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Amaia Lamarins

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UNIVERSITY OF PAU AND PAYS DE L'ADOUR

DOCTORAL SCHOOL 211 - SCIENCES EXACTES ET LEURS APPLICATIONS

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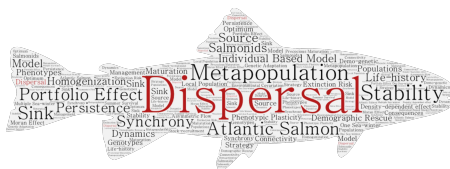
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Adaptation, persistence and management of Atlantic salmon in a metapopulation context

Defended on December 7th, 2022, by

Amaïa LAMARINS



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Abstract

In a context of rapid environmental changes and anthropogenic pressures, there is an urgent need to better understand the responses of species and to provide recommendations on how we can manage and conciliate human activities with the functioning of ecosystems. However, there is often a mismatch between the scale of species functioning, threats, and management actions. In particular, even if dispersal is a ubiquitous trait in organisms, implications of connectivity and spatial structure for adaptation, persistence, and management of populations are still poorly appreciated for numerous species. This is the case of Atlantic salmon (*Salmo salar*), for which eco-evolutionary dynamics, exploitation and management of populations are rarely considered within a metapopulation perspective. Yet, growing evidence shows individuals and gene flow among populations of salmon. Motivated by this context, this thesis aims to use an innovative multi-scale approach, from genes to metapopulation, to 1) better understand the capacities of adaptation and persistence of exploited populations of Atlantic salmon and 2) explore management practices that would meet both objectives of conservation and exploitation. Using a spatially explicit demo-genetic agent-based model, I simulated a network of interconnected populations of Atlantic salmon based on the metapopulation of Brittany. Through several scenarios, I explored the influence of a gradient of dispersal rates, various spatial genetic structures, the spatial configuration of populations, and spatial management strategies on the demographic (e.g., stability, persistence) and eco-evolutionary (e.g., life history traits, genetic diversity) dynamics of interconnected and exploited local populations. This thesis highlighted a non-linear relationship between dispersal rates and the stability of the metapopulation, resulting in an optimal portfolio effect for dispersal rates around 20% in a homogeneous network. At local population scale, I demonstrated phenotypic changes induced by density-dependent effects modulated by dispersal, as well as an increase in genetic diversity within populations. Simulations also showed adaptation of local populations was fostered by dispersal between initially diverse populations, providing general support for the adaptation network theory. However, the spatial configuration of populations also played an important role in their evolutionary trajectories by modulating dispersal patterns. Ultimately, this thesis showcased a slight benefit from a spatialized management strategy protecting source populations from exploitation, especially for high dispersal rates. Contrasted and complex evolutionary consequences emerged from the different

management strategies in interaction with dispersal. I conclude that it is critical to account for complex interactions between dispersal, eco-evolutionary processes, and spatial structure of populations to better understand and manage Atlantic salmon response to environmental change and anthropogenic pressures. This thesis also encourages empirical knowledge about dispersal rates and metapopulation structure of this species, and advocates for conservation actions according to the portfolio and adaptation network approach, protecting connectivity and biocomplexity in the face of uncertainty. My thesis opens up further perspective of work and illustrates the potential of our modelling approach as a prospecting tool for theoretical and applied research on metapopulations.

Keywords: dispersal, spatial structure, adaptation network, management, Atlantic salmon, exploitation, model, demo-genetic, portfolio effect

Résumé

Dans un contexte de changements environnementaux rapides et de pressions anthropiques, il est urgent de mieux comprendre les réponses des espèces et d'apporter des recommandations sur la manière de gérer et de concilier les activités humaines avec le fonctionnement des écosystèmes. Cependant, il existe bien souvent un décalage entre l'échelle du fonctionnement des espèces, celle de leurs menaces, et celle des actions de gestion. En particulier, bien que la dispersion soit un trait ubiquité parmi les organismes, les implications de la connectivité et de la structure spatiale pour l'adaptation, la persistance, et la gestion des populations sont encore peu considérées pour de nombreuses espèces. Cela est le cas du saumon Atlantique (*Salmo salar*), une espèce pour laquelle les dynamiques éco-évolutives, l'exploitation et la gestion des populations sont rarement appréhendées dans une perspective métapopulationnelle. Pourtant, des évidences croissantes montrent des flux d'individus et de gènes entre populations de saumon. Motivée par ce contexte, cette thèse a pour objectif d'utiliser une approche innovante et multi-échelle, du gène à la métapopulation, afin de 1) mieux comprendre les capacités d'adaptation et de persistance de populations exploitées de saumon Atlantique et 2) d'explorer des pratiques de gestion qui respecteraient des objectifs de conservation mais aussi d'exploitation. À l'aide d'un modèle démo-génétique à base d'agent et spatialement explicite, j'ai simulé un réseau de populations interconnectées de saumon Atlantique basé sur la métapopulation de Bretagne. À travers plusieurs scénarios, j'ai exploré l'influence d'un gradient de taux de dispersion, de diverses structures génétiques spatiales, de la configuration spatiale des populations, et de stratégies de gestion spatialisées sur les dynamiques démographiques (e.g., stabilité, persistance) et éco-évolutives (e.g., traits d'histoire de vie, diversité génétique) de populations locales interconnectées et exploitées. Cette thèse a mis en évidence une relation non-linéaire entre les taux de dispersion et la stabilité de la métapopulation, avec un effet portfolio optimal pour des taux de dispersion autour de 20% pour un réseau homogène. À l'échelle des populations locales, j'ai démontré des changements phénotypiques induits par des effets densité-dépendants modulés par la dispersion, ainsi qu'une augmentation de la diversité génétique au sein des populations. Les simulations ont également montré que l'adaptation des populations locales était favorisée par la dispersion entre des populations initialement diversifiées, confortant ainsi la théorie des réseaux d'adaptation. Cependant, la configuration spatiale des

populations a également joué un rôle important sur leurs trajectoires évolutives en modulant les patrons de dispersion. Enfin, cette thèse a illustré un léger avantage pour une stratégie de gestion protégeant les populations sources de l'exploitation, en particulier pour des taux de dispersion élevés. Des conséquences évolutives contrastées et complexes ont également émergé des différentes stratégies de gestion en interaction avec la dispersion. Je conclus de cette thèse qu'il est essentiel de tenir compte des interactions complexes entre la dispersion, les processus éco-évolutifs et la structure spatiale des populations pour mieux comprendre et gérer la réponse du saumon Atlantique aux changements environnementaux et aux pressions anthropiques. Cette thèse encourage également les connaissances empiriques sur les taux de dispersion et la structure des métapopulations de cette espèce, et plaide pour des actions de conservation selon l'approche portfolio et de réseau d'adaptation, en protégeant la connectivité et la biocomplexité. Ma thèse ouvre de nouvelles perspectives de travail et illustre le potentiel de notre approche de modélisation comme outil de prospective pour la recherche théorique et appliquée sur les métapopulations.

Mots-clés: dispersion, structure spatiale, réseau d'adaptation, gestion, saumon Atlantique, exploitation, modèle, démo-génétique, effet portfolio

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Introduction

Rapid environmental changes and anthropogenic pressures such as exploitation, contamination, fragmentation and climate change lead to a global decline of biodiversity, threatening ecosystems functioning and the services they provide to the human society. With these increasing pressures, conflicting demands emerge between conservation and exploitation of natural resources among stakeholders which manifest themselves at local, regional and global scales. In this context, there is an urgent need to better understand response of species to these pressures and to provide recommendations on how we can manage and conciliate human activities with the functioning of species and ecosystems. This is particularly critical for aquatic ecosystems which face many threats (e.g., water extirpation, loss of connectivity) and provide resources to the society, economy, and human welfare.

However, there is often a mismatch between the scale of species functioning, threats, and management actions. In particular, *population* is usually the scale of study and management (e.g., a river, a meadow) while most populations of species are spatially interconnected by movement of individuals, i.e., dispersal, and form a *metapopulation*. This metapopulation functioning might have consequences on the ability of species to respond to environmental changes but also for their management. Moreover, increasing attention is given for a more comprehensive consideration of the processes facilitating the adaptation of organisms to changing ecosystems, which include acclimatization (phenotypic plasticity), genetically based evolution through natural selection (also known as genetic adaptation), and movement toward more suitable habitats (dispersal). Considering the multiple eco-evolutionary processes as well as their interactions is then mandatory to appreciate the response of organisms. Finally, there is also a mounting interest in the value of diversity for the persistence, resilience and management of populations. We need to adopt a portfolio approach by considering and protecting the biocomplexity at multiple levels (from genes to ecosystems) in the face of upcoming and unpredictable environmental changes.

This thesis focuses on a salmonid species, the Atlantic salmon (*Salmo salar*). Salmonids species, and Atlantic salmon in particular, are relevant species in this

context. They are emblematic, patrimonial, economic, threatened species, for which there is a strong demand for improving their conservation while maintaining their exploitation. They are also characterized by a broad diversity of life histories, which give them great interest in the context of the portfolio approach. Importantly, salmonids are emblematic species of philopatry (commonly called *homing* in the Salmosphere) and the implications of dispersal are particularly overlooked for their management.

Motivated by this context, this thesis aims to use an innovative multi-scale approach (from genes to metapopulation) to 1) better understand the capacities of adaptation and persistence of exploited populations of Atlantic salmon and 2) explore management practices that would meet both objectives of conservation and exploitation within a metapopulation framework. The main questions I investigated are the following:

How connectivity (i.e., metapopulation functioning) and diversity influence meta-populations eco-evolutionary dynamics, stability and persistence?

Are there management strategies that meet both conservation and exploitation objectives by considering metapopulation structure?

In this introductory chapter, I introduce the main knowledge and identify gaps in the field covered by the thesis, i.e., metapopulation eco-evolutionary dynamics, management, within the context of salmonids and more specifically of Atlantic salmon. After having identified the main gaps, I decline the objectives of the thesis and introduce the following chapters and the manuscript structure.

1.1 METAPOPOPULATION ECO-EVOLUTIONARY DYNAMICS, PERSISTENCE AND MANAGEMENT

1.1.1 Species facing environmental changes

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. The persistence of species facing environmental changes is strongly related to their capacity of adaptation via eco-evolutionary processes (Reed et al., 2011b). In a simple way, species either accommodate, adapt, move, or disappear. Indeed, eco-evolutionary processes include the processes of acclimatization (i.e., phenotypic plasticity, or accommodation) and genetically based evolution through natural selection (i.e., genetic adaptation; Ghalambor et al., 2007; Brandon, 2014). Dispersal, whether spatial or temporal, can also favor species responses to environmental changes by spreading the risk of reproductive failure (Buoro and Carlson, 2014).

1.1.2 Spatial dispersal: a multicausal life history trait

1.1.2.1 Dispersal definition

Spatial dispersal (hereafter dispersal) can be defined as the movement of individuals between the natal area and the first breeding area (natal dispersal), or between two successive breeding areas (breeding dispersal), with potential consequences for gene flow (Clobert et al., 2001; Ronce, 2007; Matthysen, 2012). Dispersal is often named "migration" but I consider the migration term referring to any movement of individual without an ultimate influence on reproduction location, such as seasonal migration. 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). It can be active (e.g., a bird flight between two forests) or passive (e.g., a seed falling from a tree). Dispersal is thus highly variable, ranging from small passive movements to complex processes involving exploration behavior and social interactions (Matthysen, 2012). A conceptual approach described dispersal as a multi-phase life history process (Clobert et al., 2009), composed of the three following stages : i) emigration or departure (leaving natal habitat), ii) transfer or transience (movement), and iii) immigration or settlement (arrival in the novel habitat). Dispersal decisions often rely on information of individuals themselves and their environment (biotic,

abiotic, social; informed dispersal, [Clobert et al., 2009](#)).

1.1.2.2 Multicausality of dispersal

Dispersal is known to be multicausal ([Matthysen, 2012](#)), i.e. a diversity of proximate causes, non exclusive, are identified in the literature. Each of the three stages (emigration, transfer, and immigration) can be influenced by i) individual phenotypic condition (e.g., size, [Anholt, 1990](#); sex, [Li and Kokko, 2019](#)), ii) environmental factors (e.g., kin competition, [Moore et al., 2006](#)), and social interactions, as well as their interactions ([Box 1.1](#); [Clobert et al., 2009](#); [Matthysen, 2012](#); [Bitume et al., 2013](#)).

Box 1.1: Proximate causes of dispersal

Phenotypic-dependence

In a similar environment, some individuals will disperse whereas others will not, i.e. dispersal is not random, which may explain phenotypic variation between dispersing and philopatric individuals ([Cote et al., 2010](#)). Inter-individual variation in dispersal propensity can be related to several phenotypic traits ([Bowler and Benton, 2005](#); [Clobert et al., 2009](#)) and involves suites of traits (dispersal syndromes, [Clobert et al., 2009](#); [Cote et al., 2010](#)). For instance, sex-biased dispersal is very common in the animal kingdom ([Gros et al., 2008](#); [Li and Kokko, 2019](#)), while age and body size are also individual traits which may trigger dispersal ([Dufty and Belthoff, 2001](#)). An active metabolism combined with strong wing muscles and an appropriate body shape is an example of a dispersal syndrome in insects that rely on wings to disperse long distances ([Zera and Denno, 1997](#)). These inter-individual variations often interact with the context or condition in which individuals are (see condition-dependence).

Condition-dependence

Individuals often evolve in a spatially and temporally variable environment, and their internal propensity to disperse is largely interacting with external factors of their environment (abiotic and biotic, [Bowler and Benton, 2005](#); [Clobert et al., 2009](#), [Fig. 1.1](#)). According to a large body of literature, the main factors reported in empirical studies are listed below:

- **Density:** during the emigration process, positive density-dependent propensity to disperse has been demonstrated for a diversity of taxa (e.g.,

vole, Aars and Ims, 2000, spider, De Meester and Bonte, 2010, butterfly, Nowicki and Vrabec, 2011), reducing exploitative and interference competitive interactions (Bowler and Benton, 2005). By contrast, other studies demonstrated negative density-dependent relationship between emigration rate and density (e.g., Ims and Andreassen, 2005). Group-living advantages such as predation dilution, facilitation of foraging and mating opportunities, and other Allee effects may explain this pattern. However, the combination of these different factors is often not well represented by linear relationships and more complex shapes are expected (Kim et al., 2009; Harman et al., 2020). During the settlement process, density dependent immigration is also observed when larger population sizes reflect favourable environmental conditions and attract more immigrants (e.g., Fernández-Chacón et al., 2013).

- **Habitat quality:** closely related to population density, the quality of an habitat may influence emigration behavior, such as food availability (Hanski et al., 2002). Habitat quality may also influence immigration process; empirical evidence showed greater immigration into higher quality patches (Schneider et al., 2003).
- **Interspecific interactions:** competitive, host-parasite, prey-predator interactions with other species may also determine the suitability of an habitat for an individual and dispersal (Bowler and Benton, 2005).
- **Sex ratio:** variation in dispersal may emerge from variation in the sex ratio if competition is asymmetric between sex and if the sex ratio determines the mating success (Colwell and Naeem, 1999).
- **Relatedness:** dispersal can be triggered to avoid inbreeding and kin competition by kinship of individuals in the same habitat. This proximate cause assumes that individuals have the capacity for kin recognition (Bitume et al., 2013).
- **Patch size and isolation:** as a result of the edge to size ratios, patch size is negatively correlated with emigration rate for a variety of taxa (e.g., butterflies, Baguette et al., 2000, other insects, Kindvall, 1999, voles, Andreassen and Ims, 2001), although confounding effects of covarying

factors such as density (Hambäck and Englund, 2005) or relatedness (Léna et al., 1998) may explain these patterns. Patch size can also affect immigration by increasing the probability to be located by a dispersing animal (Kindvall and Petersson, 2000). Additionally, the isolation of a patch can determine the chance on successful movement due to the accumulating costs of dispersal with distance moved (Bowler and Benton, 2005).

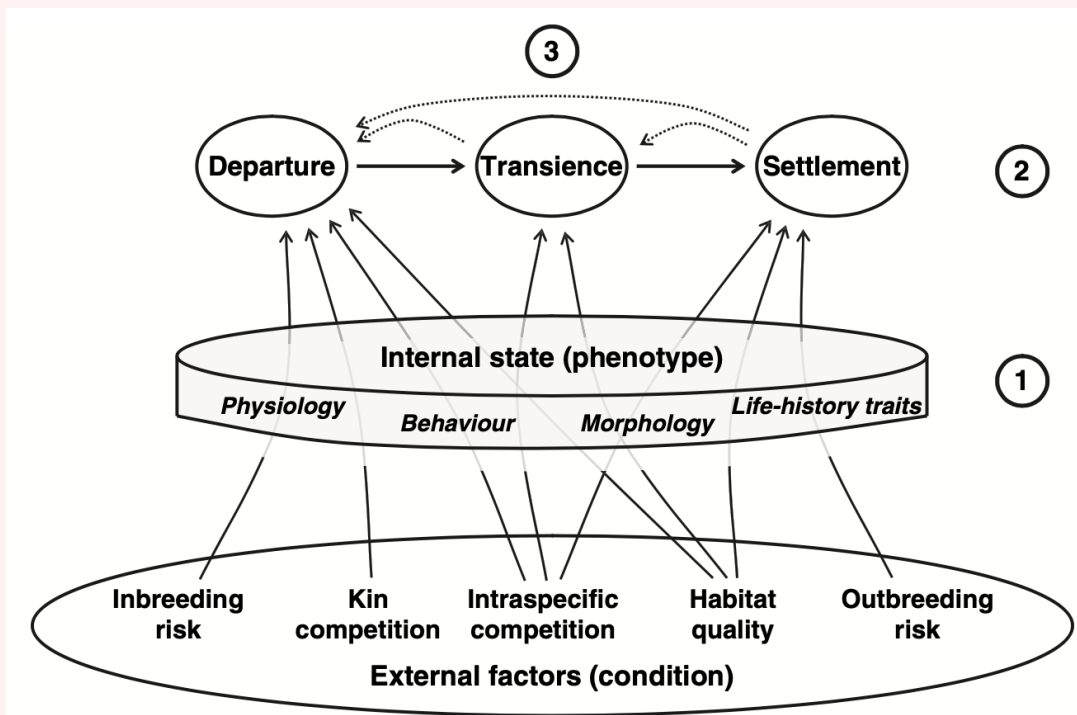


Figure 1.1: Conceptual framework of the proximate causes influencing dispersal. Internal (phenotypic-dependence) and external (condition-dependence) factors can influence each of the three dispersal stages. From Clobert et al., 2009.

This very brief overview highlights the diversity of factors which, in interaction, may influence dispersal at the individual level. Note also that the shapes of condition-dependent dispersal relationships are not fixed and may evolve (Kisdi, 2012). Globally, conditional dispersal enables organisms to escape local unfavorable conditions and to prospect actively for more favourable conditions (Matthysen, 2012) over the short term.

1.1.2.3 Fitness and ultimate causes of dispersal

Even if dispersal behavior is likely to be triggered by the proximal causes, dispersal is also driven by ultimate causes (Box 1.2). Indeed, the interindividual variability in dispersal propensity is very likely to have a genetic basis (Saastamoinen et al., 2018), especially via the genetic basis of the multiple traits that contribute to the capacity to disperse (e.g., production of wings, Zera and Brisson, 2012). Occurring at the individual scale, the dispersal behavior is characterized by several costs and benefits and can be under selection to reduce its costs and maximize individual fitness (Bonte et al., 2014). From an evolutionary perspective, the evolution of dispersal as a life-history strategy results from the balance between these costs and benefits, i.e., dispersal is adaptive when the gain in fitness of moving to a new location is higher than its costs (Box 1.2). Importantly, inclusive fitness (Hamilton, 1964), i.e., direct individual fitness added to the fitness of kins weighted by their relatedness, has to be considered to fully understand the costs-benefits balance driving dispersal.

Box 1.2: Ultimate causes of dispersal

Ultimate causes of dispersal which favor the evolution of dispersal traits include (Gandon and Michalakis, 2001; Bowler and Benton, 2005):

- **Competition avoidance:** by leaving crowded habitats and settling in low density environments, dispersal behavior may reduce deleterious effects of mate and resource competition with conspecifics or heterospecifics (Bitume et al., 2013), and allows to prospect for more favorable conditions (e.g., availability and quality of mates).
- **Kin interactions:** kin selection on individuals selects for traits which increase inclusive fitness, i.e., the fitness of the individual and its relatives, despite the direct costs of the trait (Hamilton, 1964). Thus, dispersal can be selected for to limit kin competition within the population of birth and spread competition among other populations with non siblings individuals. Kin competition has been the cornerstone of theoretical arguments for the evolution of dispersal in stable environments. It was first showcased by Hamilton and May (1977) and further demonstrated by several studies (Gandon and Michalakis, 1999; Bach et al., 2006; Poethke et al., 2007). Conversely, philopatry may be selected for in the case of cooperative behavior between related individuals (García-Ruiz et al., 2022).

- **Inbreeding avoidance:** the deleterious effects of inbreeding are expected to select for dispersal, allowing related individuals to be spread over habitats (Gandon, 1999).
- **Habitat stochasticity:** Theoretical studies showed that stochasticity in demographic dynamics (Travis and Dytham, 1998) and patch quality should select for dispersal (McPeck and Holt, 1992), although it might not always be the case (Poethke et al., 2003). From the viewpoint of reproducing individuals, dispersal can be seen as a risk spreading (Den Boer, 1968) or bet hedging strategy: dispersal increases the variance in expected fitness by distributing offspring from the same parents over different conditions of several habitat patches.

Costs associated with dispersal are also multiple; they may be classified into energetic (e.g., movement energetic expenditure), time (e.g., time not invested in foraging behavior), risk (e.g., predation risk), and indirect opportunity costs (e.g., quality of destination habitat), as defined in Bonte et al. (2012), and may apply during the three stages of the dispersal process. Departure costs gather the cost of development of structures enabling dispersal (e.g., wings) at the expense of fitness related life history traits (e.g., body size, Solbreck, 1986, mating opportunities, Sack and Stern, 2007), of exploration and preparation behaviors (Young and Monfort, 2009). During the transfer phase, the energetic cost of movement (Roff, 1977) and increased mortality probability due to predation exposure or resource limitation (e.g., Pietrek et al., 2009) are often the main costs identified. Lastly, settlement costs include mortality in unsuitable or crowded habitats (Ólafsson et al., 1994) or lower fitness in the recipient environment because of local adaptation (outbreeding, Marr et al., 2002).

Thus, dispersal may emerge as a life history strategy related to individual fitness, but can also affect ecological and evolutionary patterns by modifying population dynamics (via the movement of individuals) and population genetics (through gene flow). In turn, population dynamics and genetics may influence selective pressures on dispersal-related traits and feedback on the evolution of dispersal. Density-dependence of dispersal is the most evident way of feedback between dispersal and population dynamics (Clobert et al., 2004). Dispersal thus appears as a central trait in ecological and evolutionary processes of species, and is central to the theory of metapopulations

by favoring the flow of individuals among inter-connected populations with potential consequences for metapopulation eco-evolutionary dynamics, stability, and persistence.

1.1.3 Metapopulation eco-evolutionary dynamics

1.1.3.1 Metapopulation definition

A metapopulation can be defined as an assemblage of spatially discrete populations (hereafter local populations) of the same species, connected together by some degree of dispersal (Levins, 1969, 1970). Given that species commonly occupy metapopulations naturally, and the rate and scale at which habitat fragmentation is occurring around the globe (Harrison and Bruna, 1999), developing conceptual frameworks to describe spatial population dynamics is a central focus of conservation biology (Tilman and Kareiva, 1997; Dieckmann et al., 2000; Marsh and Trenham, 2001).

Levin's metapopulation model and theory first formalized the process of local extinction and colonization of a collection of patches that are either occupied or vacant, which is characteristic of metapopulations (Levins, 1969, 1970). The simplicity of this model made it very powerful and provided key insight on the regional persistence, despite local extinctions, provided by metapopulation functioning and sufficient dispersal among patches. This work initiated a large body of theoretical and experimental work on metapopulation ecology and raised awareness of the significance of spatial structure for population dynamics.

Further, metapopulation theory was extended by Hanski (2004), who integrated and highlighted the influence of population size and isolation on patches turnover rate into his model (Hanski, 1998). It was followed by several variants from structured metapopulation models including demographic dynamics of patches (Gyllenberg et al., 1997) and ultimately spatially explicit models (Hanski, 1994).

Metapopulation theory may be applied to a broad range of organisms which occupy spatially distinct habitats interconnected by dispersal, and thus a large range of metapopulation structures may be encountered. Several types of metapopulations have been described based on patch configuration (size and distance), the level of connectivity, and the relative rates of extinction and colonisation (Box 1.3 Fig. 1.2; Harrison, 1991; Harrison and Taylor, 1997).

Box 1.3: Metapopulation types

- The **classical Levins-type** metapopulation is characterized by local populations occupying discrete patches of suitable habitat at substantial risk of extinction, with potential colonization, leading to a high population turnover among patches and an intermediate occupancy.
- The **mainland-island** metapopulation type is very close to the island biogeography theory (MacArthur and Wilson, 1963, 1967) that was developed in parallel and in interaction with the metapopulation theory. It is characterized by high levels of variation in patch size and asymmetrical connectivity, with individuals occupying small and isolated patches and larger patches constituting a mainland source. **Source-sink dynamics** (Pulliam, 1988) follow the same type of metapopulation, but movement of individuals between patches is driven by differences in patch quality rather than patch size. Excess individuals from highly productive patches (sources) disperse to low productivity patches (sinks) that cannot support populations on their own (Pulliam, 1988; Dias, 1996). Dispersal may thus allow a species to occur at sites where local recruitment alone would not be sufficient for population persistence.
- The **patchy** populations type presents high levels of connectivity and may occur when colonisation exceeds extinction.
- Conversely, **non-equilibrium** populations type occurs when local extinction greatly exceeds colonisation so that vacant patches are never or very rarely re-colonised. If local extinction is high, non-equilibrium populations eventually become extinct.

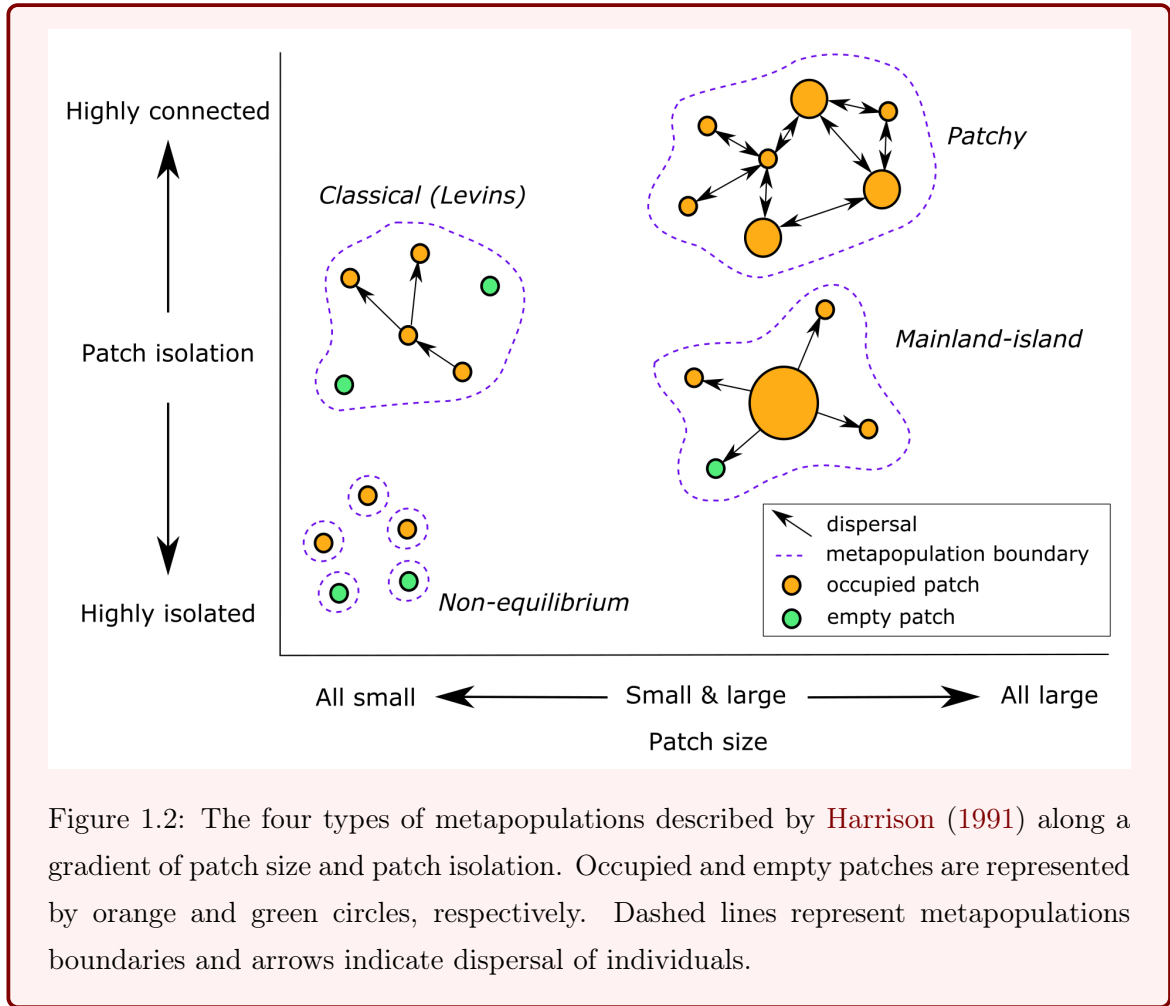


Figure 1.2: The four types of metapopulations described by [Harrison \(1991\)](#) along a gradient of patch size and patch isolation. Occupied and empty patches are represented by orange and green circles, respectively. Dashed lines represent metapopulations boundaries and arrows indicate dispersal of individuals.

The omnipresence in nature of classical metapopulations was recently questioned and most spatially structured populations can be classified as patchy or mainland-island metapopulations ([Fronhofer et al., 2012](#)). Although it is tempting to classify different spatially structured populations into different metapopulation types for the ease of use ([Harrison and Taylor, 1997](#)), the existence of a great diversity of landscapes most probably leads to a great diversity of “metapopulation structures” ([Hanski and Gaggiotti, 2004a](#)). Thinking in terms of metapopulation types with delineated patches can be conceptually useful but should be considered a simplification.

1.1.3.2 Dispersal and metapopulation eco-evolutionary dynamics

Dispersal, via the movements of individuals and gene flow, may strongly affect the eco-evolutionary dynamics of local populations and metapopulations as a whole.

Demographic consequences

First, from a demographic perspective, dispersal of individuals from neighbouring occupied patches favors long-term persistence of metapopulations by the colonisation of new patches during range expansion or the recolonisation of patches that has gone extinct (Ebenhard, 1991). This process is a crucial component of metapopulations; while single population may not survive for long, the movement of individuals between patches ensures metapopulations can persist in the long-term. The immigration of individuals into small populations close to extinction, known as demographic rescue effect (Brown and Kodric-Brown, 1977; Hill et al., 2002), is also an essential positive effect of dispersal which may greatly contribute to local populations growth (Reichert et al., 2021) and reduce risk of extinction. However, a strong level of connectivity between populations have been shown to increase population synchrony and the probability of simultaneous extinctions (Heino et al., 1997). Dispersal can indeed act to synchronize population dynamics over a spatial scale that depends on dispersal distance (Lande et al., 1999; Paradis et al., 1999; Ranta et al., 1999; Larroque et al., 2019) and with an intensity which depends on dispersal level. In experimental metapopulations of drosophila, high rates of dispersal led to population synchrony while lower rates did not (Dey and Joshi, 2006).

Direct and plastic phenotypic changes

From an evolutionary perspective, the immigration of individuals into populations may also have phenotypic effects. These phenotypic effects may be direct, especially in the case of non random dispersal with respect to phenotype, changing the distribution of phenotypes in the populations to which and from individuals migrate (Benton and Bowler, 2012). More indirectly, phenotypic changes might also be induced by changes of population dynamics via plasticity. For instance, changes of local densities, stage-structure, and competition induced by migration patterns can influence life history traits (see chapter 3). Moreover, 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 (Pacoureaux et al., 2017), and even sexual selection (Clutton-Brock et al., 1997), and all of these factors can influence the dynamics of populations.

Evolutionary consequences

Moreover, dispersal can induce gene flow altering the genetic composition within and between populations (Barton, 1992). Individual movements away from a patch can also reduce inbreeding and its deleterious effects (Keller and Waller, 2002), but immigration is likely to promote outbreeding, especially if the spatially separated populations are locally adapted to heterogeneous environments (Felsenstein, 1976; Lenormand, 2002; Débarre et al., 2013). Indeed, the mean fitness of a local population is reduced if migrants come from populations adapted to other conditions and likely to be poorly adapted to local conditions (migration load, Whitlock, 2004). However, this effect may depend on the intensity of gene flow which is not always proportional to dispersal intensity. Gene flow can be higher than dispersal (e.g., via disassortative mating, or hybrid vigour, Ebert et al., 2002), while maternal or environmental effects can create phenotypic mismatches and reduce the establishment of immigrants (Marshall et al., 2010). Another effect of dispersal on evolutionary dynamics can be observed at range margins, where founder effects can drive mutations fixations rapidly (McInerny et al., 2009). Population structure and connectivity may also have themselves an effect on the evolutionary mechanisms leading to trait evolution. For instance, genetic drift being a function of effective population size, its speed might be influenced by connectivity level (Wang and Caballero, 1999). In a context of uniform selection among habitats, the efficiency of selection (weaker response to selection) may be affected by the kin structure generated by population structure; if a genotype perform better than other, it will reduces resource availability for others, that are likely relative individuals sharing similar alleles (Whitlock, 2004). Through the change of density, dispersal might finally influence selective pressures on traits such as competition.

Life history traits evolution

Despite the description of several examples of how spatial structure of metapopulation might significantly affect the evolution of life history traits, a phenomenon called 'the metapopulation effect' by Olivieri and Gouyon (1997), the evolution of life history traits is mostly studied in single large homogeneous populations, and studies on evolution of traits in a metapopulation perspective often focus on the evolution of dispersal propensity (Friedenberg, 2003; Fjerdingstad et al., 2007). Indeed, a large amount of theoretical work has been done on the evolution of dispersal in a metapopulation context. Several studies focused on the evolution of dispersal in the case of spatial and temporal heterogeneity (Ronce and Olivieri, 1997; Ronce et al.,

2000; Heino and Hanski, 2001; Parvinen et al., 2020), while others examined it in the context of habitat loss (North et al., 2011). Theoretical work also demonstrated the evolution of dispersal in response to kin competition (Bach et al., 2006; Poethke et al., 2007), density and condition dependent dispersal (body condition dependent, Bonte and De La Peña, 2009, density dependent, Travis et al., 1999). Studies on the evolution of other life histories in a metapopulation context are still relatively scarce (but see age at maturity, de Jong et al., 2000, reproductive effort, Ronce and Olivieri, 1997). Additionally, little is known about how metapopulation structure, e.g. via the genetic structure or demographic asymmetries, may constrain or favor the evolution of life history traits, playing both on the directionality of selection and the amount of genetic variation (Ronce and Olivieri, 2004).

Eco-evolutionary feedbacks

Overall, dispersal and spatial structure of populations may have a complex influence on local populations demographic and evolutionary dynamics due to the multiplicity of implications of dispersal and their interaction. In particular, dispersal patterns may influence local populations dynamics and genetic composition, which in turn may affect dispersal patterns themselves. In other words, spatial population dynamics therefore arise as an emergent property of a system of spatially connected patches, where each patch is itself a system of linked genetic, phenotypic and population dynamics which may influence and be influenced by dispersal patterns (Benton and Bowler, 2012, Fig. 1.3). Metapopulations eco-evolutionary dynamics may be particularly complex to understand due to these eco-evolutionary feedbacks that are receiving growing attention. They have been reviewed with the angle of connectivity change in Bonte et al. (2018), since habitat fragmentation can affect the cost-benefit balance of dispersal and impose a different selective pressure, which ultimately impacts populations dynamics and connectivity. Experimental work led by Fronhofer and Altermatt (2015) also illustrated such feedback; in their study, range expansion selects for increased dispersal, likely due to spatial selection and kin competition, which in turn feeds back on distribution of population densities, which are low in range cores and high in margins, likely via trade off with foraging efficiency. A theoretical study from the same authors showed that network topology and connectivity lead to dispersal evolution which feeds back on the network genetic structure and occupancy (Fronhofer and Altermatt, 2017). However, clear demonstration of these eco-evolutionary feedbacks are still scarce, likely due to the complexity of simultaneously track trait changes and

population demography in a network of populations. Yet, acquiring insights in how the eco-evolutionary feedbacks between population dynamics, dispersal, life history evolution and the spatial structure of the landscape affect the distribution of species is essential for population conservation.

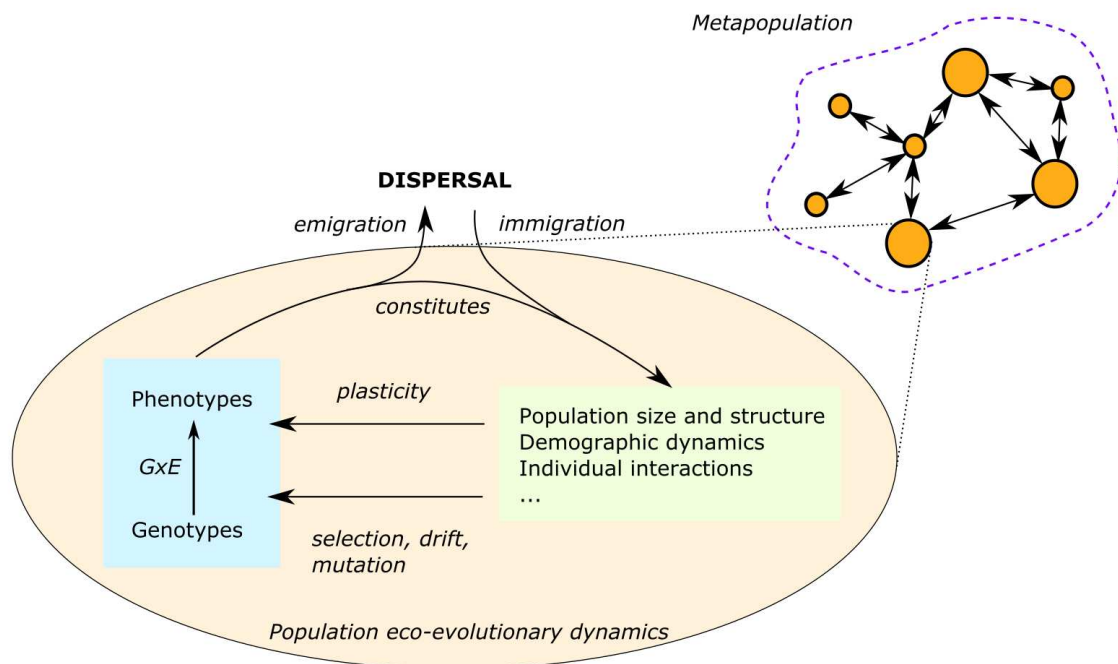


Figure 1.3: Conceptual framework of population eco-evolutionary dynamics within a metapopulation context. Local population shows its own eco-evolutionary feedback between demographic dynamics and genetic / phenotypic composition, while dispersal may interfere through emigration and immigration. As a life history trait, dispersal is also included in the eco-evolutionary feedback linking demographic and genetic dynamics. Adapted from [Benton and Bowler \(2012\)](#).

GAP 1: Eco-evolutionary dynamics of metapopulations

There is a lack of knowledge about the life history traits evolution within metapopulation, in particular how spatial structure of genetics and demography influence evolutionary dynamics and the feedback on genetic and demographic patterns.

1.1.4 Stability, persistence, and adaptation of metapopulations

By affecting the eco-evolutionary dynamics of local populations, dispersal may therefore influence the persistence, stability and adaptation of spatially structured populations. Regarding the persistence and capacity of adaptation of species to environmental changes, most attention has been focused at the population scale, where local adaptation to local selective pressure such as environmental conditions or anthropogenic activities (e.g., exploitation) provides persistence of populations. However, in the case of metapopulations, a set of locally adapted populations with potential variable selective pressures may generate biocomplexity (Hilborn et al., 2003), both at the levels of phenotypic/genotypic characters (life histories) but also in terms of asynchrony of demographic dynamics.

Biocomplexity and the portfolio effect

This biocomplexity may generate a diversity of response of populations to environmental changes and has a stabilizing effect increasing persistence of the whole network. This effect has been called the portfolio effect (PE) and is similar to the risk-spreading function of financial portfolios. The portfolio effect in ecology and evolution describes how diversity or biocomplexity of components of a system, which can lie in the demographic, phenotypic or genotypic levels, favor the ecological stability of the whole system (Schindler et al., 2015, Fig. 1.4). It is very close to the diversity-stability relationship demonstrated in community ecology where the diversity of species increases the stability and resilience of a community and ecosystem (Elmqvist et al., 2003; Loreau and de Mazancourt, 2013; Thibaut and Connolly, 2013), and can apply at various scales. In particular, the portfolio effect can describe how asynchronous responses of individuals (within-population, Bolnick et al., 2011; Abbott et al., 2017), populations (between-population, Schindler et al., 2010; Harrison et al., 2020) or species (interspecific, Vargas et al., 2022) increase the stability of the whole system. At the metapopulation scale, genetic distance and spatial variation in the environment can lead to local adaptation and adaptive divergence in life history traits. Different demographic dynamics across populations may emerge from this diversity of response in addition to stochasticity between populations dynamics, ultimately fostering populations network stability (Hilborn et al., 2003; Braun et al., 2016). There has been increasing interest in a portfolio approach to conservation decision-making to foster the resilience of populations to environmental perturbations (Anderson et al., 2015; DuFour et al., 2015; Hobbs et al., 2017). However, while the portfolio approach

recognizes the importance of a diversity of populations, it fails to appreciate the role of the interconnection between them in forming a network.

Homogenizing effect of dispersal

The diversity of populations maintained by metapopulation functioning and the resulting 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 (Paradis et al., 1999; Kendall et al., 2000; Liebhold et al., 2004; Carlson and Satterthwaite, 2011). Several studies showcased the erosion of portfolio effects by increased synchrony levels of populations (Moore et al., 2010; Satterthwaite and Carlson, 2015; Sullaway et al., 2021). While synchronization between populations is mainly attributed to the synchronization of environmental conditions (Moran effect), dispersal can also affect the synchronization of population dynamics but these effects are context dependent (Yang et al., 2022). Moreover, dispersal and gene flow might reduce 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), and therefore reduce genetic diversity between populations via this homogenizing effect (Lenormand, 2002; Settepani et al., 2014; Tinnert and Forsman, 2017). Thus, dispersal could lead to a global reduction of the biocomplexity and diversity of responses to environmental changes within the metapopulation (Fig. 1.4). However, this constraining effect of gene flow on adaptive divergence might depend on dispersal level (Garant et al., 2007) and local adaptation can also reduce immigrant's fitness and dispersal consequences in terms of gene flow (Mobley et al., 2019). Altogether, these “detrimental” effects of dispersal can affect metapopulation stability and persistence, leading to “anti- rescue” effects (Harding and McNamara, 2002).

Rescue effects of dispersal

However, additionally to demographic rescue effects, studies have demonstrated that in sink populations, moderate levels of migration may also provide other rescue effects when combined with diversity within a network of populations (Carlson et al., 2014 for review). First, the genetic rescue (Keller and Waller, 2002; Whiteley et al., 2015) describes the influx of genetic variation provided by gene flow which reduces inbreeding

within local populations and prevents the fixation of deleterious alleles. Second, the evolutionary rescue (Bell and Gonzalez, 2011; Gonzalez et al., 2013) describes the genetic adaptation of a population to environmental change that would otherwise have caused its extinction and have first been looked at in populations closed to dispersal (Gomulkiewicz and Holt, 1995; Carlson et al., 2014). But the central role of dispersal in evolutionary rescue, via the increase of standard genetic variation and/or the introduction of individuals with heritable adaptive alleles which may favor genetic adaptation of the population, have further received attention (Bell and Gonzalez, 2011; Uecker et al., 2014).

Altogether, dispersal and biocomplexity, interacting together, might foster persistence, adaptation and stability of metapopulations through adaptation networks, as defined by Webster et al. (2017) (Fig. 1.4). These adaptation networks allow ecological and evolutionary options within the network that favor adaptation to uncertain environmental changes. It is thus essential to study the relative contribution of these mechanisms in a dynamic system of spatially structured populations to better understand the potential for management actions which could favor the stability and resilience of natural resources. However, dispersal and diversity of response are rarely studied in a unified framework and studies exploring management practices in this context are scarce.

GAP 2: Adaptation network

The adaptation network theory still needs to be evaluated in a unified framework, with dispersal and diversity of response effects interacting together.

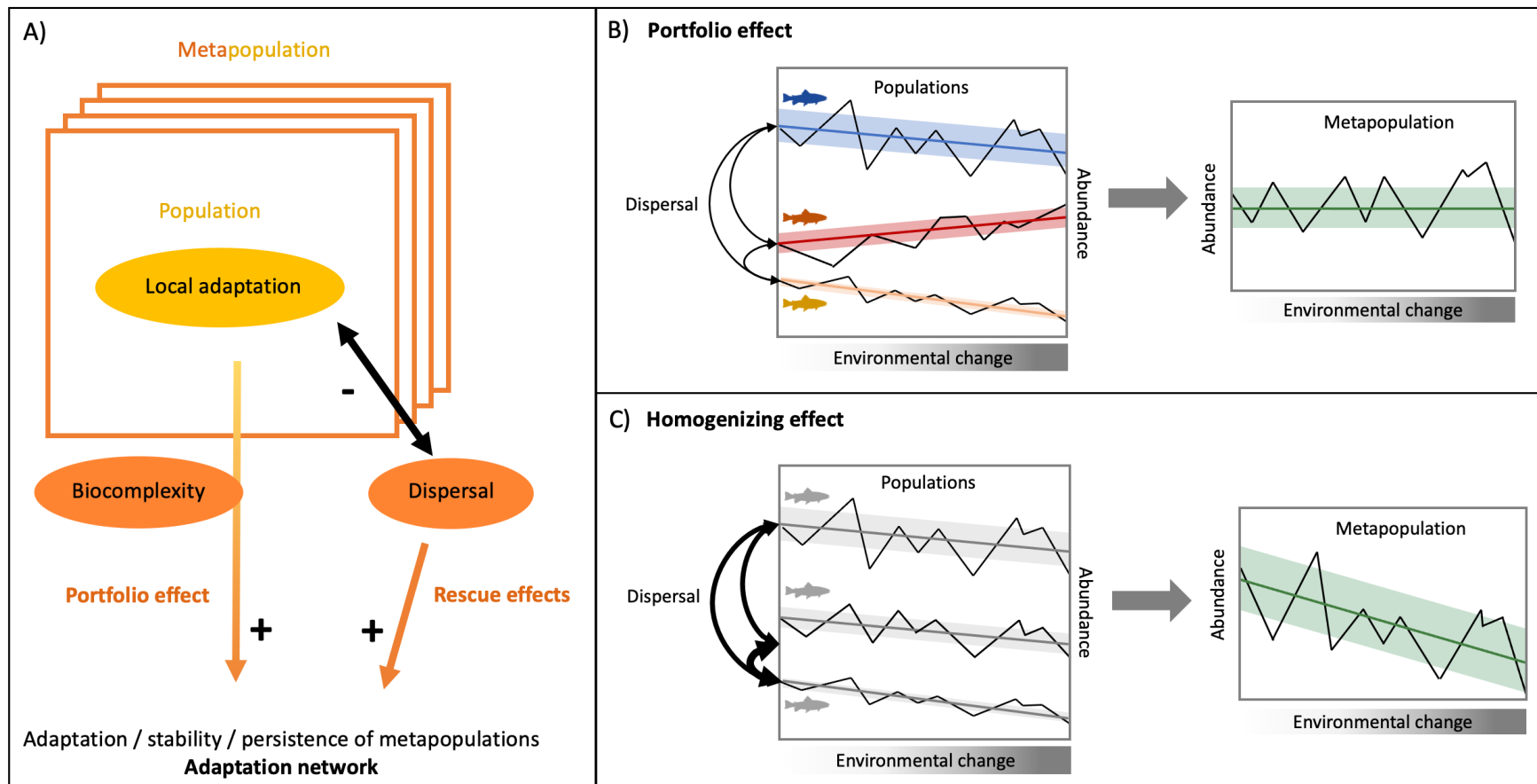


Figure 1.4: A) Conceptual framework of an adaptation network, with biocomplexity emerging from the diversity of local populations dynamics providing portfolio effects and interacting with dispersal and its rescue effects, ultimately fostering the adaptation, stability and persistence of metapopulations. B) Schematic illustration of the portfolio effect: a diversity of populations dynamics and life histories lead to the stability of the metapopulation dynamics. C) Schematic illustration of the homogenizing effect of dispersal, which synchronizes populations dynamics and homogenizes life histories, ultimately reducing the stability of the metapopulation.

1.1.5 Management of metapopulations

Targeting key populations

Considering metapopulation dynamics into the design of management practices is a promising path to follow. But it faces difficulties related to i) the complexity of metapopulation functioning, ii) the general lack of knowledge of the systems to be managed, and iii) the limitations of means and resources to monitor them. As pointed out by [Cabeza et al. \(2004b\)](#), designing reserves among a network of habitats or populations is a fundamental problem in conservation biology. Given the limited resources for conservation (political and economical), and the maintenance of human activities, it is not possible to protect all habitats and there is a need to identify areas to be set aside as reserves primarily. In the literature, several guidelines emerge from work based on biodiversity i.e. species richness. In particular, there is an emphasis on the design of reserve networks instead of single sites preservation, and selection of protected areas is often based on the ideas of representativeness and complementarity. Indeed, area protection is often hindered by a lack of knowledge, for example about the existence and location of species, and protected areas often contain a sample of biodiversity. Thus, selection of protected areas based on their representativeness and complementarity of available biodiversity aims to conserve most of biodiversity in a limited number of areas ([Kirkpatrick, 1983](#); [Margules et al., 2002](#)). For example, algorithm based on species richness index or coverage targets and occurrence probabilities derived from habitat models have been proposed to identify ideal reserves spatial configuration ([Cabeza, 2003](#); [Cabeza et al., 2004a](#)).

These simple approaches lead to the selection of reserves based on static patterns of species presence/absence only. Yet, spatiotemporal populations dynamics may change these patterns and targeted criteria may not be met anymore, compromising long-term persistence of species. For example, [Margules et al. \(1994\)](#) showed that original site selection was inadequate to preserve initial plant species after 11 years, because it didn't account for species spatial turnover. An alternative could be to consider stochasticity in population dynamics. For instance, [Moilanen and Cabeza \(2002\)](#) performed simulations with a stochastic metapopulation model (IFM) to integrate stochasticity in the spatiotemporal dynamics of a metapopulation of an endangered butterfly. They were able to identify a set of patch clusters giving the lowest metapopulation extinction rates in a certain time scale. Another stochastic model highlighted that unexpected habitat patches (sinks) could play an important role in the resilience of a metapopulation of birds ([Foppen et al., 2000](#)). Also, the design of

reserves within a metapopulation would largely depend on factors such as dispersal ability: if the dispersal ability of a species is limited, it might be better to protect sites close together; by contrast, protecting more scattered sites would be relevant if long distance dispersal is possible (Cabeza et al., 2004b). Unfortunately, network design is mainly based on presence-absence of species and considering the dynamics of populations and landscapes have been mostly overlooked despite recommendations that conservation biologists should consider local population dynamics for management of metapopulations (Baguette and Schtickzelle, 2003).

Considering the evolutionary dynamics in the design of protect areas might also be of major importance. For example, Poethke et al. (2011) showed theoretically that improvement of habitat quality of a fraction of patches might result in a reduced dispersal propensity as an evolutionary response which might prevent recolonization events. This response can ultimately lead to a global decline of populations and increased extinction risk. Thus, dispersal itself may evolve as a response to management practices (e.g., stocking, selective exploitation), a topic that has not yet been fully explored.

Conservation under the portfolio approach

An alternative management strategy that could address the issue of the lack of knowledge of the system to be managed, as well as the complexity of the mechanisms at stake, is the portfolio approach. Indeed, approaches built on a predict-and-prescribe paradigm, whereby conservation priorities are based on predictions of the responses of species to projected environmental conditions, might be flawed. Based on low predictive power and uncertainty of future conditions, such approaches have proven risky for conserving financial portfolio and they may also apply to ecosystem management. Alternatively, portfolio conservation advocates to manage for uncertainty by promoting population response diversity to foster stable ecological system and the ecosystem services they provide (DuFour et al., 2015; Hobbs et al., 2017). According to Moore and Schindler (2022), efforts to conserve biodiversity and generate habitat complexity will help to maintain species stability and persistence, via a diversity of future options for an unpredictable future. Webster et al. (2017) propose an approach to natural resource management focusing on creating adaptation networks to generate ecological and evolutionary options that favor the adaptive processes of acclimatization, natural selection, and ecological reorganization. By prioritizing portfolios of biological and ecological combinations, management

could increase the probability that winning combinations can arise, persist and spread facing environmental changes. [Anderson et al. \(2015\)](#) illustrated this with a metapopulation model, showing that preserving a diversity of thermal tolerance could ensure persistence of salmon populations facing environmental changes. They suggest that management practices should conserve not only the populations but also the processes promoting thermal tolerance diversity, i.e. the genetic diversity and habitat heterogeneity. Similarly, [Walsworth et al. \(2019\)](#) showed that, considering evolutionary capacity of coral reefs, protecting habitat diversity and connectivity fosters adaptation to climate change rather than focusing conservation on thermal refugia. This approach is attracting more and more attention ([Colton et al., 2022](#); [Moore and Schindler, 2022](#)), but remains only rarely evaluated in theoretical and applied research of metapopulations conservation.

GAP 3: Metapopulation management

Management of populations rarely considers the metapopulation structure. If this is the case, the evolutionary processes and their consequences are often underestimated. Management via the portfolio approach still needs to be investigated.

1.2 SALMONIDS AS A RELEVANT CASE OF STUDY

1.2.1 Species of several interests

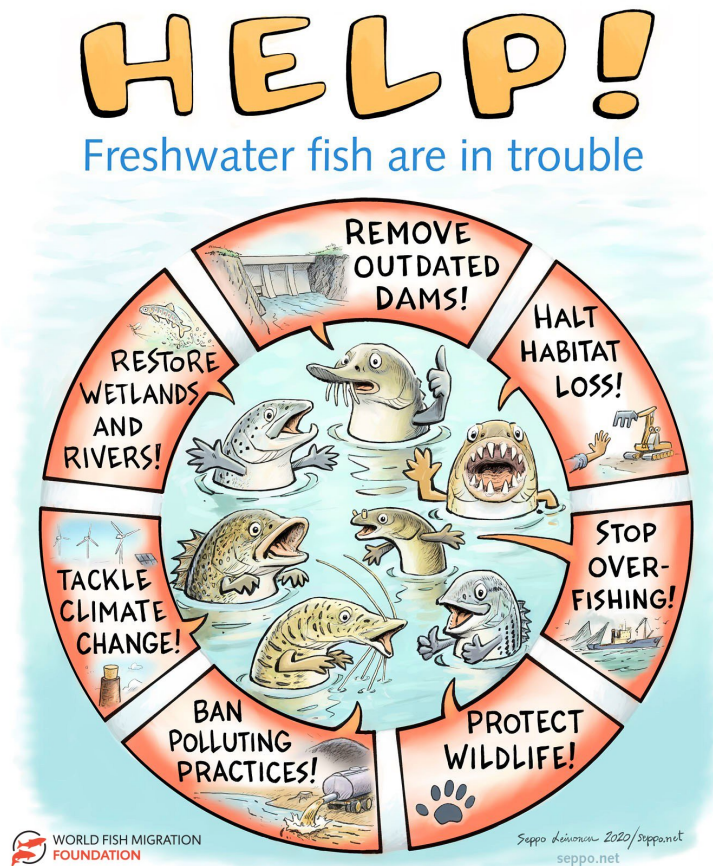


Figure 1.5: Illustration of the main threats affecting freshwater fishes.

