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Fisheries-induced selection against schooling behaviour in marine fishes

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Group living is a common strategy used by fishes to improve their fitness. While sociality is associated with many benefits in natural environments, including predator avoidance, this behaviour may be maladaptive in the Anthropocene. Humans have become the dominant predator in many marine systems, with modern fishing gear developed to specifically target groups of schooling species. Therefore, ironically, behavioural strategies which evolved to avoid non-human predators may now actually make certain fish more vulnerable to predation by humans. Here, we use an individual-based model to explore the evolution of fish schooling behaviour in a range of environments, including natural and human-dominated predation conditions. In our model, individual fish may leave or join groups depending on their group-size preferences, but their experienced group size is also a function of the preferences of others in the population. Our model predicts that industrial fishing selects against individual-level behaviours that produce large groups. However, the relationship between fishing pressure and sociality is nonlinear, and we observe discontinuities and hysteresis as fishing pressure is increased or decreased. Our results suggest that industrial fishing practices could be altering fishes' tendency to school, and that social behaviour should be added to the list of traits subject to fishery-induced evolution.

1. Introduction

Humans have become a global 'superpredator'. Advances in technology have dramatically increased our ability to capture a variety of prey species, to the extent that we have the potential to alter the evolutionary and ecological processes of the species we harvest [1,2]. Fishing can impact a variety of physiological and life-history traits, often in non-random directions, through fisheries-induced evolution [3,4]. For example, the consistent harvest of the largest individuals in a population over many generations has driven the evolution of smaller-sized individual fish [5]. This targeting of specific phenotypes (e.g. large size) can also indirectly alter reproductive rates, growth rates and time to maturation [6–8]. While the fisheries-induced evolution of life-history traits has received increasing attention, the analogous evolution of behavioural traits remains less intensely studied, but may be of equal importance to fisheries and ecological systems.

Fishing is known to directly alter the evolutionary trajectory of fish behaviour, as behavioural traits can affect an individual's vulnerability to capture by humans [9,10]. For example, boldness is a heritable trait associated with higher levels of aggression, activity and exploratory behaviour. In addition to making fish more effective at guarding eggs and improving foraging success [11], boldness results in more frequent encounters with natural predators [10,12], as well as increased encounter rates with passively operated fishing gear (e.g. long-lines and traps). This can lead to increased capture rates of bolder individuals [12], and indeed, empirical evidence has demonstrated that the widespread use

of passive fishing gear has led to increased shyness among individuals in fished populations relative to unfished populations [10,12]. This decrease in boldness could lead to important consequences regarding the foraging success of the fish, the food web dynamics of the affected ecosystems, and the profitability of a fishery reliant on fish that are increasingly difficult to capture [10,12]. Similarly, migration timing, a heritable behaviour in salmon, can affect their vulnerability to capture if fishers' effort is not distributed evenly over the season [13]. Another obvious candidate behavioural trait that may be affected by human exploitation is schooling and shoaling behaviour, although to our knowledge these effects have yet to be explored.

Within their natural habitat, individuals can accrue a variety of fitness benefits from group living [14,15], including increased access to resources (at the cost of intragroup competition), increased reproductive success, reduced energy output due to hydrodynamic efficiencies and predator avoidance [14,16]. Classically, predator avoidance is considered to be one of the main fitness benefits driving the evolution of gregariousness, particularly among small prey species [17,18]. Living in groups may reduce predation risk for an individual by lowering the probability of encountering a predator (in the case of random-search predators). Furthermore, when a predator is encountered, group living may dilute the risk of a predator attack, reduce a predator's ability to track and successfully attack individuals, and allow individuals to evade predators by using information propagated socially through the school [19–21].

There is experimental evidence that fish can exhibit preferences to be in groups of particular sizes [22–24]. Furthermore, evidence exists that fish (and other taxa) estimate numerical quantities, including group size, logarithmically [25,26], with as yet no upper bound known to the magnitude of numerical quantity (group size) that fish can estimate [27]. Indeed, changes in predation pressure and predator abundance have resulted in substantial differences in the degree of sociality in minnows and guppies, with fish exposed to less predation exhibiting a reduction in schooling tendencies [28,29].

The tendency to live and move in large groups has made schooling fish susceptible to modern mass-capture fishing technologies designed specifically to capture entire fish schools, such as purse seining, in which a large wall of netting is drawn around an entire fish school using a small vessel and then closed from the bottom, trapping the school [30]. In fact, in 2014, 29% of global commercial fishing effort was via purse seining and other encircling nets [31]. Although some benefits of group-living can reduce predation risk from predators that can only consume a small number of individuals in a school [21], they are not effective when nearly the entirety of a school may be consumed at once [30]. A minority of natural predators can achieve this. For example, humpback whales can deploy bubble nets to corral fish schools and simultaneously capture many individuals in a single lunge feeding attack [32]. However, the scale of such attacks is small compared to human fishing—bubble nets have average diameters of 30–50 m [32], while commercial purse seiners can span 640 m [33], more than an order of magnitude larger and substantially less permeable than an ephemeral bubble net. Humans are therefore probably unique in their potential to exert sustained high-intensity negative selection pressure on large groups of fish.

