the population, possibly spending more time in transit to and from fishing grounds, or shift efforts to other species. Relocations of

fisheries in the northeast United States, for example, have shown a tremendous time lag relative to the range shifts of their targeted populations (Pinsky and Fogarty, 2012). It should be noted that while temperate and tropical fisheries are generally predicted to decline in response to future climate changes, fisheries in polar regions may actually experience an increase in productivity (Campana et al., 2020), though species interactions between native species in these areas and an influx of species experiencing range shifts is unknown. It is also important to note that, to date, the vast majority of research has focused on marine species while changes in the habitable shifts of freshwater species remains relatively unknown. This is a major area for future research given the large human populations across South America, Africa, and Asia, that are dependent on freshwater fisheries and are in geographical areas predicted to be strongly impacted by warming.

3 Gear encounter and interaction

Even if a fish and fishing gear are in the same general location at the same time, there are numerous environmental, physiological, and behavioral factors that will determine whether a fish encounters and interacts with the gear (Lennox et al., 2017). Encounter rates are modulated by fish activity such that, depending on the specific gear being used, more active individuals may be more likely to encounter a deployed gear within their home range or core activity spaces. Larger home ranges will also increase the probability of a fish overlapping with the active space of a gear across space and time. Active, compared to passive, fishing gears have different modes of function such that passive gears are more reliant on the activity rates of the fish than active gears, which actively pursue fish. In addition, passive gears may require the fish to be stimulated to interact, relying on the behavior and physiology of the individual to compel it to the gear. Here, we briefly review how stressors can enhance or reduce the rates at which fish become vulnerable followed by an assessment of how stressors affect the nature of these interactions between fish and fishers.

Catchability and availability are population-level traits relevant to fisheries that are modulated by the behavior and physiology of individuals (Arreguín-Sánchez, 1996), rendering them vulnerable or invulnerable to capture. Vulnerability is an unobservable individual trait that only becomes confirmed once a fish interacts with a gear. The internal state of the animal must be such that it is physiologically and behaviorally primed to be captured, in other words, something is motivating the individual to move or feed in an area where gear is active. Fish that are hiding or satiated are generally not vulnerable to gear and will not encounter or interact with gear. Fish that are hungry and at ease in their environment are expected to be readily vulnerable to fisheries. Within a population, individual variation in metabolism (Redpath et al., 2009), boldness (Redpath et al., 2010), sociality (Louison et al., 2018), and other traits will determine the activity levels and risk taking of fish, including relevant

traits such as flight initiation distance, risk tolerance, etc., that affect the individual's response to stressors and vulnerability to capture.

When an animal's environment shifts, their physiology undergoes corresponding changes that affect the individual's likelihood of encountering or interacting with fishing gear. The effects of such stressors are threshold-dependent, such that individuals and species may have tolerance limits that enhance performance up to an optimum before decreasing performance, with consequences for their vulnerability to fisheries capture. Extreme environmental stressors such as high temperature or hypoxia, for example, shift the animal's physiology and will alter habitat selection or behavior. [Van Leeuwen et al. \(2021\)](#) showed how warm water temperatures in rivers affect catches of Atlantic salmon, implying that the environmental change affected the interaction of fish with the fishing gear. Migrating salmon are not feeding and are perhaps a special case, but similar effects can be anticipated when fishing with passive gears that rely on the fish's volition to be captured. Angling, longlining, fyke netting, and other traps should therefore have reduced efficacy in extreme weather. Active gears, however, may experience enhanced catch when individuals are beyond their physiological optimum and less able to escape gear such as trawls, unable to move as well to avoid capture. [Killen et al. \(2015a,b\)](#) demonstrated how anaerobic capacity, which may be reduced at warm temperatures for fish, affects trawl captures and [Thambithurai et al. \(2019\)](#) revealed similar patterns for environmental hypoxia. Taken together, fish living in rivers, lakes, and coastal zones where water temperatures are increasing with climate change should be increasingly vulnerable to active gears and decreasingly vulnerable to passive ones. Areas of the deep sea where oxygen minimum zones are rising may also yield less reactive fish that are more easily trawled. Acidification caused by acid rain in freshwater and warming on reefs may also affect swimming performance and vulnerability to fisheries in these highly exploited environments. Environmental pollutants may have variable effects on fish, with stimulants such as anxiolytic drug effluents stimulating behavior that would enhance gear encounters and vulnerability ([Brodin et al., 2013](#)). Other pollutants, such as noise, repel fish from affected sites and can be expected to reduce gear encounter rates proximate to the source, reducing gear encounter and capture probabilities ([Filous et al., 2017](#)). [Koeck et al. \(2020\)](#) showed that memory and learning play a key role in a population's vulnerability to capture but this probably also competes against food availability and hunger. Stressors that increase hunger or shorten memory retention in fish may have profound effects on their willingness to explore and interact with gear.

