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Implications of dispersal in Atlantic salmon: lessons from a demo-genetic agent-based model

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Abstract

Despite growing evidence of spatial dispersal and gene flow between salmonid populations, the implications of connectivity for adaptation, conservation, and management are still poorly appreciated. Here, we explore the influence of a gradient of dispersal rates on portfolio strength and eco-evolutionary dynamics in a simulated population network of Atlantic salmon (*Salmo salar*) by extending a demo-genetic agent-based model to a spatially explicit framework. Our model results highlight a non-linear relationship between dispersal rates and the stability of the metapopulation, resulting in an optimal portfolio effect for dispersal rates around 20%. At local population scale, we also demonstrate phenotypic changes induced by density-dependent effects modulated by dispersal, and a dispersal-induced increase in genetic diversity. We conclude that it is critical to account for complex interactions between dispersal and eco-evolutionary processes and discuss future avenues of research that could be addressed by such modeling approaches to more fully appreciate responses of Atlantic salmon to environmental changes and investigate management actions accordingly.

Keywords: Atlantic salmon, demo-genetic agent-based model, dispersal, eco-evolutionary dynamics, metapopulation, portfolio effect, synchrony

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1. INTRODUCTION

Rapid environmental changes and associated selection pressures are affecting the adaptive capacity and persistence of many species globally (Ceballos et al. 2015). Consequently, there is considerable interest in understanding species responses to current and predicted global changes (Urban et al. 2016). This ambitious goal requires not only a consideration of the different processes and mechanisms facilitating species adaptation, persistence, and stability but also their interactions. Ideally such processes and interactions would be studied in a single, integrative framework and the field of eco-evolutionary dynamics provides such a context (Hendry 2017). Ultimately, this framework should guide management and conservation practices to maintain adaptive capacity and persistence of natural resources.

The main eco-evolutionary processes underlying species adaptation and responses to environmental changes include phenotypic plasticity (or acclimatization) and genetic adaptation of traits in response to natural selection (Reed et al. 2011). These processes shape a great diversity of life-history traits that can be phenotypic (e.g., growth, behavior) or phenological (e.g., reproduction timing). These life-history traits are not only influenced by environmental and genetic factors, but also by complex interactions between individuals (e.g., sexual selection) and demographic processes such as density-dependence effects. Accounting for relevant eco-evolutionary processes (e.g., sexual selection) and their underlying mechanisms (e.g., genetic architecture and transmission) in empirical and theoretical approaches is necessary to fully appreciate populations dynamics and responses to environmental changes.

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Dispersal or the movement of individuals from their natal population to a different breeding population, is ubiquitous in nature and is also a process that promotes species responses to environmental change by spreading the risk of reproductive failure (Ronce 2007, Buoro and Carlson 2014). There is growing appreciation – from both theory and empirical studies - of the causes and consequences of dispersal (Clobert et al. 2009, 2012). For example, dispersal and gene flow among interconnected populations can induce genotypic and demographic consequences on recipient populations (Cayuela et al. 2018). This may prevent the extirpation of local populations via rescue effects (see Carlson et al. 2014 for review) but also lead to "anti-rescue effects" (Harding and McNamara 2002) and reduce metapopulation diversity through the homogenizing effect of dispersal (Paradis et al. 1999, Lenormand 2002). Within a metapopulation context (Hanski 1998), the connectivity among populations is critical because it has consequences for the dynamics of local populations and the whole metapopulation. Thus, we would expect eco-evolutionary dynamics of a metapopulation to differ from that of a single population taken in isolation, highlighting the need to consider eco-evolutionary processes, feedback loops, and the spatial structure of populations within a single, coherent framework.

More generally, the resilience of ecological systems, such as a metapopulation, relies on the connectivity and the diversity of responses of its components (Elmqvist et al. 2003, Webster et al. 2017). Indeed, there is growing recognition that a diverse network of populations can promote overall stability of population complexes and resource flows (e.g., fishery yields, Schindler et al. 2010). Ecological portfolio theory emphasizes the importance of biocomplexity, or life history diversity within and among populations (Hilborn et al. 2003, Abbott et al. 2017), as well as asynchronous dynamics among populations as factors contributing to stability of population complexes (Schindler et al. 2010, 2015). The portfolio effect has been studied extensively in imperiled and exploited salmonid species, especially for

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Pacific salmonids (e.g., Moore et al. 2010, Carlson and Satterthwaite 2011, Anderson et al. 2015). However, the potential influence of dispersal among salmon populations on portfolio strength has received less attention (but see Yeakel et al. 2018).

Dispersal rates are often considered low in salmonids (Schtickzelle and Quinn 2007, Birnie-Gauvin et al. 2019), even though identification of dispersers (or "strayers") and dispersal rates remain difficult to assess in wild populations. For instance, Atlantic salmon (*Salmo salar*) is well known for its great diversity of life-history strategies linked to phenotypic plasticity (Mangel and Satterthwaite 2016, Erkinaro et al. 2019) and genetic basis of life history traits (e.g., age at maturation, Barson et al. 2015, Lepais et al. 2017), but it is also commonly presented as a highly philopatric species (Salmenkova 2017). Yet, evidence of dispersal behavior and gene flow have been reported between several populations of Atlantic salmon (e.g., Consuegra et al. 2005, see Keefer and Caudill 2014 for review), allowing recolonization and expansion (Makhrov et al. 2005, Perrier et al. 2010, Pess et al. 2014). However, few studies have estimated dispersal rates between wild populations of Atlantic salmon (but see Jonsson et al. 1991, 2003, Consuegra et al. 2005, Jonsson and Jonsson 2017), and even fewer discuss or assess the potential consequences of metapopulation functioning on conservation and management of Atlantic salmon populations (but see Castellani et al. 2015, Bowlby and Gibson 2020). As suggested by Schtickzelle and Quinn (2007), future work should strategically consider salmon dynamics from a metapopulation perspective.

Modeling approaches can overcome the difficulties associated with examining dispersal consequences in nature. Among them, classical metapopulation theory, demographic, patch occupancy models (Hanski 1998, 1999, Sutherland et al. 2014; Bowlby and Gibson 2020 for salmonids), as well as evolutionary analytical models (Berdahl et al. 2015, Yeakel et al. 2018),

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have advanced general concepts in metapopulation functioning and persistence. Mechanistic eco-evolutionary models such as Demo-Genetic Agent-Based Models (DG-ABMs, also called Eco-Genetic ABMs) provide a complementary and flexible approach for simulating the complexity of a species life cycle (DeAngelis and Grimm 2014, Stillman et al. 2015) and assessing the demo-genetic consequences of dispersal in a unified framework. By integrating variation and interactions between individuals, as well as explicit genetic basis of traits and their transmission, this approach allows life-history traits to evolve in interaction with demographic effects in response to environmental and anthropogenic pressures (Dunlop et al. 2009, Johnston et al. 2019). Recently, several generic metapopulation DG-ABMs have emerged such as Nemo (Guillaume and Rougemont 2006), SimAdapt (Rebaudo et al. 2013), RangeShifter (Bocedi et al. 2014, 2021) or CDMetaPOP (Landguth et al. 2017). Several specific DG-ABMs represent the complex life cycle of salmonid species (e.g., Thériault et al. 2008, Ayllón et al. 2016), but only two studies incorporate dispersal between populations to our knowledge. Landguth et al. (2017) simulate a network of non-native Eastern Brook Trout (*Salvelinus fontinalis*) populations and evaluate efficiency of fish removal management strategies taking into account dispersal between patches. Lin et al. (2017) extended a single population model of sockeye salmon (*Oncorhynchus nerka*) to two populations to assess the consequences of dispersal on local adaptation and demography. We build on this general approach, but with a focus on Atlantic salmon, to explore dispersal implications within a realistic network of populations and an eco-evolutionary framework.

