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Opinion

Environmental forcing alters fisheries selection

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Fishing-induced evolution (FIE) threatens the ecology, resilience, and economic value of fish populations. Traits under selection, and mechanisms of selection, can be influenced by abiotic and biotic perturbations, yet this has been overlooked. Here, we present the fishery selection continuum, where selection ranges from rigid fisheries selection to flexible fisheries selection. We provide examples on how FIE may function along this continuum, and identify selective processes that should be considered less or more flexible. We also introduce fishery reaction norms, which serve to conceptualise how selection from fishing may function in a dynamic context. Ultimately, we suggest an integrative approach to studying FIE that considers the environmental conditions in which it functions.

Man the hunter has become a mechanized techno-beast, a highly efficient predator.
Árnason et al. 2009

FIE

FIE, hypothesised at the beginning of the 20th century [1] and formally established as a subject over the past 50 years [2–5], centres on the idea that both recreational and commercial fishing can not only cause direct mortality, but also evolutionary change, by removing individuals with specific traits from a population. A striking characteristic of fishing mortality is that it far outweighs natural mortality [6], and thus is a prime candidate to cause evolution in targeted populations. The rate and intensity of FIE has been questioned, with work suggesting that FIE, although existent, is not an immediate issue for fish populations (compared with direct effects of fishing mortality), or is lacking genetically based evidence [7,8]. However, there have also been calls for FIE theory to be formally integrated into fisheries management as a precautionary measure [9]. Much of the research surrounding FIE has been carried out using theoretical approaches or laboratory experiments using model species [10–13], whilst quantitative evidence of selection arising from fishing and resulting in evolutionary change in wild populations remains rare or contradictory [14,15]. Most research on FIE has centred on traits such as adult body size, onset of maturity, and growth [16–19], yet more recent work has expanded to include numerous traits across behaviour and physiology, such as shoaling, exploratory behaviour, and metabolism [20–23]. What makes selection possible across behavioural and physiological traits is the existence of consistent genetically based variation among individuals [24]. The importance of selection on traits beyond body size for population dynamics and renewal ability remains largely unknown, as does the effect of the environment on the selective processes underpinning FIE.

The fishery selection continuum

The capture of a fish by fishing gear occurs over a number of steps, which differ depending on the type of gear [25,26]; selection across each step may act synergistically or antagonistically, and is under environmentally dynamic control (Figure 1). In general terms, once steps three and four are reached, towed gear may typically select more on performance traits (e.g., swimming), stationary gear on behaviours (e.g., boldness or activity), and baited gear on sensory capacity or hunger, although selection across gear types may also overlap [25,27]. As fish move through the capture

Highlights

Fishing-induced evolution (FIE) – the evolutionary impact on fish populations as a result of fishery harvest – is an important source of contemporary evolution.

Changes in the environment in which fishery selection occurs can influence FIE.

