

Move and you're dead: commercial trawl fisheries select for fish that don't move far.

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Abstract

Recent research on harvest-induced evolution of behaviour in (especially aquatic) animals has focused on the shy-bold axis, but foraging and dispersal behaviour have received little attention. Here, we consider the selective effect of systematically localised trawl harvesting from a wild population of mobile animals that vary in their movement range (resulting in a continuum between wide-ranging and sedentary behaviours). We use a spatially explicit individual-based model of an empirically-based demersal fish population and trawl fishing in a realistic seascape. We test whether a sustained spatially concentrated pattern of fishing can select for or against wide-ranging vs. more sedentary behaviour as the fish perform biased random foraging in a seascape of spatially varying resource quality, leading to an approximation of the ideal free distribution. The simulation predicted a strong micro-evolutionary shift towards more sedentary behaviour as wide-ranging animals flow into a population sink caused by concentrated fishing. The shift towards short-rangers increased with fishing intensity and the spatial precision with which fishing activity matches fish

abundance; it decreased with habitat spatial complexity (fragmentation of suitable habitat). Most cases led to the effective extinction of trait values at the upper end of the ranging continuum, indicating important implications for the management of exploited fish stocks.

Keywords: fisheries induced evolution; ideal free distribution; dispersion; spatial population structure; behavioural syndrome.

Introduction

Harvest selection can cause evolutionary pressures in wild populations (reviewed by Heino and Godø, 2002; Jørgensen *et al.*, 2007; Allendorf and Hard, 2009,). Selective removal of large individuals by fishing is associated with shifts in size-dependent life-history traits, e.g. growth rate and sexual maturation (reviewed by Law, 2000; Heino and Godø, 2002; Enberg *et al.*, 2012; Claireaux *et al.*, 2018; modelled by Andersen *et al.*, 2007). Such phenotypic change characterizes fisheries-induced evolution (FIE), in which harvesting exerts evolutionary selection pressure (Rijnsdorp, 1993). Shifts in fish life history traits due to FIE could lead to reduced reproductive fitness (modelled by Andersen *et al.*, 2007) and impaired capacity of populations to recover from exploitation (reviewed by Enberg *et al.*, 2012; Heino *et al.*, 2013).

, In addition to size-dependent life-history traits, various components of fish behaviour are also understood to be heritable (Kirpichnikov, 1981), and therefore susceptible to selection by harvest (reviewed by Uusi-Heikkilä *et al.*, 2008; Conrad *et al.*, 2011; Diaz Pauli and Sih, 2017). Fish behaviour is closely linked to harvest selection in passive fishing gears, where capture risk is essentially the likelihood that an individual will encounter a static net or attack a lure (reviewed by Heino and Godø, 2002; Arlinghaus *et al.*, 2017; modelled by Alós and Palmer, 2012; experimentally studied by Sutter *et al.*, 2012;). Most studies on FIE of behavioural traits have therefore concentrated on passive gears and behavioural traits associated with individual patterns of activity or aggression. The research focus has been on adding a shy-bold axis of behavioural phenotypes (see experiments by Biro and Post, 2008; Diaz Pauli *et al.*, 2015; Sbragaglia *et al.*, 2019; modelled by Andersen *et al.*, 2018). The shy-bold axis has been expressed as spatial ranging behaviour (empirically studied by Monk and Arlinghaus, 2018; Alós *et al.*, 2016; modelled by Alós *et al.*, 2012; Alós *et al.*, 2019), including diel vertical migrations in Atlantic cod (Olsen *et al.*, 2012). Ranging strategy is a major component of fitness for mobile predators and correspondingly subject to strong

selective pressures (Curio, 1976; Hastings, 1983; Sims *et al.*, 2006; Baguette *et al.*, 2013; Cressman and Křivan, 2013).

The shy-bold axis, e.g. ranging behaviour, has not been widely explored in relation to active fishing gear, where research has focused on escape behaviours, e.g., swimming speed and endurance (reviewed by Wardle, 1993; Walsh *et al.*, 2004; experimentally studied by Killen *et al.*, 2015), but also schooling behaviour (modelled by Guerra *et al.*, 2020). This research gap may be important if fish are less likely to learn to avoid active, compared to passive, gears (Arlinghaus *et al.*, 2017; Koeck *et al.*, 2020). A broader issue is that most previous studies of FIE on behavioural traits have focused on the consequences of fish interacting with gear in relatively small-scale and homogeneous environments. Considering selection on fish ranging behaviour by active gears operating across large-scale seascapes introduces the potentially important effects of spatial heterogeneity in both habitat and fishing pressure.

Ranging widely may involve risks, but it can also yield an advantage (Jager *et al.*, 2011) by increasing the likelihood of finding high quality habitat (Humphries *et al.*, 2010) that provides essential functions such as refuge (Gregory and Anderson, 1997) and feeding opportunity (e.g. Hinz *et al.*, 2005). Fish use various foraging strategies to locate favourable habitat patches (Levin *et al.*, 1984) and then tend to remain within them (Botsford *et al.*, 2009). Gradients of habitat quality can guide simple search strategies over large distances (Humphries *et al.*, 2010), so demersal fish could approach an optimal spatial distribution (the ideal free distribution - IFD) with a simple area-restricted search (as shown by Farnsworth and Beecham, 1999). Area-restricted searching is a taxis-diffusion process (the macroscopic approximation of a biased-random walk, in which bias follows an environmental gradient, e.g. the chemotaxis of bacteria), and this may lead to Levy-like trails in space (Bovet and Benhamou, 1988; Benhamou, 1992; Farnsworth and Beecham, 1999). We use the term 'ranging' for the general phenomenon of movement due to some combination of dispersion and gradient searching (equivalent to 'adaptive dispersion' (Cressman and Křivan, 2013)) and 'movement rate' for the mean displacement per time interval (e.g., daily) that results. The example of 'partial migration', in which most individuals move short distances, but a few pursue long-range excursions (Chapman *et al.*, 2012; Currey *et al.*, 2014) indicates that ranging behaviour can vary strongly within a population. In this study, we examine the effect of such diversity in movement rate, assuming that it is at least partially heritable. This would imply that if there is a distribution of ranging genotypes in a fish population, it may be subject to FIE.