4 Capture and escape or release

Despite the diverse range of fishing gears across fisheries sectors, fish cannot be captured without causing some level of injury or stress which can interact

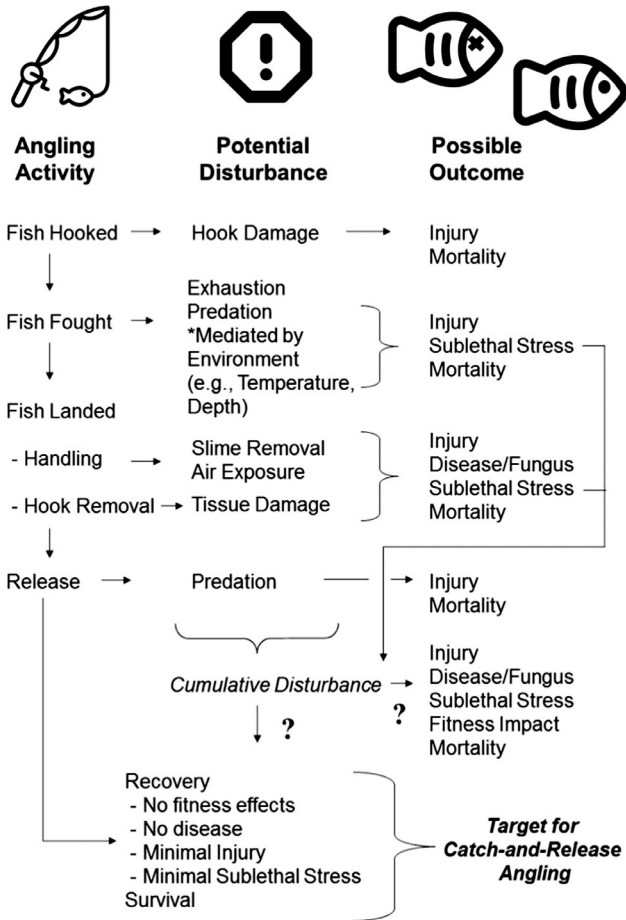


FIG. 1 Flow chart of the potential disturbances, mediators of physiological stress, and potential fish fates occurring throughout an angling event in a recreational fishery. Question marks highlight areas where the cumulative effects of numerous stressors on the potential for recovery after release are largely unknown.

with various environmental stressors, possibly leading to immediate or delayed mortality after release or escape (Fig. 1). The number of fish that are released to comply with fisheries regulations, the conservation ethic of the fisher (e.g., as is common with voluntary catch-and-release in recreational fisheries) or because of a lack of market value (e.g., in some commercial fisheries), is by no means small. In the recreational sector alone, Cooke and Cowx (2004) estimated that as many as 30 billion fish may be released on an annual basis. Understanding the fate of fish that are released and developing strategies to reduce injury, stress, and mortality are thus of high priority to fisheries managers and fishers alike, especially in the face of numerous concurrent

environmental stressors which may exacerbate the physiological stress experienced during capture or impair recovery. Although it is common to think of fishing in terms of fish that are captured and released, fish can also interact with fishing gear and escape without being landed. For example, a fish could escape from a commercial gill net or break the line when being reeled in by an angler (Chopin and Arimoto, 1995). These interactions can lead to sublethal impacts and collateral mortality but are just beginning to be explored in many fisheries (Falco et al., 2022), including interactions with various environmental factors. Here we consider the physiological consequences of different aspects of the fish capture process and the potential modulating effects of additional environmental stressors. We preface this text by noting that given the incredible diversity of fish species, fisheries techniques/gears, fisher behaviors, and environmental conditions that fish experience, our attempts to generalize will always yield exceptions.

4.1 Interactions with fishing gears

From the moment a fish is hooked, entrapped, or entangled, there is a neuro-endocrine cascade that leads to a stress response and associated physiological adaptations (Barton, 2002). Fish will first attempt to escape and may pull on the line, struggle in a net, and/or search for an escape path from a pursuing gear. Beyond activation of the HPI axis, fish will often engage in high intensity locomotor activity that includes burst swimming. Burst swimming is fueled by anaerobic metabolism so tissue energy stores such as ATP, glycogen and PCr are rapidly depleted leading to an oxygen debt and state of physiological exhaustion (Kieffer, 2000). Warmer acclimation temperatures and exposure to hypoxia can both alter liver and muscle glycogen levels, possibly affecting the times needed for fish to become exhausted (Yang et al., 2015). At the same time metabolites accumulate in tissues and acid-base imbalances occur creating metabolic acidosis (Wood et al., 1983). Rapid depletion of tissue energy stores, and associated acidosis in fish tissues generally coincides with the onset of fish exhaustion but does not necessarily equate to fish capture. For fish caught on rod and reel, the onset of fatigue prevents fish from further resisting capture, after which point they are easily landed. However, fish caught on longlines or in gill nets may show repeated incidences of struggle and recovery throughout these gears' soak times (Guida et al., 2016), while exhausted fish pursued by a trawl often escape capture by passing under/over the net mouth (Ryer, 2008).

