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CONSEQUENCES OF DISPERSAL ON ATLANTIC SALMON METAPOPULATION PERSISTENCE AND DYNAMICS OF LOCAL POPULATIONS

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ABSTRACT

Spatial dispersal is a ubiquitous trait in organisms. It is central in the theory of metapopulations, with potential consequences on their stability and persistence, as well as on local population dynamics. Although dispersal and metapopulation functioning have been suggested for salmonid, the consequences of dispersal are still underappreciated, likely because assessing dispersal in nature is challenging. We used a demo-genetic individual-based model mimicking an Atlantic salmon metapopulation connected by a distance dispersal kernel. Our model depicts a complex relationship between dispersal and the metapopulation portfolio effect. In particular, we show that low dispersal rates favor metapopulation stability, via the demographic rescue of small populations and stabilizing effects of dispersal. However, higher dispersal rates tend to synchronize populations, leading to anti-rescue effects. We also show density-dependent effects of dispersal on local populations, especially in sink ones, with consequences on life-history strategies and especially age at maturation, mainly via phenotypic plasticity. Altogether, we suggest that the spatial structure of Atlantic salmon populations should be considered in management and conservation strategies because the dynamics of local populations rely on the whole metapopulation functioning via spatial dispersal.

Keywords: dispersal, metapopulation, persistence, local population dynamics, Atlantic salmon, individual-based model

RÉSUMÉ

La dispersion spatiale est un trait très répandu chez les organismes. La dispersion est une notion centrale dans la théorie des metapopulations, avec de potentielles conséquences sur leur stabilité et leur persistance, ainsi que sur les dynamiques de population locale. Bien que la dispersion et qu'un fonctionnement en métapopulation aient été suggérés chez les salmonidés, les conséquences de la dispersion sont encore sous-estimées, probablement car mesurer la dispersion en milieu naturel est difficile. Nous avons utilisé un modèle démo-génétique individu-centré qui mime une métapopulation de saumon Atlantique connectée par un kernel de dispersion par la distance. Notre modèle décrit une relation complexe entre la dispersion et l'effet portfolio de métapopulation. En particulier, nous montrons que de

faibles taux de dispersion favorisent la stabilité de la métapopulation, via le sauvetage démographique des petites populations et les effets stabilisants de la dispersion. Cependant, de forts taux de dispersion tendent à synchroniser les populations, réduisant la stabilité de la métapopulation. Nous montrons également des effets densité-dépendants dans les populations locales, notamment chez les puits, avec des conséquences sur les stratégies d'histoire de vie et en particulier l'âge à la maturation, par plasticité phénotypique essentiellement. Finalement, nous suggérons que la structure spatiale des populations de saumon Atlantique devrait être considérée dans les stratégies de gestion et de conservation, car les dynamiques des populations locales dépendent du fonctionnement de la métapopulation dans son ensemble, à travers la dispersion spatiale.

Mots-clés: dispersion, métapopulation, persistance, dynamiques de population locale, saumon Atlantique, modèle individu-centré

RESUMEN

La dispersión espacial es un rasgo ubicuo en los organismos. Es central en la teoría de las metapoblaciones, con posibles consecuencias sobre su estabilidad y persistencia, así como sobre la dinámica de la población local. Aunque la dispersión y el funcionamiento de la metapoblación se han sugerido para los salmónidos, las consecuencias de la dispersión siguen siendo subestimadas, probablemente porque evaluar la dispersión en la naturaleza es difícil. Usamos un modelo demo-genético individual-centrado imitando una metapoblación de salmón atlántico conectada por un kernel de dispersión por distancia. Nuestro modelo representa una relación compleja entre la dispersión y el efecto portfolio de metapoblación. En particular, demostramos que las bajas tasas de dispersión favorecen la estabilidad de la metapoblación, a través del rescate demográfico de poblaciones pequeñas y los efectos estabilizadores de la dispersión. Sin embargo, las tasas de dispersión más altas tienden a sincronizar las poblaciones, llevando a efectos anti-rescate. También mostramos los efectos densidad-dependientes de la dispersión en las poblaciones locales, especialmente en los sumideros, con consecuencias sobre las estrategias de la vida-historia y especialmente la edad en la maduración, principalmente a través de la plasticidad fenotípica. Finalmente, sugerimos que la estructura espacial de las poblaciones de salmón del Atlántico se tenga en cuenta en

las estrategias de gestión y conservación porque la dinámica de las poblaciones locales se basa en el funcionamiento de toda la metapoblación, a través de la dispersión spatial.

Palabras claves: dispersión, metapoblación, persistencia, dinámica de población local, salmón del Atlántico, modelo individual-centrado

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INTRODUCTION

Understanding the drivers of ecological stability is needed to better appreciate the response of populations to environmental changes and define sustainable management practices that favor their conservation and resilience. The resilience of species to environmental changes is strongly related to their capacity of adaptation via eco-evolutionary processes (Reed et al., 2011). Eco-evolutionary processes include the processes of acclimatization (phenotypic plasticity) and genetically based evolution through natural selection (genetic adaptation; Brandon, 2014; Ghalambor et al., 2007). Dispersal, whether spatial or temporal, can also favor species responses to environmental changes by spreading the risk of reproductive failure (Buoro and Carlson, 2014).

Spatial dispersal between populations (hereafter dispersal) is the movement of individuals between their place of birth and where they will reproduce, with potential consequences for gene flow (Nathan et al., 2012; Ronce, 2007). While dispersal is a ubiquitous trait in nature (Clobert et al., 2012), its strength depends on species ability to disperse and on landscape permeability (Schtickzelle et al., 2006). Dispersal occurs at the individual scale and has several benefits and costs for both individuals and populations. For example, dispersal allows avoidance of competition and inbreeding, colonization of new habitats, but it also comes with costs such as an increased risk of predation and a lower fitness in the recipient environment because of local adaptation (Baguette et al., 2013; Bonte et al., 2012; Keefer and Caudill, 2014). Dispersal is characterized by three stages - emigration, transfer, and immigration – all of which can be influenced by individual phenotypic condition (e.g. size, Anholt, 1990; sex, Li and Kokko, 2018), environmental factors (e.g. kin competition, Moore et al., 2006), and social interactions, as well as their interactions (condition and context-dependent dispersal; Bitume et al., 2013; Clobert et al., 2009; Fronhofer et al., 2018; Matthysen, 2012). It is also very likely that the tendency to disperse can have a genetic basis (Saastamoinen et al., 2018). Indeed, dispersal propensity can also be under selection to reduce its costs, maximize individual fitness and favor species persistence in the long-term (bet-hedging theory; Buoro and Carlson, 2014; Ronce, 2007).

Dispersal is central to the theory of metapopulations because it favors the flow of individuals among inter-connected populations with consequences for metapopulation

stability, and local population dynamics and persistence (Benton and Bowler, 2012; Harding and McNamara, 2002). Metapopulations were defined as populations of sub-populations (hereafter, local populations) with a continuous process of local extinction and colonization (Levins, 1969), and with an influence of population size and isolation on their turnover rate (Hanski, 1998). Several types of metapopulations have been described, such as the mainland-island or the source-sink metapopulations, with some highly productive source populations giving individuals to low productivity sink populations (Dias, 1996). Through the colonization of new habitats, dispersal decreases the extinction risk of a metapopulation (Ebenhard, 1991), reduces the risk of local population extirpation, in particular for small populations, and favors their persistence to environmental changes via rescue effects. Three types of rescue have been identified (see Carlson et al., 2014 for review): demographic rescue (i.e. input of individuals from other populations; Brown and Kodric-Brown, 1977), genetic rescue (i.e. genes flow that reduces inbreeding and deleterious allele's fixation; Keller and Waller, 2002) and the evolutionary rescue (i.e. introduction of individuals with heritable adaptive alleles in a context of maladaptive environmental change; Bell and Gonzalez, 2011; Gonzalez et al., 2013). However, there is still few empirical evidence of these processes of rescue.

The stability and persistence of metapopulations are also favored by the diversity of local populations' responses to environmental changes, also called "biocomplexity", which generates asynchrony among local populations. Indeed, divergent natural selection due to spatial variation in the environment gives rise to adaptive divergence in traits and life history across local populations (Hilborn et al., 2003), which sets the stage for portfolio effects (Schindler et al., 2015, 2010). The portfolio effect describes how the diversity within and between populations increases the stability of the metapopulation (Anderson et al., 2013). For instance, the asynchrony among fish populations (i.e. the diversity of demographic temporal fluctuations) stabilizes the total fishery yield (Hilborn et al., 2003; Schindler et al., 2010). Within populations, the asynchronous responses of individuals to environmental variation could reduce the variability in population growth rates and abundance, and thus reduce the probability of local extirpation (Abbott et al., 2017; Bolnick et al., 2011) and increase metapopulation persistence. The portfolio effect is therefore closely related to the positive relationship between diversity and stability.

However, the diversity of populations maintained by metapopulation functioning and the stability of the metapopulation can also be altered by dispersal. Indeed, dispersal might synchronize the dynamics of local populations, resulting in the correlation of temporal fluctuations in population density between localities with potential negative consequences on the persistence of metapopulations (Carlson and Satterthwaite, 2011; Kendall et al., 2000; Liebhold et al., 2004; Paradis et al., 1999). Moreover, dispersal and gene flow might reduce the local adaptation and the mean fitness of the recipient populations via the introduction of maladapted individuals into habitats with particular environmental conditions (Ronce and Kirkpatrick, 2001; Schiffers et al., 2013). Additionally, theoretical approach and few empirical studies show that gene flow has a homogenizing effect which reduces genetic differentiation between populations (Lenormand, 2002; Settepani et al., 2014; Tinnert and Forsman, 2017). Thus, dispersal could lead to a potential reduction of the biocomplexity and diversity of responses to environmental changes within the metapopulation. However, this homogenizing effect of dispersal is still controverted (Jacob et al., 2015). Altogether, these "detrimental" effects of dispersal can affect metapopulation stability and persistence, leading to "anti-rescue" effects (Harding and McNamara, 2002).

By providing immigrants to or emigrants from local populations, dispersal may also impact local population dynamics, potentially inducing demographic, phenotypic, and genotypic changes. Besides changes in gene frequency because of the direct input of immigrants' genotypes (Barton, 1992), dispersal can induce phenotypic and genotypic changes in the recipient populations via density-dependent effects. The effect of the movement of individuals on population size, density, and consequences for life histories of individuals, in both the donor and the recipient habitats, is briefly mentioned in Benton and Bowler (2012). They suggest that emigration from a population could free some resources in these populations because access to resources is density-dependent (Keeley, 2001), while the rising density from immigration into the recipient populations would affect phenotypes such as growth rate due to density-dependent effects. In fact, many biological and ecological processes are density-dependent, such as survival (Frederiksen and Bregnballe, 2000), reproduction (Wauters and Lens, 1995), growth (Pacoureau et al., 2017), and even natural selection (Clutton-Brock et al., 1997), and all of these factors can influence the dynamics of populations.

Salmonid fishes represent an excellent system for exploring the influence of dispersal on metapopulation and local population dynamics. Indeed, salmonids species should be considered in a metapopulation perspective (Garant et al., 2000; Rieman and Dunham, 2000), since the three conditions defined by Schtickzelle and Quinn (2007) are filled: the spawning habitat is discrete, there is asynchrony between the dynamics of local populations, and there are evidences of dispersal (Keefer and Caudill, 2014). However, the consequences of dispersal remain overlooked in salmonids despite evidences of various dispersal strategies across species (Schtickzelle and Quinn, 2007). Within the salmonids, Atlantic salmon (*Salmo salar*) is often presented as an emblematic example of a philopatric species, while the somewhat pejorative term "strayers" is often used to describe individuals that disperse among populations (for salmonids, Schtickzelle and Quinn, 2007; for Atlantic salmon, Consuegra et al., 2005). Yet, genetic analyses demonstrated the existence of strong gene flow between populations suggesting a metapopulation functioning (e.g. Consuegra et al., 2005; Consuegra and García de Leániz, 2006; Perrier et al., 2011). However, such genetic analyses do not provide evidence of contemporary dispersal. The few attempts to measure dispersal rates in nature using capture-mark-recapture programs reported dispersal rates around 6%-10% on average (Jonsson et al., 2003; Kuparinen et al., 2010). It is important to note, however, that such estimates are often affected by observational bias (e.g. not all potential recipient populations are monitored, spatial heterogeneity in capture effort, etc.) and do not reflect the effective dispersal (reproductive success of dispersers). Moreover, spatio-temporal variation in dispersal propensity should be expected (for spatial, Kuparinen et al., 2010; for temporal, Jonsson et al., 2003). The natural colonization of rivers also provides empirical evidence of long-distance dispersal in Atlantic salmon (Perrier et al., 2009). The difficulty to assess dispersal in the wild might explain why the metapopulation context of this species is still poorly appreciated as for other salmonids (Birnie-Gauvin et al., 2019), and why the consequences for the dynamics of local populations, their persistence as well as their conservation and management practices are ignored (Schtickzelle and Quinn, 2007).