Our ultimate goal is to shed light on the potential implications of dispersal on the portfolio effect and eco-evolutionary dynamics in Atlantic salmon. To do so, we extended a demo-genetic agent-based model of Atlantic salmon (IBASAM, Piou and Prévost 2012) to a metapopulation context. The original IBASAM model was developped to evaluate eco-

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evolutionary responses to climate change and selective exploitation (Piou and Prévost 2013, Piou et al. 2015). It includes most of the knowledge available today on the eco-evolutionary processes and mechanisms of this species. However, IBASAM was designed to mimic a single population with complete philopatry, so we incorporated a dispersal process to simulate a realistic network of fifteen Atlantic salmon populations (Bouchard et al. 2022). By doing so, our model allows an investigation of the consequences of dispersal on local populations and network dynamics at the demographic, phenotypic, and genotypic levels. In this article, we first describe the main features of the model. Second, we test a gradient of dispersal rates and examine consequences for network stability, synchrony, local extinction risk, and life-history traits. Finally, we highlight pending questions that could be addressed with a more explicit consideration of dispersal, including basic studies related to eco-evolutionary dynamics of Atlantic salmon metapopulations and practical management questions relevant to connected populations of this exploited species.

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2. MODEL DESCRIPTION: MetaIBASAM, A SPATIALLY STRUCTURED VERSION OF IBASAM

The model presented here is a simple extension of the Individual-Based Atlantic Salmon Model (IBASAM) proposed by Piou and Prévost (2012) incorporating a dispersal process, which we call "MetaIBASAM". There are several existing modeling frameworks that would allow exploration of metapopulation dynamics of salmonids; we highlight the most relevant to our work in Table 1, including their key strengths, and summarize our rationale for extending IBASAM here. In particular, we sought a mechanistic model with potential for eco-evolutionary feedback loops (which excluded strictly demographic and analytical models; e.g., Bowlby and Gibson 2020, Yeakel et al. 2018), integrating dispersal (which excluded demo-genetic models based on single population; e.g., IBASAM), and simulating the complexity and specificity of the Atlantic salmon life cycle (which excluded more generic and specific metapopulation demo-genetic models; e.g., Nemo, RangeShifter and models from Landguth et al. 2017 and Lin et al. 2017). For all of these reasons, we moved forward expanding the IBASAM model to the metapopulation scale.

MetaIBASAM aims to simulate a network of interconnected Atlantic salmon populations and to explore the consequences of dispersal at demographic, phenotypic, and genotypic levels in a unique and coherent framework. This simulation tool is a demo-genetic agent-based model representing explicitly the life cycle of the species, individual life histories from birth to death, reproduction, and transmission of individual traits to successive generations. The full description of IBASAM is available from earlier studies (Piou and Prévost 2012, 2013, Piou et al. 2015), but we present the key features, model improvements (i.e., growth potential

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heritability and growth-survival trade-off) and the main addition to MetaIBASAM: the dispersal process.

2.1. Key features of IBASAM

2.1.1. Modeling the life cycle of Atlantic salmon at the individual scale

IBASAM aims to mimic the Atlantic salmon life cycle. Atlantic salmon is an anadromous species with a freshwater phase where reproduction (in winter) and development of juveniles (in spring) occur, and an ocean phase where anadromous fish migrate and grow. During summer, juveniles face two alternative tactic decisions: maturing in freshwater (precocious maturation, males only reproducing the next winter), or migrating to the sea the following spring (as “smolt”). Those who do not mature in freshwater or migrate to the sea in their first spring can stay one more year in freshwater before maturing or migrating to the ocean. Individuals that migrate to the ocean join a common growth area (Olmos et al. 2019) where they can mature after only one year at sea (“one sea- winter” or 1SW) or stay in the ocean for multiple years (“multiple sea-winter” or MSW) before returning, most of the time, to their natal river to reproduce. Atlantic salmon are iteroparous but most of them die following their first breeding season (low degree of iteroparity, Bordeleau et al. 2020). Salmonids are considered emblematic of species with philopatric behavior (Salmenkova 2017), but dispersal occurs regularly (in Atlantic salmon, Jonsson et al. 2003, Consuegra et al. 2005).

Within the model framework, each individual is described and followed during its complete life cycle. Individuals are characterized by 44 variables including, e.g., sex, age, size, location, state of migration/maturation, among others. Processes such as growth or survival occur at the daily scale, but individual features (e.g., size) are monitored only at the end of two seasons (winter and summer). A set of traits are genetically determined and can be transmitted to their

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offspring, including maturation tactics and growth capacity, using a bi-allelic multilocus system (see section 2.1.3.).

2.1.2. Density and environment effects on life-history traits

In the model, life-history traits of individuals are influenced both by density-dependent and density-independent processes (Fig. 1). For instance, survival from the egg stage to emergence and growth of juveniles in freshwater are impacted by water temperature and stream flow (Baum et al. 2005, Jonsson et al. 2005), but also by negative density-dependence effects (Imre et al. 2005). The seaward migration decision ("smoltification") is based on a probabilistic size-dependent reaction norm (Buoro et al. 2010). Marine conditions also affect individual life-history traits through growth and size-dependent survival at sea.

2.1.3. Heritable traits and selective pressures

Life-history traits can also evolve in response to selective pressures in IBASAM. Maturation decision in river and sea has been implemented using the environmental threshold model (Piché et al. 2008, Lepais et al. 2017). The maturation decision is based on a comparison between the individual value of the threshold (genetically determined) and the individual energetic reserves (growth-related and environmentally determined, Fig. 1). The maturation thresholds (varying between river and sea, as well as male and female) can thus evolve under natural selection, which then influences the age at maturation in the population (precocious males *vs.* time at sea). These traits are supported by a genetic architecture which is a combination of the quantitative genetics framework and the Mendelian inheritance system. Specifically, the phenotype expression of the traits above results from the additive effect of its genetic and environmental components based on heritability and the genetic value (so-called breeding value) controlled by a bi-allelic multilocus genotype with a variable number of loci.

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Sexual selection is known as an important selective pressure in fish (Kodric-Brown 1990). In IBASAM, there is an advantage in reproductive success for larger females (higher fecundity and access to anadromous males), and a sexual selection for large anadromous males by females (Fleming 1996, 1998). Though a fraction of the maturing parr can also reproduce based on observations of "sneaker" behavior (Fleming 1996), there is no sexual selection by females.

2.2. Model improvements: a genetic basis of growth and a growth – survival trade-off

While growth depends mainly on environmental conditions encountered by individuals, we introduced a genetic basis for the growth potential parameter as suggested by Gjerde et al. (1994). However, preliminary analysis showed that including a genetic basis to growth potential led to its evolution toward higher values, resulting in larger individuals over time (see Supporting information 1). Indeed, because sea survival and reproductive success depend positively on size and growth (Piou and Prévost 2012), natural and sexual selection tend to favor larger individuals with higher growth potential. To limit this directional selection and represent mortality costs of rapid growth as reported in experimental studies (Bochdansky et al. 2005, Biro et al. 2006), we implemented a growth–survival trade-off in river (Fig. 1, Supporting information 1; survival at sea is size-dependent). Combined with the size-dependent survival at sea and reproductive success, the growth-survival trade-off induces a stabilizing selection for growth and size and an optimal fitness value of growth potential (Fig. 2 A), ensuring stable size distributions in a neutral context (without selection, Supporting information 1).

2.3. Dispersal modeling: extending IBASAM into a metapopulation context

MetaIBASAM considers the connectivity between populations by implementing a dispersal process, i.e., adults can disperse toward other rivers of the system during their breeding

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migration. While there is growing interest in understanding factors influencing salmon dispersal (see Keefer and Caudill 2014 for review, and Westley et al. 2015 for a discussion of collective behavior), quantitative estimations of dispersal are rare and the underlying mechanisms remain poorly understood. In line with models proposed by Landguth et al. (2017) and Lin et al. (2017), we assume that (1) philopatry is constant over space and time, (2) dispersal is not phenotypically and genotypically determined. However, in our model the choice of recipient population is based on a dispersal kernel that depends on distance from the natal river and the attractiveness of the recipient population (see Nathan et al. 2012 for review).

At the time of adult riverward migration, dispersing individuals are randomly selected from their population of origin j with a probability to disperse P_j, independently from their individual characteristics (Equation 1). The probability P_j is function of a constant philopatry rate (noted h), i.e., without variation between populations, fixed at initialization. Then, for the subset of dispersing individuals, the recipient population j' is determined by sampling into a multinomial distribution of parameter $p_{j,j'}$, which is the probability to disperse from the population j to the population j'.

$$P_j = 1 - h_j = \sum_{j' = 1, j \neq j'}^{n} p_{j,j'} \qquad (1)$$

With P_j the total dispersal rate of the population j and h the philopatry rate.