Salmonid fishes are relevant species to explore metapopulation functioning and response to environmental changes. First, most of these species are of patrimonial interest and have considerable value in recreational and commercial fisheries. Second, most of them are migratory species, sharing their life cycle between several habitats; in particular, they are anadromous, i.e. they are born in river and migrate to the sea to grow before coming back to rivers to reproduce. This complex life cycle makes them sensitive to several threats, such as barriers to migration (e.g., dams, Lindley et al., 2006), habitat loss (McClure et al., 2008), multi-origin pollution (Arkoosh et al., 1998), climate change (Jonsson and Jonsson, 2009; Crozier et al., 2021) and overfishing

(Christensen et al., 2003). Like other freshwater fish, they are threatened by the combination of these threats (Fig. 1.5).

Third, salmonid species are also well known for their great diversity of life history strategies such as semelparity vs iteroparity, migratory vs non-migratory, variation in age and size at maturation, or size at migration (Hutchings and Jones, 1998). This diversity of life history strategies is linked to phenotypic plasticity (Pavlov et al., 2008; Mangel and Satterthwaite, 2016; Erkinaro et al., 2019) and variability in the genetic basis of traits (e.g., age at maturation, Barson et al., 2015; Lepais et al., 2017).

1.2.2 Salmonids in a metapopulation context

Salmonid fishes represent an excellent system for exploring the influence of dispersal on metapopulation and local population dynamics. Indeed, they should be considered in a metapopulation perspective (Garant et al., 2000; Rieman and Dunham, 2000), as the three conditions defined by Schtickzelle and Quinn (2007) are fulfilled: i) the spawning habitat is discrete, ii) there is asynchrony between the dynamics of local populations, and iii) there are evidences of dispersal (Keefer and Caudill, 2014). Quinn (1984) proposed philopatry and dispersal as alternative and evolutionary stable strategies in salmonids (Kaitala, 1990). Hendry et al. (2004) also discussed how salmonids could provide insight into the evolution of philopatry and dispersal, commonly called "homing" and "straying" respectively for salmonids. Indeed, salmonids are often represented as an emblematic example of philopatric species which perform "homing" to the natal river (Salmenkova, 2017), while the somewhat pejorative term "strayers" is often used to describe individuals that disperse among populations (Schtickzelle and Quinn, 2007). The principal mechanism of homing identified is an olfactory imprinting of the chemical characteristics of the water of natal sites during the juvenile stage (Hasler and Scholz, 1983). By contrast, "straying" is rather explained by mistakes of individuals to return to their natal river, and consequences of dispersal for eco-evolutionary dynamics remain overlooked in salmonids despite evidences of various dispersal strategies across species (Schtickzelle and Quinn, 2007; Atlantic salmon, Jonsson et al., 2003; Sockeye salmon, Peterson et al., 2016; Chinook salmon, Pearsons and O'Connor, 2020).

Literature review

To illustrate this, I performed a literature review on the Web of science advanced research query using the following keywords: "Species (see below) AND (dispersal

OR straying *OR* gene flow) *NOT* (juvenile *OR* lice)". Note that this literature research is limited from 1955 to 21st February 2022 and to articles reported in WOS, excluding grey literature (e.g., technical reports). The search focused on the following species: Atlantic salmon (*Salmo salar*), Coho salmon (*Oncorhynchus kisutch*), Chum salmon (*Oncorhynchus keta*), Pink salmon (*Oncorhynchus gorbuscha*), Sockeye salmon (*Oncorhynchus nerka*), Chinook salmon (*Oncorhynchus tshawytscha*), Steelhead trout (*Oncorhynchus mykiss*), and Brown trout (*Salmo trutta*).

From the 8 queries we performed on the WOS, only 42% (n=310 over 7 species) on average of the studies were relevant to our literature review about dispersal consideration in salmonids (Table 1.1, see Lamarins and Buoro, 2023 for the final database). Among them, a lot of studies focused on the genetic structure, evolutionary history of populations without estimating the gene flow or migration rate (47% of the studies on average, especially for Chum and Sockeye salmon in proportion). Several of the reported studies do estimate dispersal but on hatchery, farm escapees, or transplanted fish (15% of the studies on average, especially on Atlantic salmon, Chinook salmon and steelhead trout) which have been shown to stray more than wild individuals (Quinn, 1993; Jonsson et al., 2003). In other words, only a small number of studies report dispersal between wild populations (33% of the studies on average) and even less provide estimates (27% of the studies on average). In their review, Keefer and Caudill (2014) reported differences in the number of studies between species: 6 studies measuring emigration rates in Atlantic salmon, while 10 for Steelhead, 18 for Chinook salmon (both ecotypes), but also 5, 2, 4, and 1 for Coho, Sockeye, Pink and Chum salmon, respectively. However, most of these estimates are influenced by hatchery fish. My literature review revealed a small and similar number of studies estimating emigration rates between wild populations of these species (Table 1.1, n=4, 2, 3, 1, 1, 4, and 1 respectively).

Methods generally include genetic differentiation, identification, tagging, sometimes otolith chemistry, and a combination of them, allowing to estimate gene flow, emigration rate and immigration rate (Table 1.2). In contradiction with the review of Keefer and Caudill (2014), I did not notice a predominance of emigration rates estimations relative to immigration, but rather a good representativity of gene flow, emigration and immigration rates allowing a global view of dispersal in all species. A very small proportion (16%) of wild dispersal studies intended to identify individual (e.g., sex), environmental (e.g., temperature), or population (e.g., density) factors influencing dispersal rates (Table 1.2, see Lamarins and Buoro, 2023 for the studies references).

Table 1.1: Summary of the literature review. For each species, I report the number of studies listed by the WOS query, and the subset focusing on genetic differentiation (both on hatchery and wild fish), estimating dispersal on hatchery fish or on wild fish, and the number of studies modeling metapopulation dynamics with a consideration of dispersal. For studies using models or reporting dispersal in wild populations, I also report the number of studies discussing or evaluating the implications of dispersal for conservation or management (***). * Non relevant studies gather work focusing on the wrong species, juvenile dispersal, introgression impacts, or parasite dispersal. ** I only consider estimates of anadromous dispersal (not gene flow between residents).

Species	Atlantic	Coho	Chum	Pink	Sockeye	Chinook	Steelhead	Brown trout
WOS total	193	26	28	130	51	85	136	148
Non relevant*	104	14	14	120	24	42	71	98
Genetic differentiation	34	4	12	5	17	14	22	21
Hatchery dispersal	25	1	0	0	0	12	33	2
Wild dispersal (estimates)	27 (18)	(5)	(2)	(5)	9 (7)	14 (12)	9 (4)**	25 (19)**
Model including dispersal	3	2	0	0	1	3	1	2
Conservation perspective***	None	18	5	1	4	6	5	21
	Discussed	10	1	1	1	3	4	5
	Evaluated	2	1	0	0	1	1	1

Table 1.2: For the subset of studies estimating dispersal for wild populations (72 in total, in ()), distribution of the type of connectivity measured (gene flow, emigration rate, or immigration rates, or combinations), and number of studies evaluating factors influencing dispersal propensity (individual, population, or environmental factors) - specific studies identified are indicated in [], and refer to the WOS list of references available at: <https://doi.org/10.57745/RCMAGH>.

Species	Atlantic	Coho	Chum	Pink	Sockeye	Chinook	Steelhead	Brown trout
Gene flow	9 [1-9]	2 [19-20]	0	0	2 [31-32]	3 [38-40]	1 [50]	10 [54-63]
Emigration rate	3 [10-12]	0	0	3 [26-28]	1 [33]	2 [41-42]	2 [51-52]	2 [64-65]
Immigration rate	5 [13-17]	2 [21-22]	1 [24]	1 [29]	2 [34-35]	5 [43-47]	1 [53]	3 [66-68]
Em. + Im. rates	0	1 [23]	0	1 [30]	0	1 [48]	0	0
Gene flow + Em. rate	0	0	1 [25]	0	0	0	0	0
Gene flow + Im. rate	0	0	0	0	2 [36-37]	1 [49]	0	4 [69-72]
All	1 [18]	0	0	0	0	0	0	0
Dispersal factor	5 [3,7,10,11,13]	0	0	1 [26]	2 [31,35]	2 [47,48]	1 [50]	1 [54]

Finally, this literature review revealed that studies considering the metapopulation perspective and evaluating dispersal implications for conservation or management for salmonid dynamics are very rare (12 over the 8 species, Table 1.1). This subset of studies were largely performed through modeling analysis and focused on the demographic consequences only, or interplay with local adaptation, or applied problems around buffering introgression by farm fish or barrier removal choice. For example, [Bowlby and Gibson \(2020\)](#) and [Fullerton et al. \(2011\)](#) investigated the demographic consequences of dispersal within salmonids metapopulations; however, they did not explore genetic consequences and their potential interplay with demography (i.e., eco-evolutionary feedback loops). The theoretical work of [Lin et al. \(2017\)](#) is particularly relevant to our objective, however they only focused on two populations. [Castellani et al. \(2015\)](#) evaluated the role of immigration on introgression buffering. Moreover, less than half (34% on average) of the studies reporting or estimating dispersal discussed the implications of dispersal for salmonid conservation and management (Table 1.1, see [Lamarins and Buoro, 2023](#) for the studies references). When they did, the discussions mostly focused on the preservation of genetic diversity and local adaptation by limiting or promoting gene flow, and the recolonization and restoration potential vs stocking practices. [Bett et al. \(2017\)](#) reviewed the observed consequences of dispersal in small populations of Pacific salmon and “encourage further discussion and research on the potential effects of recipient straying”.

Altogether, studies focused on genetic differentiation or based on hatchery straying, likely because studying the connectivity between wild populations is very challenging. Thus, dispersal is increasingly appreciated in salmonids but still understudied in wild populations, with few studies estimating emigration and immigration rates at large temporal and spatial scales. These rare studies, despite some limitations (e.g., limited detection of strays, small samples, [Jonsson and Jonsson, 2017](#)), show a high variability between years ([Jonsson et al., 2003](#)) and locations ([Consuegra et al., 2005](#)), suggesting the need for regional evaluation of connectivity. Despite early studies highlighting homing and straying as evolutionary strategies ([Kaitala, 1990](#); [Hendry et al., 2004](#)), the implications of straying in salmonids dynamics remain underappreciated.

GAP 4: Dispersal in salmonids

Evidence of dispersal ("straying") in salmonids are numerous, but their implications for salmonids persistence, adaptation, and management remain overlooked.

1.2.3 The case of Atlantic salmon (*Salmo salar*)

Atlantic salmon distribution ranges from rivers from Portugal, Spain and New England (USA) in the south of its range to sub-Arctic Canada and Russia in the north. Across its range, this species provides economic, social and cultural benefits to the human society. Salmon is for example culturally important in many indigenous communities, but the most obvious benefit is fishing: Atlantic salmon is harvested for a long time by a diversity of fisheries operating in river (recreational fisheries) but also in estuary and at sea (commercial fisheries). Nowadays, most of the catches are in river (ICES, 2021). Although the presence of barriers to migration continues to play a major role, intense exploitation before the 1980s likely contributed to a decline of salmon abundance observed at the range scale via the pre-fishery abundance (Fig. 1.6). The rate of decline was the most dramatic between 1980 and 1990, and slowed down after 1990, likely related to the creation of the NASCO (North Atlantic Salmon Conservation Organization) and global limitations of commercial fishery from 1983. Since then, the total catch number dramatically decreased but populations continue to decline (Fig. 1.6).

1.2.3.1 A complex life cycle

Atlantic salmon share their life cycle between the river, where they reproduce, and the sea, where they grow (Fig. 1.7). During the winter, returning adults and mature juveniles (called "sneakers") spawn in stream gravels and lay their gametes into a nest (called "redd"). Then, eggs develop and hatching occurs the following spring, where alevins rely on their yolk sac for their nutrition, until they emerge from the gravels as "fry" and start feeding. During summer, these juveniles (called "parr") may adopt three life history strategies: they can either i) mature in freshwater (precocious maturation, mainly males) and reproduce in river the following winter, ii) migrate to the sea as "smolts" the following spring, or iii) stay an additional year in freshwater. Parr adopting the migration strategy undergo a strong physiological and morphological change known as "smoltification", allowing them to adapt to the salt water. Migrating smolts then grow at sea 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 the river to reproduce and continue the cycle. Most spawning individuals die after spawning but some survive, undergo another migration to the sea and may spawn another time as iteroparous individuals (Bordeleau et al., 2020).

This complex life cycle shows the diversity of life histories that can be followed

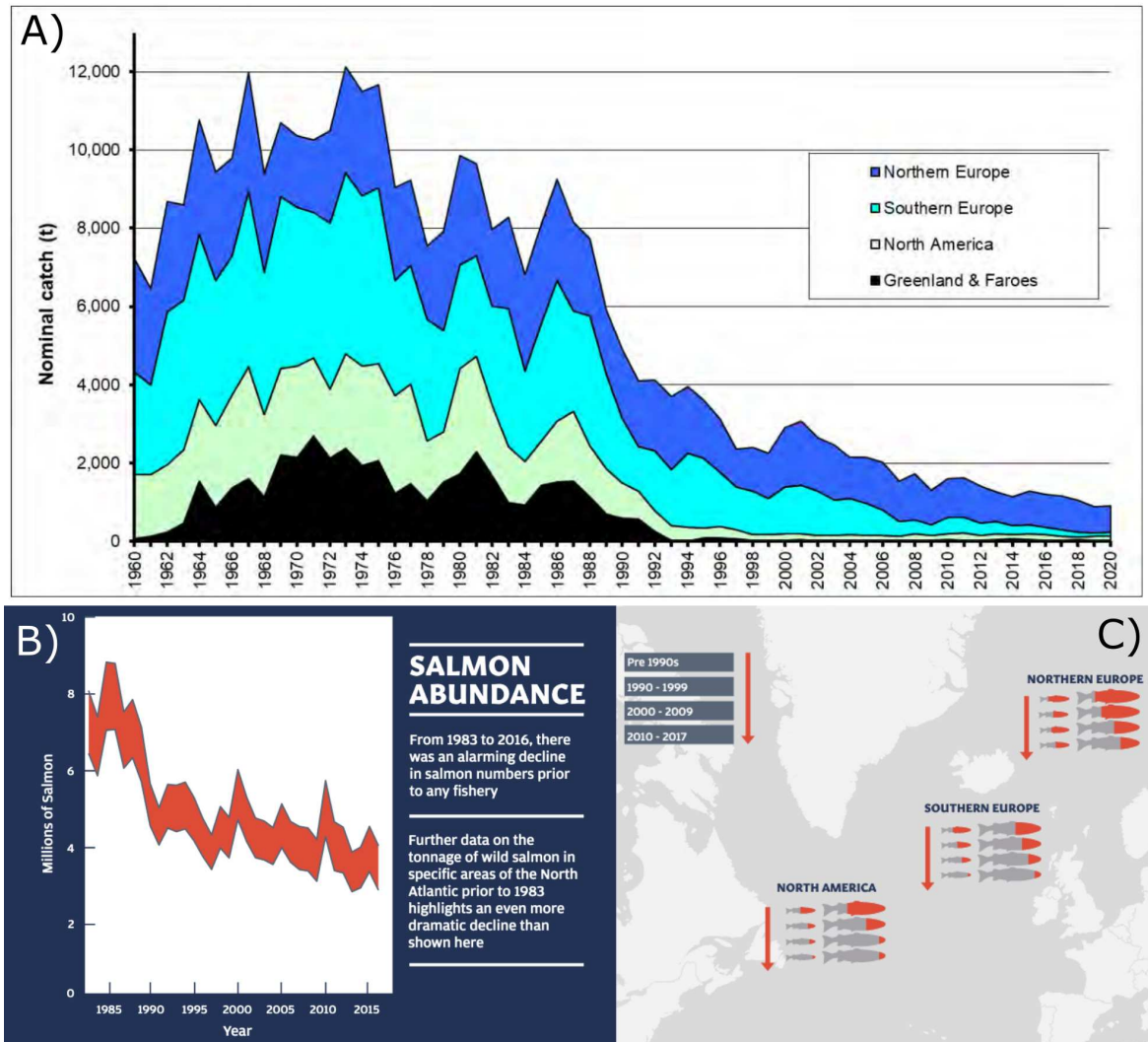


Figure 1.6: Temporal trends of the Atlantic salmon (A) catches, (B) abundance, and (C) exploitation rates over the distribution range. From [ICES \(2021\)](#) and [NASCO \(2019\)](#) reports. (A) Total reported catches (in tonnes). (B) Pre-fisheries abundance (C) Proportion of 1SW / MSW harvested.

by Atlantic salmon individuals, from residency to anadromy, from semelparity to iteroparity, with variable age at maturation, migration, and reproduction ([Fleming, 1998](#); [Hutchings and Jones, 1998](#); [Klemetsen et al., 2003](#)).

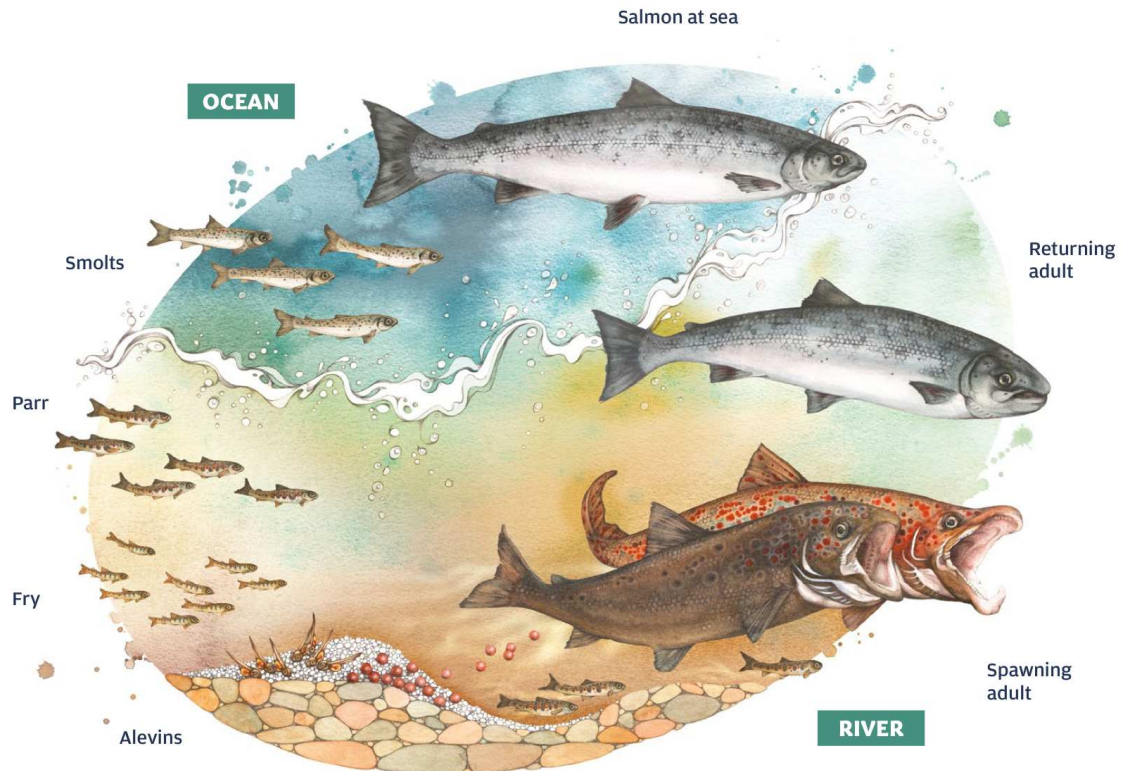


Figure 1.7: The Atlantic salmon life cycle. Illustration: Jenny Proudfoot, from NASCO (2019) report.

1.2.3.2 Dispersal

As highlighted by the literature review (Table 1.1), dispersal of Atlantic salmon is still overlooked in wild populations. In most of the representation of their life cycle, such as Fig. 1.7, dispersal is not represented as an alternative strategy of philopatry. 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, 2007; Perrier et al., 2011), although such genetic analyses do not provide evidence of contemporary dispersal and gene flow is not necessarily a metric for dispersal. Instead, a very few studies estimated dispersal rates in wild populations using capture-mark-recapture programs (Jonsson et al., 1991, 2003; Consuegra et al., 2005; Kuparinen et al., 2010). However, 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](#)). Based on both genetic and tagging methods (see [Lamarins and Buoro, 2023](#)), the average emigration and immigration rates reported for wild Atlantic salmon populations are 14.4% and 15.6%, respectively, although based on a small number of studies ([Jonsson et al., 1991, 2003](#); [Castric and Bernatchez, 2004](#); [Consuegra et al., 2005](#); [Fraser et al., 2007](#); [Dionne et al., 2008](#); [Kuparinen et al., 2010](#); [Valiente et al., 2010](#); [Jonsson and Jonsson, 2017](#)). The natural colonization of rivers also provides empirical evidence of long-distance dispersal in Atlantic salmon ([Perrier et al., 2010](#)). 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](#)).

1.2.3.3 The Brittany case of study

At the southern range of its distribution, Atlantic salmon is particularly threatened and classified on the national UICN red list of threatened species. Indeed, its distribution over the french rivers dramatically reduced over centuries. The last watersheds where wild populations are persisting are mostly located in the south-west of France, in the Nivelle and Adour watersheds, and in the Brittany and Normandy coastal rivers (Fig. 1.8).



Figure 1.8: Distribution of colonized rivers by Atlantic salmon in France from the 18th to the 21st century. From Bretagne Grands Migrateurs.

Populations established in Brittany are particularly interesting in the context of my thesis. First, juvenile and adult abundances are monitored for up to three decades, and

used to determine conservation limits (Lebot et al., 2022). Second, a genetic study led by Perrier et al. (2011) showed a low genetic differentiation among Brittany populations despite their large spatial distribution, suggesting that dispersal and gene flow are occurring within this network of rivers. Third, one river from Brittany, the Scorff, is one of the four study sites within the research observatory network (ORE DiaPFC) and benefits from a long term monitoring program started in 1993. It is also an "index" river used by the Atlantic salmon working group of the International Council for the Exploration of the Sea (ICES). Through parr sampling, smolt and adult trapping, a lot of knowledge can be acquired on the population dynamics and life histories strategies. For example, Buoro et al. (2010) provided insight into evolutionary trade-offs between life history strategies of Atlantic salmon by using data from this monitoring program. As the salmon catches have to be reported, we have good estimates of exploitation rates by rivers, on average 15% and 6% for MSW and 1SW, respectively (Lebot et al., 2022). However, dispersal and metapopulation structure are not considered in management. The river is still defined as the main management scale (ICES, 2021), and exploitation rates are applied by population. Estimated return rates are often confused with marine survival (an important indicator) without taking dispersion into account.

1.3 THESIS AIMS AND MANUSCRIPT STRUCTURE

Objectives

Through this introductory section, I identified 4 main gaps of knowledge on metapopulation eco-evolutionary dynamics and management of salmonids. First, GAP 1 identified a lack of knowledge on the influence of spatial structure of genetic diversity and population dynamics on the evolutionary dynamics of populations, while GAP 2 emphasizes the need to study adaptation networks in a single framework. GAP 3 highlights that management of population rarely considers metapopulation functioning and evolutionary processes, and GAP 4 acknowledges that this is particularly the case for salmonids for which dispersal implications are overlooked.

Disentangling multiple effects of metapopulation functioning with complex and diverse spatial structures, life history strategies and eco-evolutionary processes is a striking challenge but inevitable if we want to elucidate the role of adaptation network and to favor the persistence of Atlantic salmon populations facing an uncertain future.

Manuscript organisation

This thesis aimed to contribute in filling these gaps through three main chapters (3, 4 and 5) by using *in silico* experiments, i.e., simulations of Atlantic salmon life cycle (Fig. 1.9). The second chapter explains the rationale and puts forward the type of modelling approach used in this thesis. This chapter highlights that the study of populations dynamics would gain from being studied in a framework representing eco-evolutionary processes and explicit spatial structure of populations. Then, using this modelling approach, chapter 3 addresses GAP 4 by investigating the implications of dispersal for the stability, persistence and diversity of Atlantic salmon populations. In addressing GAPS 1 and 2, chapter 4 examines the adaptive capacity of populations within an adaptation network, and focuses on the influence of spatial structure on the eco-evolutionary dynamics of populations. Chapter 5 builds on GAP 3 by comparing alternative spatialized management strategies that take into account the metapopulation structure and evolutionary processes within a single framework. Chapter 6 presents a new version of our modelling approach I am developing to overcome the limitations of the first version of the model that I encountered during my work, while integrating new findings about A. salmon ecology. This version is still under development and was not used for analysis presented below. Finally, I discuss my main results and propose perspectives for future work on the topic in Chapter 7.

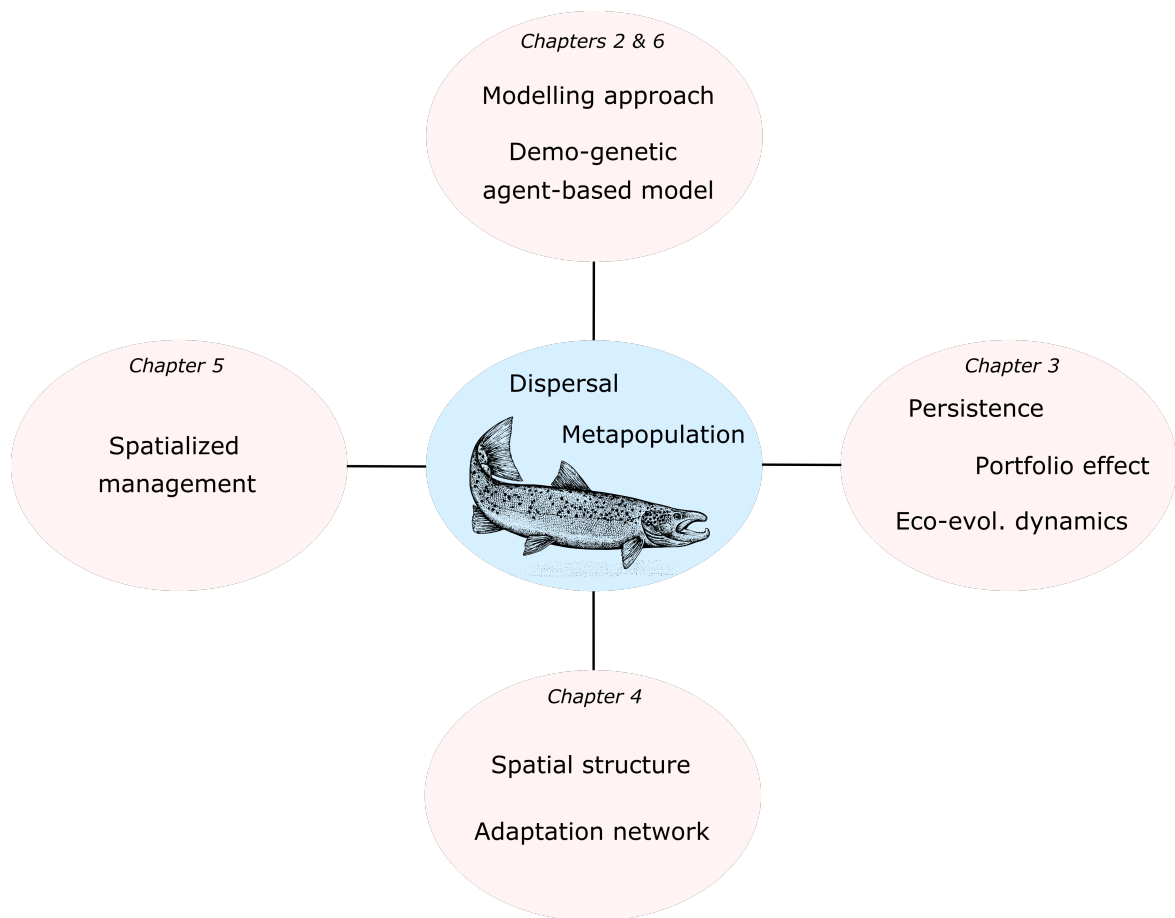
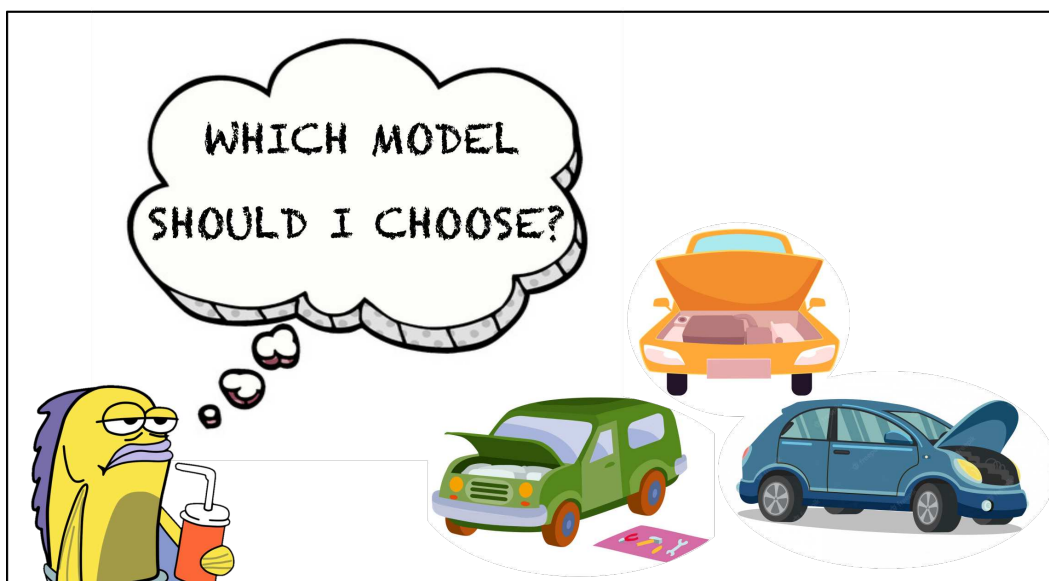


Figure 1.9: Overview of the chapters of the thesis.

The benefits of eco-evolutionary agent based modelling approaches



"All models are wrong, but some are useful." - George E. P. Box

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In this second chapter, I introduce the rationale and overview of the modeling approach I used to study eco-evolutionary dynamics and perform *in silico* experiments led in the chapters 3, 4, and 5. Further details on the model used are presented in chapter 3.

2.1 CHALLENGES EVALUATING DISPERSAL AND METAPOPULATION DYNAMICS IN NATURE

Evaluating metapopulation dynamics primarily requires estimations of dispersal rates within a network of populations. Several quantitative methods allow estimations of philopatry or dispersal rates at ecological time scales. First, direct measurements can be obtained via mark-release-recapture techniques. For example, tagging juveniles and sampling returning adults for the presence of tags in a local population allows to estimate the proportion of fish immigrating from other populations (number of untagged adults divided by the total number of adults, e.g. steelhead, [Schroeder et al., 2001](#)). Surveys of the surrounding populations also help estimating the proportion of fish that disperse from the local population (number of tagged adults at all non natal sites divided by the total number of tagged adults, i.e. at natal and non natal sites, e.g. Atlantic salmon, [Jonsson et al., 2003](#); [Consuegra et al., 2005](#)). However, this emigration rate is often underestimated, because all potential non natal sites are rarely sampled, or with limited sampling efforts. Through chemical signatures, otoliths also provide natural tags that can be analyzed on returning adults to estimate immigration rate for example (e.g., sockeye salmon, [Hendry, 2001](#); chinook salmon, [Hamann and Kennedy, 2012](#)). Further, methods of individuals assignment to source populations via phenotypic or genotypic features using discriminant functions, mixed stock analyses or assignment tests allow discrimination between immigrants and residents and estimations of dispersal rates ([Hansen et al., 2001](#); e.g., sockeye salmon, [Lin et al., 2008](#); chinook salmon, [Ford et al., 2015](#)). More indirect methods estimate the amount of gene flow based on measurement of among populations genetic divergence at neutral genetic loci (e.g., Atlantic salmon, [Elo, 1993](#)), for example using Wright's method ([Wright, 1931](#)). However, assumptions such as the Hardy-Weinberg equilibrium, random migration and equal populations are often not met ([Whitlock and McCauley, 1999](#)). These indirect estimates are also reflecting evolutionary history and past dispersal, and may be of limited use for population ecologists.

Despite the diversity of methods, investigating metapopulation eco-evolutionary

dynamics and the response of dispersing species to environmental changes with field study can be very challenging. Indeed, it requires monitoring programs at very large spatial and temporal scales, considering many processes, mechanisms, and organization levels, from genes to metapopulation (Baguette et al., 2017). For example, the understanding of eco-evolutionary loops is hindered by the challenges to simultaneously track trait changes and population demography in networks of populations. Moreover, the exploration of various management strategies and their ecological and evolutionary consequences is nearly impossible in nature because addressing these questions would involve experimental intervention on natural populations, such as modifying the quality of source or sink habitats, or altering dispersal patterns. Applying this approach to natural populations may thus not only be technically difficult, but also questionable on ethical and legal aspects.

Modelling approaches may address these different challenges. First, there are few or no limitations on the scales of study, whether spatial or temporal. Indeed, one can work from the gene to the ecosystems, and on ecological or evolutionary time scales. Second, models can be used as virtual laboratories, evaluating a multitude of scenarios without degrading the habitat or threatening the species. Models also allow the tracking of many response parameters simultaneously, such as genetic structure, population demography, or life history traits diversity. However, there are many different modelling approaches available to address metapopulation dynamics, each with their own benefits and limits. Another challenge is to choose which approach is the most appropriate for the question at hand and depending on the amount of data available for parameterization.

2.2 THE NEED OF ECO-EVOLUTIONARY, SPATIALLY-EXPLICIT, AND AGENT-BASED APPROACHES

In general, existing modelling approaches have been used for various purposes and do not satisfy all the criteria needed for an ideal metapopulation model, such as variation in patch size, explicit spatial location of populations, explicit modelling of local population dynamics, stochasticity, evolutionary processes... First, the Levins model was developed to provide general analysis of classical metapopulation dynamics by assuming infinite habitat patches, equally connected, and by ignoring local population dynamics and focusing on patch occupancy (Hanski, 1999). Structured metapopulation models, extending the Levins model, include local population

dynamics but they also do not consider the explicit spatial structure of the populations (Hanski, 1999).

Spatially explicit approaches have been extensively used to consider the influence of the spatial structure of habitat and populations on the metapopulation dynamics. Lattice models, where the set of habitats patches is represented by a regular lattice, are very common in the literature (e.g., Bascompte and Sole, 1996). They may be appropriate for general questions but they are not ideal for representing real landscapes. Spatially realistic simple models (Hanski, 1999), a variant of the Levins model considering spatial locations of a finite number of patches, consider the colonization process as function of distance, and extinction as function of patch size. The incidence function model (IFM) also considers explicit patch size and distance, but includes more stochasticity and uses Markov chains (Hanski, 1999). These previous models, based on dynamics of patch occupancy (called SPOMs, Stochastic Patch Occupancy Models), i.e. assuming network of habitat patches with only two possible states, occupied or empty, are parsimonious models that have been widely employed. They allow to simply isolate and understand the effects of metapopulation components, but at the expense of realism.

Baguette (2004) questioned the general capacity of SPOMs to predict the dynamics of metapopulations in the "real, natural world". He argued that these models particularly apply to classical metapopulation types, but that this type occur very rarely in nature. Moreover, it is increasingly important to capture the processes resulting in the observed dynamics of metapopulations, especially in the face of a changing world (Evans, 2012). Incorporating complex biological details leads to process-based models, by adding within patch dynamics for example. In particular, individual based simulation models (IBM), with careful parameterization, are increasingly being used to simulate the complexity of species life cycle and generate new insights and predictions on how complex spatial systems respond to changes (DeAngelis and Grimm, 2014; Stillman et al., 2015). For instance, Radchuk et al. (2013) used an IBM to predict population viability of a butterfly species (*Boloria eunomia*) under climate change scenarios by considering the effects of environmental factors on the survival of immature life stages. These bottom-up models, by integrating variation and interactions between individuals, can be more powerful and accurate than patch-based metapopulation models (Harrison et al., 2011).

However, an evolutionary perspective is required to study species responses to environmental changes (Urban et al., 2016). Demo/eco-genetics IBMs are particularly adapted to the study of metapopulation eco-evolutionary dynamics; by including

the genetic basis of traits and their transmission, they allow life history traits evolution and their interaction with demographic effects (Dunlop et al., 2009). In such modeling approaches, individual fitness is not defined *a priori* and rather emerges from individual variation in fitness related traits and inter-individual interactions, themselves resulting from populations dynamics. Populations dynamics results in turn from individuals decisions and traits (genotype, phenotype), and eco-evolutionary loops may arise (Stillman et al., 2015). Thus, demo-genetic approaches seem particularly suited for the study of adaptation networks, allowing to explore the consequences of dispersal at different scales, from genes to metapopulations, in a unified framework (Baguette et al., 2017).

Overall, I believe that a modelling approach which is i) spatially explicit, ii) agent/individual-based, and iii) demo-genetic provides a coherent framework to evaluate metapopulation eco-evolutionary dynamics and the theory of adaptive networks.

2.3 IMPORTANCE OF INTERINDIVIDUAL INTERACTIONS IN ECO-EVOLUTIONARY POPULATION DYNAMICS

This section corresponds to an article published in the *Evolutionary Applications* journal (Lamarins et al., 2022b), which puts forward models that meet the challenges previously identified for the study of eco-evolutionary responses of metapopulations. In particular, we focused on the importance of integrating interindividual interactions in eco-evolutionary models to better reflect the dynamics of populations. This work is part of a scientific network gathering researchers interested in this modeling approach and is the result of a collective effort.

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Importance of interindividual interactions in eco-evolutionary population dynamics: the rise of demo-genetic agent-based models

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Abstract

The study of eco-evolutionary dynamics, which favours the convergence of ecological and evolutionary time scales, is of growing interest in the current context of global change. However, many eco-evolutionary studies overlook the role of interindividual interactions, which are hard to predict and yet central to selective values. Here, we aim to put forward models that simulate interindividual interactions in an eco-evolutionary framework: the demo-genetic agent-based models (DG-ABMs). Being demo-genetic, DG-ABMs consider how ecological and evolutionary processes are intertwined. Being agent-based, DG-ABMs follow populations of interacting individuals with sets of traits that vary among the individuals. We argue that the ability of DG-ABMs to take into account the genetic heterogeneity - that affects individual decisions/traits related to local and instantaneous conditions - differentiates them from analytical models, another type of model largely used by evolutionary biologists to investigate eco-evolutionary feedback (EEF) loops. Based on the review of studies employing DG-ABMs and explicitly or implicitly accounting for competitive, cooperative, or reproductive interactions, we illustrate that DG-ABMs are particularly relevant for the exploration of fundamental, yet pressing, questions in evolutionary ecology across various levels of organisation. By jointly modelling the effects of management practices and other eco-evolutionary processes on interindividual interactions and population dynamics, DG-ABMs are also effective prospective and decision support tools to evaluate the short- and long-term

evolutionary costs and benefits of management strategies and to assess potential trade-offs. Finally, we provide a list of the recent practical advances of the ABM community that should facilitate the development of DG-ABMs.

Keywords: eco-evolutionary dynamics, demo-genetic models, eco-genetic models, agent-based models, DG-ABMs

2.3.1 Introduction

Understanding and anticipating populations' response to changes in environmental and anthropogenic pressures requires conceptual and modelling approaches coupling ecological and evolutionary processes. This is largely motivated by the increasing realisation that ecological and evolutionary responses of populations can occur on similar temporal scales, with potential consequences on dynamics from gene to ecosystem (Carroll et al., 2007). The burgeoning literature investigating eco-evolutionary dynamics illustrates this growing interest (Dunlop et al., 2009; Schoener, 2011; Romero-Mujalli et al., 2019; Oddou-Muratorio et al., 2020; Bassar et al., 2021).

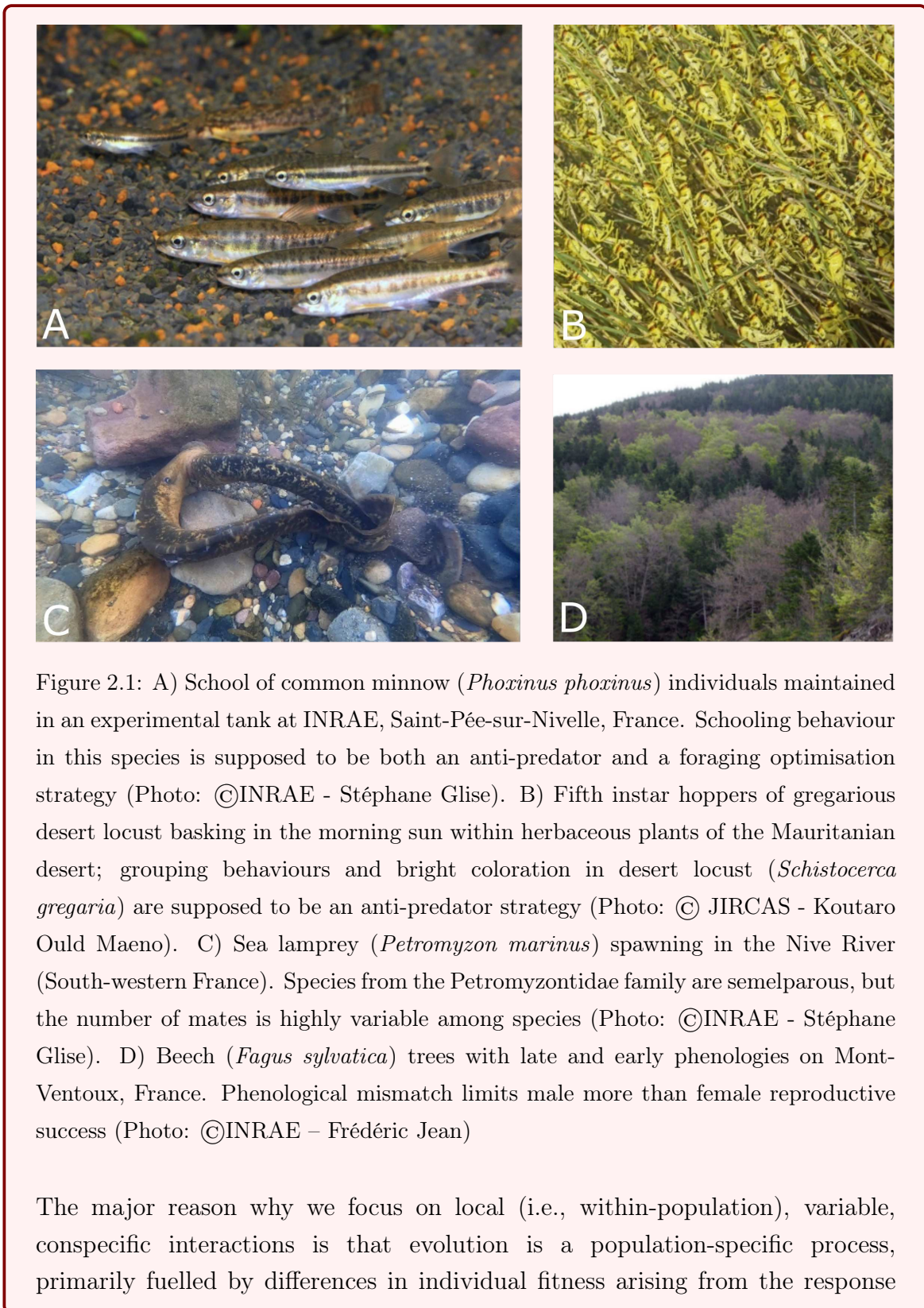
The conceptual framework of eco-evolutionary dynamics depicts feedback loops between response processes at different levels of biological organisation in a contemporary time scale (Pelletier et al., 2009; Hendry, 2017; Govaert et al., 2019). These feedback loops acknowledge that (1) genetic diversity and its architecture determine the demographic structure and population dynamics through phenotypic expression; (2) demographic structure and population dynamics determine evolutionary processes, i.e., genetic drift, selection and gene flow, which in turn (3) determine genetic diversity. As an illustration of such feedback, the competition between trees within a forest results in a selection process contributing to genetic evolution, while the genetic composition of the tree population drives interindividual competition and forest productivity (Pretzsch, 2021). To account for feedback loops, eco-evolutionary models must integrate inheritance mechanisms and the multiple driving forces controlling the dynamics of the distributions of heritable traits across generations (Bassar et al., 2021).

One of these key drivers of selection are the interactions between individuals within populations, as they directly or indirectly affect individual fitness at the core of any evolutionary dynamics (Maynard Smith, 1974; Webber and Vander Wal, 2018). We focus here on *within*-population interindividual interactions (i.e., competition, cooperation, and mating) affecting the demographic dynamics (growth, reproduction, mortality) and ultimately individual fitness or even inclusive fitness (Box 2.1). In essence, the outcome of such interactions is eminently stochastic and context-dependent, and population structure itself is part of the context. It is now recognised that the structure of social networks within a population may affect natural selection and traits evolution through indirect genetic effects (traits affected by genes in other individuals, Wade et al., 2010; Kazancıoğlu et al., 2012; Fisher and McAdam, 2017; Marjanovic et al., 2022). Additionally, these networks are themselves dynamic,

since changing the social environment may influence an individual's later decisions in a social interaction, leading to rapid shifts in networks' structures (Farine and Whitehead, 2015). For instance, individuals are able to modify their mating tactics, which diminishes the selection they endure (Oh and Badyaev, 2010), and thus affects selection at the population level. Likewise, the distribution of phenological traits (e.g., flowering or maturation time) shapes mating opportunities within plant and animal populations, and possibly leads to assortative mating (here, the positive correlation of phenology between mates). Compared to random mating, assortative mating can either deplete or increase the genetic variance available for selection depending on whether the environment is stable or changing, with contrasted consequences on genetic adaptation (Godineau et al., 2022). Unfortunately, the interindividual interactions are usually little appreciated in eco-evolutionary models, with potential consequences on our understanding of the full range of eco-evolutionary responses.

Box 2.1: Interindividual interactions involved in population eco-evolutionary dynamics

Here, we focus on interactions between conspecific individuals within a population- mainly competition, cooperation, and mating - which directly drive the processes of mortality, growth, and reproduction (e.g., Fig. 2.1 A, C, D below) and whose variations subsequently induce evolutionary changes. This also includes the variety of ecological interactions indirectly impacting demography, such as exchange of information (e.g., on predator, or resource availability), movement (e.g., to escape predation or competition) or group behaviour (e.g., affecting predator's avoidance or resistance, Fig. 2.1 A, B below).



to abiotic and biotic environments, the latter including the social context. Interspecific interactions may also shape the within-population social context and contribute to evolution: for instance, the existence and strength of plant-pollinator interactions define the social context within which selfing may evolve (Katsuhara et al., 2021). Trophic interactions may contribute to the resource context within which functional traits related to resource acquisition may evolve (Kang and Thibert-Plante, 2017). On a macroevolutionary timescale, intra- and inter-specific competition for resources can drive speciation (Gavrilets et al., 2007; Weber et al., 2017). However, considering interspecific interactions without genetic variation in at least one of the partners of the interaction is not enough to model the dynamic feedback loop between ecological interactions, fitness, and the genetic composition of the population. This is particularly why predation was not considered as a focal interaction in this review: indeed, when predation is investigated from the point of view of the variation of a prey's trait conferring variable avoidance ability from the predator, or from the variation of a predator's trait conferring variable ability to catch prey, then it becomes a trait involved in competition among prey to escape predators, or among predators to catch prey (e.g., Labonne and Hendry, 2010).

Our objectives here are to put forward models that explicitly or implicitly account for variable within-population interindividual interactions in an eco-evolutionary framework: the demo-genetic agent-based models (DG-ABMs). After defining these models, we survey the literature to illustrate how DG-ABMs can be used to investigate fundamental issues in evolutionary ecology, as well as to assist the management of natural populations facing environmental changes.

2.3.2 How to model eco-evolutionary feedback loops: from analytical models to DG-ABMs

At the very core of the eco-evolutionary models is the need of specifying the genetically variable and heritable traits, their impact on the focal organism's life history, and the ecological embedding that determines how life-history traits affect and are affected by environmental conditions and the demographic context (Dieckmann and Ferrière, 2004). This can be achieved by various approaches (Fig. 2.2). First, there is a long tradition in evolutionary ecology to rely on analytical models (differential-

equation and difference equation models) which offer elegant solutions and provide general knowledge on elementary eco-evolutionary feedback (EEF) loops, generally at the cost of simplifying hypotheses. Among the most common analytical formalisms of EEF loops are (1) adaptive dynamics models (Dieckmann and Ferrière, 2004), which incorporate ecological realism, in particular, the notion that the success of any given strategy depends on its frequency within the population, but often bypass the complexity of genotype-phenotype relationship (for instance by assuming asexual reproduction, clonal inheritance); (2) evolutionary quantitative genetics models (Slatkin, 1978; Pease et al., 1989; Kirkpatrick and Barton, 1997), which integrate the genotype-phenotype map with population demography (e.g., density-dependence) but where other ecological changes remain independent from the population dynamics; and (3) integral projection models (IPM, Smallegange and Coulson, 2013), which use population models classically developed in population dynamics to describe the evolution of continuous characters in a quantitative genetics framework. We purposely do not mention traditional optimisation models, such as stochastic dynamic programming used to represent individual behaviour (e.g., life history decisions) and development (e.g., growth and sexual maturity) and their consequences for population dynamics (Mangel, 2015), as these models do not specify the genetic basis of traits, which is mandatory for EEF. The main limitation of the above-listed analytical approaches is that they consider evolutionary and ecological processes (be they deterministic or stochastic) to be homogeneous within groups of individuals (the population or life stages), whereas group composition constantly varies in terms of phenotypes and genotypes, affecting individual decisions, linked to local and instant conditions, and their outcome at the group level (i.e., emerging effects).

Yet the question of individual heterogeneity and its effects has long preoccupied eco-evolutionary ecologists. For several decades, simulations using agent-based models (ABMs, also called individual-based models or IBMs in ecology) were used to investigate more complex scenarios and explore unexpected EEF, with approaches spreading on a spectrum of complexity well described by DeAngelis and Mooij (2005). On the one side of the spectrum, some ABMs were developed to validate and/or explore the predictions made with analytical models, replace these models and/or eventually nurture their future development. To keep these ABMs as simple as possible, individuals usually have a minimum number of attributes and fitness does not depend on interindividual interactions. For instance, by coupling a niche-based model with individual-based demo-genetic simulations, Cotto et al. (2020) investigated the evolutionary constraints related to alpine plant response to a changing climate. The

	Analytical models	DG-ABMs
Scale	Population	Individual
Population dynamics	Uniform within-populations or within classes	Not uniform, possible structure
Within-population variation	Simplified (2 variants) or Gaussian distribution, no structure	Distribution free, possible structure (e.g. spatial)
Transmission		
Inter-individual interactions	Uniform within-populations	None ↔ Not uniform, explicitly modelled
Trait-fitness relationship	Input, not flexible	Outcome, flexible, allows emerging effects
Management practices	Mean impact, not flexible	On individuals and interactions, allows emerging effects

Figure 2.2: Different approaches to model eco-evolutionary feedback loops. This scheme summarises the main differences between two major modelling approaches used to investigate eco-evolutionary dynamics: analytical models on the left and Demo-Genetic Agent-Based Models (DG-ABMs) on the right. Their main difference is that analytical models consider evolutionary and/or ecological processes to be homogeneous within groups of individuals (the population or life-stages), whereas DG-ABMs can account for phenotypic and genotypic variation in groups of individuals, its effects on individual decisions/traits linked to local and instant conditions, and their outcome at the group level (i.e., emerging effects). In particular, some (although not all) DG-ABMs model interindividual interactions, and their effects on individual fitness, which emerge in part from these interactions.

key originality of their approach is to model individuals as spatial points across a complex climatic landscape, where the individual phenotypes are explicitly linked to climatic variables and where the optimal phenotype is prescribed by the niche-based model and varies through time. They use a classical multi-stage life cycle model (from seeds to adults) where individual survival and ultimately fitness increases when the multivariate phenotype is close to the optimal phenotype but is independent of the phenotype of other individuals. This typical top-down approach aims at extending classic analytical models into more complex domains with the assistance of ABMs.

On the other side of the spectrum, some ABMs employ a specific bottom-up approach to fully integrate individual interactions and their outcome over time and space within a population, the result of which will dictate the strength and direction

of evolutionary processes at the population level (Huston et al., 1988; DeAngelis and Mooij, 2005). These ABMs acknowledge that individuals have inherently non-uniform interactions with each other, and that the consequences of the variation in traits mediating interindividual interactions are better described by rule-based simulations than by mathematical models. Accordingly, these approaches depict the interactions between individuals and their effects on individual fitness, accounting for the social context, and observe the resulting dynamics in terms of distributions of heritable traits and demography. We hereafter refer to these ABMs as Demo-Genetic Agent-Based models, DG-ABMs (another possible acronym would be Eco-Genetic ABMs).

DG-ABMs can be defined as individual-based (meta)population dynamics models with heritable trait variation and phenotype-dependent interactions between individuals (Box 2.2). A key feature of DG-ABMs is that fitness variation emerges mechanically from interactions between individuals (as opposed to assuming an *a priori* fitness function) and gives rise to the evolution of patterns structuring the population diversity and its dynamics (e.g., genetic architecture, spatial genetic structure). Typical examples of emerging fitness variation are spatially structured individual-based models focusing on dispersal evolution (Bach et al., 2006; Poethke et al., 2007; Kubisch et al., 2013). Indeed, these studies demonstrated that genetic structure and kin competition emerge from the spatial design of their DG-ABMs, when coupled with the genetic basis of dispersal and competition (here implicitly accounted for). Hence, dispersal evolves to reduce kin competition and increase inclusive fitness, ultimately driving back kin structure within populations. This is radically different from assuming a prescribed relationship between traits and fitness, as done in analytical models and some ABMs (e.g., Cotto et al., 2020). We argue here that this bottom-up construction of fitness in DG-ABMs provides different and new insights into various fundamental and applied questions in ecology and evolution, and illustrate further our point of view by a review of the literature.

Box 2.2: An overview of demo-genetic agent-based models (DG-ABMs) and on how they model interindividual interactions

Conceptual scheme of DG-ABMs (Fig. 2.3).

Modelling interindividual interactions: ABMs have the general capacity to represent both direct interactions among agents (i.e., when one agent identifies one or more other agents and directly affects them, e.g., by having some kind of contest with them, eating them, or choosing them to mate) and

mediated/indirect interactions (when one agent affects others indirectly by producing or consuming a shared resource).

The choice to model these interactions explicitly or implicitly in DG-ABMs depends on the interaction type, the degree of realism/complexity desired, and on the focal, evolvable trait(s) involved in the interaction (see Table 2.1 for examples of these traits). Direct reproductive interactions are most often explicitly modelled, through variable mate preference or competitiveness among potential mates (e.g., [Chevalier et al., 2022](#)), or assortative mating for a variable phenological trait (e.g., [Soularue and Kremer, 2014](#)). This is also the case of direct cooperative interactions, where the mechanisms involved (e.g., in grouping behaviour) are usually explicitly represented ([Van Der Post et al., 2015](#); [de Jager et al., 2020](#)).

Indirect interactions such as competition for resources can be implicitly modelled through density-dependence functions. For instance, most DG-ABMs investigating fisheries-induced evolution assume that increasing density will lead to increasing competition, the competition strength also depending on individual size ([Piou and Prévost, 2012](#); [Ivan and Höök, 2015](#)). By contrast, some DG-ABMs consider competition in an explicit prey-predator ([Costa et al., 2016](#)) or consumer-resource ([Kang and Thibert-Plante, 2017](#)) system; in these cases, the level of the resource and the consumption process at each time step are explicitly modelled, and the traits involved in the interaction can be more realistically represented (e.g., gill-raker count in [Kang and Thibert-Plante, 2017](#)).

DG-ABMs applications: DG-ABMs also offer the opportunity to study eco-evolutionary dynamics at multiple levels of organisation and spatio-temporal scales. At population scale, habitat structuring and variation in the abiotic environment can be included to account for selection, stochastic events and subdivision of the social environment. These models also allow simulations of several populations' dynamics connected through dispersal with potential gene flow, such as in a metapopulation case. At a higher level, community dynamics can be modelled through interspecific interactions between individuals from directly or indirectly interacting species.