The use of other technological innovations used to detect fish schools, such as spotter planes, drones, side-scan sonar

and fish-aggregation devices with electronic capability to sense fish schools, has further increased the efficiency of purse seine fisheries [34,35]. As a result, schooling fish are some of the most fished stocks in the world. While schooling and aggregating fish represent only 12% of marine fish species, they represent 30% of marine fish species of commercial importance (electronic supplementary material, figure S1) and in 2016 obligate schooling fish (e.g. herring and anchovy) represented 20% of the global catch of both finfish and invertebrates [36]. In terms of global capture production, eight of the ten most caught species were obligate schooling fish, and the remaining two species in the list (*Gadus chalcogrammus* and *G. morhua*) form temporary schools or aggregate seasonally [36,37]. Such strong fishing pressure has already depleted numerous schooling fish populations [30,38], and a laboratory experiment that simulated fishing pressure found that larger shoal sizes were more vulnerable to capture than small shoals of zebrafish [39]. What remains unknown, however, is whether the selective and behaviourally targeted nature of this harvest could have the potential to affect individual social tendencies.

It is not clear how the fitness benefits of schooling behaviour in a pre-Anthropocene ocean may be counterbalanced against increased risk of harvest mortality in the Anthropocene, and what the implications of any changes could be to fisheries or the ecological communities of these fish. Furthermore, while fisheries can directly target schools of particular sizes, they likely only indirectly affect individual fish behaviour. The group size that an individual resides in is the result of not only that individual's preference, but also the preferences of the other fish in the school, as well as the preferences of others in the population at large. For example, a fish cannot belong to a large group even if that is its preference, if all other fish in the population prefer to be solitary. In addition, random fission–fusion dynamics may arbitrarily alter group sizes regardless of preferences [40].

Using an evolutionary fission–fusion model, we modelled a population of fish which is susceptible to both fishing by humans and predation by natural predators (figure 1). Evolutionary models have been previously used to describe changes in individual behaviour within a social context, in collective predation avoidance and group foraging scenarios [41–43]. The aim of this model is not to emulate a specific natural system, but rather to explore a potential, and to date under-researched, behavioural consequence of targeting large schools (and fishing out natural predators). While in our model fishing targets large schools (an emergent property resulting from several fission and fusion processes, both random and driven by the group-size preferences of the individuals), selection operates on individual-level group size preference, allowing us to study how fishing pressure may ultimately affect individual behavioural traits.

2. Methods

(a) Model summary

Our model resembles previous fission–fusion models (e.g. [44–47]), but being non-spatial and rate-based it most closely resembles those of [46,47]. However, our model has the important distinction that the base unit is the individual, not the group. By explicitly modelling individuals, we are able to include individual-level behavioural traits and give individuals some agency

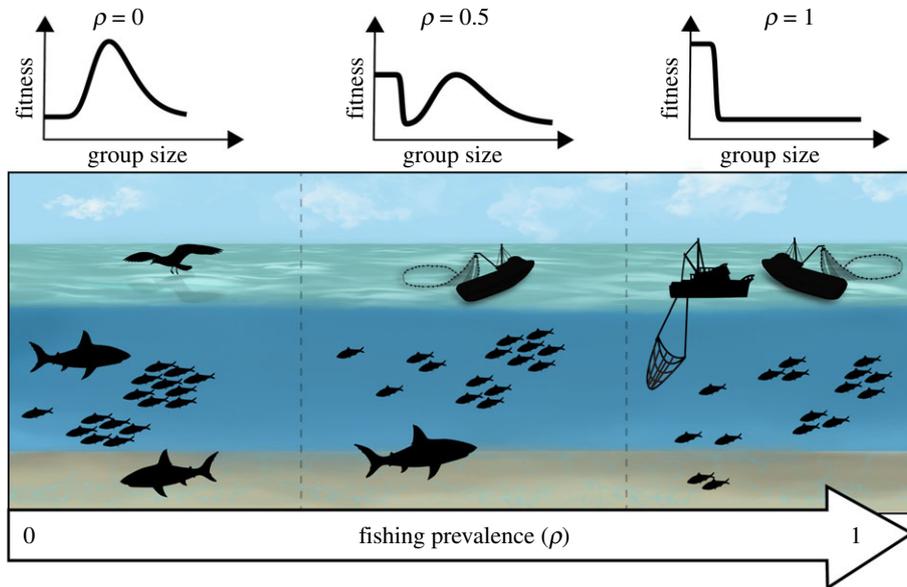


Figure 1. Illustration of the selection pressures present in the model. Individual fish are subject to both predation from natural predators (left) and modern fishing (right). The parameter ρ controls the relative importance of these two selection pressures ($\rho = 0$ means only natural predators, $\rho = 1$ means only human predators, while intermediate values of ρ indicate a mixture of natural and human predators). The curves provide a qualitative illustration of the selection on group size in the different scenarios; see the electronic supplementary material for quantitative descriptions of these functions. (Online version in colour.)

over the fission–fusion processes. Further, this allows us to evolve the individual-level traits, which potentially influence those fission–fusion processes and the subsequent distribution of group sizes. In this section, we give a brief qualitative description of our model; we refer readers to the electronic supplementary material for the full quantitative details of the model.