This matrix of dispersal probabilities p represents the connectivity between populations and is derived from a dispersal kernel (Fig. 2 B). Here, we assume that dispersal probability $p_{j,j'}$ between two populations j and j' is a function of the distance between their estuaries, $D_{j,j'}$. We use the Laplace distribution, a leptokurtic distribution commonly used for fish (Pépino et al.

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2012), which maximizes the connectivity between close populations while still allowing some flow of individuals between distant rivers (long-distance dispersal, Equation 2). Because the attractiveness of rivers for anadromous salmonids can vary as a function of the population size, likely because of chemical attraction to congeners, collective behavior, and/or the influence of river discharge (Jonsson et al. 2003, Berdahl et al. 2016; see Keefer and Caudill 2014 for review), we weigh the distance kernel by a parameter $g_{j'}$, the relative size of the destination population with other populations, to represent its attractiveness (Equation 3). The larger the populations, the more attractive they are to dispersing individuals.

$$p_{j,j'}(D_{j,j'}, b) = g_{j'} \times \frac{1}{2b} \times exp^{(-\frac{D_{j,j'}}{b})} \quad (2)$$

$$\text{with } g_{j'} = \frac{\log10\,(A_{j'})}{\sum_{A_1}^{A_{npop}} \log10\,(A_{j'})} \quad (3)$$

With b the mean dispersal distance in the metapopulation and $A_{j'}$ the production area of juveniles of river *j'*, considered as a proxy of population size.

Altogether, the dispersal kernel assumes that a given migrant fish will tend to disperse to the nearest population from its natal river but this will be moderated by the "attractiveness" (i.e., the relative population size) of nearby rivers (Fig. 2 B). Even with a constant dispersal rate over space and time, the spatial structure of the population network, the demography of local populations, and the dispersal kernel lead to various immigration rates between populations.

2.4. Model parameterization and outputs

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MetaIBASAM consists of a set of IBASAM sessions - with one session simulating one population - running in parallel and exchanging information about the dispersers (e.g., phenotypic, genetic values, and genotypes). Similar to IBASAM, MetaIBASAM was parameterized in a pattern-oriented modeling framework (Grimm et al. 2005) using values extracted from the literature and empirical studies (see Piou and Prévost 2012, and Supporting information 2), and adjusted using a long-term monitoring program of the salmon population in the Scorff River (Brittany, France). We adjusted the parameters of the growth-survival trade-off (see Supporting information 1 and 2) to ensure that abundances and size at different life stages are within the range of observed values on the Scorff River. All other parameters of each population are kept identical to the IBASAM version (Piou and Prévost 2012), except for survival rates at different life stages and a temperature-survival related parameter (*dr*) that have been adjusted (Supporting information 2) to updated environmental conditions (see section 3.1). The parameter *b* of dispersal kernel was adjusted to limit dispersal under 50km for at least 80% of dispersers individuals, as suggested by Jonsson et al. (2003) and Keefer and Caudill (2014). Daily water temperature, water discharge, marine growth conditions, and exploitation are the main environmental and anthropogenic factors affecting individuals in the model (Fig. 1).

IBASAM is coded in C++ language, and an R package named MetaIBASAM has been developed (https://github.com/Ibasam/MetaIBASAM). Each IBASAM can be parametrized by users to represent a unique population with its own demographic (area, distance), phenotypic, genetic (initial distribution), environmental (water temperature, discharge), and anthropogenic (exploitation rate) characteristics. One simulation of MetaIBASAM returns all information on individuals (e.g., unique ID, population of origin, current population, body size, genetic values) and nests (e.g., ID of parents, number of eggs) two times per year for each population.

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3. APPLICATION: CONSEQUENCES OF A GRADIENT OF DISPERSAL RATES ON LOCAL POPULATIONS AND METAPOPULATION DYNAMICS

3.1. Scenario and parameterization

To investigate the consequences of dispersal on Atlantic salmon metapopulation dynamics and persistence, we ran the model for a gradient of dispersal rates P from 0% to 50%, corresponding to a large range of variation encompassing rates of straying that have been reported in the wild (e.g., Consuegra et al. 2005; see Keefer and Caudill 2014 for review). The spatial structure of the network in the model is inspired by the salmon populations of Brittany (France; Bouchard et al. 2022, see also Supporting information 2), for which one population (Scorff) was used to calibrate IBASAM, and gene flow among populations was demonstrated (Perrier et al. 2011). The network is composed of fifteen major populations (small coastal rivers) of different river sizes and distances between each pair. We gathered the area of juvenile production of each population (population area A_j), measured annually by the angling club federations, and the distance between their estuaries (Supporting information 2). Note that the objective was not to accurately mimic each population but to define a realistic spatial configuration and diversity of demographic characteristics to explore eco-evolutionary questions. Beyond population size and distance between pairs of populations, all other parameters are the same for all populations (e.g., environmental conditions, trait distributions at initialization, etc.) for all dispersal scenarios. In doing so, we can isolate the effect of dispersal on portfolio strength from the effects of biocomplexity and diversity of population responses.

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We simulated a daily time series of water temperature and water discharge for each river, with the same regime (average and amplitude) but no spatial covariation to focus on the role of dispersal and spatial structure in populations dynamics. The different models and data used to simulate these series, as well as the parameters estimated, are detailed in Supporting information 3. The daily effects of marine growth conditions on the fish are drawn from a normal distribution of similar mean and standard deviation between the populations. Exploitation rates (7% and 15% for 1SW and MSW individuals respectively, Lebot et al. 2022) were kept identical across populations.

Simulations were initialized for each population using a random draw of individuals corresponding to 25% of rivers production area A_j only to limit the computing time without loss of generality. Phenotypic and genetic values were sampled using the same distributions implemented in IBASAM (see Piou and Prévost 2012). Since generation time for this species is approximately 2.5 years in French populations, we simulated each dispersal scenario and population network over 50 years, which is sufficient time to detect any changes in the population dynamics and evolution of life-history traits. For each dispersal scenario, we simulated 100 replicates with a 10-year burn-in period. We ran the simulation using R version 3.6.3 and the package MetaIbasam version 0.0.6. Code and R scripts are freely available at https://github.com/Ibasam/Portfolio.

3.2. Simulations outcomes analysis

3.2.1. Network spatial structure

In our application set up, each population was independently “stable”, i.e., was not growing or declining. Thus, while source-sink populations are commonly determined based on

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demography (growth rate) and immigrants rates, we classified each population as sink, neutral, or source based on the ratio of incoming individuals (immigrants) to outgoing individuals (emigrants) in the sea-adult returns. We considered populations with a ratio above one as *sinks*, those with a ratio below one as *sources*, whereas the *neutral* populations have a ratio near one.

Regardless of the fixed dispersal rate, source-sink dynamics within a network of fifteen populations emerged from the model due to asymmetric dispersal that was driven by differences in population size and spatial structure (Fig. 3 A and B). For example, larger populations generated more emigrants, and more isolated populations received less immigrants but "sent" the same proportion of emigrants. The ratio between immigrants and emigrants was highly variable between populations, as well as the proportion of immigrants, which ranged from 4% to 27% for dispersal rates of 10%. But the source-sink dynamics among populations within the network remained similar between dispersal scenarios or over time (Fig. 3 A).

3.2.2. Demographic consequences of dispersal: population network stability, synchrony, and persistence

For each dispersal scenario and simulation, we measured the stability and diversity of the network using the portfolio effect and synchrony metrics. The portfolio effect (hereafter PE) is a metric measuring the stabilizing effect of population diversity on metapopulation dynamics (Schindler et al. 2010), by comparing the measured metapopulation variance over the time series to the theoretical variance expected if the metapopulation was considered as a unique population. To do so, we used the mean-variance method from the R package *ecofolio* (Anderson et al. 2013). Using this approach, if this ratio equals 1, it means that the network is as stable as expected if it was a single population. If the ratio exceeds 1, it suggests evidence

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of a portfolio effect. For example, a ratio of 1.25 means that the variance of the metapopulation dynamic is reduced by 25% as compared to a scenario where the metapopulation acts as a single population, and so on.