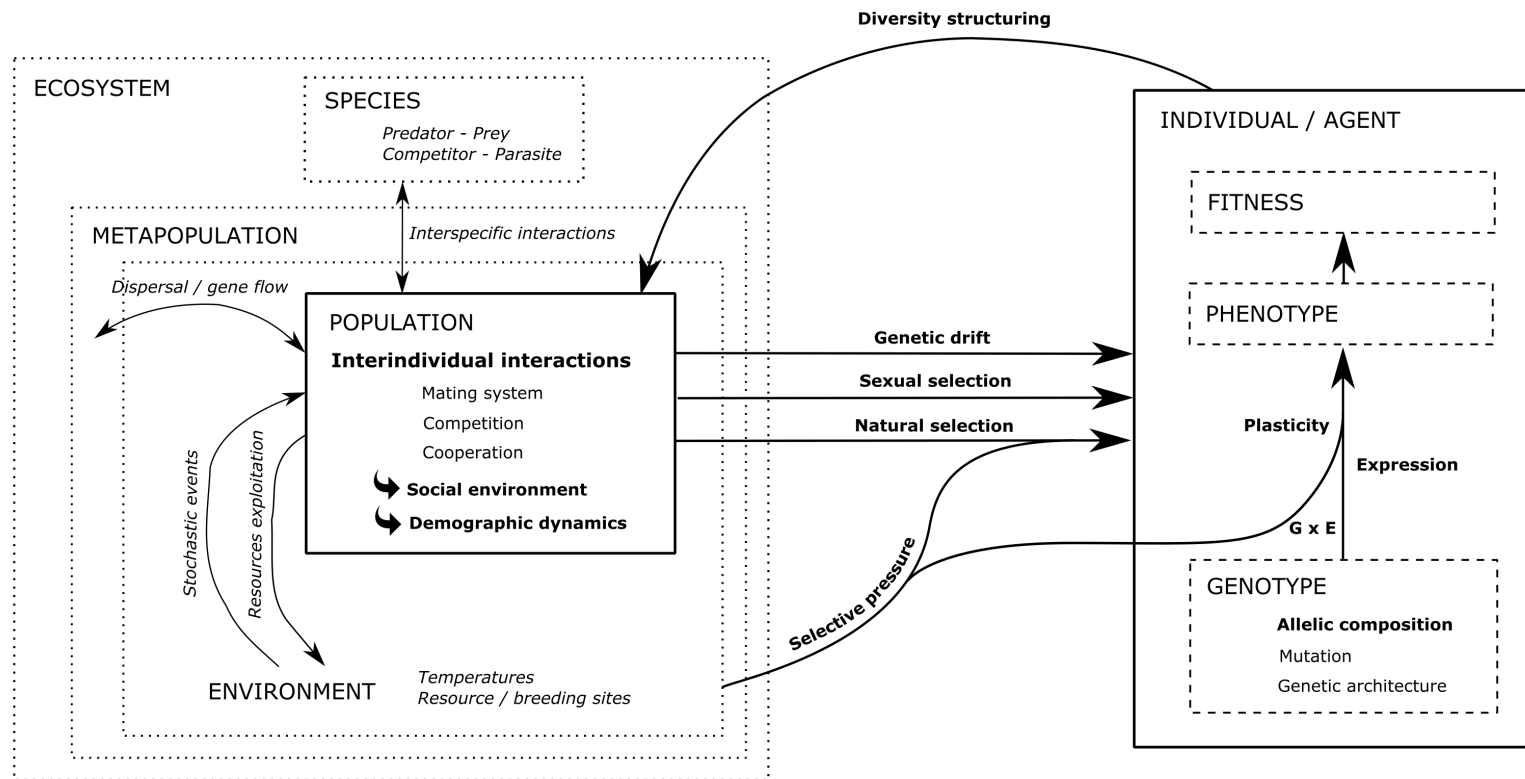


Figure 2.3: Individuals (or agents) are characterised by their phenotypic traits, determined by their genotype, the environment, and interactions between them (denoted Gx E). The agents together define the population, hence determining its diversity and structure, where interindividual interactions shape the social environment. This social environment influences population dynamics, which ultimately drives evolutionary processes (drift, selection, gene flow). Fitness variations (e.g., survival, fecundity variation) emerge from different outcomes of interindividual interactions (e.g., mating, competition, cooperation, information exchange) and give rise to evolution of traits via the trans-generational response to selection. This framework, highlighting the feedback loop central to eco-evolutionary approaches, is the core part of DG-ABMs and is identified by solid (units) / dashed (units' properties) line boxes and bold arrows.

2.3.3 Objective and method for the literature review

In their recent review of individual-based modelling of eco-evolutionary dynamics, [Romero-Mujalli et al. \(2019\)](#) illustrated how ABMs have been applied to assess organisms' and populations' responses to environmental change, but overlooked whether these ABMs accounted or not for interindividual interactions. Here, we specifically reviewed DG-ABMs in which fitness variation emerges mechanically from interactions between individuals.

To that aim, we searched the Web of Science Core Collection between 1955 and 2022 for various combinations of key-words (Suppl. Mat. Fig. 2.4 and 2.5). A first query using (Individual-based model* OR IBM*) AND (eco-evol* OR demo-genet* OR demogenet* OR ecogenet* OR eco-genet*) returned 138 publications. By using the terms (Agent-based model OR ABM) instead of (Individual-based model* OR IBM*), we obtained 15 publications indicating that the eco-evolutionary community has not appropriated the term ABM despite its broader meaning (e.g., [Railsback and Grimm, 2019](#)). Of all these 153 publications (see Table S1 in [Lamarins et al., 2022b](#)), only 54 included the terms ((interindivid* OR inter-individ* OR individ*) AND interact*). After excluding reviews, technical publications, book chapters, preprint and duplicated studies (Suppl. Mat. Table 2.3), we retained 120 publications. Finally, as we were interested in studies using a DG-ABM approach, we checked if these 120 remaining publications (1) use an IBM; (2) simulate dynamics over multiple generations; (3) represent (direct or indirect) interactions between conspecific individuals; (4) represent individual variation in the interaction-related trait(s); (5) consider that part of this variation is heritable. With this method, we filtered out 45 additional publications that did not satisfy these five criteria, resulting in a total of 75 publications using DG-ABMs where interindividual interactions affect fitness. Using a snowball approach, we found 14 additional references cited in or citing the 75 selected publications (see Table S3 in [Lamarins et al., 2022b](#) and [Lamarins et al., 2022a](#) for the final database). Note that the difficulties we encountered in selecting studies using DG-ABMs with interindividual interactions from the WOS illustrate the need for clearer referencing based on key-words better shared by the community.

2.3.4 Synthesis of the literature review

In the selected 89 studies, competition was by far the most considered interaction (79 studies), followed by reproductive interactions (38 studies) and cooperative interactions (4 studies only). We found 32 studies accounting for two types of

interaction simultaneously.

On average, 1.9 traits (between 1 and 19 traits) per study were considered as evolvable. The nature of evolvable trait(s) depended on the interaction type, the species/kingdom considered and the level of generality/realism/precision of the model (following the classification of models properties of [Levins, 1966](#)). We distinguished eight categories of evolvable traits (Tables 2.1 and 2.2): 1) traits related to growth and/or maturation thresholds (36 studies); 2) traits related to mating (12 studies); 3) dispersal traits (12 studies); 4) traits related to cognitive behaviour and information exchange (six studies); 5) traits related to energy acquisition or allocation (six studies); traits related to 6) defence (five studies) or 7) virulence (two studies); 8) and finally, abstract traits - meaning that they do not correspond directly to a measurable trait - generally related to competitive ability or/and assortative mating (17 studies). We found seven studies considering two types of traits simultaneously. While some of these traits directly mediate interindividual interactions (e.g., mating traits for reproduction, behavioural traits for cooperation), most of them indirectly impact interactions. For instance, dispersal traits or movement preferences are often associated with avoidance of competition and/or predation, or mate search for reproduction ([Travis et al., 2012](#); [Fronhofer and Altermatt, 2017](#)). Traits related to growth, maturation and energy acquisition or allocation, influence individual size, which often plays a major role in the outcome of competition.

Table 2.1: Interindividual interactions and associated evolvable traits modelled in DG-ABMs. To illustrate the categories of traits considered as evolvable in the reviewed DG-ABMs, we listed some examples (see Lamarins et al., 2022a) depending on the interaction type considered (IT): competition (C), reproduction (R) or cooperation (Coo).

IT	Evolvable traits category	Examples	Examples of references (species/kingdom)
C	1) Growth/ maturation	Size at emergence	Fielding 2004 (grasshopper); Ayllón et al. 2016, 2018 (trout)
		Threshold for size at migration	Piou and Prévost 2012, 2013 (salmon)
		Growth rate	Kang and Thibert-Plante 2017 (alewife); Moya-Laraño 2011 (generic); Travis et al. 2010 (plant)
	2) Abstract trait	Competitive abilities	Gascuel et al. 2015; Pontarp et al. 2015; Ward and Collins 2022 (all generic for species community)
	4) Dispersal trait	Prospecting of habitat quality	Fronhofer et al. 2011; Ponchon et al. 2021 (generic)
		Dispersal distance	LaRue et al. 2019 (sea rocket); Leidinger et al. 2021 (plant)
	5) Behaviour	Movement preference Drifting	Hrycik et al. 2019 (perch) Mazzucco et al. 2015 (shrimps)
	6) Energy, allocation	Functional traits related to energy acquisition	Ivan and Höök 2015 (perch); Mollet et al. 2016 (plaice)
7) Defence	Toxin production	de la Peña et al. 2011 (plant-herbivores)	
	Abstract defence	Costa et al. 2016; Urban et al. 2019 (generic)	
8) Virulence	Pathogen virulence	Papaix et al. 2018; Rimbaud et al. 2018 (plant pathogen)	
R	1) Growth/ maturation	Threshold for size at maturity	Ayllón et al. 2016, 2018 (trout); Piou and Prévost 2012, 2013 (salmon); Kane et al. 2022 (trout)
		Slope/intercept of the maturation reaction norm	Dunlop et al. 2007 (bass)
	3) Mating	Selfing or self-incompatibility Mate choice (preference, competitiveness), mate search	Kirchner et al. 2006; Katsuhara et al. 2021 (plant) Berec et al. 2018; Chevalier et al. 2022 (generic) ; Labonne and Hendry 2010 (guppy) ; Nathan et al. 2019 (trout)
Coo	2) Abstract trait	Mutualistic or antagonistic trait	Maliet et al. 2020 (generic)
	5) Cognitive behaviour	Grouping, schooling behaviour Attachment density	Van Der Post et al. 2015 (generic); Reuter et al. 2016 (fish) de Jager et al. 2020 (mussel)

Table 2.2: Association between the category of evolvable traits considered in each DG-ABM, and the type of eco-evolutionary feedback considered.

Trait category	Type of eco-evolutionary feedback					Number of studies
	Ecology-focused	Microevolution-focused	Macroevolution-focused	Management-focused	Spatial-focused	
Growth/Maturation	6	2	3	16	3	30
Abstract trait	2	7	8			17
Dispersal	2				9	11
Mating	2	5		1		8
Cognitive behaviour	2	1	1		2	6
Defence	1	2			1	4
Energy acquisition or allocation	2	1		1		4
Virulence				2		2
Mating and growth/maturation			1	2		3
Mating and Energy acquisition or allocation		1				1
Growth/maturation and Defence				1		1
Growth/ maturation and Dispersal					1	1
Growth/ maturation and Energy acquisition or allocation				1		1
Number of studies	17	19	13	24	16	89

These evolvable traits are at the core of the EEF loop in DG-ABMs, since fitness variation emerges from interactions among individuals that differ in these traits, giving rise to population dynamics in terms of both distribution of evolvable traits and demography. We distinguished five main types of EEF in the reviewed DG-ABMs (Table 2.2). We found 17 “Ecology-focused” DG-ABMs, with a high level of realism in the demographic and ecological processes, and incorporating a “dose” of evolutionary processes to gain a better understanding of the ecological/demographic behaviour. In these DG-ABMs, evolvable traits were most often growth/maturation traits, but six other trait categories were considered. Then, we found 19 “Microevolution-focused” DG-ABMs, with a high level of generality in the evolutionary processes, and incorporating a “dose” of demographic and ecological processes to gain a better understanding of the evolutionary behaviour at a contemporary timescale. Similarly, there were also 13 “Macroevolution-focused” DG-ABMs, dedicated to the understanding of speciation at a macroevolutionary time scale. In these “Micro- or macroevolution-focused” DG-ABMs, the evolvable trait was most often abstract, but mating traits were also often considered. Then, we identified 24 “Management-focused” DG-ABMs, used to address how management practices interfere with the EEF loop with a high level of precision; in these DG-ABMs, evolvable traits were most often growth/maturation traits. Finally, we found 16 “Spatial-focused” DG-ABMs, used to investigate EEF in a spatially explicit context (e.g., metapopulation). These DG-ABMs investigated in particular the evolution of dispersal traits.

Another characteristic of DG-ABMs is the type of inheritance framework used to model genetic variation in the evolvable traits. We found that 64 studies (71.9%) used a Mendelian inheritance process either in a population genetic framework (one locus, possibly multi-allelic, which directly determines the phenotype) or combined with a quantitative genetic framework (several loci, together with the environment, which govern trait variation). Besides, 22 studies (24.7%) used an infinitesimal quantitative genetic framework (where each offspring inherits the mean of the two parent’s genetic values), and two studies (2.2%) tested for population versus quantitative genetic framework. Note that our definition of DG-ABM is larger than the one suggested by some authors (e.g., [Frank and Baret, 2013](#)), who proposed to reserve the term “eco-genetic” to models based on a quantitative genetics framework, and the term “demo-genetic” to models based on a population genetics framework. Beyond these general typologies, we illustrate below the main applications of the reviewed DG-ABMs, through selected examples.

2.3.5 DG-ABMs to better understand eco-evolutionary feedback loops

Accounting for variable within-population interindividual interactions in a bottom-up approach allows DG-ABMs to better investigate the emergence of fitness variation resulting from several complex eco-evolutionary processes and the interactions between them. Accounting for the stochastic and context-dependent outcomes of competitive, cooperative, or reproductive interactions can change the predicted evolution of life-history traits compared to an approach where the relationship between traits and fitness is prescribed. Below, we emphasise relevant studies from our literature review which investigate these three types of interaction.

We start with examples of DG-ABMs considering explicit **competitive** interactions within species. [Fielding \(2004\)](#) investigated competition in grasshoppers and showed that contrasted optimal values of life history traits can emerge from different types of localised interindividual interactions, i.e., exploitative or size-based competition. In their DG-ABM of trout population, [Ayllón et al. \(2016\)](#) observed the emergence of different eco-evolutionary outcomes due to explicit competitive interactions for food in a changing environment. These two DG-ABMs with explicit competitive interactions were built from well-tested demographic models, and additionally considered that the same traits (size at emergence and maturity size threshold) could evolve and interact with the spatial distribution of food resources to shape population dynamics. Most often in the reviewed DG-ABMs focusing on single species adaptive dynamics, competition is implicitly considered, e.g., through a density-dependence function. In a perch species, [Ivan and Höök \(2015\)](#) showed variable patterns of energy allocation along individual ontogeny, resulting from the interplay between plastic and adaptive responses to selection and density-dependent competition for food. Using a DG-ABM representing competition among individuals choosing different life-history tactics, [Piou and Prévost \(2013\)](#) and [Piou et al. \(2015\)](#) showed that climate change may modify salmon population dynamics through plastic responses of individual size. These two DG-ABMs acknowledge the main role of individual size on competition, and incorporate both genetic and plastic variation in this trait to gain a better understanding of the adaptive population dynamics in future, changing environments.

Integrating behavioural interactions between individuals and EEF is logically critical to understand the evolution of sociality and **cooperation**. [Van Der Post et al. \(2015\)](#) investigated how grouping, a taxonomically widespread social process, co-

evolved with two cooperative social behaviours: anti-predator vigilance and foraging. In a simulation experiment where behavioural processes were specified through 19 variable traits, but not the cost and benefits of each decision strategy, they showed eco-evolutionary interactions between group size and vigilance with an evolutionary trajectory towards bigger groups and less vigilance, eventually leading to fission into small groups with high vigilance and back. Accounting for heritable interindividual differences and environmental heterogeneity in resource distribution, [Reuter et al. \(2016\)](#) were able to relate landscape structure to the evolution of schooling behaviour and collective foraging in fish. Although these studies mostly focused on how cooperation can emerge in models where costs and benefits are not explicitly specified but related to other behavioural traits, reverse strategy, where cooperation is the evolvable trait, could also be used to investigate adaptive dynamics.

Reproductive interactions are an obvious major driver of demographic dynamics, and “Ecology-focused” DG-ABMs are particularly suitable to investigate this issue in an eco-evolutionary framework. For instance, to explore how mating behaviour and population size jointly affect fitness components or population growth rate through Allee effects, [Berec et al. \(2018\)](#) considered the rate of mate search as evolvable and found different optimal values of search rates for populations at different densities, resulting in lower Allee thresholds in populations kept at lower densities. DG-ABMs are also relevant to examine the interplay between demographic processes and the mating system when self-incompatibility ([Kirchner et al., 2006](#)) or sterility ([Nonaka and Kaitala, 2020](#)) occur as a direct consequence of the genotype.

Reproductive interactions are also known to drive evolutionary dynamics ([Maan and Seehausen, 2011](#)), and explicit representation of mating interactions is important as sexual selection can sometimes oppose natural selection ([Labonne and Hendry, 2010](#)), or eventually reinforce it ([Soularue and Kremer, 2014](#)). Mate choice strongly depends on the population structure, making the outcome challenging to predict yet rarely random ([Klug and Stone, 2021](#)). DG-ABMs, by allowing to represent explicitly sexual interactions, are particularly adapted to explore the evolution of traits considering the dynamic aspects of mating systems, such as when sexual preference and competition over mating partners occur, while still accounting for natural selection ([Nathan et al., 2019](#); [Chevalier et al., 2022](#)). In this context, growth traits, or traits related to life-history decisions such as migration or maturation, are often chosen as key traits to jointly consider size-dependent survival and reproductive interaction and their possible interactions ([Piou et al., 2015](#); [Ayllón et al., 2019b](#)). Another application is the investigation of sexual dimorphism, which can arise when a given trait is subject

to different selection pressures in males vs females (or even opposing pressures in the case of sexual conflict), but has a shared genetic basis between the sexes. Höök *et al.* (2021) showed how sex-specific plasticity for size could evolve by looking at perch evolutionary response to environment. Kane *et al.* (2022) showed that optimal migration propensity differed among males and females in trout, and that populations could adapt to environmental change across a range of intersex genetic correlations for migration propensity, which influence the magnitude of sexual conflict.

2.3.6 Extending in space, time and levels of organisation

In most examples detailed above, eco-evolutionary dynamics are modelled within a non-spatially explicit population. However, the spatial arrangement of habitats shapes animal movements or gametes propagation, and therefore also shapes social interactions and sexual networks (He *et al.*, 2019). Since they allow fine-scale explicit representation of habitats as well as individual movements, DG-ABMs are well suited to represent **spatial evolutionary dynamics**. Focusing on the evolution of dispersal, Fronhofer and Altermatt (2017) showed how EEF can emerge from a simple spatially-explicit DG-ABM. Depending on network topology and connectivity, variable evolutionary stable dispersal strategies emerged from their model via kin competition, and lead to EEF by changing back the network's demography and genetic structure. Hrycik *et al.* (2019) explored the importance of environmental cues in perch vertical movement. By allowing movement rules in response to these cues to evolve, they illustrated the role of DG-ABMs in determining appropriate movement rules in spatially-explicit ecological modelling. Travis *et al.* (2010) used a mechanistic DG-ABM approach to model the evolution of seed dispersal in plant populations, accounting for likely trade-offs between traits in a patchy landscape. Additionally, sexual selection can determine the reproductive success of immigrants in populations and thus the strength and direction of demo-genetic consequences of dispersal (e.g., demographic rescue, evolutionary rescue vs gene swamping). For instance, Soularue and Kremer (2014) highlighted the major importance of gene flow and assortative mating in shaping the genetic differentiation between populations in a heterogeneous environment.

Interactions between conspecific individuals are at the core of DG-ABMs. In addition, considering explicitly higher levels of organisation (e.g., community level) to represent **interspecific interactions** may ultimately change the evolutionary outcomes expected from single species systems (Weber *et al.*, 2017; terHorst *et al.*,

2018). We found examples of such multispecies DG-ABMs used to investigate mating interactions: for instance, using an ABM in which two plant species share the same pollinators, [Katsuhara et al. \(2021\)](#) highlighted that the evolution of selfing without pollinator assistance (autonomous selfing) may increase population growth rates of inferior competitors and consequently favour long-term coexistence via an evolutionary rescue. Furthermore, [McDonald et al. \(2019\)](#) showed that the strength of intraspecific competition for mates may result from sexual interactions with heterospecifics, which may interfere with sexual selection (i.e., interspecific reproductive interference).

Most of the reviewed multispecies DG-ABMs focused on competitive interactions, in an explicit prey-predators' or community context. For instance, [Kang and Thibert-Plante \(2017\)](#) illustrated that considering trophic interactions and the genetic basis of functional traits within a single model could improve the understanding of evolutionary morphological changes in fish. [Hillaert et al. \(2020\)](#) showed that in a fragmented habitat, the presence of predators selects for increased herbivore movement and hence larger herbivore size. Demo-genetic models of plant-virus interactions allowed to investigate the emergence of plant viral genotypes breaking down plant qualitative resistance genes ([Fabre et al., 2009](#)). Ecological interactions at the community level may drive selection within species, and selection may affect in return the processes of species assembly at a community scale ([Leidinger et al., 2021](#)). Finally, as multispecies DG-ABMs represent both intra-and interspecific complexity, they are especially suited to address macroevolutionary consequences of interspecific interactions, such as speciation ([Gavrilets et al., 2007](#); [Weber et al., 2017](#)). We found several examples of macroevolution-focused DG-ABMs developed to investigate adaptive radiation, i.e., the rapid diversification of a single lineage into many species with a great diversity of ecological strategies ([Gascuel et al., 2015](#); [Pontarp et al., 2015b](#); [Ward and Collins, 2022](#)). These models generally consider a limited number of abstract, phenotypic traits reflecting the competitive ability of the focal individual with all the other individuals of the local patch. The distance between these ecological phenotypes within a patch drives exploitative competition, while heritable variation of the ecological phenotype fuels the processes of local adaptation and speciation.

Overall, it appears that DG-ABMs have a large potential to address fundamental eco-evolutionary questions accounting for multiple drivers of fitness, and are increasingly used in an integrative way, allowing effects to flow up and down between organisation levels.

2.3.7 DG-ABMs to assist management strategies

Another key feature of DG-ABMs is their capacity to model the effects of management practices on individuals and their interactions, together with that of other eco-evolutionary processes. Hence, by allowing emerging effects, DG-ABMs can also be efficient prospective tools to elaborate and assess management strategies. When management consists of **demographic control of populations**, in particular through individual phenotype-based choices, it can deeply impact all demographic processes and population genetic composition, and therefore the intensity and direction of the evolutionary processes (Lefèvre et al., 2014). For example, selective fishing (or harvesting) directly affects competition among surviving fish (or trees), while genetic composition determines optimal fishing (or harvesting) patterns. In particular, different DG-ABMs were used to understand how selective fishing can affect the demography and evolution of fish populations (fisheries-induced evolution), through cascading and sometimes counterintuitive effects on population demographic structure, growth and maturation thresholds (Wang and Höök, 2009; Piou et al., 2015; Wang et al., 2017; Ayllón et al., 2018). By simultaneously modelling the plastic and genetic responses of individuals, DG-ABMs can also disentangle the role of selective fishing and environment in the observed and predicted population declines and phenotypic changes (Piou et al., 2015).

When evolutionary dynamics and **land use planning decisions** are linked, DG-ABMs also represent valuable decision support tools. For example, Papaïx et al. (2018) and Rimbaud et al. (2018) used a spatially explicit demo-genetic model to assess the joint effect of crop cultivar deployment strategies in space and time and key pathogen life-history traits on epidemiological dynamics, resistance durability and long-term evolutionary control. Using a DG-ABM, Mims et al. (2019) found strong effects of spatial connectivity on demo-genetic outcomes in reintroduced bull trout populations, and allowed identification of watershed areas with higher persistence probabilities.

In the case of **hybridization** between native/wild and introduced/domesticated gene pools, DG-ABMs allow to study the impact of management on the dynamics of crossing within and between gene pools, which depends on differential social interactions (e.g., mating preference) and genetic performances (e.g., local adaptation) between gene pools (Castellani et al., 2015; Nathan et al., 2019). In this context, DG-ABMs are an effective means of developing genetic enrichment strategies in a prospective approach (which genetic resources and which deployment modalities for which risks?), and conversely of evaluating strategies aimed at preserving the local

gene pool from unwanted introgression.

In these different case studies, DG-ABMs offer a relevant framework to evaluate the short- and long-term evolutionary costs and benefits of management actions and to assess potential trade-offs between them. For example, they allow to address the issue of exploiting a population or a metapopulation (e.g., fishing, wood production) while preserving its genetic value and diversity, or to determine how to minimize the risks of demo-genetic collapses of populations facing climate change. Furthermore, by controlling the social context of populations, management drives the overall ecological processes and thus affects biotic and abiotic stressors, the susceptibility of populations to these stressors, and selection intensity (Jactel *et al.*, 2009).

2.3.8 Taking advantage of ABMs for DG-ABMs

The above-listed examples from our literature review illustrate the diversity of interindividual interactions, adaptive traits and ecological processes that can be investigated using DG-ABMs. This diversity is a strength, but requires active strategies to better identify possible links between similar models developed to answer different questions, and to structure the community of developers and users of these models. Identified as agent-based models, DG-ABMs can benefit from multiple advances in the ABM community. The flexibility of the approach ranges from very simple and generic models to very complex and specific models, depending on model assumptions and objectives (Edmonds and Moss, 2005). A wide panel of tools and methodologies are available to explore DG-ABMs (Thiele *et al.*, 2014). The exponential increase of genomic databases should help in the calibration/validation of DG-ABMs (Rudman *et al.*, 2018). The use of description protocols such as Overview, Design concepts and Details (ODD) protocol ensures the replicability and enhances the understanding of the models (Grimm *et al.*, 2020). The TRACE framework (Grimm *et al.*, 2014) is also a powerful tool for planning, documenting, and assessing model development, analysis and application. Software for ABM development have increased in simplicity, quality, speed of computation and reliability and allow sharing pieces of code easily (Dufour-Kowalski *et al.*, 2012); in particular, quantitative genetic libraries can be plugged into existing population dynamic models to describe the genetic architecture of adaptive traits (e.g., “Genetics” library in CAPSIS, Dufour-Kowalski *et al.*, 2012; Oddou-Muratorio and Davi, 2014). Software for complex model exploration have been proposed (Reuillon *et al.*, 2013). Complex and multi-authored models may use modelling notebooks to keep trace of all steps

of conceptualisation, model development, implementation and exploration in order to enhance the confidence of end-users of DG-ABMs in the management communities (Ayllón et al., 2021). Finally, the publication of model codes on specific dissemination platforms is encouraged in the ABM community (e.g., <https://www.comses.net/codebases/>). All these recommendations should benefit the development of DG-ABMs.

Intrinsically, DG-ABMs conception requires a multidisciplinary approach integrating multiple levels of knowledge and can be used in interdisciplinary research projects as a tool of interaction among disciplines. Agent-based models are also used as frontier objects in several contexts (Le Page and Perrotton, 2017; Reilly et al., 2021). As such, DG-ABMs are important tools in interacting with management or other end-user communities that need to incorporate evolutionary processes in their decisions. Although this has not been done so far, DG-ABMs could even be developed as part of a participatory modelling approach (Le Page et al., 2010) to integrate the knowledge of a diverse community of experts that need to manage constantly evolving ecosystems. Finally, they should become essential to adaptive management with an evolutionary perspective (Groot and Rossing, 2011).

2.3.9 Conclusion

In complement to the analytical models traditionally employed by evolutionary ecologists to investigate EEF loops, this review puts forward DG-ABMs, which are individual-based (meta)population dynamics models with heritable trait variation and phenotype-dependent interactions between individuals. Our literature review illustrates how the bottom-up construction of fitness in these DG-ABMs allows them to provide new insights into various fundamental and applied questions in ecology and evolution.

Previous reviews of the literature have indicated that ABMs in general are not used to address general questions in ecology and evolution, but have a more “narrow” or “pragmatic” scope (DeAngelis and Grimm, 2014). We advise modellers working on eco-evolutionary processes to carefully consider the benefits of accounting for the effects of interactions between individuals on fitness in their approach, since it might significantly affect the direction and magnitude of evolution. This is true for theoretical investigations as well as for more applied objectives, since these eco-evolutionary mechanisms also operate on rather short time scales (a handful of generations). Using a dedicated term - such as DG-ABM - would facilitate a distinction between categories of

modelling approaches, highlighting the specifics of eco-evolutionary models accounting for interindividual interactions and their variations, and the potential differences in their respective predictions.

2.3.10 Supplementary materials

The Table 2.3 focuses on original publications of models that were not retained. The sub-categories a) to d) correspond to other models than IBMs. The sub-category e) corresponds to models applied on a time scale of maximum 1 generation, i.e., without evolution. The sub-category f) corresponds to models which do not represent neither explicit nor implicit interactions between conspecific individuals. Finally, the sub-category g) corresponds to models including interindividual interactions, but either without individual variation in the interaction-related trait(s), or with purely plastic variation in these traits. The category “Not appropriate” gathers: 15 reviews, seven technical publications (introducing a new software without specific investigation of an eco-evolutionary issue), five publications related to cell biology model (without any link to ecology), three book chapters, one conference proceeding, one preprint and one duplicated study.

Table 2.3: Publications excluded during the literature review.

Category	Sub-Category	Number of publications
Original publication of a new model but...	a) Concept paper	1
	b) Niche model	1
	c) Differential equation model	1
	d) Integral Projection Model (IPM)	2
	e) ABM without evolution	7
	f) DG-ABM without interactions	16
	g) DG-ABM with interactions but without eco-evolutionary feedback	18
DG-ABM with interindividual interactions affecting fitness	74	
Not appropriate (review, software, proceeding publication)	33	
Total	74	

Figure S1a: Distribution over time of the 138 selected publications associated to “IBM” and “eco-evolution” keywords. Keywords: (Individual-based model* OR IBM)* AND (eco-evol* OR demo-genet* OR demogenet* OR ecogenet* OR eco-genet*). WOS 1955/01/01-2022/07/01.

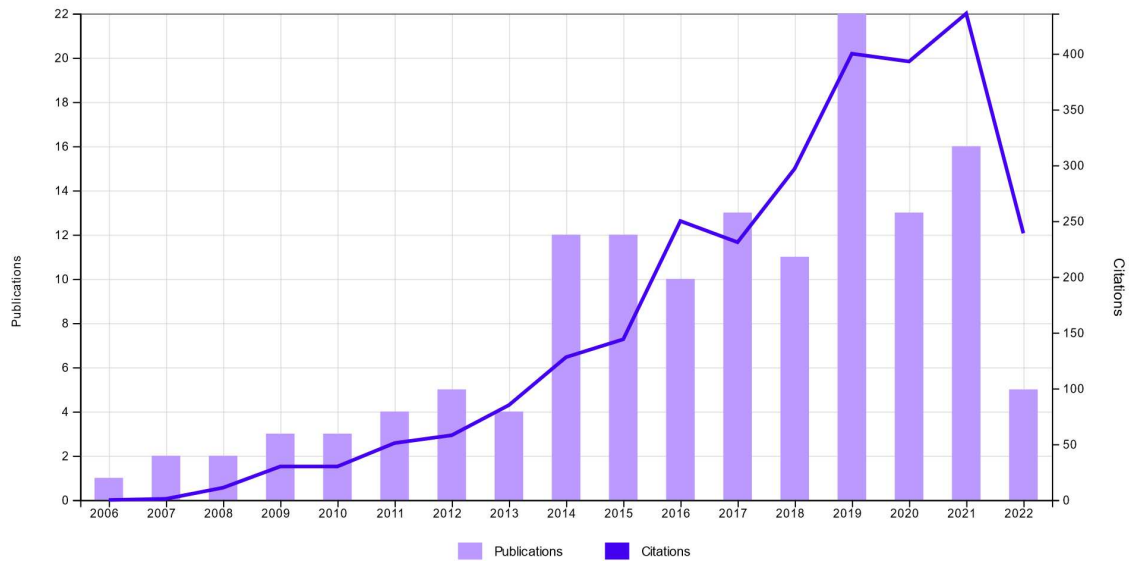


Figure S1b: WOS categories of the 138 selected publications associated to “IBM” and “eco-evolution” keywords. Keywords: (Individual-based model* OR IBM)* AND (eco-evol* OR demo-genet* OR demogenet* OR ecogenet* OR eco-genet*). WOS 1955/01/01-2022/07/01.

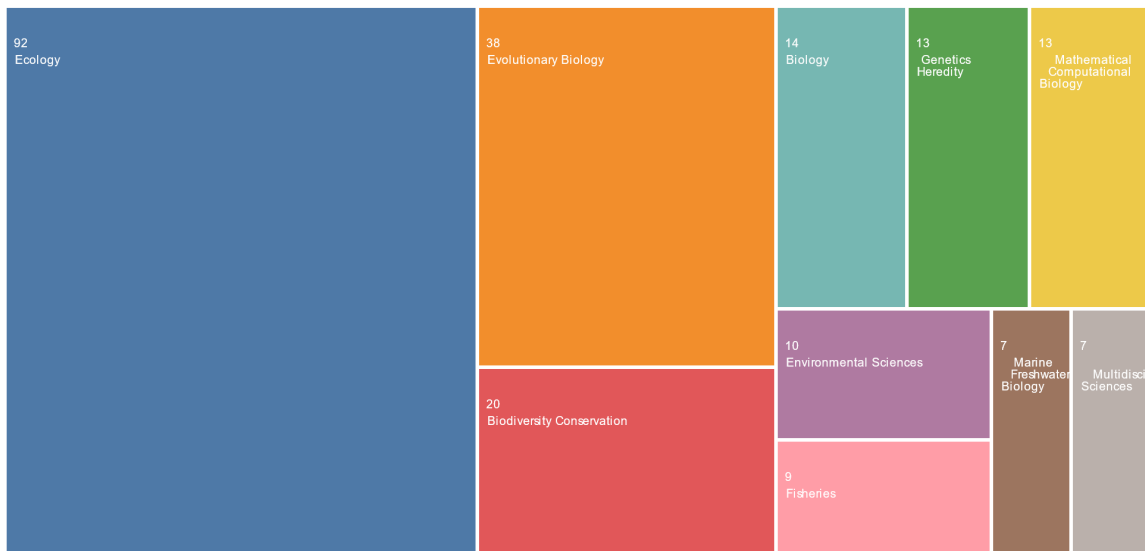


Figure 2.4: Graphical summary of the publications associated with the first WOS query.

Figure S1c: Distribution over time of the 15 selected publications associated to “ABM” and “eco-evolution” keywords. Keywords: (Agent-based model* OR ABM)* AND (eco-evol* OR demo-genet* OR demogenet* OR ecogenet* OR eco-genet*). WOS 1955/01/01-2022/07/01.

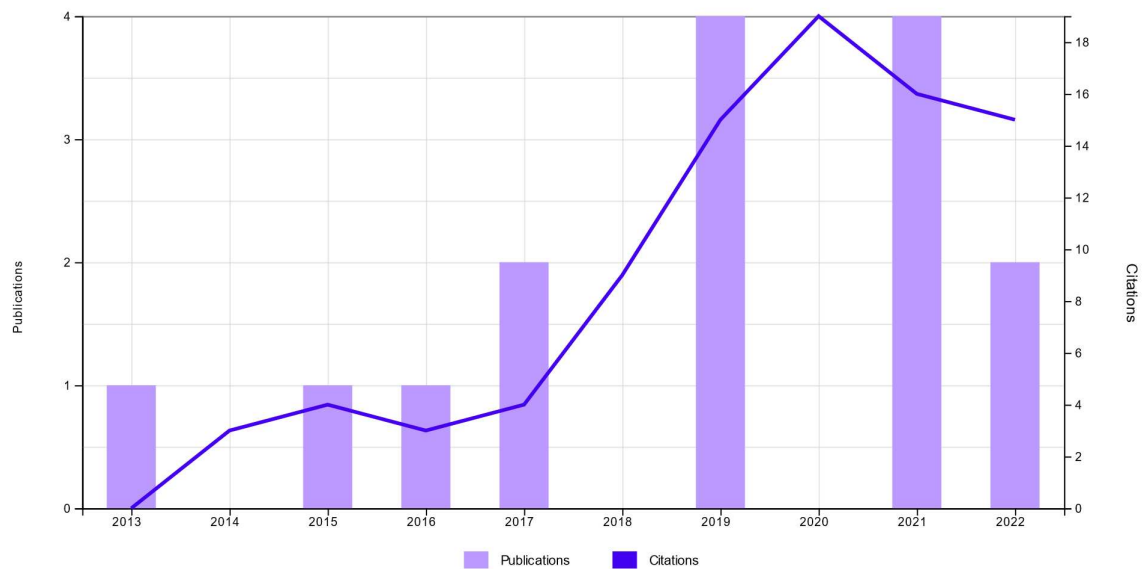


Figure S1d: WOS categories of the 15 selected publications associated to “ABM” and “eco-evolution” keywords. Keywords: (Agent-based model* OR ABM)* AND (eco-evol* OR demo-genet* OR demogenet* OR ecogenet* OR eco-genet*). WOS 1955/01/01-2022/07/01.



Figure 2.5: Graphical summary of the publications associated with the second WOS query.

2.4 EXISTING METAPOPOPULATION DG-ABMs

In the light of these conclusions, we aimed at using a demo-genetic agent-based approach to explore metapopulation eco-evolutionary dynamics in the case of Atlantic salmon. A large number of DG-ABMs are already existing for fishes and salmonids especially. However, these models have been built for single closed populations, without dispersal. For example, Jager et al. (2001) evaluated the consequences of life history variation on population viability of the white sturgeon (*Acipenser transmontanus*). Such models have also been used to evaluate the impact of exploitation and selective mortality on the evolution of life history traits in brook charr (*Salvelinus fontinalis*, Thériault et al., 2008), smallmouth bass (*Micropterus dolomieu*, Dunlop et al., 2007) and freshwater fish similar to lake whitefish (*Coregonus clupeaformis*) and walleye (*Sander vitreus*, Wang and Höök, 2009). The effects of environmental conditions and anthropogenic disturbances can also be examined with DG-ABMs, such as the effects of floods on growth rates of the marble trout (*Salmo marmoratus*, Vincenzi et al., 2012), of temperature increase on migration timing of sockeye salmon (*Oncorhynchus nerka*, Reed et al., 2011a), or the influence of migration barriers and stocking on the abundance and genetics of the brown trout (*Salmo trutta*, Frank and Baret, 2013).

A very few DG-ABMs consider the metapopulation perspective for salmonids species. The model of Castellani et al. (2015) on Atlantic salmon incorporates the influence of immigration, but does not consider emigration and is also built for a single population. The model of Ayllón et al. (2016) on brown trout is spatially explicit but rather focuses at the microhabitat scale. More generic models have nevertheless been developed to simulate dynamics of metapopulations. Nemo provides an evolutionary and populations genetics modelling framework to simulate life history trait evolution in a metapopulation context, with a large diversity of population models available (Guillaume and Rougemont, 2006). SimAdapt has been developed to simulate adaptation and population dynamics with a particular focus on the influence of the landscape, which is represented as a cellular automaton (Rebaudo et al., 2013). RangeShifter also allows to simulate complex population dynamics on spatially explicit landscapes (grid cells), with a detailed process of dispersal divided into 3 phases (emigration, transfer and settlement, Bocedi et al., 2014). ALADYN also provides a modeling framework of adaptive dynamics but in a continuous landscape (Schiffers and Travis, 2014). Finally, CDMetaPOP allows the simulation of patch demographic and genetic dynamics interconnected by dispersal (Landguth et al., 2017). However, these

models generally represent simple life cycles, far from the complexity of salmonids life histories. Two exceptions of DG-ABMs applied to salmonid metapopulations have been found in the literature. [Landguth et al. \(2017\)](#) applied their DG-ABM (CDMetaPOP) to brook trout, with a dispersal process, density-dependent and independent life history traits, but a fixed spatially explicit fitness for each genotype (not emerging from eco-evolutionary dynamics). [Lin et al. \(2017\)](#) extended a model from [Bromaghin et al. \(2011\)](#) on sockeye salmon, but it focuses on two populations only.

On Atlantic salmon, only population-level DG-ABMs have been developed. The model IBSEM of [Castellani et al. \(2015\)](#) focused on the influence of gene flow from non-local and domesticated conspecific individuals on genetic and demographic changes of a wild population. The model IBASAM of [Piou and Prévost \(2012\)](#) has been used to evaluate the evolutionary and demographic consequences of climate change and exploitation scenarios on Atlantic salmon populations ([Piou and Prévost, 2013](#); [Piou et al., 2015](#)). There is thus room for an extension of such models to the metapopulation scale.

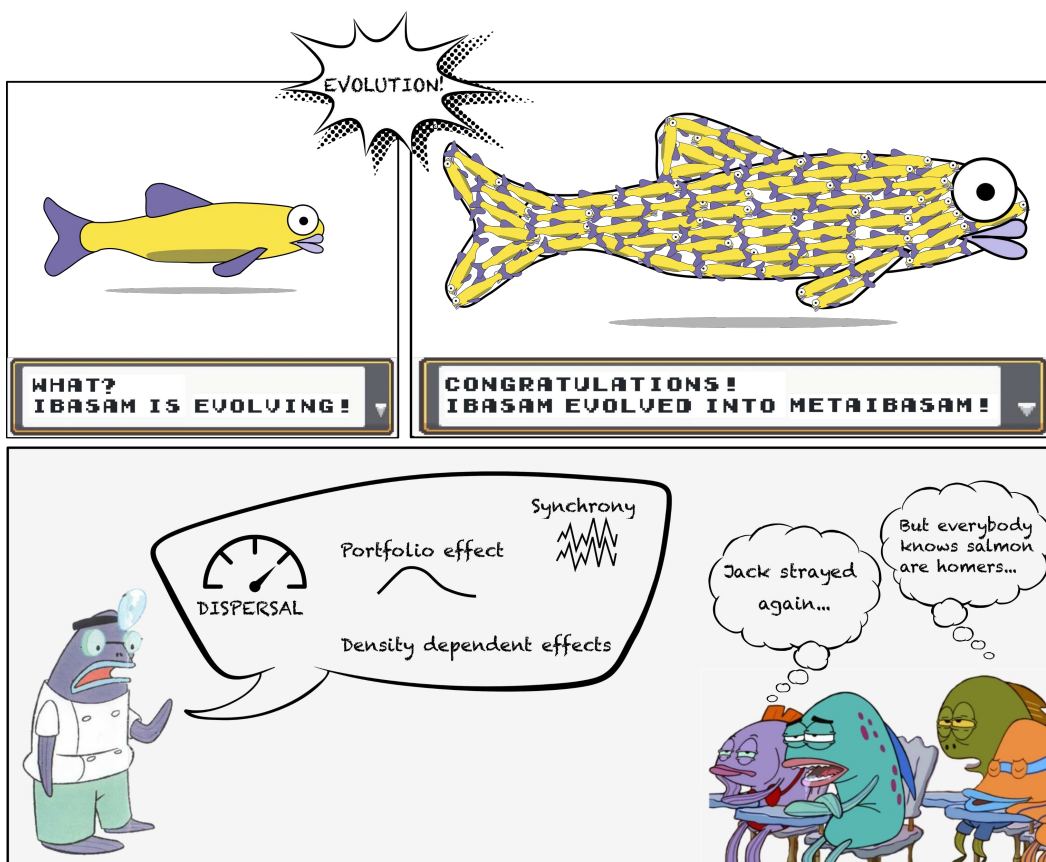
2.5 CHAPTER HIGHLIGHTS

In this chapter, I explained the rationale of using a modelling approach which is i) spatially explicit, ii) agent/ individual-based, and iii) demo-genetic to evaluate metapopulation eco-evolutionary dynamics and the theory of adaptation networks. I also identified gaps regarding existing metapopulation DG-ABMs, especially lacking for salmonid species and their complex life cycle. The main lessons of this chapter are the following:

Chapter 2 highlights

- Multiple challenges related to the study and measure of dispersal in the wild hamper our understanding of the eco-evolutionary dynamics of metapopulations;
- Modelling approaches may address these issues;
- Stochastic Patch Occupancy Models (SPOMs) have been widely used to study metapopulations but they only provide a limited insight into metapopulation dynamics;
- Spatially explicit agent-based demo-genetic approaches (DG-ABMs) provide a coherent framework to study these dynamics, in particular through the emergence of fitness related to inter-individual interactions and heritable fitness related traits;
- This approach appears as a relevant tool to explore response of metapopulations to selective pressures and their management;
- Few DG-ABMs are applied to metapopulations, even less to salmonids, and none for Atlantic salmon.

Implications of dispersal in Atlantic salmon



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In the light of Chapter 2 conclusions, we here propose a DG-ABM (Demo-Genetic Agent-Based Model) that includes the processes and organisational scales required to study the adaptation and management of Atlantic salmon populations within a metapopulation context and that will be used in the following chapters. In this chapter, the model is presented as well as an application study investigating the consequences and implications of dispersal in Atlantic salmon populations. The model presented here (MetaIBASAM) is an extension of a previously developed model at the population scale (IBASAM) by the ECOBIOP lab, and it is noteworthy that its extension is the result of several contributions and is far from being exclusively mine. This chapter corresponds to an article published in the *Canadian Journal of Fisheries and Aquatic Sciences* (Lamarins et al., 2022c), and first includes the main body of the article and then the supplementary materials.

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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

3.1 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., 2011b). 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.

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 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), 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 developed to evaluate eco-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.

3.2 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 3.1](#), 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.

Table 3.1: 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	<ul style="list-style-type: none"> • 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	<ul style="list-style-type: none"> • Not explicit SS/ two populations • Em: inherited probability/ density-independent or dependent • Im: random destination 	<ul style="list-style-type: none"> • Inherited ecological trait • Fitness: mismatch trait-site optimum (fixed) 	No

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References	Model type	Species	Dispersal/ Connectivity	Eco-evolutionary dynamics	Key mechanistic processes
Guillaume and Rougemont (2006); Rebaudo et al. (2013); Bocedi et al. (2014); Schiffrers and Travis (2014); Landguth et al. (2017)	Demo-genetic agent-based model of metapopulation (Nemo, SimAdapt, RangeShifter, ALADYN, CDMetaPOP)	Generic	<ul style="list-style-type: none"> • SS: grid landscape • Em: fixed emigration rate/ density-dependent/ individual trait • Im: random destination among nearest/ distance dispersal kernel 	<ul style="list-style-type: none"> • 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	<ul style="list-style-type: none"> • SS: grid landscape • Em: fixed emigration rate • Im: distance dispersal kernel 	<ul style="list-style-type: none"> • Multi locus system • Spatially explicit fitness for each genotype (fixed) 	<ul style="list-style-type: none"> • Growth \sim temperature • Survival \sim patch fitness, density • Maturation \sim size • Sexual selection

Continued on the next page

References	Model type	Species	Dispersal/ Connectivity	Eco-evolutionary dynamics	Key mechanistic processes
Lin et al. (2017)	Demo-genetic agent-based model of two populations (extension from Bromaghin et al., 2011)	Sockeye salmon	<ul style="list-style-type: none"> • SS: two populations • Em: fixed emigration rate 	<ul style="list-style-type: none"> • Multivariate quantitative genetic model • Fitness: mismatch trait-site optimum (fixed) 	<ul style="list-style-type: none"> • No growth: inherited length, age at maturation • Survival \sim density, phenotype • Sexual selection
MetaIBASAM	Demo-genetic agent-based model of metapopulation (extension from IBASAM, Piou and Prévost, 2012)	Atlantic salmon	<ul style="list-style-type: none"> • SS: multiple populations, size and distance • Em: fixed emigration rate • Im: dispersal kernel (distance and attractivity) 	<ul style="list-style-type: none"> • Bi-allelic multi locus system • Emerging fitness from fitness-related traits 	<ul style="list-style-type: none"> • Growth \sim temperature, flow, density, genetic • Survival \sim temp., flow, density, growth potential, size • Maturation (precocious and at sea) \sim energetic reserves and genetic thresholds • Size dependent migration • Sexual selection

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

3.2.1 Key features of IBASAM

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

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. 3.1). 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.

3.2.1.3 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. 3.1). 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.

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.

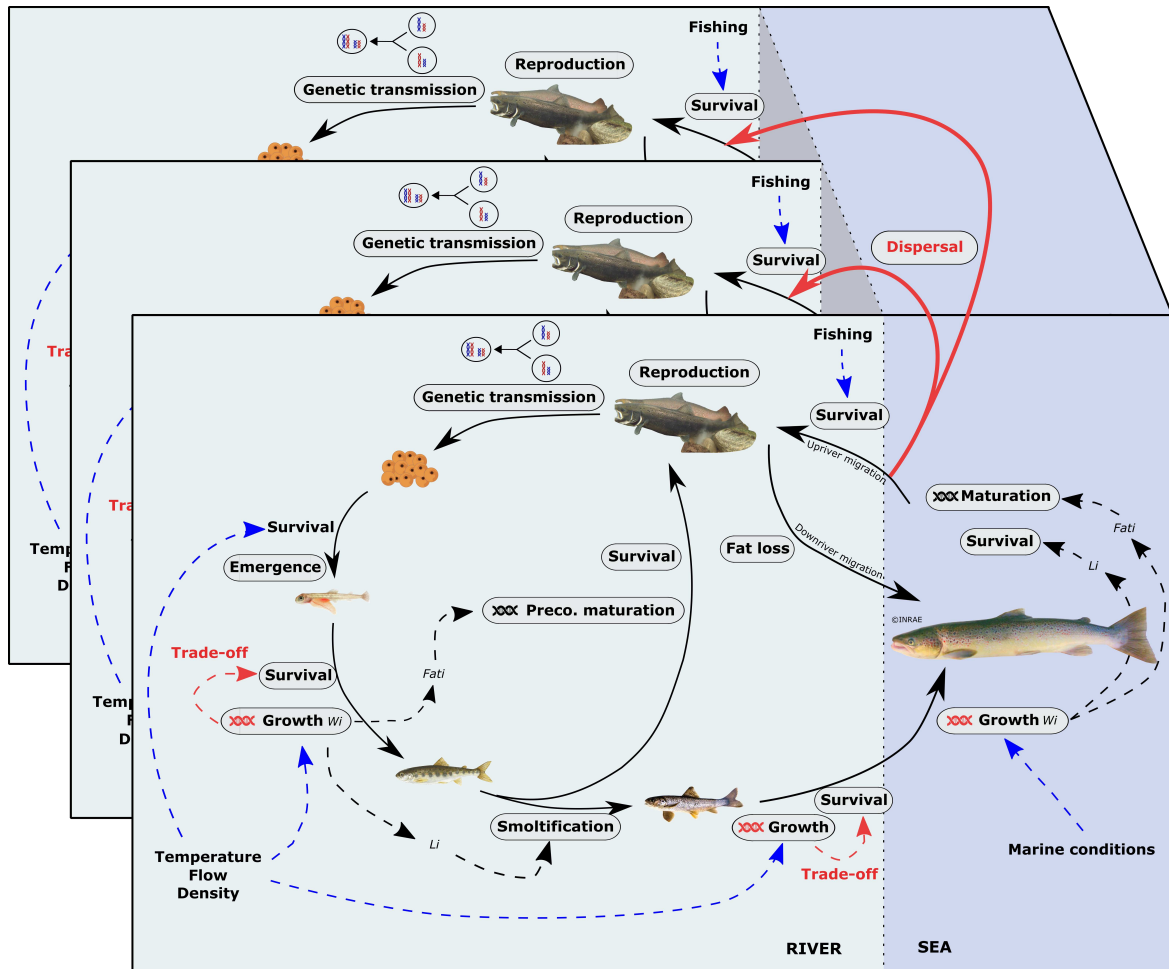


Figure 3.1: Conceptual framework of the MetaIBASAM model, adapted from Piou and Prévost (2012). Processes at individual levels are highlighted in grey, where the DNA icon indicates heritable traits linked to these processes (maturation thresholds and growth potential). The dashed arrows represent the 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.

3.2.2 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 Suppl. Mat. 3.5.1). 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. 3.1, Suppl. Mat. 3.5.1; 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. 3.2 A), ensuring stable size distributions in a neutral context (without selection, Suppl. Mat. 3.5.1).

3.2.3 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 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 3.1). The probability

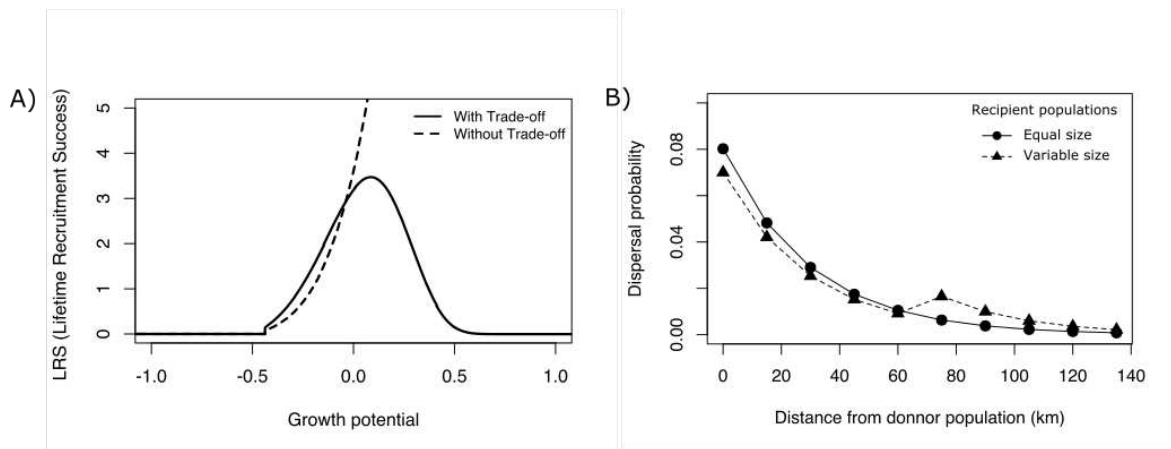


Figure 3.2: Additions into MetaIBASAM from IBASAM. In A), theoretical optimal value of phenotypic growth potential (in log scale) based on mean individual Lifetime Recruitment Success (measured as the mean egg number per female; see processes details in Suppl. Mat. 3.5.1) with (fill) and without (dashed) 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.

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' .

$$P_j = 1 - h_j = \sum_{j'=1, j \neq j'}^n p_{j,j'} \quad (3.1)$$

With P_j the total dispersal rate of the population j , h the philopatry rate, and n the number of populations.

This matrix of dispersal probabilities p represents the connectivity between populations and is derived from a dispersal kernel (Fig. 3.2 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 (Pépin et al., 2012), which maximizes the connectivity between close populations while still allowing some flow of individuals between distant rivers (long-distance dispersal, Equation 3.2). 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 3.3). The larger the populations, the more attractive they are to dispersing individuals.

$$p_{j,j'}(D_{j,j'}, b) = g_{j'} \times \frac{1}{2b} \times \exp\left(-\frac{D_{j,j'}}{b}\right) \quad (3.2)$$

$$\text{with } g_{j'} = \frac{\log_{10}(A_{j'})}{\sum_{j'=1}^n \log_{10}(A_{j'})} \quad (3.3)$$

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. 3.2 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.

3.2.4 Model parameterization and outputs

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 Suppl. Mat. 3.5.2), 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 Suppl. Mat. 3.5.1 and 3.5.2) 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 (Suppl. Mat. 3.5.2) to updated environmental conditions (see section 3.3.1). 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. 3.1).

IBASAM is coded in C++ language, and an R package named MetaIBASAM has been developed (<https://github.com/Ibasam/MetaIBASAM>). Each IBASAM can be parameterized 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.

3.3 APPLICATION: CONSEQUENCES OF A GRADIENT OF DISPERSAL RATES ON LOCAL POPULATIONS AND METAPOPOPULATION DYNAMICS

3.3.1 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 Suppl. Mat. 3.5.2), 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 (Suppl. Mat. 3.5.2). 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.

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 Suppl. Mat. 3.5.3. 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>.

3.3.2 Simulations outcomes analysis

3.3.2.1 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 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. 3.3 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. 3.3 A).

