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Author(s): Kuparinen, Anna; Uusi-Heikkilä, Silva

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Atlantic cod recovery from the Allee effect zone: contrasting ecological and evolutionary rescue

Anna Kuparinen  | Silva Uusi-Heikkilä 

Department of Biological and Environmental Sciences, Jyväskylä, Finland

Correspondence

Anna Kuparinen, Department of Biological and Environmental Sciences, P.O. Box 35, 40014 Jyväskylä, Finland.
Email: anna.k.kuparinen@jyu.fi

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Abstract

The ability of a population to recover from disturbances is fundamental for its persistence. Impaired population recovery might be associated with a demographic Allee effect. Immigration from adjacent populations could accelerate the recovery not only by promoting population growth beyond the Allee effect threshold but also by bringing in advantageous genotypes. We explore the nature and role of ecological and evolutionary rescue in an Atlantic cod (*Gadus morhua* Gadidae) population fished below its Allee effect threshold. We utilize an eco-evolutionary model and simulate scenarios, where the target population evolves in response to selective fishing and sample immigrants from (a) a source population similarly adapted to fishing (post-fishing genotypes) or (b) an unexploited source population with natural genetic and phenotypic diversity (pre-fishing genotypes). Immigration of pre-fishing genotypes enhances the recovery due to the larger body sizes and the flow of associated genes. Post-fishing immigrants can also promote the population abundance recovery, but they increase uncertainty about recovery times as compared to pre-fishing immigrants and do not promote evolutionary recovery. Our results stress the importance of maintaining genetic and phenotypic diversity and suggest that marine protected areas can serve as an important source of immigrants to promote both the demographic and evolutionary recovery of exploited populations.

KEYWORDS

adaptation, depensation, harvest-induced evolution, harvesting, population collapse, population rebuild, resilience

1 | INTRODUCTION

The rate of population recovery is inversely related to the risk that the population goes extinct, and thus, population recovery ability is of great importance to species conservation and risks related to disturbances, human-induced alterations and environmental stochasticity (Dulvy et al., 2004; Lande, 1993; Mace et al., 2008). In the absence of substantive habitat losses, impaired population recovery is often associated with a demographic Allee effect, that

is below some population size threshold the population growth slows down as the population abundance reduces (Stephens, Sutherland, & Freckleton, 1999). In practice, the demographic Allee effect is manifested by the positive association between per-capita population growth rate and the population abundance and the point at which this association turns from positive to negative is the threshold for the demographic Allee effect (Stephens et al., 1999) or the Allee effect threshold (Hutchings, 2015). Such a population growth pattern is opposite to the common assumption that

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at low abundances populations should grow fast owing to low intraspecific competition (Stephens et al., 1999). Nonetheless, unexpectedly slow or virtually absent recovery of populations reduced to low abundances have been observed across taxa, suggesting demographic Allee effects and the resulting depensatory population dynamics might be widespread among natural populations (Hutchings, 2015).

In the presence of demographic Allee effects, or any other factor that reduces per-capita population growth or viability at low abundance, immigration can be key to the “rescue” of a population. From an ecological perspective, immigrants arriving when abundance is at its lowest can be critical to bring the population abundance/density above the threshold below which the demographic Allee effect is manifest (Hutchings, 2015). In addition to the direct ecological rescue affecting census population size (N_t), immigrants can also benefit population recovery from a genetic point of view. An increase in effective population size (N_e) can reduce the probability of drift and inbreeding depression in small populations; this phenomenon is sometimes termed “demographic rescue” (Carlson, Cunningham, & Westley, 2014). The rescue driven by immigrants can also be “evolutionary” if the gene flow mediated by immigrants causes an adaptive evolutionary change in the population that restores positive population growth (Carlson et al., 2014). Conversely, immigrants can also be maladapted, carrying genotypes that adversely affect the sink population. The question of whether evolutionary rescue can occur depends heavily on the selection that shaped the immigrant source population in the past (Fitzpatrick & Reid, 2019). Consequently, both ecological and evolutionary rescues are dependent on, firstly, source populations dispersing immigrants and, secondly, the genetic composition of the source populations. In practice, this requires not only connectivity among local populations but also spatial heterogeneity in the abundance and adaptive genetic diversity of the local populations.

Atlantic cod (*Gadus morhua* Gadidae) is in many ways an iconic species for studying recovery following depletion. Following several fishery collapses, most northwest Atlantic populations have shown unexpectedly slow or absent recovery (Hutchings & Kuparinen, 2017; Hutchings & Reynolds, 2004). For example, in the Gulf of St Lawrence (Canada), natural mortality of cod has increased to unsustainably high levels (Swain, 2011; Swain & Mohn, 2012) because of a predator-driven Allee effect (Neuenhoff et al., 2019; Swain, Hugues, & Benoît, 2015). More generally, meta-analyses across 207 populations of marine species, of which 19 were cod, revealed evidence of a demographic Allee effect in cod at abundances <10% of the population carrying capacity (approximated by maximum observed spawning stock biomass; Keith & Hutchings, 2012). Similarly, in numerous intensively harvested (and later collapsed) cod populations, the life histories shifted towards earlier maturation and smaller adult body size (Hutchings, 2005; Olsen et al., 2004). These general observations prompt one to ask whether slow cod recovery might be related to the demographic Allee effect coupled with life-history changes, which are likely to negatively affect cod population growth rate (Hutchings, 2005), particularly at low abundance (Kuparinen, Stenseth, & Hutchings, 2014).