Increases in water temperature and reductions in oxygen availability will likely increase the rate of energetic resource depletion and the onset of acidosis in fish tissues as they attempt to escape or unhook themselves from fishing gears (Gale et al., 2013), exacerbating stress responses and subsequent physiological disruption. In the case of rod and reel fisheries, environmentally-induced reductions in swim performance (e.g., Domenici et al., 2013) may

decrease the fight times of angled fish in certain instances, although fish can sometimes be landed before such severe physiological disruptions occur (Shea et al., 2022). In contrast to rod and reel fishing, the extended soak times of longlines or gillnets mean that there is greater opportunity for the extended/repeated struggling of caught fish to cause significant disruptions to fish homeostasis, with potential consequences for both recovery after release/escape (see below), and fish condition upon the retrieval of the gear. Physiological disruptions likely exacerbated by high temperatures and reduced oxygen availability, such as elevated lactate and decreased blood/tissue pH, are often associated with reductions in meat quality from harvested fish (Anders et al., 2020). Under future climate change scenarios, minimizing the stress experienced by commercially important fish species may become increasingly important. In future, fishers may need to evaluate the tradeoffs between lost income due to declining fish condition, and the relative cost of performing multiple, shorter gear sets to try and reduce the severity of physiological disruptions of target fish.

4.2 Handling

Once a fish is landed, how it is handled can play a large role in the ultimate outcome of the fishing interaction for the fish. In some cases a fisher may reach down into the water and slide out the hook or cut the line without bringing the fish into a vessel or onto shore. In such instances, handling is negligible but to do so may require a fish that is already exhausted from the fishing interaction (e.g., an angler using a protracted fight time to enable exhaustion). However, it is more common for a fish to be fully landed whereby they are brought into the “possession and control” of the fisher (e.g., in a landing net, on a boat deck, in the hands of the fisher, or on shore). In some cases, fish are crowded in nets (e.g., a purse or beach seine) at time of landing, which can lead to localized depletion of dissolved oxygen (i.e., hypoxia) and stress (Tenningen et al., 2012). It is common for fish to be exposed to air during handling. Air exposure is not surprisingly a rather severe stressor for fish characterized by collapse and adhesion of gill filaments, severe bradycardia, inability to respire, and a host of biochemical alterations. Beyond some threshold tissue damage arising from lack of oxygen is so severe that a fish will die. In a synthesis of air exposure studies, Cook et al. (2015) suggested 10s as a conservative, cross-species and context value for a suggested maximum air exposure target when species- or context-specific values are unavailable. In some cases, this is easily achievable but in other cases such as challenges with removing fish from the gear, fisher inexperience, or the volume of fish that need to be sorted and handled (e.g., in non-selective gears such as seines where fish are landed *en masse*), air exposure can last 20min or more (Raby et al., 2012). Such durations may not necessarily be injurious but require research to understand outcomes and best practices for handling such

situations, and the effects of other additional stressors such as thermal history and prior oxygen availability (e.g., hypoxia during the time of capture). In trawl fisheries, air-temperature during on-deck sorting may strongly affect the degree of physiological stress experienced by fish, and so warming conditions or heat-waves may cause an increase in the mortality that occurs during this stage of the fishing process.

4.3 Recovery and fitness impacts

When fish are released after capture they can be in a range of physiological conditions. Some fish are able to maintain equilibrium and are vigorous while others are near death and unable to swim (Davis, 2010). Even fish that are able to swim may experience cognitive impairments that lead to them having difficulty in assessing risk and making risk averse decisions (Cooke et al., 2014). Fish with locomotor impairments may be subject to predation (Raby et al., 2014). Some researchers have evaluated different tactics for facilitating recovery of exhausted fish in an attempt to expedite physiological recovery and reduce mortality. Farrell et al. (2001) showed that use of a recovery box allowed coho salmon that were classified as lethargic to be vigorous as little as 15 min later (with accompanying recovery of tissue energy stores) while Brownscombe et al. (2013) restored locomotor activity of bonefish by temporarily holding them in flow-through recovery bags. Yet, the science is mixed and in other instances there is little evidence that recovery can be facilitated (e.g., Robinson et al., 2013). In other words, it is much better to ensure that fishing and handling practices are optimized such that fish are not exhausted at time of release than trying to facilitate recovery of exhausted fish.

The mechanisms by which fish die after release or escape are varied. Some fish that are bleeding may survive long enough to be released but die later. However, minor injuries such as scale loss or abrasion can in time (days to weeks) provide an entry route for opportunistic pathogens such that fish can die well after release. Given that stress such as that arising from capture and handling can also impair immune function (Tort, 2011), such minor injuries can turn into major infections. In some cases, fish are sufficiently exhausted that they are unable to recover, presumably due to tissue oxygen limitation and associated damage to the heart and/or brain (Farrell et al., 2009) or because of extreme acid-base imbalance (Wood et al., 1983). As noted above, if fish are exhausted and unable to escape from predators then they can be killed by predators, while exhausted fish which are obligate ram-ventilators may be unable to sufficiently oxygenate their gills through swimming, preventing recovery. While rates of recovery from exhaustive exercise show a large degree of variation among ecologically distinct species, elevated temperatures are typically associated with elevated metabolic debt after exercise, as well as increased rates and occurrence of post release

mortality in released fish (Clark et al., 2017). Specifically, elevated temperature and hypoxic conditions during recovery can slow recovery of intramuscular ATP, PCr, and lactate, and plasma levels of glucose following exhaustive exercise (Suski et al., 2006). For example, Wilkie et al. (1996) revealed that angling of Atlantic salmon in warm summer water impairs restorative processes and increases the susceptibility of Atlantic salmon to delayed post-angling mortality. Under continued warming scenarios, the probability of and rate of recovery after exhaustive exercise may be lowered in fish, potentially elevating both post release mortality, and rates of depredation in future (Gale et al., 2013). In addition to the impact of capture and handling stress, environmental temperature has also been shown to directly influence the efficacy of fish immune response. While low temperatures are known to inhibit fish immune response (Butler et al., 2013), elevated temperatures can both reduce the immunocompetency of fish, as well as increase proliferation of pathogens (Shameena et al., 2021).