The synchrony index ϕ_x, reflecting the degree of population synchrony in their demographic evolution over time, was measured as the ratio between the detrended network variance σ_x^2 and the squared sum of populations detrended standard deviation σ_{xi} (adapted from Loreau and de Mazancourt 2008, Equation 4). This index is expressed between 0 (asynchrony) and 1 (synchrony).

$$\varphi_x = \frac{\sigma_x^2}{(\sum_i \sigma_{x_i})^2} \quad (4)$$

For each dispersal scenario and simulation, a population's stability was measured through the coefficient of variation of adult returns number over the 40 last years. A population viability analysis was also performed for each scenario. In particular, we evaluated the quasi-extinction risk for each population as the proportion of simulations where the abundance was at least two consecutive years below an "at-risk" threshold (defined as 5% of the population carrying capacity *Rmax*, adjusted in Piou and Prévost 2012, Supporting information 2).

Our analyses revealed a non-linear relationship between dispersal and stability of the population network, resulting in an optimal portfolio effect for dispersal rates around 20%, i.e., 80% of a population returning to its natal site (Fig. 4 A). With strict philopatry (i.e., no dispersal), the PE was on average above 1, meaning that the population network was more stable than expected if it was the sum of the local populations. Indeed, the dynamics of all populations were stable and asynchronous (φ~0.1; Fig. 4 B). Between dispersal rates of 0%

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and 10-20%, the PE was increasing, suggesting a stabilizing effect of low dispersal rates followed by a gradual decline in the PE with dispersal rates above 20%. This declining trend of network stability with high dispersal rates can be explained by the synchronizing effect of dispersal, which counter-balances its initial positive effect. Indeed, we found that the synchrony of population dynamics was increasing linearly with dispersal (+70% from 0 to 50% of dispersal, Fig. 4 B).

At the local population level, dispersal tended to decrease the coefficient of variation of the abundance of adult returns, suggesting a stabilizing effect of dispersal on population dynamics (Fig. 4 C). Dispersal rates also reduced the extinction risk of small and sink populations, whereas the extinction risk of other populations appeared insensitive to dispersal (Fig. 4 D). Altogether, these results suggest a demographic rescue of populations by dispersal, especially for those behaving as sink populations.

3.2.3. Intra- and interpopulation phenotypic and genotypic diversity

Our results showed that dispersal per se can induce phenotypic diversity between populations. Indeed, we observed a slight decrease of median juvenile and adult size with dispersal for sink populations and an increase in source populations, which might have consequences on life-history tactics illustrated by shifts in the age at sea maturation (Fig. 5, A, B, D). Note that we assessed phenotypic changes on philopatric individuals only, to test the consequences of dispersal on each population's trait distribution without the direct influence of immigrants. As immigrants do not differ from philopatric adults in terms of size and growth potential at initialization, this unexpected result could be explained by density-dependent effects on river growth. Indeed, dispersal increased juveniles density in sink populations (due to higher

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immigration than emigration) and decreased it in source ones (Supporting information 4), affecting juvenile growth and adult life history traits as a consequence. This effect was less visible when considering phenotypic traits of all individuals (philopatric adults and immigrants) of populations (Supporting information 5).

As expected due to similar genetic distribution parameters at initialization between populations, no interpopulation genotypic diversity emerged with dispersal (Fig. 5 C). However, dispersal rates rapidly increased intrapopulation genetic variance in sink populations (Fig. 6).

4. DISCUSSION

We aimed to draw attention to the consequences of dispersal on the portfolio effect and eco-evolutionary dynamics of Atlantic salmon. To do so, we extended a demo-genetic agent-based model (IBASAM, Piou and Prévost 2012) into a metapopulation framework by integrating a dispersal process to simulate a set of fifteen interconnected populations of Atlantic salmon (MetaIBASAM). MetaIBASAM is freely available and can be modified to mimic various networks of Atlantic salmon populations and their demo-genetic characteristics. Although similar models exist (see Table 1), whether generic or applied to salmonid species, our model was designed to reproduce the life cycle of Atlantic salmon by integrating the knowledge available on this species. Moreover, it has been calibrated on one of the populations constituting the network of populations in Brittany. In particular, we used a simple but realistic spatial network to explore the influence of dispersal on stability and rescue effects. Our model induced a source-sink dynamic, though all populations showed stable dynamics. Despite this parsimonious design (populations only differ in their size and distance between each pair), we

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showed that dispersal rates from 10% to 50% can have significant consequences on persistence (at both local and metapopulation levels), stability, phenotypic and genetic features. Below we expand on these results and also highlight the potential of demo-genetic ABMs (such as MetaIBASAM focused on Atlantic salmon) to identify knowledge gaps and investigate dispersal, adaptive capacity, and responses of metapopulations to environmental change and management practices.

Evidence of a non-linear relationship between dispersal and portfolio effect: stabilizing *vs* synchronizing effects of dispersal

Our study emphasizes a non-linear relationship between dispersal rates and the stability of the metapopulation, resulting in an optimal portfolio effect for dispersal rates around 20% with the particular parameterization of our model. Using a network of two populations, Yeakel et al. (2018) also found non-linear effects of dispersal on metapopulation robustness (PE) and identified two optimums (strongest PE, called alternative stable state regimes in their paper) at levels of dispersal below 10% and 30% of the population respectively. Interestingly, the optimal dispersal rate that we report is consistent with the few empirical studies reporting dispersal rates in Atlantic salmon (Jonsson et al. 2003, Jonsson and Jonsson 1991, 2017, Keefer and Caudill 2014). However, it is important to note that it might depend on the adjustment of the dispersal kernel parameter and reported rates in the literature are highly variable and likely biased (e.g., site/year dependence, low sample size, hatchery influence; Jonsson et al. 2003, Consuegra et al. 2005, Jonsson and Jonsson 2017, Keefer and Caudill 2014). When the dispersal rate was below 20% in our model, dispersal had a stabilizing effect on population dynamics and fostered the demographic rescue of small, sink populations by increasing population size and/or limiting demographic stochasticity. Using a theoretical two-patch

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metapopulation model, Hill et al. (2002) also demonstrated that dispersal rates between 0% and 20% increased the time before extinction two-to four-fold, and a recent Population Viability Analysis revealed the benefit of population connectivity for persistence of diadromous fishes more generally under high productivity scenarios (Bowlby and Gibson 2020). However, we found that the positive effects of dispersal on metapopulation stability are overcome by increased synchronization of population dynamics with higher dispersal rates (>20%), which could increase the metapopulation risk of collapse (Carlson and Satterthwaite 2011). The "anti-rescue" effects (Harding and McNamara 2002) associated with higher dispersal rates have been demonstrated both theoretically and empirically on patterns of synchrony (Paradis et al. 1999, Yeakel et al. 2018), but also on genetic homogenization (Tinnert and Forsman 2017), and reduced local adaptation (Schiffers et al. 2013).

The parsimonious configuration we simulated, using phenotypically and genetically homogeneous populations, did not allow us to fully consider the homogenizing effect of dispersal. But introducing more variability between populations in their demographic dynamics (e.g., unstable trends) or in their phenotypic and genotypic composition would open up new perspectives to better address the portfolio effect. However, we found that intrapopulation genetic variance was enhanced in sink populations receiving immigrants from nearby populations, potentially increasing adaptive capacity (Jump et al. 2009, Seaborn et al. 2021). In our study, populations did not show inbreeding depression, but one can assume that dispersal might reduce it through genetic rescue. More surprisingly, interpopulation phenotypic diversity also emerged from the dispersal process. Indeed, the asymmetric flows between source and sink populations within the network induced phenotypic changes via density-dependent effects on the growth of individuals rearing in the river, ultimately influencing their life-history strategies (e.g., age at maturation) through phenotypic plasticity. Altogether, we show that there

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may be a dispersal optimum at the metapopulation level that favors its stability (i.e., portfolio effect), and selection should favor local dispersal rates (within populations) that tend towards this metapopulation optimum. Thus, metapopulation optimum value would depend on species characteristics (e.g., propensity to disperse), spatial configuration (e.g., distance between populations), but also local population features (e.g., population size, density, environmental conditions, attractiveness, local adaptation, costs of migration, etc.).