Active gear fishers, e.g. trawlers, typically aim to maximize catch per unit effort in seascapes where target fishes form patchy sub-populations in space (Metcalf, 2006) associated with specific benthic habitats (Fraser *et al.*, 2008; Sell and Kröncke, 2013). Fishers often use experiential, or even inherited, knowledge of habitat and fish–habitat associations to select fishing locations (Bergmann *et al.*, 2004; Serra-Pereira *et al.*, 2014). Their focus on more productive areas results in a ‘footprint’ of fishing activity that is very uneven in space but often stable in time (Shephard *et al.*, 2011, 2012; de Castro *et al.*, 2015), with areas of consistently higher fish density expected to experience greater than average trawling activity. Fishing typically selects for larger individuals and this effect is exacerbated by size-selectivity of trawled fishing gear. Fine-scale spatial coupling between fishing activity and the body-size distribution of the fish community has been observed (Shephard *et al.*, 2011; Smith *et al.*, 2013; Castro *et al.*, 2015; Arroyo *et al.*, 2019). If the spatial distribution of phenotypes within a population is not homogenous, this too could be subject to selective pressure from spatially heterogeneous fishing (Law, 2000).

All this sets up the hypothesis that spatially heterogeneous, but temporally consistent, patterns of fishing can cause selection on ranging behaviour, which may lead to FIE, especially in demersal fish populations. If fishing is localised in patches where resources for fish are relatively abundant, then fish having a relatively large spatial range may be attracted to these high reward / high mortality areas, while more sedentary fish that are not already in those areas are less likely to enter them and so have a lower risk of capture. Current fisheries-management practices (and supporting models) do not have the spatial resolution to take account of this effect, but Křivan and Jana (2015) and Takashina and Mougi (2015) have shown how spatially heterogeneous fishing can substantially affect maximum sustainable yield (MSY). This process has also been demonstrated with an individual-based model in the case of passive fishing gear (Alós and Palmer, 2012), where differences in ranging behaviour among fish can produce misleading results for fisheries managers (Alós *et al.*, 2019) and a wide range of MSY outcomes in the context of protected area size (Sadykov and Farnsworth, forthcoming). In the long run, the high mortality areas may constitute a population sink for the wider-ranging fish and if their ranging trait is genetically determined this will change the gene-frequency of the population and thereby constitute FIE.

To test the plausibility of the selection prediction of this hypothesis we consider a spatially explicit, individual-based simulation based on de Castro *et al.* (2015) that includes inheritance and makes the following assumptions:

1. Demersal fish populations exhibit a spectrum of a heritable ranging-trait;
2. Individuals follow a resource gradient towards higher quality habitats;
3. Individual fitness depends on habitat quality experienced, integrated over time (among other things);
4. Fish have no individual behavioural response to the distribution of fishing intensity;
5. Fishing intensity tends to be concentrated in areas of high habitat quality.

Assumption 1 is necessary to examine the effect of hypothesised heritable diversity in ranging behaviours. Whilst the heritability of ranging behaviour in fish has yet to be quantified, its simple foundation in taxis has been shown for a wide range of organisms from bacteria upwards and the mechanisms of its genetic control have been comprehensively identified in the nematode *Caenorhabditis elegans* (Luo *et al.*, 2014). Taxis is the standard (and very effective) model for animal searching, including in vertebrates (Farnsworth and Beecham 1999), which share the ancient ‘fold-change detection’ biochemical system (Adler and Alon, 2018). Assumptions 2 and 3 describe fitness maximising, subject to assumption 4, so they amount to assuming ‘adaptive dispersion’, which is a founding assumption of IFD-like models. Assumption 4 is supported by empirical evidence (Wilson and Hollowed, 2003; Walline and Wilson, 2012). For the special case of passive gears, however, there is evidence that fish can learn to avoid e.g., traps and baited hooks (Arlinghaus *et al.*, 2017; Koeck *et al.*, 2020) and that they may have behavioural adaptations to natural predators (detecting the ‘landscape of fear’ (Laundre, 2010)) and any humans that appear as natural predators (Bergseth *et al.*, 2016). It is also possible that trawling reduces whole benthic community biomass, possibly resulting in diminished habitat attractiveness (Hiddink *et al.*, 2020). Conversely, trawling can expose benthic infauna to predation, thereby attracting bottom-feeding fish to areas where fishing takes place, at least for some species and over some (short) time scales (Kaiser and Spencer, 1994; Collie *et al.* 2016). Trawling is also a huge acoustic phenomenon (vessel noise, interaction of trawl and trawl doors with the seafloor, vibrations of the wires); this impact could repel fish over short time scales and small spatial scales. In summary, both attraction and repulsion can be present. In combination with assumption 5, attraction would strengthen the effects we study. Assumption 5 represents the view that fishers seek to maximise their catch per unit effort by strongly concentrating in areas of perceived high fish abundance, which, by assumptions 2 and 3, coincide with time-stable areas of relatively high resources for the fish (Amoroso and *et al.*, 2018). We acknowledge limitations (such as gear operability, knowledge and management restrictions) to perfect matching of fishing to abundance and examine the effects of several degrees of matching.

The result of fishery concentration is ‘over-matching’ to the fish resource (using the IFD terminology, following e.g. Sutherland (1983)).