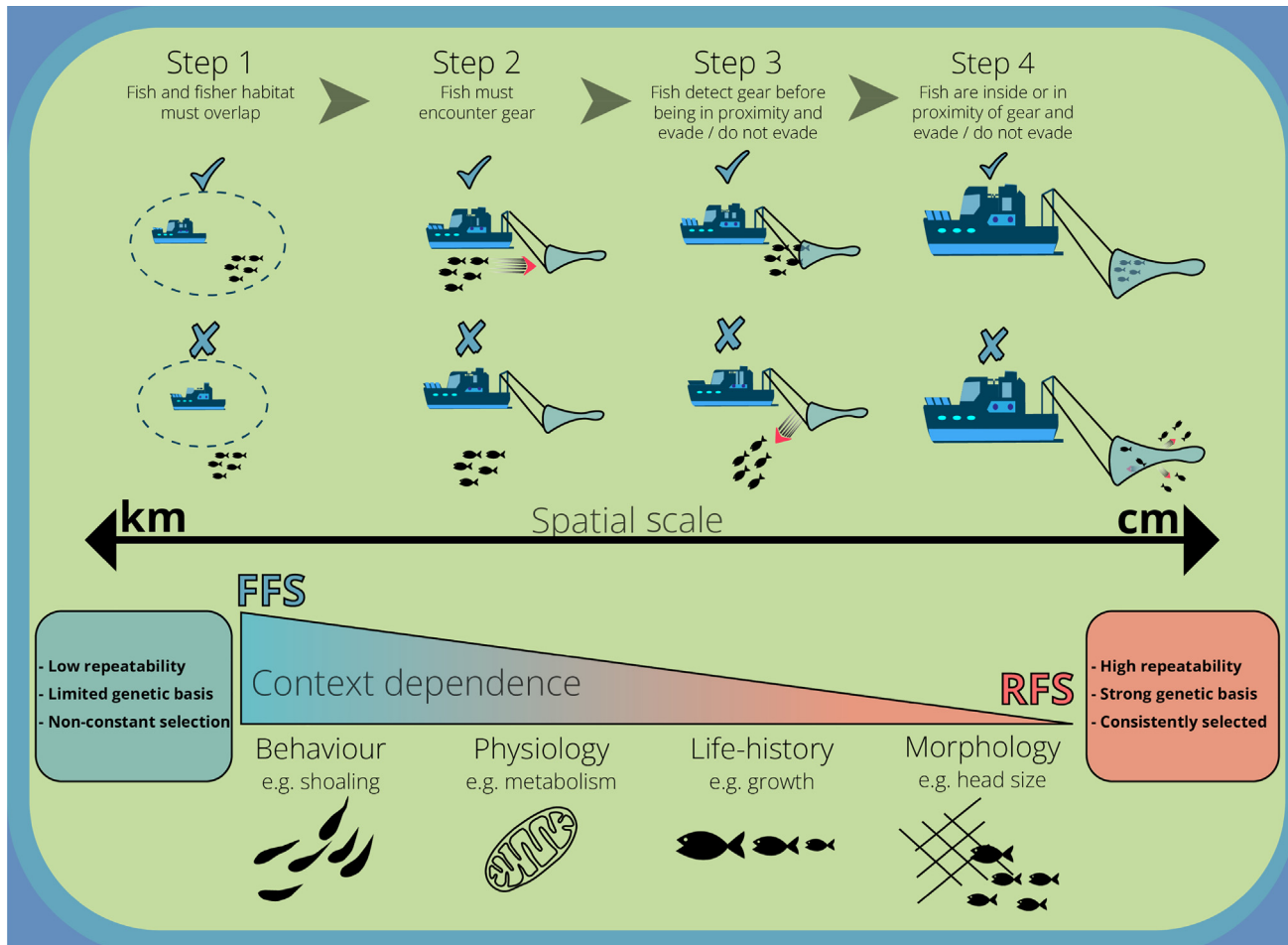
Certain traits remain liable to selection in different contexts (rigid fishery selection), whilst others are only selected for in specific contexts (flexible fishery selection).

Future research on contemporary evolution must consider that selection functions in a dynamic environment.