Although mortality is the outcome of greatest concern to fisheries managers, sublethal impacts can also be relevant to fitness. For example, stress associated with fishing that occurs prior to or during reproduction may suppress reproductive hormones (Pankhurst and Dedualj, 1994), delay reproduction (Ostrand et al., 2004), impede spawning migration (Thorstad et al., 2007), influence gamete development (Hall et al., 2009) or offspring quality (Ostrand et al., 2004), impair parental care (Kieffer et al., 1995), and even reduce reproductive success (Richard et al., 2013). Reproductive indicators related to fitness are challenging to study in wild fish but these aforementioned examples suggest that more research is needed. Other fitness impacts can occur as a result of feeding impairments (Siepker et al., 2006) or other pathways that impact growth (Meka and Margraf, 2007) although compensatory growth is common (Cline et al., 2012).

5 Feedbacks between fisheries and stressors

In addition to the effects on individual fish that have so far been described in this chapter, fisheries have wide ranging impacts on exploited ecosystems, and fishing is itself a “multi-stressor,” potentially causing pervasive, sublethal impacts to fish populations with consequences for species of both commercial and recreational interest (Fig. 2). For example, while fisheries harvest is a direct source of mortality for many fish species, the concurrent destruction of critical habitat (Wheeler et al., 2005) and associated noise of vessel traffic (Celi et al., 2016) which also occurs, each constitute additional stressors in their own right. Furthermore, the selective nature of fisheries harvest has likely altered the life history (Heino et al., 2015), behavioral (Uusi-Heikkilä et al., 2008) and physiological (Hollins et al., 2018) traits of exploited fish populations, with potential consequences for their capacity to adapt to the other stressors discussed in this chapter (Crespel et al., 2021a).

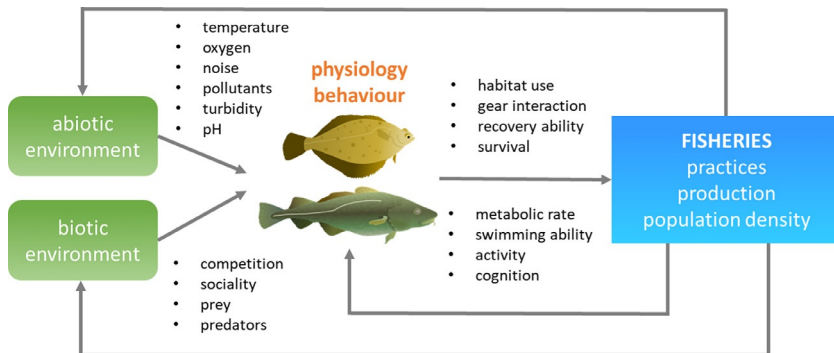


FIG. 2 Potential feedbacks among environmental variables, fish, and fisheries practices. Various abiotic and biotic factors will have direct and indirect effects on the physiology and behavior of fish. This includes natural environmental variation but also anthropogenic stressors. The physiological state and behavior of fish will determine their vulnerability to being captured as well as the physiological stress they experience during the capture process. The fishing process itself will then feedback to affect environmental conditions, especially due to noise, pollution, habitat degradation, and changes in the population densities of targeted species. These alterations will go on to further modify fish physiology and behavior.

The following section discusses the indirect stressors fisheries activity exert on fish, and the role that fisheries harvest may play in limiting the adaptive potential of exploited fish populations to further environmental disturbances.

Fishing practices may directly alter habitats in a way that increases the stress experienced by fish living within a given region. For example, demersal trawls can clear large swathes of structured, complex benthic ecosystems which provide critical sheltered habitat for fish species (Koslow et al., 2001; Kritzer et al., 2016; Yesson et al., 2017). In addition to potentially depriving fish of habitat-structure necessary to complete critical life history functions (Caddy, 2008), lack of adequate shelter can increase the risk of predation in demersal fish species (Brooker et al., 2013; Quadros et al., 2019), potentially leading to sublethal stress effects which can impact individual fitness. For example, a lack of available shelter has been shown to increase measures of basal metabolic demand in fish (Chrétien et al., 2021; Millidine et al., 2006), potentially due to increased costs of vigilance (Killen et al., 2015b). These increased metabolic costs may reduce resources available for growth and reproductive investment, with subsequent reductions in fitness or capacity to adapt to further stress, or otherwise increase energetic demand in a resource limited environment. Fishing activity can also induce further stress responses by exposure to vessel noise, which has been shown to elevate metabolic demand and heart rate in exposed fish (Graham and Cooke, 2008; Simpson et al., 2016), as well as increasing circulating levels of biochemical stress indicators (Celi et al., 2016). Cumulatively, these indirect-fisheries stressors may contribute to reductions in fitness of wild fish populations

inhabiting exploited ecosystems, with potential consequences for future fisheries yield. The potential fitness impacts of these indirect fisheries-stressors have yet to be studied in the wild, but any observed impact would be difficult to attribute to indirect effects of fisheries, as the selective nature of fisheries harvest (Heino et al., 2015), and density dependent effects (Crespel et al., 2021a,b) might also be expected to impact life history traits in similar ways.