Model significance, limits, and perspectives

Like any modeling study, our results are influenced by the model structure (functional relationships, parameterization, etc.) and hypotheses retained in MetaIBASAM. However, our study showcases the utility of agent-based models as virtual laboratories for exploring the possible consequences of poorly understood processes and mechanisms on eco-evolutionary dynamics, in particular dispersal which is difficult to study in the wild. Here, we used MetaIBASAM to demonstrate the implications of dispersal on the persistence and dynamics of a network of Atlantic salmon populations. Although it was not our intention to represent the dynamics of a particular Atlantic salmon metapopulation, the network modelled here was realistic both in its complex spatial scale and structure. This provided a unique source-sink metapopulation with a diversity of local dynamics, showing variable consequences of dispersal on local populations depending on their spatial distribution and demographic features. Additionally, by its integrative nature, our modeling approach took into account all eco-evolutionary processes involved and allowed the emergence of non-trivial patterns because of complex interactions between these processes. Overall, our approach emphasizes the importance of assessing the demographic, phenotypic, and genetic consequences of dispersal in metapopulations in a single framework.

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However, despite the model complexity, some processes are still represented in an overly simplified manner, especially the *causes* of dispersal. Like other models focused on salmonids (see Table 1), we simulated dispersal as a random individual process, with a probability of dispersing that was constant in space and time, and limited to a fixed expansion range. Yet, it has been shown in several species and also suggested for salmonids that dispersal depends on individuals traits (e.g., sex-biased dispersal, Li and Kokko 2019, genetic basis, Saastamoinen et al. 2018) or populations characteristics (e.g., density-dependent dispersal, Berdahl et al. 2016). These features might modify the intensity and direction of flow of individuals and the consequences of our dispersal scenarios, because dispersal could evolve towards dispersal rates which optimize the portfolio effect. For example, Berdahl et al. (2015) tested a model including joint evolution of dispersal and local adaptation and showed that dispersal should evolve towards lower values in the context of heterogeneous populations environments. Additionally, we did not represent explicitly the consequences (e.g., costs) of dispersal, such as additional mortality or reduced reproductive success (Mobley et al. 2019). However, this is limited by the lack of knowledge on processes and mechanisms of dispersal in salmonids (but see Jonsson et al. 2003 for Atlantic salmon and Bett et al. 2017 for Pacific salmon). Thus, there is considerable room for improvement in our model, and below we highlight some potential research avenues and ideas that could be addressed by MetaIBASAM and any other demo-genetic ABM of salmonid metapopulation, based on burgeoning theoretical and empirical research on causes and implications of dispersal.

1/ *We need more studies to understand dispersal mechanisms and their consequences on eco-evolutionary dynamics of metapopulations*.

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Along with additional work estimating dispersal rates between wild populations, empirical studies focusing on individual and population factors influencing dispersal are needed to better appreciate the causes and consequences of dispersal in salmonids. Increasing attention focuses on the three distinct phases of dispersal (emigration, transfer, and settlement, Bonte et al. 2012), and theoretical models are starting to explicitly include phases of dispersal since it may strongly influence patterns of dispersal (e.g., Travis et al. 2012, Bocedi et al. 2014). However, identification of these three phases and knowledge of the underlying mechanisms are still limited in salmonids. By integrating these mechanisms (e.g., condition and density-dependence, genetic basis) in our model, we could expect dispersal rates to vary in space (between populations) and time. This could sharpen our results on the relationship between dispersal and metapopulation stability.

2/ *We need to evaluate how diversity between and within populations may shape an adaptation network fostering response to environmental changes.*

Our study focused on the consequences of dispersal scenarios to shed light on the influence of connectivity alone on eco-evolutionary processes. However, adaptation network theory (Webster et al. 2017, Fig. 7) states that the resilience of ecological systems, such as metapopulation, relies on the connectivity as well as response diversity of its components (Elmqvist et al. 2003). Recent theoretical studies of coral reefs have emphasized that population diversity is beneficial for metapopulation persistence and stability in the context of a changing and uncertain climate (Walsworth et al. 2019, McManus et al. 2021a). Moreover, among population variability in thermal tolerance (e.g., Eliason et al. 2011, McKenzie et al. 2021) could increase species resistance to climate change especially if associated with dispersal (fostering evolutionary rescue). Evaluating the adaptation network theory in this context should

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provide information on the ability of metapopulations with variable degrees of diversity to persist under various projected climate scenarios (Fig. 7).

3/ *We need to assess the interplay between diversity and dispersal by considering spatial structure and local adaptation.*

Dispersal and diversity are key processes influencing metapopulation functioning and persistence and previous studies have highlighted the importance of potential interactions between the two (Berdahl et al. 2015, Fig. 7). For example, considerable research has focused on gene flow impeding local adaptation (Moore et al. 2013). The strength of gene flow may vary with the intensity of dispersal (Garant et al. 2007) and the reproductive success of immigrants (Mobley et al. 2019). Interestingly, several recent theoretical studies focused on this interplay between diversity and dispersal (e.g., Tomasini and Peischl 2020, McManus et al. 2021b) but often on two patch population models or metapopulations with constant spatial structure (e.g., Tomasini and Peischl 2020). Another line of work has recently identified the spatial configuration of the metapopulation as a major component of metapopulation demographic and evolutionary dynamics (Papaïx et al. 2013, Bonte and Bafort 2019), suggesting a need to explore the consequences of the interplay between diversity and dispersal under different spatial configurations. It is very likely that different spatial structures and patterns of local adaptation in Atlantic salmon metapopulations may lead to different evolutionary and population dynamics given the amplitude and characteristics of immigrants (e.g., adapted populations can become maladapted and vice versa).

4/ *We need to consider the implications of spatially structured populations for management.*

Our results highlight the importance of interpreting the dynamics of local populations and defining management strategies by considering the potential connectivity between populations.

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Prior work has warned about the danger of ignoring spatial structure and connectivity of populations (Cooper and Mangel 1999), but few studies have compared different management strategies while also considering the spatial structure of populations (but see Tufto and Hindar 2003, Moore et al. 2021). While mixed-stock fisheries explicitly consider variation in productivity among harvested stocks, rarely is connectivity considered. Our preliminary results suggest that any alteration in a source population could affect demography and phenotypic traits of surrounding populations. Moreover, selective exploitation within spatially structured populations could drive complex evolutionary trajectories in the whole network – whether local populations are exploited or not - because selective exploitation can induce evolution of life history traits (Piou et al. 2015, Ayllón et al. 2018).

Conclusions

In summary, we have introduced a metapopulation version of IBASAM, MetaIBASAM, a demo-genetic agent based model of Atlantic salmon populations, which we believe provides a useful and flexible framework to fill knowledge gaps about the role of dispersal in Atlantic salmon metapopulation eco-evolutionary dynamics and portfolio strength. We highlight the importance of dispersal for metapopulation stability and evolutionary pathways. Additionally, we discuss ideas for future directions using the model to explore responses of interconnected Atlantic salmon populations to environmental change and spatially structured management. Finally, we advocate for a management of populations within the adaptation network framework (Webster et al. 2017, Fig. 7) because maintaining diversity and evolutionary options within a network of populations is a critical step for fostering species persistence and stability in the face of environmental change (Walsworth et al. 2019).

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COMPETING INTERESTS STATEMENT

The authors declare there are no competing interests.

AUTHORS' CONTRIBUTIONS STATEMENT

AL: conceptualization, methodology, formal analysis, writing (original draft, review and editing), MB: conceptualization, methodology, writing (review and editing), SMC: conceptualization, writing (review and editing), FH: methodology, CP: methodology, JP: methodology, EP: methodology.

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DATA AVAILABILITY STATEMENT

Modelling code and R scripts are freely available at https://github.com/Ibasam/Portfolio. Adult abundance and size data from the Scorff population used for model calibration have been

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obtained via the ORE-DiaPFC observatory and can be accessible on https://github.com/ORE-DiaPFC/Abondance/tree/master/Scorff, and on demand, respectively.

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Table 1: Comparison between MetaIBASAM and existing modeling frameworks to explore metapopulation dynamics of salmonids (generic models also included). SS=spatial structure; Em=emigration; Im=immigration.