(i) Individual-level traits

In our model, each individual j is characterized by a parameter, a_j , which determines the size of group (the number of individuals) in which that individual prefers to live. The evolvable trait a_j , along with a fixed parameter κ (set by empirical data on numerosity estimation by animals across taxa; see the electronic supplementary material, for details), together set the location and width of the group size preference curves shown in figure 2*a,b* (and electronic supplementary material, figure S2). At a particular moment in time, each individual in the population belongs to a unique group (which can be of size 1, allowing for singletons). If the individual finds itself in a group that is larger than its preferred group size, the probability that fish will initiate a fission event (leaving the group and potentially taking some of its groupmates with it) increases with increasing group size. If a fish is in a group that is smaller than its preferred size, it increases the likelihood that its group will merge with another. These two processes are depicted by the increasingly orange and purple portions, respectively, of the curves in figure 2*a,b*.

(ii) Model processes

The total number of individuals in the model is fixed throughout a simulation, but the number and sizes of groups change over time as a result of three fission–fusion processes (figure 2*c*). At each discrete time step, one of the following three processes occurs. (i) *Spontaneous fission* represents groups' tendency to split due to stochastic environmental effects. Spontaneous fission occurs at a rate proportional to the number of groups. A group is randomly selected and a random fraction of the individuals in that group split off into a new group. (ii) *Driven fission* is caused by individuals that prefer a smaller group splitting off from their group. Driven fission occurs at a rate proportional to

the sum of the tendency of each individual to leave the group (figure 2*b*). During this event, a random individual from the entire population who prefers a smaller group is selected to lead the formation of a new group. Other individuals in the leader's group, that also prefer to be in a smaller group, leave with the leader (each with probability given by the curve in figure 2*b*) to form the new group. We limit the number of fish that leave to form the new group to half of the original group size, so that the fish that prefer to be in a smaller group minimize their resulting group size. (iii) *Fusion* combines spontaneous and driven fusion into a single process. Fusion occurs at a rate proportional to the product of (a) the number of potential pairs of groups and (b) the average fraction of individuals that prefer a larger group weighted by each fish's value of the curve in figure 2*a*. Two groups are selected, each with a probability that increases linearly with the weighted fraction of individuals in that group that prefer a larger group. The strengths of driven fission, spontaneous fusion and driven fusion (each relative to spontaneous fission) are controlled by the parameters, α , β and γ , respectively (see electronic supplementary material, table S1 for a list of model parameters).

Because the fission and fusion dynamics depend on the preferences of all of the fish in the population, and because the size of the group subsequent to a fission or fusion event is probabilistic, an individual's preferences can only indirectly contribute to the size of the group in which it actually finds itself.

(iii) Selection regimes

We modelled a continuum of environments that our populations could experience, ranging from 'natural' pre-Anthropocene conditions to 'modern' conditions dominated by industrial fishing. Under natural conditions, we assume that grouping helps individuals avoid predation, but as groups become too large, intragroup competition dominates, such that individual fitness peaks at intermediate group sizes and is proportional to a lognormal curve (figure 1; electronic supplementary material, figure S3). Under industrial fishing conditions, we assume that natural predation is replaced by human predation (i.e. industrial fishing), as intense overharvesting by humans has led to the decline of many predator populations and elevated humans to