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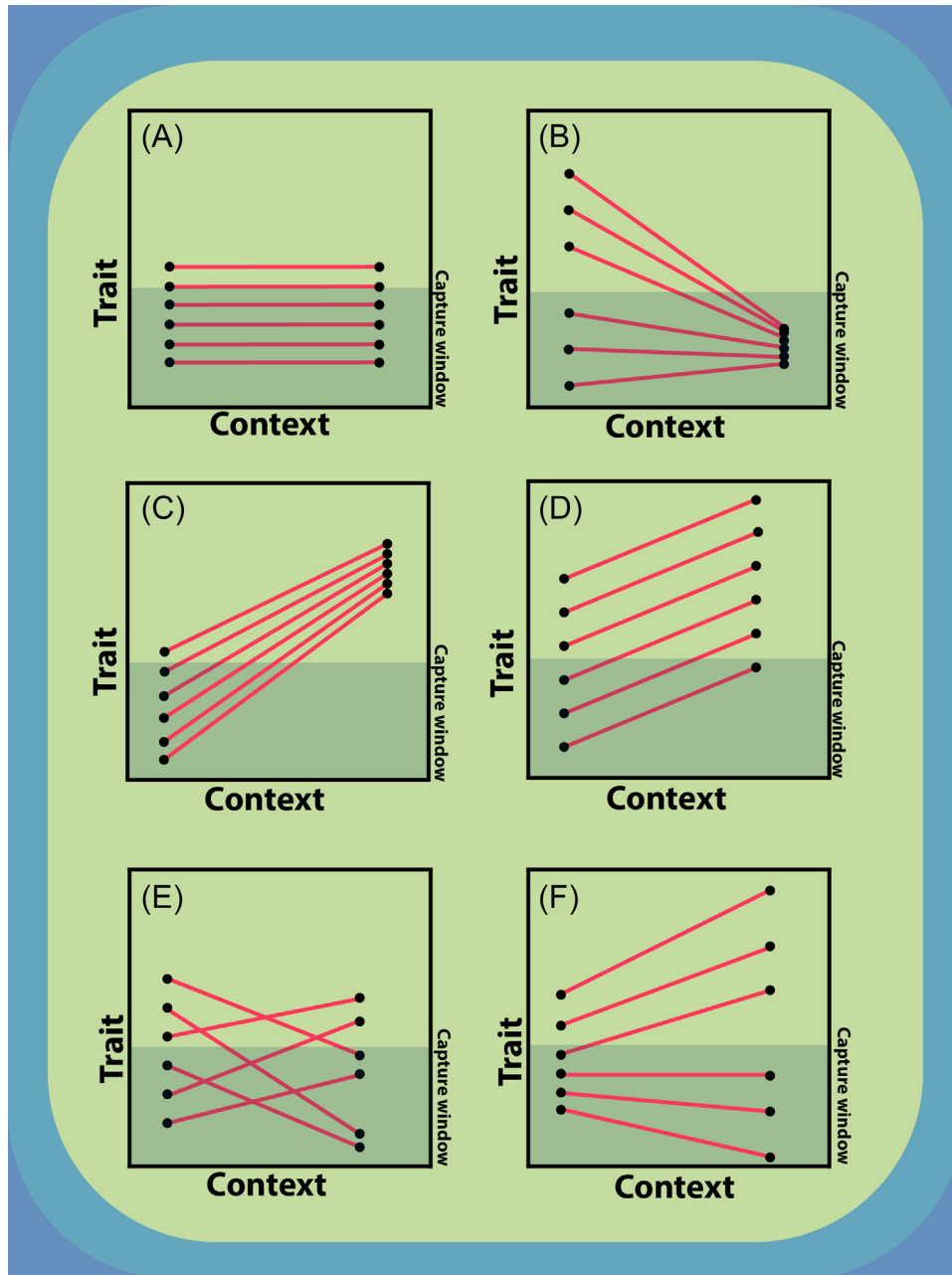
Figure 1. The fishery selection continuum. Although in this example a trawler is shown, distinct capture steps are present with all gear types. In some cases, such as with static gear, step 3 can differ with fish actually being attracted to the gear, and capture might be based on how attracted they are to the gear rather than on their ultimate fate. For a fish to be captured, conditions at each step must be met; failure at any step would mean a fish escapes (indicated by blue crosses). Discarding is considered to represent an additional phase following step 4 (see Box 1). However, it is not depicted in this image as our focus was primarily on the capture/noncapture of the fish rather than on their ultimate fate. The triangle shows how context-dependent selection is, ranging from rigid fisheries selection (RFS) to flexible fisheries selection (FFS). The effects of biotic and abiotic variables are considered weakest toward RFS and strongest toward FFS. For instance, behaviour can be very context-dependent, and thus selection on behaviour is malleable, whereas selection on head morphology is immutable in the short term. The trait categories provide some guidance as to how traits lie along the continuum (behaviour > life-history > physiology > morphology). However, it should be noted that in some specific cases, where traits are particularly repeatable, or not repeatable (regardless of category), their position along the continuum can shift. The coloured boxes display general trait characteristics that influence the location of a trait along the continuum.