Removal of fish from wild populations by fisheries harvest not only elevates the mortality experienced by fish stocks, but can constitute a strong selective pressure to which they must adapt (Heino et al., 2015). Where mortality extends to immature life history stages in exploited fish populations, fisheries harvest selects for individuals which can successfully reproduce at earlier ages and smaller sizes (Enberg et al., 2012; Heino et al., 2015), driving population level change in life history traits. Fisheries harvest is also selective for specific life history (Heino et al., 2015), behavioral (Uusi-Heikkilä et al., 2008), and physiological (Hollins et al., 2018) traits in fish such that individuals exhibiting certain phenotypic traits are more likely to be caught than others of the same species. If there is a heritable genetic basis for individual traits which determine capture vulnerability in fish, these phenotypic changes can constitute a true evolutionary response, in a phenomenon known as fisheries induced evolution (FIE). Fisheries harvest therefore has the capacity to drive phenotypic change in exploited fish populations, with consequences for the adaptive potential of those populations when faced with further environmental stressors.

In addition to influencing population resilience and recovery potential through impacts on life history traits, fisheries selection may also directly alter the physiological traits present in exploited fish stocks (Enberg et al., 2012; Hollins et al., 2018). Individual variation in physiological traits has been shown to correlate with risk of capture in both active (Killen et al., 2015a; Hollins et al., 2019) and passive fishing gears (Koeck et al., 2019; Redpath et al., 2010) and has also been shown to underpin a range of behaviors which influence capture vulnerability (Andersen et al., 2016; Arlinghaus et al., 2017; Diaz Pauli and Sih, 2017; Metcalfe et al., 2016). For example, angling was shown to selectively remove individual rainbow trout with low neuroendocrine stress responsiveness and high activity rates (Koeck et al., 2019), leaving an uncaptured population composed of more stress-responsive, low activity individuals. Experimental studies have shown that active gears also have the capacity to selectively remove individuals with specific physiological traits. In a simulated trawl fishery, European minnow (*Phoxinus phoxinus*) with greater anaerobic metabolic capacity were more likely to avoid trawl capture (Hollins et al., 2019; Killen et al., 2015a,b) through a mechanism of higher swim performance, suggesting physiological selection in trawl fisheries may lead to fish populations with high anaerobic capacity and associated swim performance. However, relationships between individual behavioral and physiological traits and capture vulnerability in both active and passive gears have

been shown to be highly context dependent (Hollins et al., 2019, 2021), as these traits themselves show high plasticity (Killen et al., 2016). This makes the net outcome of any physiological selection difficult to predict, as the distribution of traits within a population, and thus the potential for any selection to occur, will be strongly mediated by environmental conditions. For example, in low oxygen and high temperature conditions, swim performance in targeted fish populations may be so reduced, and capture rates resultantly high, that selection is effectively obviated (Thambithurai et al., 2019). Nevertheless, many physiological traits show evidence of heritability (Ferrari et al., 2016; Volckaert et al., 2012) and repeatability (Norin and Malte, 2011), as well as correlations with other traits relevant in determining capture vulnerability in fishing gears (Hollins et al., 2018; Metcalfe et al., 2016), or influencing capture vulnerability in their own right (Hollins et al., 2019; Killen et al., 2015a,b). Therefore, where the direction of fisheries selection on physiological traits has been consistent (e.g., low activities and swim performances may be consistently selected against in trawls; Diaz Pauli et al., 2015; Hollins et al., 2019; Killen et al., 2015a,b; Thambithurai et al., 2019), resulting phenotypic change in the physiological traits of exploited fish populations seems possible.

Any fisheries-induced phenotypic change in physiological traits of wild fish populations could have consequences for ecosystems and population resilience to environmental disturbance/stress. For example, the physiological traits of fish populations which experience heavy trawl fishing may be skewed toward individuals with high anaerobic metabolic capacity, a trait which is also associated with prolonged recovery times after exhaustive exercise (Clark et al., 2017), but also resilience to low oxygen availability at high temperatures (Sørensen et al., 2014). The impacts of severe ocean weather events, such as localized extremes in temperature increase or oxygen deprivation (Bates et al., 2018) may therefore be lessened in these fish populations. However, unlike aerobic metabolism, anaerobic metabolism cannot be sustained for long periods due to continual accumulation of lactate and subsequent onset of metabolic acidosis, a process which will be accelerated under conditions of ocean warming (Clark et al., 2017). Shifts toward high performance phenotypes as a result of fisheries selectivity may therefore have further implications for fish species targeted by both trawls and catch and release/recreational fisheries, (e.g., Atlantic cod), where the stress of capture/handling/release may lead to higher rates of mortality under future climate change scenarios. The distribution of physiological traits which determine baseline energetic demand (e.g., standard metabolic rate) in fish populations may also have been altered by fisheries selectivity owing to their likely role in determining behaviors related boldness and feeding motivation (Metcalfe et al., 2016), and the relevance of those behaviors in determining capture vulnerability in passive gears (Biro and Post, 2008; Lennox et al., 2017; Redpath et al., 2010). The relative benefits/costs of high SMR are context specific (Norin and