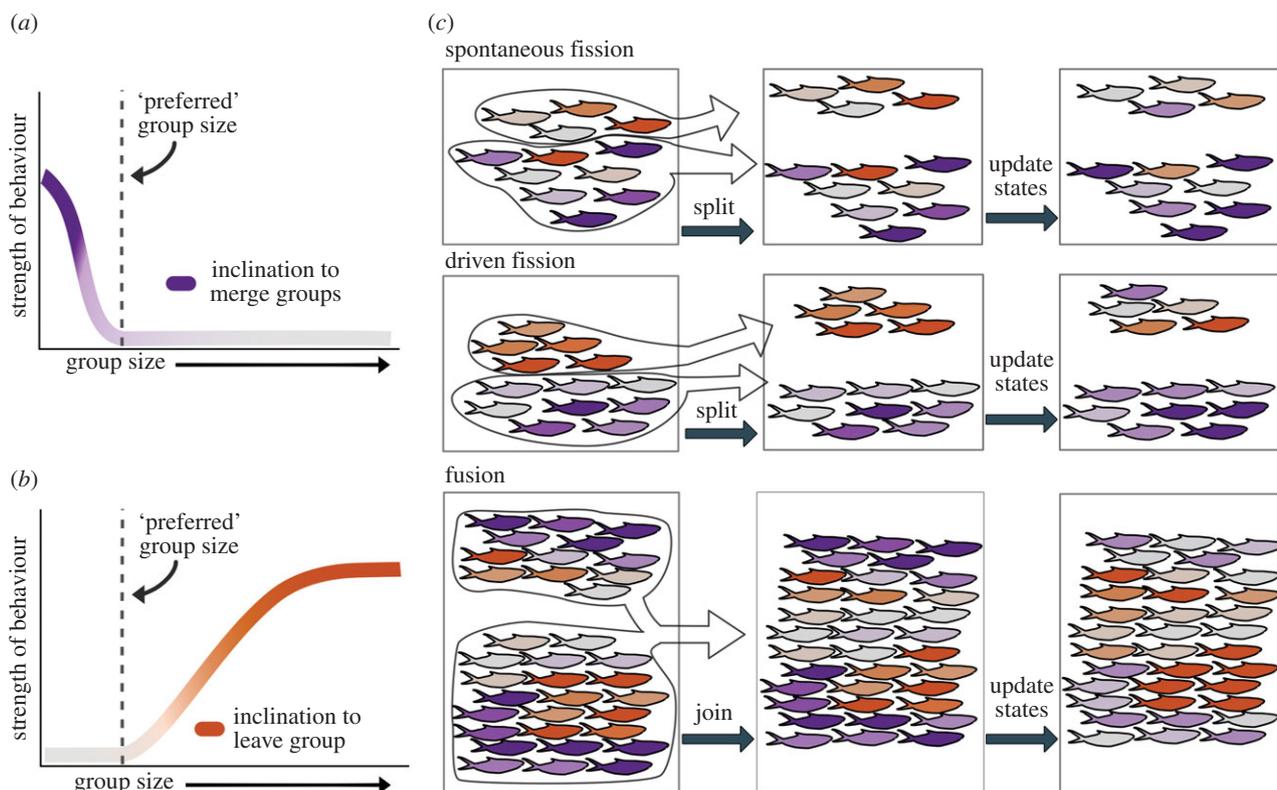


Figure 2. Illustration of the fission–fusion processes in the model. (a) Strength of a fish’s inclination to merge groups as a function of its experienced group size, with the fish’s preferred group size indicated by the vertical dashed line. (b) Strength of a fish’s inclination to leave its group as a function of its experienced group size, with its preferred group size indicated by the vertical dashed line. Each fish may have a different preferred group size, and therefore different levels of discontent and inclinations to merge or leave its current group; see the electronic supplementary material, for details. Depending on the ratio of its experienced group size and its preferred group size, a fish may prefer a larger group (purple), a smaller group (orange) or may be relatively satisfied with its current group (grey). The discontentment of the fish in a group influence the relative probabilities that the group splits or merges with another group. (c) Ways in which groups split or merge. *Spontaneous fission*: a randomly selected group splits into two new groups with random membership. *Driven fission*: a randomly selected fish, weighted by its inclination to leave its current group, splits off, taking with it all other fish in its group (up to half of the group) that also prefer a smaller group. *Fusion*: two groups merge, each selected with a probability that increases with their tendency to merge (see electronic supplementary material, for equations). Following any fission or fusion event, the discontentment of the fish affected by the event are updated. (Online version in colour.)

the ocean’s top predators [1,48]. In this scenario, groups above a certain size threshold are preferentially targeted, so fitness is proportional to a logistic function (figure 1; electronic supplementary material, figure S3). We tuned the environment with a single parameter ρ , which represents the relative frequency that a population would experience natural versus modern conditions: if $\rho=0$, a population only experiences natural predation pressure, while if $\rho=1$, a population would only experience industrial fishing.

(iv) Selection algorithm

We allowed the preferred group sizes, determined by the trait a_i , to evolve via a selection algorithm. In each generation, we modelled a large number (approx. 16 000) of fission and fusion events, periodically calculating (every 164 events) the survival probability of each individual (see electronic supplementary material, for procedural details) as a result of the fishing and predation pressure in a particular simulated environment (determined by the value of ρ ; figure 1). At the end of a generation, individuals reproduce proportional to their overall survival probability (i.e. fitness). Offspring retain their parent’s group-size-preference trait (a_i), plus some small, normally distributed, mutation. The values of the evolving traits typically stabilize after several dozen generations. We wait until well after the evolution has stabilized (500–2000 generations) and then we observe the distribution of group size preferences, as well as the distribution of realized group sizes, in the evolved fish population.

3. Results

We first observed how group size preference changes under fisheries-induced selection. As the prevalence of fishing (ρ) increases, the evolved group sizes preferred by fish in the population decreases. The mean preferred group size (determined by a_i) undergo an approximate threefold reduction as ρ increases from 0 to 1 (solid curve in figure 3). However, equally striking as the size of the reduction is its highly nonlinear nature.

As the prevalence of fishing increases, the evolved values of preferred group sizes exhibit two discontinuities (one at $\rho \approx 0.49$ and another, smaller and possibly less robust one, at $\rho \approx 0.93$). The locations of these threshold values strongly depend on whether the prevalence of fishing is increasing (figure 3, solid curve) or decreasing (figure 3, dashed curve), over time. If fishing of a population initially increases such that it crosses one of these discontinuities and then subsequently decreases (e.g. due to a policy change reducing fishing or increasing the population of natural predators), the transition back to larger group size preferences occurs at a different, and generally lower, threshold (one at $\rho \approx 0.91$ and another at $\rho \approx 0.29$). We stress that the exact values of these thresholds are not important, given the heuristic nature of the model. However, the fact that they occur at different values depending whether ρ is increasing or decreasing demonstrates