process, the spatial scale at which interactions occur decreases; this brings forth the notion of 'pre-gear selection' and 'post-gear selection'. Pre-gear selection should be regarded as selection on fish traits that occurs prior to fish coming into contact with the fishing gear, whilst post-gear selection occurs once fish have contacted gear (e.g., Figure 1, step 4). Pre-gear selection is generally more affected by environmental fluxes than post-gear selection, as fish struggle to evade gear once nearby, regardless of environmental influence on physiology or behaviour. Nevertheless, there are some performance-based traits or behaviours that might maximise escape potential in these late capture phases, and are still influenced by the environment, such as fast-start responses. These performance traits are known to be affected by environmental oxygen availability and temperature for example [28].

Environmental fluxes can affect selection through effects on fish performance, behaviour, and physiology, as well indirectly through fishing activity (e.g., weather influences fisher behaviour which will, in turn, influence selection). Parasitic infection, for instance, shifts selection patterns in simulated fishing [29]. Importantly, both subtle and extreme changes in the environment can impact selection, but may do so differently. For example, Atlantic cod (*Gadus morhua*) vertical space use is heavily influenced by temperature [30], and given the existence of intraspecific temperature preference [31], shifts in water temperatures can influence encounter rates between fish and gear, and thus alter the intensity of selection. By contrast, a temperature change near a species' maximum or minimum tolerance threshold can have equally important but different implications on the capture process (e.g., impaired metabolic functioning and hindered escape ability). Dynamics between environmentally driven habitat use and selection are further complicated by gear-associated restrictions or fisher behaviour. For instance, fishing activity can be limited to specific depths, temporal windows, or zones [32]. This can lead to stronger selectivity on phenotypic properties involved with habitat preference [14,33] or migration timing [34]. In general, dynamics between the environment and the stability of selection make it difficult to predict fisheries-induced evolutionary changes, especially in behavioural traits.

Fishery selection is split into two components along the fishery selection continuum (Figure 1): rigid and flexible fishery selection (RFS and FFS). RFS is selection that is almost immutable regardless of environmental condition, for example, selection occurring on fish size driven by mesh width. Unless there are processes driving selection at greater spatial scales (Figure 1, steps 1–3) that precludes a fish being available for capture, once a fish is in contact with gear, escape options are limited, and capture will be primarily a function of whether a fish can fit through a net mesh and escape. This mechanism is equally important for active gear such as trawl nets (which chase the target fish), as for static gear such as gill nets (forming a curtain in which fish get snagged) [26]. By contrast, selection on some traits can be strong in some situations, but weaker in others (flexible fisheries selection), especially across behavioural and physiological traits which can be highly context-dependent [24] (Figure 1). For example, whereas in a nonturbid environment trawling can select on swimming capacity, within a turbid environment sensory acuity (e.g., hearing or eyesight) might represent the most important trait to escape from fishing gear, and swimming performance might be less important. This means that swimming capacity would not lie at the extreme rigid end of the continuum.