Because exploring the causes and consequences of dispersal is difficult in nature, powerful and flexible modeling approaches such as Individual-Based Models (IBMs) seem relevant as a virtual laboratory (Zurell et al., 2010). This approach provides an opportunity to mimic the long-term evolution of traits in a complex biological system and explore the

outcomes for population persistence (e.g. Piou et al., 2015; Piou and Prevost, 2013, 2012). Using this approach, one can test the effects of different scenarios, such as environmental change or anthropogenic disturbance, on population persistence. By scaling up IBMs to metapopulations, we would be able to explore the consequences of dispersal at different scales, from genes to metapopulations, in a unified framework (Baguette et al., 2017). With careful parametrization, these kinds of models can provide more accurate results than patch-based metapopulation models (Harrison et al., 2011).

Our ultimate goal is to draw attention to the underappreciated consequences of dispersal on Atlantic salmon populations. To do so, we focus on two objectives: (i) investigating the role of dispersal in metapopulation stability and persistence via the portfolio and rescue effects, and (ii) evaluating potential consequences of dispersal on the dynamics of local populations and life-histories. We use a demo-genetic individual-based metapopulation model, mimicking the Atlantic salmon metapopulation in Brittany (France), as a virtual laboratory to explore these two objectives. Through its demo-genetic structure, we explore the demographic, phenotypic and genotypic consequences of a gradient of dispersal rates by measuring the portfolio effect, synchrony and homogenization of the abundance of local populations, as well as the extinctions risks and changes in key life-history traits (size and age at maturation) of local populations. We predict that dispersal would increase the metapopulation stability and the portfolio effect, by rescuing sink and small populations from extinction, highlighting the demographic rescue effect. However, high dispersal rates could have detrimental effects on metapopulation dynamics and portfolio effects by synchronizing populations. Altogether, this suggests the existence of an optimal dispersal rate in terms of reducing extinction risk and increasing metapopulation stability. Finally, we predict that dispersers that emigrate from neighboring populations would shape the dynamics of both the donors and the recipient local populations, and influence evolutionary processes and life-history traits due to density-dependence effects.

MATERIAL AND METHODS

1. Salmon metapopulation modeling

1.1. IBASAM: a demogenetic individual-based model for simulating a unique population

We used IBASAM (Individual Based Atlantic Salmon Model), an Atlantic salmon population simulator that integrates most of the knowledge of *Salmo salar* currently available. It was originally developed to study the effects of environmental changes induced by climate change and selective exploitation on a unique population of southern Atlantic salmon (Piou et al., 2015; Piou and Prevost, 2012). IBASAM is a demo-genetic individual-based model developed to mimic the Atlantic salmon life cycle. It represents explicitly the life histories of individuals within populations and incorporates a genetic structure allowing the transmission of genetically determined traits.

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

In the IBASAM model, Atlantic salmon breed in river in winter and each female builds a nest ("redd") in stream gravels, where eggs develop. Individuals, called "fry", emerge from the gravels in April and start feeding. During summer, fish can "decide" to either mature in freshwater as parr (precocious maturation, males only) and reproduce in river, or migrate to the sea as "smolts" the following spring. Those who survived and/or did not succeed to engage maturation or migration stay one more year in freshwater before migrating to the sea. Individuals that migrate to the sea grow there at least one year, and can mature after one sea-winter (1SW) or stay in the ocean for multiple years ("multiple sea-winter" or MSW) before returning to their natal river to reproduce. The mature anadromous individuals begin an upstream migration to reach spawning sites in rivers and continue the cycle. Within the model framework, each individual is described and followed during its complete life cycle, from birth to death, including reproduction, between river and sea, and along the year.

Individuals are characterized by 44 variables including sex, age, size, localization, state of migration/maturation and a set of genetic traits transmitted to their offspring. These genetic traits are represented through a bi-allelic multilocus system and support the phenotypic expression of maturation thresholds and growth capacity at sea. IBASAM is structured in 10 sub-models (see GitHub for more details and code), each representing the major life cycle events of each individual (e.g. reproduction and genetic traits transmission,

emergence, growth and survival, migration to sea, maturation and migration) and environmental conditions in river (temperature and flow time series) and in the sea, which can affect the survival and growth of salmon at different life stages (Fig.1).

1.1.2. Modeling the eco-evolutionary processes

An important feature of IBASAM is that it integrates explicitly the eco-evolutionary processes (e.g. phenotypic plasticity and genetic adaptation), allowing individuals to respond to selection pressures and the simultaneous study of genetic adaptation and phenotypic evolution (Piou and Prevost, 2012; Fig.1). In the model, life-history traits of individuals are influenced by density-dependent and density-independent processes. For instance, eggs-to-emergence survival and growth of juveniles are impacted by temperature and stream flow (Baum et al., 2005; Jonsson et al., 2005) but also by negative density-dependence effects (Bal et al., 2011; Imre et al., 2005; Jonsson et al., 1998).

Life history traits can then evolve in response to selective pressures. For the maturation decision, for example, an environmental threshold model has been implemented with a genetic variation in thresholds between individuals (Lepais et al., 2017; Piché et al., 2008). The maturation decision is based on a comparison between the individual value of the threshold (genetically determined) and the individual's energetic reserves (growth-related and environmentally determined, Fig.1). The maturation thresholds (in river or in sea) can thus evolve under natural selection, which then influences the age at maturation in the population (precocious males vs 1SW vs MSW individuals). Moreover, 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, 1998, 1996). The reproductive success of precocious maturing males is dependent on the contribution of anadromous male to reproduction and of their size, leading to a density/frequency-dependent selection (for more details, see Suppl. mat. 1). Because age at maturation is influenced by growth conditions, survival and reproductive success of alternative life history tactics, any changes in age at maturation can be attributed to phenotypic plasticity (e.g. in response to changing growth conditions) and/or genetic adaptation via thresholds evolution.
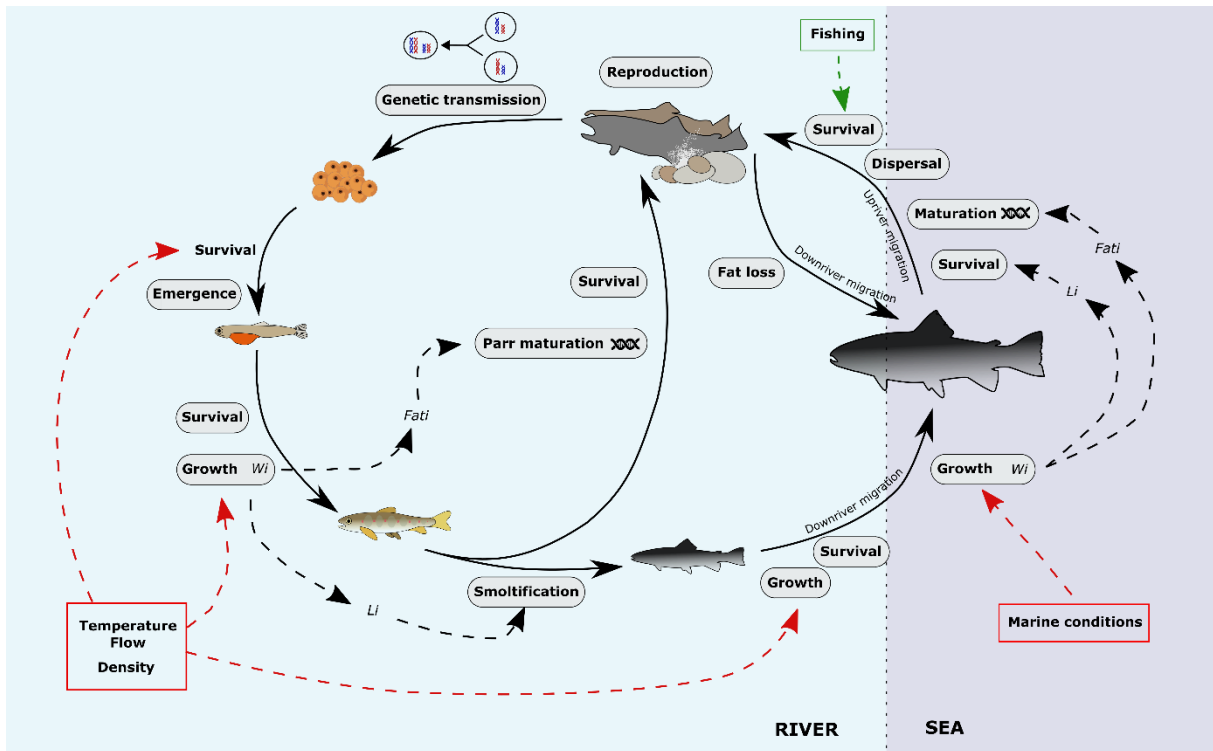
Fig.1: Conceptual framework of the MetaIBASAM model, adapted from Piou & Prévost 2012. Processes at individual levels are highlighted in grey, where the DNA icon indicates heritable traits (genetic thresholds). The dashed arrows represent the influence of both environmental and anthropic factors (red and green rectangles, respectively), or the influence of state variables of individuals (in italics).

1.2. MetaIBASAM: a network of multiple populations connected by dispersal

IBASAM was originally designed to mimic a single population and assumes a philopatry rate of 100%, i.e. all anadromous fish return to their natal river. The model has been extended to consider the metapopulation context (hereafter MetaIBASAM, Fig.1), by allowing dispersal between populations during individual migration of adults into rivers to breed (dispersal sub-models; Hugon, 2018). MetaIBASAM is then a spatially-structured version of IBASAM. Although some studies investigated and characterized some aspects of salmon dispersal (sex-biased dispersal, collective behavior, etc.; Yeakel et al., 2018, see Keefer and Caudill, 2014 for review), the underlying mechanisms remain poorly understood. Here, we adopted a parsimonious approach by assuming that (1) philopatry is constant over space and time, (2) dispersal is not phenotypically and genotypically determined, and (3) the choice of the recipient population is mainly based on distance, a pattern commonly observed in fish and many other organisms (Nathan et al., 2012).

First, we assumed a philopatry rate (noted h) that is constant over time and space, i.e. without variation among populations. At the time of adult migration, dispersing individuals

are randomly selected from their population of origin with a probability *1-h* or P_j, independently from their individual characteristics (Equation 1). Second, for the subset of dispersing individuals, the recipient population is determined by sampling a multinomial distribution of parameter $p_{j,j'}$, which is the probability to disperse from the population *j* to the population *j'*.

$$P_j = 1 - h = \sum_{j'=1}^{n} p_{j,j'} \tag{1}$$

With P_j the total dispersal rate of the population *j*.

This matrix of dispersal *p* represents the connectivity between populations and is based on a dispersal kernel. Dispersal kernels are density probability functions determining the probability of dispersal as a function of some features (Nathan et al., 2012). Dispersal kernels are typically used as a means of scaling the effect of distance on connectivity, and assumes that the dispersal process is radially symmetric. Here, we assumed 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 used the Laplace distribution, a leptokurtic distribution commonly used for fish (Kuparinen et al., 2010; Pépino et al., 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 seems to vary as a function of the population size, likely because of congeners chemical attraction, collective behavior, and river discharge (Berdahl et al., 2016; Jonsson et al., 2003; see Keefer and Caudill, 2014 for review), we weighted the distance kernel by a parameter $g_{j'}$, the relative size of the destination population, to represent its attractiveness (Equation 3).

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

$$\text{with } g_{j'} = \frac{\log(A_{j'})}{\sum_{A_1}^{A_{npop}} \log(A_{j'})} \tag{3}$$

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. *b* was adjusted to 29.5 to limit

dispersal under 50km for at least 80% of dispersers individuals, as suggested by Jonsson et al. (2003) and Keefer and Caudill (2014).

Altogether, the dispersal kernel assumes that a given anadromous fish will tend to disperse to the nearest population from its natal river but this will be moderated by the "attractiveness" of nearby rivers.

We classified each population as sink, neutral or source based on the ratio of incoming individuals (immigrants) to outgoing individuals (emigrants) in the anadromous returns (according to Randon et al., 2018 for Allis shads). A population with a ratio above one was considered a sink, those with a ratio below one were defined as sources, whereas the neutral populations have a ratio near one (Suppl. mat. 2).