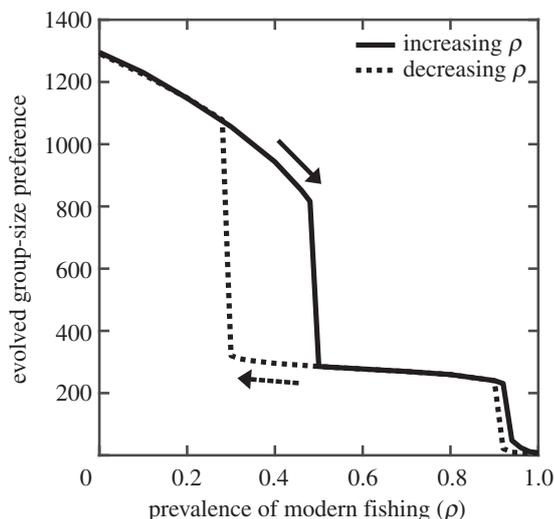


Figure 3. Evolved group size preferences. The curves indicate the mean preferred group size of the population after the group-size preference trait, a_j , has evolved to steady state. The solid curve depicts a situation where fishing pressure, ρ , gradually increases, while the dashed curve corresponds to a situation where ρ gradually decreases. Both curves exhibit two discontinuities. These curves show the mean of three independent replicates.

that the system exhibits hysteresis [49]. The existence of hysteresis suggests that the consequences of fishing are not reversible in a straightforward manner. Instead, the model predicts that fishing likely needs to be reduced much further in order for the fish population to evolve preferences similar to those observed in the absence of fishing.

The presence of hysteresis also suggests that for certain values of fishing prevalence—where the solid (increasing fishing pressure) and dashed (decreasing fishing pressure) curves in figure 3 substantially differ—there is bi-stability in the evolved group size preferences. In these regimes, stochastic fluctuations could dramatically alter the system by shifting the system from one stable state to another, even while fishing pressure is held constant. We note that we see the same qualitative picture (two discontinuities in evolved group-size preference) across a 100-fold range in the strength of the driven processes relative to the spontaneous ones (see sensitivity analyses in the electronic supplementary material).

As prevalence of modern fishing (ρ) passes through any of these critical threshold values (or tipping points) the evolved system undergoes distinct qualitative changes [50]. These changes are apparent in the distributions of group sizes in the evolved populations (figure 4). The two discontinuities (in each direction) in the evolution of the group size preferences essentially divides the system into three different regions (figure 3). In each of these regions, we observe a qualitatively distinct ‘family’ of group size distributions. Figure 4 shows the probability density functions of group sizes for various values of ρ . Even though the values of ρ for the different curves are evenly spaced, the curves are clustered into three distinct ‘families’.

The driven processes tend to introduce a characteristic scale to the group size distributions corresponding to the range of evolved preferred group sizes. This is seen as a ‘hump’ in the distributions in figure 4. However, the stochastic fission–fusion processes still lead to many groups outside of this typical range. This is especially true for smaller groups, and we note that when larger groups are preferred, singletons

actually become the mode of the distribution. Common to nearly all of the distributions is a power-law-like relationship for small group sizes (relatively straight lines on log–log plot in figure 4*b*), a characteristic group size (hump) and an exponential decay for larger group sizes (straight lines on log–linear plot in figure 4*a*). These three features are found in empirical estimates of group size distributions for a wide range of marine fishes [45,47,51].

The abrupt changes in the evolved group size preferences also have strong implications for the average group size in the population. Figure 5 shows the average group size from three perspectives: that observed by an omniscient observer (i.e. the population mean group size), by an individual fish (i.e. the mean group size experienced by an individual fish) and by fishers measuring catch size (i.e. the mean catch size)—see the electronic supplementary material, for details on calculating these quantities. The mean group size experienced by a fish is generally different from the population mean group size because many more fish experience a given large group compared with a given small group, such that a fish will generally experience a group size larger than the population mean, which may have fitness consequences for individuals. The mean catch size will also tend to be larger than the population mean because fisheries preferentially target large schools. We find that the discontinuities and hysteresis in the evolved group size preferences correspondingly lead to discontinuities and hysteresis in the mean group sizes from all three of the perspectives.

By multiplying the observed distribution of group sizes (figure 4) by the fishing selection pressure curve (figure 1), it is possible to estimate the proportion of the evolved fish population available to be fished (electronic supplementary material, equation S6). Assuming that the minimum group size targeted by fishers remains constant, the fraction of the population available to fishers is predicted to precipitously decline as the prevalence of modern fishing increases through the first discontinuity (figure 5*b*). After fishing prevalence continues past the second discontinuity, the fraction of fish available to fishers approaches zero.

4. Discussion

We modelled the fisheries-induced selection of social behaviour in schooling fish, indicating that as the prevalence of mass-capture fishing pressure increases relative to natural predation (ρ), individual preferences shift towards smaller group sizes. Thus, the targeted fishing of large schools can select against behaviours that lead to large schools, despite selection acting only on individual-level traits (here group-size preference) while fitness is determined by an emergent group-level property (here group size) [41]. This is non-trivial because the size of a group a fish resides in depends not only on its own preference, but also the preferences of the rest of the population, as well as the stochasticity generated by the fission–fusion processes.