References	Model type	Species	Dispersal/Connectivity	Eco-evolutionary dynamics	Key mechanistic processes
Bowlby and Gibson 2020, Fullerton et al. 2011	Population dynamics models, graph theory	Salmonids	-Explicit SS: multiple populations, size and distance -Em: fixed emigration rate -Im: distance dispersal kernel	No	No
Berdahl et al. 2015, Yeakel et al. 2018	Analytical model/adaptive dynamics, quantitative genetic model	Generic, Salmonids	-Not explicit SS/ two populations -Em: inherited probability/density-independent or dependent -Im: random destination	-Inherited ecological trait -Fitness: mismatch trait-site optimum (fixed)	No
Guillaume and Rougemont 2006, Rebaudo et al. 2013, Bocedi et al. 2014, Schiffers and Travis 2014, Landguth et al. 2017	Demo-genetic agent-based model of metapopulation (Nemo, SimAdapt, RangeShifter, ALADYN, CDMetaPOP)	Generic	-SS: grid landscape -Em: fixed emigration rate/density-dependent/individual trait -Im: random destination among nearest/distance dispersal kernel	-Multi locus system -Spatially explicit fitness for each genotype (fixed)	Simple life cycle
Landguth et al. 2017	Demo-genetic agent-based model of metapopulation (CDMetaPOP)	Brook trout	-SS: grid landscape -Em: fixed emigration rate -Im: distance dispersal kernel	-Multi locus system -Spatially explicit fitness for each genotype (fixed)	-Growth ~ temperature -Survival ~ patch fitness, density -Maturation ~ size -Sexual selection
Lin et al. 2017	Demo-genetic agent-based model of two populations (extension from Bromaghin et al. 2011)	Sockeye salmon	-SS: two populations -Em: fixed emigration rate	-Multivariate quantitative genetic model -Fitness: mismatch trait-site optimum (fixed)	-No growth: inherited length, age at maturation -Survival ~ density, phenotype -Sexual selection
MetaIBASAM	Demo-genetic agent-based model of metapopulation	Atlantic salmon	-SS: multiple populations, size and distance -Em: fixed emigration rate	-Bi-allelic multi locus system	-Growth ~ temperature, flow, density, growth potential

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	(extension from IBASAM, Piou and Prévost 2012).	-Im: dispersal kernel (distance and attractivity)	-Emerging fitness from fitness-related traits	-Survival ~ temperature, flow, density, growth potential, size -Maturation (precocious and at sea) ~ energetic reserves and genetic thresholds -Size dependent migration -Sexual selection

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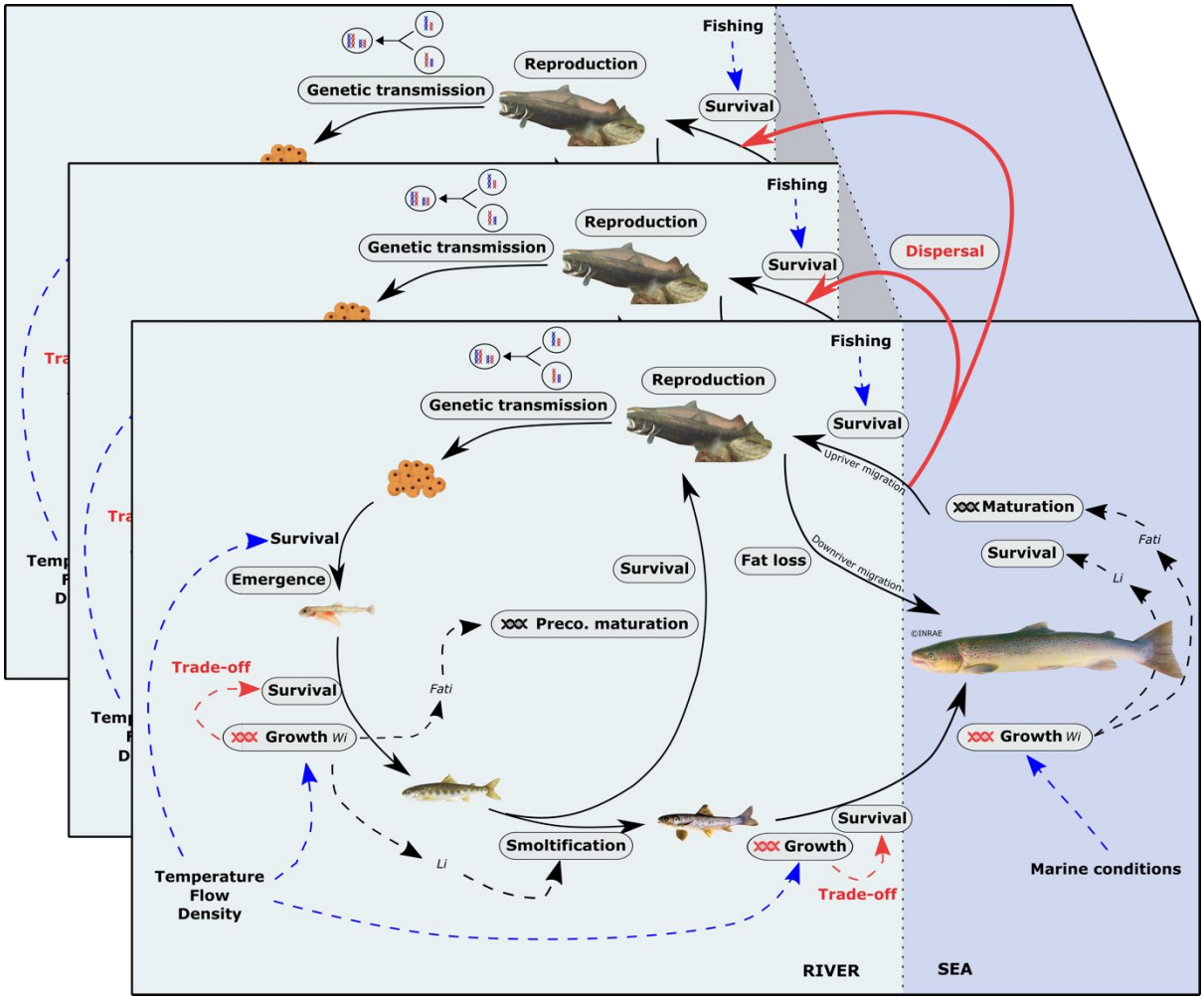

Fig. 1: Conceptual framework of the MetaIBASAM model, adapted from Piou and Prévost 2012. Processes at individual levels are highlighted in grey, where the DNA icon indicates heritable traits linked to these processes (maturation thresholds and growth potential). The dashed arrows represent the influence of both environmental and anthropogenic factors (in blue), or the influence of state variables of individuals (in italics). New additions from IBASAM, the dispersal process, growth potential heritability and growth-survival trade-off, are identified in red. Each big rectangle represents a population, exchanging individuals with neighboring populations via dispersal.

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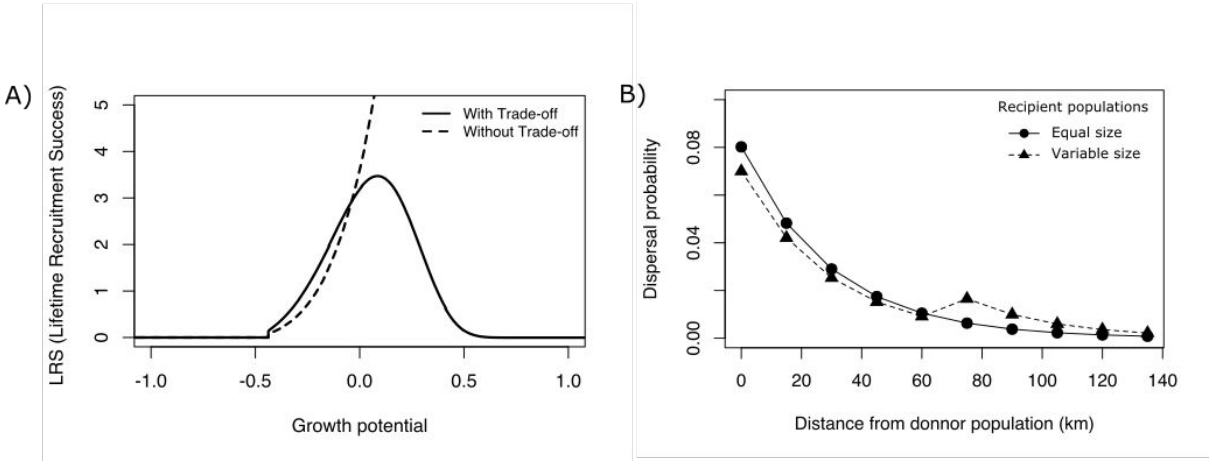

Fig. 2: Additions into MetaIBASAM from IBASAM. In A), theoretical optimal value of phenotypic growth potential (in log scale) based on mean individual Lifetime Recruitment Success (measured as the mean egg number per female; see processes details in Supporting information 1) with (fill) and without (dashed) the implemented growth-survival trade-off. In B), dispersal kernel representing the probability to disperse, for a total dispersal rate of 20%, from one donor population to ten others populations as function of their distance (in km) and their relative size. In circles and fill line, all populations present the same size; in triangles and dashed line, the five first are three times smaller than the five last populations.