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In the present study, we explore how recovery can be affected by a combination of demographic Allee effects, life-history evolution and ecological or evolutionary rescue mediated by immigrants. We focus on cod as a conceptual, empirically defensible study system, given the empirical evidence of an Allee effect in this species (Keith & Hutchings, 2012). By utilizing an eco-evolutionary simulation model parameterized for cod (Kuparinen, Hardie, & Hutchings, 2012; Kuparinen, Keith, & Hutchings, 2014), we simulate the recovery dynamics of a depleted (target) cod population and investigate how recovery is affected by (a) fishing-induced evolution (FIE) in the depleted population, (b) the rate of immigration during the initial years of recovery and iii) the evolutionary history of the immigrants. Regarding the third point, we touch upon the question of the importance of maintaining adaptive genetic diversity within populations and species. Namely, we contrast two scenarios: one in which immigrants arrive from a depleted population that shares a similar evolutionary history as the target population, and one in which immigrants arrive from a pristine, unexploited population. Such a source population might, for example, originate from a marine protected area (Roberts et al., 2017).

2 | METHODS

The primary objective of the present study was to explore how the recovery of an overfished population can be affected by immigrants arriving during the initial years of recovery. We contrast the following scenarios: i) the sink population either has or has not experienced fishing-induced evolution (FIE) and ii) immigrants to the sink population are either similarly adapted to fishing (i.e. experienced FIE; Figure 1) or not adapted to fishing. To this end, we utilize an individual-based eco-evolutionary simulation model for cod dynamics (Kuparinen et al., 2012; Kuparinen, Keith, et al., 2014). The model is parameterized using individual-based empirical data (Kuparinen et al., 2012), and

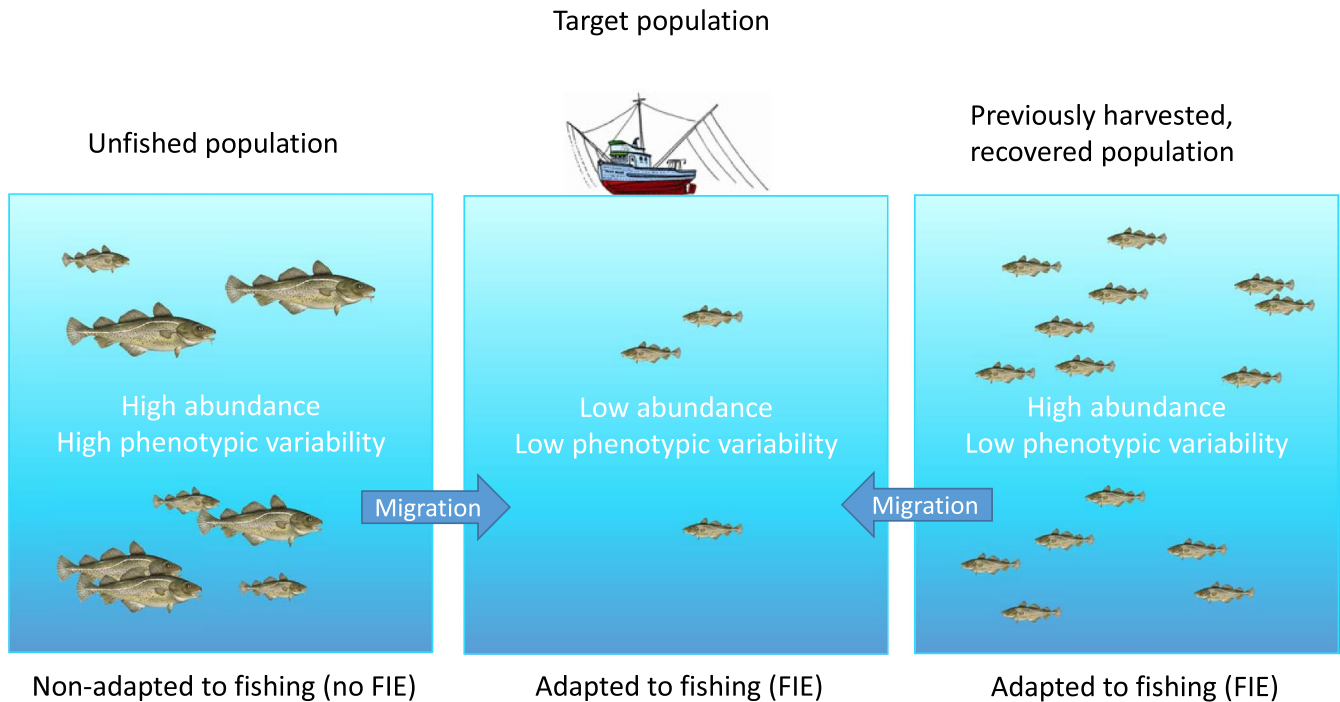


FIGURE 1 A schematic illustration of the study design. The target population is depleted into a low abundance after which fishing is ceased. Fish have undergone fisheries-induced evolution (FIE) and phenotypic variability has decreased (an alternative scenario where no FIE has occurred is contrasted in the simulations, but since this is not very realistic and not further analysed in the results, this scenario is not described in the figure). After fishing has ceased, immigrants arrive either from (1) a population that has experienced FIE or from (2) a population that has not experienced FIE. In practice, these source populations could be considered as (1) a previously exploited population that has experienced FIE and has recovered in abundance but not evolutionarily (right side in the figure) and (2) a population that has not been exposed to fishing (left side of the figure).

low-abundance dynamics are affected by the empirically estimated demographic Allee effect for cod (Table 1, Keith & Hutchings, 2012). We provide an overview of the model features below and in Table 1.