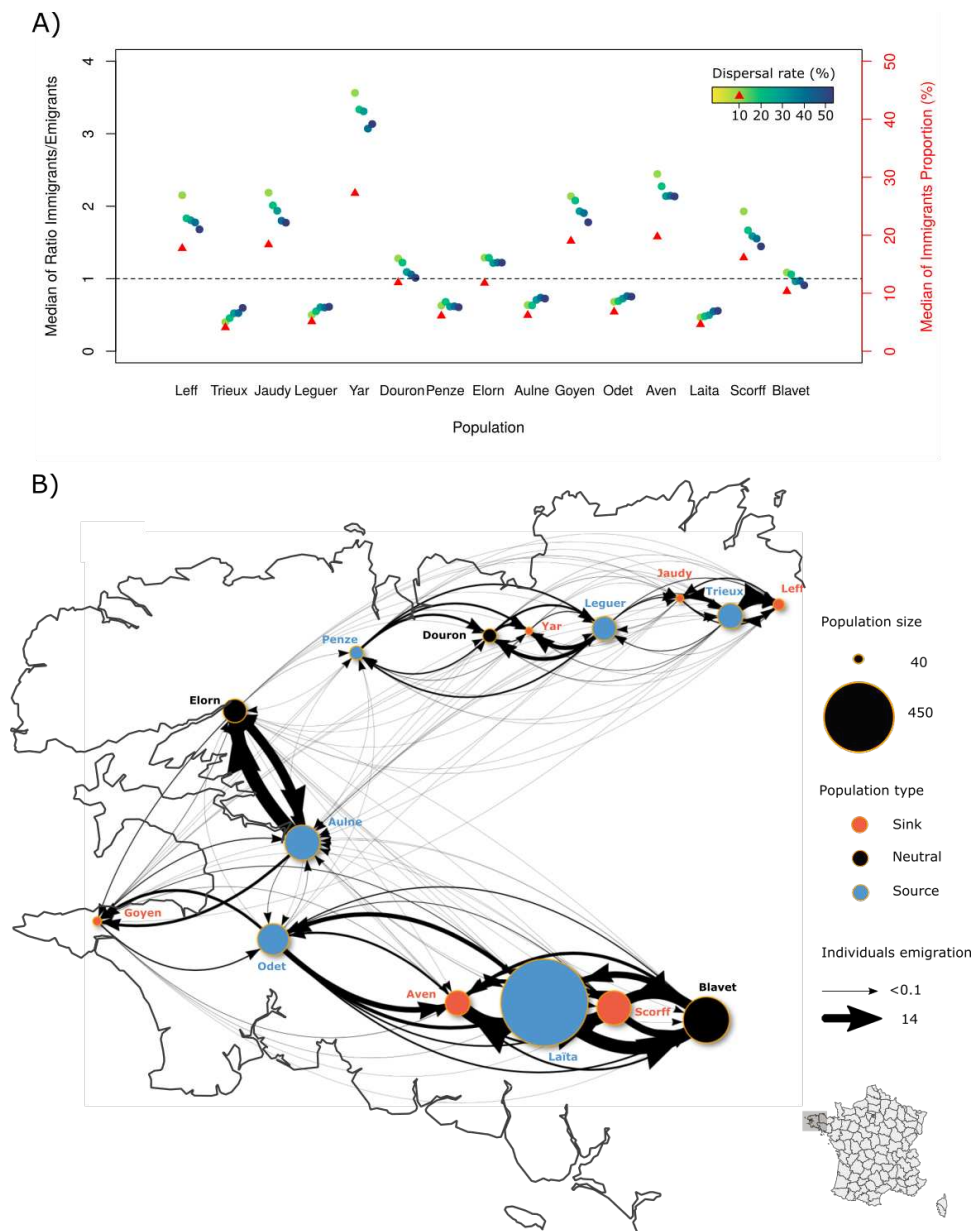


Figure 3.3: A) In points, median over simulations of the ratio between immigrants and emigrants number of the 5 last years for each population and dispersal scenario. In red triangle, median over simulations of the proportion of immigrants of the 5 last years for each population at 10% of dispersal rate. B) Visualisation of the network emerging from MetaIBASAM simulations 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.

3.3.2.2 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 (Box 3.1).

Box 3.1: Stability 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* (Fig. 3.4, 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 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.

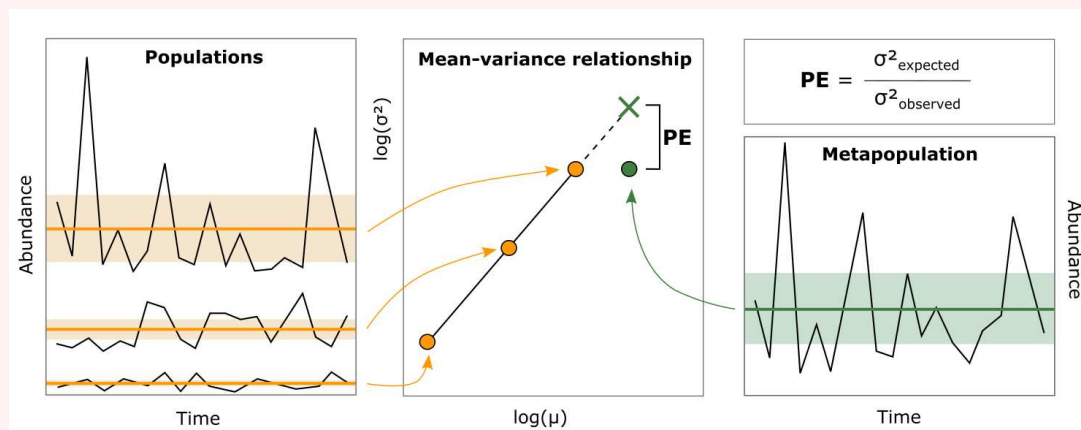


Figure 3.4: Estimation of the PE according to the mean-variance method. The mean-variance relationship is obtained from the mean (orange lines) and the variance (orange shaded regions) of each population abundance time series, and extrapolated to reach the observed metapopulation mean (green line and 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 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 3.4, Fig. 3.5). This index is expressed between 0 (asynchrony) and 1 (synchrony).

$$\phi_x = \frac{\sigma_x^2}{(\sum_{i=1}^n \sigma_{xi})^2} \quad (3.4)$$

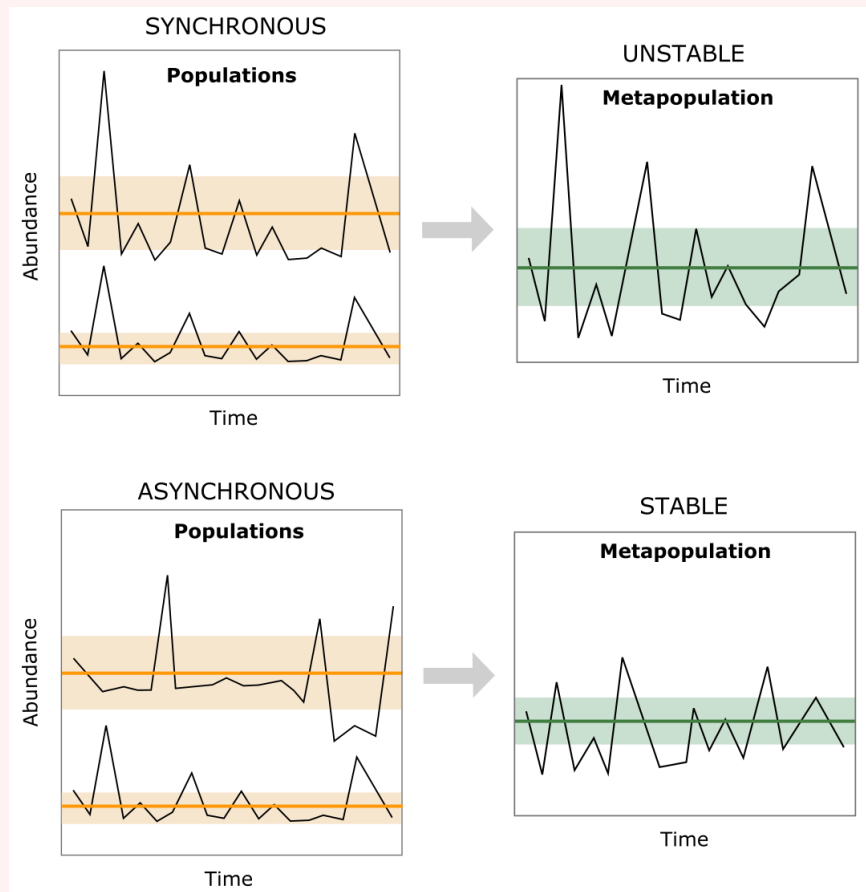


Figure 3.5: Schematic representation of local populations synchrony / asynchrony (on the left) and the resulting variability and stability of the metapopulation (on the right).

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 R_{max} , adjusted in [Piou and Prévost, 2012](#), Suppl. Mat. 3.5.2).

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. 3.6 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 ($\phi \sim 0.1$; Fig. 3.6 B). Between dispersal rates of 0% 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. 3.6 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. 3.6 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. 3.6 D). Altogether, these results suggest a demographic rescue of populations by dispersal, especially for those behaving as sink populations.

3.3.2.3 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. 3.7, 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,

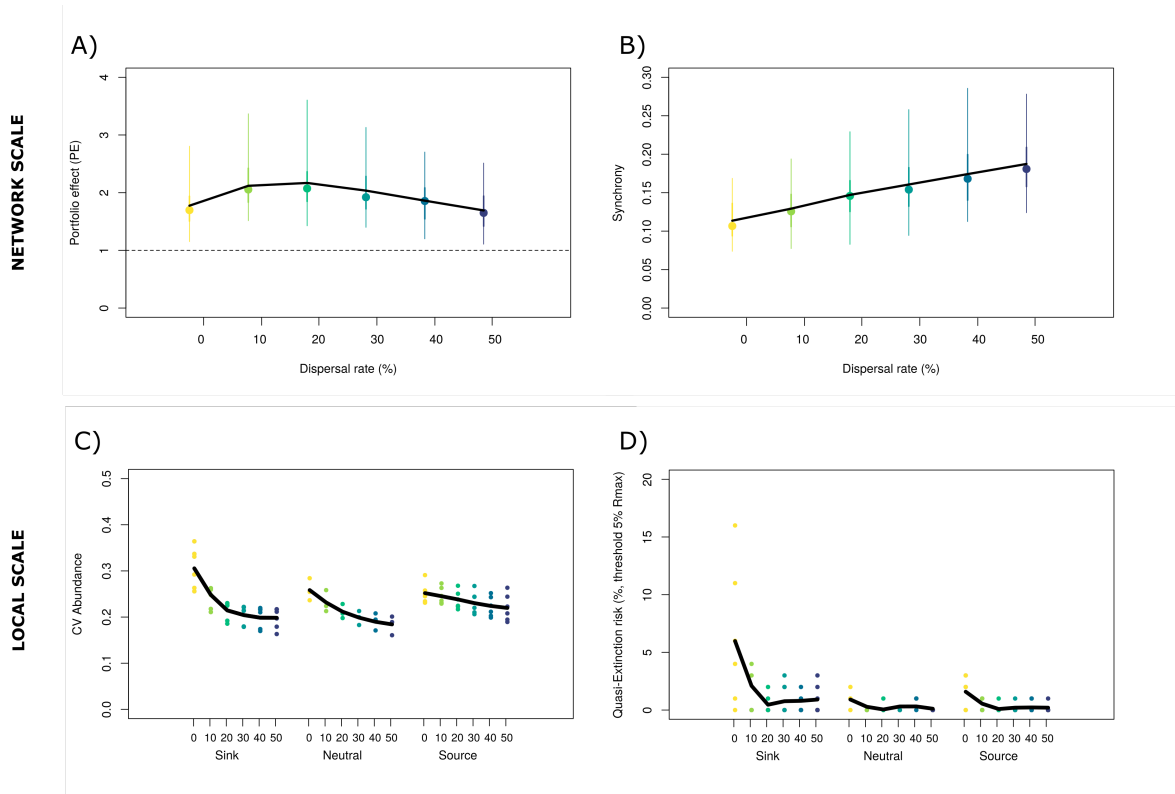


Figure 3.6: Distribution (median, 95% confidence interval) over simulations of the detrended metapopulation PE (A) and synchrony (B) metrics for each scenario of dispersal. Median over simulations of local populations CV of detrended returns abundance (C) and quasi extinction risk (D) for each scenario 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).

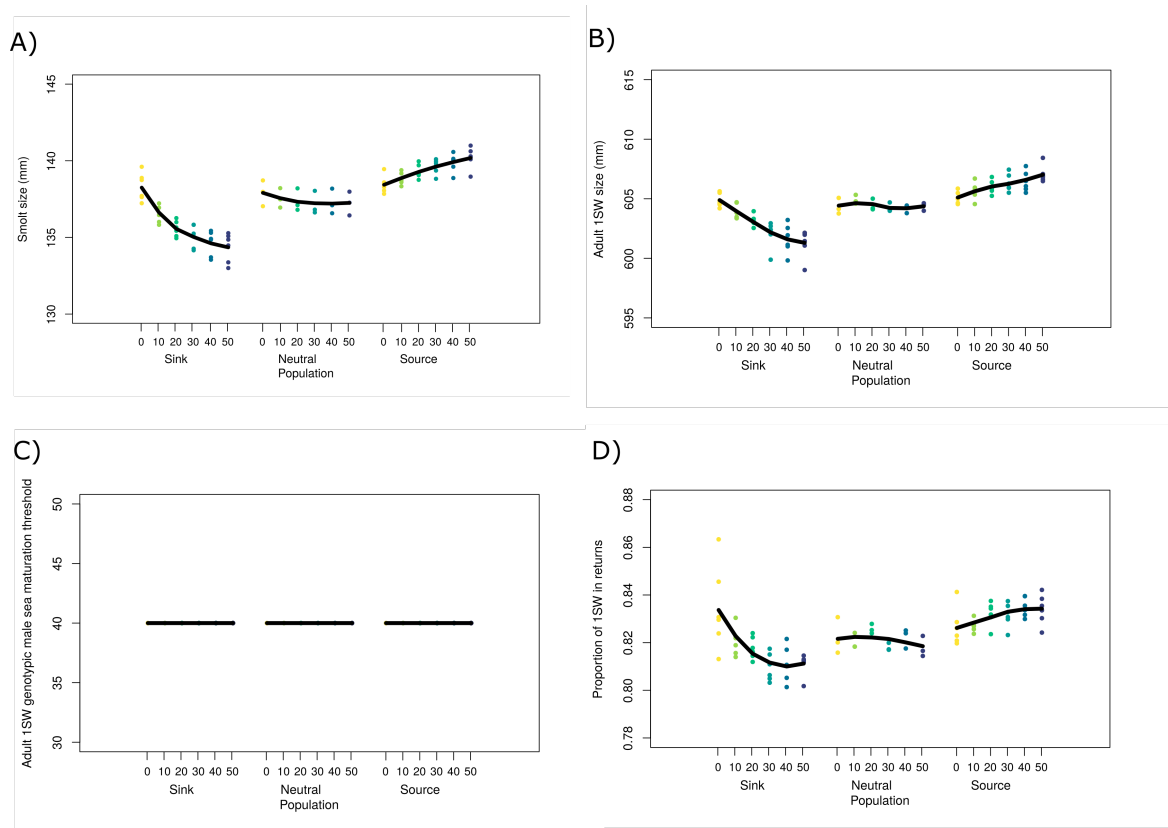


Figure 3.7: Median over simulations of populations last 5 years median smolt size (A), philopatric adult 1SW size (B), philopatric adult 1SW genotypic value of male sea maturation threshold (C), and proportion of 1SW in philopatric adult returns (D) for each scenario of dispersal. Each point is a population, 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).

this unexpected result could be explained by density-dependent effects on river growth. Indeed, dispersal increased juveniles density in sink populations (due to higher immigration than emigration) and decreased it in source ones (Suppl. Mat. 3.5.4), 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 (Suppl. Mat. 3.5.5).

As expected due to similar genetic distribution parameters at initialization between populations, no interpopulation genotypic diversity emerged with dispersal (Fig. 3.7 C). However, dispersal rates rapidly increased intrapopulation genetic variance in sink populations (Fig. 3.8).

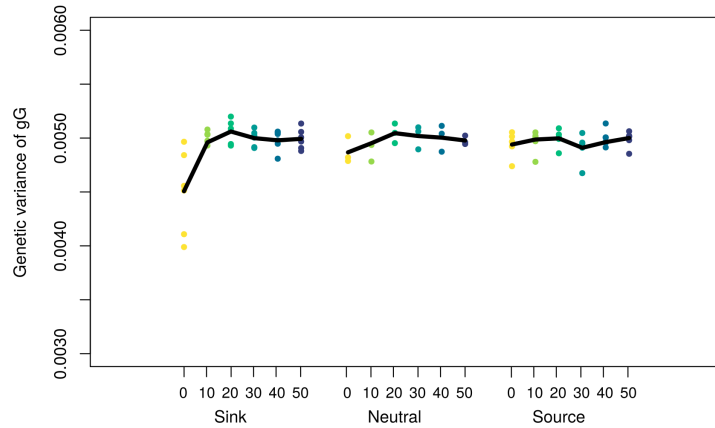


Figure 3.8: Median over simulations of populations last 5 years genetic variance (of philopatric 1SW genotypic growth potential), for each scenario of dispersal. Each point is a population, categorized by its type (sink/source/neutral), and a local regression is added to represent a global trend as a function of dispersal rates and category of populations (sink/source/neutral).

3.4 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 demographic 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 3.1](#)), 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 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, 1991](#); [Jonsson and Jonsson, 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 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 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.

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 3.1), 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.

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. 3.9) 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 provide information on the ability of metapopulations with variable degrees of diversity to persist under various projected climate scenarios (Fig. 3.9).

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. 3.9). 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. 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. 3.9) 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).

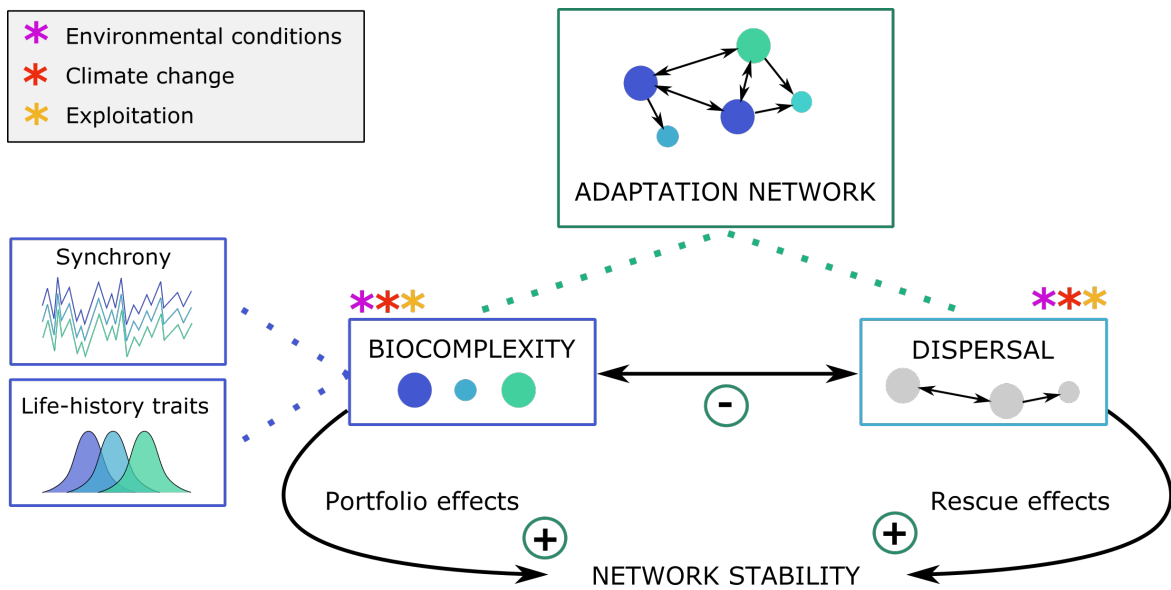


Figure 3.9: Theoretical framework of the adaptation network theory. Both biocomplexity (e.g., trait diversity, populations synchrony) and dispersal can foster network stability through portfolio and rescue effects. The homogenizing effect of dispersal and divergent effect of local adaptation on populations 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.

3.5 SUPPLEMENTARY MATERIALS

3.5.1 Growth-survival trade-off in river

Formula and parameters

In river, the daily survival probability ($Sp_{i,t}$) of an individual i at time t , depending on its age and maturing status, is mitigated by its phenotypic growth potential (in log scale pG_i) through a growth-survival trade-off coefficient ($CoeffSurvRIV_i$) according to the Equation 3.5, 3.6, and 3.7.

$$Sp_{i,t} = Sp_{i,t}^{status} \times CoeffSurvRIV_i \quad (3.5)$$

Where $Sp_{i,t}^{status}$ can take one of the population parameters survival values as function of the individual i status at day t (Piou and Prévost, 2012).

$$CoeffSurvRIV_i = \frac{\exp(-kappaRIV \times pGres_i^{sigRIV}) - \exp(-kappaRIV)}{1 - \exp(-kappaRIV)} \quad (3.6)$$

$$with pGres_i = \min(1, \frac{\exp(pG_i)}{maxRIV}) \quad (3.7)$$

Where $maxRIV$, $sigRIV$ and $kappaRIV$ are populations parameters. Since the literature regarding growth-survival trade-offs is limited (but see Bozdansky et al., 2005; Biro et al., 2006), the values of these parameters (Table 3.2) were adjusted based on anadromous returns number and size distributions monitored on the Scorff river that were used for calibrating IBASAM (Piou and Prévost, 2012).

Table 3.2: Parameters values of growth-survival trade-off in river.

Parameter type	Parameter name	Parameter value
Maximum growth rate	$maxRIV$	5
Shape of the trade-off function	$sigRIV$	3.7
Shape of the trade-off function	$kappaRIV$	0.001

Consequences on life-history traits evolution

Implementing the growth-survival trade-off in river limited the evolution of growth potential genetic value and adult size towards high values, as showed by MetaIBASAM simulations on the Scorff river only (without dispersal) with and without the trade-off (Fig. 3.10).

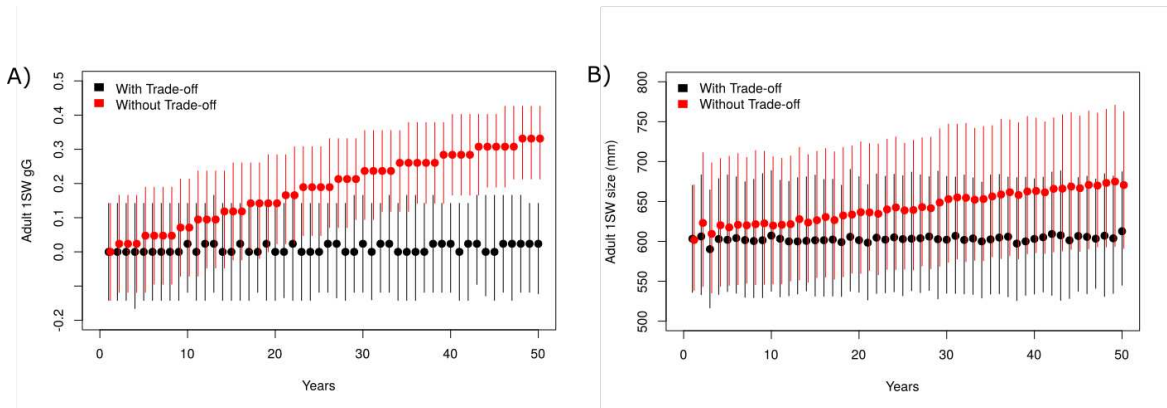


Figure 3.10: Temporal evolution of (A) growth potential genotypic value (in log scale) and (B) 1SW adult size in 10 simulations of one population (Scorff) with (black) and without (red) growth-survival trade-off implemented in the model.

Theoretical optimal value

As an illustration, and with the main model formula and parameters values used in the application study, we can compute the lifetime recruitment success of a range of individuals growth potential values to identify the theoretical optimal value of this parameter. Shortly, we created similar juveniles (weight, length, fat reserves) except for their growth potential. We computed growth (with constant temperature averaged at 15°C in summer and 11°C in winter, density effect fixed at 0.6) and survival rate (depending on individuals growth potential according to the trade-off, Fig. 3.11 A and B) after one year in river. Then, we simulated all individuals migrate to sea and computed their growth and survival rate (size-dependent) after one year in sea (Fig. 3.11 C). Finally, by considering all individuals are breeding females, we computed egg number depending on individual weight (Fig. 3.11 D). Ultimately, the Lifetime Recruitment Success is the product of the river survival rate, sea survival rate, and egg number for each value of individual growth potential, and presents an optimal value of growth potential around 0.1-0.2 (log scale; Fig. 3.2 A, Fig. 3.10 A). Thus, our

parameterization, in a neutral context (i.e., no additional selective pressure), leads to optimal value of growth potential around 1: despite variability between individuals, there is on average no effect of growth potential on survival.

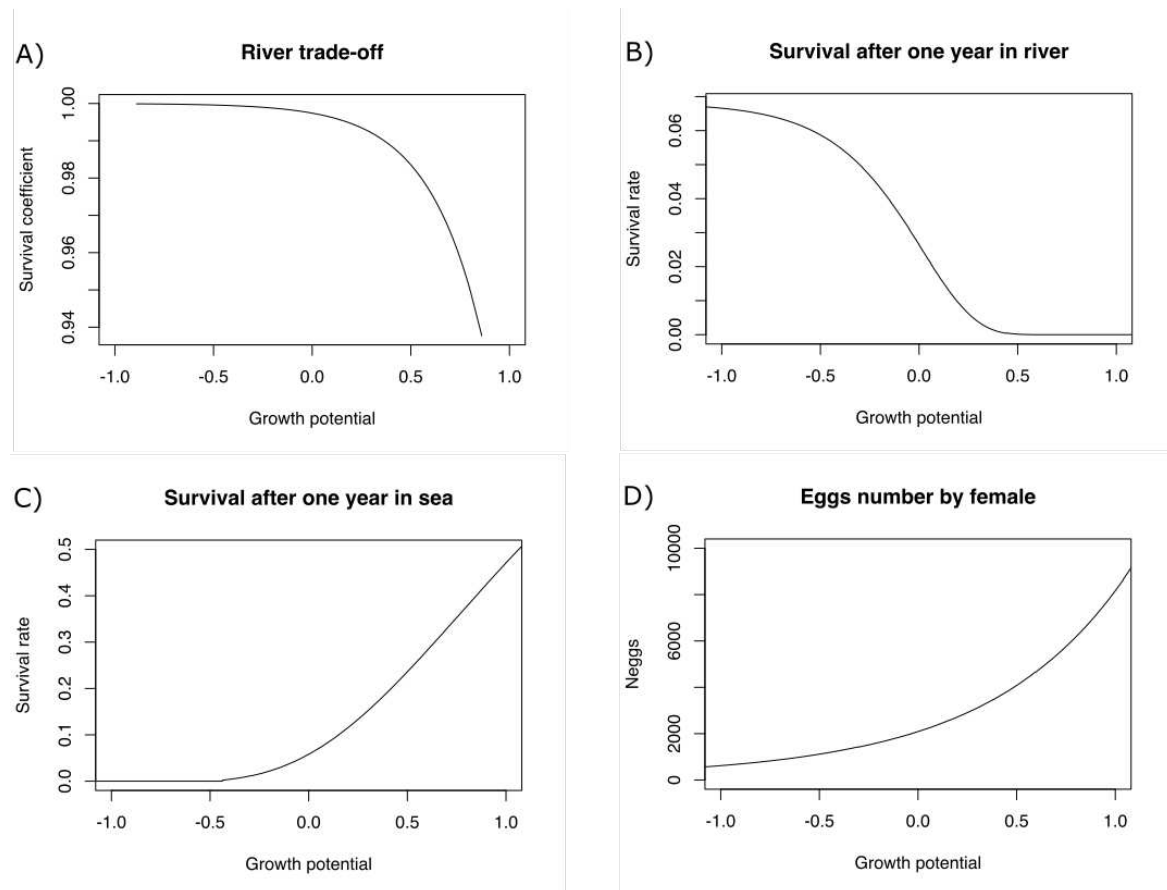


Figure 3.11: Processes details to compute the theoretical growth potential optimal value. A) Shape of the growth-survival trade-off for a range of phenotypic growth potential values (in log scale). B) Shape of the relationship between river survival (after one year), C) sea survival (after one year), D) egg number and phenotypic growth potential (in log scale).

3.5.2 MetaIBASAM parameterization

The Table 3.3 describes modified or new parameters compared to IBASAM, that have been collected from the literature or adjusted to observed data. Species parameters are here common to all populations, whereas populations parameters describe the spatial structure of the network, based on salmon populations in Brittany rivers (Fig. 3.12).

Table 3.3: Description and selected values of modified or new model parameters compared to IBASAM (Piou and Prévost, 2012). Population indicator is from 1 to 15.

Parameter type	Parameter name	Parameter value	Reference / adjustment
Species parameters			
Mean dispersal distance in the metapopulation (km)	b	29.5	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 survival probability by individual stage	$Sp0+$, $Sp1+$, $Sp1Mat$, $Sp1Smolt$, $SpMat$, SpN , $SpAnad$	0.986621, 0.9939184, 0.9883022, 0.9987859, 0.9931622, 0.9997455, 1	Adjusted to Scorff data
Parameters of growth-survival trade-off function in river	$maxRIV$, $sigRIV$, $kappaRIV$	5, 3.7, 0.001	Adjusted to Scorff data
Heritability at initialization of individual growth potential	$heri$	0.14	Gjerde et al. (1994)
Parameter of river growth – temperature function	dr	0.5	Adjusted to Scorff data
Populations carrying capacity (juveniles / 100 m ²)	$Rmax$	10	Adjusted to Scorff data (Piou and Prévost, 2012)
Populations parameters			
Populations area of juvenile production (m ²)	$A_{[1:15]}$	72305, 213733, 47561, 197283, 37104, 95451, 106753, 164699, 252659, 53603, 249049, 142686, 669028, 229027, 326121	Brittany angling clubs federations
Populations distance between each pair of estuaries (km)	$D_{[1:15;1:15]}$	See distance matrix (Table 3.4)	

Table 3.4: Distance matrix between river estuaries (km). Population indicator is from 1 to 15.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	0	0	16	67	77	82	106	232	254	317	369	403	420	438	438
2		0	16	67	77	82	106	232	254	317	369	403	420	438	438
3			0	51	61	66	90	216	238	301	353	387	404	422	422
4				0	10	15	39	165	187	250	302	336	353	371	371
5					0	5	29	155	177	240	292	326	343	361	361
6						0	24	150	172	235	287	321	338	356	356
7							0	126	148	211	263	297	314	332	332
8								0	22	85	137	171	188	206	206
9									0	63	115	149	166	184	184
10										0	52	86	103	121	121
11											0	34	51	69	69
12												0	17	35	35
13													0	18	18
14														0	0
15															0

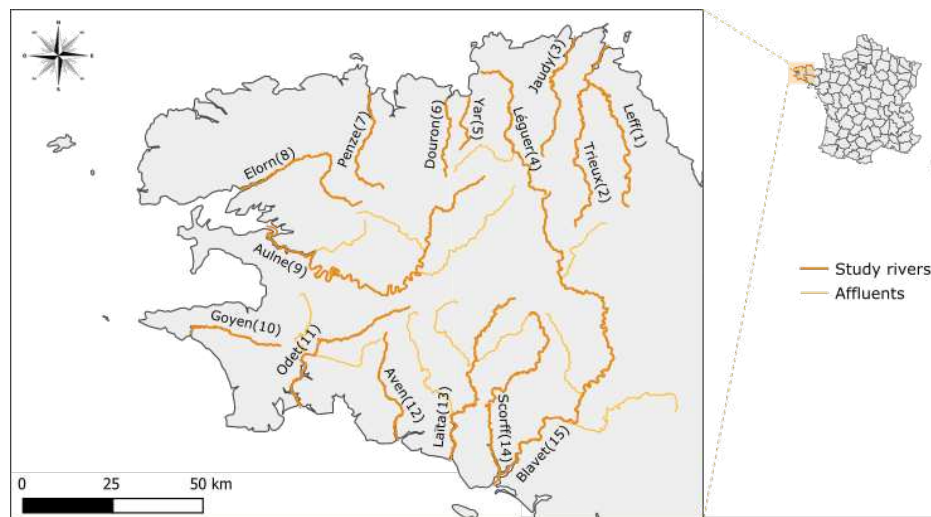


Figure 3.12: Mapping of the coastal rivers related to the 15 populations of Brittany included in the model. The population indicator is between brackets. The base map and hydrographic system come from a French Government open data base (<https://www.data.gouv.fr>) with a RGF93 map projection.

3.5.3 Environmental conditions simulation

In MetaIBASAM, the objective is to simulate realistic environmental conditions; for the model application, we simulated environmental conditions similar to Brittany. Because water temperature was partially observed (23% of missing data due to logger failure) on the Scorff river only, we first estimated the parameters of the relationship between daily water temperature, discharge, and air temperature using a sigmoid model to be able to compute water temperature from air and flow data that are more abundant.

3.5.3.1 Sigmoid model of the relationship between air, water temperature and water discharge on the Scorff

Model description

Different approaches have been proposed to assess water temperature. For example, [Arismendi et al. \(2014\)](#) reviewed and evaluated two widely used methods based on air temperatures. [Piotrowski and Napiorkowski \(2019\)](#) present new modifications of logistic regression models based on air temperature, water discharge and radiation fluxes. Alternatively, [Bal et al. \(2014\)](#) used a hierarchical times series modelling approach for air and water temperature, discharge, based on seasonal sinusoidal signals. For consistency, we opted for a method of calculation based on air temperature and flow as described in the report Explore2070 ([OFB, 2012](#)). To do so, we used daily time series of water discharge and air temperature between 1960 and 2017 and water temperature between 1995 and 2017 on the Scorff river (databases HYDRO, [Leleu et al., 2014](#), SAFRAN, [Vidal et al., 2010](#), ORE DiaPFC, [Jeannot, 2019](#)). We defined the best model based on DIC and RMSE criteria, and checked model convergence, as well as posterior and predicted values distributions with *qqplot*. Then, the robustness and predictive performance of the best model was tested by cross-validation. The cross-validation was implemented using the half of the available time series to fit the model and make the forecasting on the other half. For each river, the water temperature at a day t depends on the air temperature of the 15 days before with an autoregression of order 15, as suggested in Explore 2070 (coefficients a), but also of the flow of the same day, with a coefficient b . α and θ are respectively the maximum and minimum water temperature and evolve in time, as function of the minimum/ maximum air temperature and the minimum flow, as suggested in [Bal et al. \(2014\)](#) (Equation 3.8). The minimum and maximum air temperature and water discharge are centered.

$$\begin{aligned}
Twater_t &\sim norm(\mu_t, tau) T(0,) \\
\mu_t &= \theta_y + \frac{\alpha_y - \theta_y}{1 + \exp(-x_t)} \\
x_t &= \sum_{i=0}^{15} a_{i+1} \times Tair_{t-i} + b \times IQ_t + c \\
IQ_t &= \frac{1}{\frac{module}{10} + Q_t} \\
\theta_y &\sim norm(\mu_y^\theta, tau^\theta) T(0, 15) \\
\mu_y^\theta &= \theta_1 + (\theta_2 \times minTair_y) + (\theta_3 \times minFlow_y) \\
\alpha_y &\sim norm(\mu_y^\alpha, tau^\alpha) T(0, 35) \\
\mu_y^\alpha &= \alpha_1 + (\alpha_2 \times maxTair_y) \\
\varepsilon_y^\theta &= \theta_y - \mu_y^\theta \\
\varepsilon_y^\alpha &= \alpha_y - \mu_y^\alpha
\end{aligned} \tag{3.8}$$

Bayesian estimates

The parameters are estimated in a Bayesian framework with 20000 iterations using the following non-informative prior (Table 3.5, Fig. 3.13).

Table 3.5: Prior and posterior distributions of the parameters of the water-air temperature-flow discharge relationship. Posterior distribution is summarized by the median value and 95% credible interval.

Parameter	Prior	Posterior
θ_1	Uniform (0.1, 10)	0.87 [0.19; 1.29]
θ_2	Normal (0, 0.001)	0.18 [-0.06; 0.55]
θ_3	Normal (0, 0.001)	2.38 [0.84; 4.83]
tau^θ	Gamma (0.1, 0.1)	1.97 [0.68; 4.86]
α_1	Normal (0, 0.001) T(0,)	28.08 [27.44; 28.80]
α_2	Normal (0, 0.001)	0.19 [-0.08; 0.46]
tau^α	Gamma (0.1, 0.1)	0.67 [0.33; 1.27]
$a_{[1:16]}$	Normal (0, 0.001)	See Fig. 3.13
b	Normal (0, 0.001)	-0.23 [-0.25; -0.21]
c	Normal (0, 0.001)	-2.15 [-2.18; -2.13]
tau	Gamma (0.1, 0.1)	1.41 [1.37; 1.46]

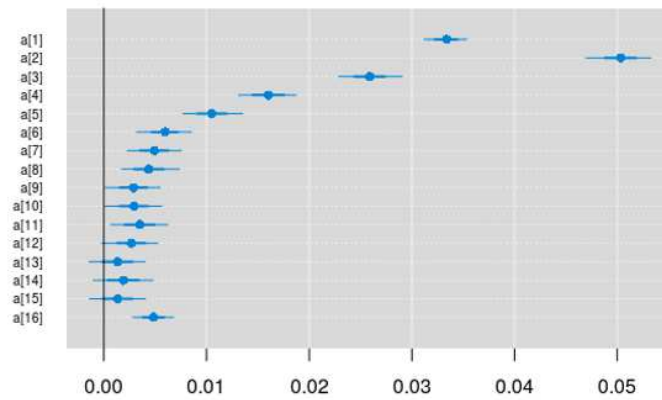


Figure 3.13: Posterior distributions of the autoregressive parameter a of the water-air temperature -flow discharge relationship. Median values and 95% credible intervals are represented.

Distribution of predictions

The distribution of predicted values of 10 random iterations was checked (Fig. 3.14); only low values of water temperature are overestimated with the model, which represents on average 9 days per year of the observed data and 1.7% of the simulated data (median over the 100 simulations for 1 population).

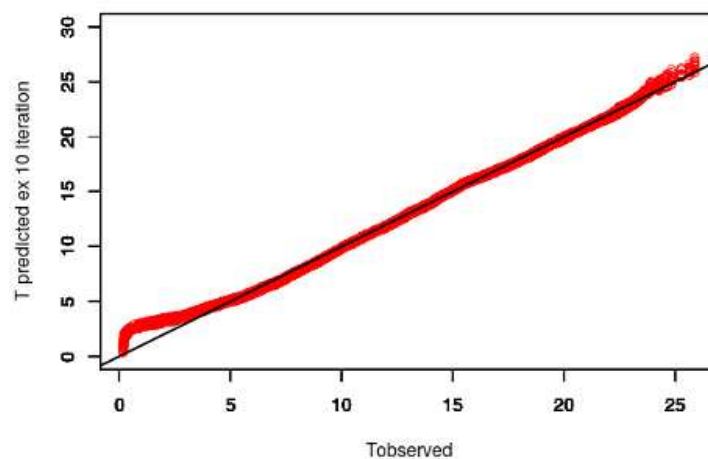


Figure 3.14: Quantile-quantile diagram between the observed and predicted (over 10 iterations of the model) water temperatures.

3.5.3.2 Sinusoidal model of air temperature and water discharges regimes of the Scorff

Then, we assessed the air temperature and hydrological regimes in the Scorff river using a sinusoidal model with autoregressive errors from the same datasets.

Model description

To characterize rivers flow conditions, we used a sinusoidal autoregressive model with order 1 and estimates parameters for each river j (Equation 3.9).

$$\begin{aligned} \log\left(\frac{Q_{t,j}}{\bar{Q}_j}\right) &\sim \text{norm}(\mu_{t,j}, \text{tau}_j) \\ \mu_{t,j} &= \alpha_j + \text{amp}_j \times \sin\left(\frac{2 \times \pi \times (t - t_0)}{n}\right) + AR_{t,j} \\ AR_{t,j} &= \text{ar1} \times AR_{t-1,j} \end{aligned} \quad (3.9)$$

With Q the daily discharge in m^3/s , \bar{Q}_j the module of the flow over the time period, α the mean flow, amp the amplitude, t_0 the phase, n the number of days per year and ar1 the autoregressive parameter.

To characterize the air temperature conditions for each river, we used the same sinusoidal model with order 1 autoregression and estimates parameters for each river j .

We used a Bayesian approach to estimate parameters of interest for both models, with the Nimble package. We considered a simple model with parameters α and amp constant over time. We ran both models for 10 000 iterations with the following priors (Table 3.6 and Table 3.7), tested their convergence with the diagnostic of Gelman, and used *qqplot* to see if the predicted values of the model fit the observed values of flow and air temperature.

Table 3.6: Prior and posterior distributions of the parameters of the water flow sinusoidal model. Posterior distribution is summarized by the median value and 95% credible interval.

Parameter	Prior	Posterior
α	Uniform (-4, 4)	-0.42 [-0.47; -0.38]
amp	Uniform (0.01, 4)	0.99 [0.93; 1.05]
ar1	Uniform (0, 1.1)	0.94 [0.93; 0.94]
t_0	Uniform (300, 365)	325.95 [322.46; 329.47]
tau	Gamma (0.01, 0.01)	22.66 [22.21; 23.11]

Table 3.7: Prior and posterior distributions of the parameters of the air temperature sinusoidal model. Posterior distribution is summarized by the median value and 95% credible interval.

Parameter	Prior	Posterior
α	Uniform (-20, 20)	10.71 [10.59; 10.81]
amp	Uniform (0, 20)	5.87 [5.71; 6.03]
$ar1$	Uniform (0, 1.1)	0.79 [0.78; 0.80]
$t0$	Uniform (100, 200)	117.51 [115.98; 119.04]
tau	Gamma (0.01, 0.01)	0.32 [0.31; 0.32]

3.5.3.3 Simulation of water flow and water temperature for each river

From the median posterior value of the parameters of sinusoidal models and the water-air-discharge relationship, we simulated daily times series of water discharge and water temperature using a daily random draw independent for each river to ensure no environmental spatial covariation (i.e., environmental synchrony).

3.5.4 Populations' density of juveniles (parr 0+)

We measured the density of juveniles in populations for each dispersal scenario and observed an increase of density in sink populations with dispersal, as immigration is higher than emigration (Fig. 3.15). Conversely, dispersal decreases density in source populations, where emigration is higher than immigration. This changes in density affect individual's growth and life history traits during individual's life cycle.

3.5.5 Populations' life-history traits by considering all individuals phenotypes (philopatric adults and immigrants)

By considering all individuals traits in populations, we can barely observe changes in adult size and age at maturation with dispersal (Fig. 3.16).

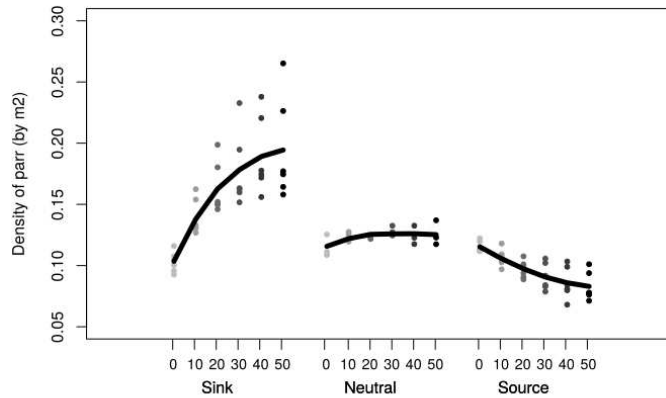


Figure 3.15: Median over simulations of populations last 5 years median parr density (by m²) for each scenario of dispersal. Each point is a population, categorized by its type (sink/source/neutral), and a local regression is added to represent a global trend as a function of dispersal rates and category of populations (sink/source/neutral).

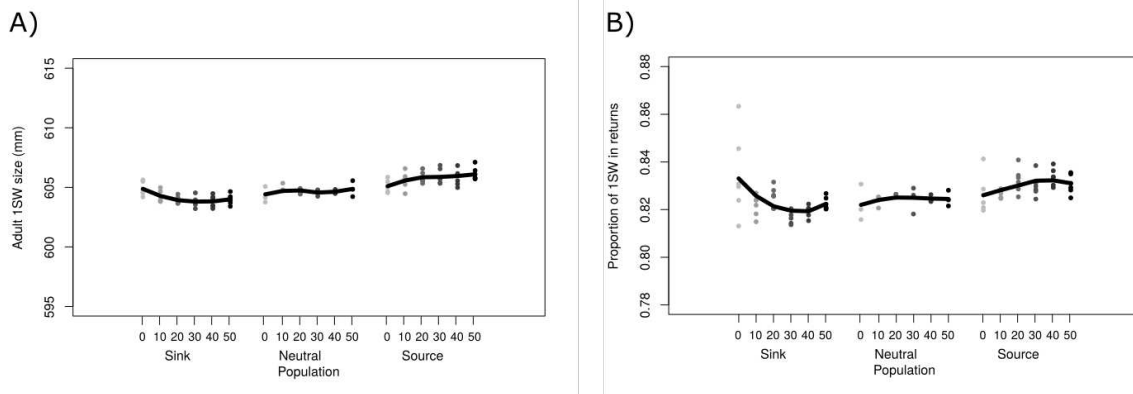


Figure 3.16: Median over simulations of populations last 5 years median adult 1SW size (A) and proportion of 1SW in adult returns (B) for each scenario of dispersal. Each point is a population, categorized by its type (sink/source/neutral), and a local regression is added to represent a global trend as a function of dispersal rates and category of populations (sink/source/neutral).

3.6 CHAPTER HIGHLIGHTS

In this chapter, I hope to have clearly illustrated the rationale, description and potential applications of our modeling approach, which meets both the needs to integrate eco-evolutionary dynamics and connectivity of populations in a single framework. Ultimately, the main lessons of this chapter are the following:

Chapter 3 highlights

- MetaIBASAM, a spatial extension of IBASAM, is a demo-genetic agent based model of Atlantic salmon populations connected by dispersal;
- MetaIBASAM builds on more generic eco-evolutionary models of metapopulations;
- Within a source-sink metapopulation, a gradient of dispersal rates between 0% and 50% can have non-linear consequences on metapopulation stability, and local populations demographic, phenotypic, as well as genetic patterns, summarized in Fig. 3.17;
- Demo-genetic ABMs such as MetaIBASAM have the potential to investigate eco-evolutionary dynamics in a metapopulation perspective and their implications for management;
- Atlantic salmon populations cannot be treated as isolated systems and spatial dispersal is an important component for understanding the dynamics of metapopulations and the resilience of population complexes.

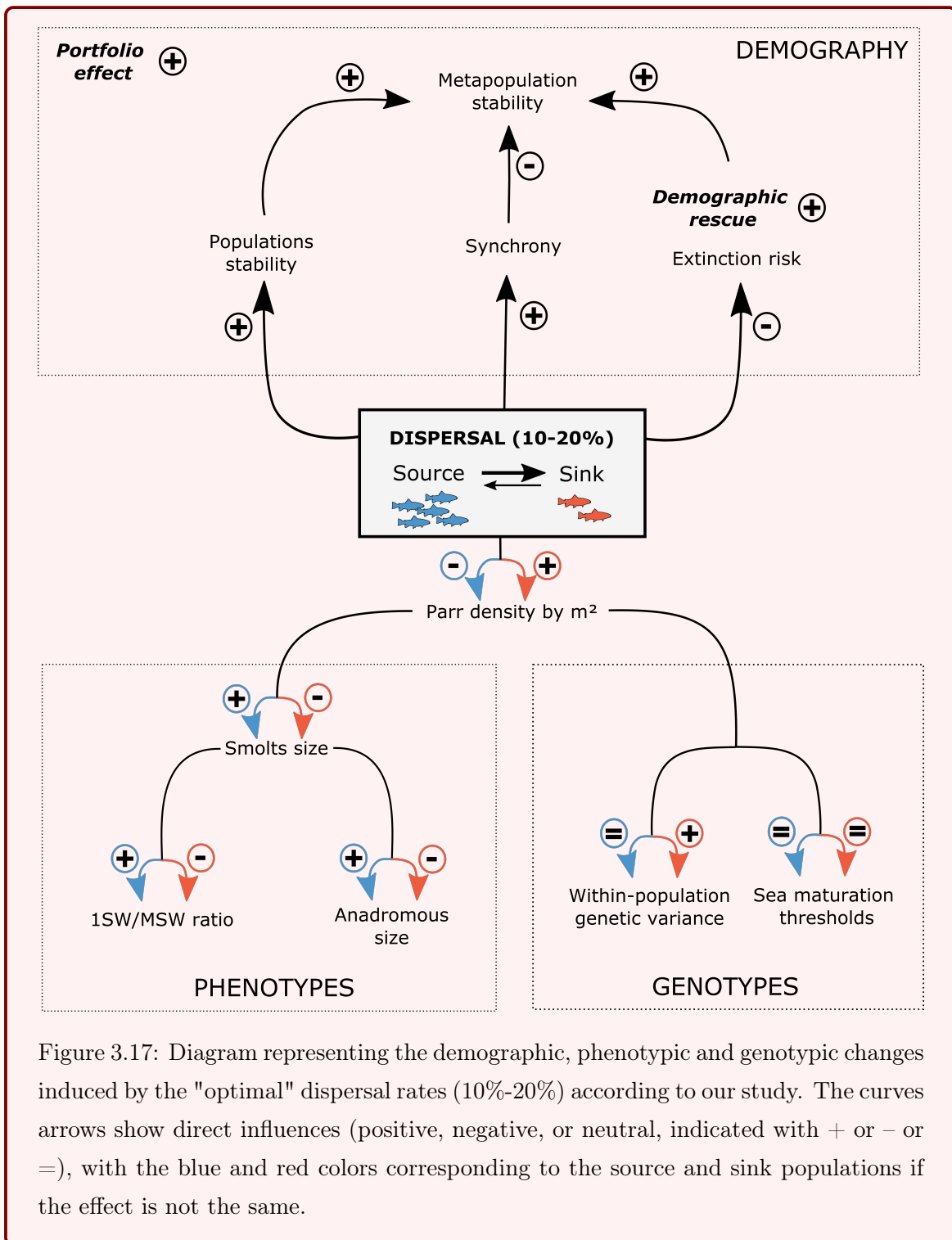
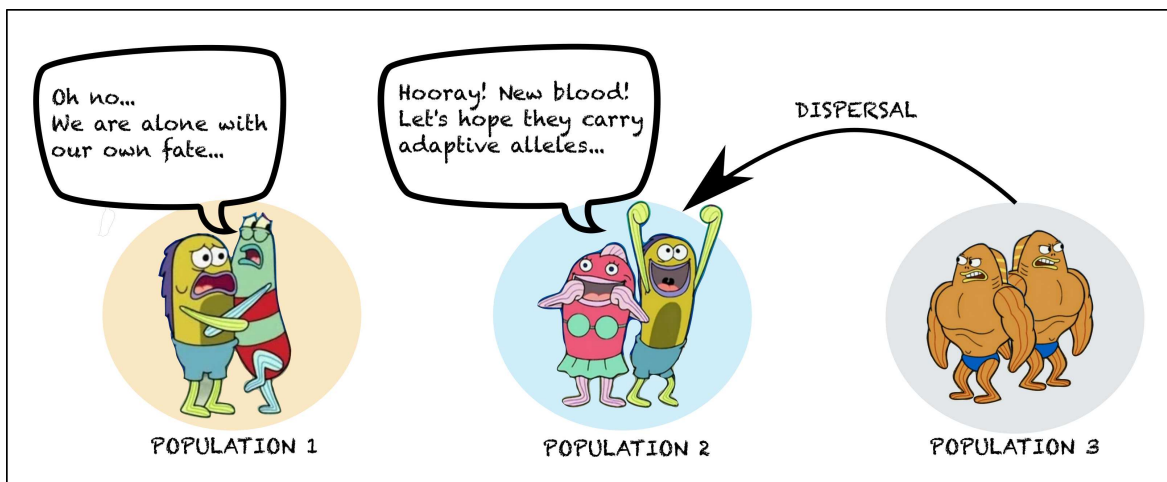


Figure 3.17: Diagram representing the demographic, phenotypic and genotypic changes induced by the "optimal" dispersal rates (10%-20%) according to our study. The curves arrows show direct influences (positive, negative, or neutral, indicated with + or - or =), with the blue and red colors corresponding to the source and sink populations if the effect is not the same.

The parsimonious design of this study, i.e., using phenotypically and genetically homogeneous populations, allowed to showcase the eco-evolutionary effects of dispersal in a "neutral" context, i.e. through density changes. Even if this genetic and phenotypic structure is very likely in some networks such as the metapopulation of Brittany, many other networks are characterized by a variability of environmental conditions, or genetic structure among populations. Considering more variability of populations dynamics would allow to evaluate the consequences of dispersal in a context of diversity and to better examine the adaptation network theory. The next chapter seeks to investigate this interplay between dispersal and diversity, with a focus on the influence of the spatial structure of the network.

The importance of network spatial structure as a driver of eco-evolutionary dynamics



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Following the conclusions of Chapter 3, the next step of this thesis was to evaluate the consequences of dispersal in a context of diversity among populations, and to examine the adaptation network theory. A large body of literature already provided insight into the interplay between dispersal and diversity, emphasizing that the evolutionary trajectories of local populations may be influenced by the intensity of gene flow, the intensity of selection, trait heritability, and environmental variation (García-Ramos and Kirkpatrick, 1997; Schiffers et al., 2013; Berdahl et al., 2015). However, they mainly use the framework of divergent selection and highlight the homogenizing effect of dispersal. In this chapter, we rather put our work in a context of no divergent selection, and among populations diversity is generated by perturbations. Thus, this work aims to investigate the adaptive capacity of local populations after a perturbation within a network of diversified populations. Additionally, the spatial structure of populations is rarely considered as a driver of populations dynamics, but may be of crucial importance in the evolutionary dynamics of local populations; it is thus a major emphasis of this chapter. This chapter corresponds to an article submitted for publication to the *American Naturalist* journal.

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The importance of network spatial structure as a driver of eco-evolutionary dynamics

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Abstract

Investigating eco-evolutionary responses of populations to environmental changes requires better understanding of the spatial context in which they evolve. While the interplay between local adaptation and dispersal in guiding evolutionary outcomes has been studied extensively, it is often in a context of divergent selection and simplified spatial structure. Alternatively, we used a spatially-explicit demo-genetic agent-based model to simulate a network of interconnected populations of Atlantic salmon facing a perturbation shifting their genetic composition and creating diversity among populations. We analyzed the influence of the spatial structure of genetic diversity and populations on the evolutionary dynamics under convergent selection (toward a common optimum). Our simulations showed adaptation of local populations was enhanced by dispersal between initially diverse populations, providing general support for the adaptation network theory. However, the spatial configuration of populations also played an important role in their evolutionary trajectories. Overall, the adaptive capacity of the network depended on the “opportunity for adaptation” provided by immigration patterns that emerged from the connectivity structures of the scenarios tested. We highlight the importance of spatial diversity and population structure on the ability of species to respond to environmental change, with implications for management and conservation of spatially structured populations.

Keywords: demo-genetic agent-based model, perturbation, spatial structure, evolutionary dynamics, adaptation network

4.1 INTRODUCTION

Dispersal and adaptation are two evolutionary processes that can promote species persistence to environmental changes. However, gene flow (a consequence of dispersal) can also alter trajectories of recipient populations and limit local adaptation. Indeed, the extensive literature on the balance between gene flow and selection emphasizes that divergent selection across populations favors adaptive divergence while gene flow can have a homogenizing effect (Hendry et al., 2001b; Ronce and Kirkpatrick, 2001; Lenormand, 2002). Many studies from diverse taxa provide evidence of this tension by documenting negative correlations between genetic (or phenotypic) variation and degree of gene flow (e.g., in fish, Lu and Bernatchez, 1999; Hendry et al., 2002; in insects, Nosil and Crespi, 2004; in plants, Sambatti and Rice, 2006).