1.3. <u>Model parameterization and calibration: the case of the Brittany metapopulation</u>

1.3.1. Local population dynamics

In this study, MetaIBASAM aims to represent the salmon metapopulation of Brittany composed of 15 major populations (Fig.2). However, IBASAM was parametrized using values extracted from the literature and empirical studies (see Piou and Prevost, 2012 and references therein), and calibrated using a long-term monitoring program of the salmon population in the Scorff river (an index population monitored within the framework ORE DiaPFC by INRA). While the objective was not to accurately represent each population using MetaIBASAM, we aimed to differentiate each population dynamics and the parameters needed to define the matrix of connectivity (see above). To do so, we gathered the area of juvenile production (population area A_j) and the stock-recruitment relationship parameters (i.e., the carrying capacity $Rmax_j$ and the maximal egg-fry survival α_j) which govern populations' dynamics (Suppl. mat. 3). Areas of juvenile production for each monitored rivers have been provided by the Bretagne Grands Migrateurs association and local angling clubs. The parameters of the stock-recruitment relationship, between eggs and fry, have been estimated for each populations (Fig.3), based on abundances time-series of eggs deposited (stock, based on the mass-fecundity relationship) and parr 0+ juveniles (recruitment) by fitting a Beverton-Holt model in a Bayesian Hierarchical framework (perso. com. C. Lebot, RENOSAUM project), with the parameters of the Scorff river as a reference (Equation 4).

$$R_j = \frac{S_j}{\dfrac{1}{\alpha * M_j} + \dfrac{S_j}{Rmax * M_j}} \qquad (4)$$

With R_j and S_j being the recruitment (fry abundance/100m²) and the stock (eggs abundance/100m²), respectively, of the population j. α and $Rmax$ parameters are the maximal egg-fry survival and the carrying capacity of the Scorff river, respectively (Piou and Prevost, 2012). M_j is a proportional coefficient for each population j estimated to fit the stock and recruitment data observed for each population in Brittany (perso. com. C. Lebot, Suppl.mat.3).

Other unknown parameters of the model were kept identical to the Scorff River population implemented in IBASAM, as in Piou and Prevost, 2012, except the survival rates at different life stages that have been adjusted to obtain realistic abundances (Suppl. mat. 4).
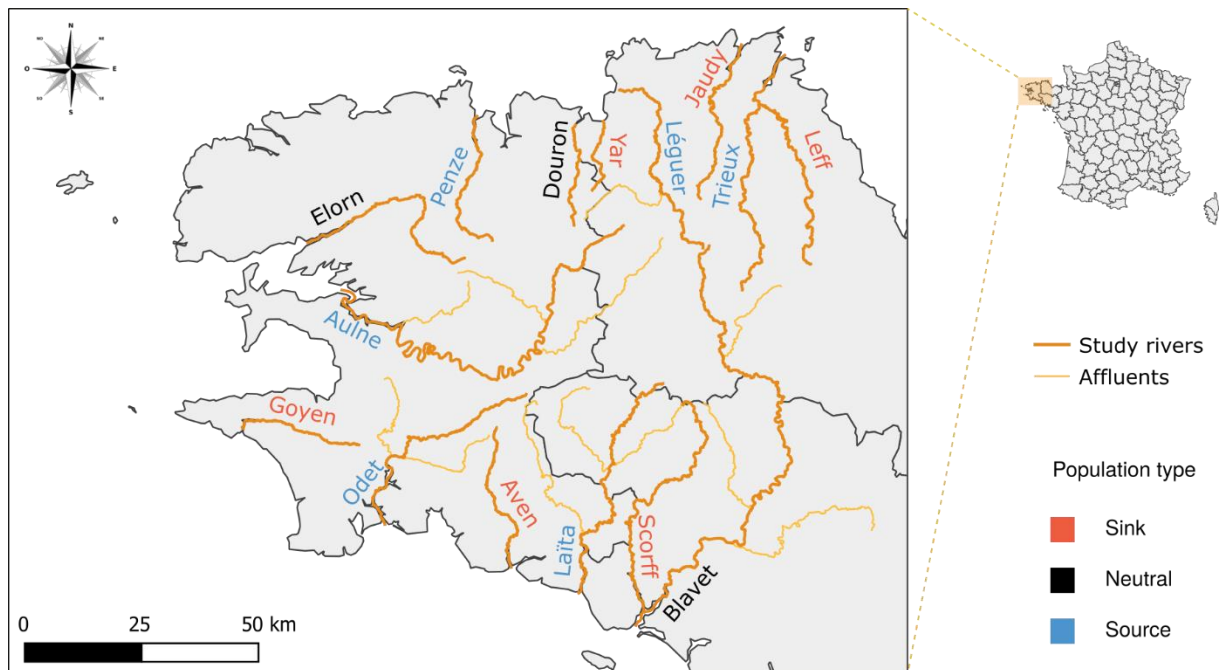

Fig.2: Studied populations in Brittany rivers. The type of each population was defined according to the ratio Immigrants/Emigrants (Suppl. mat. 2).
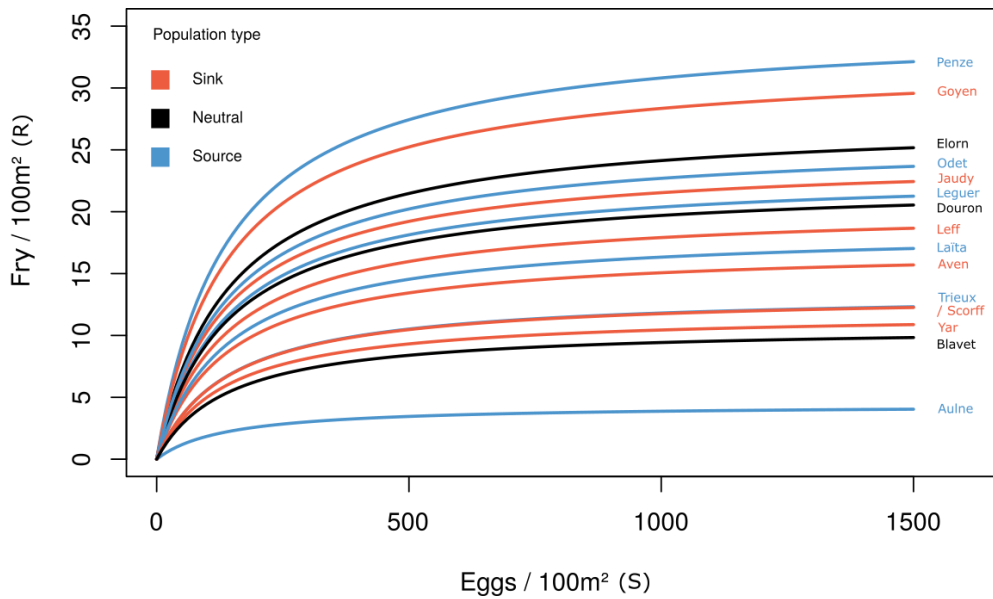
Fig.3: Theoretical stock-recruitment relationships implemented for each population in MetaIBASAM (data provided by C. Lebot, RENOSAUM project, and Piou & Prevost 2012).

1.3.2. Environmental and anthropic conditions

Water temperature, water discharge, and exploitation are the main environmental and anthropic factors affecting individuals in the model. We simulated river temperature and flow through sinusoidal models with autoregressive errors, using the Scorff River parameters (Piou and Prevost, 2012), but with a daily random draw independent for each river, ensuring no environmental spatial covariation. Marine growth conditions are the same for all the populations, and anadromous exploitation rate (individuals selected at random) is about 7% for 1SW and 15% for MSW individuals, based on empirical data estimations (perso. com. C. Lebot). Maintaining similar conditions among populations allowed us to avoid confounding effects of environmental or anthropogenic conditions and to focus on dispersal effects on population dynamics and life-history changes.

2. Scenarios and simulations

We first ran the model for a gradient of dispersal, from 0% to 100%, to evaluate the consequences of dispersal on metapopulation dynamics, functioning, and persistence. Then, we analyzed the phenotypic and genotypic consequences of dispersal for a range of dispersal rates between 0% and 40%, corresponding to more realistic scenarios of dispersal for Atlantic salmon (e.g., Consuegra et al., 2005; Keefer and Caudill, 2014).

The simulations were initialized for each population by a random draw of individuals (25% of rivers production area). Phenotypic and genetic values were sampled in the same distribution as the Scorff population (e.g. size, genetic traits, as in Piou and Prevost, 2012). Because generation time for this species is about less than 2.5 years in French populations, we ran simulations for 50 years, which is sufficient time to detect any changes in the metapopulation dynamics and evolution of life-history traits. For each of the 11 scenarios, we simulated 100 replicates with a 10-year burn-in period.

3. Simulation outcomes analysis

3.1. Metapopulation stability, synchrony, and evenness

For each scenario, we measured the stability and diversity of the metapopulation using the portfolio effect, synchrony, and evenness (homogenization) metrics. The portfolio effect (hereafter PE) is a metric measuring the stabilizing effect of populations' diversity on metapopulation dynamics, by comparing the measured metapopulation variance over the time series and the theoretical variance expected if the metapopulation was considered as a unique population (Fig.4). To do so, we used the mean-variance method with a detrended linear regression from the R package *ecofolio* (Anderson et al., 2013). For example, if this ratio is above 1.25, it means that the metapopulation is 25% more stable than expected. However, if the PE equals 1, it means that the metapopulation is as stable as expected if it was a unique population.
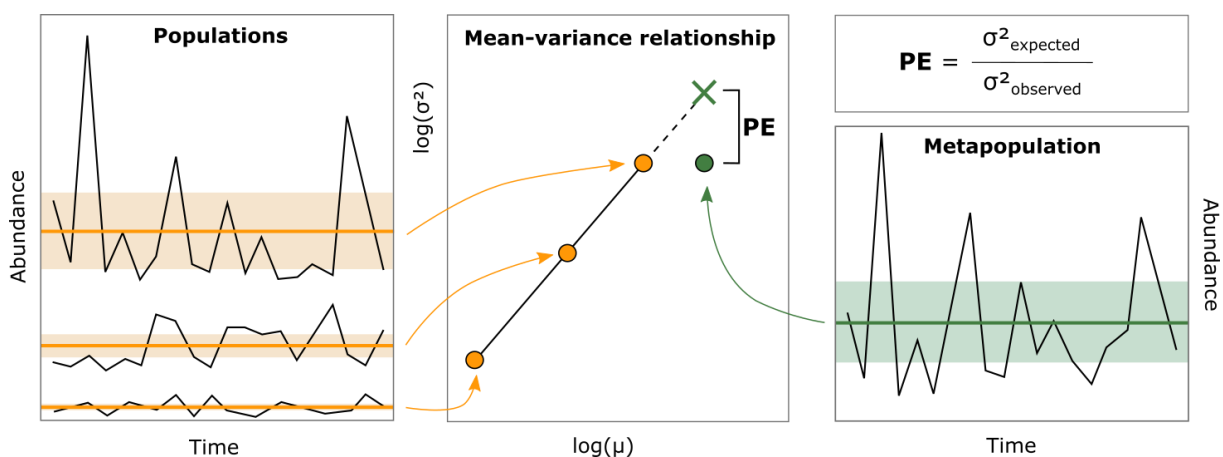
Fig.4: Estimation of the PE according to the mean-variance method. The mean-variance relationship is obtained from the mean (orange lines) and the variance (orange shaded regions) of each population abundance time series, and extrapolated to reach the observed metapopulation mean (green line and circle). The comparison between the expected (green cross) and observed (green circle and shaded region) metapopulation variability estimates the PE.

The synchrony index φ_x, reflecting how populations are synchronous in their demographic evolution along time, was measured as the ratio between the metapopulation variance σ_x^2 and the squared sum of populations' standard deviation σ_{xi} (Loreau and de Mazancourt, 2008, Equation 5). This index is expressed between 0 (asynchrony) and 1 (synchrony).

$$\varphi_x = \frac{\sigma_x^2}{(\sum_i \sigma_{x_i})^2} \tag{5}$$

In order to identify which populations are the most synchronous, we performed pairwise Pearson correlations for each pair of populations and each simulation. The proportion of simulation where these correlations are above 0.2 or under -0.2 were analyzed as a proxy of synchrony trend for each pair of populations. We also computed the metapopulation evenness, representing how populations are similar in terms of abundance, for each year of simulation from the Shannon index, and averaged it over the last 5 years of simulations.

3.2. Local population dynamics and viability

For each scenario, metapopulation and populations abundance (averaged over the last 5 years) were analyzed (as a percentage of relative change to the null scenario) and we performed a population viability analysis (PVA, Beissinger and McCullough, 2002). In particular, we evaluated the quasi-extinction risk for each population as the proportion of simulations where the abundance is at least one year below an "at-risk" threshold (defined as 10% of the population carrying capacity *Rmax*). These results are here only presented for two examples populations by type (sink / neutral / source), one big and one small.

For dispersal rates from 0% to 40%, we also measured the density of individuals (by m²), averaged over the 5 last years by population and then averaged by type of population for each simulation. The proportion of immigrants in the anadromous stock, averaged over the last 5 years, was measured for each population for a dispersal rate of 10% only.

3.3. Phenotypic and genotypic changes

We analyzed the phenotypic and genotypic consequences of dispersal by type of population and for dispersal rates from 0% to 40%, since patterns were globally similar within the type of populations and different between them. We focused on resident individuals, allowing us to study the consequences of dispersal on each population, and avoiding the noise brought by immigrants that would have experienced different conditions during their juvenile stage in their population of origin. Changes in life-history strategies were measured via the success of early mature males strategy, defined as the proportion of eggs by redds fertilized by 0+ (or 1+) parrs, and via the 1SW/MSW ratio (number of 1SW and MSW residents anadromous), indicating the age at maturation. We also measured the body size of parrs, smolts and resident anadromous as phenotypic changes. We monitored genetic changes by means of the genetically determined thresholds of maturation, both in river (for males parr) and in sea (for males and females resident anadromous). All these traits were averaged over the 5 last years by population and then averaged by type of population for each simulation. Their distribution across simulations are presented by type of population.