Whether or not areas of consistently high fishing intensity retain high resource quality for predatory fish is complicated (see Collie *et al.*, 2016), but the expectation here is that fishing depletes competition, effectively increasing the *per-capita* resource availability. The faster that fish disperse, moving to maximise their experience of resource abundance (adaptive dispersal), the sooner they arrive in higher-resource areas. Assuming that removal by fishing is independent of fish dispersal rate (i.e. fish of different dispersal rates are equally likely to be caught in any one haul), the dynamic balance between arrival and removal leads to higher abundance of fast than slow dispersers in the high-resource areas because fast individuals are replaced more rapidly. The combination of the assumptions implies that the higher mortality rate experienced by widely ranging fish in the high-resource areas may be compensated (to some extent) by the greater food intake rate obtained from better matching resources. This makes the micro-evolution of a population structure a spatio-dynamic function of fisheries interactions with trait distributions. It is sufficiently complicated to be non-trivial and hard to predict. In the spatially explicit simulation, we will examine the dynamics in relation to three environmental factors: the overall fishing intensity, its spatial distribution relative to habitat quality and the spatial complexity of the underlying habitat.

Methods: a spatially distributed individual-based simulation with inheritance of the dispersion (ranging) trait

We use a spatially explicit, individual-based model of a single species in which individuals have a continuous heritable trait determining their rate of dispersion (ranging behaviour). Dispersion in this context means how many metres they move per day in a straight line. The model also includes feeding and growth, reproduction, natural mortality and fishing mortality. Each of these processes is detailed below and in the supplementary material.

The simulation arena was a grid of $N_c = 400 \times 400$ cells of 0.25 km side, representing 10^4 km². Each cell was characterised by an initial value of resource abundance for the fish, on an arbitrary scale [0, 1]. Fractal maps of resource abundance of increasing spatial complexity (low, medium and high) were generated by the midpoint displacement method (McClure, 2014), hence “habitat complexity”

(Figure 1). The resource was an abstract food source represented in a simple way – i.e. it is not a prey species, does not diffuse or evade the predator.

All simulations started with a population of 10^5 individuals located randomly within the seascape. The initial population length structure was generated by randomly sampling (with replacement) sizes taken from the observed length distribution in fisheries-independent surveys of a natural population of a large gadoid species in the Celtic Sea (ICES, n.d.). This procedure was used to start simulations with a realistic length structure, without representing any particular species. The simulations progressed with a 1-day time step for fifty years.

Movement

Individuals moved across the simulated seascape using an area-restricted gradient search (Turchin, 1991; Benhamou, 1992) with the only objective of maximising resource intake (preserving assumption 4 that they are insensitive to or unaware of the fishing mortality risk), each at a rate governed by their ranging trait, following the methods of Farnsworth and Beecham (1999). In other words, each individual moved in the direction along the maximum local resource *gradient* in the cell where they are located, thus moving to richer areas (see Bovet and Benhamou, 1988; Turchin, 1991; Farnsworth and Beecham, 1999). Given that resource density is defined for each cell, all individuals in the same cell moved in the same direction in a given time-step. Individual fish performed biased random walks each at a rate governed by their ranging trait with step-length $d_{i,p}$. Area-restricted search assumes that individuals can detect the local resource gradient at their current location (illustrated by Figure S1) and that they are able to follow it toward the most favourable area in the vicinity, which is not necessarily the global optimum. Notice that the consumption of the resource, which depends on the local fish population density, caused its spatial distribution (and gradient thereof) to change at each time-step. This in turn continuously modified the direction of movement of fish as they followed their gradient searches in an attempt to maximise their intake rate: by this means an Ideal Free Distribution (IFD) could emerge.

Feeding and growth

The individuals consumed the resource at a constant rate, independent of their size. The resource level R_j in the j th patch was consumed by N_j fish each at a mean feeding rate R_c ($1/30 \text{ ind}^{-1} \text{ d}^{-1}$), whilst being replenished at a rate R_r ($4/30 \text{ d}^{-1}$) so that at time t , $\dot{R}_j = R_r - N_j(t) R_c$. In practice, this was calculated iteratively and the values of R_j were bound by 0 and the initial value in each patch

at the beginning of the simulation. Density-dependence arose through this process of scramble competition. The values of R_c and R_r were chosen to allow the population to persist for some time at the higher population densities while also allowing for resource depletion and, therefore, dynamic changes of the resource gradient.

Somatic growth rate of fish (in length L) followed a von Bertalanffy function, $\Delta L_i / \Delta t = K(L_\infty - L_i)$, up to maximum (asymptotic) length L_∞ (Table S1). We assume K to be linearly related to the habitat quality experienced by the individual each day, but constrained by the arbitrary limits K_{\min} and K_{\max} (Table S1) which correspond to habitat quality 0 and 1, respectively. All individuals in a cell increase in length according to the value of K for that cell and their present length. Consumption of the resource in a cell causes a decrease in habitat quality and, consequently, a reduction of K and a corresponding reduction of growth rate for all individuals in the cell.

Reproduction and inheritance

Reproduction occurred only during the first three months of each year, which allowed the development of a realistic, multimodal size-structure. The number of recruits was limited by a maximum population size, which was set at 1.5×10^5 for practical computational constraints, implying an asymptotic recruitment, so that at carrying capacity, recruitment exactly matched mortality losses. New recruits entered the population at age 1, and matured at a rate defined by the age-dependent maturation reaction-norm (Equation 4 in the Supplementary Material). Recruits were introduced at random locations in the seascape, not within some range of their parent. The latter possibility could have affected the speed of genetic changes in the population, but we did not explore this option.