While gene flow can be a source of homogenization and maladaptation, it can also benefit adaptation to changing conditions (Garant et al., 2007; Blanquart and Gandon, 2011). Maladaptation of populations may arise from many eco-evolutionary origins (Brady et al., 2019), but perturbations constitute an important factor. Natural or human-induced perturbations may alter the phenotypic and genetic compositions of populations (i.e., diversity *within* populations), deviating them from their optimum and making them maladapted (e.g., extreme climate events, Chan et al., 2005; Shama et al., 2011; Vincenzi et al., 2017; stocking, García de Leániz et al., 2004; Stringwell et al., 2014; selective harvest, Langvatn and Loison, 1999; Anderson et al., 2008). But perturbations may also have differential effects on a network of populations and thereby influence the diversity *among* populations. Recovery and evolutionary dynamics of populations after perturbations have been investigated extensively (e.g., Vincenzi et al., 2014; García-Ulloa et al., 2021), but mostly at local scales, focusing on isolated populations (but see Bell and Gonzalez, 2011; Uecker et al., 2014). This is unfortunate because the interplay between dispersal and diversity among populations may determine the recovery of maladapted populations. Indeed, dispersal and gene flow between spatially structured populations can provide demographic, genetic (i.e., increase of *within* population genetic diversity), and evolutionary rescue effects (Carlson et al., 2014; Fitzpatrick et al., 2020; Tomasini and Peischl, 2020) favoring resilience and adaptation of populations.

Importantly, gene flow cannot occur without dispersal but dispersal does not necessarily lead to gene flow, which might explain observed local adaptation patterns despite high rates of dispersal (Moore et al., 2013). Indeed, the reproductive success of immigrants can be lower than philopatric individuals (e.g., in salmonids, Mobley

et al., 2019; in seabirds, Barbraud and Delord, 2021). Therefore, understanding the factors contributing to gene flow also requires a consideration of the factors contributing to dispersal, including the spatial structure of populations. Many theoretical studies have assumed simple spatial structure of a linear environment (e.g., Andrade-Restrepo et al., 2019), two demes (e.g., Pontarp et al., 2015a), or populations structured as grid cells, with equal size and distance among them (e.g., Schiffers et al., 2013). However, other experimental and theoretical studies with more complex spatial structure of populations have revealed that spatial structure itself has a major influence on demography, including potential consequences for metapopulation persistence (Vuilleumier et al., 2007; Gilarranz and Bascompte, 2012; De Roissart et al., 2015; Bonte and Bafort, 2019), synchrony (Yeakel et al., 2014; Larsen et al., 2021), invasion success (Holenstein et al., 2022), prey-predator dynamics (Holland and Hastings, 2008), as well as metacommunity biodiversity (Carrara et al., 2014).

Similarly, the spatial structure of a network of surrounding populations is expected to play an important role in the evolutionary dynamics of the local populations. Indeed, heterogeneous spatial structure can induce asymmetry in dispersal with potential consequences on eco-evolutionary dynamics (e.g., via density-dependent effects). For example, De Roissart et al. (2016) experimentally showed divergence in life history traits of spider mites with variation in patch size, while theoretical studies have revealed the influence of spatial distribution of habitats on specialization (Débarre and Gandon, 2010; Papaïx et al., 2013) and adaptation to environmental change (McManus et al., 2021b). Another line of work has explored how the configuration of dendritic riverine networks influences patterns of genetic diversity (Labonne et al., 2008; Paz-Vinas and Blanchet, 2015; Thomaz et al., 2016). We build on these findings to investigate the impact of spatial structure on the evolutionary dynamics of local populations, specifically (i) the spatial genetic structure (i.e., spatial distribution of diversity *among* populations) and (ii) the spatial configuration of the network (i.e., distance between populations and their respective carrying capacities).

Investigating the interplay between dispersal and genetic diversity by considering eco-evolutionary feedbacks and the spatial structure of a network is challenging. It requires precise monitoring of populations at various spatio-temporal scales and levels of organization (from genes to the metapopulation, Baguette et al., 2017) as well as knowledge of the eco-evolutionary processes at work. Analytical and adaptive dynamics modeling approaches have been developed to provide parsimonious frameworks (e.g., Papaïx et al., 2013; McManus et al., 2021b) but may not be sufficient to understand the complex eco-evolutionary feedbacks occurring in nature

(Bonte and Bafort, 2019; Govaert et al., 2019). *In silico* modeling approaches such as Demo-Genetic Agent-Based Models (DG-ABMs, or individual-based) including evolutionary processes and genetic mechanisms, offer an alternative (Baguette et al., 2017). Importantly, DG-ABMs do not assume an *a priori* fitness function. Instead, variation in fitness emerges from eco-evolutionary processes, individual decisions, interactions and feedbacks, resulting in the evolution of patterns structuring genetic diversity and population dynamics. By also allowing the explicit representation of the spatial structure of populations, these models facilitate the emergence of unanticipated eco-evolutionary feedbacks (Travis and Dytham, 1998). However, implementing such complex biological systems into a generic model can be challenging. Models based on well-known case studies with predefined parameters based on empirical knowledge, on the other hand, retain the complexity of the real world while exploring unobserved but realistic scenarios (e.g., dispersal patterns).

In this study, we used a spatially-explicit demo-genetic agent-based model simulating a network of interconnected populations of Atlantic salmon (MetaIBASAM, Lamarins et al., 2022c) to examine the eco-evolutionary dynamics resulting from the interplay between dispersal, genetic diversity *among* populations, and their spatial configuration. Several adaptive traits could evolve (growth potential and maturation thresholds), and their optimal value emerged dynamically from the interactions between eco-evolutionary processes. At initialization, populations genetic compositions were shifted, simulating a sudden and temporary perturbation, moving them away from their optimum. We created diversity *among* populations under different spatial genetic structures (none, gradual and random), so that perturbations may not have the same impact on all populations. We then tested a gradient of dispersal rates combined with these various spatial genetic structures and spatial configurations of populations. The spatial configuration was then modified incrementally, beginning with a simple case (equal distances and carrying capacities among populations) and progressing to the complexity of an observed Atlantic salmon metapopulation in Brittany (France). We evaluated for these scenarios the dynamics of return to local optimum for each populations on an ecological time scale (out-of-equilibrium dynamics). We expected patterns of adaptation to be influenced by the interaction of dispersal and genetic diversity *among* populations. Additionally, we expected the spatial configuration of local populations to influence their evolutionary dynamics within the network by influencing the number and traits of immigrants.

4.2 METHODS

4.2.1 Model overview

We used a spatially explicit demo-genetic agent-based model, called MetaIBASAM, simulating the eco-evolutionary dynamics of interconnected populations of Atlantic salmon (Lamarins et al., 2022c). MetaIBASAM mimics the life cycle of the salmon and incorporates the extensive knowledge available to date on the species. Atlantic salmon (*Salmo salar*) is an anadromous species that divides its life cycle into two phases: the freshwater phase, where reproduction and development of juveniles take place, and the marine phase, where growth and maturation occur. Although this species remains emblematic of philopatry, some adults disperse to non-natal rivers during their breeding migration, though this is often overlooked (Birnie-Gauvin et al., 2019).

The demo-genetic agent-based model used here has been described in two previous studies: Piou and Prévost (2012) focused on a single population and Lamarins et al. (2022c) extended the model to consider multiple populations connected by dispersal. We provide an overview of the main features of the model here and refer the reader to the earlier papers for additional details. First, the model simulates explicitly the complete life cycle of each individual, from birth to death, with growth, life history tactics and reproduction, tracking individual life history traits in each population of the network. Second, it includes eco-evolutionary processes, such as environmental effects (e.g., temperature and density dependent effects on growth and survival) and the genetic basis of traits (growth potential and maturation thresholds), allowing their transmission to successive generations. Optimal values of genetic traits emerge dynamically from interactions between the model's eco-evolutionary processes and the resulting fitness. The optimum of growth potential, for example, an important individual and heritable trait that influences life history tactics and fitness components, is the result of a trade-off between growth and survival in river and at sea (Lamarins et al., 2022c, Suppl. Mat. Fig. 4.7). Finally, during the spawning migration of adults from the sea to the rivers, a parsimonious dispersal process allows individuals to disperse between populations, with a constant emigration rate over time and space, independently from the individual's features. The choice of recipient population is a function of its distance from the natal population, moderated by its carrying capacity through a dispersal kernel (Lamarins et al., 2022c). We did not apply any direct costs of dispersal (e.g., no additional mortality), and the reproductive success of dispersing

individuals was subject to the same factors as philopatric individuals (i.e., sexual selection and offspring survival). Altogether, each population of the network has its own eco-evolutionary dynamics, which is influenced by dispersal (i.e., demographic changes) and gene flow.

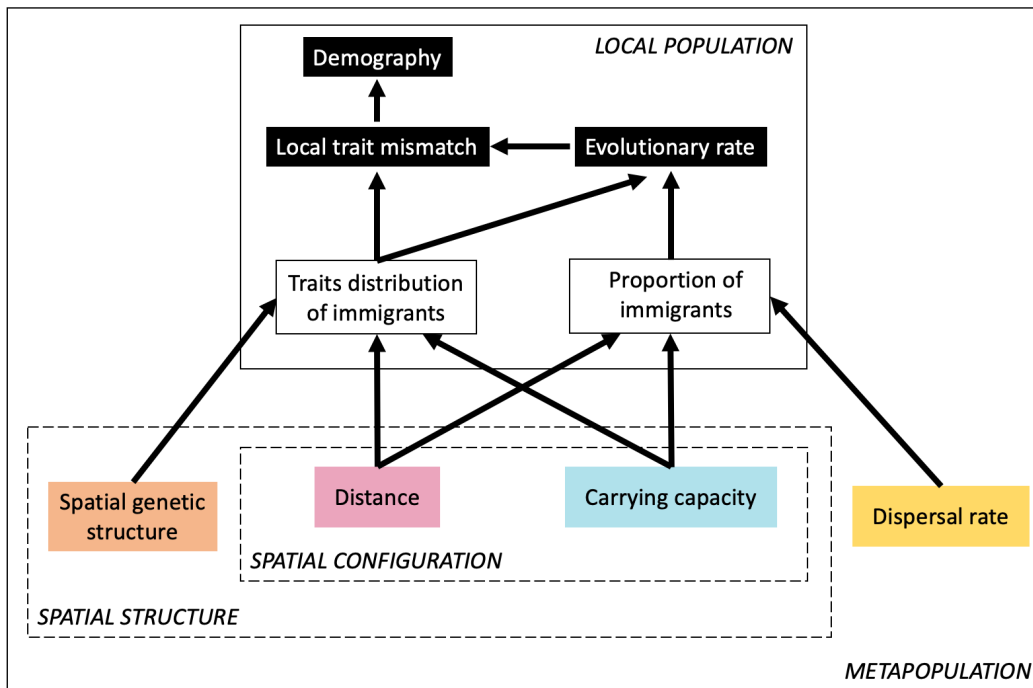


Figure 4.1: Schematic representation of the interplay between dispersal and both components of spatial structure, i.e., the spatial genetic structure of populations, and their spatial configuration (distance and carrying capacities), on the eco-evolutionary trajectories of local populations. Dispersal intensity (rate, in yellow), when combined to diversity *among* populations, is expected to influence the proportion of immigrants and the evolutionary rates (see Equation 4.2) of local populations. Spatial genetic structure (in orange), when combined with dispersal, can modify the genetic traits distribution of immigrants, and ultimately the local trait mismatch and evolutionary rates of local populations. The spatial configuration of populations (distance and/or carrying capacity, in pink and blue) can modulate both the composition and quantity of immigrants, and ultimately the evolutionary trajectories of local populations. Finally, the evolutionary trajectories of local populations can influence their demography and dynamically feedback on the metapopulation spatial genetic structure and dispersal patterns.

4.2.2 Scenarios, simulations, and model parameterization

Our goal was to investigate the eco-evolutionary dynamics of maladapted populations resulting from the interplay between dispersal, genetic diversity *among* populations, and their spatial configuration (Fig. 4.1). Our general approach can be outlined as follows. First, we applied a perturbation affecting the genetic composition of populations to equal or varying degrees and generating diversified *spatial genetic structures*. Then, we modified the *spatial configuration* of populations (i.e., distance and carrying capacity of populations). Finally, we tested these spatial scenarios for a gradient of dispersal rates from 0% to 30%, i.e., around the theoretical optimal rates (10%-20%) that maximize the demographic stability of the metapopulation in this model (see Lamarins et al., 2022c). Below we detail each of these three steps.

First, we tested the effects of the spatial genetic structure of maladapted populations in a simple spatial configuration, i.e., equal carrying capacity and distance between populations (Fig. 4.2 A-C), which maintained similar emigration and immigration rates between neighbouring populations (i.e., symmetrical dispersal, Suppl. Mat. Fig. 4.8 and 4.9). Using this simple spatial configuration, we compared a scenario with no spatial genetic structure (Fig. 4.2 A) with two scenarios including spatial genetic structures: a gradual (Fig. 4.2 B) and a random distribution of diversity across the network (Fig. 4.2 C). To set both populations maladaptation (as induced by a perturbation) and spatial genetic structure, populations were initialized with distributions of genetic traits (maturation thresholds and growth potential) shifted away from their emerging optimum. More precisely, in scenario A, all populations genetic distributions were shifted by +15% of the mean compared to Piou and Prévost (2012) and Lamarins et al. (2022c). By contrast, each population had its own distribution of genetic traits at initialization in scenarios B and C, with a mean shift across populations of +15% and a range from 0% to +30% between populations (Fig. 4.2 B and C). The initial genetic diversity within populations (i.e., variance) and all other parameters were kept the same for all populations in all scenarios (e.g., environmental conditions regimes, exploitation rates, stage-survival rates, heritabilities, etc.; Lamarins et al., 2022c). Based on the optimal fitness value of growth potential emerging from the model simulations presented by Lamarins et al. (2022c), most populations were maladapted at the start of the simulations in all scenarios (optimum around 0 at log scale, Fig. 4.2 and 4.7). This allows us to evaluate the adaptive capacity of populations after a perturbation within various configuration of the network.

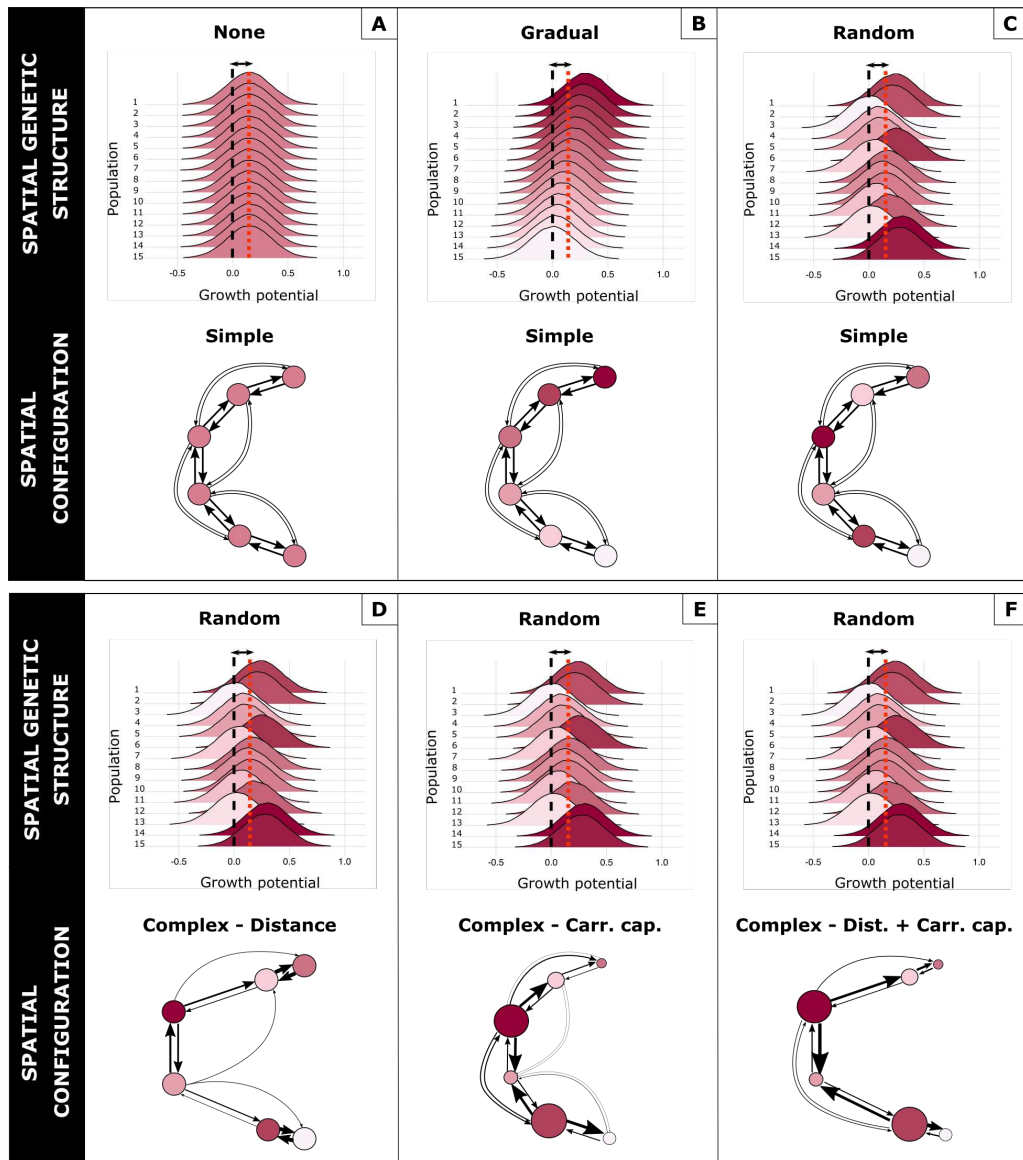


Figure 4.2: Schematic representation of the spatial genetic structure and the spatial configuration of the network for each scenario (A-F). At the top of each scenario box are represented the distributions of genotypic growth potential (log scale, optimum represented by the black dashed line) at initialization of simulations for the 15 populations (average over populations represented by the red dashed line). At the bottom of each scenario box, the circles represent populations (distance between them, size relative to their respective carrying capacities, color indicating the mean of the genetic distribution of growth potential at initialization), the arrows represent the dispersal of individuals (thickness of the line indicating the intensity resulting from the dispersal kernel and spatial configuration). The full simulated network is shown in Suppl. Mat. Fig. 4.9.

Second, we investigated how different network spatial configurations, such as unequal carrying capacity and population distance, impacted asymmetrical dispersal and eco-evolutionary dynamics but under the scenario of random spatial genetic structure only (Fig. 4.2 D-F, Suppl. Mat. Fig. 4.8 and 4.9). The model simulated the dynamics of fifteen populations, parameterized according to Lamarins et al. (2022c) in a pattern-oriented modeling framework (Grimm et al., 2005), and inspired by the spatial configuration of the salmon metapopulation of Brittany (France, Perrier et al., 2011; Bouchard et al., 2022), i.e., adjacent rivers along a coastline (Fig. 4.2). This spatial configuration contrasts with most studies of riverine systems, which have focused on the configuration of dendritic networks *within* basins (e.g., Paz-Vinas and Blanchet, 2015; Fronhofer and Altermatt, 2017), but is particularly relevant to dispersal *among* basins and across gradients of diversity. We sequentially modified the distance between populations (Fig. 4.2 D), carrying capacities (Fig. 4.2 E), and both (Fig. 4.2 F), based on the distance between populations and the area of juvenile production of each population as measured in the Brittany Atlantic salmon metapopulation by Lamarins et al. (2022c).

For each of the 24 scenarios (4 dispersal rates x 6 network genetic and spatial structures), we simulated 50 replicates over 50 years. With a generation time of approximately 2.5 years, our simulation time was sufficient to detect the evolution of life-history traits but short enough to remain in a non-equilibrium state to be able to contrast our scenarios. Simulations started for each population with a random draw of individuals from the population distribution parameters according to the scenarios. To limit computational time, simulations were performed for only 25% of the observed river's carrying capacity, as in Lamarins et al. (2022c). We ran the simulations using R version 3.6.3 and the package MetaIBASAM version 0.0.6 (<https://github.com/Ibasam/MetaIBASAM>). Code and R scripts are freely available at <https://github.com/Ibasam/SpatialStructure>.

4.2.3 Simulation outcomes analysis: Local adaptation / maladaptation

For every scenario, the evolution of genetic traits was monitored for each population by following the average value of philopatric adult traits over the years, averaged over the simulation replicates. Hereafter, we only show evolution patterns of the genotypic growth potential because it was the trait under the strongest selection compared to maturation thresholds (Suppl. Mat. Fig. 4.10, 4.11, 4.12 and 4.13), and because its

phenotypic patterns were similar to those of the genotypes, though less contrasted due to additional environmental variance (see Suppl. Mat. Fig. 4.15 and 4.16). To compare patterns of local adaptation versus maladaptation in populations, we adapted the “mismatch metrics” proposed by McManus *et al.* (2021b). We computed the local population’s trait mismatch (hereafter, LTM) for each scenario as the difference between the median trait value of philopatric individuals of a year t of all simulation replicates and the optimal value of the trait (0 for growth potential, Equation 4.1).

$$LocalTraitMismatch_{i,t} = |\delta_i - X_{i,t}| \quad (4.1)$$

Where δ_i is the optimal genetic trait value of the population i and $X_{i,t}$ is the median of the genetic trait of the philopatric individuals from the population i at a year t over all simulation replicates of a given scenario.

We also calculated the rate of evolution for each population by comparing absolute LTM values at the start of simulations (averaged over years 1 to 5, $LTM_{i,1:5}$) to the end of simulations (averaged over years 45 to 50, $LTM_{i,45:50}$), divided by the time required to reach its final LTM value ($T(LTM_{i,45:50})$, Equation 4.2).

$$EvolutionaryRate_i = \frac{|LTM_{i,1:5} - LTM_{i,45:50}|}{T(LTM_{i,45:50})} \quad (4.2)$$

We chose this metric because the final value of LTM for a population is not always the optimum value at initialization (here, 0), and because this final value can be reached before the simulations are completed.

To unveil the influence of immigrants to the local dynamics of recipient populations, we monitored the distribution of genetic traits of incoming immigrants in each of the local populations over time, as well as the proportion of immigrants.

Within population diversity was monitored via the coefficient of variation of the genetic trait of (i) philopatric individuals and (ii) immigrants over all simulation replicates for each population, each year, and each scenario.

Finally, the demographic consequences of evolutionary trajectories and populations adaptation were measured by the number of returning adults (philopatric and immigrants) averaged over simulation replicates, for each population, each year, and each scenario.

4.3 RESULTS

4.3.1 Dispersal and diversity among populations with a simple spatial configuration

At the network scale, the three scenarios of the spatial genetic structure showed the same pattern of traits evolution without dispersal (0%). While maturation thresholds didn't change (Suppl. Mat. Fig. 4.10, 4.11 and 4.12), growth potential evolved toward the optimum ($LTM_{optimal} = 0$), illustrated by a lower trait mismatch at the end of simulations compared to initialization (-46%, -43% and -44% on average compared to $\overline{LTM_{initial}} = 0.15$ for scenarios of none, gradual, and random genetic structure, respectively, without dispersal; Fig. 4.3 A). However, the interplay between diversity among populations and dispersal showed various patterns of trait mismatch and evolutionary rates of the local populations across the three scenarios of diversity (Fig. 4.3 A and B). Without diversity among populations, the final LTM of populations remained high (-46% on average compared to initialization) regardless of the dispersal rate, while the evolutionary rates remained low (Fig. 4.3 A and B, black color). In contrast, the final LTM of populations decreased with increasing dispersal when combined with genetic diversity among populations, and this pattern was stronger when genetic diversity was distributed randomly (orange color; e.g., -79% on average compared to initialization with 10% dispersal) compared to gradually (green color; -56% on average compared to initialization with 10% dispersal; Fig. 4.3 A). The evolutionary rates of populations increased on average with dispersal for a gradual genetic structure, and even more when genetic diversity was randomly distributed among populations (Fig. 4.3 B). Finally, population recovery following perturbation was enabled by the evolution of growth potential within the population network, which was facilitated by dispersal and diversity among populations. Indeed, adaptation alone (without dispersal) did not allow the metapopulation to recover within the time frame we observed (Fig. 4.3 C). For example, in the scenario with a random distribution of diversity and no dispersal (orange color), the metapopulation abundance remained at its lowest level 50 years after the perturbation (-41% on average compared to initial metapopulation abundance) despite a reduced LTM by 44%. But when combined with dispersal, it had the highest recovery (-17% on average for 10% dispersal compared to initial metapopulation abundance) and stability (lower CV, -34% on average for 10% dispersal compared to the scenario without dispersal and diversity) in the metapopulation's demography (Fig. 4.3 C and D). These results suggest that

resilience of metapopulation is enhanced within a diversified and connected network of populations.

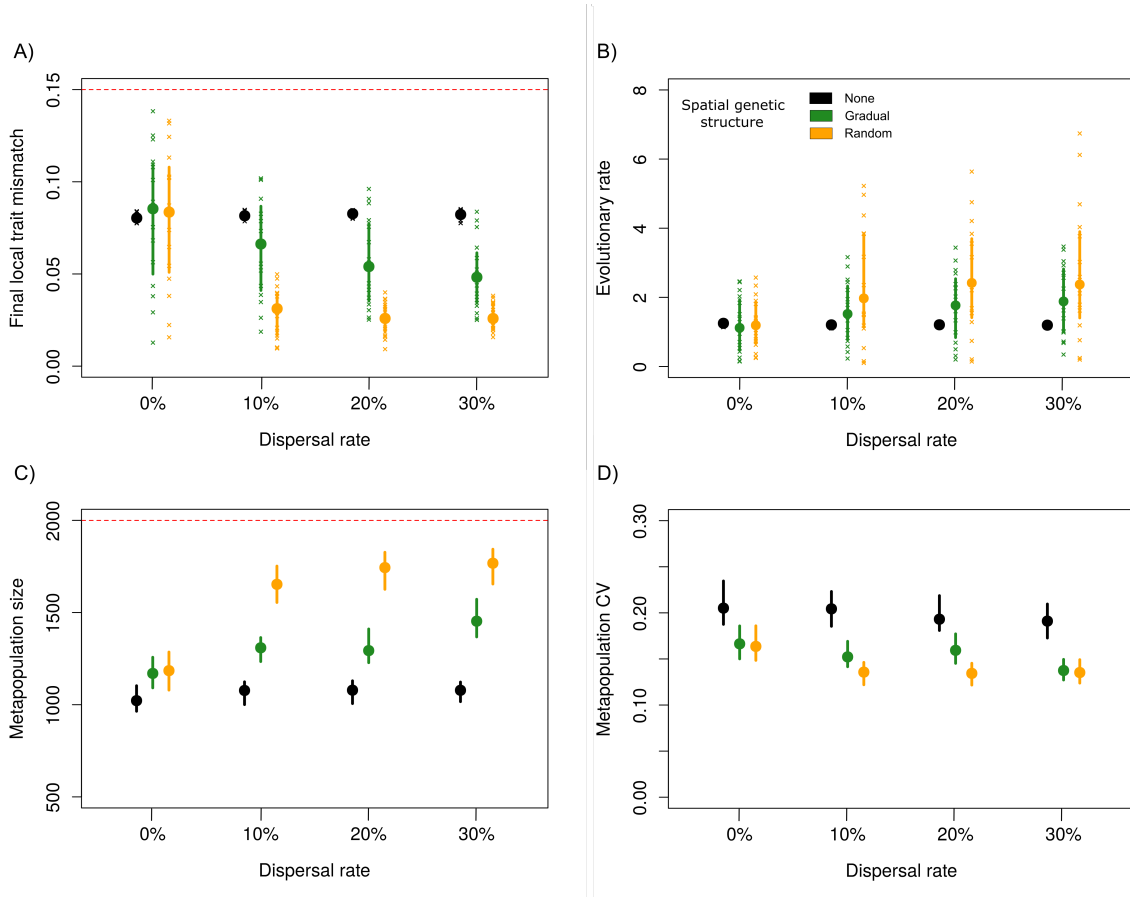


Figure 4.3: Above, distributions (median, quantiles 50%) of A) the final local trait mismatch (averaged over the last 5 years) and B) the evolutionary rates of the 15 local populations (represented by the crosses). Below, distributions (median, quantiles 50%) over simulation replicates of C) the metapopulation size (number of returning adults averaged over the last 5 years) and D) the coefficient of variation of metapopulation abundance (calculated over the 50 years). Distributions are represented for each scenario of dispersal rate and spatial genetic structure under a simple spatial configuration of populations. The dashed red lines represent A) the initial local trait mismatch averaged over populations and C) the initial metapopulation size averaged over simulation replicates and scenarios.

At the local population scale, the overall differences of local trait mismatch, evolutionary rates and demography between scenarios of dispersal rates and spatial genetic structures can be explained by the resulting immigration patterns (Fig. 4.4).

First, changes with increasing dispersal rates can be explained by the increase in the proportion of immigrants (Fig. 4.4 A, Suppl. Mat. Fig. 4.17 B). Indeed, increasing dispersal rates had small influence on the average value of growth potential of the immigrants; it rather increased their quantitative contribution to local populations (Fig. 4.4 A).

Second, changes with spatial genetic structures can be explained by the trait distributions of immigrants, which were more or less close to the optimum (Fig. 4.4 A, Suppl. Mat. Fig. 4.17 A). Without initial diversity among populations, evolution of growth potential was slow and at the same rate for all populations (Fig. 4.4 A, shades of grey), which didn't show any demographic recovery from perturbation whatever the dispersal rate (Fig. 4.4 B, shades of grey). Indeed, immigrants from neighbouring populations showed the same average value of growth potential that the recipient population (Fig. 4.4 A). In the scenario of gradual genetic structure (Fig. 4.4 A, shades of green), some populations started simulations with high LTM, while others with medium or low LTM, but they were surrounded by populations with close LTM. However, these small differences among populations were beneficial to populations adaptation relatively to the scenario without diversity, and the benefits increased with dispersal rate (increased immigrants proportion, Fig. 4.4 A). This was especially true for the populations starting the most maladapted (e.g., $LTM_{initial} = 0.26$), both in term of adaptation and demographic recovery (Fig. 4.4 A and B, Suppl. Mat. Fig. 4.13 and Fig. 4.19 for all populations). Indeed, demographic recovery of maladapted populations was not observed without dispersal despite adaptation, but only when dispersal occurred, providing evidence for the evolutionary rescue effect of dispersal. Finally, in the scenario with random genetic structure (Fig. 4.4 A, shades of orange), the average value of growth potential was more contrasted between immigrants and the recipient populations. In this case, populations with high initial LTM benefited quickly and strongly, both in terms of adaptation and demographic recovery, from better adapted immigrants, as soon as there were dispersal (Fig. 4.4 A and B). But the opposite also occurred, to a lesser extent though, for populations already adapted but surrounded by populations with higher initial LTM, where immigration limited their adaptation (Fig. 4.4 A and B). For populations with intermediate LTM, random structure was still beneficial if immigrants were better adapted. Even though the patterns of evolution were contrasted among populations in this later scenario, the overall effect was an improvement in terms of adaptation of the metapopulation and of its demography (Fig. 4.3). This suggests the importance of the spatial genetic structure in determining evolutionary and demographic trajectories of local

populations interconnected by dispersal.

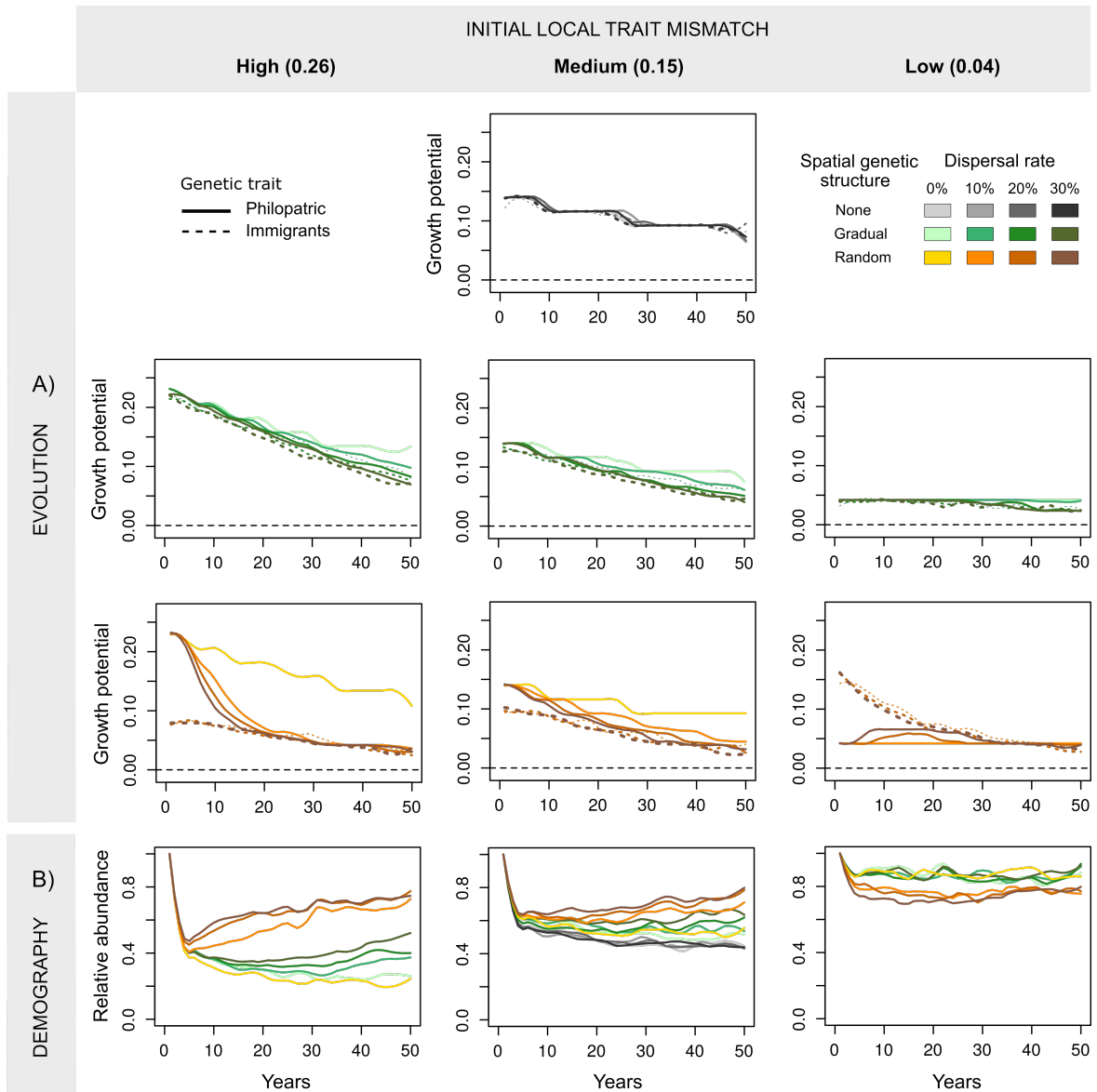


Figure 4.4: Temporal evolution of A) the genetic value of growth potential (log scale) of philopatric adults (full line) and immigrants (dotted line), and B) of the relative abundance of returning adults, averaged over simulation replicates, for each scenario of dispersal rate and spatial genetic structure under a simple spatial configuration of populations, in examples of populations of the network starting simulations at different local trait mismatch (high-medium-low). In A), the horizontal dashed black line represents the optimum value of growth potential. The thickness of the immigrants lines (color dotted lines) represents the averaged proportion of immigrants over time and simulation replicates.

4.3.2 Dispersal and diversity among populations with a complex spatial configuration

On average, no significant differences in local trait mismatch and evolutionary rates were observed at the population network scale between scenarios of population spatial configuration (distance and/or carrying capacity; Suppl. Mat. Fig. 4.18). However, variable patterns were noticeable when examined at the local population scale (Fig. 4.5 A, Suppl. Mat. Fig. 4.14 for all populations), showing contrasted evolutionary trajectories of populations induced by the variable spatial configurations tested. For example, variations in distances within the network (red color; scenario D in Fig. 4.2) reduced adaptation of some populations (i.e., higher local trait mismatch and/or lower evolutionary rate, such as for the populations 10 and 14), increased adaptation of others (such as for the populations 1 and 2), or did not change populations trajectories (e.g., population 13) compared to the scenario of simple spatial configuration (orange color, Fig. 4.5 A). The different patterns associated to distance variation within the network can be explained by changes of the trait distribution of immigrants relative to the optimum. For instance, the increased adaptation of population 1 was fostered by a trait distribution of immigrants which was closer to the optimum, mainly resulting from a reduced distance with population 3 which started simulation close to the optimum (Fig. 4.5 A). Conversely, the reduced adaptation of the population 10 can be explained by the isolation of this population from others that were more adapted.

Variations in carrying capacities within the network (blue color; scenario E in Fig. 4.2) also limited (e.g., populations 1, 2 and 3), fostered (e.g., populations 10, and 14), or did not change (e.g., population 13) their adaptation (Fig. 4.5 A), both through changes of the trait distribution of immigrants (e.g., farther from / closer to the optimum) and the proportion of immigrants (e.g., higher/lower immigration). For instance, the smaller and the larger carrying capacity of the population 3 and 2, respectively, modulated their contribution to the population 1, which pushed away the immigrants distribution from the optimum and reduced adaptation of population 1 compared to the scenario of simple spatial configuration (orange color, Fig. 4.5 A). Conversely, the increased contribution of population 13, a large population starting simulations close to the optimum, to both populations 10 and 14, increased their adaptation via the distribution of immigrants (e.g., in population 14) but also via their proportion in the recipient population (e.g., increased proportion in population 10, Fig. 4.5 A).

The simultaneous variation of distance and carrying capacities between populations

within the network (purple color; scenario F in Fig. 4.2) resulted in combined effects of the scenarios with distance or carrying capacity variation only on adaptation patterns (Fig. 4.5 A). Ultimately, these contrasted effects of variation in spatial configuration on local populations explain why we did not observe difference of adaptation metrics at the network scale. However, these local changes of evolutionary trajectories also had an impact on the demography of local populations, and strongly determined their dynamics of return to equilibrium (Fig. 4.5 B, see Suppl. Mat. Fig. 4.20 for all populations).

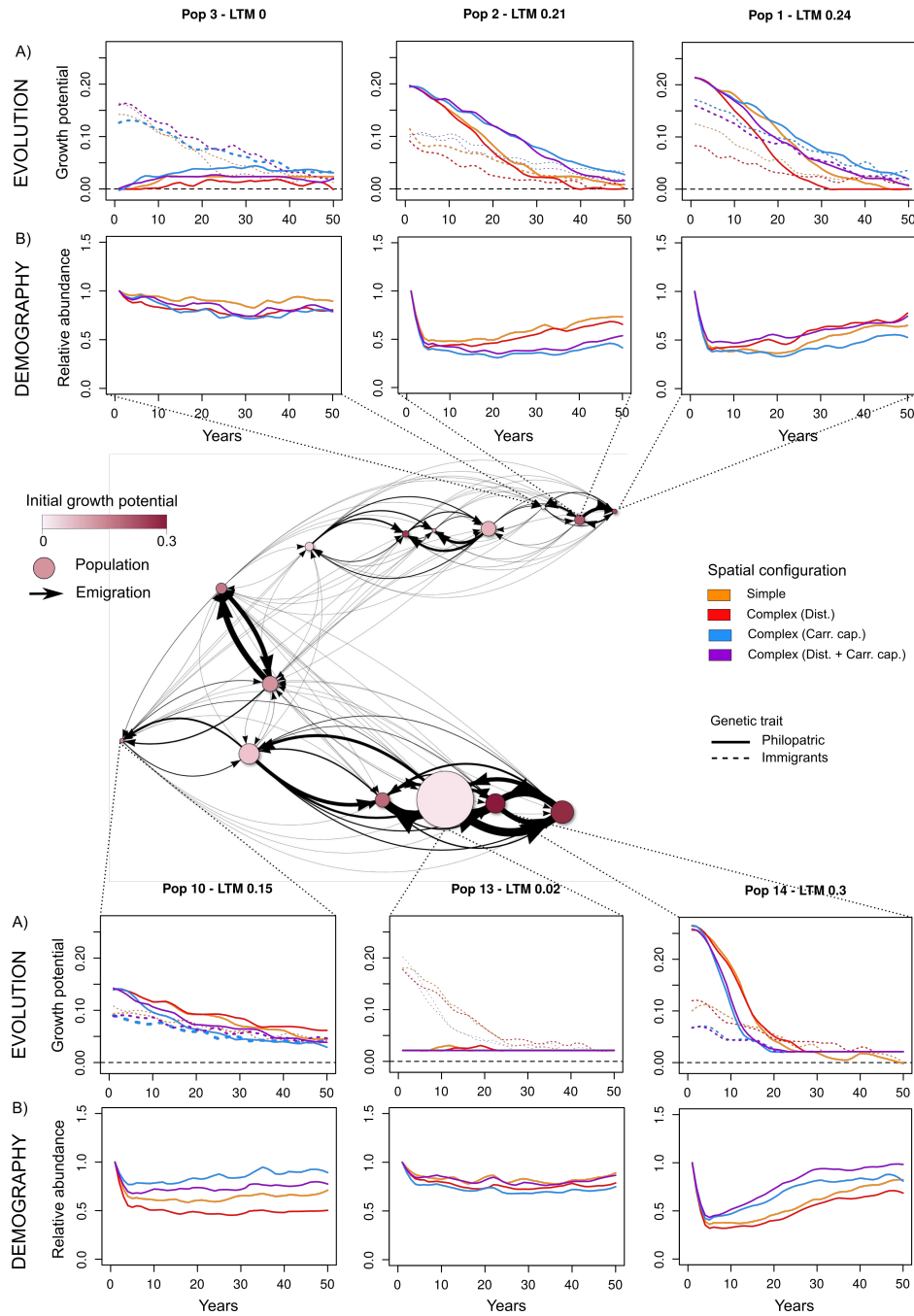


Figure 4.5: Temporal evolution of the genetic value of growth potential (log scale) of philopatric adults (full line) and immigrants (dotted line), averaged over simulation replicates, for each scenario of spatial configuration under a random genetic structure and dispersal rate of 10%. Only 6 populations of the network (each box is a single population identified by its number from 1 to 15) are represented. The horizontal dashed black line represents the optimum value of growth potential. The thickness of the immigrants lines (color dotted lines) represents the averaged proportion of immigrants over time and simulation replicates. The spatial network illustrates the spatial structure (distances, carrying capacities, spatial genetic structure) of the last scenario F, which is inspired by the network of Atlantic salmon from Brittany in France.

4.3.3 Among populations diversity and spatial configuration also influence within populations diversity

The *within* populations genetic diversity was also influenced by the spatial genetic structure (Fig. 4.6 A) as well as the spatial configuration of populations (Fig. 4.6 B). The coefficient of variation (CV) of growth potential of local populations, without dispersal or diversity, slightly decreased over time (shades of grey), but it increased with dispersal rate and diversity among populations (shades of green and orange). More particularly, we observed a linear increase of the CV with dispersal rates and with time in the scenario of gradual genetic structure, while the scenario of random genetic structure showed a rapid increase of the CV followed by a slow decrease over time (Fig. 4.6 A). These patterns are related to the diversity of immigrants composition, which was higher in the random scenario than in the gradual at the beginning of simulations, and then linearly decreased over time via the homogenizing effect of dispersal (Suppl. Mat. Fig. 4.21 A). Considering a random genetic structure and a constant dispersal rate, genetic diversity within populations was reduced with complex spatial configuration, i.e., variation in distance and/or carrying capacity, compared to the simple spatial configuration scenario (Fig. 4.6 B). Indeed, when population clusters were present, or population contributions to dispersal patterns were unequal due to variable population sizes, immigration composition was less diverse (Suppl. Mat. Fig. 4.21 B).

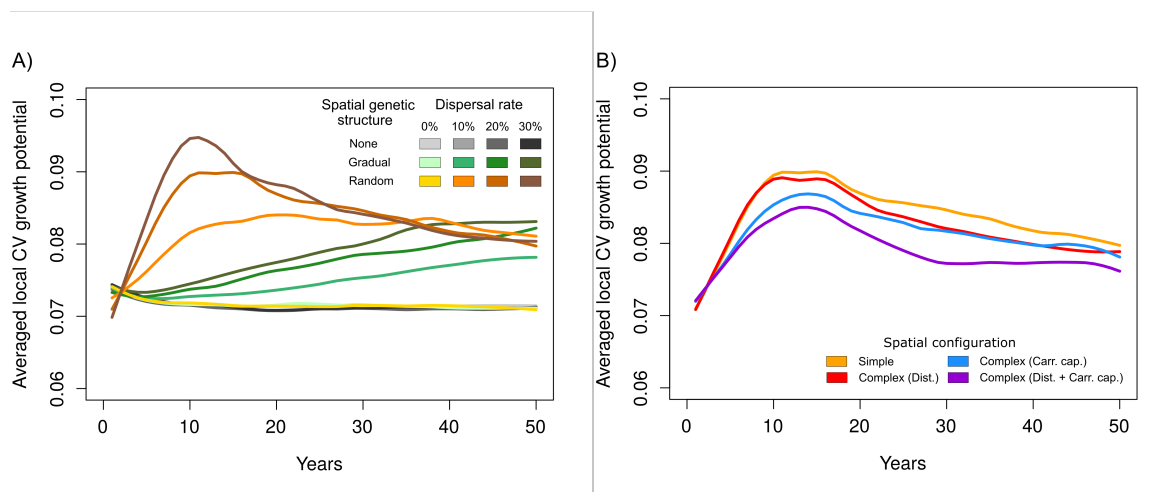


Figure 4.6: Temporal evolution of the average of the 15 local populations coefficient of variation of growth potential (in natural scale, philopatric individuals only), A) for each scenario of dispersal rate and spatial genetic structure under a simple spatial configuration, and B) for each scenario of spatial configuration under a random genetic structure and a dispersal rate of 20%.

4.4 DISCUSSION

We aimed to shed light on the importance of the spatial genetic structure and spatial configuration on the evolutionary trajectories of populations connected via dispersal. To do so, we used a spatially-explicit demo-genetic agent-based model to simulate a set of interconnected populations characterized by various degrees of dispersal, spatial genetic structures, and spatial configurations. We mimicked post-perturbation dynamics without divergent selection and evaluated local populations eco-evolutionary responses. We showed that the interplay between dispersal and genetic diversity can shape the adaptive capacity and eco-evolutionary trajectories of local populations as well as the metapopulation. We showed that adaptation alone of isolated populations did not allow demographic recovery 50 years after perturbation. But dispersal combined with genetic diversity among populations fostered adaptation and resilience for most of the populations - a result that was strengthened with increasing dispersal rates and a random genetic structure. The spatial configuration of populations (i.e., characterized by the distance between them and their respective carrying capacities) modulated their evolutionary trajectories in a variety of ways, depending on the properties (distance, carrying capacity, and genetic distribution) of the recipient population as well as the properties of surrounding populations. But overall, the different adaptation patterns observed across scenarios largely reflected an “opportunity for adaptation” provided by immigration (the number and traits of migrants). The variable evolutionary trajectories of populations based on spatial structures had implications for metapopulation resilience. Altogether, these results illustrate that the different components of an adaptive network and their potential interaction influence species’ abilities to respond to environmental changes, with consequences for management and conservation of local and sets of populations.

Interplay between dispersal and diversity among populations

Our successive scenarios allowed us to disentangle the effects of multiple components of a network on evolutionary dynamics, including the spatial genetic structure, the distance between populations, and their demography. We first manipulated the spatial genetic structure within a network using a simple spatial configuration (scenarios without genetic diversity [A], gradual [B], and random genetic structure [C]). Our simulations showed stronger adaptation for most of the populations when diversity among populations was combined with dispersal, especially for higher dispersal rates, and when genetic diversity was randomly structured compared to when it

was gradually distributed. This was best illustrated by a reduction in the local trait mismatch as well as an increase in the rate of evolution (Fig. 4.3). Indeed, dispersal rates increased the contribution of immigrants, and the spatial genetic structure determined the distribution of immigrants traits, which both determined the "opportunity for adaptation" via immigration into the recipient populations. This higher evolutionary potential of interconnected and diversified populations supports the concept of adaptation networks (Webster et al., 2017), where diversity among populations contributes to evolutionary options favoring adaptation. Here, we additionally showed that the spatial structure of genetic diversity across the network (e.g., random vs. gradual) plays an important role in the outcomes of the adaptive network.

The theoretical work of McManus et al. (2021b) also investigated the influence of environmental heterogeneity on evolutionary responses but in the context of coral reefs experiencing rapid environmental change. They demonstrated a stronger adaptive response of populations to local temperature in a network with regular dispersal compared to random dispersal, because the latter resulted in gene swamping and trait mismatch. The differences between our studies might be explained because populations were confronted with different trait optimums in their scenarios (i.e., divergent selection, which is not our case) and adaptation was favored overall if populations remained diversified (see also the similar results of Papaix et al., 2013, where aggregation and specialization leads to a better adaptation). Building on the literature, our study provides further evidence of the influence of the spatial genetic structure on evolutionary rescue of populations but in the particular case of maladapted populations in a context without divergent selection. Taking advantage of the demo-genetic modelling approach, our study also showcased the strong positive demographic consequences arising from the rescue effects provided by dispersal and the random genetic structure of populations, at both local and metapopulation scales (Fig. 4.3 and Fig. 4.4).

Spatial configuration influences local populations evolutionary trajectories

Our work also shed light on the interaction between the genetic diversity among populations and the network spatial configuration. Even if no clear difference of trait mismatch and evolutionary rate was observed on average at the network scale between simple and complex spatial configurations, contrasted patterns emerged from the model at the scale of local populations. For a given spatial genetic structure (random), our

results illustrated that variation in the distance and carrying capacity of populations can modulate dispersal patterns and contributions of populations to neighboring populations through asymmetrical flow of individuals (Suppl. Mat. Fig. 4.8 and 4.9). These variable dispersal patterns, characterized by the intensity and genetic distribution of migrants, changed the "opportunity for adaptation" of immigration to recipient populations, fostering their adaptation in some cases (e.g., increased contribution of a large or nearby adapted population), while hindering adaptation in others (e.g., decreased contribution of a small or far population). These variable evolutionary trajectories observed depending on the spatial configuration further impacted local and metapopulation demography (Fig. 4.5, Suppl. Mat. Fig. 4.18). These results emphasize the spatial context-dependence of evolutionary trajectories of diversified populations connected by dispersal, and the importance of considering their spatial configuration (distance, carrying capacity), combined with spatial genetic structure, to fully understand evolutionary and demographic dynamics of a network of populations.

Our results build on earlier work highlighting the influence of spatial configuration on demographic trajectories of populations. The increasing recognition of the importance of considering the influence of demography in dispersal dynamics and their consequences on population dynamics was recently reviewed by Drake et al. (2022b) who further emphasize the value of considering the "demographically-weighted connectivity" (which they define as "an extended conceptual representation of landscape connectivity that considers, explicitly, the population dynamics and demographics"). Considering connectivity patterns as emerging from the spatial structure of a landscape has also been empirically shown as crucial to better understand demographic dynamics of populations (Drake et al., 2022a). Our work goes further by emphasizing the importance of considering the spatial structure of genetic features of interconnected populations in addition to demography to understand evolutionary and demographic trajectories of local populations. Similarly, Ranke et al. (2021) described asymmetrical dispersal that was linked to the spatial structure of a metapopulation of sparrows (*Passer domesticus*) and expected consequences for evolutionary dynamics of populations.

Temporal dynamics of within populations diversity

Within-population diversity has been the focus of extensive study because it is considered as the basic material for evolution and adaptation of local populations to

new conditions in the future (Jump et al., 2009). Without diversity among populations, the diversity within populations remained low and even decreased throughout our simulations due to selection. Initial genetic diversity among populations of the network globally increased within-population diversity, but with contrasted temporal patterns depending on the spatial genetic structure. In our simulations, a gradual change in genetic structure progressively increased within-population diversity, while it quickly reached a maximum and then decreased with a random genetic structure. The complex spatial configuration of the network also reduced genetic diversity within populations, because immigrants were less diversified with population clustering and unequal contributions of populations to dispersal patterns. Overall, the patterns of genetic diversity within populations were influenced by the diversity of the immigrant composition, which was a result of the scenario and was temporally dynamic. Thus, we demonstrate that population spatial structure can influence within-population diversity, as well as the importance of considering the temporal context of population dynamics in addition to the spatial context when assessing the state of a local population.

Perspectives and management implications

Spatially explicit demo-genetic individual based models are powerful tools to explore eco-evolutionary dynamics of spatially structured populations. One of the most interesting properties of this type of approach is the ability to generate eco-evolutionary patterns without specifying the fitness function. For example, Fronhofer and Altermatt (2017) showed that dispersal strategies evolve in response to the spatial structure of genetic relatedness (to avoid kin competition) and network properties (topology and connectivity) influence spatio-temporal correlations in fitness expectations. More realistic design of spatial and temporal heterogeneity between populations in modeling approaches such as MetaIBASAM hold promise for providing insight into dynamics of diversified networks (Travis and Dytham, 1998).

Having said that, there is much room for improvement of our model, including a consideration of additional mechanisms that could strongly influence eco-evolutionary dynamics. Given the complexity of the model, we adopted a parsimonious approach focusing on the evolution of growth potential, an important trait in life history theory. The dispersal trait was kept as simple as possible, only influenced by distance between populations and attractivity (carrying capacity). But other important dispersal mechanisms could be explored, such as density-dependence (both for emigration and

immigration, e.g., reviewed in [Harman et al., 2020](#); in salmonids, [Berdahl et al., 2016](#)), habitat choice (e.g., based on environmental similarity, [Mortier et al., 2019](#)), as well as the genetic basis of dispersal itself ([Saastamoinen et al., 2018](#)). Including these mechanisms might change the dispersal patterns in space and time, and ultimately influence the eco-evolutionary dynamics of local populations ([Peniston et al., 2019](#)).

While we did not explore the evolution of dispersal, this is a potential fruitful direction for future studies building on our approach. Prior work has revealed that dispersal can be selected against in heterogeneous environments because of local adaptation, but dispersal can also be selected for as a spreading strategy when environments vary in space and time, to reduce kin competition, or because it favors the propagation of advantageous genes ([Lenormand, 2002](#)). Thus, we hypothesize that in our model dispersal should evolve depending on (i) the spatial structure of adaptive traits, (ii) characteristics of populations within a network (e.g., small vs. large populations to avoid kin competition) and (iii) environmental changes (e.g., increasing spatial synchrony), modifying the local trait mismatch and evolutionary rates. Regardless of the dispersal rate, gene flow could be lower than the dispersal rate because of reduced reproductive success of immigrants (i.e., pre/post zygotic lower fitness) or higher if immigrants have higher reproductive success (due to sexual selection that favors immigrants and/or higher survival of their offspring). This pattern emerged from our model simulations where reproductive success of immigrants was higher than philopatric adults in most maladapted populations, whereas it was lower in adapted populations (for females only, see Suppl. Mat. Fig. 4.22); dispersal propensity could thus evolve as function of local adaptation patterns. It is then crucial to consider both dispersal (i.e., demographic consequences) and gene flow (i.e., evolutionary consequences) together and their variation in space and time (e.g., [Peniston et al., 2019](#); [Drake et al., 2022a](#)).

We build on many studies that already advocate for the conservation of adaptation networks with population diversity and connectivity ([Webster et al., 2017](#); [Walsworth et al., 2019](#)). However, our results further emphasize that the spatial structure, i.e., spatial genetic structure and spatial configuration of populations, are important drivers of local evolutionary and demographic dynamics that must be considered when managing populations. Ideally, identifying key populations based on their influence on eco-evolutionary dynamics of the metapopulation (e.g. adaptive value, higher genetic diversity) could enhance adaptation and conservation success. Importantly, exploitation and climate change are expected to affect the spatial structure of diversity via the synchronization of environmental conditions and/or selective effects ([Parmesan](#)

and Yohe, 2003; Bellmore et al., 2022). A future avenue of research building on our approach is to investigate how a network of diverse populations cope with selective exploitation and climate change, and to determine if there are preferable management strategies considering the spatial structure of populations. More generally, we argue that management strategies should consider not only diversity *within* populations but also *among* interconnected populations to foster rescue effects and adaptation network (Webster et al., 2017; Moore and Schindler, 2022).

4.5 SUPPLEMENTARY MATERIALS

4.5.1 Growth-survival trade-off and emerging growth potential optimal value

A growth-survival trade-off has been implemented in river in MetaIBASAM, as described in Lamarins et al. (2022c), to limit directional selection towards higher values of growth potential. Combined with the size-dependent survival at sea (larger individuals survive better) and reproductive success (higher fecundity of larger individuals), the growth-survival trade-off induces a stabilizing selection for growth and size and an optimal fitness value of growth potential emerges dynamically from the model. This optimal value can be observed via the convergent evolution of populations in the scenarios without dispersal, and estimated theoretically in a neutral context (Fig. 4.7, Lamarins et al., 2022c).