2.1 | Eco-evolutionary simulation model for cod dynamics

The model tracks a population of individuals through time and at each annual time step simulates, at the level of each individual, the outcomes of the demographic processes of mortality (both natural and fishing), growth, maturation and reproduction (Table 1). Those individuals that die are removed from the population, and newborn juveniles are added to the population.

2.1.1 | Life histories

Each individual cod life history is described through its von Bertalanffy growth trajectory

$$L(t) = L_{\infty} - (L_{\infty} - L_0) \times e^{-kt} \quad (1)$$

where $L(t)$ is the body length at age t , L_0 is the average length at $t = 0$, L_{∞} is the asymptotic body length, and k is the rate at which $L(t)$

approaches L_{∞} (Charnov, 1993). Cod life histories, as reflected by their von Bertalanffy parameters, are under genetic control. Each individual has ten loci with two alleles each (coded with 0 and 1). The sum across allele values codes the genotype of the individual. This sum, coupled with some phenotypic variability sampled from a normal distribution with mean zero, linearly relates to L_{∞} . In fish, L_{∞} and k are known to be strongly and negatively correlated. In our model, the association was estimated based on empirically observed growth trajectories of 258 individuals sampled from an unfished cod population in the Canadian Arctic (Kuparinen et al., 2012).

2.1.2 | Survival

The probability that an individual dies at a given time step is determined by sampling, using a binomial trial. For cod 3 years and older, the rate of natural mortality was set to 0.12 and the survival cost of reproduction was set to the rate of 0.10, which was added to the baseline natural mortality for the mature individuals. These mortality rates were calibrated based on empirical data (Kuparinen et al., 2012). For those years when the population was fished, the annual fishing mortality rate was set to $F = 0.20$ (i.e., about 18% of population biomass was removed each year through the conversion $1 - e^{-0.20}$) with logistic trawling selectivity (Table 1). For each individual, F depended on length such that the mortality rate was the

Model component	Formulation	References
Range of L_{∞}	30–130 cm	Based on 258 empirical samples (Kuparinen et al., 2012)
L_{∞} – k relationship	$\log(k) = -0.609 - 0.013 \times L_{\infty}$	Kuparinen et al. (2012)
Density-dependent growth: progress along an individual's growth trajectory within one year, from $L(t)$ to $L(t + t')$, where $t' \leq 1$	$t' = e^{15-17.6 \times c} / (1 + e^{15-17.6 \times c})$, where c is the population biomass divided by K	Kuparinen et al. (2012)
Fishing selectivity	$e^{-12.5+0.25 \times \text{length}} / (1 + e^{-12.5+0.25 \times \text{length}})$	Myers and Hoenig (1997)
Length–weight relationship	Weight = $3.52 \times 10^{-6} \times \text{length}^{3.19}$	Kuparinen et al. (2012)
Fecundity	Eggs = $(0.48 \times [(\text{female weight} + 0.37)/1.45] + 0.12) \times 10^6$	(Hutchings, 2005) Estimated when northern cod abundance was approximately 40% of its K .
Density dependence of recruitment (a coefficient to multiply the number of eggs)	Coefficient with respect to abundance as % of K 0%–10%: 0.65; 10%–20%: 1.39; 20%–30%: 1.15, 30%–40%: 1; 40%–60%: 0.92; 60%–80%: 0.77, >80%: 0.64	Keith and Hutchings (2012)

TABLE 1 Equations for the components of the eco-evolutionary simulation model for Atlantic cod (*Gadus morhua* Gadidae)

product of F and the relative fishing selectivity at the given length (Table 1). The age of recruitment to the fishery was set to 3 years, meaning that individuals younger than 3 years were not caught by fishing.

2.1.3 | Growth

Individuals that do not die grow in accordance with their von Bertalanffy growth trajectory. An individual matures when its body size exceeds 66% of its L_{∞} (Charnov, 1993). Growth along each individual trajectory was density-dependent and was based on the ratio of population biomass to carrying capacity (K). At low density, the individual growth increment is that predicted by an individual's von Bertalanffy curve, that is a shift from $L(t)$ to $L(t + 1)$. In a dense population, the increment is smaller, according to the density-dependent coefficient given in Table 1.

2.1.4 | Reproduction

For each mature female, a mature male was assigned randomly. The number of eggs produced depended on female body size and population density. Density dependence of the fecundity followed the pattern estimated for cod by Keith and Hutchings (2012), where at biomasses <10% of K the fecundity is depensatory and, thus,

reduced by about 50% compared with the fecundity at biomasses 10%–20% of K (see Table 1 for details). For each juvenile, alleles for each locus were drawn randomly from the respective loci of the parents, using binomial trials. The allele sum was coupled with a random number drawn from a normal distribution with mean zero and variability calibrated to yield realistic heritabilities (~0.2–0.3, Mousseau & Roff, 1987). The allele sum coupled with the random number was linearly related to the value of L_{∞} (Table 1). The sex of each juvenile was assigned randomly, using binomial trials. Juvenile survival from the egg stage to age 3 was set to 1.13×10^{-6} (Hutchings, 2005), and the number of survivors was sampled from a binomial trial.