To model the inheritance of the ranging trait, because individual reproductive output, F , is weight-dependent, the random sampling of parent genes was weighted by the weight-dependent expected reproductive output of the parent, given that weight is proportional to length to the 3rd power:

$F \propto l^3$. This way, larger individuals had a higher probability of transmitting their genotype to the next generation (noting that Hixon (2014) reviewed evidence that larger females may have more than proportionally larger reproductive output, implying a power higher than 3). The distribution of genotype $d_{i,G}$ among these new recruits drove the change in the phenotype frequency of the population, so the number of recruits, which was determined by the total mortality in the previous year, set the rate of implied gene replacement and hence the pace of evolution.

We aimed to mimic heritability of the ranging trait, but excluded mutation. With an individual-based model, we had to represent inheritance explicitly to calculate gene-frequency dynamics under selection. We could have assumed that genetic variance is purely additive, but most likely the distribution of individual ranging behaviours arises from a complex mixture of (possibly) Mendelian, additive and epistatic genetic processes, combined with individual responses to environmental variation (non-inherited effects) and their genetic-environmental interactions. To avoid unsupported assumptions about the genetics (and mating), we pragmatically represented inheritance from just one of the parents and combined the (effectively random) contribution from the other parent with the environmental variance, treating the combination as total ‘unaccounted-for’ variance. Thus, by implication, we used the average effect of the genes: “the mean deviation [in trait-value] from the population mean of individuals which received those genes from one parent, the genes from the other parent being taken by random sample from the population” (Falconer, 1983, p.p. 104). Thus, the ranging phenotype for the i th individual $d_{i,P}$ was modelled as the sum of a ‘genetic’ contribution ($d_{i,G}$) inherited (unmodified) from one parent and a random contribution representing the combination of plastic (environmentally influenced) and unaccounted-for individual-level effects, including those of the other parent: in total E_i , such that $d_{i,P} = d_{i,G} + E_i$ (with units of m/day). The initial population was given values of $d_{i,G}$ drawn from a uniformly random distribution: $d_{i,G} \in [1, 1000]$ m/day. The values of E_i were annually resampled, drawn from a normal distribution with zero mean and a variance proportional to the mean genotypic trait value \bar{d}_G (which changes as the population dynamics progresses under fishing). This gives a ‘broad sense’ heritability from the single parent: $H^2 = V_G / (V_G + V_E)$ (where V represents trait variance). The resulting heritability was maintained at approximately 0.67 throughout the simulation by setting $V_E = (1/2.5)^2 (\bar{d}_G)^2$ for each annual reproduction cycle.

We do not claim that the heritability is that high in any natural system, but under the computational limitations of our simulations it may be less likely to show any clear effects with heritability set at a lower value (compare to similar value used by Forestier et al. (2020) in their study of FIE). The distribution of $d_{i,P}$ was restricted to positive values since negative dispersion is non-sensical (negative values were replaced with the minimum of the rest of the population, though it was rarely necessary in practice).

273 *Natural mortality*

274 Natural mortality is simulated by randomly removing individual fish from the population, with a
275 probability set by their daily mortality m_d , which is an exponential function of age (See eqs. [1] and
276 [2] in the Supplemental material).

277

278 *Fishing mortality*

279 Fishing mortality involves two separate aspects: overall intensity and spatial accuracy. We tested
280 three levels of each of those two factors. For each level of habitat spatial complexity, we simulated
281 all the combinations of fishing mortality and fishing accuracy, for a total of 27 results.

282 The spatial distribution of fishing mortality matched the pattern of habitat quality at the start of a
283 simulation (scaled such that the mean mortality over all space gives the experimental variable $\bar{\mu}$).
284 This mimics the ‘over-matching’ of fishing intensity to the fish resource. Notice that fishing
285 mortality remained constant and did not change during a simulation, even if the resource level
286 changed continuously.

287 Fishing spatial accuracy was simulated by adding Gaussian noise of mean zero and of different
288 standard deviations to the fishing mortality (Figure 2): 0 (for ‘perfectly matched’ fishing accuracy),
289 0.1 (medium fishing accuracy) and 0.25 (low fishing accuracy). The addition of normally distributed
290 noise weakened the correlation between fishing mortality and resource distribution, and, therefore,
291 with the density of individuals in each cell.

292 Fishing was size-selective: the probability of capture experienced by an individual in a particular
293 cell was the product of fishing mortality in that cell and trawl size-selection represented by a
294 sigmoid function of body-length (parameters in Table S1). Fishing was introduced into simulations
295 following a one year no-fishing ‘burn-in’ period to allow a fish-distribution to emerge, upon which
296 fishing would then act.

297 Simulations were run for 50 years in one-day time steps for all combinations of three levels of (i)
298 habitat complexity (low, medium and high, as in Figure 1), (ii) fishing precision (low, medium and
299 high, as in Figure 2), and (iii) magnitude of global fishing mortality (**0.1**, **0.25** and **0.5**). Although
300 there is not a direct conversion of these probabilities to the more familiar instantaneous fishing
301 mortality (F), we estimated that they correspond to F rates of: **0.07**, **0.18** and **0.32** per year,

respectively (see supplemental material). We also ran a simulation with fishing mortality set to zero.

To test whether the observed change in trait frequency is an evolutionary shift in genotype frequency or just a purely demographic response because of differential selection, we experimentally prohibited evolution by randomly re-setting the trait frequency by drawing it from the initial range [1,1000]m for each recruit.

Further details on the individual-based simulation are presented in the online Supplementary Material.