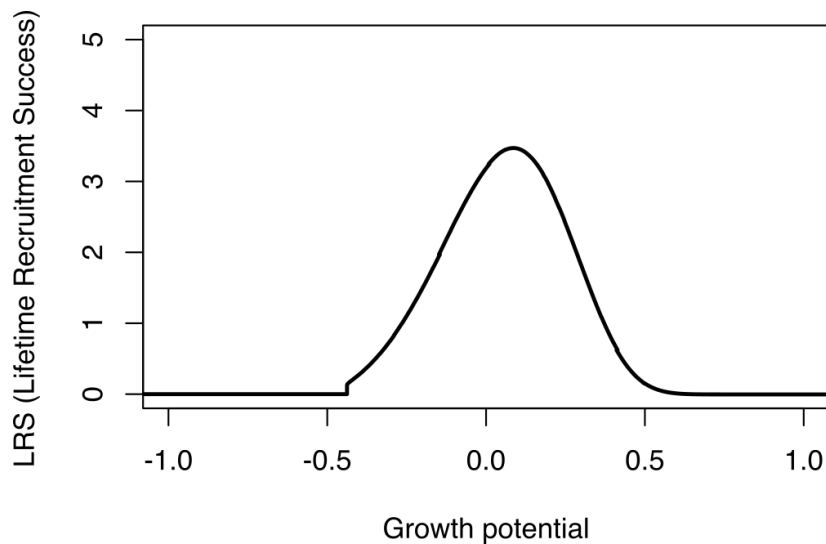


Figure 4.7: Theoretical optimal value of phenotypic growth potential (in log scale) based on mean individual Lifetime Recruitment Success (measured as the mean egg number per female; see processes details in Suppl. Mat. of Lamarins et al., 2022c).

4.5.2 Asymmetry of dispersal patterns

The ratio of the number of immigrants and emigrants in each population illustrates the asymmetry in dispersal patterns for the different scenarios tested. For the scenarios of simple spatial configuration [A-C], the ratio was around 0 (Fig. 4.8 A), i.e., the

dispersal fluxes were symmetrical, whereas variations of the ratio emerged with a complex spatial configuration [D-F] (Fig. 4.8 B), reflecting asymmetrical fluxes of migrants between populations.

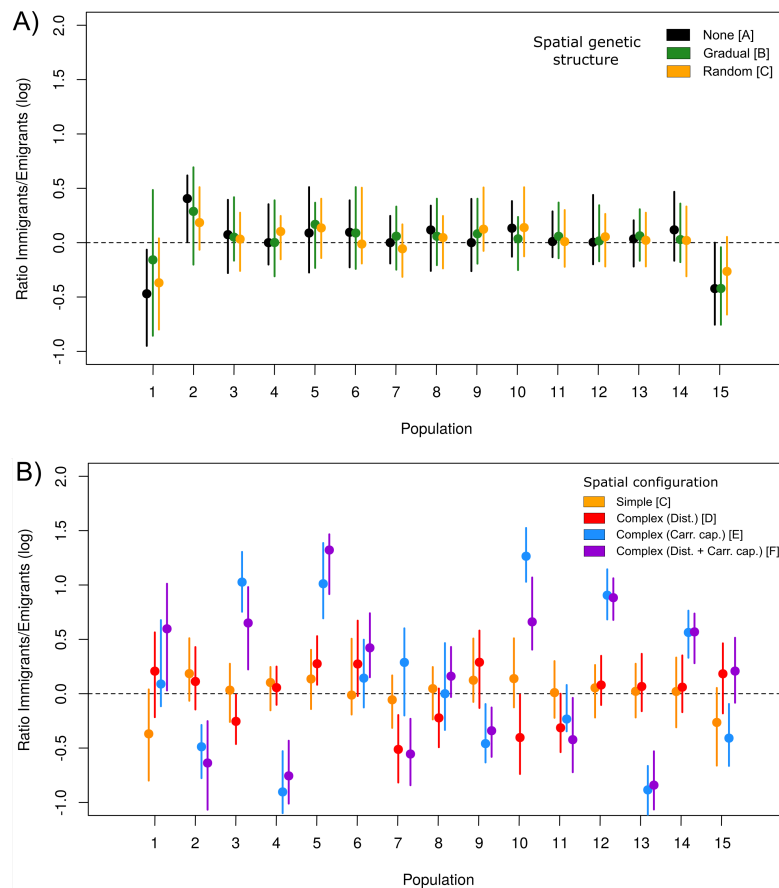


Figure 4.8: Distributions (median, quantiles 50%) over simulation replicates of the ratio Immigrants / Emigrants (in log scale), averaged over the last 5 years, of each of the 15 populations in the scenarios of A) spatial distribution of diversity and B) spatial configuration of populations, for a dispersal rate of 10%.

The simulated networks in the different scenarios, resulting from the spatial configuration (distances and carrying capacities), the spatial distribution of genetic diversity, dispersal rate, and population dynamics, are presented in Fig. 4.9. Overall, the three scenarios of simple spatial configuration showed symmetric dispersal patterns (Fig. 4.9 A-C), whereas the three scenarios of complex spatial configuration showed asymmetric dispersal patterns (Fig. 4.9 D-F).

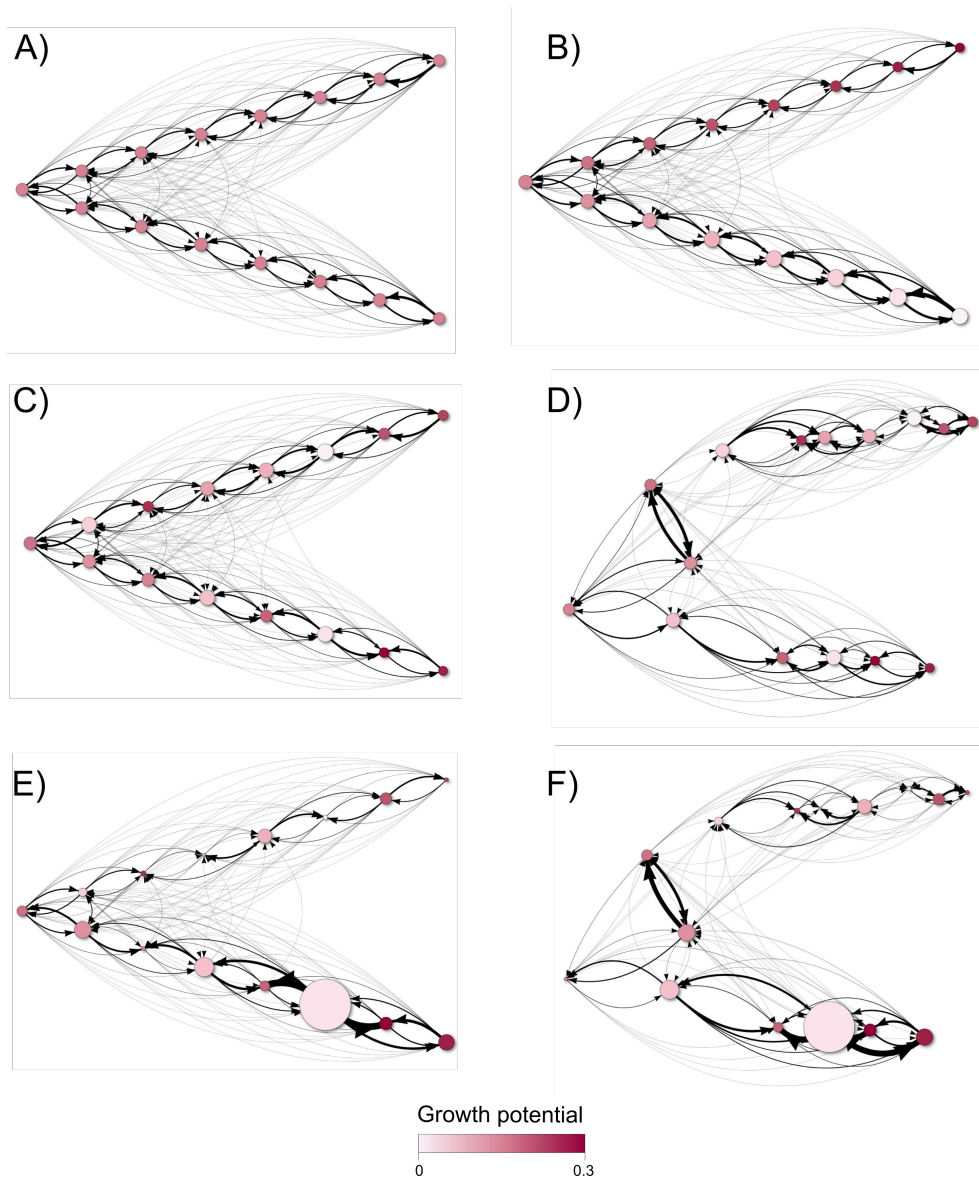


Figure 4.9: Spatial configuration and distribution of genetic diversity of the simulated networks of each scenario (A-F) for a dispersal rate of 10%. The circles represent the 15 populations (distance and size relative to distance between them and their population size during the first 5 years, color representing the mean of the growth potential distribution at initialization), the arrows represent the dispersal of individuals (thickness function of the quantity of migrants during the first 5 years emerging from the dispersal kernel and spatial configuration).

4.5.3 Temporal evolution of traits in all populations

We monitored the evolution of maturation thresholds genotypes (Fig. 4.10, 4.11 and 4.12), growth potential genotype (Fig. 4.13 and 4.14) and phenotype (Fig. 4.15 and 4.16) for each population, by following the adult traits of both philopatric individuals and immigrants, averaged over the simulation replicates, for the scenarios of spatial distribution of diversity and spatial configuration. Results indicated that growth potential was under strong selection, characterized by the evolution of populations with high initial LTM towards the optimum without dispersal (Fig. 4.13), whereas it was not the case for maturation thresholds (Fig. 4.10, 4.11 and 4.12). The effect of immigration on populations trajectories seemed nevertheless the same for maturation thresholds compared to growth potential. We thus focused our analysis of the effect of spatial structure on the evolutionary trajectories of growth potential.

Maturation thresholds

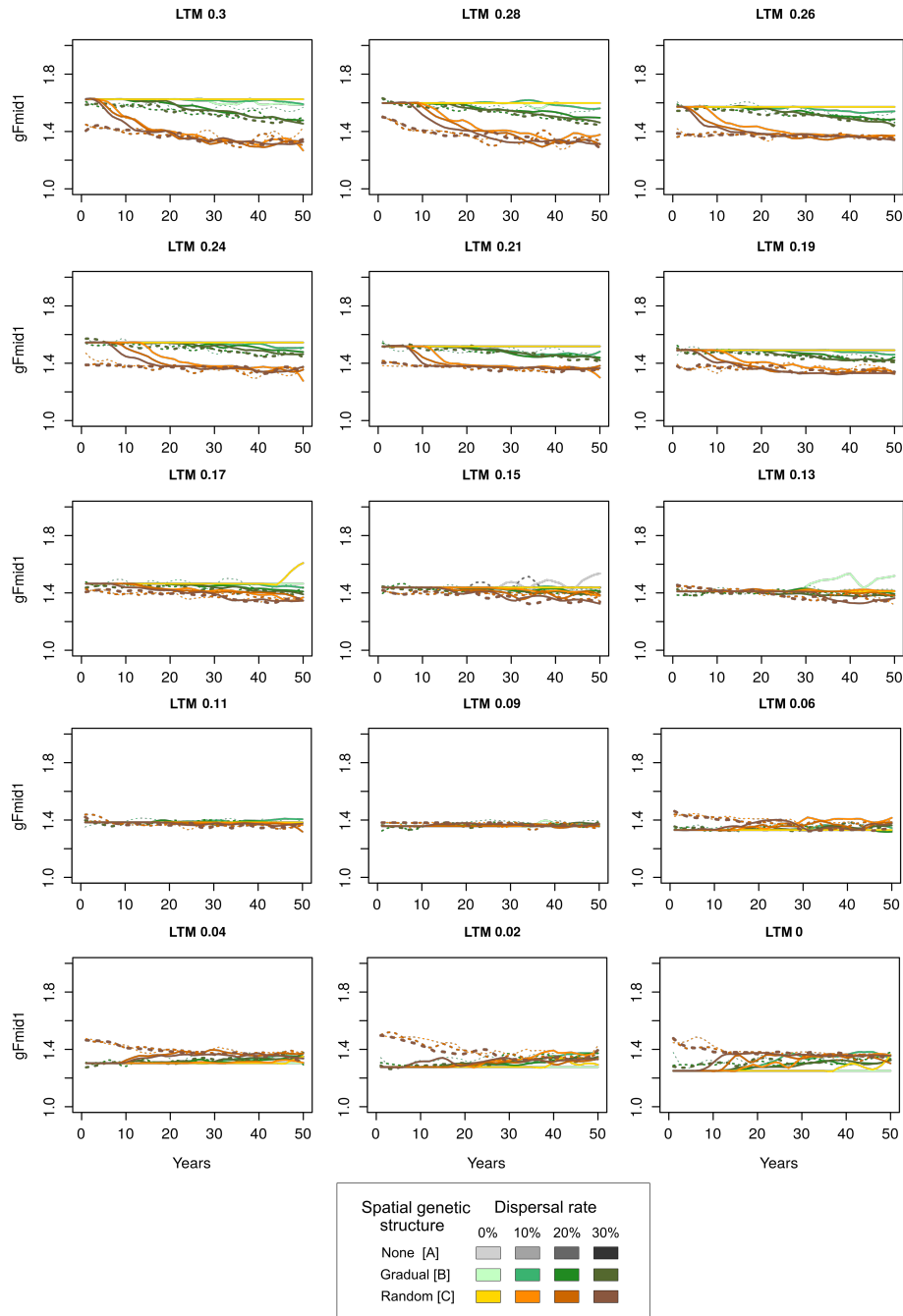


Figure 4.10: Temporal evolution of the genetic value of male river maturation threshold of philopatric adults (full line) and immigrants (dotted line), averaged over simulation replicates, for each scenario of dispersal rate and spatial distribution of diversity (none [A], gradual [B], random [C], see Fig. 4.2 of the main manuscript) in each of the 15 populations ordered by the initial LTM. The thickness of the immigrants lines (color dotted lines) represents the averaged proportion of immigrants over time and simulation replicates.

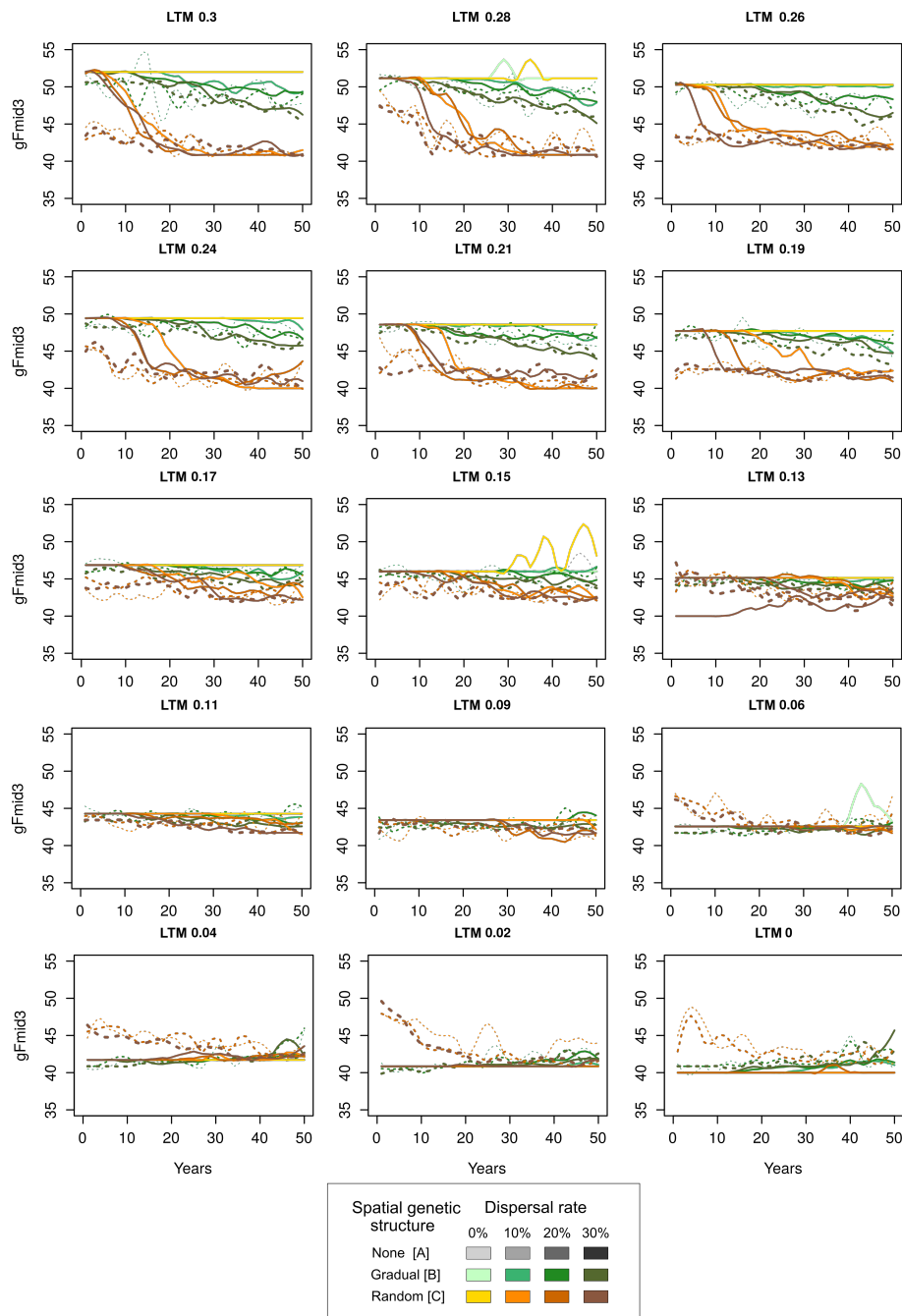


Figure 4.11: Temporal evolution of the genetic value of male sea maturation threshold of philopatric adults (full line) and immigrants (dotted line), averaged over simulation replicates, for each scenario of dispersal rate and spatial distribution of diversity (none [A], gradual [B], random [C], see Fig. 4.2 of the main manuscript) in each of the 15 populations ordered by the initial LTM. The thickness of the immigrants lines (color dotted lines) represents the averaged proportion of immigrants over time and simulation replicates.

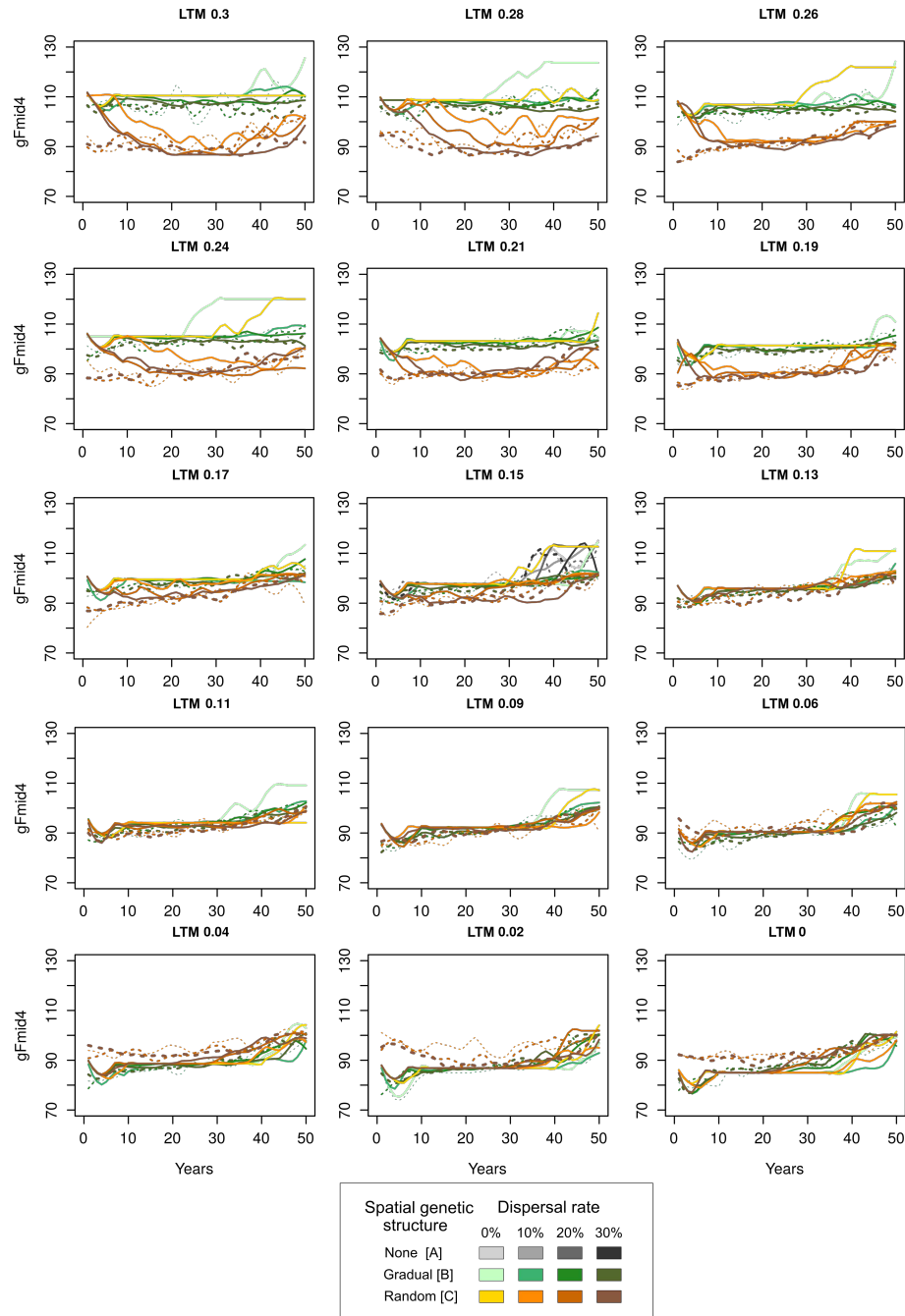


Figure 4.12: Temporal evolution of the genetic value of female sea maturation threshold of philopatric adults (full line) and immigrants (dotted line), averaged over simulation replicates, for each scenario of dispersal rate and spatial distribution of diversity (none [A], gradual [B], random [C], see Fig. 4.2 of the main manuscript) in each of the 15 populations ordered by the initial LTM. The thickness of the immigrants lines (color dotted lines) represents the averaged proportion of immigrants over time and simulation replicates.

Growth potential

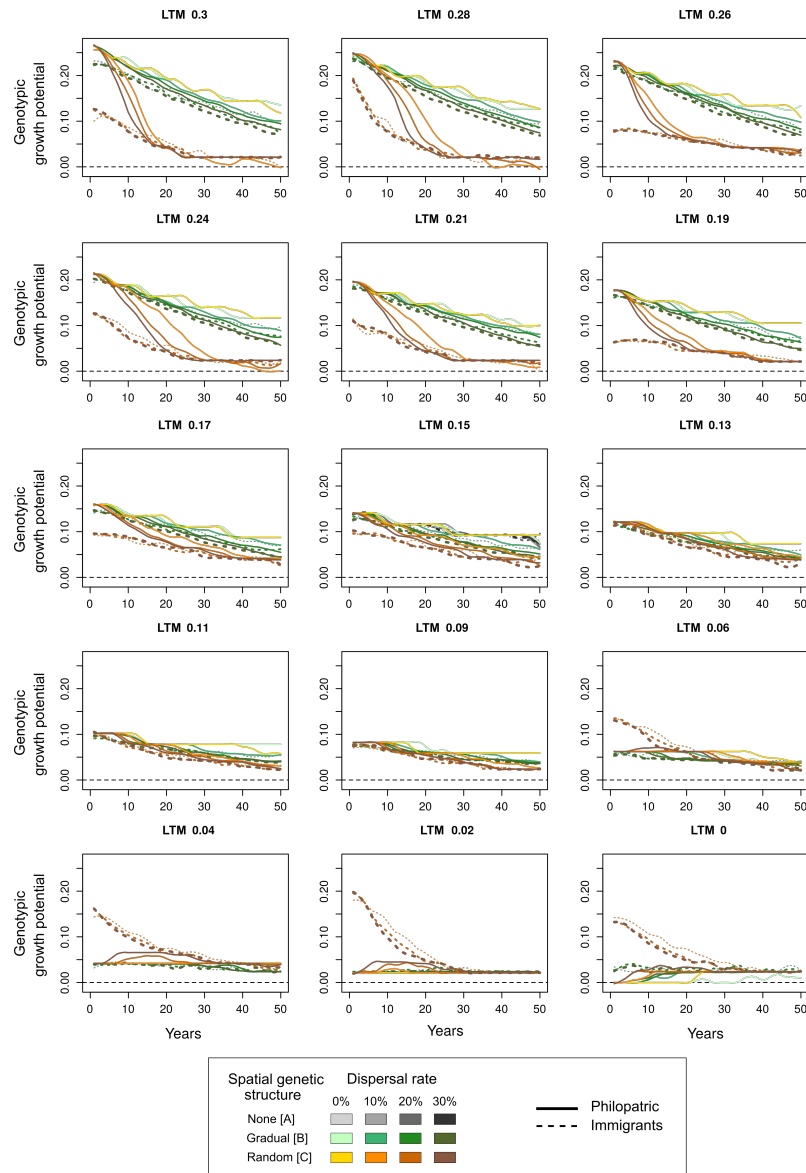


Figure 4.13: Temporal evolution of the genetic value of growth potential (log scale) of philopatric adults (full line) and immigrants (dotted line), averaged over simulation replicates, for each scenario of dispersal rate and spatial distribution of diversity (none [A], gradual [B], random [C], see Fig. 4.2 of the main manuscript) in each of the 15 populations ordered by the initial LTM. The horizontal dashed black line represents the optimum value of growth potential. The thickness of the immigrants lines (color dotted lines) represents the averaged proportion of immigrants over time and simulation replicates.

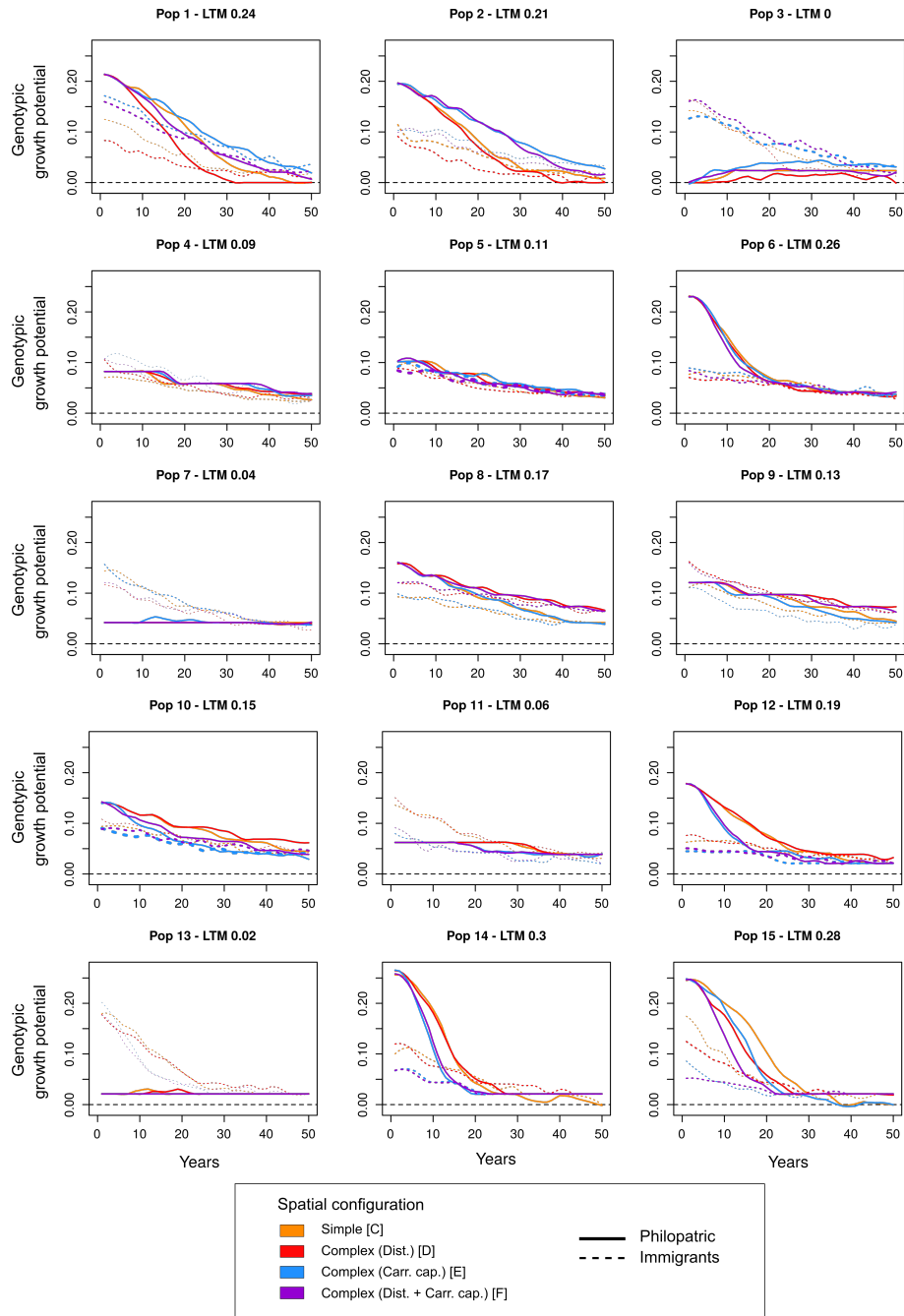


Figure 4.14: Temporal evolution of the genetic value of growth potential (log scale) of philopatric adults (full line) and immigrants (dotted line), averaged over simulation replicates, for each scenario of spatial configuration [C-F, see Fig. 4.2 of the main manuscript] under a random distribution of diversity and a dispersal rate of 10%, in each of the 15 populations. The horizontal dashed black line represents the optimum value of growth potential. The thickness of the immigrants lines (color dotted lines) represents the averaged proportion of immigrants over time and simulation replicates.

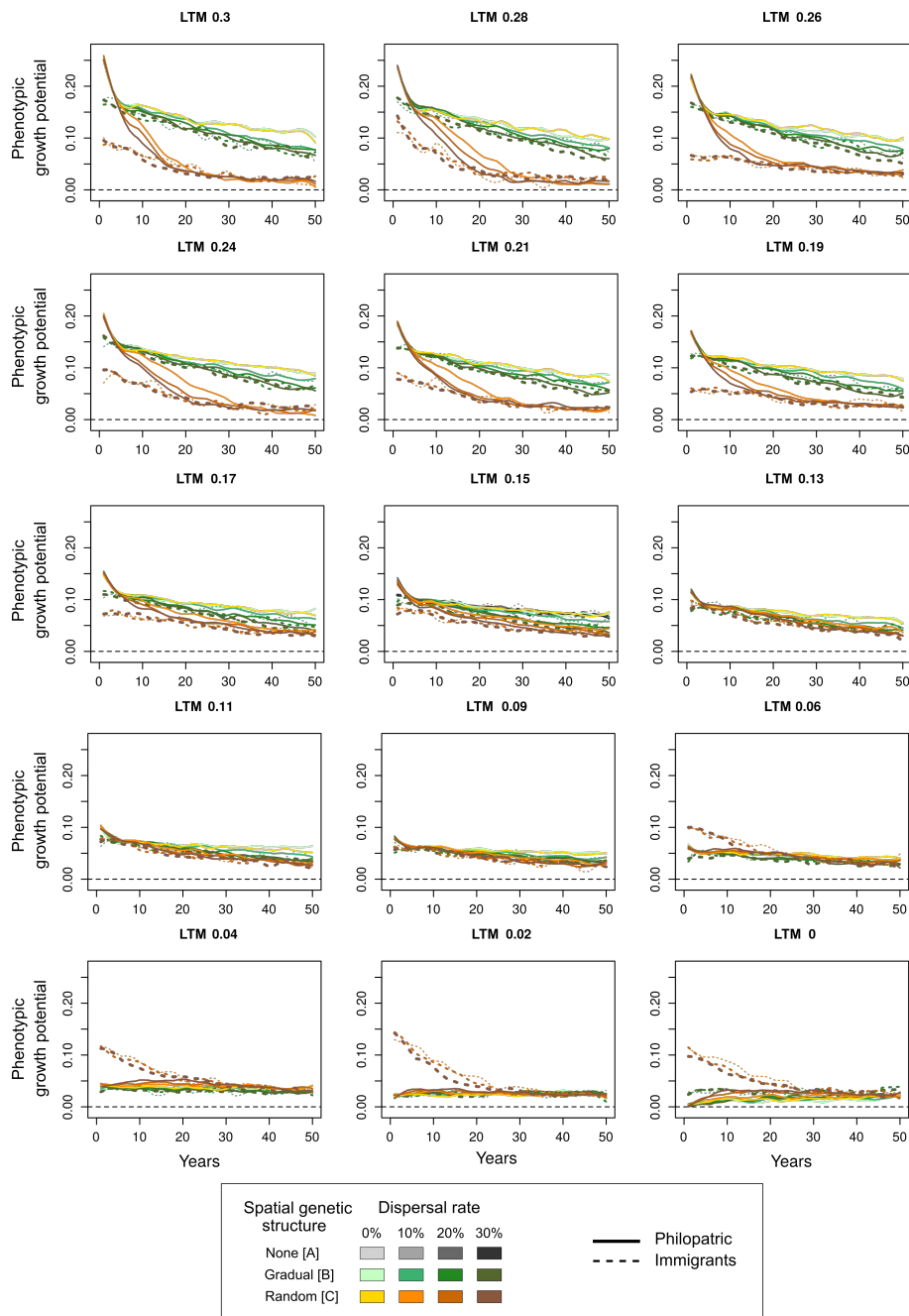


Figure 4.15: Temporal evolution of the phenotypic value of growth potential (log scale) of philopatric adults (full line) and immigrants (dotted line), averaged over simulation replicates, for each scenario of dispersal rate and spatial distribution of diversity (none [A], gradual [B], random [C], see Fig. 4.2 of the main manuscript) in each of the 15 populations ordered by the initial LTM. The horizontal dashed black line represents the optimum value of growth potential. The thickness of the immigrants lines (color dotted lines) represents the averaged proportion of immigrants over time and simulation replicates.

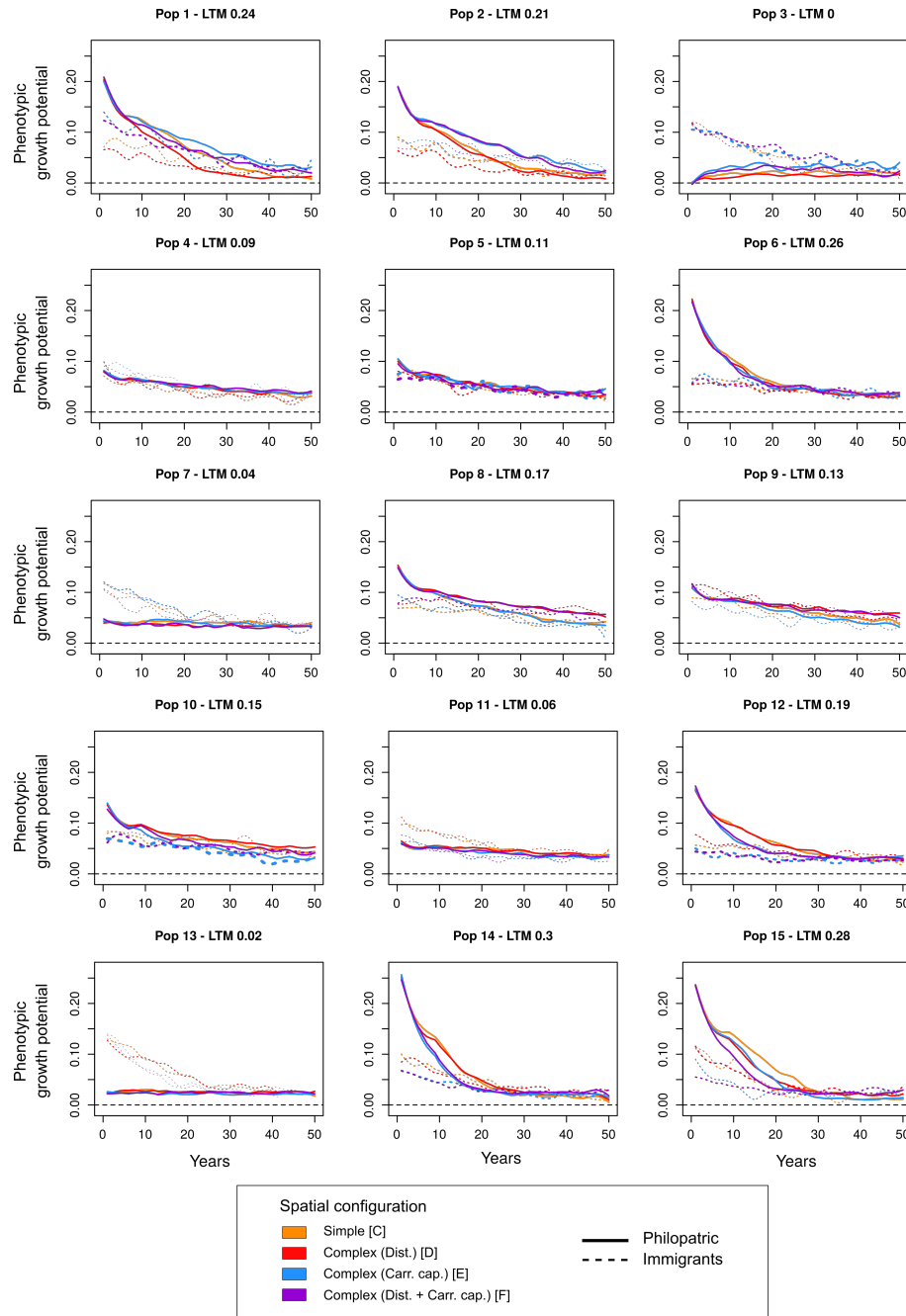


Figure 4.16: Temporal evolution of the phenotypic value of growth potential (log scale) of philopatric adults (full line) and immigrants (dotted line), averaged over simulation replicates, for each scenario of spatial configuration [C-F, see Fig. 4.2 of the main manuscript] under a random distribution of diversity and a dispersal rate of 10%, in each of the 15 populations. The horizontal dashed black line represents the optimum value of growth potential. The thickness of the immigrants lines (color dotted lines) represents the averaged proportion of immigrants over time and simulation replicates.

4.5.4 Relationships between local and metapopulation trait mismatch, and between evolutionary rate and the proportion of immigrants

To reveal the influence of immigrants to the local population dynamic, we measured the distribution of genetic traits of incoming immigrants in each of the local populations over time, i.e., the metapopulation trait mismatch (adapted at the individual level from [McManus et al., 2021b](#), Equation 4.3), as well as the proportion of immigrants (Equation 4.4), representing the qualitative (genetic characteristics of immigrants) and quantitative contribution of immigrants to the recipient population, respectively.

$$\text{MetapopulationTraitMismatch}_{i,t} = |\delta_i - X_{imm}_{i,t}| \quad (4.3)$$

$$\text{ProportionImmigrants}_{i,t} = \frac{N_{im}_{i,t}}{N_{i,t}} \quad (4.4)$$

Where δ_i is the optimal genetic trait value of the recipient population i , $X_{imm}_{i,t}$ is the median of the genetic trait of all immigrants to the recipient population i at time t , $N_{im}_{i,t}$ is the number of immigrants and $N_{i,t}$ the population size of the recipient population i at time t .

We showed a strong positive relationship between the local trait mismatch of populations and the metapopulation trait mismatch, i.e., the distribution of immigrants trait relative to the optimum (Fig. 4.17 A). The closer are the immigrants' traits to the optimum (i.e., low metapopulation trait mismatch), the more the population is locally adapted at the end of the simulation (i.e., low local trait mismatch).

We found a slight positive relationship between the evolutionary rate of populations and the proportion of immigrants when dispersal is combined with genetic diversity (no relationship in the scenario without diversity, Fig. 4.17 B). The relationship was stronger for the scenarios of complex spatial configuration including variation in carrying capacities of populations (scenarios E and F, see Fig. 4.2 of the main manuscript), leading to a higher range of proportion of immigrants. Overall, the more the immigrants contributed to the population, the faster the population evolved.

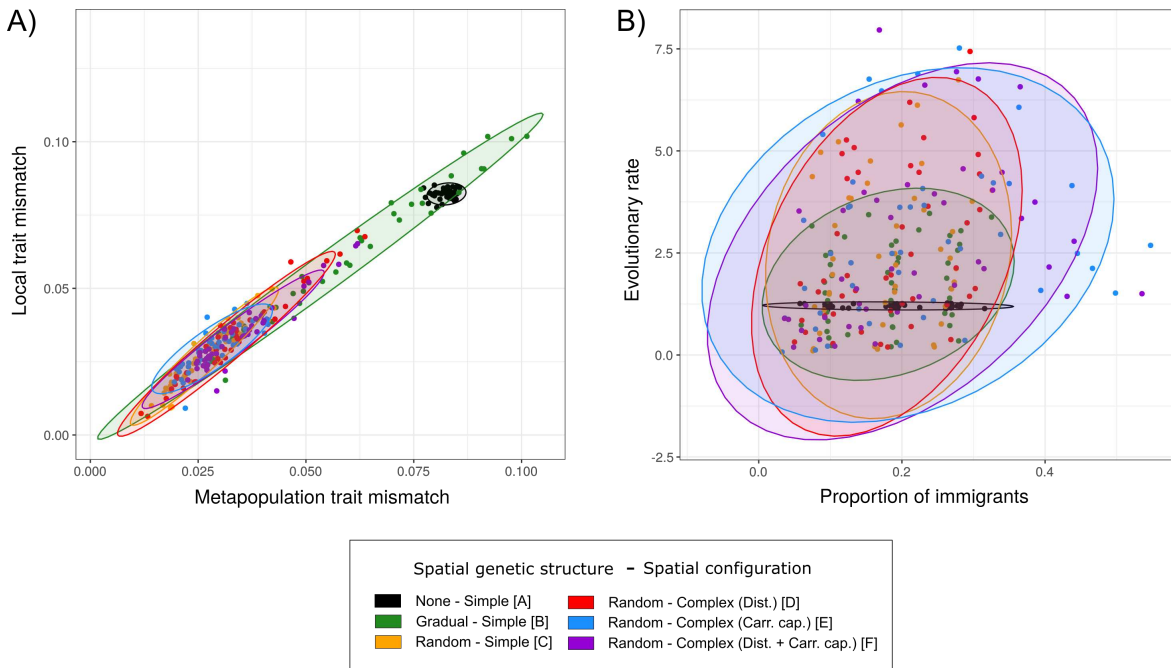


Figure 4.17: Relationship A) between the local trait mismatch and the metapopulation trait mismatch of populations (averaged over the last 5 years), and B) between the evolutionary rate of populations and the proportion of immigrants (averaged over the 50 years), for each scenario of spatial genetic structure and spatial configuration. Each point of a specific color is a population for a dispersal rate.

4.5.5 Local trait mismatch, evolutionary rate and demography according to spatial configuration

At the network scale, for a random genetic structure, the various spatial configurations of populations showed minor differences in the averaged local population trait mismatch and evolutionary rates (Fig. 4.18 A and B). A slight trend, consistent across dispersal rates, depicted lower evolutionary rates with distance variations and higher evolutionary rates with variation of carrying capacity compared to the simple spatial configuration (Fig. 4.18 B). These slight patterns may not be generalized because they strongly depend on the particular spatial configuration and genetic structure tested in this study (e.g., one large population which is adapted tend to increase the evolutionary rates of several populations). Spatial configuration also slightly affected metapopulation demography. Variation in distance and carrying capacities decreased metapopulation size and increased metapopulation CV, while the combination of the two did not affect metapopulation demography (Fig. 4.18 C and D).

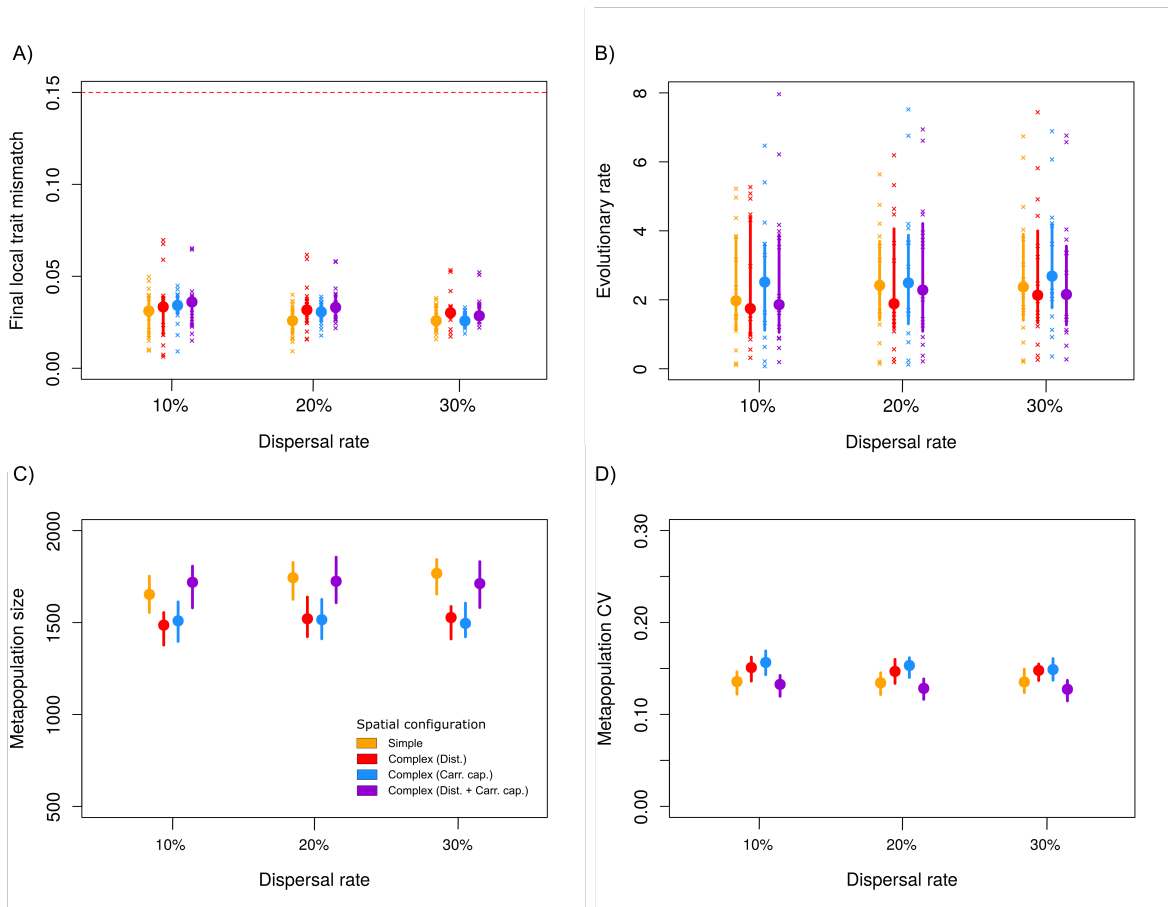


Figure 4.18: Above, distributions (median, quantiles 50%) of A) the final local trait mismatch (averaged over the last 5 years) and B) the evolutionary rates of the 15 local populations (represented by the crosses). The dashed red line represents the initial local trait mismatch averaged over populations. Below, distributions (median, quantiles 50%) over simulation replicates of C) the metapopulation size (number of returning adults averaged over the last 5 years) and D) the coefficient of variation of metapopulation abundance (calculated over the 50 years). Distributions are represented for each scenario of dispersal rate and spatial configuration under a random genetic structure.

4.5.6 Demography of local populations

We monitored the temporal demography of local populations via the number of returning adults in each population for the scenarios of spatial genetic structure (Fig. 4.19). Results showed the rapid negative demographic effect of maladaptation in the scenario A (without genetic diversity, see population with initial LTM of 0.15), which is not compensated by increasing dispersal rates. In the scenario B (gradual

genetic structure), the populations starting simulations with high mean value of LTM showed demographic effects of maladaptation, which were slightly compensated by increasing dispersal rates, whereas the populations starting simulations with a weak LTM did not show any demographic change (except the last one with a range margin effect for high dispersal rates). The scenario of random genetic structure (C) showed contrasted demographic effects depending on populations. The negative effect of maladaptation was strongly counteracted over time with dispersal in the populations starting with high LTM, whereas populations starting with low LTM showed slight effect of maladaptation with dispersal.

We also monitored the temporal demography of local populations for the scenarios of spatial configuration (Fig. 4.20). Results also showed the demographic effects of adaptation / maladaptation patterns that were modulated by variations of distance or/and changes of carrying capacities of populations compared to the simple spatial configuration (Fig. 4.20).

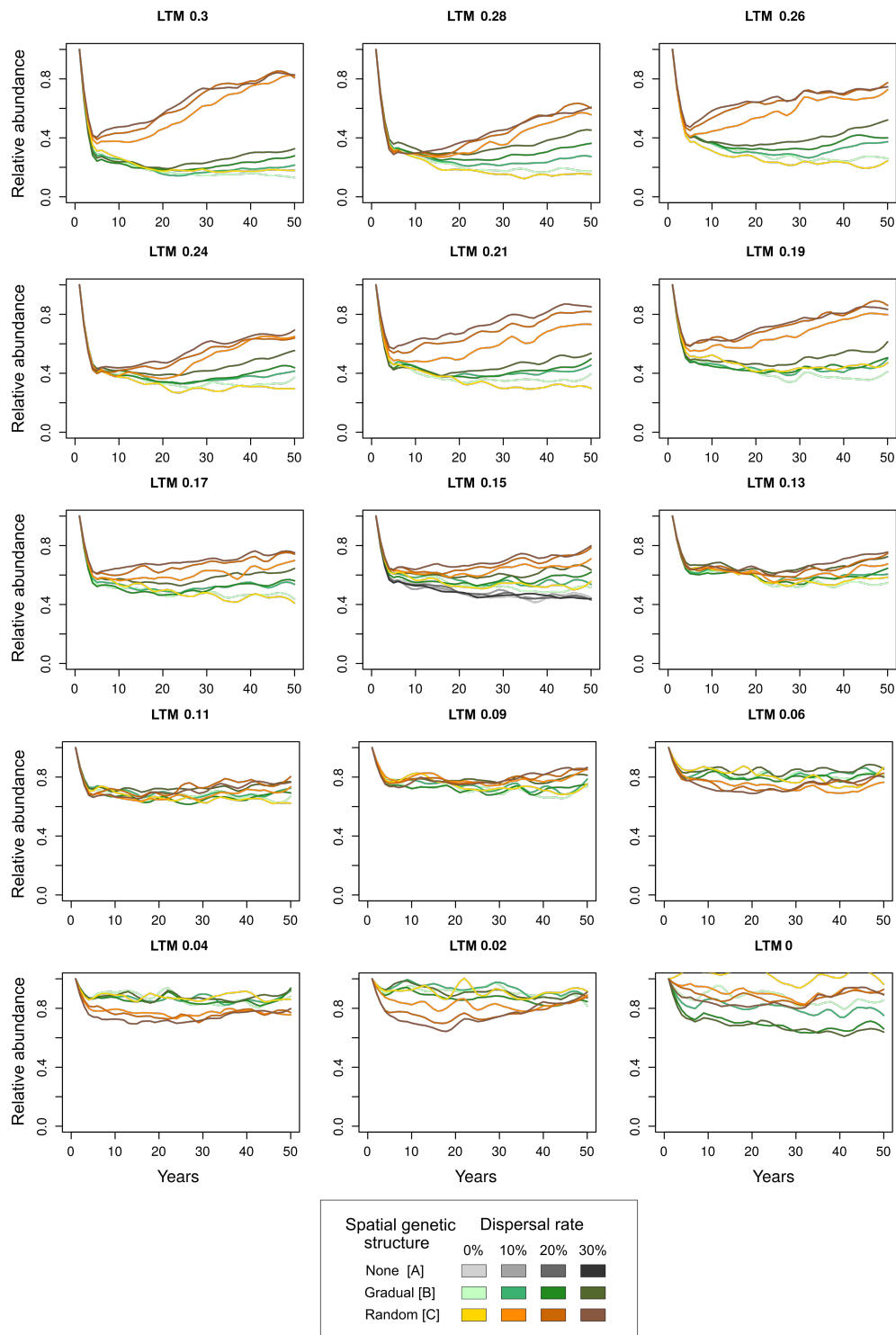


Figure 4.19: Temporal evolution of the number of returning adults (including immigrants) relative to the first year, averaged over simulation replicates, for each scenario of dispersal rate and spatial genetic structure (none [A], gradual [B], random [C], see Fig. 4.2 of the main manuscript) in each of the 15 populations ordered by initial LTM.

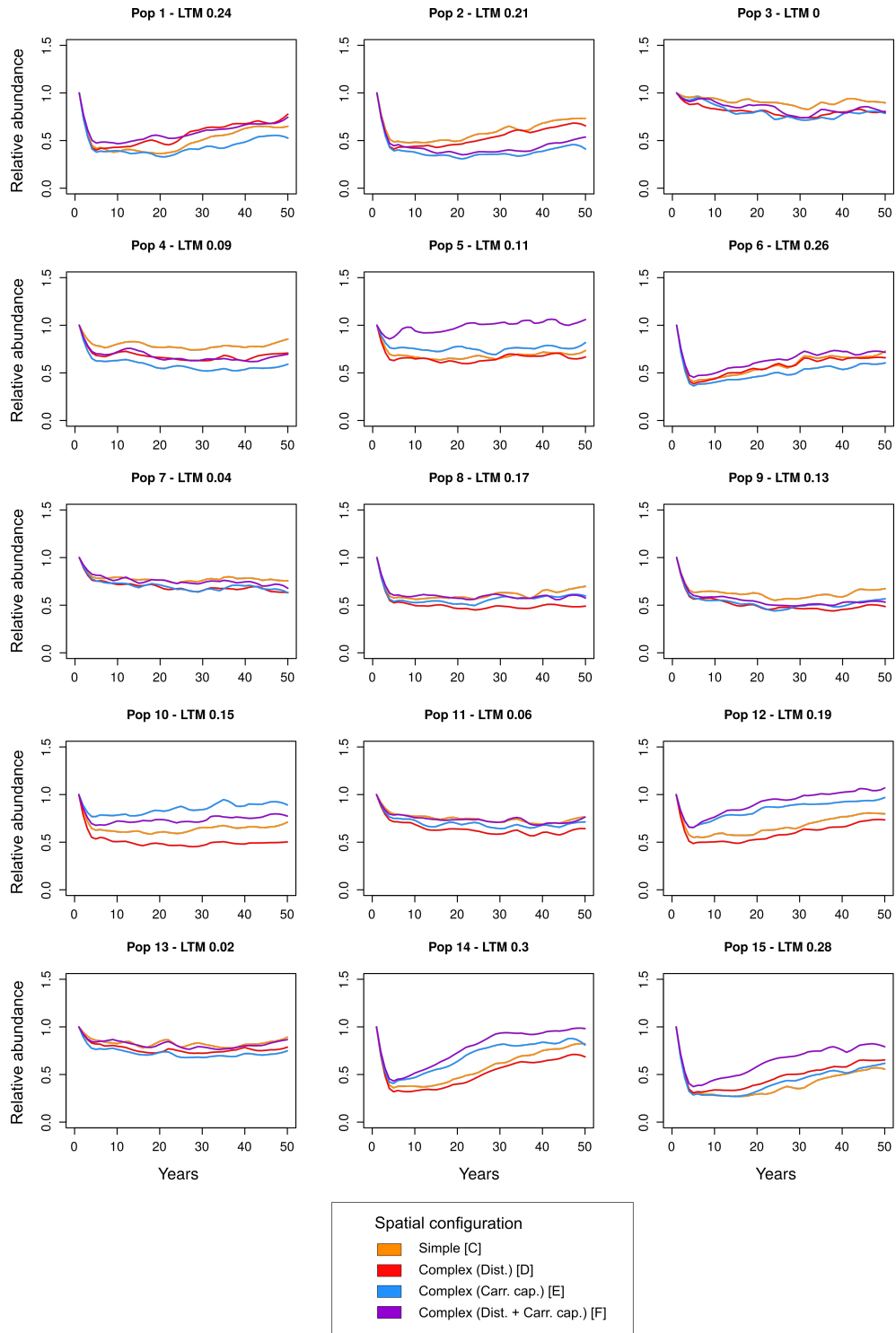


Figure 4.20: Temporal evolution of the number of returning adults (including immigrants) relative to the first year, averaged over simulation replicates, for each scenario of dispersal rate and spatial configuration [C-F, see Fig. 4.2 of the main manuscript], in each of the 15 populations.