Empirically tracking the manifestation of these selective patterns in Anthropocene fisheries is challenging as data-keeping on the size of fish schools captured is not always readily available. However, among commercially fished marine fish, we find that species classified as ‘critically endangered’ by the IUCN experience a higher proportion of harvest via gear types designed specifically to target schooling, shoaling and

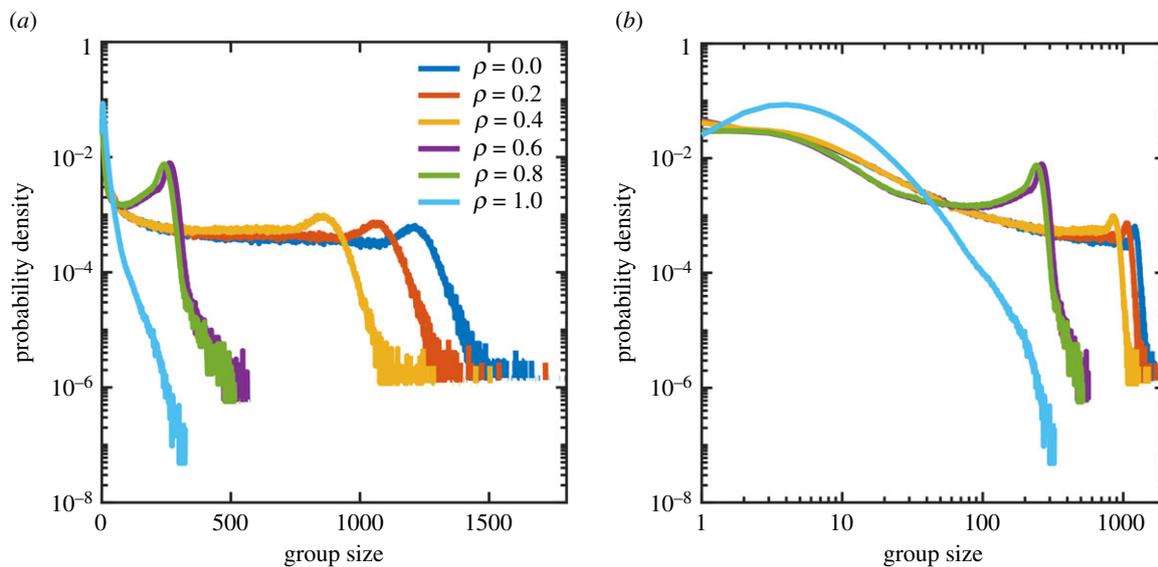


Figure 4. Group size distributions in evolved populations. (a) Probability density functions for group size in evolved populations for various values of fishing pressure (ρ) on log-linear axes. (b) Same data as in (a), but on log-log axes. Both panels correspond to data from gradually increasing the fishing pressure ρ (i.e. the solid curve in figure 3). Even though the curves are equally spaced in ρ space, there are three distinct qualitative 'families' of curves. (Online version in colour.)

aggregating behaviour, such as seines and trawls, relative to species classified under a less high risk IUCN Red List status (figure 6). While circumstantial, this pattern could suggest that such targeted fishing practices have already affected these species' behavioural tendencies. To date, concern regarding management of fisheries that target schooling and aggregating species has primarily focused on risk of extinction and stock collapse operating under the assumption that schooling behaviour remains unchanged with increased fishing pressure [52,53]. For example, fishing may cause hyper-aggregation and range contraction, driving a fish population to extinction while maintaining constant catch rates [52,54]. Population extinction can also arise due to Allee effects, when population densities fall below a critical point, leading to insufficient social interactions important for a population's survival [55]. Our model suggests a new possibility, where the collapse of a fishery may be due to the evolution of social behaviour within the population, rather than the extinction of a population. Such evolution could have equally important ecological and economic consequences [56,57].

While evolving social preferences can save a population from collapse, it may still cause unfavourable ecological consequences. Indeed, considering the high proportion of commercial global fisheries that target schooling fish, [36], a large number of populations, and therefore ecosystems, stand as potential candidates to experience these negative effects. For example, a slight overharvest of pelagic schooling fish can negatively impact an ecosystem by altering prey sources for other marine predators [58]. While these results were attributed to the impact of decreased abundance rather than changes in schooling behaviour, most species of low trophic-level pelagic fish have a tendency to form schools, and a wide range of natural predators rely on, and exploit, this grouping tendency when hunting (e.g. humpback whales) [32,59]. Small schooling fish are also important for various species of seabirds that rely on pelagic predators, such as tuna, to drive prey to the water's surface [60]. In coastal ecosystems, aggregating fish are important for subsidizing and sustaining a high biomass of top predators [61], in addition to creating nutrient hotspots of bioavailable nitrogen in predominantly oligotrophic habitats [62]. Therefore,

fish schools, and their decline, have the potential to alter many important ecosystem functions and food webs globally [63].