2.2 | Simulation design

The objective of the simulations was to explore a scenario in which a cod population was exploited to a very low abundance, after which fishing ceased and the population received immigrants during the initial years of recovery. We set this immigration period to 10 years to examine how a short immigration period might influence recovery. By investigating a short immigration period and by keeping rates of immigration low, we could also keep the scenarios with and without immigration comparable (the robustness of our findings was nonetheless tested with an immigration period of 20 years).

Although our simulation set-up is hypothetical, not referring to any specific cod population or area, our model is based on a

well-parameterized study system (Kuparinen et al., 2012; Kuparinen, Keith, et al., 2014) for which a demographic Allee effect has been quantified (Keith & Hutchings, 2012). The scenarios with immigration stem from the fundamental theory of the ideal free distribution; if one population has declined well below its K , it will receive immigrants from abundant nearby populations until individual fitness is, on average, equal between the source and the sink populations (Cressman & Krivan, 2006; Fretwell, 1972; Fretwell & Lucas, 1969).

Simulations were initiated by sampling one of 100 populations pre-adapted to their demographic parameters in the absence of fishing. Target population equilibrium dynamics were simulated first for 100 years in the absence of fishing, after which fishing with mortality rate $F = 20$ and logistic fishing selectivity was introduced. At the beginning of fishing, the average age and size at maturity were ~ 7 years and 53.4 cm, and k and L_{∞} were, on average, 0.2 and 81 cm, respectively. The sex ratio was 1:1, and no loci were fixed (allelic frequencies were 0.71–1.53 out of possible range of 0 to 2). Fishing continued until the population biomass dropped below 5% of K (Figure 2; Figures S1–S4). At this point, the target population biomass ($BM_{5\%}$) was recorded and the 10-year immigration period was initiated in the following year. Given that immigration rates were fractions of $BM_{5\%}$, each population experienced the same relative rate of immigration with respect to its “collapse” abundance. Annual immigration rate scenarios of 1%, 2.5%, 5%, 7.5% or 10% of $BM_{5\%}$ were contrasted with the scenario in the absence of immigration.

The simulation design was repeated in the absence and presence of FIE in the target population during the fishing period. Immigrants were sampled from a genotype pool recorded either prior to the beginning of fishing (pre-fishing genotypes) to mimic a source population not exposed to fishing, or at the end of the fishing period (post-fishing genotypes) to mimic a source population that had been exposed to levels of fishing and FIE similar to that of the target population. During and after the immigration period (or the same period without immigrants, as a contrast), the populations were allowed to recover in the absence of any fishing. The times required for population abundance to recover to 25%, 50% and 75% of the unexploited abundance were recorded. Similarly, the development of population biomass, abundance and the annual average L_{∞} was tracked through each simulation run. For each simulation scenario (presence/absence of FIE; no-immigrant/post-fishing genotype immigrants/pre-fishing genotype immigrants; 1%, 2.5%, 5%, 7.5% and 10% immigration rates), we produced 50 replicated simulation runs. Simulations and analyses were carried out in R 3.4.2 (R Core Team, 2017).

3 | RESULTS

Across the simulation scenarios, fishing led to a consistent and rapid population decline to below 5% of K within 43–61 and 43–58 years in the absence and presence of FIE, respectively (95% observation