Results

The results indicated that increased fishing mortality favours reduced ranging behaviour, while spatial complexity in habitat and low accuracy of targeting work in the opposite direction (Figure 3). Evolution in ranging phenotypes and genotypes reflect the balance between these factors. Following 50 years of simulation, the population phenotype and genotype distributions both showed mean (median) values that shifted from their initial uniform distribution towards slow-ranging in most scenarios (Figure 3 for phenotype and Figure S2 for genotype). The shift towards slow rangers increased with fishing intensity (Figures 3 and S2, from left to right) and fishing accuracy; it decreased with habitat spatial complexity (Figures 3 and S2, orange, green and blue). The cases that did not show a strong shift in genotype (Figure S2) had lower levels of fishing mortality, particularly at the greatest habitat complexity or least fishing precision (Figure S2). These factors reduce the absolute difference in mortality rate among phenotypes. The shape of the distributions of ranging behaviour became strongly skewed in cases where the mean was strongly affected, e.g. at greater values of F and accuracy of targeting. The temporal progression of this shift can be seen in Figure S3.

The disruptive effect of fishing was clarified by the simulation with fishing mortality set to zero. In this 'unexploited' case, the phenotype distribution remained rather uniform, but fast rangers had a clear advantage at high habitat complexity (Figure S4). In the scenario where trait evolution was prohibited, the ranging-rate distribution showed only a modest shift towards slow ranging from the

initial uniform distribution, as compared with a substantial shift when simulated genetics was included (Figure 4).

Discussion

Studies of FIE have tended to focus on shifts in size-dependent life-history traits. More recent work has considered selection on behavioural traits, but generally in relation to passive gears in relatively homogeneous environments. We explored how fishing could select across a ranging behaviour trait in a fish population occupying a seascape with different levels of habitat complexity and of spatial matching between local fishing pressure and fish abundance. Our simulations showed that when fishing mortality was great enough and sufficiently well correlated to habitat quality (consistently over time) and the habitat not too fragmented, fast rangers increased their risk of capture by more rapidly finding the higher-resource and, hence, higher-mortality areas, which were made more attractive, in terms of *per-capita* resource availability, by the local fish population depletion was caused by targeted fishing mortality. A population sink is maintained in the high-quality high-mortality area and fast-dispersing or wide-ranging fish are more likely to fall into this trap. These fish supply the fisheries from a wider area, potentially leading to the perception of a plentiful supply of fish on preferred fishing grounds (Rose and Kulka, 1999) which reinforces spatial targeting by trawlers and the result is inevitably one of (at least) micro-evolution.

We interpret these results as follows: free movement allows organisms to distribute in space to maximise their individual fitness. If they all share the same relationship with the environment (and we assumed that), then they tend towards an IFD. Because trawl fishing is unnatural, we assume that fish have not evolved an avoidance response to its distribution, so they effectively approach an IFD based on only the resource component, not the threat component of fitness (see Beecham and Farnsworth (1999) for an analysis of both together). The result is that high mortality areas remain high *per-capita* resource areas and act as population sinks, driven by a resource-orientated IFD. Areas of relatively low fishing pressure constitute a *de-facto* refuge (Shephard *et al.*, 2012), which Křivan (2013) showed could allow prey to co-exist with a predator when otherwise they would be extinguished by it. Differential mortality among phenotypes is not sufficient to produce this effect because competition among individuals is also needed to drive the movement into high-resource high-risk patches (as Cressman and Křivan (2013) showed for a predator-prey system).

Our results suggest that if fishing is consistently correlated with (heterogeneous) habitat quality and fish differ in a heritable ranging trait, fishing may create an evolutionary selection pressure favouring fish with more sedentary ranging behaviour. This conclusion concurs with (and expands on) previous findings from dispersal models with similar (IFD-like) assumptions: spatial (in the absence of temporal) heterogeneity “selects against dispersion” (Hastings, 1983). It critically depends on the organisms not reacting to the spatial distribution in mortality risk created by fishing (our assumption 4). Křivan and Jana (2015) quantified the effect of responding to the spatial distribution of mortality (in relation to dispersal from protected areas), showing that reacting to mortality risk could eliminate the effect of dispersal on fitness. As noted in the introduction, noise from trawling activity may possibly repel fish. On the other hand, some species of bottom-feeding fish might be attracted, at least over short time scales, to recently trawled areas where benthic prey became exposed (Kaiser and Spencer, 1994; Collie *et al.*, 2016). If the latter effect persisted long enough, it would increase the spatial correlation between resource availability and fishing activity and even enhance the effects that we found. In practice, a complex system (as this is) with a stochastic time-varying environment will never fall into a static equilibrium, but will orbit the equilibrium attractor. In these circumstances, organisms never perfectly match an IFD, they can only approach it (Farnsworth and Beecham, 1999).

An empirical test of our prediction that fish become less mobile because of trawling could be carried out by tagging fish in both highly fished and largely unfished regions, and comparing their subsequent mobility. The hypothesis would be that fish tagged on the fishing grounds would tend to be recaptured further away than those tagged on the unfished grounds. This contrast would reflect the expectation that individuals in fished areas have a greater probability of being fast rangers as fish with this trait are more likely to arrive in higher quality more fished areas. Proportions of slow and fast-ranging individuals could be compared between fished and unfished areas.

The model with zero fishing did not appear to produce systematic selection on the ranging trait in low or medium complexity habitats, although we would be unlikely to detect differences caused by random drift and weak selection. There was slight selection in high-complexity habitats. We acknowledge that we only used a single landscape of each complexity type, and there would be benefit in running replicate landscapes to ensure that our results apply generally. This result differs from the prediction of Hastings (1983) concerning dispersion because our ranging trait does not control undirected movement; it sets the rate of biased-random gradient-search foraging (i.e.

including directed movement), which effectively declines to near zero as the IFD is approached. The result is that in the absence of fishing, as IFD is approached, the difference among ranging traits is effectively eliminated. High-complexity habitats tended to impede this homogenisation because the gradient search often became trapped in (spatially) local optima, and the population could not approach an IFD. As a result, some areas of the habitat maintained higher than optimal population densities with correspondingly lower *per-capita* resources. Wide-ranging phenotypes were better able to escape from this sub-optimal distribution, achieving larger sizes and fecundities. We may conjecture that this advantage is frequency-dependent (it only operates when the trait is relatively rare) so slow phenotypes are conserved in a natural (unfished) system. If the ranging trait is under genetic control, there are several mechanisms to preserve the diverging phenotypes in the population: if the population mean of the trait is close to the fitness maximum, stabilising selection is likely via e.g. heterozygote advantage, otherwise, non-additive effects, such as over-dominance may be operating – see Falconer (1983, p.p. 303-310).