Metcalfe, 2019; Reid et al., 2012), but fish populations comprised of low SMR individuals may be less able to translate abundant food resources or productivity pulses into enhanced growth, potentially limiting biomass available for fisheries harvest.

The role of aerobic and anaerobic metabolic traits in determining the fitness and abundance impacts of future climate change on fish populations is a contentious issue (Ejbye-Ernst et al., 2016), and so how fisheries selection on physiological traits may interact with the environmental stress of climate change is not clear. That being said, reductions in the diversity of traits present within animal populations are expected to reduce overall population resilience and limit the capacity for populations to adapt to environmental change (Schindler et al., 2010). This destabilizing effect of fisheries selection may exacerbate the impact of environmental stressors on wild fish populations, and may underlie observations of exploited fish species showing greater distributional shifts in response to climate change than unexploited populations (Hsieh et al., 2008).

The high mortality and often size-selective nature of fisheries harvest can truncate size and age structure in wild fish populations (Enberg et al., 2009; Kuparinen and Hutchings, 2012; Swain, 2011), which can lead to unpredictable recruitment success (Hsieh et al., 2006, 2010; Longhurst, 2002), and possibly increase population susceptibility to concurrent environmental stressors (Hsieh et al., 2006; Lehodey et al., 2006). Therefore, while these population-level phenotypic changes may have limited direct impact on overall economic yield in fisheries in the short term, their implications for the resilience of exploited fish stocks, and the capacity for those stocks to recover should fishing effort cease, may be more severe (Eikeset et al., 2013; Enberg et al., 2009; Kuparinen and Hutchings, 2012; (Swain, 2011)). For example, in the Atlantic cod populations off southern Labrador and eastern Newfoundland, Canada (hereafter “Northern cod”), fisheries induced reductions in size at age were apparent by 1960 (Hutchings and Rangeley, 2011; Olsen et al., 2004), but subsequent fisheries “collapse” did not occur until the 1980s and 1990s. In response to precipitous population declines, a moratorium on targeted fishing for Northern Cod was implemented in 1992. Despite this, Northern cod stocks have not recovered, and remain at approximately 2–3% of their 1960 biomass (Hutchings and Rangeley, 2011). Evolutionary reductions in size at age, and earlier maturation have likely limited the rates of population growth in Northern cod through mechanisms of reduced population fecundity (Hutchings and Rangeley, 2011; Swain, 2011), but are insufficient to explain their lack of recovery in its entirety. Indeed, despite drastically reduced fishing mortality experienced by the Northern cod population, overall mortality has actually increased since the moratorium on fishing activity was established (Swain, 2011). This elevated mortality is partially attributed to increased post reproductive mortality in smaller cod (Hutchings and Rangeley, 2011; Swain, 2011), however, increased rates of predation, reductions in egg

quality, and interactive effects between earlier maturation and challenging environmental conditions (e.g., resource limitation) are likely even greater contributors to sustained low Northern cod biomass (Hutchings and Rangeley, 2011; Venturelli et al., 2009).

The evolutionary legacy of the collapsed Northern cod population highlights how fisheries harvest can alter the demographic traits of exploited fish populations, and also how these changes can cause synergistic ecosystem interactions to further hinder population recovery. While overall alterations to size at age and growth rate have clear implications for the reproductive output and recovery potential of wild fish populations (Enberg et al., 2009, 2012; Heino et al., 2015), truncated size and age structures of exploited fish stocks may also render populations more vulnerable to the continued impacts of climate change. The influence of environmental conditions on recruitment success in fish populations varies, with some showing tight linkages with variables such as temperature, while for others recruitment success is better predicted by standing biomass, or age at maturity (Longhurst, 2002; Rindorf et al., 2020). FIE impacts on these life history traits may therefore strengthen links between climate and recruitment in heavily fished species, contributing to more variable patterns of abundance over time (Hsieh et al., 2006) and exacerbating the impacts of climate change on future fisheries yield (Ottersen et al., 2013).