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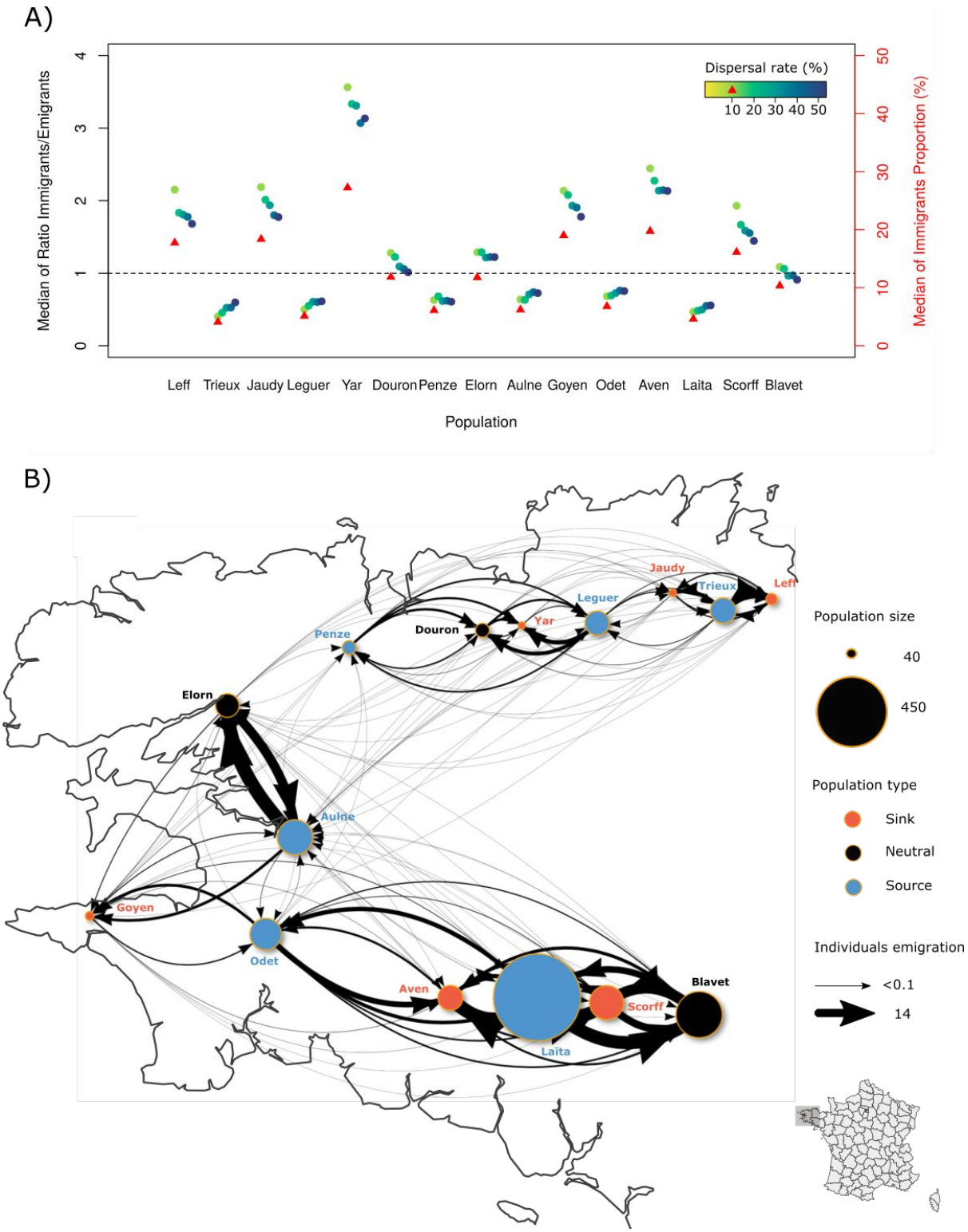

Fig. 3: A) In points, median over simulations of the ratio between immigrants and emigrants number of the 5 last years for each population and dispersal scenario. In red triangle, median over simulations of the proportion of immigrants of the 5 last years for each population at 10% of dispersal rate. B) Visualisation of the network emerging from MetaIBASAM simulations

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with dispersal rates of 10%. Circles represent the populations (with the size function of the median 5 last years population size, and color function of population type) and arrows the emigration of individuals (with the width function of the median 5 last years emigrants number) along the shorelines. The base map of Brittany shoreline comes from a French Government open data base (https://www.data.gouv.fr) with a RGF93 map projection.

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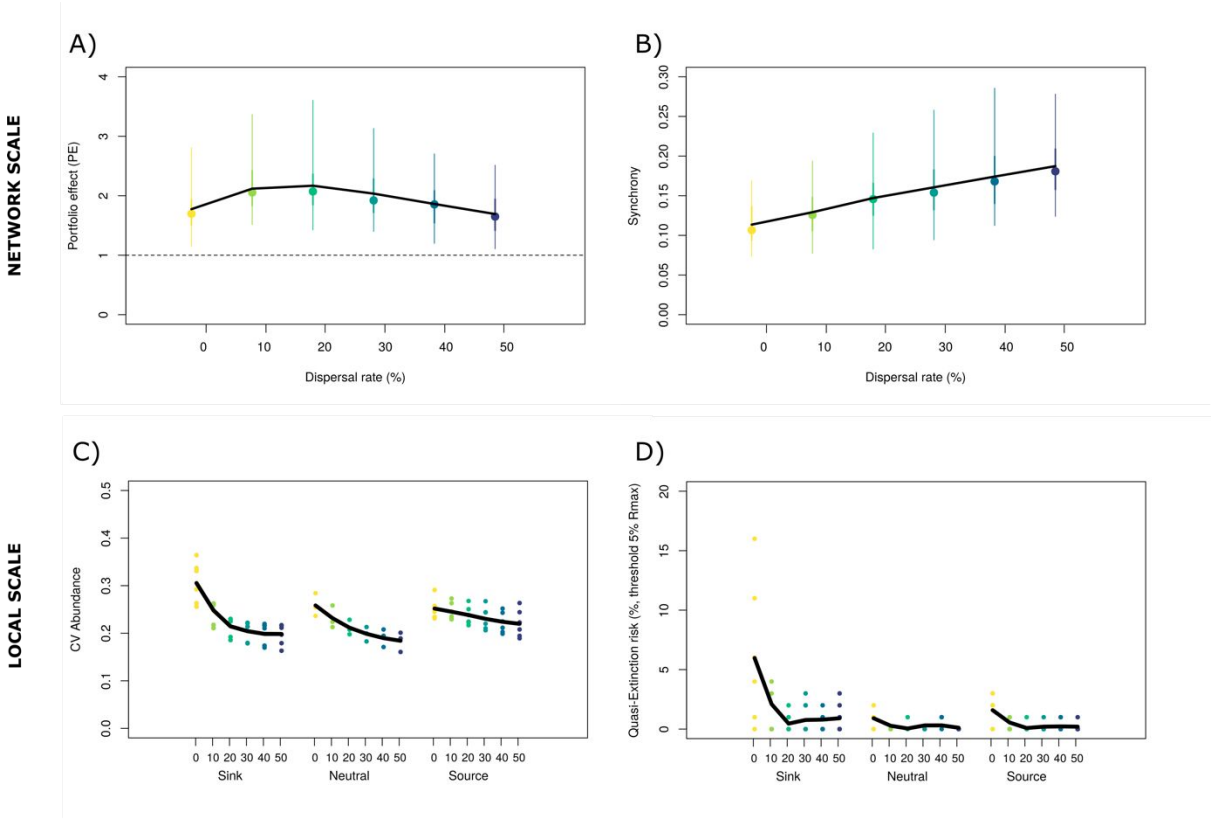

Fig. 4: Distribution (median, 95% confidence interval) over simulations of the detrended metapopulation PE (A) and synchrony (B) metrics for each scenario of dispersal. Median over simulations of local populations CV of detrended returns abundance (C) and quasi extinction risk (D) for each scenario of dispersal. Each point is a population, categorized by its type (sink/source/neutral) and a local regression is added to represent the evolution of population stability (C) and persistence (D) as a function of dispersal rates for each category of populations (sink/source/neutral).