Our study cannot estimate the strength and speed of the evolutionary response to fishing mortality and habitat complexity, partly because the heritability of ranging behaviour in fish remains unknown. In this context, we implemented inheritance at a rate where the genotypes of the survivors of fishing mortality would be more likely to be passed on to the next generation. The relatively high heritability needed for that in the current model does not reflect a view on the (as yet unmeasured) heritability of the trait, but is useful for determining the extent to which model outcomes can be attributed to trait diversity: the same procedure as followed by Forestier et al. (2020), who allowed inheritance of parental traits +/- 20% (implying $H^2 \sim 0.7$) for modelling FIE. Nevertheless, independently of inheritance, we demonstrated a selection pressure towards more sedentary behaviour, and so it is very likely that under any form of genetic control of the ranging trait this selection pressure will lead to its evolution.

As well as raising dispersion or ranging behaviour as a potential subject of FIE, our study connects the developing field of behavioural FIE with the study of the evolutionary effects of dispersive behaviours, notably those that tend towards ideal free distributions (Hastings, 1983; Levin *et al.*, 1984; Houston and McNamara, 1988; Turchin, 1991; Farnsworth and Beecham, 1999; Cressman *et al.*, 2004; Cressman and Křivan, 2013; Křivan, 2013; Křivan and Jana, 2015). By adding this spatial foraging behaviour, our analysis captures important ecological and fishery characteristics likely to drive FIE in commercial-scale trawl fisheries, where life-history traits of target populations are heterogeneous in space (Sala-Bozano and Mariani, 2011). The FIE of dispersal rate in fish could be

important for long-term sustainability because movement patterns underlie population distribution (Turchin, 1991; Wiens *et al.*, 1993) and individual foraging success in heterogeneous resource landscapes (Ritchie, 1998; Farnsworth and Beecham, 1999; Jager *et al.*, 2011) and resource abundance substantially shapes feeding success in demersal fishes (Lloret *et al.*, 2002; Lloret and Planes, 2003; Hinz *et al.*, 2005). We note also that our hypothesised dispersion-rate trait may be correlated with the shy-bold axis, especially in relation to foraging as an exploratory behaviour (see e.g. Sih *et al.*, 2004; Ólafsdóttir, 2016).

In addition to foraging success, dispersion rate also influences the degree of spatial mixing within animal populations, and hence it may affect the extent of sub-structuring and genetic divergence, although this will be counteracted in some species by specific reproductive behaviours, like spawning aggregations at spawning grounds. Demersal fish populations often show fine-scale spatial structure (Metcalf, 2006) and subpopulations frequently show phenotypic variability (e.g. Wright *et al.*, 2011; Wright and Tobin, 2013) that may have a genetic as well as environmental basis (Harrald *et al.*, 2010; Hemmer-Hansen *et al.*, 2014). If the phenotypic variability in dispersion rate (related to home range) has a genetic basis (presently unknown), then harvest selection could drive an evolutionary change.

Our results are consistent with the FIE of home-range size reported by Villegas-Ríos *et al.* 2017. For passive-gear, Alós and Palmer (2012) also found consistent catching bias towards more active fish (sparing less active), but obtained mixed results in relation to home-range size: they depended on the details of fishing gear and individual movements. Using a repeatability measure, Thorbjørnsen *et al.* (2021) recently showed that home-range size is likely to be heritable and affects survival across an MPA boundary, such that effectively wide-ranging fish with home-ranges within the MPA are at a disadvantage relative to those with small ranges within. Those with large ranges in adjacent unprotected areas gained survival benefit from the MPA over those with small ranges in the unprotected area. Our results therefore reinforce the prediction made by Baskett and Barnett (2015) that marine reserves could select for shorter (slower) ranging individuals, confirmed by comprehensive mathematical analysis (Sadykov and Farnsworth, forthcoming). We can speculate that a population of slow rangers may show a reduced mixing rate, with increased incidence of fine-scale structure, or even population fragmentation and extinction of local genotypes, especially among rare and relatively sedentary species such as the threatened blue and flapper skates (*Dipturus intermedius* and *D. flossada*) (Dulvy *et al.*, 2000). This suggests that if marine protected areas were more integrated into networks (especially closer together) they may be more effective

in conserving the population structure of such species (Moffitt and Wilson White, 2011; Foster *et al.*, 2017).

Other management implications of potentially reduced genetic diversity may include lower resilience of fish populations, for example in the context of climate change. A population of less mobile fish may have a reduced capacity to modify spatial range in response to ocean warming. Moreover, under our hypothesis the population would become concentrated in low-productivity areas; this would probably mean that the fish population itself would show low productivity, with knock-on effects on recruitment, because they are “stuck” in these impoverished zones. Also, if such slow-moving remnants were “found” by fishermen, they could be rapidly depleted. This effect would also mean that fishing effort was moved into novel areas, with concomitant habitat impacts and other collateral impacts. In general, since the ecosystem approach to fisheries management requires conservation of ‘natural’ trait distributions, we recommend adding dispersion (ranging) rate to the list of behavioural traits for which “fisheries should not be ignored” (Diaz Pauli and Sih, 2017).