RESULTS

1. Metapopulation dynamics and demographic consequences of dispersal

1.1. Spatial structuration of the metapopulation

Based on the model assumptions, the model represents a metapopulation of source-sink type, with sources populations being the largest relatively to their neighbors (e.g. Leguer, Aulne) and sinks populations being the smallest (e.g. Yar) or close to a source population (e.g. Scorff close to the Laïta; Fig.5). The Laïta appears to have the highest contribution to the metapopulation (22% of anadromous for a dispersal rate of 10%). There is also a high inter-population variability in the proportion of immigrants (Fig.6), with the Yar population being composed of up to 30% of immigrants, while the Trieux and Laïta are only composed of 4.5% of immigrants for dispersal rates of 10%. Fig.5 also shows that long-distance dispersal between populations can occur, for example between the Blavet and the Elorn.
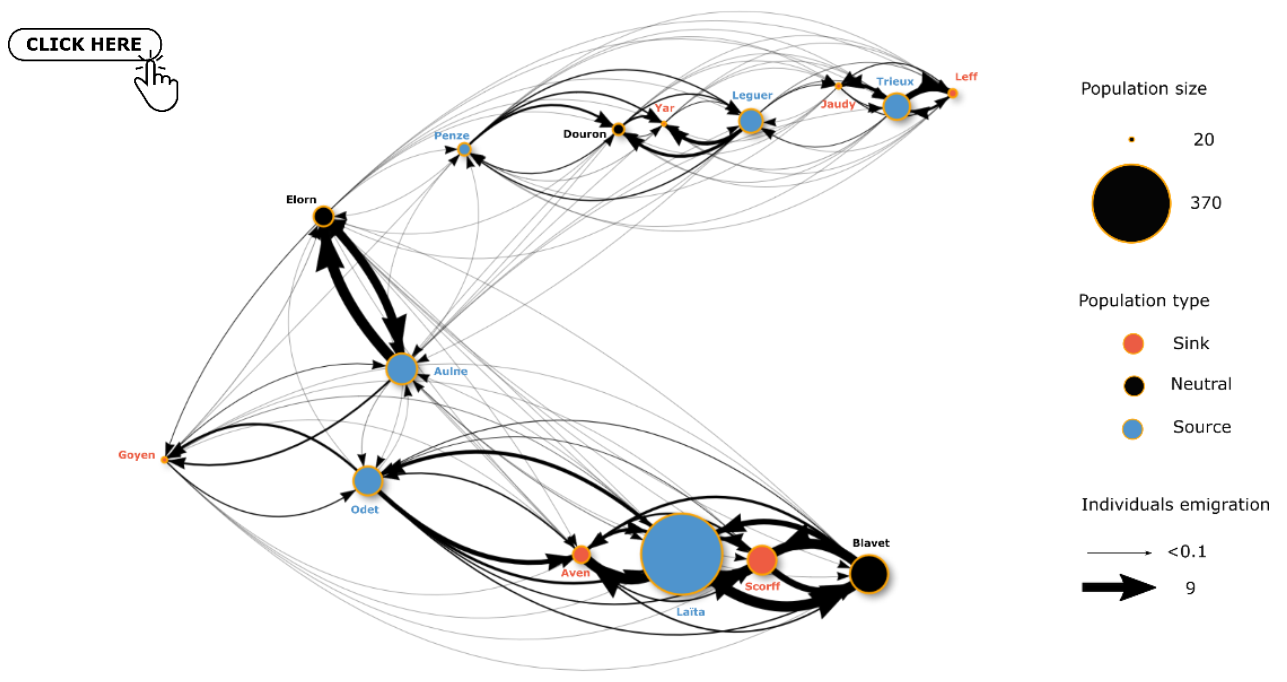
Fig.5: Schematic representation of the metapopulation network generated by the model, for a dispersal rate of 10%, and averaged over the 5 last years of simulations. The circles represent the populations, colored by type, and their size is a function of their abundance. The type of populations (sink, neutral, source) was defined according to the ratio Immigrants/Emigrants for each population (Suppl. mat. 2). The arrows represent the emigration of individuals and their width is a function of the number of dispersers. The button "click here" redirects to a shiny app with the same graph with interactive options.
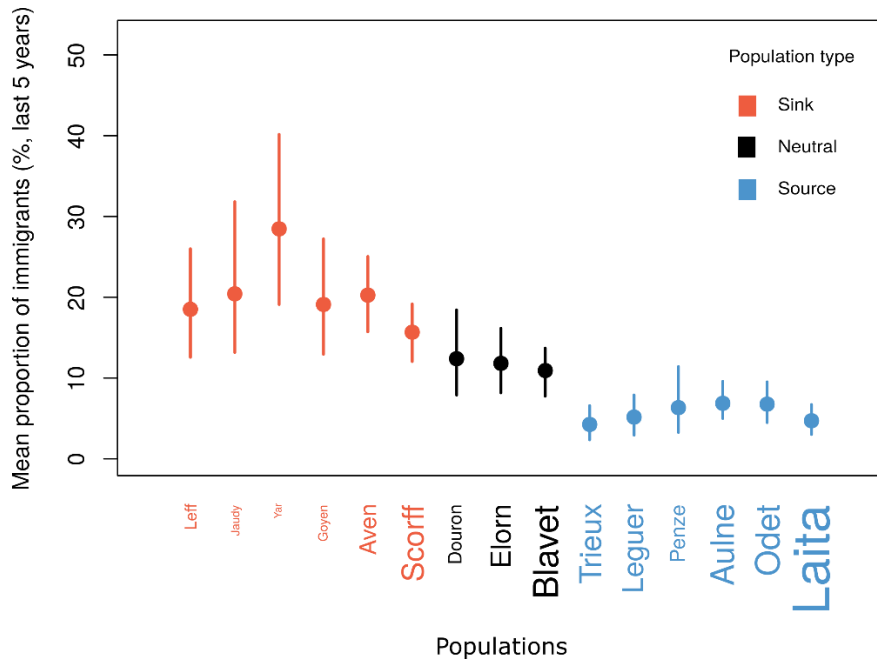
Fig.6: Distributions of simulation replicates for the proportion of anadromous immigrants (in %) in each population. The proportion of immigrants was averaged over the 5 last years of the time series. Means (black circles) and 95% intervals (lines) are reported, and the size of population labels is a function of their abundance.

1.2. Metapopulation stability, synchrony, and evenness

Our results show a non-linear relationship between dispersal and portfolio strength. With strict philopatry (i.e. no dispersal), the PE is estimated at 1.61 on average, meaning that the metapopulation is 61% more stable than expected if it was the sum of the local populations. With an increasing dispersal rate, the PE increases to a peak of 1.79-1.74 for dispersal rates around 10-20%, and then declines gradually and ultimately stabilizes around 1 for dispersal rates above 50% (Fig.7 a). Altogether, these results suggest that for dispersal rates below 50%, the metapopulation stability is greater than expected if the metapopulation was considered as a single population, with an optimal PE achieved with dispersal rates around 10-20%. However, the metapopulation behaves as a single population (PE ~ 1) when dispersal rates exceed 50%.

Indeed, we observe a 75% increase of metapopulation synchrony and a 5% increase of evenness with dispersal above this threshold (Fig.7 b and c), suggesting that the initial PE could be associated with high diversity and low synchrony, and the dynamics and size of the local populations are becoming more similar (less diversify) with high dispersal. However, these relationships are not linear. For example, there is a rapid increase from a synchrony of 0.09 (strict philopatry) to 0.17 (50% dispersal) on average, and then a slowdown from dispersal

rates of 50% to reach a maximum synchrony of 0.19 for 90% dispersal (Fig.7 b). At the population scale, populations are becoming more synchronous with elevated dispersal rates (Fig.7 d), but this is only the case for the most proximate populations (with distances below 50km). For example, the Scorff and the Blavet, two nearby populations in the south of Brittany, have a correlation of their anadromous time series above 0.2 or below -0.2 for 25%, 44%, and 98% of simulations for dispersal rates of 0%, 20% and 80% respectively (Fig.7 d).
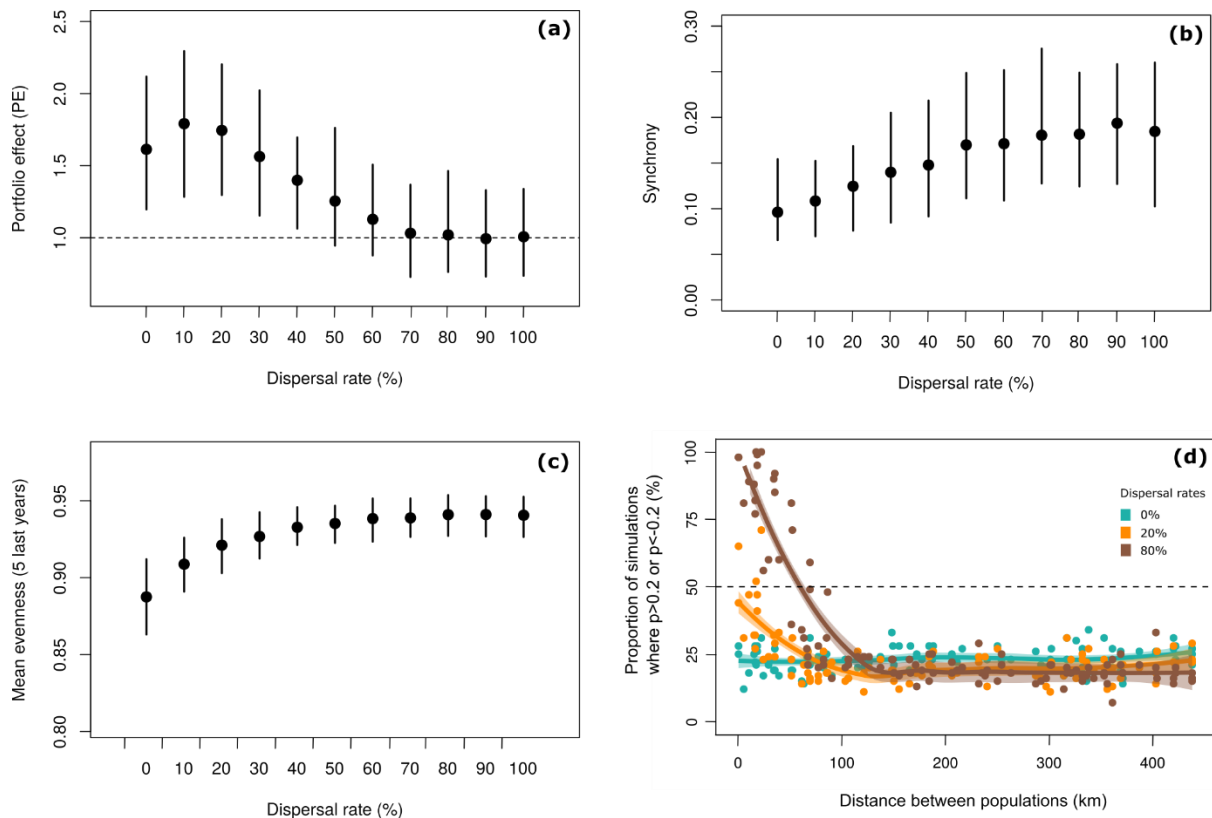
Fig.7: Distributions of simulation replicates for the (a) portfolio effect (PE), (b) synchrony and (c) mean evenness between 15 sub-populations, as a function of dispersal rates. The PE and synchrony metrics were calculated using the 50 years of the anadromous time-series, and the evenness metric was calculated for each of the last 5 years only and then averaged. Means (black circles) and 95% intervals (lines) are reported. In (d), the synchronous trend between pairs of populations, as a function of the distance between them for dispersal rates of 0%, 20%, and 80%. The synchronous trend is represented by the proportion of simulations where the Pearson correlation (p) between the pairs of populations is above 0.2 or below -0.2. A proportion higher than 50% means that the two populations tend to be correlated, whereas a proportion below 50% means an uncorrelated trend. The line represents the fitted model between the synchronous trend and the distance using a loess regression.