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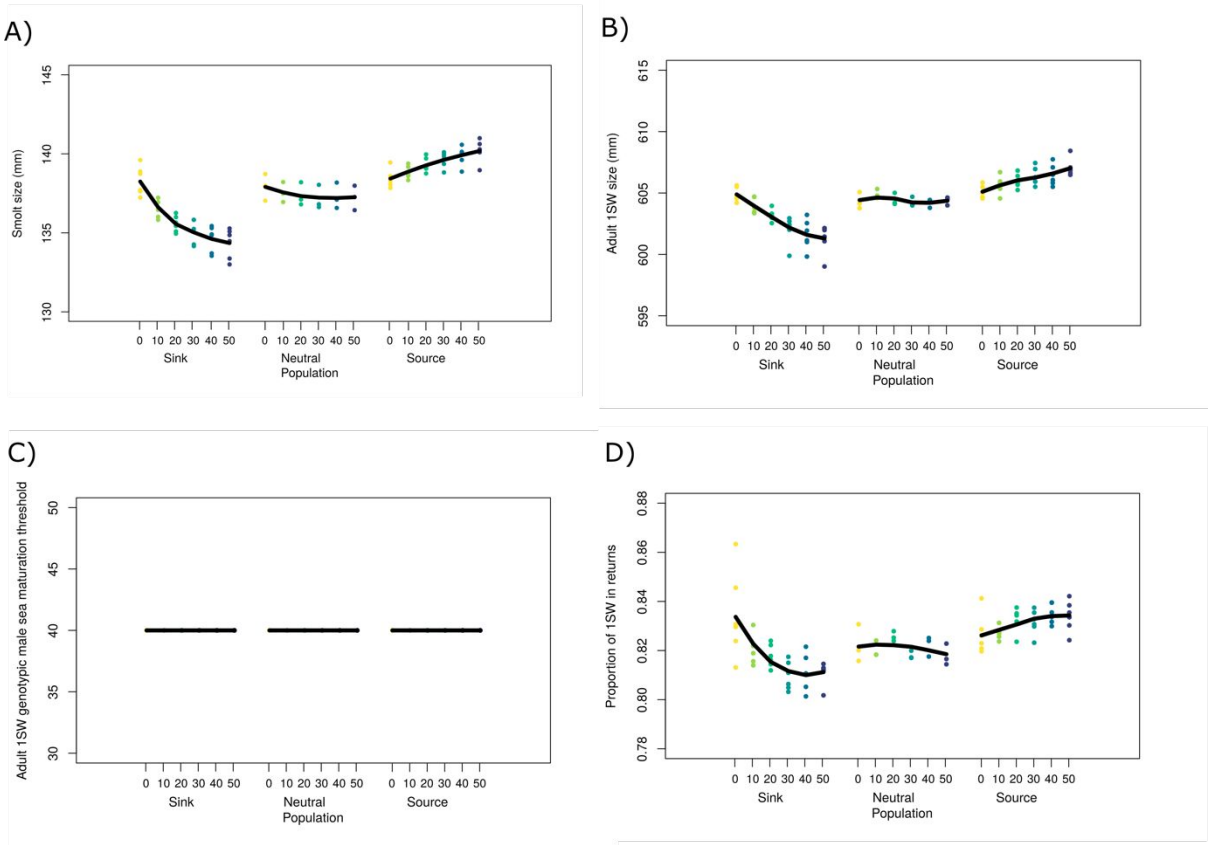

Fig. 5: Median over simulations of populations last 5 years median smolt size (A), philopatric adult 1SW size (B), philopatric adult 1SW genotypic value of male sea maturation threshold (C), and proportion of 1SW in philopatric adult returns (D) for each scenario of dispersal. Each point is a population, categorized by its type (sink/source/neutral), and a local regression is added to represent a global trend as a function of dispersal rates and category of populations (sink/source/neutral).

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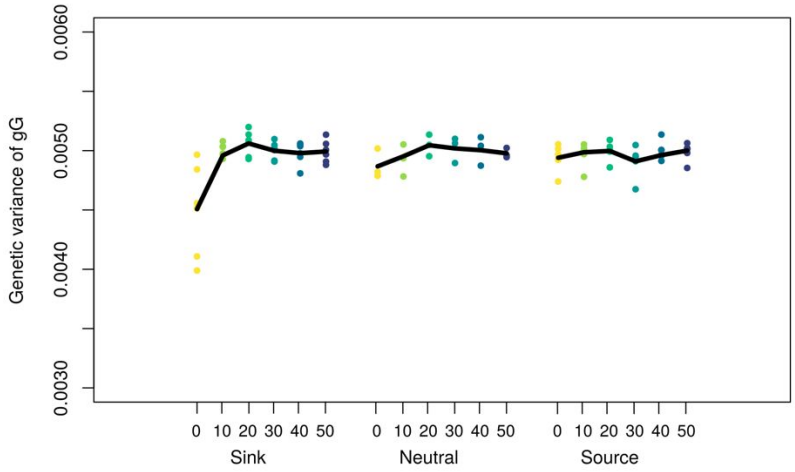

Fig. 6: Median over simulations of populations last 5 years genetic variance (of philopatric 1SW genotypic growth potential), for each scenario of dispersal. Each point is a population, categorized by its type (sink/source/neutral), and a local regression is added to represent a global trend as a function of dispersal rates and category of populations (sink/source/neutral).

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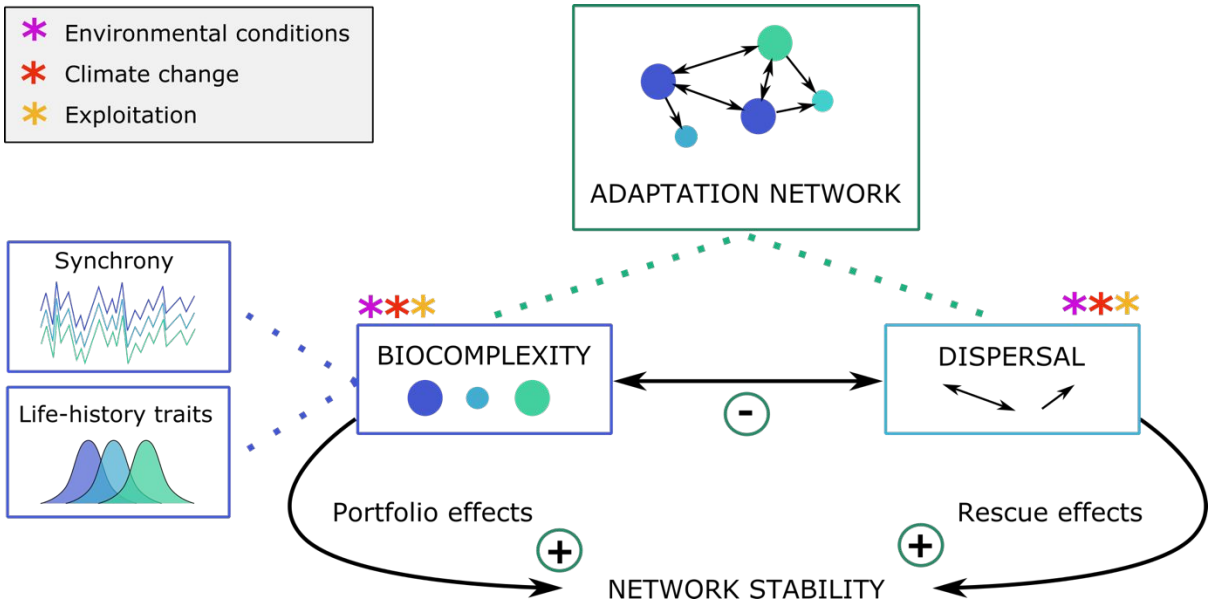

Fig. 7: Theoretical framework of the adaptation network theory. Both biocomplexity (e.g. trait diversity, populations synchrony) and dispersal can foster network stability through portfolio and rescue effects. The homogenizing effect of dispersal and divergent effect of local adaptation on populations can also induce negative feedbacks between biocomplexity and dispersal. Examples of promising future directions with MetaIBASAM are identified by asterisks. In particular, how various environmental conditions, climate change, and exploitation management affect network stability are questions that could be addressed in this framework.

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