Supplementary material

Details on the model, Table S1 and Figures S1-S4 are in the online Supplementary Material.

Statement of conflicts of interest

We are not aware of any conflicts of interest.

Acknowledgements

This publication has emanated from research conducted with the financial support of Science Foundation Ireland (SFI) under grant number 14/IA/2549 and also FISHKOSM.

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Figures

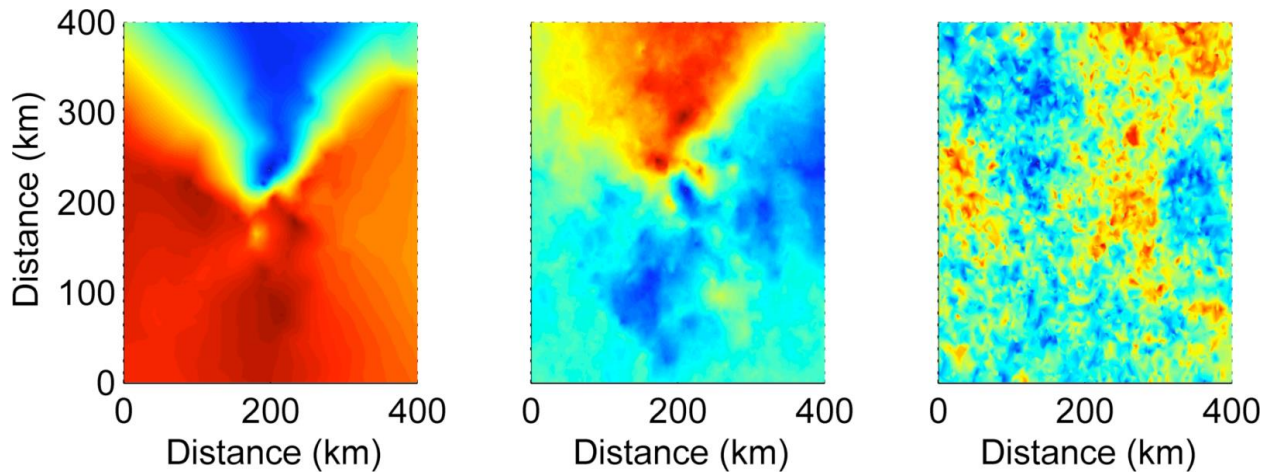


Figure 1. Synthetic seascapes. From left to right: low, medium and high complexity. The colour code for resource abundance is from dark red (highest) to blue (lowest).

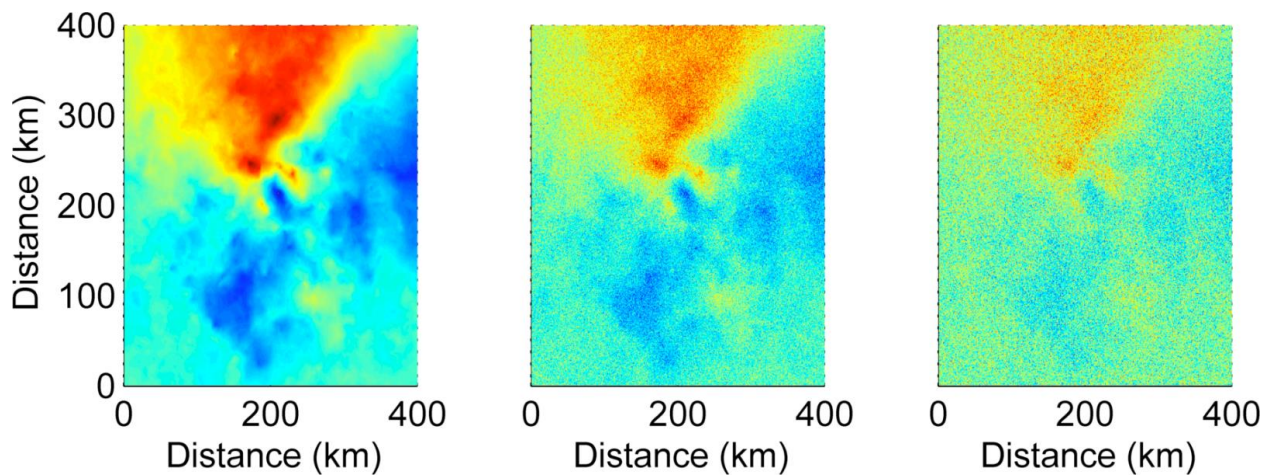


Figure 2. Synthetic distributions of fishing mortality. From left to right: high, medium and low matching precision of fishing. Each of these levels of precision can be used with each of the seascapes in Figure 1, creating nine scenarios in total. This figure illustrates high, medium and low matching precision applied to the medium complexity seascape of Figure 1 (middle panel). The colour code for fishing mortality is from dark red (highest) to blue (lowest).