When considering where a trait lies on the continuum, and how it might respond to fishery selection, four key factors should be taken into account: trait variance, stability, heritability, and its correlation with other traits. Variance, or among individual variation in a trait, must exist if selection is to function (as indicated by the vertical spread of points in Figure 2). This permits some individuals to escape and others to be captured (i.e., some individuals lying within and some outside the capture window) (Figure 2). The strength of selection is also a function of how stable a trait is in the face of environmental shifts (typically more applicable to behaviours). A trait that is stable under different contexts means that it would skew towards the rigid end of the continuum, whilst a trait that changes depending on context would be toward the flexible end of the continuum. Olfaction, hearing, gustation, and vision play crucial roles in mediating physiological and behavioural responses to the environment, making them examples of traits that can undergo context-specific selection in fisheries. However, there is currently limited evidence of intraspecific variation in these traits [35–37]. The response of a trait to selection and its potential evolution is also dictated by a trait's heritability (proportion of the variation attributable to genetic factors). Across organisms, heritability of morphological traits is considered highest, followed by physiology, behaviour, and life-history [38]. A high heritability means that, for a given trait, a higher proportion of a phenotype will be passed to the next generation [39]. Thus, in a scenario where selection on traits



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Figure 2. Fishery selection in a dynamic environmental context displayed via fishery reaction norms. Lines represent individual/genotype, and slopes are indicative of changes in trait expression along differing environmental context. Intercepts show interspecific differences in trait value, whilst slopes show how a trait changes as a function of context. Capture windows (shaded boxes) represent the trait space in which fish are vulnerable to fishing. Though shown as rectangles with hard boundaries, capture windows are themselves under dynamic environmental control; they can occupy trait space across the graph or be restricted to a specific area, and reflect a probability of capture for a specific phenotype. (A) Flat response with consistent differences between individual/genotype and no plastic response to the environment, an example of rigid fisheries selection (RFS). (B,C) Sloped, non-parallel fishery reaction norms; a loss in population variation is present and all/no individuals fall within the capture window, no selection occurs on the right of the

(Figure legend continued at the bottom of the next page.)

is not context-dependent, and fixed at the same rate, we would expect morphological traits to evolve quickest in response to fishing. Finally, the fact that fishing vulnerability is not one trait but is made up from a combination of traits (physiological, behavioural, morphological, meristic), typically with a polygenetic basis, means that response to fishery selection can manifest itself across a number of correlated traits, and may cause unknown shifts in genotype [40,41]. For instance, recent work has shown that trawling selects on growth rate through correlated selection on swimming performance [42]. If selection acts on two correlated traits, each sitting at different ends of the fishery selection continuum (Figure 1), then one would expect a mutual response in both traits. However, the correlated response would be greater if the trait being selected on were at the rigid end of the continuum, as opposed to the flexible end, as the environment would modulate selection at the FFS end. Ultimately, correlated responses to selection would depend on the strength of the correlation, the heritability of each of the traits in question, and the consistency of selection.

Selection across the continuum is not only a function of the biological trait being selected in the fish, but also a function of the fishing action itself. The ‘fishing repeatability’ may influence selection by either being stable or being stochastic (i.e., can the activity be replicated in exactly the same manner each time, or does its effectiveness and selective strength differ according to context?). In Figure 1 only biological traits related to the fish are shown, but one can think about a similar and equally important continuum for fishing gear and fisher behaviour. Similarly to how biological traits are shown as categories of the length of the continuum, categories associated with fishing practice must also span the length of a continuum (e.g., timing of fishing, gear specifics), and will be more or less likely to be influenced by context.

Fisheries reaction norms

Environmental influences on selection have received little attention in evolutionary theory, and even less in FIE research [24,29,43,44]. Gear type, specific capture step (Figure 1), type of disturbance, and time of occurrence will all modulate the type of impact that environmental context has on selection. A way to understand and visualise how fishing selection can differ dynamically under changing environmental context is to do so graphically, using reaction norms [45], with an additional component displaying fishery capture (Figure 2). Importantly, environmental impacts can amplify (e.g., increase trait variance), nullify (e.g., decrease trait variance or repeatability), or reverse directional selection in fishing. In the following text, we highlight how a suite of environmental drivers can influence selection; we mainly use trawling as an example as it is one of the most widespread fishing methods, but effects on selection across gear types should be expected. A more detailed case study is provided in Box 1, where hypoxia and its potential effects on selection are discussed across each capture step.