4.5.7 Diversity of immigrants composition

The diversity of immigrants genetic traits incoming to local populations was monitored over time for each scenario and averaged over populations. The CV of immigrants composition was higher for the scenarios of among populations diversity compared to the scenario without diversity (Fig. 4.21 A). It linearly increased with time and dispersal rates for the gradual genetic structure, while it was very high at the beginning of simulations and then linearly decreased over time and with increasing dispersal rates with a random genetic structure (Fig. 4.21 A). For a dispersal rate of 20% and a random genetic structure, immigrants composition was on average lower when spatial configuration was complex, especially for variations in carrying capacities and after 20-30 years of simulations. At the end of simulations, differences were dampened (Fig. 4.21 B).

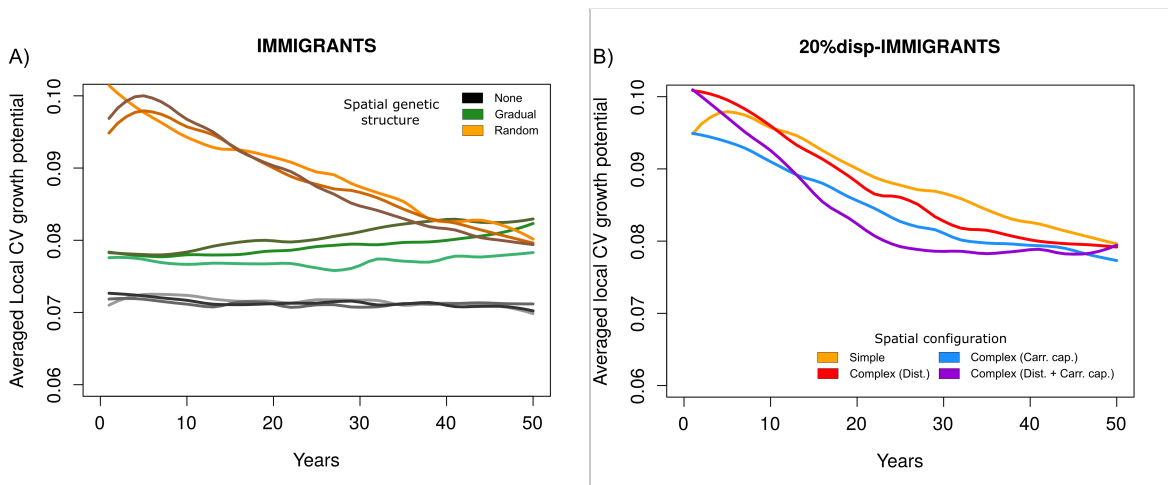


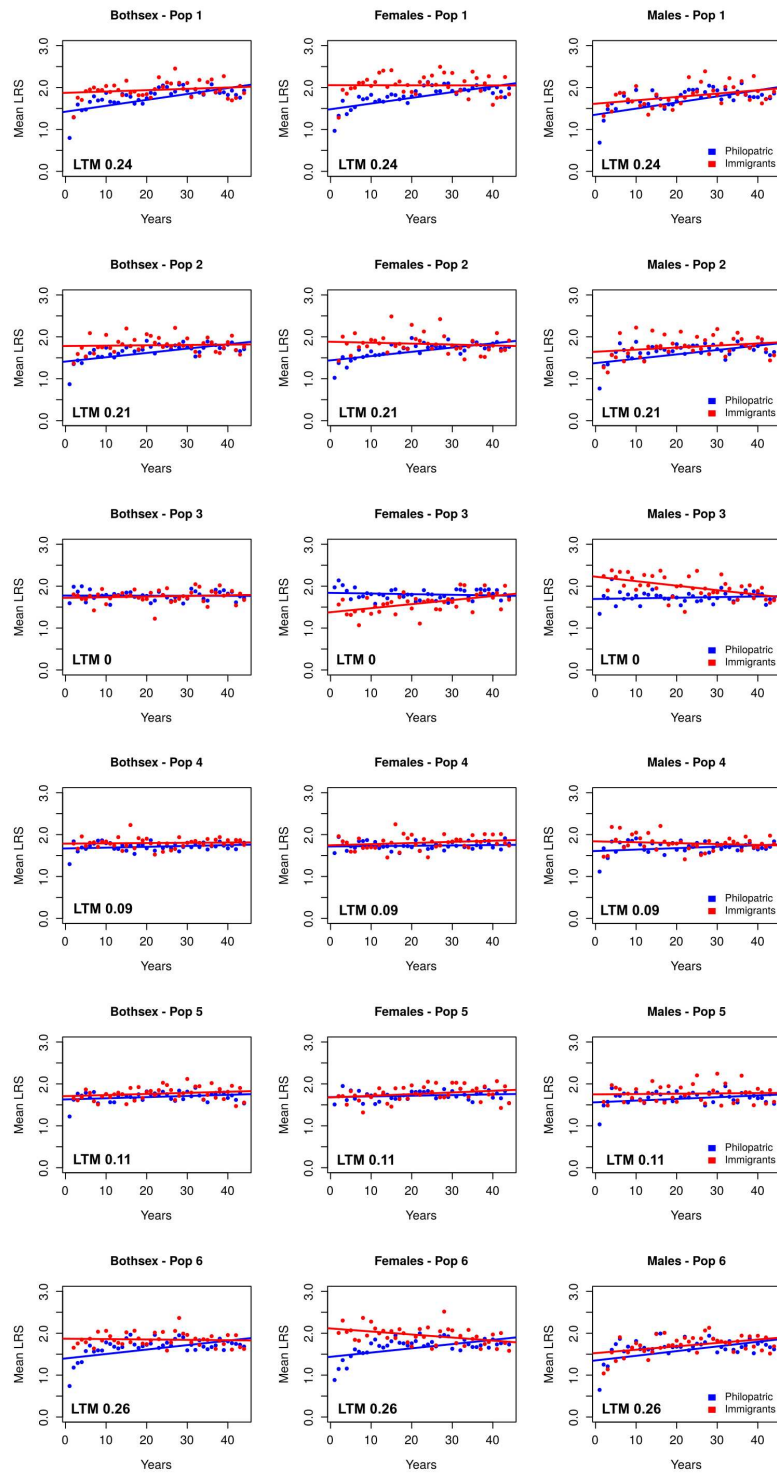
Figure 4.21: Temporal evolution of the coefficient of variation of growth potential (in natural scale) among immigrants, averaged over the 15 recipient populations, A) for each scenario of dispersal rate and spatial genetic structure under a simple spatial configuration, and B) for each scenario of spatial configuration under a random genetic structure and a dispersal rate of 20%.

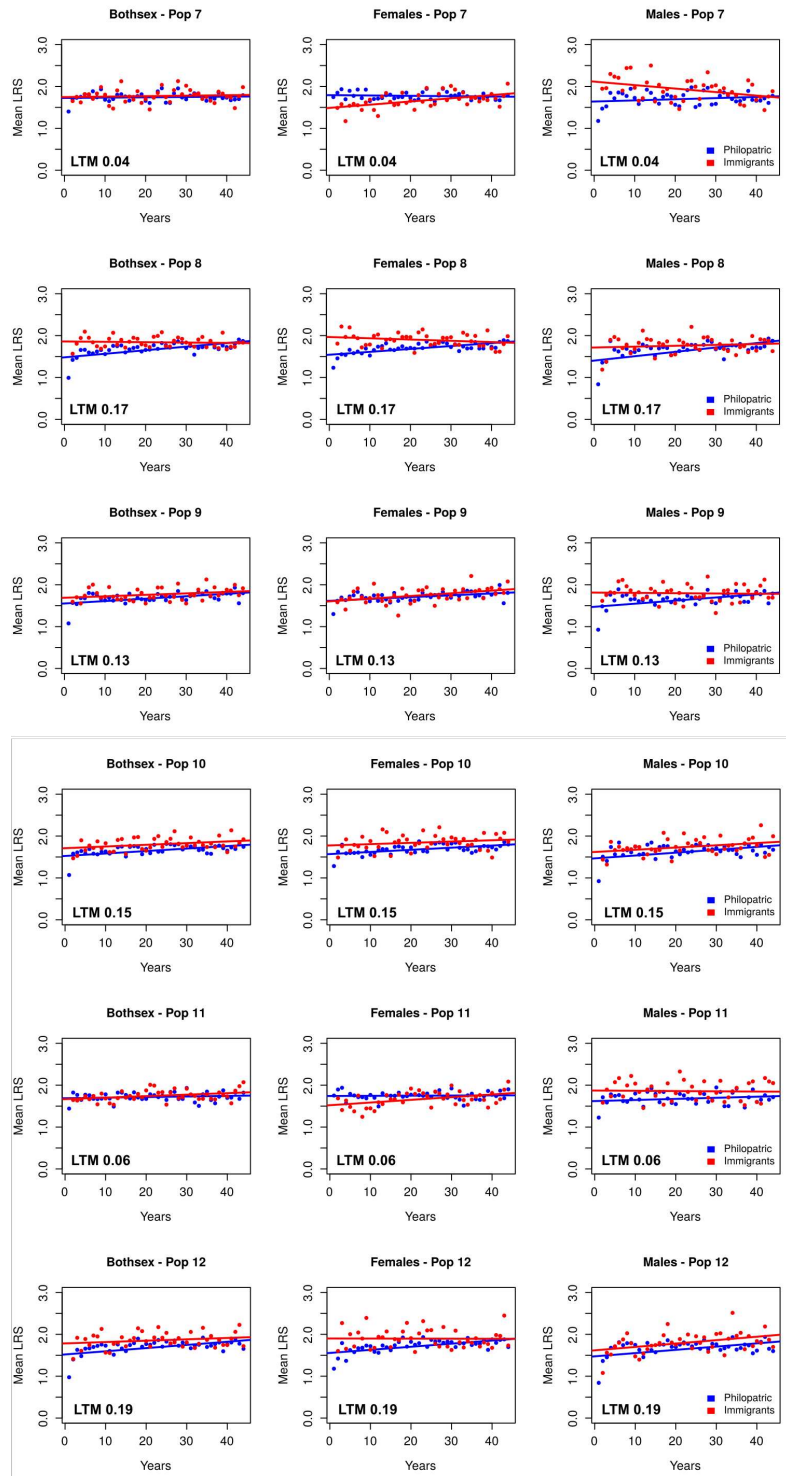
4.5.8 Reproductive success

To explore potential differences in the reproductive success of immigrants vs philopatric individuals, we computed the Lifetime Reproductive Success (LRS) as the number of returning adult per returning adult for each sex and both sex together. We compared

the temporal evolution of the average LRS over individuals and simulations between philopatric and immigrants for a dispersal rate of 10% in the scenario of random distribution of diversity, which was the most contrasted in terms of differences between the traits of philopatric individuals and immigrants.

Results (Fig. 4.22) showed contrasted patterns across populations and between sex. Indeed, for populations starting simulations with a high LTM, the LRS of incoming immigrants was higher than philopatric individuals at the beginning of simulations, regardless the sex. Then, while these populations evolve towards the optimum, the LRS of philopatric individuals increased and was similar to that of immigrants at the end of simulations. Conversely, for populations starting simulations with a low LTM, the LRS of females immigrants was lower than philopatric females, while the males immigrants showed higher LRS than philopatric males at the beginning of simulations. These differences between sex is likely due to the high size-dependent sexual selection on males. For populations starting simulations with a medium LTM, the LRS of immigrants and philopatric individuals was similar for both sex.





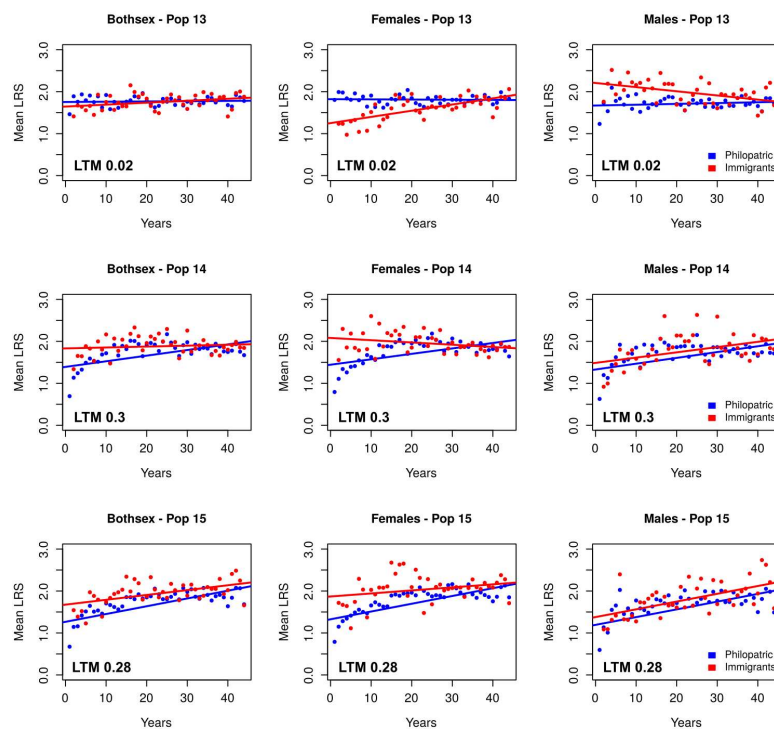


Figure 4.22: Temporal evolution of the average Lifetime Reproductive Success (LRS) of philopatric individuals (in blue) and immigrants (in red), averaged over simulation replicates, for each population, by sex or with the sexes combined, for a dispersal rate of 10% and a random spatial distribution of diversity (scenario C).

4.6 CHAPTER HIGHLIGHTS

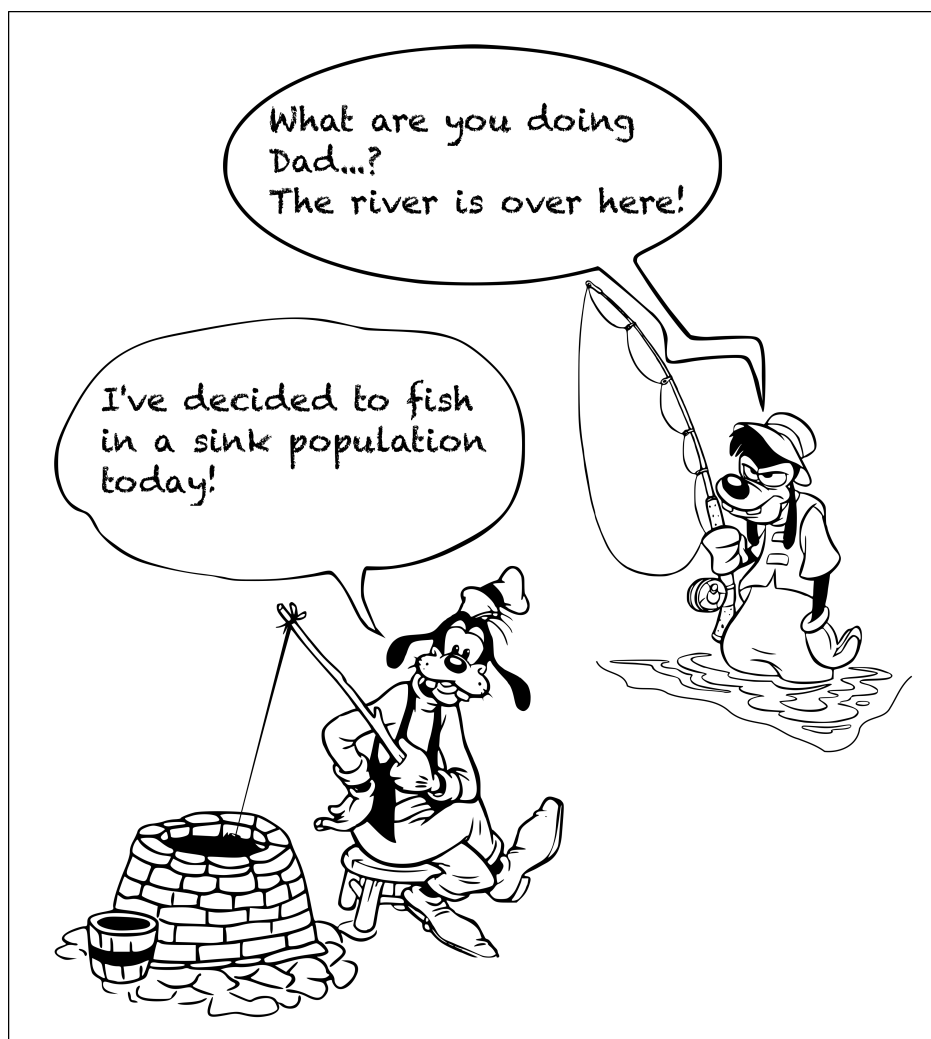
In this chapter, I hope to have clearly illustrated the importance of considering the diversity among populations (additionally to the within-population diversity) and their spatial configuration to better appreciate metapopulation and local populations eco-evolutionary dynamics. The main lessons of this chapter are the following:

Chapter 4 highlights

- In a context without divergent selection, dispersal, combined with genetic diversity among populations, can foster adaptation of local populations after perturbations. This is particularly true with increasing dispersal rates and a random spatial genetic structure;
- The spatial configuration of populations (distance and carrying capacity) may also modulate the evolutionary trajectories of local populations, depending on the properties of the recipient population as well as the properties of surrounding populations;
- Immigration may provide an “opportunity for adaptation” for local populations, which supports the concept of adaptation networks;
- Results suggest that management of local populations would benefit from a consideration of the spatial structure and features of surrounding populations that are connected by dispersal, and provide support for a management of populations diversity according to the portfolio approach.

After having identified the importance of considering the spatial structure of populations, a future avenue of research building on our approach was to investigate how a network of populations would cope with selective exploitation and to determine if there are preferable management strategies for considering the spatial structure of populations.

Management strategies of exploited Atlantic salmon metapopulation



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In the light of Chapter 3 and 4 conclusions, which showed the importance of considering dispersal patterns and network spatial structure to better appreciate eco-evolutionary dynamics of populations, we then investigated the implications of these findings for the management of exploited populations of Atlantic salmon. Indeed, conservation or exploitation strategies could interfere with metapopulation functioning if ignored. For instance, exploitation of a productive population could also affect neighbouring populations highly supported by immigration, or focusing conservation actions on the genetic diversity of a focal population without considering the potential influence of immigration could also be misleading. Selective exploitation also induces evolutionary changes which could be variable within a metapopulation. Therefore, we explored in this chapter the demographic and evolutionary consequences of spatialized management strategies of exploited Atlantic salmon, within a metapopulation context, by using MetaIBASAM. This chapter follows up on preliminary analyses carried out by an intern I supervised (Tewann Beauchard). The results presented in this chapter are still being analyzed and a publication is being prepared with the collaboration of Mathieu Buoro, Stephanie Carlson and Etienne Prévost.

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Management strategies of exploited Atlantic salmon metapopulation

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Abstract

While the eco-evolutionary consequences of dispersal and exploitation are increasingly recognized, consideration of these effects - potentially in interaction - for management and conservation is limited. Here, we evaluated population exploitation in a metapopulation perspective, by using the case of Atlantic salmon which is still managed at the local population scale while dispersal has been demonstrated. Specifically, we compared a management strategy that was not spatialized with other that accounted for the asymmetry of dispersal patterns (i.e., focusing on sink or source populations), in order to meet both conservation and exploitation objectives. We used a demo-genetic agent-based model to examine both demographic and evolutionary consequences of these strategies for various dispersal rates and a gradient of local exploitation rates. We showed differences in the consequences of spatialized management strategies and a benefit of protecting source populations from exploitation for a certain range of exploitation rates and dispersal rates, in terms of abundance but not in terms of stability. Simulations also showed contrasted eco-evolutionary consequences between management strategies, indicating that interactive effect of plastic, evolutionary responses and immigration dilution are difficult to disentangle. Overall, our results show that without knowledge on metapopulation functioning, the safest strategy remains to spread the exploitation effort over all populations.

Keywords: management strategies, eco-evolutionary consequences, exploitation, Atlantic salmon, dispersal

5.1 INTRODUCTION

In the context of global change, there is a growing tension between exploitation and conservation of natural resources. Indeed, the recent global decline in biodiversity has led management authorities and researchers to revisit how they manage threatened species and how they exploit others, and this is particularly critical in a context of accelerating climate change. A general consensus is to better acknowledge and consider the ecology of species as part of management decisions, as well as ecosystems functioning and the relationships between harvested resources and harvesters in the case of exploited species. Although there is a growing recognition of these essential elements, major common challenges remain - how to conserve?, how to manage?, what to prioritize?, what are the best strategies? (what?, where?, when?, e.g., [McDonald-Madden et al., 2011](#)). But answers to these questions might depend on the local context and the objectives to be reached, such maintaining abundance, stability, or productivity.

However, general guidelines emerge from the literature. Among them, several studies argue that we need to better consider the ecological features of the studied system to determine the appropriate scale of management. For instance, [Moore \(2015\)](#) discussed the implications of river networks connectivity for the management of watersheds, considering water, sediments and animals all together. Importantly, he stressed the need to align the scale of management with the scale of the river system, since upstream activities can affect downstream parts (e.g., chemical contamination) and vice versa (e.g., dams affecting upriver migration) through the bidirectional connectivity of rivers. Another typical example is the effectiveness of Marine Protected Areas (MPAs) on coral reefs conservation around the globe (see [Mora et al., 2006](#) for review). Although MPAs prevent marine organisms from being harvested in a specific area, individual movements outside this area may limit the effectiveness of this conservation action.

Indeed, dispersal is a ubiquitous trait in organisms and a major eco-evolutionary process which may extend and obscure the scale of management to be considered. Because of the movements of individuals between spatially structured populations, metapopulation functioning raises questions about management strategies and several ideas have been discussed in the literature ([Akçakaya et al., 2007](#)). First, managing at population scale might be misleading, because the abundance of a patch does not always capture its productivity. In a source-sink metapopulation, a management action on a local patch could be perceived as successful when the observed demographic

changes could be solely due to increased immigration, or conversely, could be perceived as detrimental when the changes are due to increased emigration. [Cooper and Mangel \(1999\)](#) illustrated this "danger of ignoring metapopulation structure for conservation" with the example of salmonids but it can apply to any species with a metapopulation functioning. Moreover, an often overlooked aspect is that a local management action (e.g., restocking, habitat restoration) may not only impact the local population, but also other populations that are interconnected through dispersal. Thus, focusing at a larger scale than local population is highly recommended when dispersal occurs within a system of populations. However, some studies also shed light on the risk of focusing on a too large scale of management. This is especially the case of mixed stocked fisheries, where harvesting of a set of populations as a whole large stock have been shown to lead to overexploitation and risk of collapse of sub-populations of various species (cod, [Hutchinson, 2008](#); herring, [Okamoto et al., 2020](#); [Stier et al., 2020](#); sockeye salmon, [Moore et al., 2021](#); croaker, [Ying et al., 2011](#)).

Thus, sustainable management of metapopulations requires a larger view than population scale but still acknowledging and considering the specificities and drivers of local populations dynamics, although it might strongly depend on the demographic and genetic connectivity of the network ([Hawkins et al., 2016](#)). This comprehensive view requires a good knowledge of local and regional ecological processes governing populations dynamics such as dispersal patterns. However, others have also already pointed out that "developing harvest strategies for spatially complex fish populations remains a major challenge" ([Benson et al., 2015](#)). It is still not intuitive to know what is the best strategy to adopt within a set of interconnected populations, what populations to prioritize when there is resource limitation or conflicting objectives between conservation and yield (in the case of harvested species). Some studies advocate for the protection of certain populations over others based on various criteria such as population size ([Okamoto et al., 2020](#)), whether they are source or sink ([Crowder et al., 2000](#); [Tufto and Hindar, 2003](#); [Fullerton et al., 2016](#)), their influence on spatial synchrony ([Engen et al., 2018](#)), or a set of connectivity metrics ([Kininmonth et al., 2019](#)). As discussed by [Bradford and Braun \(2021\)](#), protecting some populations over others, such as the productive source ones, might improve the demographic resilience of the metapopulation in the short term. But in the longer term, it could be relevant to maintain a diversity of habitats, of populations genetics and dynamics, because this biocomplexity provides resilience of metapopulations to environmental changes ([Anderson et al., 2015](#); [Walsworth et al., 2019](#); [Moore and Schindler, 2022](#)). It could also provide stability of yields in the case of exploited species ([Hilborn et al.,](#)

2003; Schindler et al., 2010; Freshwater et al., 2019; Connors et al., 2022). Thus, managing a diversity of populations also appears crucial to improve metapopulation stability and resilience.

However, consequences of actions on metapopulations are not only at demographic level but can also induce changes at phenotypic and genotypic levels. Selective exploitation, by focusing the harvesting effort on certain populations and/or phenotypes, might lead to evolutionary changes (Allendorf and Hard, 2009) and reduce genetic diversity, in addition to other indirect effects such as decreasing prey biomass (Czorlich et al., 2022). A large body of literature documented this effect in the field of fisheries, called "fisheries-induced evolution" (Kuparinen and Merilä, 2007; Heino et al., 2015). But less attention has been devoted to this effect from a metapopulation perspective. We showcased in chapter 4 that evolutionary trajectories of populations can be largely driven by the spatial structure and connectivity of a network when dispersal occurs. Thus, based on this evolutionary effect of exploitation, in addition to demographic effects (e.g., density dependence), one can assume that the spatial structure of exploitation may influence the evolutionary dynamics of exploited and interconnected populations. However, it seems unclear if the best management strategy would be to spread conservation effort over populations or to focus exploitation on some and preserve others from this selective pressure to dampen the evolutionary effect through connectivity and rescue effects (Carlson et al., 2014). We thus build on many studies already emphasizing the need to not consider local populations as isolated systems but in the system which creates them, but intend to fill the gap where both demographic and evolutionary consequences of management strategies of exploited populations are rarely considered at the metapopulation scale.

In this study, we aim at investigating the demographic and evolutionary consequences of alternative management strategies within a source-sink metapopulation by using the case of exploited Atlantic salmon (*Salmo salar*) populations. Indeed, Atlantic salmon is an emblematic species, exploited for a long time (ICES, 2021), and for which dispersal is still overlooked regarding its management and exploitation (ICES, 2021) despite several warnings provided by various studies on salmonids (Cooper and Mangel, 1999; Schtickzelle and Quinn, 2007; Bradford and Braun, 2021). In particular, we explore spatialized management strategies based on whether populations were source, sinks or neutral, for various dispersal rates and local exploitation rates, by using a demo-genetic agent-based model (MetaIBASAM, chapter 3). We examine the demographic and evolutionary consequences of these strategies and attempted to identify if one of them better meet both conservation

and exploitation goals. We expect that contrasted demographic patterns would emerge depending on populations exploitation, especially because source populations would be crucial for sink persistence, but also that various evolutionary consequences would result from selective exploitation. Finally, we hypothesize that consequences of exploitation will depend on dispersal intensity.

5.2 METHODS

5.2.1 A spatially realistic demo-genetic agent-based model

Exploring the eco-evolutionary consequences of selective exploitation and management measures in a metapopulation framework is difficult or impossible in the wild. However, simulation models are relevant tools in the decision-making process, because they allow to assess and compare the performance of alternative management actions before their implementation on real populations. However, different modeling approaches can be used, showing both benefits and limits depending on the management objectives. [Pelletier and Mahévas \(2005\)](#) reviewed models that have been developed to investigate the consequences of various management actions on fisheries. Most of them are simulation models, spatially explicit (which is needed for spatial fisheries), but do not consider demographic processes (usually metapopulation models with patch occupancy) or simplified version of it. Individual based modeling approaches allow to simulate explicitly individual movements in the landscape and the emergence of population dynamics, providing support for management of commercial fisheries of sea bass for example ([Walker et al., 2020](#)). However, spatially explicit models rarely consider genetics ([Zurell et al., 2022](#)). Yet, it is increasingly obvious that management strategies should be designed taking genetics and evolutionary processes into account ([Hoffmann et al., 2015](#); [Mijangos et al., 2015](#)). Promising modeling approaches, such as demo-genetic agent based models (DG-ABMs), provide a framework to study management strategies in a metapopulation context by integrating eco-evolutionary feedback, although their development remains challenging. Such models have been used to investigate consequences of exploitation but only at population scale (e.g., [Thériault et al., 2008](#); [Marty et al., 2015](#); [Ayllón et al., 2019a](#)).

We used a simulation model, initially developed by [Piou and Prévost \(2012\)](#) to assess the effect of environmental change and selective fisheries on the demography and life history traits of a single population of Atlantic salmon (IBASAM, [Piou and Prévost, 2013](#); [Piou et al., 2015](#)). It was further extended in chapter 3 to

explore eco-evolutionary dynamics of this species in a metapopulation framework (MetaIBASAM). The model is demogenetic (i.e., incorporating both demographic and genetic processes, as well as their feedback), agent-based (i.e., representing each individual, its features, and potential interactions with others), and spatially realistic (i.e., considering populations spatial configuration and heterogeneity). It simulates the eco-evolutionary dynamics of 15 interconnected populations of Atlantic salmon, as described in chapter 3. We hereafter provide a brief overview of the model structure but additional details are available in the previously cited papers and chapters.

For each population of the network, the life cycle of individuals is explicitly simulated and individuals features (e.g., sex, age, size) are monitored. The Atlantic salmon is an anadromous species with a great diversity of life history strategies (Erkinaro et al., 2019). Reproduction and juvenile (called "young of the year", hereafter YOY) growth occur in rivers, where two alternative strategies are adopted by juveniles: maturing in freshwater (precocious maturation allowing juveniles to reproduce the next spawning season), or migrating to the sea (as smolts, then becoming anadromous). While in the sea, individuals grow and may mature after only one year at sea ("one sea-winter" or 1SW) or more ("multiple sea-winter" or MSW) before returning to rivers. A high proportion of mature adults return to their river of birth (philopatry) but dispersal to non-natal rivers also occurs regularly (Jonsson et al., 2003; Consuegra et al., 2005). Atlantic salmon has been extensively harvested for a long time (ICES, 2021) by a diversity of fisheries (in rivers, sea, and estuaries) and is considered as a threatened species. Exploitation is currently reduced and mainly focusing on returning adults in rivers (ICES, 2021), but harvest rates are often estimated at the scale of local populations (e.g., Lebot et al., 2022), and the river is mainly defined as the management scale (ICES, 2021) despite the metapopulation structure of the species leading to harvest of mixed-stock.

In the model, density-dependent and independent processes (e.g., water temperature, water flow) can affect life history processes such as growth and survival, and a set of traits (growth potential, precocious and anadromous maturation thresholds) also include an underlying genetic basis, allowing eco-evolutionary feedbacks to emerge from the model. Local populations are connected by dispersal of individuals, which occurs during the spawning migration of adults from the sea to the rivers, i.e., before fishing. Dispersal patterns are defined via a fixed dispersal rate (i.e., emigration rate) and a dispersal kernel determining recipients populations considering their distance from the natal population, and their carrying capacity (i.e., attractivity). The model was parameterized in a pattern-oriented modeling framework

(Grimm et al., 2005) as in Piou and Prévost (2012) and chapter 3, and inspired by the spatial structure (i.e., distance and carrying capacities) of the salmon metapopulation of Brittany (France, Perrier et al., 2011; Bouchard et al., 2022).

5.2.2 Scenarios of local exploitation rate, management strategies, and dispersal rate

MetaIBASAM allows to include exploitation mortality (i.e., angling) on returning adults from the sea to the rivers (i.e., after immigration), through the removal of a proportion of individuals from the population according to a local exploitation rate. Exploitation can also be setup as selective regarding adults' features (e.g., age class, Piou et al., 2015), as different rates have been estimated between life history types (MSW and 1SW, 15% and 6% on average, respectively, on populations of Brittany, Lebot et al., 2022).

In this study we focused on the consequences of variable management strategies at the scale of the metapopulation and tested scenarios following a gradient of local exploitation rates from 0 to 50% (Table 5.1), independently from adult features (but still selective on adults vs juveniles). We crossed this gradient of local exploitation rates with three management strategies (Fig. 5.1) based on populations type (i.e., sink, neutral, source, based on the ratio of Immigrants/Emigrants defined in chapter 3). First, we simulated populations with an equal exploitation rate between populations (hereafter scenario "Exploitation"), as it is currently applied in management practices. We contrasted this scenario with two others protecting a specific type of population from exploitation: 1) protecting source populations (i.e., exploitation on sink and neutral, hereafter "Source conservation") and 2) protecting sink and neutral populations (i.e., exploitation on source populations only, hereafter "Source exploitation"). We ensured that each of these two scenarios leads to a 50% exploitation (or conservation) of the total metapopulation size.

Each of these combinations (exploitation rates x management strategies) were tested with dispersal rates of 15% and 30% (Table 5.1) to evaluate the consequences of the tested management strategies in a metapopulation structure with various dispersal intensity. We also compared these scenarios with a no-dispersal control scenario, i.e., independent populations as currently considered by managers, but varying exploitation rates to assess the risk of ignoring metapopulation functioning.

All cross-combinations of scenarios (73) were simulated with 50 replicates each. Simulations were initialized for each population by a random draw of individuals

Table 5.1: Scenarios design of dispersal rates, local exploitation rates, and management strategies.

Dispersal rate	Manag. strategy	Local exploitation rate										
		0	5%	10%	15%	20%	25%	30%	35%	40%	45%	50%
0%	Exploit.	-	-	-	-	-	-	-	-	-	-	-
	Exploit.	-	-	-	-	-	-	-	-	-	-	-
15%	Source conserv.		-	-	-	-	-	-	-	-	-	-
	Source exploit.		-	-	-	-	-	-	-	-	-	-
30%	Exploit.	-	-	-	-	-	-	-	-	-	-	-
	Source conserv.		-	-	-	-	-	-	-	-	-	-
	Source exploit.		-	-	-	-	-	-	-	-	-	-

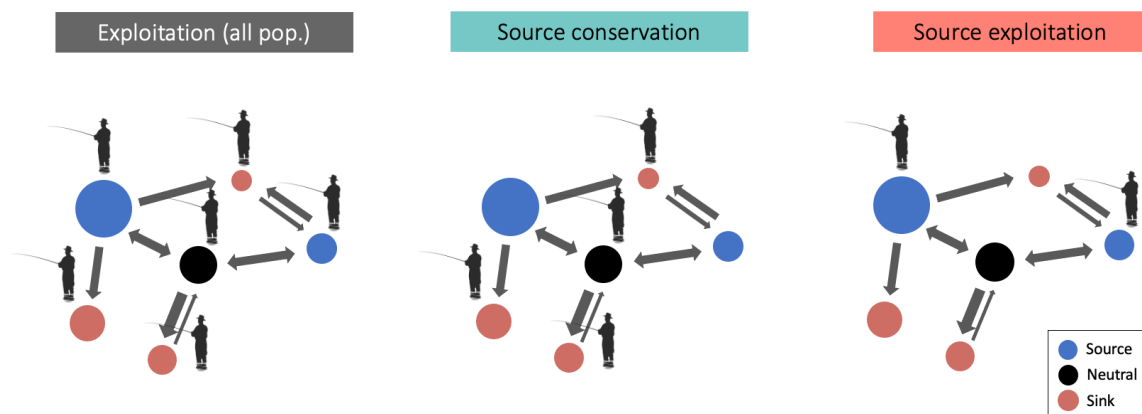


Figure 5.1: Schematic representation of the three management strategies tested in the study. A first non-spatialized strategy ("Exploitation"), is compared with two spatialized management strategies, "Source conservation" (exploitation of sink and neutral populations) and "Source exploitation" (conservation of sink and neutral populations).

(sampled in the same genetic and phenotypic distributions, see chapter 3), and for 25% of river's carrying capacity to limit computational time. A 10-year burn-in period without dispersal and without exploitation allowed populations stabilization. Thus, all other parameters than carrying capacity and distance were kept similar for all populations (e.g., environmental conditions, trait distributions at initialization, etc.)

for all scenarios. Then, we simulated populations by applying treatments (dispersal and fishing rates) over 40 years, which was sufficient time to detect any changes in the population dynamics and evolution of life-history traits (generation time of 2.5). All simulations and analysis were performed using R version 3.6.3 and the package `metaIbasam` version 0.0.6 (<https://github.com/Ibasam/MetaIBASAM>). Code and R scripts are available at <https://github.com/Ibasam/FishStrat>.

5.2.3 Simulations outcomes analysis

Regarding the double objective of conservation and exploitation, we evaluated the consequences of our spatialized management strategies at several levels, both in terms of abundance, stability, life history traits distribution, and yield. Also, to be able to compare the scenarios between them (i.e., same exploitation effort), the exploitation rate was measured at the scale of the metapopulation (hereafter metapopulation exploitation rate, or *MER*), which was computed *a posteriori* for each scenario by averaging over the last 5 years and over all simulations using (Equation 5.1):

$$MER_y = \frac{\sum_{i=1}^{n_{pop}} N_{pop_{i,y}} \times LocalExpRate_{i,y}}{\sum_{i=1}^{n_{pop}} N_{pop_{i,y}}} \quad (5.1)$$

Where y is the year, n_{pop} the number of populations, $N_{pop_{i,y}}$ the number of returns before fisheries for the population i at year y , and $LocalExpRate_{i,y}$ the local exploitation rate defined according to the scenario for the population i at year y .

Thus, each variable was evaluated at metapopulation scale, averaged over simulations, and function of the metapopulation exploitation rate, the management strategy and the dispersal rate simulated. To analyze the demographic dynamics, we examined the Pre-Fishery Abundance (hereafter *PFA*) as the sum of returning adults over populations the last 5 years, metapopulation stability using the Portfolio effect (hereafter *PE*) and synchrony, which are metrics of stability that were computed based on the number of returns as in chapter 3. To analyze eco-evolutionary dynamics, we examined for each population and the whole metapopulation (using averaged values over the last 5 years) : 1) *genetic* changes by monitoring maturation thresholds and growth potential, 2) *phenotypic* changes using body size of juveniles (YOY and smolts) and adults (1SW and MSW), and 3) *life history strategy* changes via the ratio of MSW/1SW and proportion of maturing juveniles (YOY only).

5.3 RESULTS

We summarize the results below by distinguishing between demographic, phenotypic, and genetic effects. For each of these sections, we sequentially present the effects of 1) exploitation, 2) dispersal, and 3) spatialized management strategies.

5.3.1 Demographic consequences

At the scale of the metapopulation, increasing exploitation rates decreased the PFA, whatever the dispersal rate and the management strategy, in a nonlinear trend (Fig. 5.2 A). Metapopulation functioning via dispersal did not affect the PFAs at metapopulation scale compared to the scenario without dispersal. However, various patterns were observed between management strategies. In particular, whatever the dispersal rate and MER, the “Source exploitation” strategy (red color) showed dramatically lower PFA than the “Exploitation” strategy (black color), especially for higher MER (Fig. 5.2 A and B). In contrast, the “Source conservation” strategy (blue color) showed more complex results which varied with the MER and the dispersal rate (Fig. 5.2 A and B). For a dispersal rate of 15%, this scenario showed higher PFAs than the “Exploitation” for a range of MER between 0% and 15%, followed by a lower PFA, whereas for a dispersal of 30%, this scenario showed higher PFAs for a range of MER between 0% and 20%.

Regarding metapopulation stability, increasing exploitation rates decreased the portfolio effect and increased the synchrony of populations, whatever the dispersal rate and management strategy (Fig. 5.3 A and C). As expected, metapopulation functioning via dispersal enhanced the stability of the metapopulation especially for intermediate level of dispersal (15%, Fig. 5.3 A) as shown in chapter 3. However, the relationships between the MER and portfolio effect or synchrony varied between the simulated management strategies. Compared to the “Exploitation” strategy, the “Source exploitation” strategy showed higher synchrony level (Fig. 5.3 C and D), especially for high MER, but no difference in the measure of the portfolio effect (Fig. 5.3 A and B). In contrast, the “Source conservation” strategy showed similar synchrony level but lower portfolio effect for high MER compared to the “Exploitation” strategy. Indeed, the “Source conservation” strategy tended to decrease the PE as the MER increased, suggesting dramatic increase in the variability of PFAs in local sink and neutral populations which are heavily exploited (high local exploitation rates).

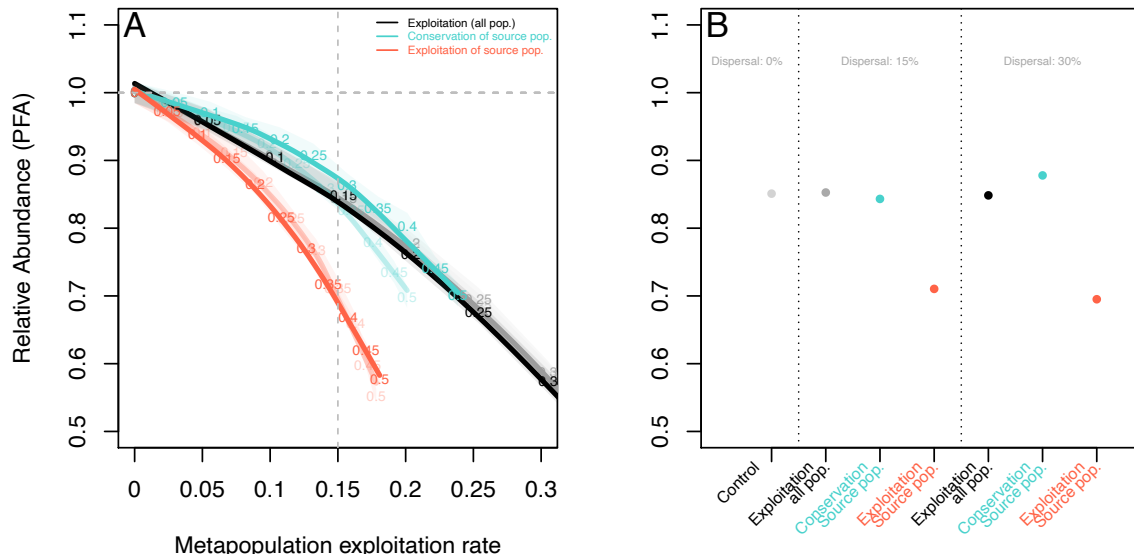


Figure 5.2: Relative abundance of returns (PFA) of the metapopulation for the different management strategies (colors) and dispersal rates (colors intensity) compared to the scenario without exploitation for increasing metapopulation exploitation rate (MER) (A), and for a MER of 15% (B).

5.3.2 Evolutionary consequences

We did not observe any change in the average values of the neutral gene with increasing MER, dispersal rates, or management strategies (Fig. 5.4 A), indicating that any change in fitness-related traits is unlikely to be due to genetic drift. Increasing exploitation induced several changes in the genotypic traits underlying life history strategies of individuals (Fig. 5.5 and 5.4). Whatever the dispersal rate, precocious male maturation threshold (Fig. 5.5 A) and genotypic growth potential (Fig. 5.4 C) decreased with increasing MER. Anadromous male maturation threshold (Fig. 5.5 C) decreased slightly with increasing MER while female maturation threshold (Fig. 5.5 E) did not change on average with variations of MER. We did not observe significant genotypic changes with dispersal, except a lower averaged growth potential (Fig. 5.4 D).

According to the management strategy, we observed contrasted evolutionary patterns for some traits, especially for high MER (above 15%). The “Source exploitation” strategy depicted lower growth potential than the “Exploitation” strategy whatever the dispersal rate (Fig. 5.4 D), but didn’t show strong effect on other genotypic traits. In contrast, compared to the “Exploitation” strategy, the

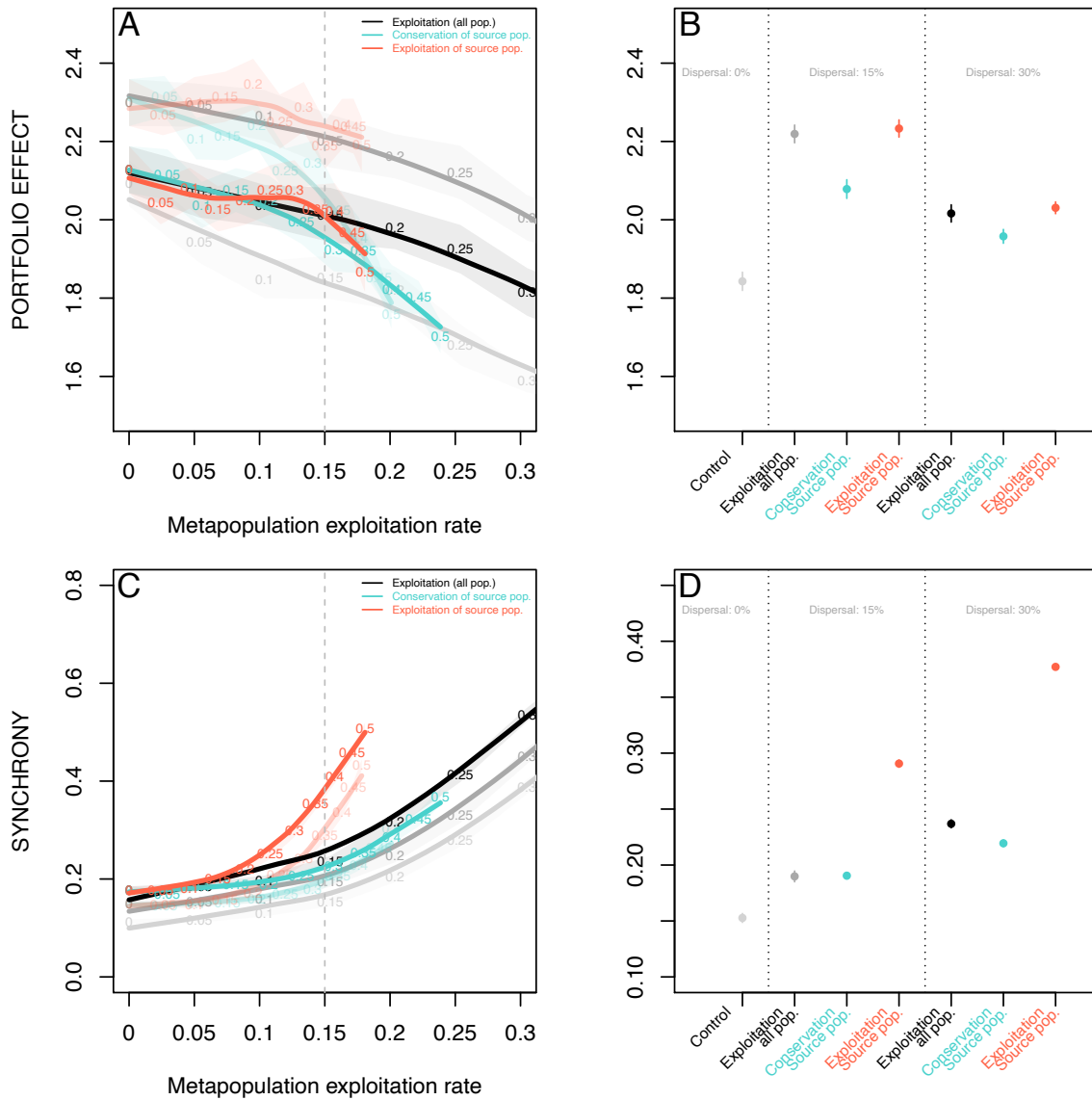


Figure 5.3: Portfolio effect (A, B) and synchrony (C, D) of the metapopulation for the different management strategies (colors) and dispersal rates (colors intensity) for increasing metapopulation exploitation rate (MER) and a MER of 15%.

“Source conservation” strategy induced higher growth potential (Fig. 5.4 D), higher anadromous male maturation threshold for dispersal rates of 15% but lower for rates of 30% (Fig. 5.5 D), while the opposite trend was observed for female maturation threshold (Fig. 5.5 F). Meanwhile, no difference in the precocious maturation threshold emerged at the metapopulation scale among the three management strategies (Fig. 5.5 B).

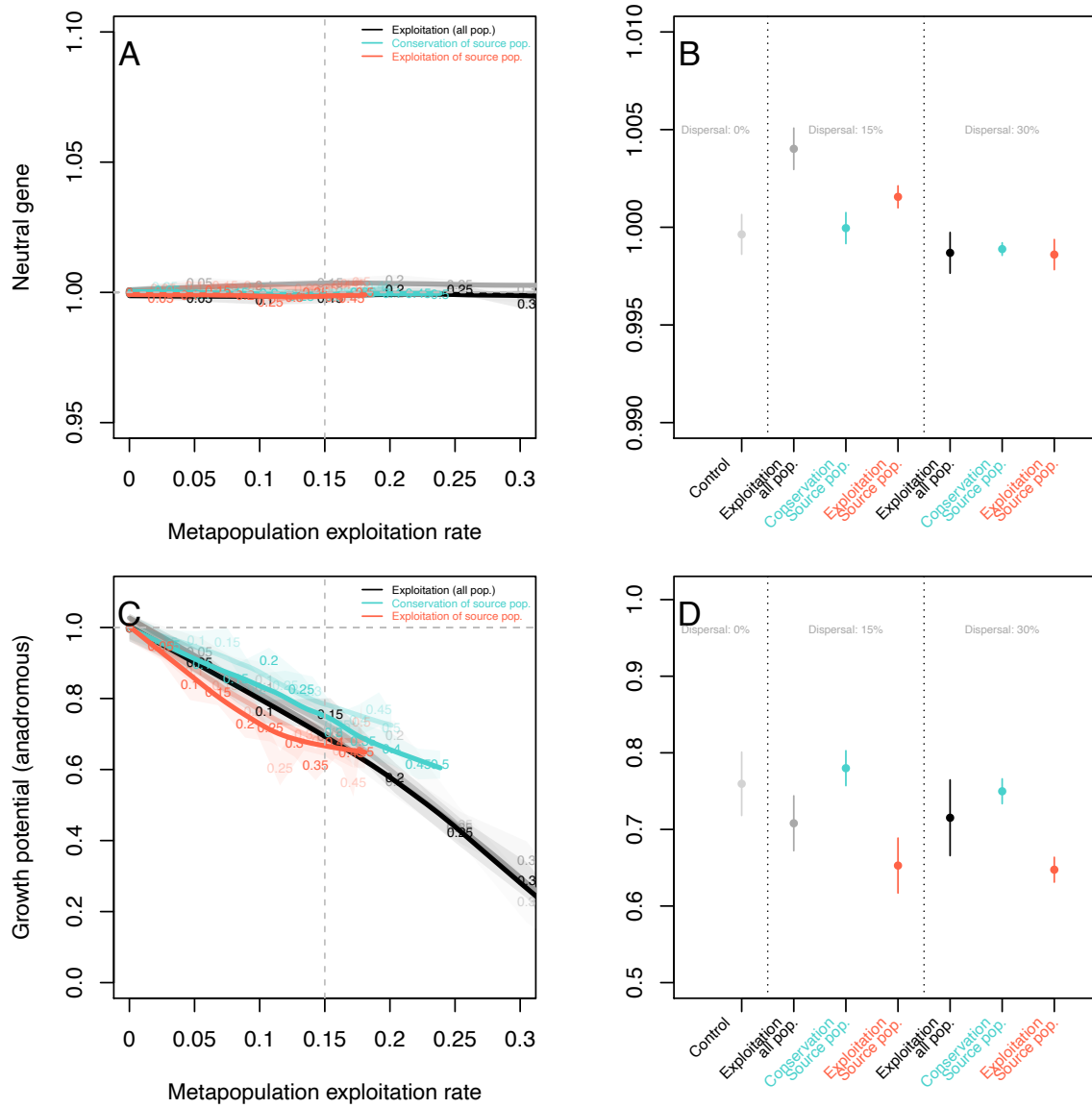


Figure 5.4: Relative average genetic values of neutral gene (A, B) and growth potential (C, D) over returning adults (last 5 years) over the metapopulation, for the different management strategies (colors) and dispersal rates (colors intensity) compared to the scenario without exploitation, for increasing metapopulation exploitation rate (MER) and a MER of 15%.

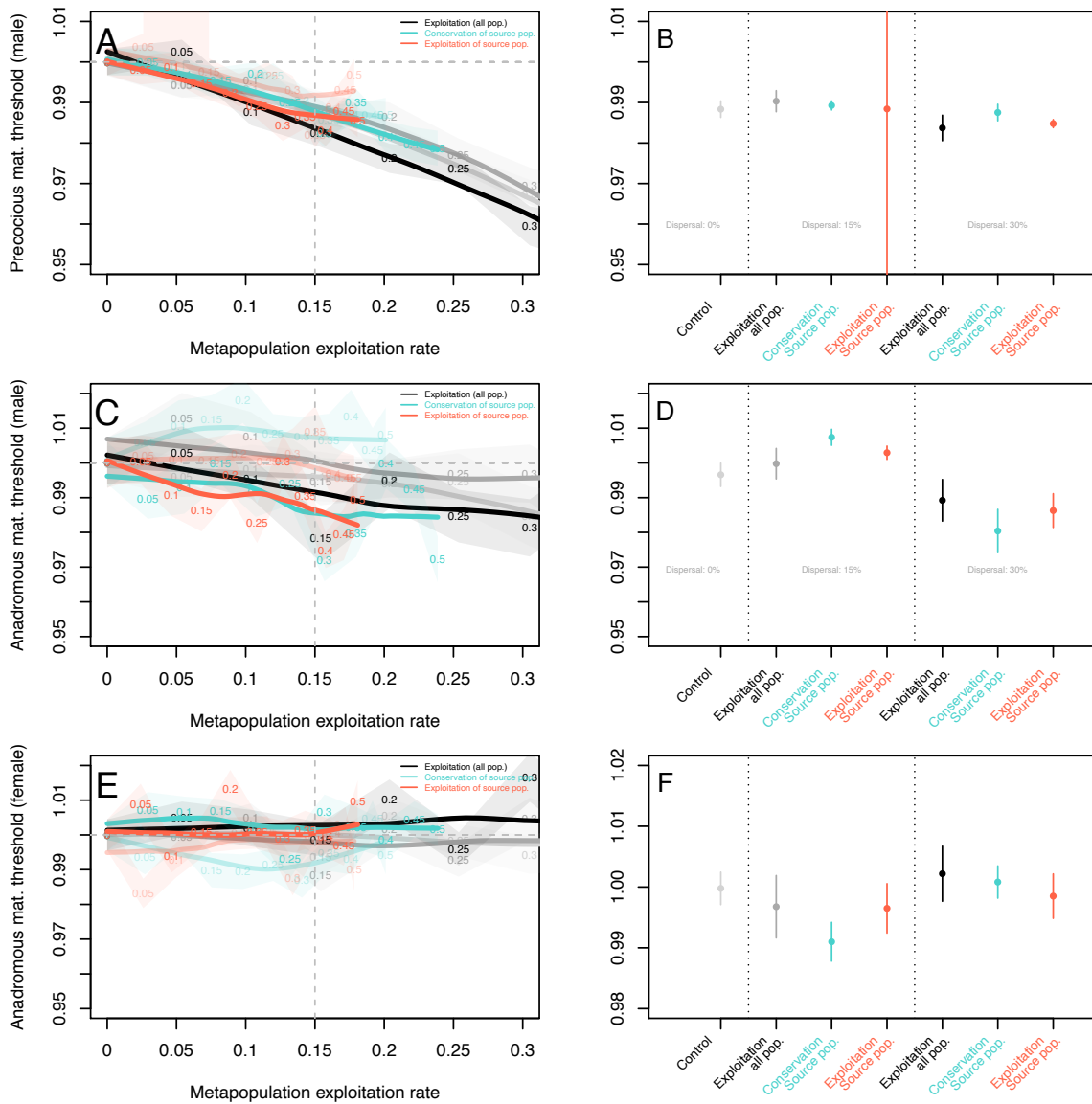


Figure 5.5: Relative average genetic values of precocious male maturation threshold (A, B), male (C, D) and female (E, F) anadromous thresholds, over returning adults (last 5 years) over the metapopulation, for the different management strategies (colors) and dispersal rates (colors intensity) compared to the scenario without exploitation, for increasing metapopulation exploitation rate (MER) and a MER of 15%.