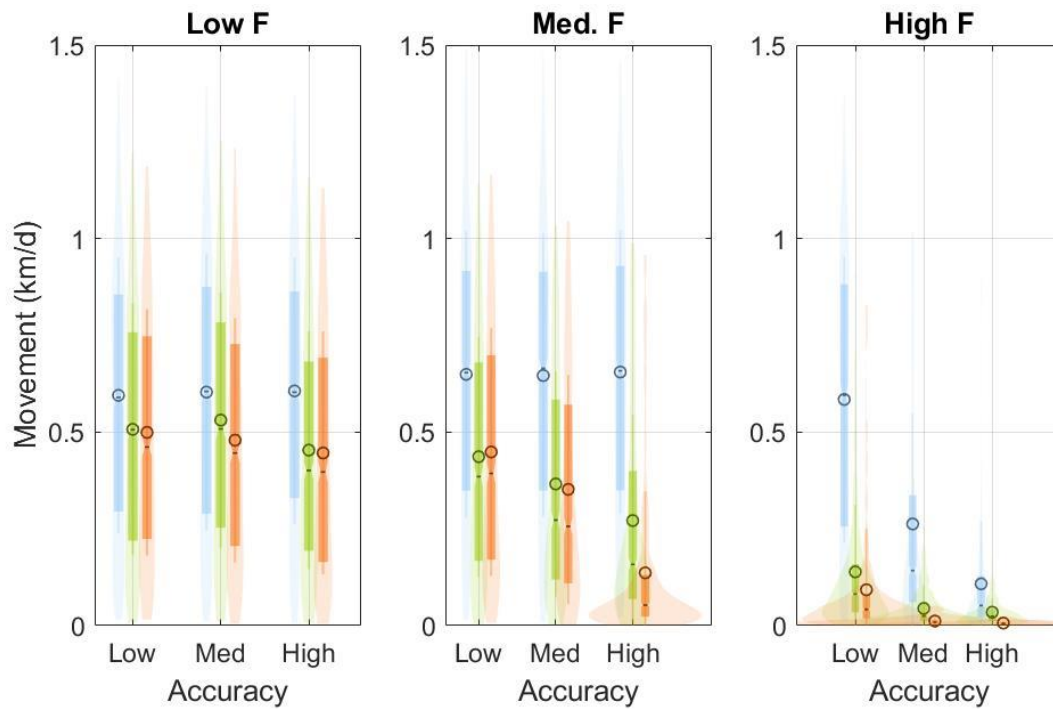
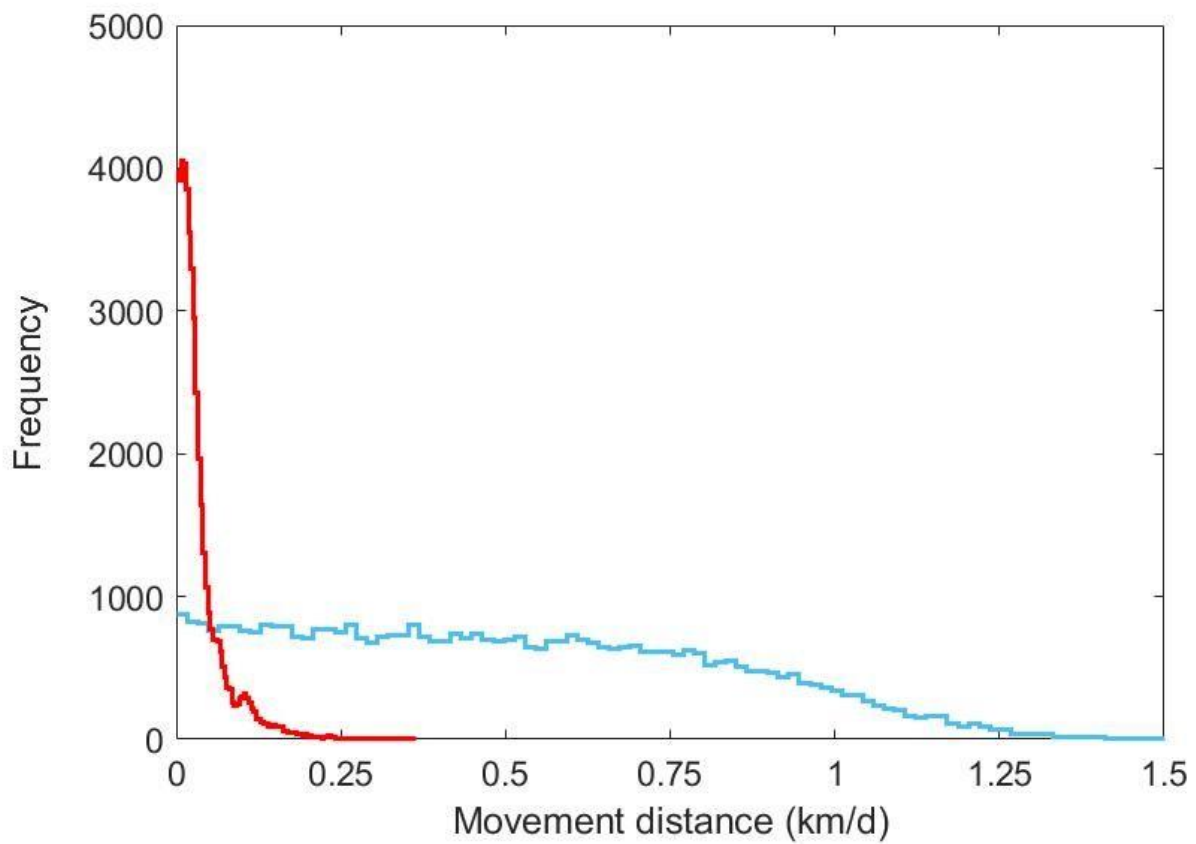


Figure 3. Phenotypic dispersion rate box-plots after a fifty-year simulation. Each subplot represents a level of fishing mortality, F (left to right: low, medium and high). Within each subplot, fishing accuracy is the abscissa. The colours represent spatial complexity: blue is high, green is medium and orange is low. The bars extend from the 5% to the 95% percentiles; the thin vertical lines are 1 standard deviation; the solid dot at the centre of the bars is the median and the empty circle is the mean. The semi-transparent violin plots depict the frequency distribution of the dispersion rate in each case. Notice that for high fishing mortality the violin plots are not fully visible to the right because the distribution is very skewed



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773 *Figure 4. Comparison of the distributions of phenotypic dispersion rates when the trait is heritable (red line) and*
 774 *when is not (light blue line). Situation at the end of a 50 year simulation with high fishing mortality (0.5), perfect*
 775 *accuracy and medium habitat complexity.*

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