Because of the diversity-stability relationship, one would expect a decrease of the metapopulation stability (coefficient of variation CV and PE) with diversity, due to an increase of synchrony with dispersal. Surprisingly, the metapopulation stability (CV) remains constant and not affected by dispersal (Fig.8), suggesting that dispersal modifies the slope of the mean-variance relationship (Fig.9). For example, for dispersal rates of 20%, the mean-variance

relationship leads to an expected variability of metapopulation higher than observed, whereas for a dispersal rate of 80%, the expected variability is close to the observed one. However, at the population scale, we observe the expected pattern so that all the local populations are becoming more stable with an exchange of individuals among them (Fig.8).
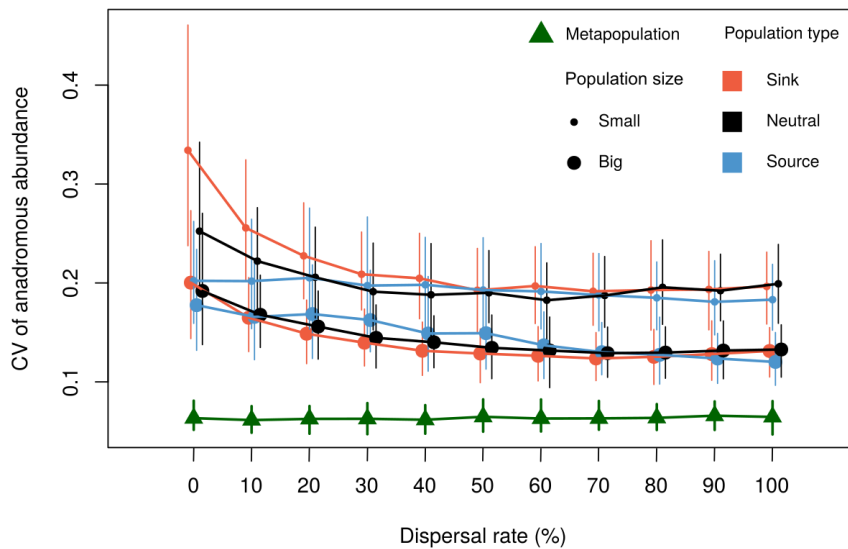
Fig.8: Distributions of simulation replicates of the variability (coefficient of variation CV) of anadromous abundance time series for the metapopulation (green triangles) and some local populations (circles) along a gradient of dispersal rates. Two populations by type of population, one small (small circles) and one big (large circles) are represented (sink: Jaudy and Scorff; neutral: Douron and Blavet; source: Leguer and Laïta). Means (circles or triangles) and 95% intervals (vertical lines) are reported.
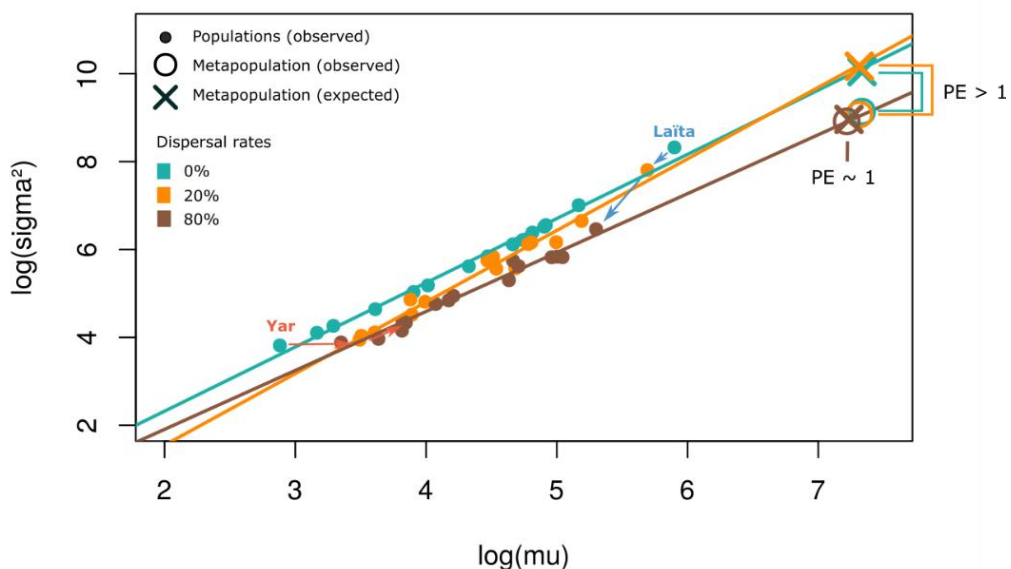
Fig.9: Mean-variance relationship, leading to the PE estimations, averaged over simulations and for dispersal rates of 0%, 20%, and 80%. The observed log(mean) and log(variance) in populations abundance are represented by the small circles, and by the large circles for the metapopulation. The metapopulation log(variance), expected via this linear relationship for the observed log(mean), is represented by the large cross.

1.3. Local populations dynamics and Population Viability Analysis

Our results show a small decline of metapopulation abundance along a gradient of dispersal, with a maximum loss of 15% of metapopulation abundance with 100% dispersal (Fig.10 a). However, at the population scale, results differ across population type (sink, source, neutral) and size (small, big). With dispersal, there is an increase in the abundance of sink populations compared to a scenario with no dispersal, especially for small populations. For example, the size of the Jaudy and Scorff populations increases by 74% and 32%, respectively, with a 50% dispersal rate (Fig.10 a). From dispersal rates near 50%, their abundance stabilizes and then decreases for the highest dispersal rates, suggesting that the contribution of immigration is declining with high dispersal. In contrast, there is a constant decline in the abundance of source populations, whatever their initial size due to dispersal. For example, there is on average a 33% decrease in the Laïta size for a 50% dispersal rate (Fig.10 a), suggesting that source populations are affected by dispersal, by sending much more individuals than they receive (Suppl. mat. 2).
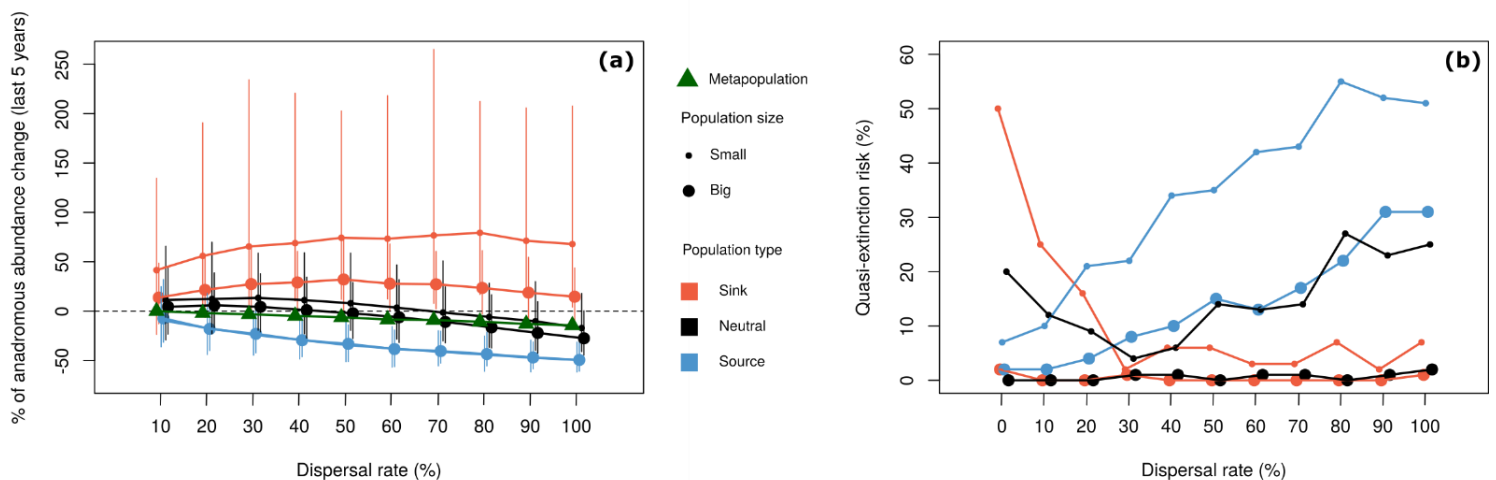
Fig.10: In (a), distributions of simulation replicates of the change (in %) in metapopulation (green) and some local populations abundance, compared to the null scenario (0% dispersal), and in (b), quasi-extinction risk (in %, for a 10% of carrying capacity threshold) of these local populations along a gradient of dispersal. In (a) and (b), two populations by type of population, one small and one big are represented (sink: Jaudy and Scorff; neutral: Douron and Blavet; source: Leguer and Laïta). In (a), means (circles and triangles) and 95% intervals (lines) are reported.

The relationship between the quasi extinction risk and dispersal rate varies with the type and the size of populations (Fig.10 b). Without dispersal, small sink populations, such as the Jaudy, have a high risk of extinction (e.g. 50%) that sharply declines with even small rates of dispersal (e.g. to 2% and 6% for dispersal rates of 30% and 50%, respectively), suggesting a demographic rescue effect. Larger populations, such as the Scorff, are not vulnerable to

extinction, even without dispersal. On the contrary, source populations are increasingly affected by increasing dispersal rates. This is especially the case for the smallest of the source populations, where the extinction risk can exceed 50% when dispersal rates exceed 80% (see, for example, the Leguer, Fig.10 b). Meanwhile, the extinction risk of neutral populations appears insensitive to dispersal.

As a consequence of the asymmetric flows between populations with dispersal, the density of anadromous (not shown) and parr individuals within populations changes in different ways in source, neutral, and sink populations (Fig.11). Indeed, density is constant for neutral populations, whereas it sharply increases by 74% in sink ones and decreases by 28% in source ones from dispersal rates of 0% to 40%.
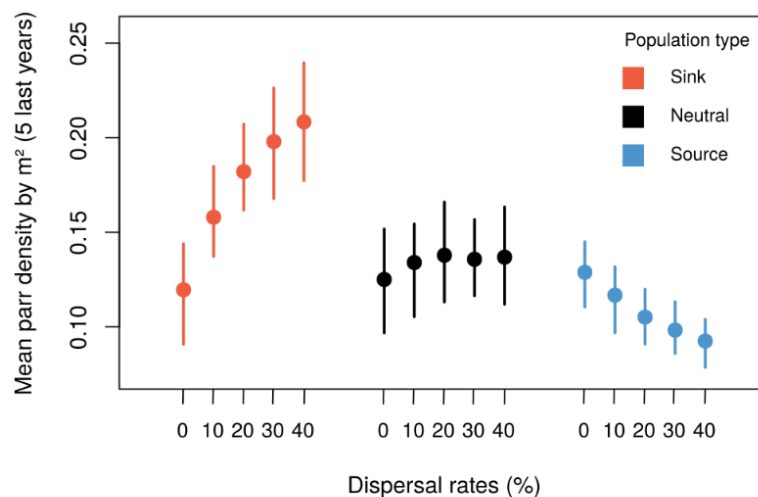
Fig.11: Distributions of simulation replicates of the density of parr individuals by m², averaged by type of population over the last 5 years, as a function of dispersal rates from 0% to 40%. Means (circles) and 95% intervals (lines) are reported.

2. Phenotypic and genotypic consequences of dispersal

Life history strategies such as age at maturation are also affected by dispersal. The changes of ratio 1SW/MSW (Fig.12 b) and the success of early mature 0+ strategy (males only, "precocial parr"; Fig.12 a) with increasing dispersal show the same pattern: it declines in sink populations (by 25% and 24%, respectively for a dispersal rate of 40%) and increases in source ones (by 8% and 13%, respectively for dispersal rate of 40%), while remaining constant in neutral ones. However, the success of the early mature 1+ strategy is less affected by dispersal rates (Suppl. mat. 5). Either phenotypic, genetic changes, or both, can induce these life-history changes with dispersal.

Our results indicate changes in body size of young stages with different dispersal rates and the patterns differ among the different types of populations. In sink populations, parr and smolts are smaller (by 5% and 2% with dispersal rate of 40%, respectively) with dispersal, whereas the inverse pattern is observed in source ones (where parr and smolts are larger by 3% and 1% with dispersal rate of 40%, respectively; Fig.12 c and d). There is no trend in parr and smolts body size with dispersal in neutral populations. Whatever the type of population, there is no change in the body size of anadromous fish with dispersal (less than 1%, Suppl. mat. 6).

Irrespective of the dispersal rate, we found no evidence of genetic drift of neutral genes in any populations (results not shown), suggesting that any change in non-neutral genes is due to selection. In the case of non-neutral genes, there is no change in the genetic thresholds of maturation (in river or in sea) in the neutral and source populations with dispersal (Fig.12 e and f). However, in sink populations, the genetic thresholds of male river maturation (precocious) and female sea maturation slightly increase by 2% and 4%, respectively, with a dispersal rate of 40% (Fig.12 e and f).