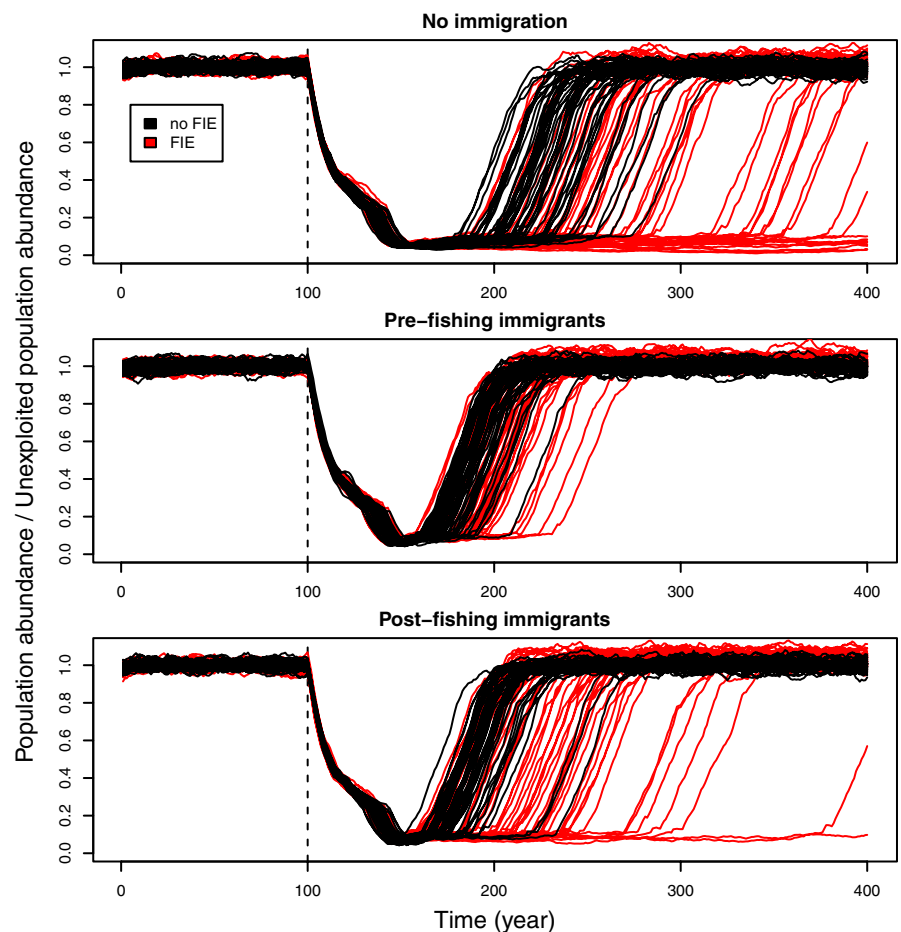


FIGURE 2 Simulated abundance trajectories for immigration rate 7.5% (for immigration rates 1%, 2.5%, 5% and 10%, see the electronic appendix). Grey vertical line marks the beginning of fishing. Fishing ceased as the biomass-to- K ratio went below 5%.

interval; respective medians were 52 and 50 years). Recovery patterns strongly differed between the evolution and immigration scenarios. The differences were primarily generated by differences in the time that the population remained in the Allee effect zone. Once the biomass had exceeded the Allee threshold, the recovery trajectory was steep and predictable (Figure 2 shows 7.5% immigration; for other scenarios, see Figures S1–S4). In the absence of FIE, all populations recovered eventually, while in the presence of FIE some populations never recovered. The occurrence of no recovery was much higher (8 of 50 simulation runs) in the absence of immigration as compared to any immigration scenario (pre-fishing immigrants: 0–1 of 50 simulation runs; post-fishing immigrants: 1–6 of 50 runs).

The highest frequency of no recovery was in the absence of immigration (except in 1% rate of post-fishing genotype immigrants), followed by pre-fishing genotype immigrants. The lowest incidence of no recovery was in the presence of pre-fishing genotype immigrants.

Recovery was always faster in the absence of FIE and further accelerated by immigration (Figures 2 and 3). In the absence of FIE, individuals grew to larger body sizes, enhancing the ability of the population biomass to surpass the Allee effect threshold; this was further accelerated by the biomass influx resulting from immigration, largely regardless of whether immigrants were pre- or post-fishing genotypes (Figures 2 and 3). In the presence of FIE, the recovery time was more uncertain, as reflected by greater variation among