Temperature

While temperature changes have obvious impacts on growth and development, thereby leading to changes in body size, temperature can also alter habitat use, thus reducing fish availability in fishing grounds (Figure 1, steps 1 and 2) [46]. At a finer scale, temperature can affect fish performance and behaviour [31] by reducing swim performance and influencing escape responses [47]; such effects could influence which individuals within a population are captured (Figure 1,

panels. (D) Sloped, parallel fishery reaction norms, indicating plasticity to the environment and additive genetic variation; in this case some individuals exit the capture window as they display a high context-specific plasticity. (E) A genotype by environment interaction, where some individuals which occupied a higher trait space are lower and vice versa for other individuals; in this case selection could occur but is on a different set of individuals than within the initial context. (F) Differently sloped responses indicating a genotype by environment interaction, some individuals exit the capture window and some remain within it.

Box 1. Hypoxia across the capture process

Marine oxygen levels have decreased over 50 years and will likely continue to do so [59,60]. Hypoxia (low oxygen in water [61]) can have major effects on fish, influencing species distribution, morphology, physiology, and behaviour. Little consideration has been given to how hypoxia may influence fishery selection. Unlike in natural predator–prey scenarios, where both predator and prey are affected simultaneously by hypoxia, only the prey fish is being influenced in a fishery scenario. This means that we may see significant impacts on how selection occurs during fishing in hypoxic conditions, especially because variability in individual responses to hypoxia can impact inter-individual susceptibility to capture [61], and potentially modify selection outcomes [62]. Individual capture steps (see Figure 1 in main text), associated fishery reaction norms, and some of the potential effects of hypoxia are discussed for trawling gear as follows.

Step 1

Fish exposed to hypoxia exhibit behavioural changes (e.g., activity shifts) alongside physiological responses (e.g., altered cardiac rate, and haemoglobin affinity) to preserve homeostasis. Emigration out of affected areas may remove some or all individuals from the pool of fish available for capture (see Figure 2C in main text); these effects can be accentuated by differences in among-individual tolerance to hypoxia. Habitat compression, a process whereby fish congregate on the edges of hypoxic fronts [63], can lead to increased densities of fish and render individuals within a population more vulnerable to exploitation, leading to little selection (see Figure 2B in main text). Under mild hypoxia, at a wide spatial scale, a scenario such as the one presented in Figure 2E in main text may arise, where owing to differential within-species behavioural response some individuals which were previously not available to a fishery are now available, and vice versa. Under a high level of hypoxia, due to a strong effect on physiology, selection may altogether fail to operate (see Figure 2B in main text).

Step 2

Step 2 of the fishing process entails gear to be deployed in the same general area as fish, but not so close that the fish are able to sense the gear. Movement from fish in different strata of the water column, or closer to underwater structures, could influence selection at this point. Hypoxia is known to influence depth preference in fish [64]. This could serve to change selection patterns, especially when gear limitations restrict fishing across the water column. Existing evidence on FIE already suggests that fishing can selectively target phenotypes associated with specific depths [14]; therefore, in instances where hypoxia influences depth preference, a substantial change in selection patterns could occur (e.g., Figure 2D in main text). Hypoxia is also known to have strong effects on the activity of fish, both increasing [65] and decreasing activity [66], and this may impact the encounter rates between fish and gear, thereby influencing selection.