6 Environmental stressors, species interactions, and fisheries: An example with the introduction of non-native species

Ecosystem structure may be altered by many factors, including interspecific differences in response to a changing climate (Ainsworth et al., 2011; Pinsky et al., 2020; Roessig et al., 2004), the introduction of non-native species by human activities (Gozlan, 2017), and synergistic interactions between the two. The continued impacts of climate change drive increases in water temperature and acidity (Abraham et al., 2013), as well as the propagation of aquatic oxygen minimum zones (Altieri and Gedan, 2015). The combined effects of these shifting environmental conditions can constitute a significant form of physiological stress for native fauna, and biodiversity within impacted ecosystems may be altered as native fauna either leave the now disturbed environment, or struggle to compete with species more readily adaptable to changing conditions (Libralato et al., 2015). Community change in aquatic ecosystems can also occur via competitive interactions between native species and species introduced through human activity (Bando, 2006; Lovell et al., 2006; Martin et al., 2010). Establishment of invasive species can lead to population declines of native species through competitive interactions (Martin et al., 2010), but these interactions themselves will also be modulated by the continued influence of climate change (Coni et al., 2021). Fisheries may therefore be forced to continually adapt to the changing distributions/

availability of traditionally targeted species, or otherwise target newly established species of commercial value. The presence of invasive species also constitutes a biotic stressor for native fishes, possibly influencing physiological stress, habitat use, rates or energy intake, and predation, in ways that interact with various abiotic stressors.

Where non-native species have a competitive advantage over native species, or environmental conditions are otherwise no longer advantageous to native species, the availability of target fish to a given fishery may change. For example, the establishment of the invasive lionfish (*Pterois* spp.) in the Caribbean has been implicated in declines of commercially important Atlantic coral reef fish populations through both mechanisms of competition (Morris et al., 2011; O'Farrell et al., 2014), and direct predation (Green et al., 2012). While rapid somatic growth, a lack of predators, and an abundance of naïve prey have all contributed to the continued invasive success of lionfish (Côté and Smith, 2018), lionfish also exhibit physiological tolerance to a broad range of temperatures (Lower and upper critical thermal ranges of 9.5–16.5°C and 30–40°C, respectively) and salinities (daily fluctuations of 28‰) (Barker et al., 2018; Jud et al., 2015), while also showing high starvation tolerance (Fishelson, 1997). While these environmental tolerances are comparable to those of native reef fishes throughout its introduced range, predation pressure can limit the dispersal of native fish to habitats where abundant shelter is available. As lionfish experience very limited predation pressure (Côté and Smith, 2018), and also exhibit broad physiological tolerances, they have been able to successfully colonize a range of non-native habitats in an era of unprecedented environmental change. While reductions in populations of commercially and recreationally important Atlantic reef species have been attributed to the invasive success of the lionfish throughout its non-native range (Ballew et al., 2016; Côté and Smith, 2018), a commensurate shift in targeted fishing effort toward lionfish has not yet occurred, and management approaches including targeted removals, and incentivized harvest are often implemented as a form of population control (Johnston et al., 2015).

In addition to reducing the availability of resources to native organisms (van Kessel et al., 2011), with subsequent reductions in fitness, the presence of invasive species can also reduce the predictability of those resources (Carpenter et al., 2011). This can influence relationships between individual physiological and behavioral traits and fitness in fish species, (Reid et al., 2012) with potential consequences for the phenotypic composition of native fish populations (Závorka et al., 2017). For example, brown trout parr (*Salmo trutta*) with higher standard metabolic rates (SMR) show more territorial behavior to secure consistent access to high quality habitat (Závorka et al., 2017). Securing territories in this way helps ensure food resources are predictably available, which can confer fitness advantages to these high metabolic rate individuals (Reid et al., 2012; Závorka et al., 2017). However, should

the predictability of these resources change, this adaptive advantage may be lost, potentially leading to selection against individuals with high metabolic demands (Killen et al., 2011; Zeng et al., 2017). Indeed, competitive displacement disrupted the relationship between metabolic traits and territoriality observed in brown trout parr at sites where the invasive brook trout (*Salvelinus fontinalis*) was established (Závorka et al., 2017) and was accompanied by a reduction in space use and slower growth rates in brown trout in general. Traits related to space use (Härkönen et al., 2014; Koeck et al., 2019), energetic demand (Keiling et al., 2020; Redpath et al., 2010) and boldness/aggression (Klefoth et al., 2017; Redpath et al., 2010) may each play a role in determining capture vulnerability in fish, and so changes in the distribution of these traits amongst wild fish populations because of invasive species may in turn impact their availability to fisheries.

Although poorly understood, deleterious interactions between native and non-native species may be buffered by present-day environmental conditions. For example, high availability of shelter and food resources can mitigate competition between native and non-native species (Kernan, 2015; van Kessel et al., 2011; Stachowicz and Byrnes, 2006) while seasonal decreases in water temperature can prevent the expansion or establishment of warmwater invasive fish populations further outside of their natural range (Rahel and Olden, 2008). Therefore, further environmental change may eventually trigger a competitive imbalance and destabilizing effect in ecosystems where non-native species are already present but relatively non-disruptive, when differences in physiological tolerances and performance between native and non-native species may be revealed and translate to differences in fitness. Such a scenario is predicted to exacerbate the problem of invasive sea lamprey throughout the Laurentian Great Lakes (Lennox et al., 2020), which will benefit from enhanced growth and the expansion of thermally suitable habitat as the climate warms. This, in turn, will likely increase rates and lethality of parasitism on native fish species of both recreational (e.g., lake trout; Muir et al., 2012) and commercial (lake whitefish *Coregonus clupeaformis*; Ebener et al., 2008) fisheries importance (Lennox et al., 2020). Similarly to the lionfish example outlined above, no new commercial fishery targeting lamprey has emerged in response to their increased abundance, and lamprey are not a desirable species in recreational fisheries.