Altogether, these results suggest that dispersal induces different patterns between sink and source populations, driven by density-dependent effects, with phenotypic consequences at all life cycle stages. These changes are mainly due to changes in growth conditions, i.e. phenotypic plasticity rather than genetic evolution.
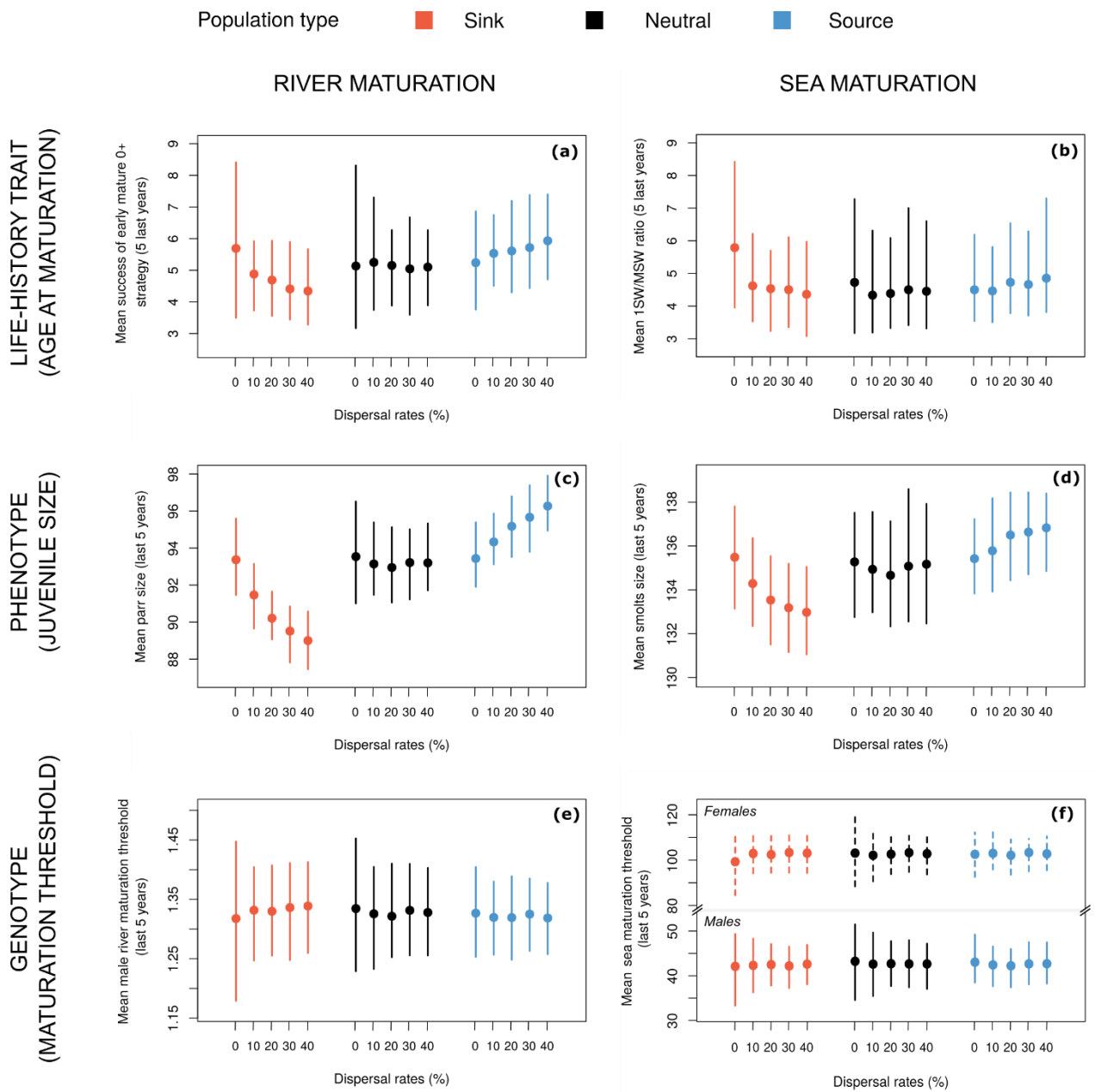
Fig.12: Distributions of simulation replicates of (a) the success of early mature strategy (males parr 0+), (b) the ratio 1SW/MSW, (c) the size (in mm) of parr and (d) smolts individuals, (e) the maturation threshold of males in river and (f) of females and males in sea, averaged by type of population over the last 5 years, as a function of dispersal rates from 0% to 40%. The success of the early mature strategy is represented by the proportion of eggs of a redd fertilized by mature parrs. Means (circles) and 95% intervals (lines) are reported.
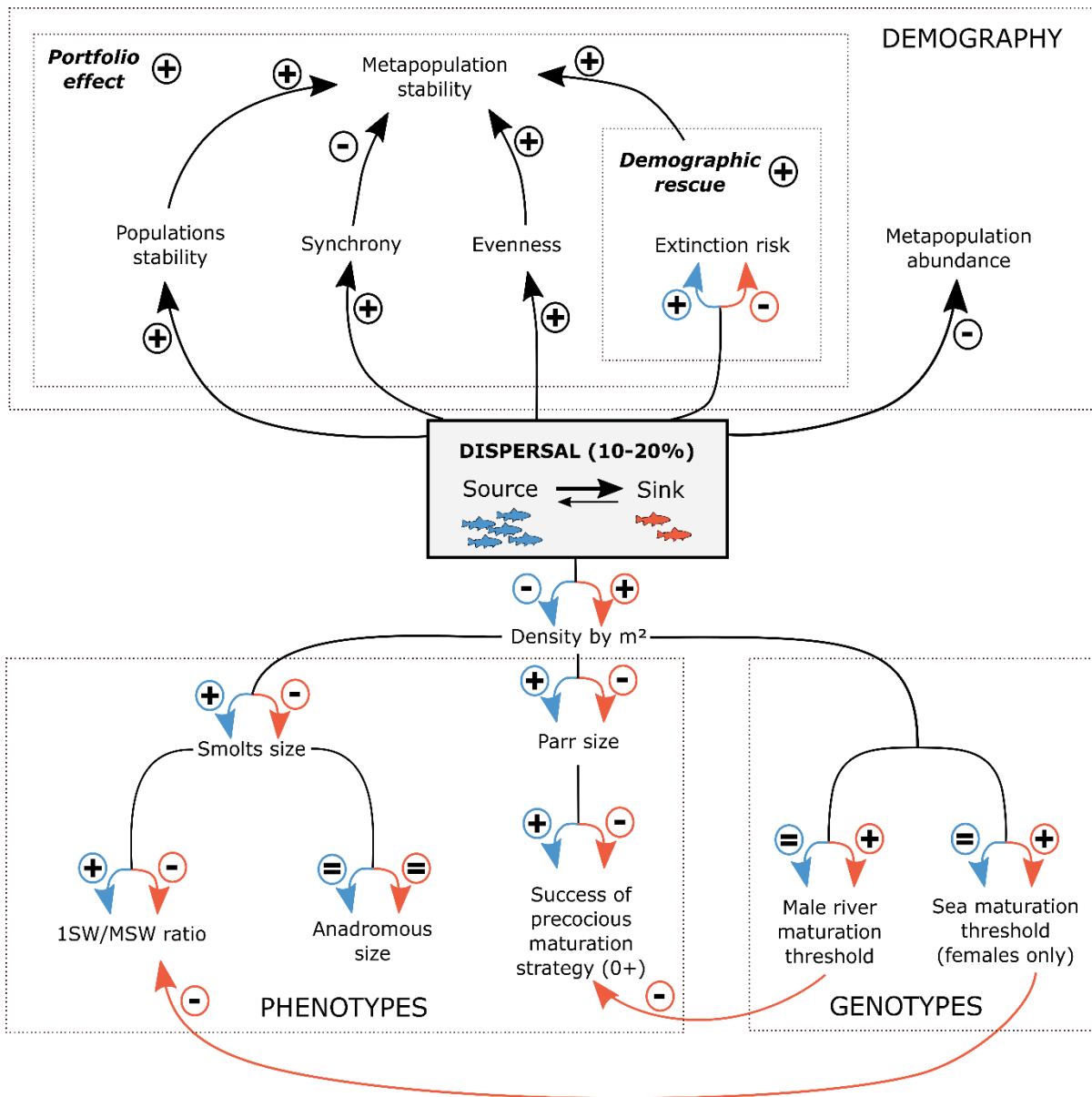
Fig.13: Diagram representing the demographic, phenotypic and genotypic changes induced by low and realistic dispersal rates (10%-20%). The curves arrows show direct influences (positive, negative, or neutral, indicated with + or – or =), with the blue and red colors corresponding to the source and sink populations if the effect is not the same.

DISCUSSION

The consequences of spatial dispersal on metapopulations persistence have been overlooked in salmonids, likely because estimating dispersal rates in nature is challenging (Keefer and Caudill, 2014; Schtickzelle and Quinn, 2007). Using a demo-genetic individual-based model mimicking an Atlantic salmon metapopulation connected by a standard distance dispersal kernel, we show that dispersal can have profound consequences for (i) metapopulation functioning and stability, and (ii) local population dynamics including demographic, phenotypic, and genetic changes (summarized in the Fig. 13). Our model induces a spatial structure of source-sink dynamics, with populations behaving as sources or sinks as a function of their size and isolation from nearby large populations. In particular, we show that low dispersal rates favor metapopulation stability and persistence of small populations, confirming the demographic rescue and stabilizing effects of dispersal. However, higher dispersal rates tend to synchronize populations and affect the source ones, leading to anti-rescue effects affecting the whole metapopulation. Additionally, we show that the asymmetric flows between local populations induce phenotypic and genetic changes via density effects, especially in sink populations. The density effects especially reduce and enhance the success of the precocial male strategy, while they favor and decrease the postponed maturation in sea, in sink and source populations respectively. These changes occur via phenotypic plasticity mainly and genetic adaptation. Altogether, these results suggest that Atlantic salmon populations cannot be treated as isolated systems and that spatial dispersal is an important component for understanding the dynamics of metapopulations and the resilience of population complexes.

A non-linear relationship between dispersal and metapopulation portfolio effect

Our study emphasizes a complex relationship between dispersal and the strength of the portfolio effect, measured at the scale of the metapopulation. The initial benefits of rescue effect induced by dispersal are counterbalanced by the rise of synchrony of populations abundance associated with high dispersal rates. Indeed, we observed that without dispersal, populations behave largely independently and the portfolio effect is well above the stability expected if the metapopulation was considered as a sum of the local populations (i.e. it is > 1, (Anderson et al., 2013). This strong PE might be explained by the asynchrony between the density fluctuations of populations and the homogenization (evenness) of their sizes, despite

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high risks of extinction for sink and small populations. While dispersal increases synchrony and homogenization of population abundance, it also increases the population size of sink and especially small populations, reducing their variability and risk of extinction, through a demographic rescue effect. For example, the extinction risk of the Jaudy, a small sink population, can reach 50% without dispersal, due to demographic stochasticity, but declines close to zero for dispersal rates of 30%. These processes of demographic rescue have not directly been demonstrated in the wild for salmonids, but Hill et al. (2002) also found that small dispersal rates increase the time before extinction, using a structured salmon metapopulation model, and natural recolonization of rivers can be associated to dispersal (Perrier et al., 2009). This positive effect of dispersal overcomes the negative effect (synchrony) and favors the stability of the metapopulation by increasing the PE by 11%, which reaches an optimum for dispersal rates around 10%-20%. Interestingly, this optimal dispersal rate in terms of generating the strongest PE corresponds to the few empirical studies reporting dispersal rates of Atlantic salmon (e.g. Jonsson et al., 2003; see Keefer and Caudill, 2014 for review).

However, synchrony continues to increase with dispersal and becomes detrimental when dispersal rates exceed 20%. The strength of the PE declines from these rates to finally reach a PE equal to 1, meaning that the metapopulation behaves as a single population with very high dispersal rates. Our results are in agreement with Yeakel et al. (2018), who also observed such a pattern using a quantitative genetic model simulating two populations connected by density-dependent dispersal. Moreover, from dispersal rates of 50%, the abundance of source populations, especially the smallest, dramatically decreases, because they send more individuals than they receive by nearby rivers, and they become vulnerable to extinction (more than 40% risk). The contribution of these source populations to the metapopulation demography is dramatically reduced, resulting in an overall decline in metapopulation abundance. These anti-rescue effects of dispersal might increase the risk of extinction of the whole metapopulation.

The synchronizing effect of dispersal among rivers was observed in many studies on other organisms and is known to increase the metapopulation variability and risk of collapse (for birds, Paradis et al., 1999; for Chinook salmon, Carlson and Satterthwaite, 2011). However, here, the metapopulation variability remains stable along a gradient of dispersal,

while all the local populations, whatever their size or type, are becoming more stable with dispersal. This stabilization of local population fluctuations might counteract the increase of synchrony between them and lead to constant metapopulation stability. This pattern was conceptualized by Thibaut and Connolly (2013) and also depicted in a study based on patch metapopulation modeling (Wang et al., 2015). In particular, Wang et al. (2015) showed that community stability depends not only on the synchrony of population fluctuations, but also on the stability of species weighted by their abundance.

While populations are becoming more synchronous with dispersal, they also become more even in terms of abundance. This homogenization of population size could be beneficial to the metapopulation stability by reducing the potential driver effect of variability of the largest populations, such as the Laïta, and by raising the contribution of the smallest populations to stability, such as the Yar, but we were not able to demonstrate it here. This concept has been explored in the context of community stability, where a positive relationship between the evenness of species abundance and the stability of the community has been found (Doak et al., 1998; Mikkelson et al., 2011). Here, we only focused on dispersal-induced homogenization of population abundance, rather than homogenization of traits, because populations were not differentiated phenotypically and genotypically. By avoiding these potential population differences, it allowed us to show the phenotypic and genotypic consequences of dispersal-induced density changes.