Step 3

Step three of the fishing process occurs when fish detect gear, but before immediately reaching it (beyond a few meters). During this phase, fish can use their sensory apparatus to assess a threat and take evasive action. Hypoxia may hinder the ability of fish to do this due to its impacts on physiology (eyesight, hearing, olfaction, and neural functioning) [67]. Hypoxia is known to negatively impact escape from natural predators, but evidence for its influence on fishing and selection is lacking. Anecdotal evidence suggests that catches in hypoxic areas sometimes increase dramatically [68], possibly pointing to a collapse in selection (see Figure 2B in main text). In hypoxia, fish might delay gear avoidance due to effects on escape-related traits such as visual acuity [69], thus making them more prone to capture. Recent work has suggested that propensity to shoal can influence selection in fishing [12,22,70]; this is also known to be significantly influenced by hypoxia [67], therefore selection on behavioural characteristics such as shoaling may break down under hypoxic conditions, leading to changes in which individuals are vulnerable (see Figure 2E in main text). By contrast, congregation along hypoxic fronts may lead to no selection as fish are tightly packed and all equally likely to be captured (see Figure 2B in main text).

Step 4

Step four in the fishing process occurs when fish are herded near the gear or within it; selection then skews towards the rigid fishery selection (RFS) end of the spectrum. Both laboratory studies and work on wild populations suggest that trawling removes slower phenotypes [71,72]. Fish use two swimming modes: sustained and burst. Sustained swimming relies on O₂ supply and uses mitochondria-rich red muscle, whilst anaerobic white muscle is typically used for escaping and bursting. Both swimming modes are influenced by hypoxia [28]. These hypoxic effects on swimming may disrupt selection and randomise capture (see Figure 2E in main text) by influencing the repeatability of swimming [62], thus changing the evolutionary impacts of fishing.

Additional thoughts

An additional capture/selection step not fully considered here is the collateral mortality associated with fishing [73]. Processes like discarding – eliminating unwanted by-catch – will certainly select for phenotypes more capable of surviving the discard process. For example, if in a population there are individuals with better sustained swimming performance, they are more likely to survive the discard process by limiting the time they are impinged on the net. These selection processes will be accentuated by how individual fish can cope with the stress of being in the net as well as hypoxia.

steps 3 and 4). Temperature also increases activity through effects on metabolism, thus affecting gear encounter rates [48]. Recent work on zebrafish has also shown that warming water temperatures, coupled with fishing harvest, can act in synergy to limit recruitment rate [49].

Turbidity

Visual acuity is crucial for antipredator behaviour, and can differ among individuals [50]. Higher turbidity may mean that the advantages held by an individual with better eyesight would be reduced (unless also held under turbid conditions), changing selection, or shifting selection towards secondary traits (Figure 1, steps 3 and 4). For instance, the principal sensory mechanism to avoid danger may change from vision to sound, meaning the distribution of phenotypes under selection will also change (unless two traits are correlated).

Parasite infection

Parasites are ubiquitous among wild fish, infecting practically every organ, and influencing both behaviour and performance by effects on locomotion, metabolism, sociality, activity, and morphology [51]. Effects of parasites on foraging behaviour, or sensory capacity, are very likely to influence which individuals within a population are liable to capture (Figure 1, steps 1–4). Similarly, increases in activity or boldness induced by parasite infection may increase likelihood of capture among infected individuals [29].

Noise pollution

Underwater environments have become increasingly noisy [52]. Fish use sound as a means of identifying and avoiding natural predators [35], and have been shown to use sound to also avoid fishing gear [53]. Anthropogenic noise has the potential to mask the sound used by fish for early avoidance of fishing gear [54], thus altering selection patterns (Figure 1, step 3).

Food availability and population density

Fishing itself changes population density, with feedbacks on selection and evolution [42]. For instance, fishing pressure on small pelagic fish (e.g., sardines) could decrease food availability for larger fish like tuna, increasing activity levels and lead to changes in selection patterns [55]. Capture in stationary or baited gears is particularly affected by limited food availability through effects on activity [56,57] (Figure 1, steps 1 and 2).