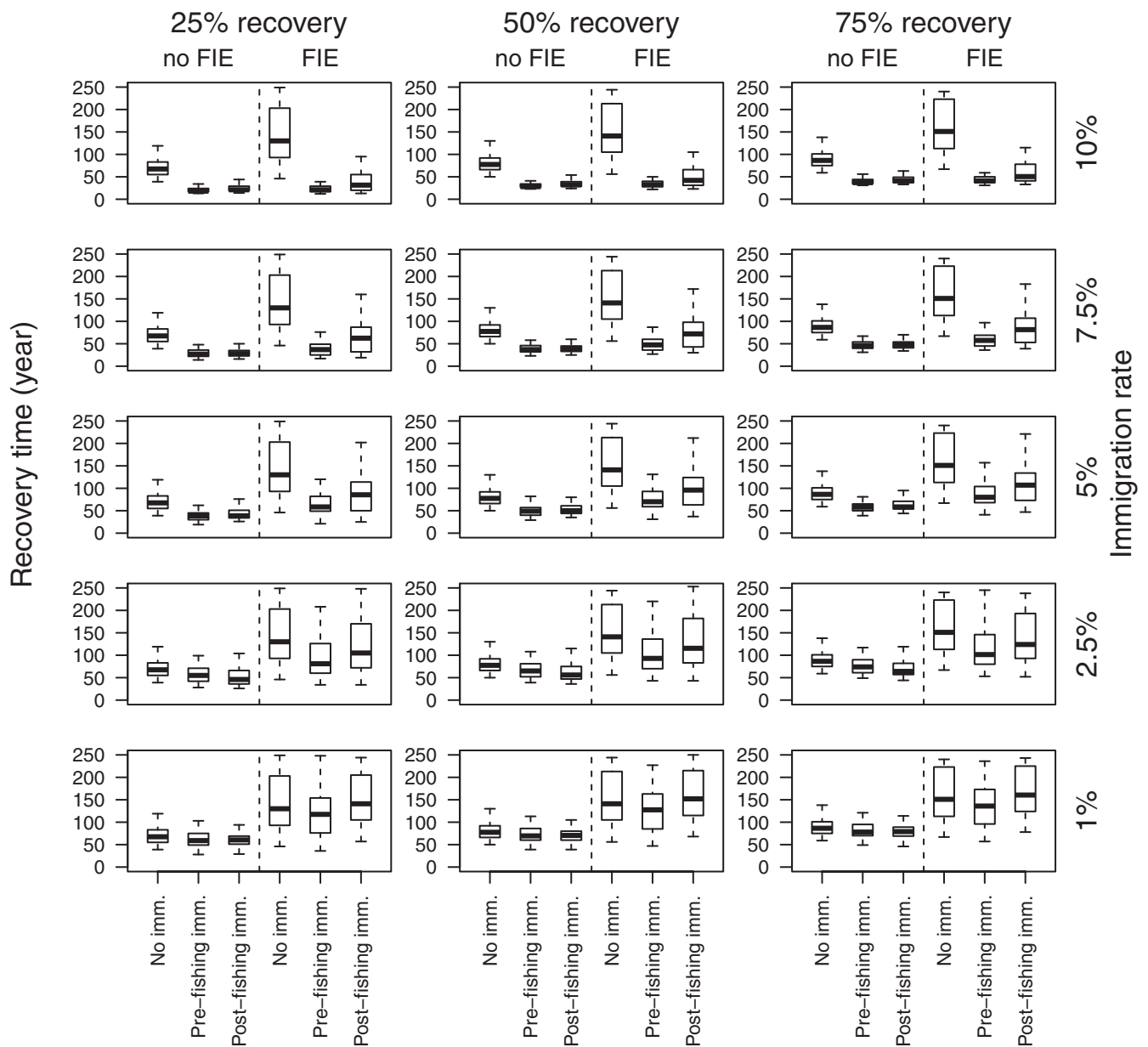


FIGURE 3 Recovery times for population abundance rebuild up to 25%, 50% and 75% of unexploited abundance. Medians are indicated by horizontal lines, boxes span the interquartile range, and whiskers encompass values 1.5 box lengths away from the box. Outliers are not shown. In two rightmost panels in the lowest row, the upper interquartile ranges and upper whiskers were estimated to infinity due to the frequent occurrence of no recovery.

the simulated replicates (Figure 2; Figures S1–S4), a pattern generated by lower population biomass growth resulting from smaller adult body sizes of individuals that had evolved in response to fishing. The relative impacts of immigration *per se* and the type of immigrants on recovery times were also larger in the presence of FIE (Figure 3). In other words, those populations that had experienced FIE benefitted more from immigration than populations that had not evolved under fishing. In the following section, we focus on the role of immigration in the presence of FIE.

Pre-fishing genotype immigrants (i.e., genotypes with high L_{∞}) accelerated recovery to a greater extent when compared to the contribution of post-fishing genotype immigrants (i.e., genotypes with low L_{∞}). This difference became more pronounced as the rate of immigration decreased (Figure 3). This is because, under the same rate of immigration, the pre-fishing genotypes aid evolutionary recovery of life histories towards larger adult body sizes, unlike the post-fishing genotypes (back towards their pre-fishing state; Figure 4).

Both in the case of post- and pre-fishing genotype immigrants, the uncertainty in recovery time increased as immigration rates decreased (Figure 3). Furthermore, in the absence of immigration or at low immigration rates, greater numbers of populations experienced no recovery at all. At the highest three immigration rates, the uncertainty in recovery was largest in the absence of immigration as compared to the immigration scenarios. In addition, the

type of immigrant affected the uncertainty differently (the heights of the boxes in Figure 3 in the presence of FIE): post-fishing immigrants caused recovery time to be more uncertain than pre-fishing immigrants. This effect became more pronounced as the rate of immigration decreased. At immigration rates of 1.0% to 2.5%, the uncertainty in recovery time associated with post-fishing immigrants was comparable to the level of uncertainty in the absence of immigration (Figure 3).

In the absence of FIE, the average L_{∞} of the population was only slightly affected by selective removal of large individuals during the fishing period. However, if FIE was allowed, the average L_{∞} evolved from about 81 cm to 74 cm during fishing (Figure 4). After FIE had occurred and fishing ceased, pre-fishing immigrants accelerated evolutionary recovery of L_{∞} towards its pre-fishing level, whereas post-fishing immigrants had a slightly negative or no effect on the evolutionary trait recovery as compared to the absence of immigration. Although the positive effect of pre-fishing immigrants on evolutionary recovery was more pronounced at high immigration rates, its influence at the lowest rate of immigration (1%) is still clearly visible (Figure 4). In the absence of FIE, post-fishing immigrants caused a small temporary reduction in the average L_{∞} after the cessation of fishing, whereas the scenario with pre-fishing immigrants did not differ from the scenarios without immigration (Figure 4).