Phenotypic and genotypic consequences of dispersal-induced density effects on local populations

Under our model assumptions, we show that the asymmetric flows between source and sink populations could lead to changes in density compared to a scenario with no dispersal, with different patterns between types of populations. These density variations have consequences not only on demography as shown above, but also on life-history strategies via phenotypic and/or genotypic changes. In particular, we emphasize changes in the size of juveniles and age at maturation especially in sink populations, where the change of density with dispersal is stronger than in source ones. Indeed, the sharp increase of density in sink populations with dispersal induces a decrease in the size of juveniles through density-dependent growth, whereas the large emigration from source populations reduces the

density effect, inducing an increase of juvenile size. These changes in size also have downstream life-history consequences, especially on smolts size and age at maturation. For example, with dispersal, smolts from sink populations spend more time at sea before maturing, since they left rivers at a smaller size (Fig. 12 d) and their fitness is weight-dependent. Also, the increase in the genetic threshold of female maturation with dispersal in sink populations might favor a postponed maturation and a higher fecundity to counteract the negative density effects induced by dispersal on eggs survival. In sink populations, via phenotypic plasticity mainly and thresholds evolution, individuals become MSW anadromous rather than 1SW (Fig. 12 b). Simultaneously, the success of the early maturation strategy also changes with dispersal-induced density effects (Fig. 12 a). In sink populations, the success and contribution of 0+ parrs to the offspring decrease with dispersal. Smaller than without connectivity, parrs individuals rarely reach the maturation threshold in river (plastic response) and this early maturation strategy is even counter selected via a slight increase of the genetically determined threshold (Fig. 12 a). This counter-selection might be induced by the high number of large MSW anadromous that have a higher ability to fertilize eggs. Thus, parr individuals would rather smoltify and mature at sea. In source populations, we show only phenotypic plasticity, leading to a trend of earlier maturation, in sea or in river, because the weakened density effect induced larger juveniles with dispersal. Consequently, we show changes of age at maturation through phenotypic plasticity mainly (both in sink and source populations) and genetic adaptation (only in sink populations).

The model allows us to measure phenotypic and genotypic consequences of dispersal on local populations, especially in sink populations, but in the literature, studies focus on density-dependent dispersal (Aars and Ims, 2000) rather than the density changes caused by dispersal. Benton and Bowler (2012) introduced the effect of individuals' movement on patch population size, and since the access to resources is density-dependent, emigration from a population could make resources available (Keeley, 2001). Inversely, immigration increases density, which could affect density-dependent phenotypes such as growth rate. To our knowledge, the phenotypic and genotypic consequences of density changes due to dispersal have been rarely explored. Instead, most studies have focused on the input of phenotypes or genotypes, changing gene frequency in the recipient populations (Barton, 1992). Our model allowed us to focus on the density effects explicitly, because there was no phenotypic or

genotypic differentiation between populations, due to similar average environmental conditions. The observed life-history changes are not surprising since salmonids are highly plastic species characterized by several life histories, especially regarding age at maturation (Thorpe, 2007). For example, growth changes induced by density were demonstrated for Atlantic salmon (Bal et al., 2011; Imre et al., 2005), and can influence age at maturation through environmentally plastic and/or evolutionary responses. Through plastic response to changes of river growth conditions with climate change, it seems that Pacific salmon spend more time in sea than before (Cline et al., 2019), and a previous study using IBASAM model depicted postponed maturation at sea following the reduction of sea growth conditions for Atlantic salmon (Piou and Prevost, 2013). The changes in river growth conditions also influence early freshwater maturation (Horth and Dodson, 2004; Thomaz et al., 1997), since the fertilization success of precocious males can be size-dependent (Jones and Hutchings, 2001). Strong selective pressures, such as selective harvest of old adults, can also lead to the evolution of harvest populations, for example towards an earlier maturation (Kuparinen and Hutchings, 2017). However, the genetic changes we measured here are marginal compared to those observed for stronger selective pressures than density, such as climate change or selective exploitation on Atlantic salmon (Piou et al., 2015; Piou and Prevost, 2013).

<u>Limits of the model and new perspectives</u>

Dispersal increases the synchrony between populations but our results suggest that the synchronizing effect of dispersal might be limited. Indeed, for the highest dispersal rates, the synchrony among populations over time was around 0.19 and seems to reach an asymptote, while it is estimated to 0.49 in wild populations in Brittany (perso. com. C. Bouchard). In our study, there was no environmental covariation between populations (around 0 on average, not shown). Yet, environmental conditions are known to synchronize the dynamics of populations, via the Moran effect (Moran, 1953; Ranta et al., 1997). Many studies investigated the relative effects of dispersal and environment on synchrony (Lande et al., 1999; Ranta et al., 1995; Ripa, 2000), and showed that synchrony would be mainly explained by the Moran effect rather than dispersal, especially at high geographical scale (Ranta et al., 1995; Ripa, 2000). In our model, only the closest populations had correlated dynamics, whereas in nature some distant populations can be highly synchronous if they experience similar environmental conditions (for salmonids, Mueter et al., 2002; for Atlantic

salmon, Olmos et al., 2019). In our study, we focused on the role of dispersal in metapopulation synchrony, but it could be interesting in further studies to explore the relative synchronizing effect of dispersal and environmental conditions by simulating different scenarios of environmental covariation, especially in the context of climate change.

Although we implemented the parameters of the stock-recruitment relationships of each population in the model (e.g carrying capacity), it seemed that we were not able to represent accurately the dynamics of the local populations, as all of them showed similar patterns as the Scorff (Suppl. mat. 7). Two hypotheses not mutually exclusive could explain these differences between the observed and simulated results. First, the egg-to-fry survival depends not only on the density but also on environmental conditions (temperature and flow), which are based on the Scorff river for all the populations in the model. Second, the stock-recruitment parameters were estimated using parr 0+ captured in September as the recruitment, whereas in the model, there are applied to emerging fish in April as the recruitment (fry), with a similar summer survival for all populations (here based on summer-survival estimated for the Scorff). Yet, summer survival varies among rivers, environmental conditions, and through time (Bley and Moring, 1988; Hwan et al., 2017). Variation in summer survival could be an important process influencing the dynamics of Atlantic salmon populations, but studies of juvenile survival during this period are rare. Estimating summer survival across rivers and time, as well as an experimental study evaluating the effect of summer flow variation on emergent-parr 0+ survival, would allow us to better represent the stock-recruitment dynamics of populations in MetaIBASAM, which might change the patterns we observed.

Finally, as with all models, our results are strongly dependent on our assumptions, especially regarding dispersal modeling. We used a simple way to represent dispersal, that is, via a distance-dispersal kernel. Consequently, dispersal was constant in space and time, which has several implications. First, we did not consider any costs of dispersal (Bonte et al., 2012), nor did we consider the potential for survival and reproductive success of dispersers to be reduced in recipient populations because of local adaptation (Mobley et al., 2019). Second, the observed patterns might change if dispersal was genetically determined (Saastamoinen et al., 2018), at least in part, and was under selection and subject to evolution (McPeek and Holt, 1992). Although the genetic basis of salmonids dispersal has only been suggested for the stage

of emigration, and not for the stages of transfer and immigration (Ferguson et al., 2019; Pearse et al., 2014), evaluating the evolution of dispersal strategies in metapopulations, in particular in a changing environment, is a challenging but needed task (Baguette et al., 2017; Travis et al., 2013). Finally, Yeakel et al. (2018) showed that the relationship between dispersal rate and metapopulation robustness depends on the strength of collective behavior. Some recent studies provide evidence for collective migration in salmonids (for review, see Berdahl et al., 2016), where reduced straying was observed in years with greater abundance of fish (see Jonsson et al., 2003, for an example from Atlantic salmon). Future work should consider alternative ways of modeling dispersal in the MetaIBASAM framework, which would help illuminate how our assumptions of the dispersal process influence our conclusions regarding consequences for metapopulation and the dynamics of local populations.

<u>Management implications</u>

This study shows that Atlantic salmon populations should not be considered as isolated entities, since the dynamics and persistence of individual populations depend, in part, on the metapopulation dynamics. We argue that the spatial structure of Atlantic salmon populations should be considered in management and conservation strategies. Indeed, because the contribution of populations in the metapopulation dynamics seemed to differ between source, sink, and neutral populations, some strategies of harvest that depend on the type of population should be evaluated to determine which strategies favor the persistence of metapopulation and strong salmon portfolios (Anderson et al., 2015; Webster et al., 2017). Management strategies would have to favor an adaptive network, by allowing connectivity between populations via dispersal, while maintaining a diversity/biocomplexity and asynchrony of populations' responses to environmental changes.

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SUPPLEMENTARY MATERIALS

Suppl. mat. 1: Summary of the sexual selection and reproductive success processes represented in the model IBASAM

At the time or reproduction, a random number of mature anadromous males $N_{males,i}$ is attributed to each mature female i according to a Poisson distribution of parameter $MeanN_{males}$, the populational mean of anadromous males fertilizing the eggs of one female (Piou & Prévost 2012).

If the number of available males is below $N_{males,i}$, all these males are attributed to the female i but if there are too many males, the probability for a male j to be attributed depends on its relative size.

$$P\left(selected|W_j\right) = \frac{W_j}{\sum_l W_l}$$

where l is an anadromous male among the available ones.

A random number of mature parr $N_{parrs,i}$ is also attributed to each female according to a Poisson distribution of parameter $MeanN_{parrs}$ (Piou & Prévost 2012), which are randomly picked up among the available ones.

Then, each female produces a redd i with a mean egg weight $EggW_i$ and a number of eggs $Neggs_i$ depending on the mother i weight.

$$EggW_i = \frac{\exp(aWegg * \log(W_i) + bWegg)}{10000}$$

$$Neggs_i = \exp(aNegg * \log(W_i) + bNegg)$$

Where $aWegg$, $bWegg$, $aNegg$ and $bNegg$ are population parameters (Piou & Prévost 2012).

Finally, for each redd i, each anadromous male k fertilizes a number of eggs ($NFertilized_{k,i}$) depending on its relative weight compared to all the other males (anadromous and parrs).

$$NFertilized_{k,i} = \frac{W_k^{aFert}}{\sum_s^{allmales_i} W_s^{aFert}} * Neggs_i$$

Where $allmales_i$ representing all the selected males for the redd i and $aFert$ a parameter adjusting the advantage due to weight (Piou & Prévost 2012).

The number of eggs fertilized by the selected mature parrs (identical number between parrs) depends on the relative weight of them compared to the weights of all the other males (anadromous and parrs).

$$NFertilizedParrs_i = \frac{\sum_k^{Nparrs_i} W_k^{aFert}}{\sum_s^{allmales_i} W_s^{aFert}} * \frac{Neggs_i}{Nparrs_i}$$

Suppl. mat. 2: Immigrants/Emigrants ratio, averaged over the last 5 years, for each population for a gradient of dispersal. Means values and 95% intervals over simulations are represented.