A shift in fish social behaviour can also have important socioeconomic implications. Foragefish, which support commercial fisheries directly as target species, or indirectly as prey of higher trophic-level target species, are valued at 16.9 billion USD [59]. Thousands of livelihoods rely on the persistence of schooling behaviour, especially since schooling behaviour minimizes the amount of effort needed to capture many fish at once. A decrease in the tendency to form large schools could affect existing fisheries by increasing the financial and physical effort, as well as carbon emissions, involved in locating fish schools until the fishery is no longer profitable. Alternatively, there could be a 'race to fish' the remaining fish schools in a population [64], for example, if rare fish become more highly valued [65], leading to both the collapse of the fishery and the fish population. In either case, the collapse of a fishery could have long-lasting social and economic impacts on the livelihoods of those that depend on it, as occurred in the collapse of the cod fishery in Newfoundland [57].

Managing fisheries through the lens of fisheries-induced evolution is gaining traction [66,67]. For example, the incorporation of evolutionary models into fisheries stock assessments [67], including trait evolution within ecosystem-based management frameworks [66], and developing marine reserves (which can buffer against the effects of trait evolution) [68,69], have been proposed to promote phenotypic variability [70] and attenuate the consequences of fisheries-induced evolution of life-history traits. However, the majority of proposed responses to fisheries-induced evolution have centred on shifts in life-history traits, with far less focus on shifts in behavioural traits (but see [69]).

Our model demonstrating the evolution of social behavioural traits due to fishing is heuristic and meant to capture general features of preference-driven fission–fusion dynamics rather than describe any particular system or species. To our knowledge, ours is the first model to endow individuals with heterogeneous group-size preferences in a fission–fusion model (but see [71], using a very different framework). While some choices were made to keep our model simple

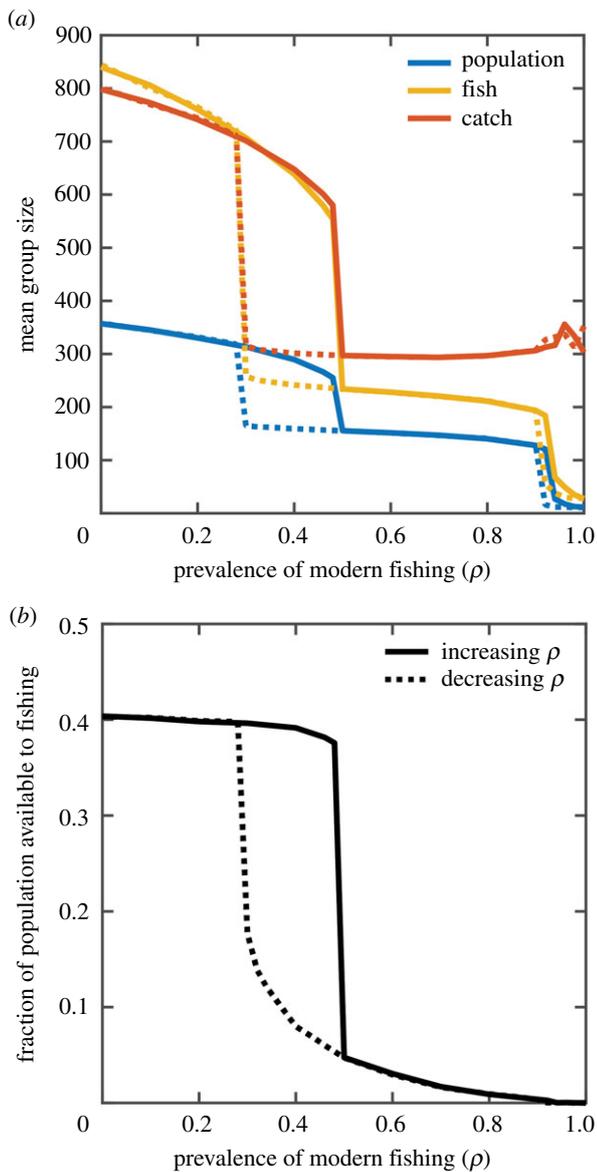


Figure 5. Effects of evolved group size preference on group size and fraction of fish vulnerable to fishing. (a) The blue curve shows the mean group size resulting from the evolved values of group size preferences, the red curve shows the mean group size caught by modern fishers from the same populations, while the yellow curve shows the mean group size experienced by the fish in the population. (b) The fraction of the evolved population that are in groups above the size targeted by modern fishing. In both panels, the solid lines correspond to the up stroke of the hysteresis cycle (solid lines in figure 3) and the dashed lines correspond to the down stroke of the hysteresis cycle (dashed lines in figure 3). These curves show the mean of three independent replicates. (Online version in colour.)

and computationally efficient (e.g. individuals can measure their group size perfectly and have distinct group size preferences, fission–fusion events occur at a fixed rate, etc.), given a paucity of data on how individual preferences interact with general fission–fusion processes in nature, we incorporated the simplest and most parsimonious assumptions into our model, such that the results should be quite general and relevant to many different species and contexts. However, to date there exists little data of whether and how individuals exhibit preferences for particular group sizes, especially in large groups. Our model suggests that experiments specifically designed to test this are necessary in order to better

understand the evolution of group size preferences among marine fish species. We note that population size was held constant in our simulations to avoid confounding effects on process rates or our estimates of average group size, as well as avoid assumptions about recruitment and other population-dynamic processes. In real systems, it is likely that population size will change (decrease) with increased fishing, contributing further (negative) consequences to population, ecosystem and economic stability.