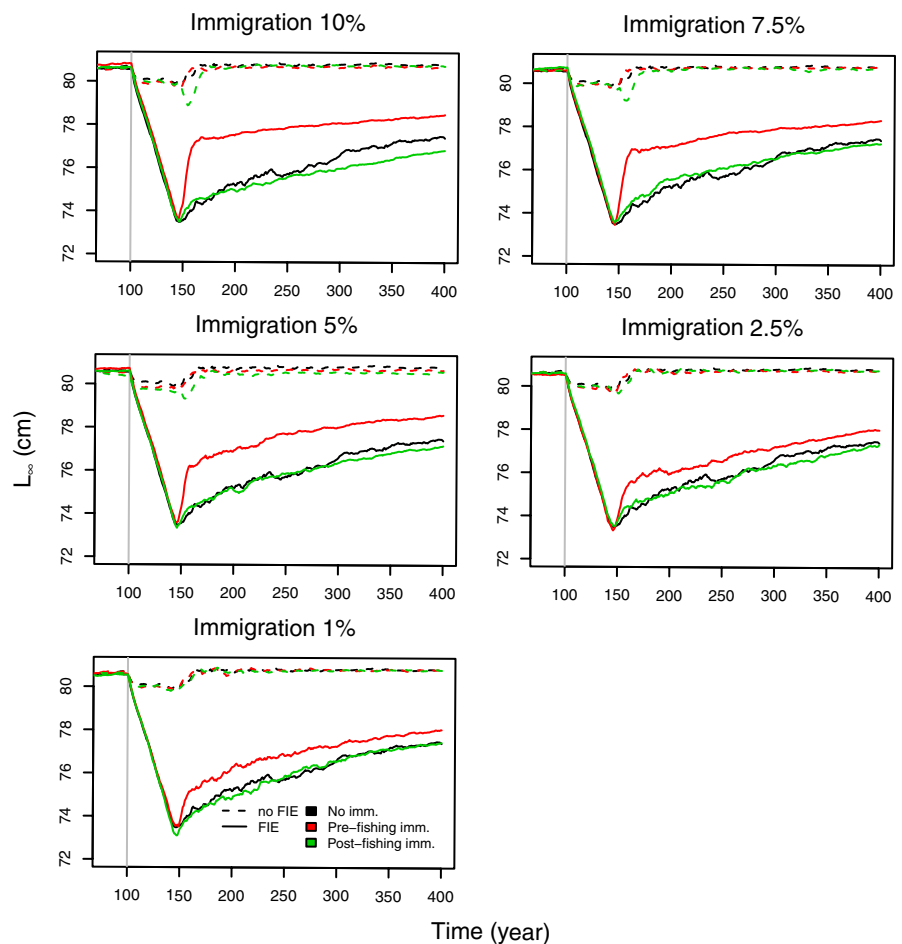


FIGURE 4 The temporal development of the L_{∞} averaged across the 50 replicated simulation runs. Grey vertical line marks the beginning of fishing.

If the simulation recovery period was extended to 20 years, the results were similar to those for the 10-year period, except that the rates of recovery were faster, particularly under higher immigration (Figures S5, S6).

4 | DISCUSSION

The present study illustrates that the recovery of depleted populations can be accelerated by immigration (Figures 2 and 3) and that uncertainty in recovery time can be substantially reduced as the rate of immigration increases (Figure 3). This finding might be expected in the light of demographic stochasticity, but the less intuitive outcome is the role of the genotypes of the immigrants. If the depletion was associated with strong directional selection reducing the frequency of certain fitness-related genotypes, restoring the genetic composition of the population may be as important as the restoration of population abundance (Figures 2 and 3). Thus, it is not irrelevant where the immigrants come from. In practice, genetic restoration of a depleted natural population requires source populations where the natural genetic and phenotypic diversity has been maintained. Such populations could occur in marine protected areas or reserves, provided that the areas are large enough to serve as sources of migrants and established sufficiently long ago to resemble pristine populations in terms of their phenotypic and genetic diversity.

Although the present study explored the consequences of overfishing, the same principles would apply to the recovery of populations and species declined owing to any disturbance (e.g., habitat fragmentation, climate change; Roberts et al., 2017) in marine and freshwater systems. In particular, the present work underscores the importance of establishing and maintaining species reserves that harbour high adaptive genetic diversity, not simply high numbers of individuals. Immigrants from such sources not only restore the phenotypic diversity of depleted populations but can also mitigate genetic Allee effects arising from inbreeding depression or deleterious mutations (Wittman, Stuis, & Metzler, 2018).

A major uncertainty in our study relates to the rate of immigration. We varied it over one order of magnitude, and the immigration scenario mimicked the principles of ideal free distribution such that the immigrants arrived during the first years after the target population collapse (Cressman & Křivan, 2006; Fretwell, 1972; Fretwell & Lucas, 1969). However, little is generally known about the magnitude of migration among cod populations and, specifically, how migration might be affected by large differences in population densities. At their current state, the migration rate estimates vary from zero (Ruzzante, Taggart, & Cook, 1999) to 0.3 (Therkildsen et al., 2013), but the existing genetic structuring of the populations suggests that migration is not common (Pogson, Taggart, Mesa, & Boutilier, 2001; Ruzzante, Taggart, & Cook, 1998, 1999; Therkildsen et al., 2013). While most cod populations are at low abundances and, thus, could hardly act as potential source populations for immigrants, after a few decades of recovery the situation might look very different. For example, following the establishment of a partially protected area

in southern coastal Norway in 2006, cod emigration to surrounding habitats has increased (Fernández-Chacón, Moland, Espeland, & Olsen, 2015). Despite uncertainties surrounding the rate of immigration, it should also be stressed that our results were markedly consistent across the simulation scenarios and, therefore, likely to reflect generic features present in recovery dynamics. While our study is hypothetical with respect to cod, in developing countries and in new fisheries it is common that one population is harvested until catches cease and then fisheries shift to a new population (Perälä & Kuparinen, 2017). Our study provides insights into design features needed for management strategies for new unexploited fisheries.