| Population	10%	20%	30%	40%	50%	60%	70%	80%	90%	100%
Leff	2.68	2.24	2.14	1.92	1.85	1.98	1.94	1.83	1.85	1.95
	[1.31;3.95]	[1.22;3.89]	[1.29;3.97]	[1.34;2.72]	[1.29;2.46]	[1.42;2.76]	[1.35;2.76]	[1.40;2.55]	[1.44;2.58]	[1.39;2.68]
Trieux	0.48	0.53	0.54	0.61	0.62	0.59	0.66	0.68	0.71	0.74
	[0.23;0.74]	[0.32;1.07]	[0.37;0.82]	[0.42;0.96]	[0.42;0.92]	[0.43;0.90]	[0.48;1.13]	[0.51;0.89]	[0.52;0.92]	[0.52;1.03]
Jaudy	2.79	2.90	2.51	2.10	1.90	1.91	1.81	1.77	1.64	1.40
	[0.78;5.60]	[1.38;5.04]	[1.18;5.55]	[1.40;3.15]	[1.14;2.89]	[1.40;2.75]	[1.16;2.47]	[1.11;2.45]	[1.14;2.52]	[1.05;1.78]
Leguer	0.60	0.57	0.64	0.55	0.66	0.65	0.65	0.64	0.67	0.73
	[0.25;1.37]	[0.36;1.06]	[0.44;1.34]	[0.40;0.86]	[0.46;0.97]	[0.43;0.88]	[0.42;0.91]	[0.43;0.88]	[0.44;0.91]	[0.50;1.19]
Yar	3.89	4.28	4.06	3.95	3.33	3.18	3.09	3.01	2.92	2.59
	[1.97;6.73]	[2.10;6.76]	[2.42;7.63]	[2.37;7.84]	[2.14;5.19]	[1.99;4.66]	[2.04;4.70]	[1.81;4.36]	[1.96;4.15]	[1.79;3.79]
Douron	1.78	1.45	1.39	1.22	1.12	1.11	0.98	1.03	0.97	0.94
	[0.86;3.71]	[0.92;2.19]	[0.74;3.37]	[0.95;1.57]	[0.64;1.82]	[0.77;1.53]	[0.71;1.34]	[0.67;1.41]	[0.59;1.37]	[0.64;1.31]
Penze	0.81	0.79	0.70	0.77	0.65	0.66	0.83	0.72	0.73	0.74
	[0.34;1.64]	[0.41;1.27]	[0.43;1.17]	[0.42;1.65]	[0.40;1.09]	[0.40;1.14]	[0.47;1.44]	[0.33;1.24]	[0.42;1.30]	[0.43;1.23]
Elorn	1.25	1.36	1.27	1.21	1.22	1.20	1.21	1.24	1.20	1.24
	[0.78;1.82]	[0.86;2.48]	[0.89;1.81]	[0.86;1.72]	[0.78;1.63]	[0.90;1.70]	[0.96;1.54]	[0.94;1.55]	[0.91;1.54]	[1.03;1.58]
Aulne	0.80	0.74	0.81	0.80	0.84	0.85	0.87	0.86	0.90	0.88
	[0.52;1.54]	[0.45;1.04]	[0.53;1.11]	[0.58;1.11]	[0.61;1.29]	[0.55;1.10]	[0.68;1.16]	[0.65;1.09]	[0.66;1.22]	[0.67;1.10]
Goyen	2.47	2.70	1.92	2.19	2.01	2.02	1.84	1.73	1.62	1.58
	[1.28;4.47]	[1.71;4.64]	[1.25;2.95]	[1.56;3.41]	[1.38;2.98]	[1.34;3.15]	[1.24;2.50]	[1.31;2.39]	[1.20;2.20]	[1.08;2.25]
Odet	0.79	0.72	0.78	0.75	0.77	0.77	0.80	0.85	0.89	0.82
	[0.42;1.47]	[0.56;0.93]	[0.58;1.08]	[0.58;0.93]	[0.59;0.98]	[0.55;0.96]	[0.67;1.03]	[0.64;1.08]	[0.68;1.17]	[0.65;1.02]
Aven	2.99	2.50	2.39	2.30	2.23	2.31	2.22	2.20	2.21	2.32
	[1.97;4.96]	[1.85;3.92]	[1.80;3.07]	[1.89;3.15]	[1.79;2.69]	[1.76;3.09]	[1.62;2.76]	[1.75;2.71]	[1.81;2.72]	[1.78;3.22]
Laïta	0.48	0.54	0.54	0.57	0.58	0.60	0.64	0.61	0.63	0.64
	[0.34;0.65]	[0.41;0.73]	[0.40;0.68]	[0.45;0.78]	[0.49;0.67]	[0.50;0.80]	[0.51;0.87]	[0.51;0.77]	[0.47;0.82]	[0.51;0.83]
Scorff	2.12	1.62	1.60	1.53	1.43	1.30	1.26	1.27	1.14	1.16
	[1.26;3.85]	[1.19;2.24]	[1.23;2.01]	[1.20;2.19]	[1.07;1.80]	[1.06;1.65]	[0.96;1.61]	[0.98;1.66]	[0.88;1.39]	[0.92;1.41]
Blavet	1.21	1.07	1.05	0.97	0.97	0.96	0.91	0.86	0.89	0.84
	[0.72;1.84]	[0.85;1.39]	[0.85;1.34]	[0.76;1.24]	[0.72;1.27]	[0.77;1.10]	[0.69;1.07]	[0.71;1.04]	[0.72;1.16]	[0.65;1.19]

Suppl. mat. 3: Parameters of stock-recruitment relationship and for the dispersal kernel implemented in the model MetaIBASAM for each population.

| Population j	Distance from Leff (km)	A_j (m²)	α_j (0+/eggs)	$Rmax_j$ (parr 0+/100m²)	M_j
Leff	0	72305	0.14777	20.38	1.53212
Trieux	0	213733	0.095890	13.47	1.00577
Jaudy	16	47561	0.178551	24.49	1.83879
Leguer	67	197283	0.164441	23.26	1.72520
Yar	77	37104	0.086614	11.87	0.89531
Douron	82	95451	0.160152	22.46	1.67624
Penze	106	106753	0.250490	35.13	2.61598
Elorn	232	164699	0.195026	27.54	2.04296
Aulne	254	252659	0.031885	4.41	0.33096
Goyen	317	53603	0.229613	32.34	2.39536
Odet	369	249049	0.185059	25.87	1.93216
Aven	403	142686	0.12444	17.14	1.28727
Laïta	420	669028	0.13271	18.62	1.38259
Scorff	438	229027	0.09588	13.4	1
Blavet	438	326121	0.07665	10.75	0.79715

Suppl. mat. 4: Survival rates at different stages implemented in MetaIBASAM.

| Life stage	Survival rate
Parr < 6 months	0.9841606*1.0025
Parr between 6 months and 1 year	0.9914398*1.0025
Parr between 6 and 1 year maturing	0.9863295*1.002
Parr future smolts	0.9967923*1.002
Other parr	0.99775*1.002
Parr > 1 year maturing	0.9911798*1.002

Distributions of simulation replicates of the success of early mature strategy (males parr 1+), averaged by type of population over the last 5 years, as a function of dispersal rates from 0% to 40%. The success of the early mature strategy is represented by the proportion of eggs in a redd fertilized by mature parrs. Means (circles) and 95% intervals (lines) are reported.
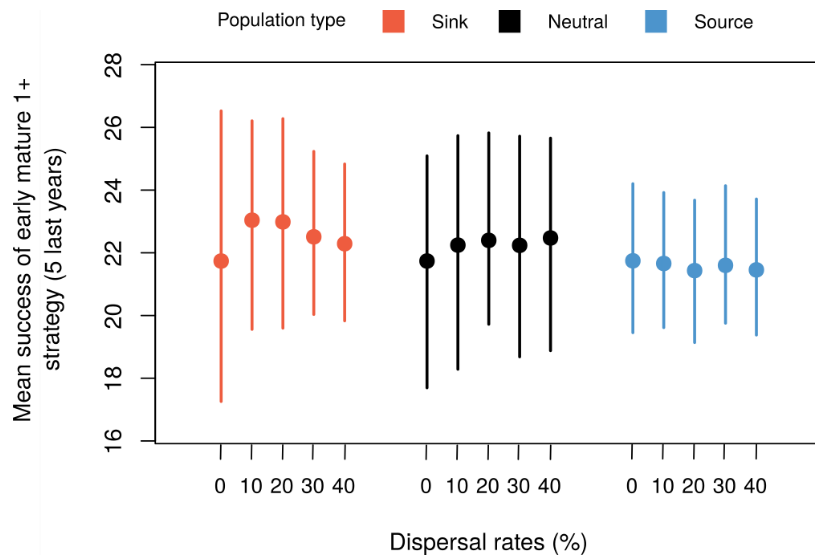
Suppl.mat.6: Distributions of simulation replicates of (a) 1SW and (b) MSW anadromous size (in mm), averaged by type of population over the last 5 years, as a function of dispersal rates from 0% to 40%. Means (circles) and 95% intervals (lines) are reported.
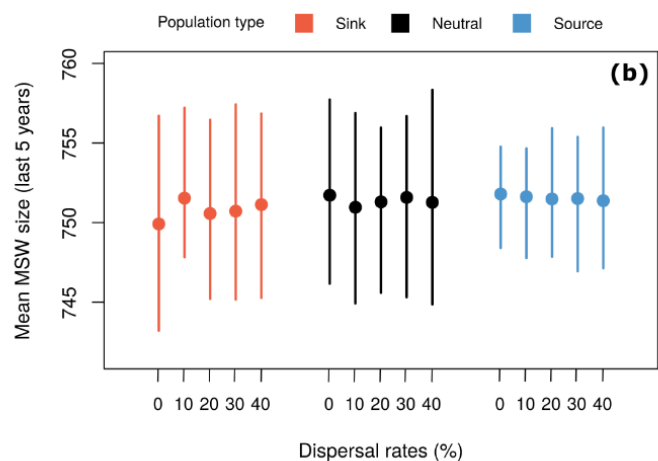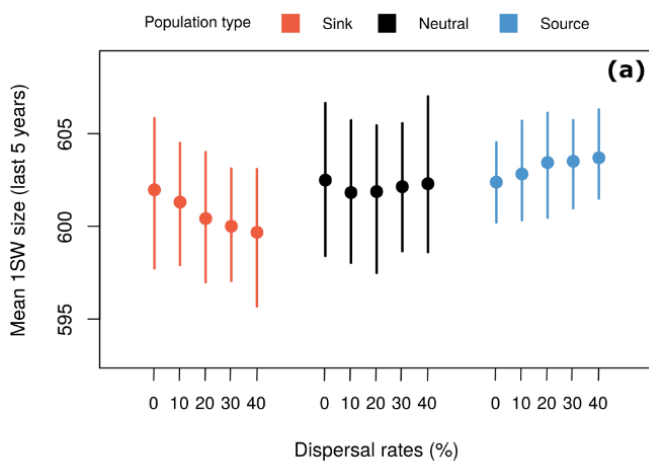
Stock recruitment relationships obtained for each population via MetaIBASAM. The stock is the number of eggs by 100m² and the recruitment is the number of parr 0+ by 100m². The filled line represents the theoretical relationship based on C. Lebot estimations for each population and the dashed line represents the Scorff's one.
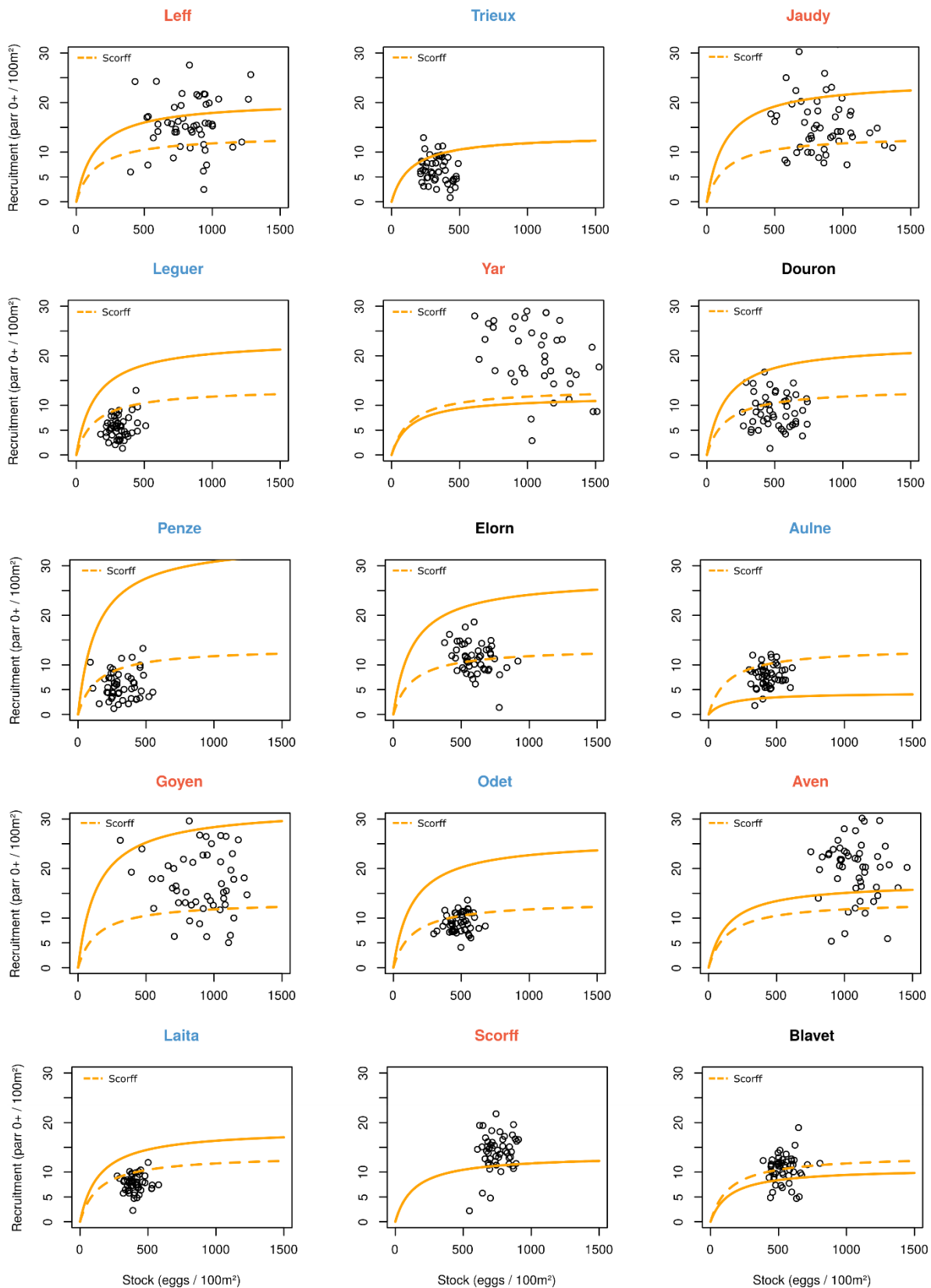
Contribution	Original idea	Bibliography	Simulations running	Results exploration	Results selection	Redaction
Main	MB	AL	AL	AL	AL	AL
Secondary		MB			MB, SC	MB, SC

AL: Amaïa Lamarins; MB: Mathieu Buoro; SC: Stephanie Carlson

Task	March	April	May	June	July	August
Bibliography	■				■	■
Simulations running		■			■	
Results exploration		■	■	■	■	
Results selection				■	■	
Redaction					■	■