Future research

Fishery-driven contemporary evolution requires further scrutiny to assess whether it poses a significant problem for exploited fish populations. Evidence is particularly lacking for behavioural and physiological traits that are not directly linked to fishery or population productivity (i.e., not growth, body size, or maturity). Within this context, a huge unknown that remains to be understood is the role of shifting biotic and abiotic conditions on selection and traits under selection, potentially leading FIE to be extremely dynamic (see Outstanding questions). Randomness in the conditions in which fish are exploited (context dependence), as well as the range of methods by which they are exploited, might mean that selection pressure is in some cases negligible, and therefore evolutionary shifts are unlikely but for the most rigid selection (e.g., size). The arguments we present are theoretical, and empirical work is needed to assess which evolutionary responses to fishing can be stable under the stochastic nature of marine and freshwater environments and fishing practices. Laboratory work involving simulations of fishing under dynamic environmental conditions using model species might, in part, serve to answer some of these questions. However, importantly, the nature of selection induced by real fisheries must be measured and its components elucidated. A way to approach this would be to carefully monitor environmental conditions whilst simultaneously assessing phenotypic differences in fish being

captured. Also, data mining of historical collections, such as those of otoliths, in combination with techniques such as whole-genome sequencing might provide insights into widescale changes to selection patterns (e.g., changes in propulsion like wind, steam, and combustion). Particular effort must also be made to understand how selection on a specific phenotype can operate across the capture process (Figure 1). Each step can drive selection toward a specific phenotype, all whilst being influenced by the environment. Thus it is important to consider fishery selection as multidimensional, first occurring at large spatial scales, and gradually ending within the gear itself. Although some effort has been made to consider selection occurring at large spatial scales, more needs to be done to comprehend selectivity at each fishery step, and whether selection at each step acts in synergy or antagonistically under dynamic environmental conditions.

While we have concentrated on the influence of short-term dynamic changes on selection processes, long-term climatic and technological trends also affect fishery selection. The unprecedented rates of warming and acidification occurring in marine environments might mean that previously less vulnerable phenotypes become more vulnerable, or vice versa. Synergistic effects of warming waters or hypoxia will undoubtedly have repercussions on the selective processes in commercial fishing. In addition, advances in fishing technology – whether related to fishing gear, navigation, or propulsion – might mean that fishery selectivity changes over time, never settling on one particularly phenotype. Contrasting fishing regimes and the effect of the environment may promote weak selection on fish populations that are subjected to commercial fishing.

Concluding remarks

Past work on FIE has overlooked the influence the environment can have on selection. Understanding how environmental factors affect among-individual variation, trait repeatability, and selective processes during distinct fishery capture phases (Figure 1) is crucial to project the evolutionary response of fish populations to harvest (see Outstanding questions). The interplay between anthropogenic and nonanthropogenic selective forces, as well as genetic drift, will drive fitness and fixation toward specific phenotypes. Only when selection is acting on the same trait repeatedly and consistently under different contexts are we likely to see a large-scale population-level evolutionary change. Furthermore, such an evolutionary change in one species targeted by fishing is likely to cause coevolution in interacting species, such that ecoevolutionary feedbacks propagate throughout the ecosystem [58].

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Declaration of interests

The authors declare no conflicts of interest.

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Outstanding questions

How much does environmental stochasticity influence selection in fisheries?

What are the most important environmental factors influencing the selective process in commercial and recreational fishing, and are these the same?

Can selection on behavioural and physiological traits lead to significant evolutionary change, given that environmental conditions can strongly affect trait repeatability?

Does randomness in the system mean that selection gradients toward some phenotypes are essentially negligible, or does selection persist regardless of the randomness? If so, what are the traits that do persist?

What are the dynamics of selection when multiple stressors are simultaneously influencing fish behaviour and physiology?

How do short-term and long-term advances and trends in fishing gear technology affect FIE?

What is the relative strength of selection at wider spatial scales compared with selection in the immediate vicinity of the fishing gear, and what is more important for evolution?

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