Allee effects occur in small and sparse populations and, although difficult to detect (but see Perälä & Kuparinen, 2017), are considered widespread in nature (Gascoigne & Lipcius, 2004; Hutchings, 2015; Shelton & Healey, 1999; Stephens et al., 1999). Immigration from adjacent populations, even at low rates, helps to push populations from the Allee effect zone, accelerating recovery and reducing the uncertainty of the recovery (Figure 2, Table 1). It is often believed that large population size is an important hedge against extinction and instrumental for population recovery (Dulvy et al., 2004; Lande, 1993; Mace et al., 2008). However, when immigrants are maladapted to the sink population's environment, an ecological (or demographic) rescue is possible (Figure 3), but an evolutionary rescue is unlikely. In our cod example, when the formerly exploited target population received post-fishing immigrants adapted to fishing, those were virtually similar to individuals in the target population and, therefore, could not contribute to the evolutionary recovery. Moreover, our results are conservative because we have considered adaptation relating only to growth and maturity; in reality, immigrants arriving from other populations also can bring maladapted traits, for example differences in spawning time.

Traditionally, fully protected areas (i.e., areas protected from all extractive activities; hereafter "reserves") are being established to restore habitats and/or promote population recovery (FAO, 2011; Lubchenko, Palumbi, Gaines, & Andelman, 2003). At this point, population sizes have likely been drastically reduced and the phenotypic and genetic diversity might be low owing to human-induced selection (e.g., selective harvesting), genetic drift and inbreeding (Frankham, 2005; Marty, Dieckmann, & Ernande, 2015). Populations in these kinds of reserves do not act as ideal sources of immigrants for an exploited population because (a) low abundance in the source population hinders dispersal and (b) individuals are potentially adapted to exploitation, thus maladapted to the natural, unexploited conditions. Although we do not refute the importance of protecting populations with critically low sizes, establishing reserves for thriving populations with large census and effective sizes is also vital. This would allow the spillover of phenotypically superior individuals favoured by natural selection (e.g., large individuals with high reproductive success) to adjacent exploited populations to occur more rapidly. Marine reserves have been documented to host more large and fertile individuals compared with fished areas (Edgar et al., 2014; MacNeil et al., 2015). However, reaching a point where the frequency of these phenotypes is high enough to facilitate their dispersal can

take decades, particularly if the population density is pushed to extremely low levels (e.g., below the Allee effect threshold; Hutchings, 2015) and if earlier exploitation have caused evolutionary changes in the population. Indeed, our simulations showed that a full recovery of cod populations can take hundreds of years, particularly in the presence of fisheries-induced evolution (Figure 2a).

It has been proposed that in order to produce the greatest conservation benefit, the reserves should be well-enforced, large ($\geq 100 \text{ km}^2$), well-established (≥ 10 years old) and isolated (Díaz, Mallol, Parma, & Goñi, 2016). While we fully agree with the first three key characteristics (although it is good to keep in mind that the largest areas are also the most isolated), a very isolated area might not bring great dispersal benefits to adjacent subpopulations because very long-distance dispersal events are rare (Manel et al., 2019). In order to support dispersal and migration spillover, networks of small, well-connected reserves might be more valuable (Green et al., 2014). The establishment of these networks requires a close collaboration with scientists and managers as the former can provide detailed information about the habitats of the protected populations. However, dispersal is not always based on active and complex behaviour of adults (Rakitin & Kramer, 1996) or juveniles because of dispersal imbalance (Walters, Hilborn, & Parrish, 2007) or competition (Bowler & Benton, 2005). In current-dominated environments, fish larvae can drift to neighbouring reserves (Baetscher et al., 2019). The dispersal routes of pelagic larvae might be difficult to predict.

Spatial design of the networks brings additional challenges. Firstly, the home ranges of pelagic species can be extremely large (Daly et al., 2018), and secondly, in some instances it is necessary to also protect the migration routes to feeding and spawning grounds (e.g., some cod populations have separate feeding and spawning grounds). Finally, effective management practices are required in the environment surrounding the networks to prevent intensive exploitation in the dispersal routes and at the edges of the reserve network. However, it is good to keep in mind that this kind of immigration might not be suitable for all species or populations in need of protection (e.g., when gene flow breaks down local adaptation; Bolnick & Nosil, 2007). Although reserve networks are powerful conservation tools, they do not provide a universal remedy to all problems, particularly to those that originate outside network boundaries. We speculate, however, that networks could alleviate problems caused by overharvesting outside the network in recently exploited populations via immigration when harvesting has ceased in the sink populations.

The present study was motivated by an attempt to establish reserves as a management measure to protect harvested fish species, by acting as a source of immigrants and a reservoir of genetic and phenotypic diversity. Namely, intensive, selective fishing outside reserves is likely to drive fishing-induced evolution in key fitness-related life-history traits, such as the age at maturity and maximum asymptotic length (L_{∞}). We showed that a large number of immigrants are important to bring about a short-term ecological rescue. However, evolutionary rescue will only be likely when immigrants are well-adapted to the no-harvest environment. Immigration will

enhance population recovery and, owing to high phenotypic and genetic variation, potentially increase a population's resilience by promoting natural resistance to threats.

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DATA AVAILABILITY STATEMENT

The present manuscript presents no new data. Codes and simulation outputs are available in Dryad: <https://doi.org/10.5061/dryad.dbrv15dx2>

ORCID

Anna Kuparinen  <https://orcid.org/0000-0002-7807-8946>

Silva Uusi-Heikkilä  <https://orcid.org/0000-0001-6503-455X>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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