7 Future research and conclusions

Within the realm of comparative physiology in general, studies are only recently beginning to consider the effects of multiple stressors on animal functioning, and the potential effects of combined stressors on fisheries are mostly unknown or speculative. Most work that has been done in this has examined effects of fishing in isolation or in combination with perhaps a single additional stressor (e.g., elevated temperature). This work has been a

key foundation for understanding the physiological effects of fishing, the potential for recovery after escape or release, collateral fishing mortality, and population-level effects. However, much more work is needed to understand the combined effects of the many stressors that fish regularly encounter in the wild, including hypoxia, chemical and sensory pollution, artificial light, altered pH, habitat degradation, and others, particularly in the context of fisheries. There is a broad range of potential research avenues in this field, but here we outline five general areas of especially high priority:

1. *The combined effects of multiple stressors during interactions with fishing gears.* Many studies have evaluated acute impacts of capture on fish in terms of immediate physiological stress response, behavioral impairment, and mortality, however many of these studies only consider a single environmental scenario (for example, at a single water/air temperature, or time of year). Experimental work evaluating these responses under prospective climate change scenarios, and in response to other environmental stressors, will further our knowledge on how the cumulative stress of capture and additional stressors may impact wild fish populations.
2. *Feedbacks between fisheries-induced evolution and vulnerability to environmental stressors.* While it is increasingly acknowledged that the impacts of fisheries selection alter the phenotypic composition of targeted fish species, the impacts of this phenotypic change are typically considered in terms life history and reproductive traits. How fisheries selection may have influenced the capacity for exploited fish stocks to adapt to climate change-induced stress, for example through the removal of stress-resilient phenotypes, is completely unknown. While investigating phenotypic change of cryptic traits in wild fish populations is extremely challenging, new analytical techniques such as retroactive estimation of metabolic rate via stable isotope analysis of otoliths provide new opportunities to investigate change in metabolic traits of fish stocks over time. Mesoscale fisheries simulations, where the traits of caught and uncaught fish are known and can be monitored in real time would also do much to elucidate how fishing changes the composition of fish populations, and how these altered populations may cope with future environmental stressors.
3. *Overlap between fisheries and shifting population distributions.* Poleward range expansions, and compression of vertical habitat use in response to changes in water temperature and oxygen concentrations have been observed in a range of fish taxa, but mechanistic links between physiological traits and habitat selection/use are still lacking, making future predictions of fish home ranges difficult. With the development of high-resolution telemetry devices, in addition to data loggers which can simultaneously measure fish acceleration, temperature, and heart rate, studies evaluating the metabolic costs/advantages of using specific habitats are increasingly viable. Studies

using these approaches in both fully wild and mesocosm experiments would be invaluable in predicting changes in encounter rates with fishing gears in response to a warming climate.

4. *Acute effects of multiple stressors on fish recovery after capture and subsequent release or escape.* Many studies have evaluated acute impacts of capture on fish in terms of immediate physiological stress response, behavioral impairment, and mortality, however many of these studies only consider a single environmental scenario (for example, at a single water/air temperature, or time of year). Experimental work evaluating these responses under prospective climate change scenarios, and in response to other environmental stressors, will further our knowledge on how the cumulative stress of capture and additional stressors may impact wild fish populations.
5. *Sublethal effects of fishing practices and modulating effects of multiple stressors.* Many studies consider the cumulative impact of stressors in terms of fish mortality, while more sublethal effects on performance and fitness are more rarely investigated, despite their relevance for fisheries management. The quality of harvested fish meat, reproductive investment, and growth trajectories may all be impacted by various stressors, however the degree to which this is occurring/may occur, and the economic implications for these changes in fisheries are mostly unknown.
6. *Ecosystem level impacts of fisheries in a multi-stressor world.* The myriad of stressors faced by fish populations in freshwater and marine environments will have ecosystem-wide effects, including alterations to food-webs and interactions with non-native species. This is especially true in the context of fisheries, which may exacerbate these effects by targeting specific trophic levels, altering competitive and selective landscapes, and potentially changing the phenotypic composition of targeted populations. Our knowledge of these effects is currently extremely limited and much more work is needed in this area.

There is no doubt that numerous anthropogenic stressors are having an important impact on freshwater and marine fisheries and will continue to do so well into the future. Understanding the mechanistic, physiological underpinnings of these effects is critical for developing potential solutions and effective science-based fisheries management. To date, research in this realm has largely consisted of controlled laboratory experiments and field sampling studies to isolate the physiological effects of fishing practices. Much more work is needed to understand the effects of multiple stressors at each stage in the fishing process and its relevance for not only those fish that are captured (and perhaps released or escaped) but also for those that are not captured (with potential selection or evolutionary effects). In addition, much more knowledge is needed regarding the potential feedbacks between fishing and various forms of environmental stressors encountered by fish in the wild.

The progress of various technologies for making fine-scale physiological measures in the laboratory and tracking fish movements and logging physiological measures in the wild will greatly facilitate research in these areas going forward.

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