While our qualitative results should be general to many schooling species, specific elements of a species's biology may be incorporated if using the model as a management tool to generate more quantitatively accurate predictions. Experiments could be performed to better understand group size preferences among individual fish species, or the dynamics of fission and fusion events among a collection of groups. One interpretation of our model is that the main benefit to group-living is predator avoidance, such that an increasing prevalence of fishing displaces natural predators in the environment, and therefore, displaces the 'natural' fitness function. However, there are certainly other benefits of sociality, including improved mate finding, foraging, navigating and moving efficiently [16,72]. Our model is still applicable in these scenarios. The ratio $\rho/(1-\rho)$ would control the relative impact of modern fishing events to the natural benefits, regardless of their source. Furthermore, our model is designed to identify the evolutionary stable state (or multiple stable states) for a given fishing pressure, rather than accurately model the trajectory that the population takes to reach that stable state. Nonetheless, understanding the time scale that governs how quickly a particular fish population may adapt to a new level of fishing pressure is important when crafting new management policies. This should include studying processes that impact this time scale for the particular fish species of interest (e.g. mating behaviours, generation times and mutation rates), in order to design policies that allow the fish population to smoothly track the changes to selection pressures that affect its fitness.

Of particular importance to the development of management strategies is the hysteresis that we observed in our model. Hysteresis implies that a recovery to pre-fishing conditions would require a greater reduction in fishing pressure compared to the level that caused the initial decline in group size preferences (figure 3). This is consistent with empirical trends of over-exploitation in fisheries (e.g. [73]), as well as other theoretical models on fisheries-induced evolution of life history traits, where reverse evolution was 20–30 times slower than fisheries-induced evolution [74]. Additionally, traits altered by fisheries-induced evolution may be maladaptive in a natural system once fishing is removed [75] (i.e. small groups will be poor at avoiding their natural predators, assuming the predators return following a decrease in fishing). Therefore, even if fishing is removed, these populations may be at risk of further population depletion until enough evolutionary time has passed to recover adaptive group size preferences in their new environment.

While there may be an extinction of 'catchable' individuals [52] at high fishing pressure (figure 5b), this may not necessarily indicate a corresponding extinction of the entire population. Catch data may therefore not be very informative for testing the predictions of our model and accurately monitoring the status of a fished population which may be subject to evolution in behavioural traits. Alternative methods should

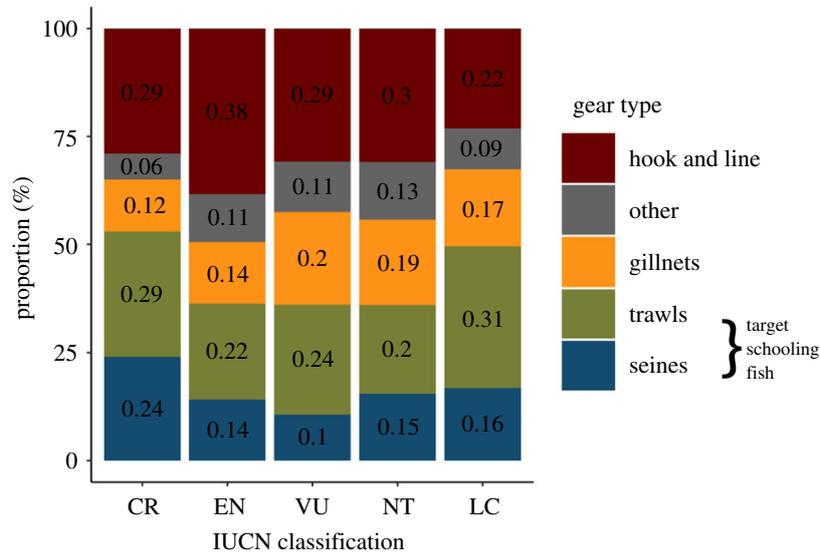


Figure 6. International Union for Conservation of Nature (IUCN) Red List status of commercially important wholly-marine fish and gear used for harvest. Trawl and seine fishing are the mass capture industrial fishing technology used to target fish schools. IUCN status abbreviations: CR, critically endangered; EN, endangered; VU, vulnerable; NT, near threatened; LC, least concern. IUCN status and gear uses were determined using the *rfishbase* package in R; see the electronic supplementary material for detailed methods. (Online version in colour.)

be developed or used to better understand the behavioural, and evolutionary, dynamics of such populations.

The model we present suggests fisheries have the potential to cause significant shifts in fish social behaviour. If these shifts are indeed occurring in existing fisheries, they currently remain undetected. As we continue to find new ways to better manage global fisheries [76], and increase attention on the effects of fisheries-induced evolution, it is important to incorporate the possibility of the evolution of behavioural traits in our models and management strategies, since these dynamics may play an important role in population and ecosystem resilience.

Data accessibility. Our code can be accessed via a link provided in the final section of the electronic supplementary material (https://github.com/berdahl/fisheries_induced_schooling).

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