5.3.3 Phenotypic and life history strategy consequences

Life history traits and strategies were also affected by exploitation at metapopulation scale (Fig. 5.6 and 5.7). Whatever the dispersal rate, the size of juveniles (YOY and smolts) increased with MER suggesting a release of density-dependent effects favouring growth of juveniles (Fig. 5.6, A and C). Among returning adults, 1SW individuals showed a slight increase in body size with MER, while no change was observed regarding the body size of MSW individuals (Fig. 5.6, E and G). The proportion between these two maturation strategies also slightly changed with variable MER (Fig. 5.7, A), and more specifically we observed more 1SW individuals relatively to MSW with increasing MER. Finally, the proportion of precocious maturing YOY increased with exploitation rates (Fig. 5.7, C).

We did not observe significant phenotypic changes with dispersal, except for the proportion of precocious maturing YOY and 1SW average body size which remained lower than the control scenario (no dispersal). These results can be explained by the decrease in the genotypic growth potential (see section above).

Management strategies did not change significantly the average body size of anadromous or smolt individuals (Fig. 5.6, D, F and H). However, the size of YOY was slightly lower in the “Source conservation” and more strongly lower in the “Source exploitation” strategy compared to the “Exploitation” strategy for high MER (Fig. 5.6, B). The same pattern was observed for the proportion of mature juveniles with high exploitation rates (Fig. 5.7, C), while no strong difference in the proportion of anadromous strategies was observed among management strategies (Fig. 5.7, A).

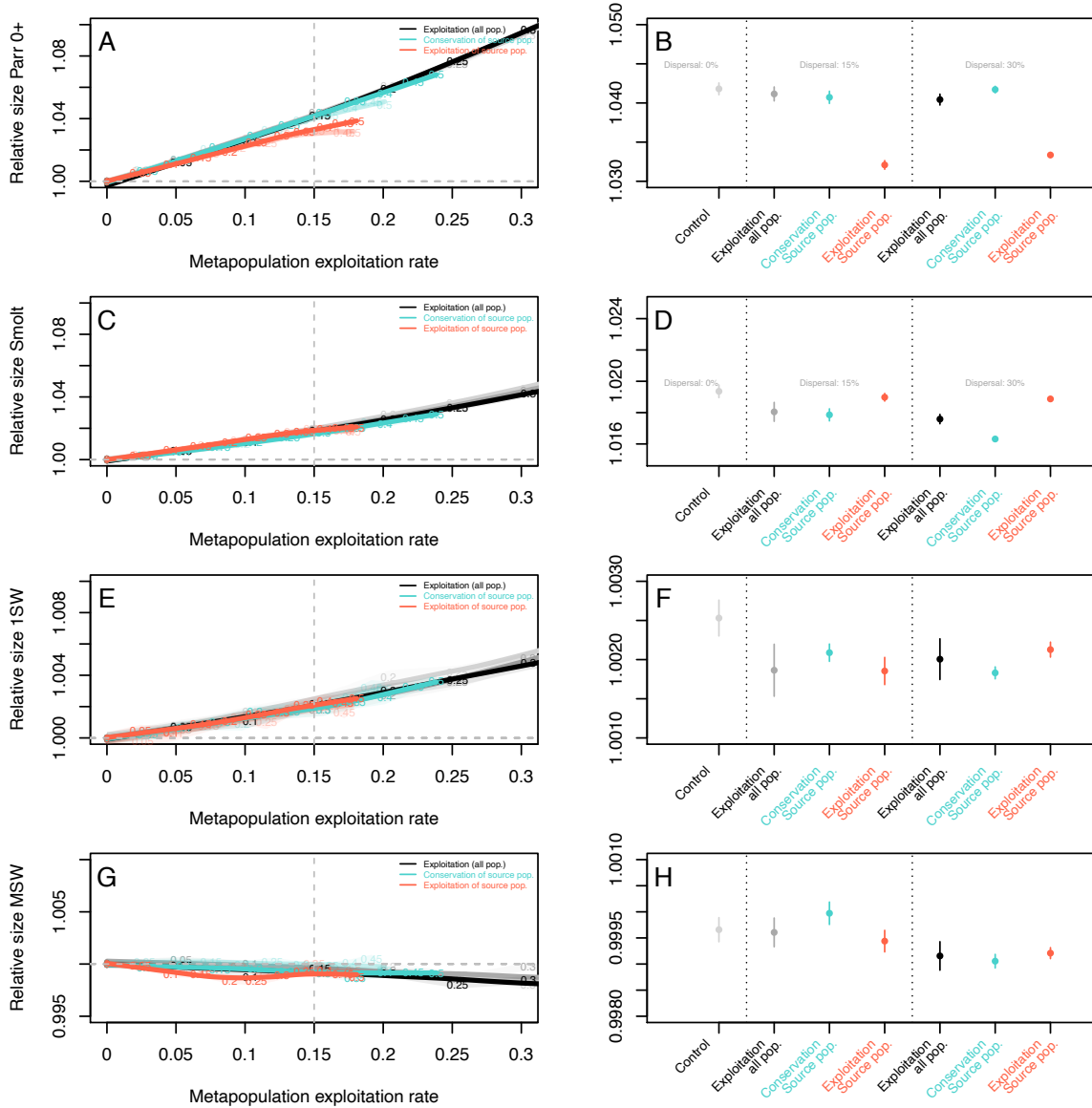


Figure 5.6: Relative average (last 5 years) of phenotypic values of returning adults (E, F, G and H), juveniles (YOY, A, B) and smolts (C, D) over the metapopulation for the different management strategies (colors) and dispersal rates (colors intensity) compared to the scenario without exploitation for increasing metapopulation exploitation rate (MER) and a MER of 15%.

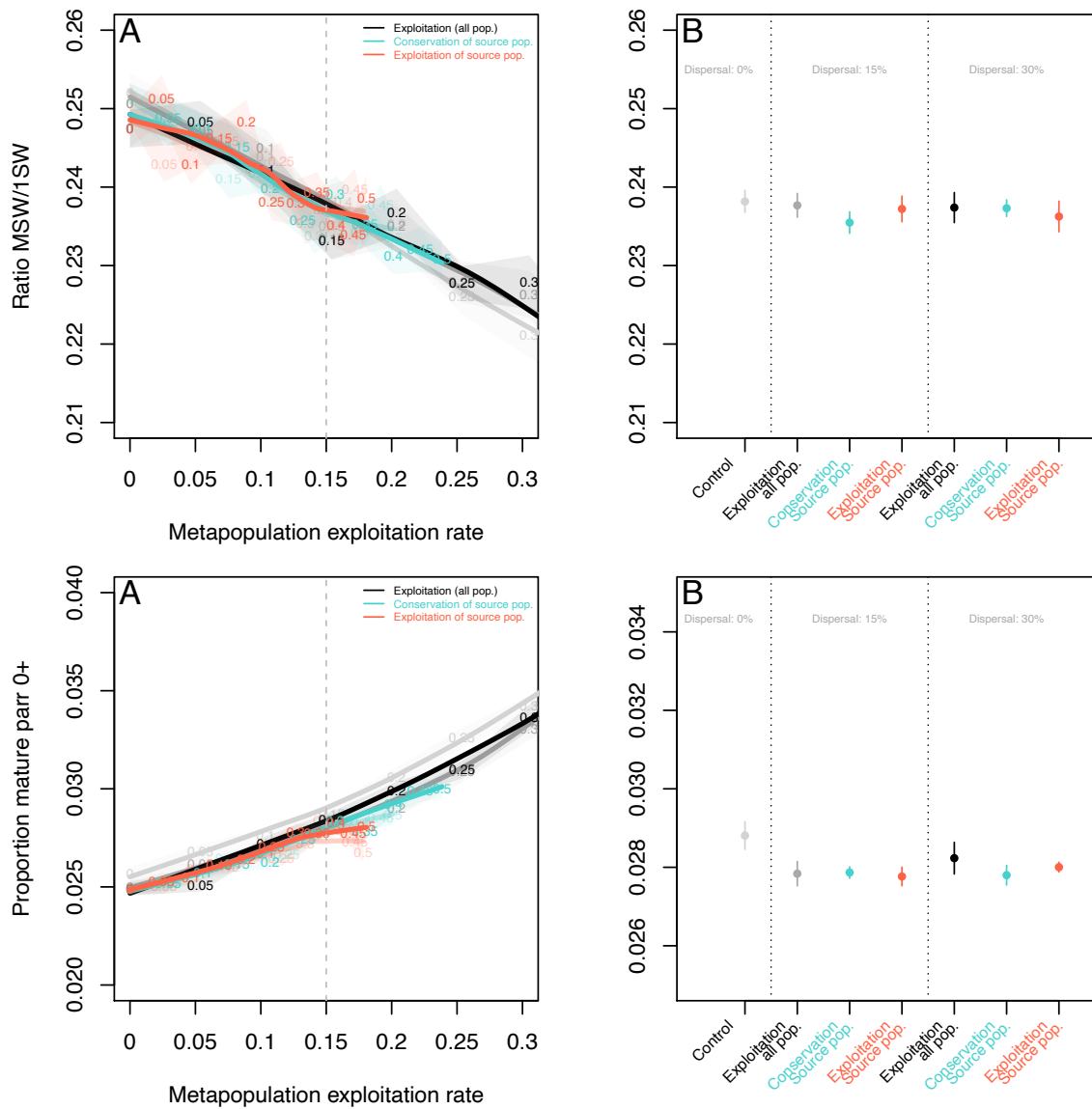


Figure 5.7: Ratio MSW/1SW (A, B) and proportion of maturing YOY (C, D) averaged (last 5 years) over the metapopulation for the different management strategies (colors) and dispersal rates (colors intensity) compared to the scenario without exploitation for increasing metapopulation exploitation rate (MER) and a MER of 15%.

5.4 DISCUSSION

While the eco-evolutionary consequences of dispersal and exploitation are increasingly recognized, consideration of these effects - potentially in interaction - for management and conservation is limited. Here, we evaluated population exploitation in a metapopulation perspective, by using the case of Atlantic salmon which is still managed at the local population scale while dispersal has been demonstrated. Specifically, we compared a management strategy that was not spatialized with other that accounted for the asymmetry of dispersal patterns (i.e., focusing on sink or source populations), in order to meet both conservation and exploitation objectives (maintaining the same exploitation rate at the scale of the metapopulation). We used a demo-genetic agent-based model (MetaIBASAM) allowing us to examine both demographic and evolutionary consequences of these strategies for various dispersal rates and a gradient of local exploitation rates via simulations of interconnected populations. Our results confirmed both demographic and evolutionary effects of non-spatialized exploitation in a metapopulation (i.e., lower abundance and earlier maturation). But considering the spatial structure of the metapopulation, we showed differences in consequences of spatialized management strategies and a benefit of protecting source populations from exploitation for a certain range of exploitation rates and dispersal rates, in terms of abundance but not in terms of stability. Simulations also showed contrasted eco-evolutionary consequences between management strategies, indicating that interactive effect of plastic, evolutionary responses and immigration dilution are difficult to disentangle. Overall, our results show that without knowledge on metapopulation functioning, the safest strategy remains to spread the exploitation effort over all populations.

Eco-evolutionary consequences of non-spatialized exploitation

From a demographic perspective, our simulations showed a decrease of the metapopulation abundance with increasing exploitation rates (both local and global). This expected result was also observed at the local population scale in [Piou et al. \(2015\)](#), even if they simulated a more selective harvest with a higher rate of exploitation of the MSW individuals than the 1SW individuals. However, we showed a non-linear decrease of the PFA with increasing MER whatever the dispersal rate. This non-linear pattern can also be observed by using a simple population dynamics model (Supplementary Materials 5.5.1), so it is not a property of our DG-ABM and it seems to be due to density-dependence effects. Regarding metapopulation stability,

our simulations demonstrated a synchronizing and destabilizing effect of exploitation, via a reduction of the portfolio effect metric. Several studies identified commercial exploitation as a key driver of the erosion of populations portfolio and increased populations synchrony using long term data (e.g., cod, [Frank et al., 2016](#); herring, [Stier et al., 2020](#)). The relationships patterns between PE and synchrony with the MER were similar between scenarios of dispersal rates, but the synchrony level was the lowest for complete philopatry, whereas the portfolio effect was maximised for dispersal rates of 15%, as showed in chapter 3.

From an eco-evolutionary perspective, our simulations showed various evolutionary trajectories of the metapopulation with variation of exploitation rates, which, combined to demographic effects (e.g., density dependence), also affected life history traits and strategies of individuals. These evolutionary and phenotypic patterns did not vary with dispersal rates. In particular, lower precocious male maturation thresholds were selected by higher exploitation rates, i.e., the anadromous strategy was selected against, avoiding individuals to be harvested before reproduction by favoring early maturation in river. Along with an increased size of juveniles (YOY and smolts) because of relaxed density dependent effects, increased exploitation rates led to a higher proportion of early maturing parr. This life history change, emerging from both plastic and evolutionary response of populations, illustrates the potential of our modeling approach to investigate eco-evolutionary response of populations to exploitation. Late maturation in sea was still selected for in females with high exploitation rates, likely because of the mass-fecundity relationship, whereas late maturation in sea was slightly selected against in males (lower maturation threshold) with increased exploitation rates. An earlier maturation in sea of males might reduce sea mortality to compensate the higher mortality induced by exploitation. Along with a slight higher size of 1SW individuals with increasing exploitation rates, the relative proportion of MSW individuals to 1SW individuals decreased. Lower growth potential were also selected for with increased exploitation, likely because of the plastic increase of juvenile size combined with a counter-selection of big juveniles with a high probability of following the anadromous strategy.

Our results strengthen the body of literature showing both demographic and evolutionary consequences of exploitation on local populations. In their study at local population scale, [Piou et al. \(2015\)](#) showed a decrease of adults maturation thresholds with exploitation but this effect was observed in response to selective fisheries on MSW individuals, whereas fishing pressure was the same between 1SW and MSW individuals in our study. However, the differential selective pressure of exploitation that we applied

between the anadromous and resident (precocious maturation) strategy explained the evolution of earlier maturation, as observed at the population level in other empirical and modeling studies (Edeline et al., 2007; Wang and Höök, 2009; Matsumura et al., 2011; Ayllón et al., 2018). However, in a metapopulation perspective, these results may only be relevant in the case of similar exploitation pressure applied over all populations, regardless their own demographic and genetic features. Besides, we go further and shed light on the difference of demographic and evolutionary outcomes between spatialized management strategies of exploitation. Here, we focused on two spatialized strategies, i.e., protecting the source populations vs. the sink and neutral from exploitation, that we compared with a strategy of exploiting all the populations at the same rate, a strategy that is currently applied in most exploited populations.

Demographic consequences of spatialized management strategies

Indeed, the relationship between the MER and the metapopulation PFA differed between management strategies. In particular, the "Source exploitation" strategy showed the lowest PFAs whatever the exploitation and dispersal rates; it seems that the high local rates of exploitation applied on the source populations were not compensated by immigration in this scenario. In contrast, the "Source conservation" strategy showed higher PFAs than the "Exploitation" strategy for a certain range of MER which depended on dispersal rate. It might first seem counter-intuitive not to protect sink populations and to harvest them instead at high local rates, but this harvest was largely compensated by immigration provided by the protected source populations of the network in this scenario. Even if immigrants were also harvested before reproduction in our model, their contribution to the local populations dampened the effect of exploitation. This compensatory effect of immigration is illustrated in Supplementary Materials 5.5.2, where Fig. 5.9, 5.10, 5.11 and 5.12 showed that the "Exploitation" strategy affected both sink and sources populations (low PFAs and low ratio Immigrants/Harvest), while the "Source exploitation" strategy strongly affected source populations (low PFAs and low ratio Immigrants/Harvest) but also the sink even if they were not harvested (lower PFAs). In contrast, the "Source conservation" strategy had little effect on the sink population (ratio Immigrants/Harvest close to 1 even with high local ER, PFA reduction lower in proportion than that of source in the "Source exploitation" scenario) and did not affect source populations. This compensatory effect on sink populations was also more significant for dispersal rates of 30% (Supplementary Materials 5.5.2 Fig. 5.9 and

5.11). Thus, in terms of metapopulation abundance, focusing conservation on sink and neutral populations by exploiting only the source populations, appeared detrimental for the whole metapopulation according to our simulations. In contrast, our model showed a slight advantage in protecting the source populations from exploitation, while exploiting the sink and neutral ones, and especially when dispersal intensity was high (30%). Note that, this compensatory effect might also depend on the carrying capacity of the habitats.

However, applying this management strategy would require an extensive knowledge of the network structure, i.e., the intensity of connectivity and its asymmetry (which populations are source or sink?). Moreover, this source-sink structure might be dynamic in time, due to internal dynamics of the metapopulation, but also external factors such as exploitation itself (Supplementary materials 5.5.3). Furthermore, focusing exploitation on one type of population (e.g., sink or source) reduced the stability of the network compared to spreading the exploitation effort over all populations in our simulations: protecting the sink and neutral populations increased the synchrony metric, while protecting the source decreased the portfolio effect, especially for high MER (above 15%). This result might be explained by the high exploitation rates applied locally to maintain global exploitation (i.e., reallocation of fishing effort), which might lead to high stochasticity in population dynamics. Altogether, we suggest that the "Exploitation" strategy might be the safest action to adopt for the management of exploitation in this metapopulation. In contrast, a recent theoretical analyse have shown that proportional harvest induced spatial synchrony and suggested that spatialized management strategies, in particular protecting the low abundance populations, would reduce this effect (Engen et al., 2018). Our findings are also not entirely in line with those of Crowder et al. (2000), who suggested with a theoretical model of coral reef fish to preserve source populations for exploitation efforts above 5% of the abundance, and to preserve sink populations for exploitation rates below 5%. In our study, we also showed the benefit of preserving source populations for metapopulation conservation but with a limit for high exploitation rates, depending on dispersal intensity. Moreover, we didn't show any advantage to preserve sink populations for low exploitation rates. But Crowder et al. (2000) only investigated exploitation rates of 15% maximum, and they modelled the dispersal process as density-dependent (i.e., dispersal occurs when carrying capacity is exceeded), in contrast to the constant rate we applied in our simulations. The study of Tufto and Hindar (2003) used a deterministic model of two populations and demonstrated that protecting the smallest populations before the largest ones would be the optimal

strategy in order to maximise both the effective size and yield.

Eco-evolutionary consequences of spatialized management strategies

Meanwhile, spatialized management strategies also showed contrasted eco-evolutionary consequences, especially for high exploitation rates (above 15%), that likely resulted from the combined effects of response to selection, plasticity, and immigration dilution. In particular, the average genetic value of individuals growth potential over the metapopulation was slightly higher in the "Source conservation" strategy than the "Exploitation", but lower for the "Source exploitation" strategy. An explanatory hypothesis could be that focusing fishing effort over the source populations induced a higher selective pressure compared to spreading fishing efforts over all populations (local exploitation rate higher), while in the "Source conservation" strategy, this higher selective pressure might be compensated by a strong influence of immigration coming from source populations and potentially bringing individuals with higher growth potentials. Compared to the "Exploitation" strategy, the average genetic value of precocious maturation threshold showed a slower decrease (i.e., were higher) for MER above 15%, while the size of juveniles (especially parr) was lower in both spatialized management strategies (and even more in the "Source exploitation" strategy). The lower juvenile size was likely a plastic response to relaxed density effect in focal populations, but might also result from a dilution by immigration of individuals with higher individual sizes in the "Source conservation" strategy, and from a lower growth potential for the "Source exploitation" strategy. Ultimately, the combination of these evolutionary and plastic responses resulted in a lower proportion of mature parr for high MER for the "Source conservation" and "Source exploitation" strategies compared to the "Exploitation". Adults maturation threshold also showed slightly contrasted results between management strategies but they were harder to explain. Male and female maturation thresholds were similar on average between the "Exploitation" and the "Source exploitation" strategies. However, male maturation threshold was higher than "Exploitation" for the "Source conservation" strategy for dispersal rates of 15% but lower for dispersal rates of 30%, whereas the opposite pattern was observed for female maturation threshold. Altogether, complex eco-evolutionary responses emerged from the spatialized management strategies, and looking at the averaged traits of philopatric and immigrants individuals at the population scale might help to disentangle the various and interactive effects that could lead to these contrasted results. But overall, our results suggest that protecting some populations

from exploitation can dampen the selective effects of exploitation.

Perspectives

Our model allowed the emergence of demographic and evolutionary outcomes as function of which type of population was exploited, but we simulated dispersal rates that were constant over space and time, as a parsimonious assumption. However, empirical studies reported variable dispersal rates over space (Consuegra et al., 2005) and time (Jonsson et al., 2003) in Atlantic salmon, and suggested that dispersal propensity might depend on individual traits (e.g., genetic basis, Saastamoinen et al., 2018) or population characteristics (e.g., density-dependence, Berdahl et al., 2016). Different patterns would probably arise if individual probability to disperse was variable in space and time. For example, with a genetic basis, one might expect dispersal rates to evolve as function of the spatial structure of exploitation. Focusing harvest on sink populations might select for dispersal in these populations but against in source populations, and vice-versa.

Moreover, we evaluated the consequences of management strategies that were very contrasted, by applying reserves (no harvest at all, such as a Freshwater Protected Area) on some populations and reporting the fishing effort on others. Another perspective of future work could be to evaluate strategies with variable exploitation rates between populations (e.g., 5% on source and 15% on sink). Examining other criteria of differential exploitation between populations than asymmetry in dispersal (i.e., sink vs source), such as population size, contribution to the network stability or effective size (Hindar et al., 2004), environmental or genetic features, would also provide insight into diverse options of spatialized management strategies of exploitation. Finally, our results confirmed the importance to favor connectivity between populations to provide opportunity of dispersal between populations and its dampening effects facing the demographic and evolutionary consequences of exploitation. Investigating the impact of enhancement or restoration management actions such as improvement of connectivity, or habitat productivity, also constitute future avenues of research in this metapopulation context.

Conclusion

Altogether, our study showcased that a spatialized management strategy protecting the sink and neutral populations did not appear as a good strategy, while protecting source populations from exploitation seemed slightly better than exploiting all populations

at the same rate, at least within our scenarios. We also showed variable evolutionary consequences depending on management strategies, and in interaction with dispersal. We argue that accounting for metapopulation structure in defining exploitation management would allow to better meet both conservation and exploitation goals, but without any information on metapopulation structure and dispersal, spreading the exploitation effort across all populations seems to be the safest strategy. We also shed light on the potential of our modeling approach as a prospecting tool for management strategies by including ecological and evolutionary complexity of the system as well as management constraints (e.g., exploitation objective, money limitations) and uncertainty (e.g., risk of misidentification of populations).

5.5 SUPPLEMENTARY MATERIALS

5.5.1 Relationship between PFA and MER using a population dynamics model

To evaluate if the non-linear relationship between the metapopulation PFA and the MER was a property of our DB-ABM, we simulated population dynamics via a simple model of population dynamics with a Beverton-Holt relationship of stock-recruitment. Similar patterns were observed between the output of this simple model and those of our DG-ABM, i.e., the slight advantage of the "Source conservation" strategy compared to the other strategies for a certain range of MER and depending on the dispersal rate (Fig. 5.8).

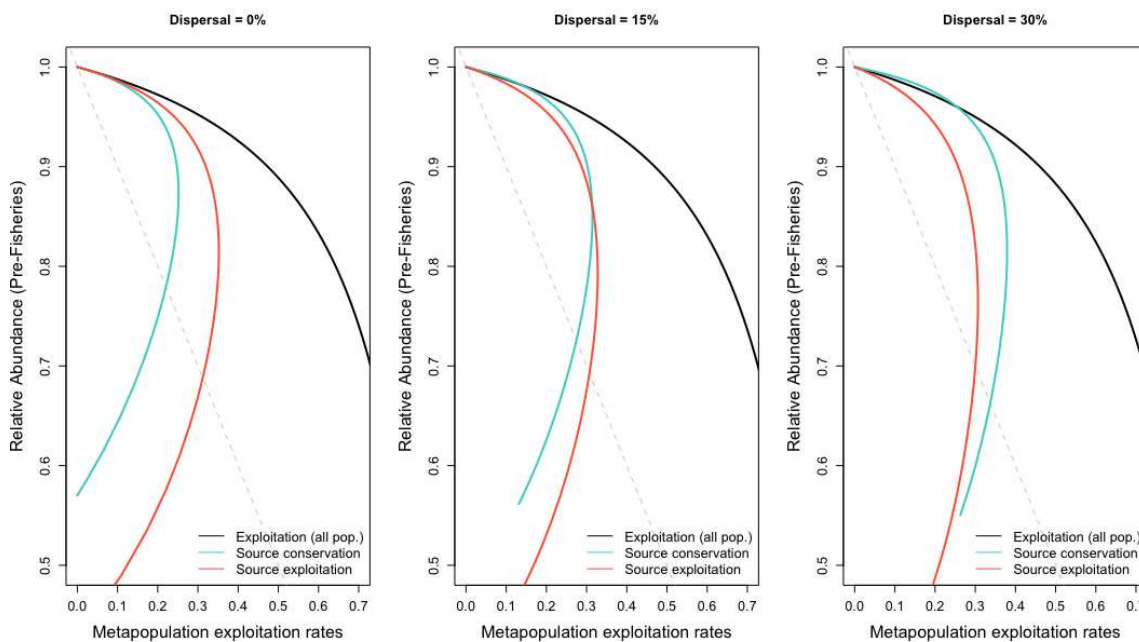


Figure 5.8: Metapopulation PFAs for scenarios of MER, dispersal rates, and management strategies using a simple population dynamics model.

The code of the model can be found below:

```

1 ##### PARAMETERS #####
2 nyear=30
3 a=10 Alpha # density-independent survival
4 Rmax=10 # carrying capacity
5 S=seq(100,10000,100)/(mean(Area)/100) #stock
6 mu=0 # Parameters for Laplace kernel
7 beta=29.5 # so that >80% of migrants disperse into the first 50km
8 dat <- read.csv2("data/dataPop.csv", header=TRUE, stringsAsFactors = FALSE, comment.char = "#")
9 pops <- dat$Population; npop <- length(pops)

```

```

10 M=as.numeric(dat$M); Area=as.numeric(dat$Area)
11 Type=dat$Type; dist <- dat$Distance #edit al - 20/03/21
12 frates_vec = seq(0,1,0.01) #local exploitation rates
13 ##### FUNCTIONS #####
14 getFishingRates <- function(scenarioFishing,scenarioFishingRate){
15   tmp <- matrix(0, nrow = npop, ncol = 1)
16   if (scenarioFishing==0){ # fishing all
17     scn_name="fishing all"
18     for (i in 1:npop) {
19       if (dat$Type[i]=="sink") tmp[i,] <- frates_vec[scenarioFishingRate]
20       if (dat$Type[i]=="neutral") tmp[i,] <- frates_vec[scenarioFishingRate]
21       if (dat$Type[i]=="source") tmp[i,] <- frates_vec[scenarioFishingRate]
22     }
23   }
24   if (scenarioFishing==2){ # fishing sinks/neutral
25     scn_name="fishing sinks/neutral"
26     for (i in 1:npop) {
27       if (dat$Type[i]=="sink") tmp[i,] <- frates_vec[scenarioFishingRate]
28       if (dat$Type[i]=="neutral") tmp[i,] <- frates_vec[scenarioFishingRate]
29       if (dat$Type[i]=="source") tmp[i,] <- 0
30     }
31   }
32   if (scenarioFishing==3){ # fishing sources only
33     scn_name="fishing sources"
34     for (i in 1:npop) {
35       if (dat$Type[i]=="sink") tmp[i,] <- 0
36       if (dat$Type[i]=="neutral") tmp[i,] <- 0
37       if (dat$Type[i]=="source") tmp[i,] <- frates_vec[scenarioFishingRate]
38     }
39   }
40   return(list(tmp,scn_name))
41 }
42 BH <- function(S) (a*S)/(1+(a*(S/Rmax)))
43
44 SimulExploitMetaPop <- function(h=1){
45   ##### I. CONNECTIVITY #####
46   distance=matrix(, npop, npop)
47   for (i in 1:npop){
48     for (j in 1:npop){
49       distance[i,j]=abs(dist[j]-dist[i])
50     }
51   }
52   ##### II. AREA #####
53   area_log=log10(dat$Area)
54   ratio_area=matrix(, nrow=1, ncol= npop); colnames(ratio_area)=pops
55   for (i in 1:npop){
56     ratio_area[1,i]=area_log[i]/(sum(area_log))
57   }
58   ##### III. DISPERSAL KERNEL #####
59   lap = function(mu, beta, distance) {(1/(2*beta))*exp(-(distance-mu)/beta)} # Laplace
60   ##### IV. CONNECTIVITY MATRIX #####
61   connect_kernel=matrix(, nrow=npop, ncol=npop)
62   for (i in 1:npop){
63     attrac_d=lap(mu, beta, distance[i,]) #attractivity based on distance
64     attrac_d[i]<-0 # ignore population of origin
65     attrac_ad=attrac_d*ratio_area # influence of area on attractivity
66     proba_attrac_ad=attrac_ad/sum(attrac_ad)
67     sum(proba_attrac_ad)
68     proba_dispersion=proba_attrac_ad*(1-h)
69     proba_dispersion[i] <- h
70     connect_kernel[i,]=proba_dispersion
71     test <- rowSums(connect_kernel) #sum of probabilities
72     if (!(any(test==1))) {
73       print ("something wrong with dispersal kernel")
74       connect_kernel <- NULL
75     }
76   }
77   pstray = connect_kernel
78
79   phi<-A<-R <-ratio <-array(,dim=c(nyear, npop))
80   N<-Exploit<-array(,dim=c(nyear, npop, length(frates_vec)))
81   PFA<-GlobExploit<-array(,dim=c(nyear, length(frates_vec)))
82   N[1,,]<- Area*0.01
83   ratio[1,]<- 1
84
85   plot(NULL,xlim=c(0,0.7),ylim=c(0.5,1),ylab="Relative Abundance (Pre-Fisheries)"

```

```

83     ,xlab="Metapopulation exploitation rates",main=paste0("Dispersal = ",(1-h)*100,"%"),cex.lab=1.5, cex.axis
      =1.2)
84     abline(1,-1, col="lightgrey",lty=2)
85     for (scn in c(0,2,3)){
86         for (f in 1:length(frates_vec)){
87             scenarioFishing = scn
88             scenarioFishingRate = f
89             fishing.rates <- getFishingRates(scenarioFishing,scenarioFishingRate)[[1]]
90             fishing.scn <- getFishingRates(scenarioFishing,scenarioFishingRate)[[2]]
91             for (year in 2:nyear){
92                 for (pop in 1:npop){
93                     ## Recruitment
94                     S <- N[year-1,pop,f] / (Area[pop]/100)
95                     R[year,pop] <- BH(S) # Recruitment / BH relationship
96                     ## Survival
97                     phi <- 1 #rbeta(1,2,10)
98                     A[year,pop] <- (R[year,pop]*(Area[pop]/100)) * phi
99                 }
100                ## Dispersal
101                tmp <- A[year,]
102                disp <- tmp * pstray
103                for (pop in 1:npop){
104                    N[year,pop,f] <- sum(disp[,pop])
105                }
106                # Pre-fisheries abundance
107                PFA[year,f] <- sum(N[year,,f],na.rm=TRUE)
108                ## Fishing
109                for (pop in 1:npop){
110                    Exploit[year,pop,f] <- N[year,pop,f] * fishing.rates[pop]
111                    N[year,pop,f] <- N[year,pop,f] - Exploit[year,pop,f]
112                }
113                GlobExploit[year,f] <- sum(Exploit[year,1:npop,f],na.rm=TRUE)
114            } # end loop year
115        } # end loop f
116
117        GlobExploitRates <- GlobExploit[nyear,] / PFA[nyear,] # last year
118        colors<-c("black","blue","#48D1CC","#FF6347")
119        points(GlobExploitRates,PFA[nyear,]/PFA[nyear,1],col=colors[scn+1],type='l',lwd=2)
120    }
121    legend("bottomright",legend=c("Exploitation (all pop.)","Source conservation","Source exploitation"),lty=1,col=
      colors[c(1,3,4)],bty="n",cex=1.2)
122 } # end function
123
124 par(mfrow=c(1,3))
125 SimulExploitMetaPop(h=1)
126 SimulExploitMetaPop(h=.85)
127 SimulExploitMetaPop(h=.7)

```

5.5.2 Compensatory effect of immigration on exploitation

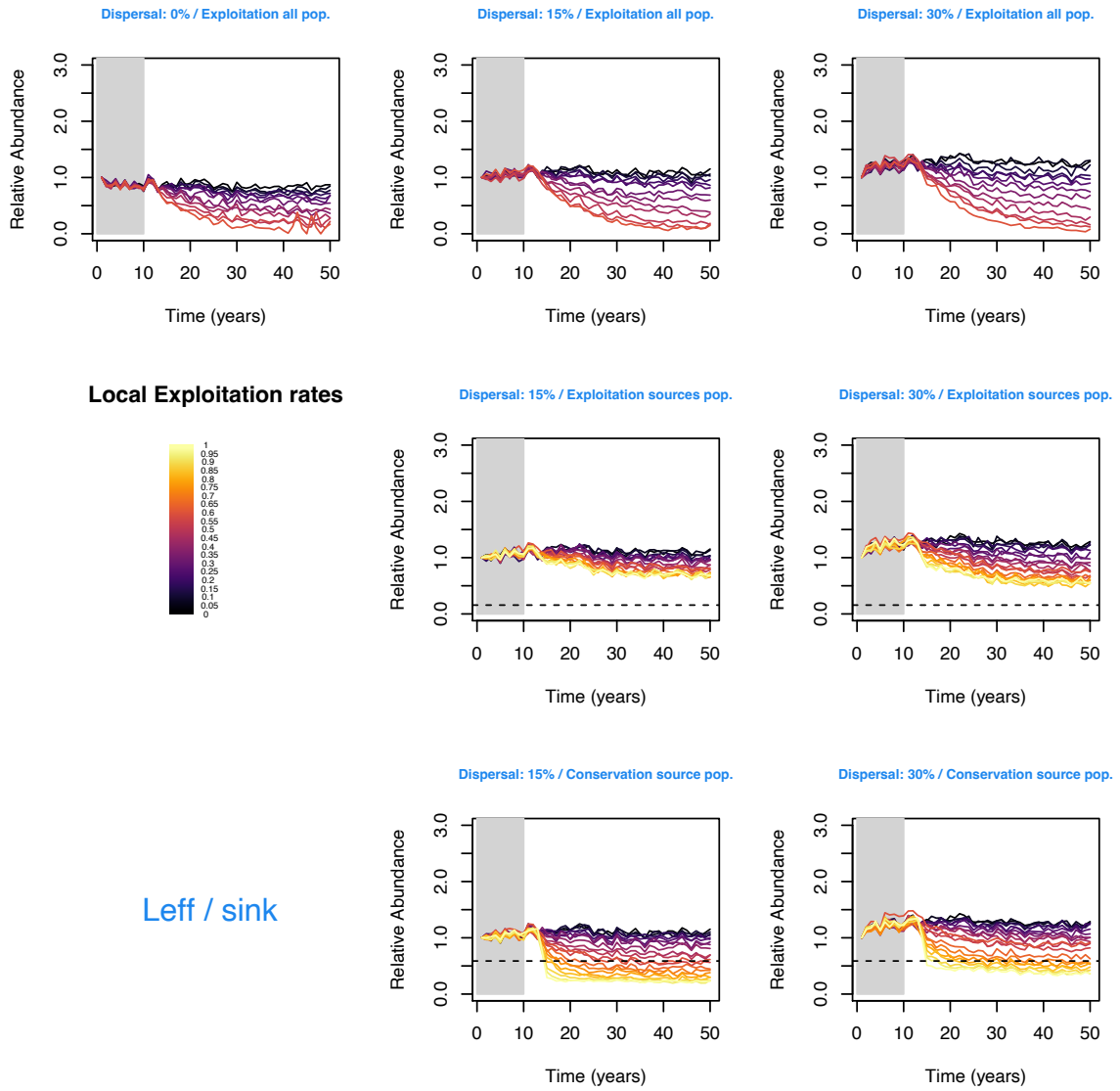


Figure 5.9: Relative PFA over time of an example sink population (the $Leff$) for a gradient of local exploitation rates, dispersal rates and the three management strategies.

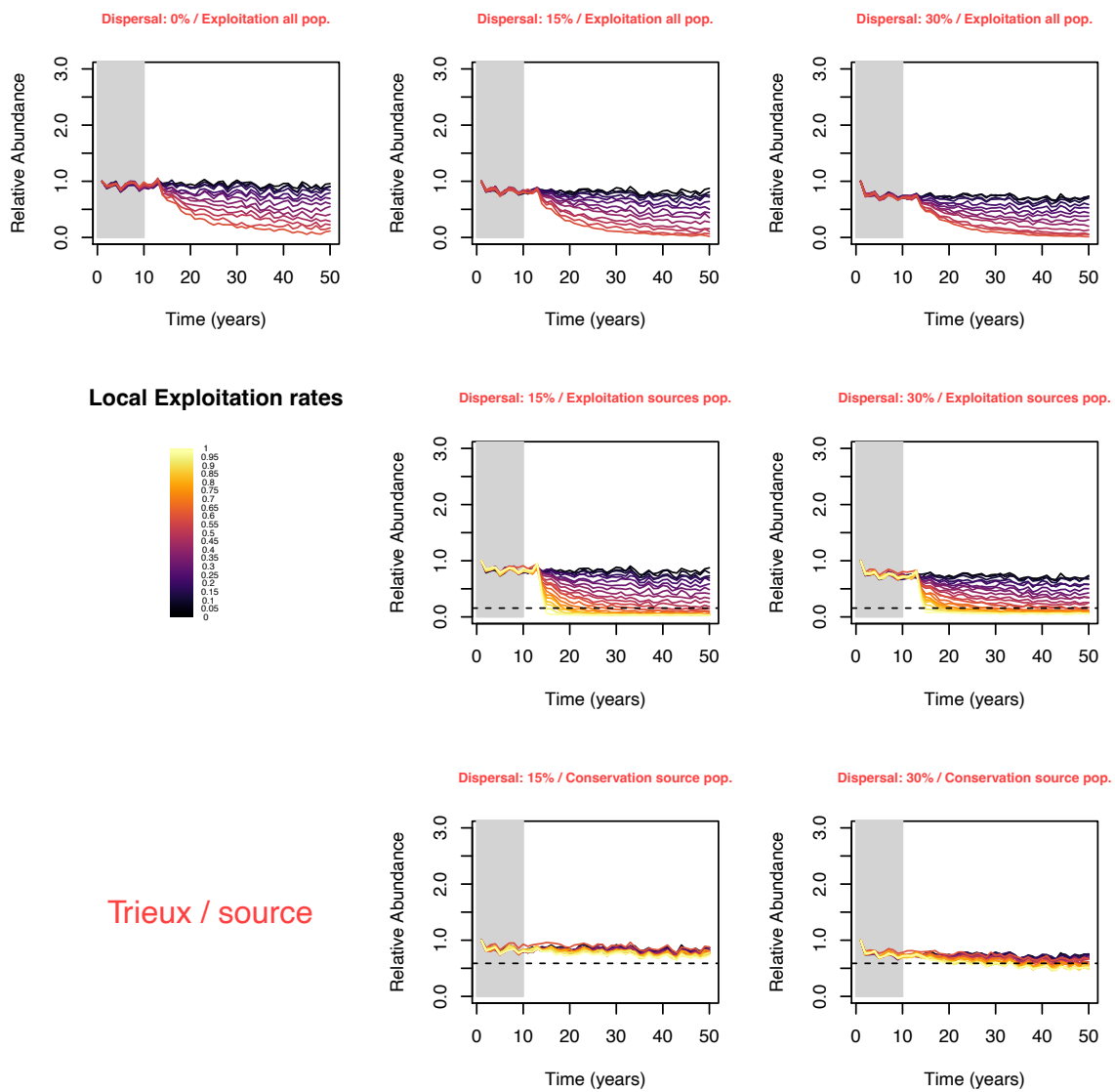


Figure 5.10: Relative PFA over time of an example source population (the Trieux) for a gradient of local exploitation rates, dispersal rates and the three management strategies.

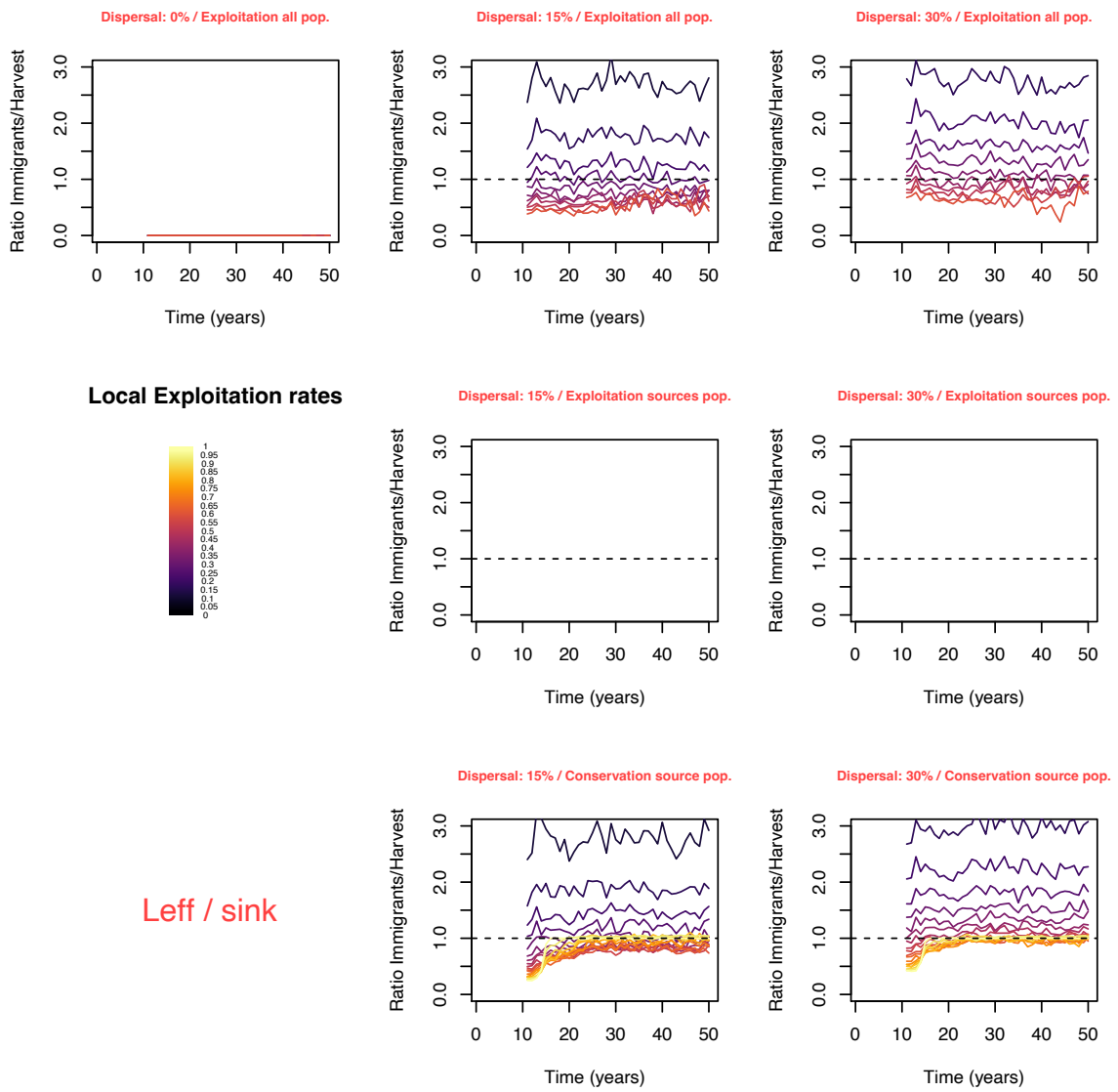


Figure 5.11: Ratio Immigrants/Harvest over time of an example sink population (the Leff) for a gradient of local exploitation rates, dispersal rates and the three management strategies.

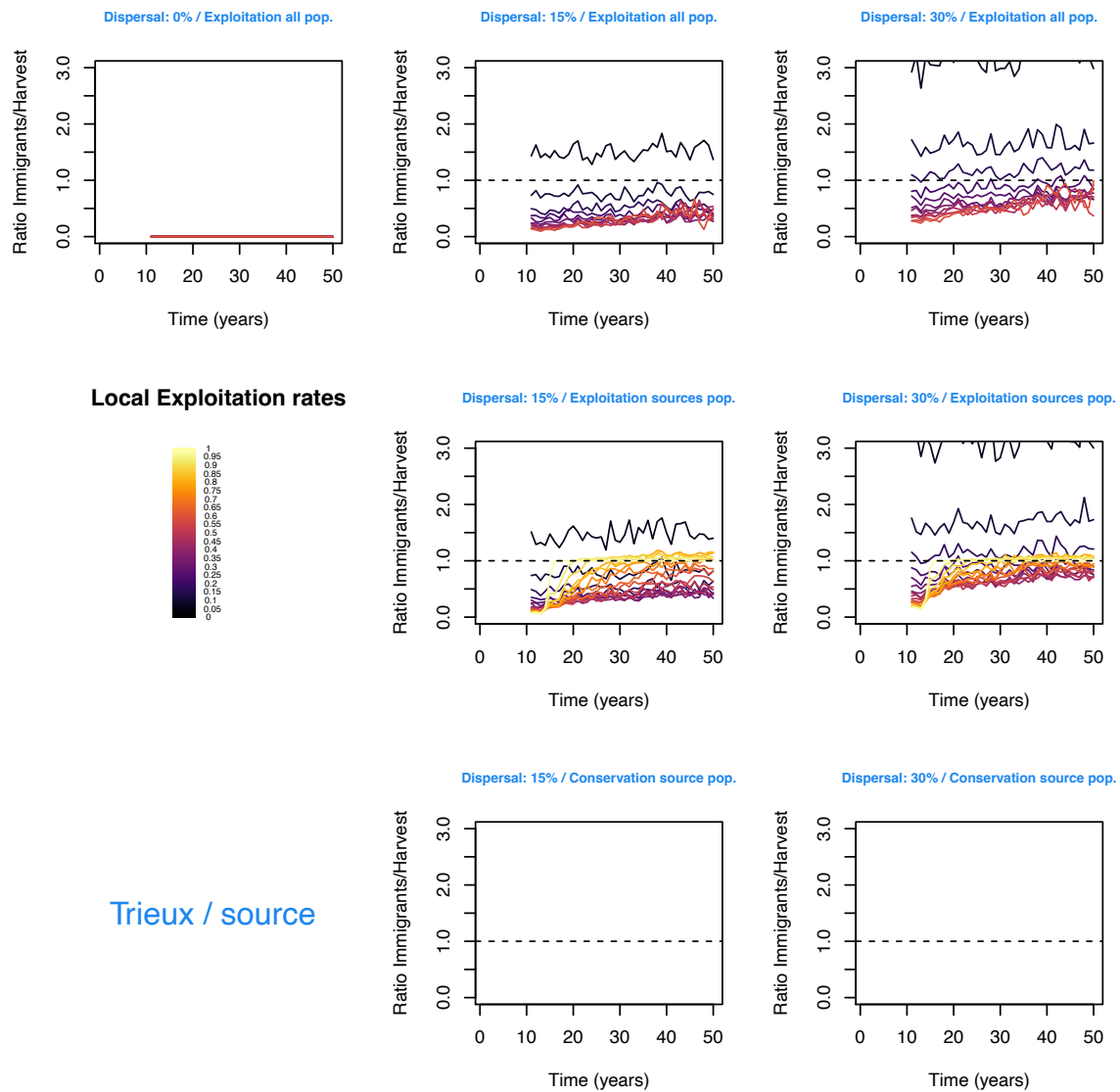


Figure 5.12: Ratio Immigrants/Harvest over time of an example source population (the Trioux) for a gradient of local exploitation rates, dispersal rates and the three management strategies.

5.5.3 Dynamics of source-sink structure with exploitation

The source-sink feature of populations was determined via the ratio of incoming immigrants over outgoing emigrants, averaged over the last 5 years of simulations. Fig. 5.13 showed that the source-sink structure of the network changed with high exploitation rates, i.e., initial sink populations became source (e.g., Goyen) and initial source populations became sink (e.g., Aulne) for high rates of exploitation of source populations (red scenario).

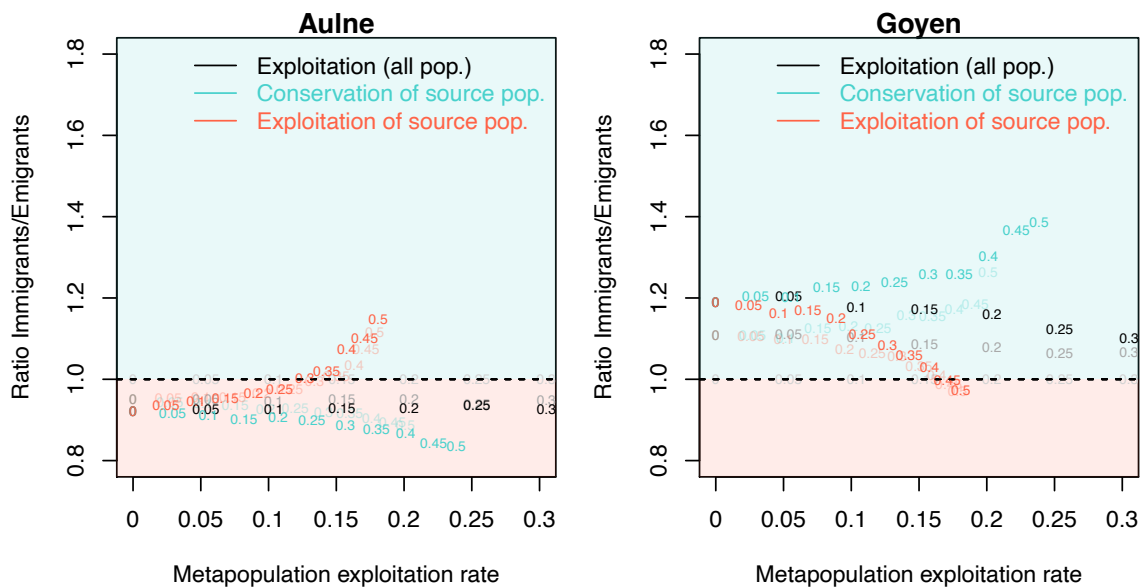


Figure 5.13: Ratio Immigrants/Emigrants of examples populations for a gradient of metapopulation exploitation rates, dispersal rates (colors intensity) and the three management strategies (colors).

5.6 CHAPTER HIGHLIGHTS

This chapter aimed at investigating innovative management strategies considering the spatial structure and evolutionary dynamics of interconnected and exploited populations of Atlantic salmon. Contrasted consequences between spatialized strategies were observed, at both demographic and evolutionary levels. The main lessons of this chapter are the following:

Chapter 5 highlights

- Studies evaluating management strategies by considering metapopulation structure and eco-evolutionary feedbacks are scarce;
- Spatialized management strategies of a network of exploited Atlantic salmon populations showed different demographic and evolutionary consequences at the metapopulation scale, in interaction with dispersal rate;
- Protecting sink and neutral populations, while reporting exploitation on source populations dramatically affected metapopulation size, while protecting source populations from exploitation performed slightly better than exploiting all populations;
- Complex evolutionary consequences require further analysis to disentangle interacting effects of immigration, density-dependence, and selection;
- Results suggest that without information on the metapopulation structure, conservation of the populations according to the portfolio approach appears as the safest strategy;
- Our modeling approach may be used as a prospecting tool to inform future management strategies of populations complex within an evolutionary perspective.

Towards a more flexible modeling approach



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6.1 INTRODUCTION

Previous chapters highlighted the potential of our modeling approach to investigate eco-evolutionary dynamics and management of metapopulations, by focusing on the case of Atlantic salmon. However, the version of the model showed some constraints regarding our questions and the growing literature extending knowledge on species life cycle and processes.

In particular, the following elements have been identified:

- the model shows limited applicability for other salmonids species; the values of the species parameters can be changed but this is not easy to access and use. Importantly, the temporal chronology of life history events is imposed and limits flexibility in the life cycle to simulate.
- The model is not truly spatially explicit, since several IBASAM models run in parallel and there are exchange of individuals between them. The absence of explicit exchange of information between populations (e.g., effective density) would not allow for example to add dispersal mechanisms such as density dependent immigration (collective behavior, [Berdahl et al., 2016](#)). Moreover, the model only focuses at the river scale, and not at a finer scale, preventing for example to simulate variable spatial features within rivers (e.g., upstream / downstream, estuary, dendritic networks). Also, it does not provide flexibility on the number of marine sea regions (only one). Yet, multiple marine areas have been identified during sea migration and growth (e.g., Feroe islands and Greenland, with potential variable conditions, [Rikardsen et al., 2021](#)) and it might be relevant to be able to dissociate them and their effects on individuals survival and decisions (e.g., maturation). Within river resolution might also be relevant to be able to integrate and study individuals movement (e.g., spawning ground area choice), genetic structure (e.g., kin distribution), dendritic basins, differential exploitation or other anthropogenic pressures (e.g., commercial fisheries in estuary vs angling in river, estuaries stressors, [Hodgson et al., 2020](#)).
- In the current version of the model, variation in the phenology of life histories is limited, although phenology changes are increasingly and ubiquitously observed in response to global changes ([Woods et al., 2022](#)). For example, several studies reported earlier migration timing in multiple salmonid species ([Kovach et al., 2013](#)), while [Jonsson and Jonsson \(2018\)](#) showed later spawning migration of Atlantic salmon individuals exposed to warmer temperatures during

development. Conversely, [Reed et al. \(2011a\)](#) theoretically showed earlier upmigration timing of sockeye salmon associated with an increased temperature. Providing more flexibility on the life history traits to monitor and model, in particular on their phenology, seems therefore necessary in this context of environmental change.

- More flexibility in the genetic architecture of life history traits of interest would keep the modelling approach in accordance with the recent literature. For example, [Barson et al. \(2015\)](#) showed a major effect locus controlling age at maturity with sex-dependent dominance, potentially reducing intralocus sexual conflict. However, the current genetic architecture of the model does not allow to take into account this key information, because its architecture is based on an infinitesimal model (or polygenic model) without dominance effects. Yet, this particular genetic architecture recently demonstrated in nature might have consequences on evolutionary potential, genetic diversity, and persistence of Atlantic salmon populations ([Kardos and Luikart, 2021](#)) and ultimately have conservation implications ([Waples et al., 2022](#)).
- Last but not least, the current version of our model does not have any end user model interface and can only be used via the execution of scripts as well as for results visualization. This issue may limit the implementation of our modeling approach for management applications and interactions with stakeholders. Indeed, a graphical and intuitive interface allowing simulations parameterization, execution, and main results visualization would be beneficial for the transfer of the model to managers.

To address these different issues, in parallel to the work presented in the previous chapters with *MetaIbasam*, we built a new version of our modeling approach, more flexible, on another platform, *Capsis* (initially developed for research on trees, [Dufour-Kowalski et al., 2012](#)) in collaboration with Jacques Labonne and François de Coligny. This chapter presents the model description following the ODD protocol (Overview, Design concepts, Details, [Grimm et al., 2020](#)), considering that model construction still requires some work and the calibration and sensitivity analyses still have to be performed. The java source code of the model is available on the *Capsis* platform.

6.2 MODEL DESCRIPTION

6.2.1 Purpose and patterns

The main purpose of IBASAM is to forecast how changes in environmental conditions (water temperature, discharge and growth conditions) and selective pressures (e.g., selective fishing) affect eco-evolutionary dynamics of salmonids. We investigate how phenotypic plasticity and genetic adaptation foster the response of populations to environmental changes, especially facing climate change. We also investigate the consequences of the metapopulation functioning via dispersal on the evolution of life history traits, populations stability, persistence and resilience. Ultimately, IBASAM is a tool to explore the effects of different management practices (e.g., spatially defined exploitation/conservation measures) under various environmental scenarios. The model is based on Atlantic salmon life cycle but can be adjusted to mimic other migratory salmonid species.

We evaluate our model by its ability to reproduce observed phenotypic and demographic patterns in a *A. salmon* population. In particular, model results are compared to size/mass distributions at different ages/life stages, life history strategies (i.e., proportion of early maturation, age at sea) and population dynamics (i.e., abundance distributions at different ages/life stages) observed in nature.

6.2.2 Entities, state variables and scales

Entities

The model includes individual agents - called *fish* - and two kinds of collectives - *redd* (spawning nest) and *fry siblings*. Fish are characterized by: an ID, a status (parr, smolt, anadromous), a sex, an age (year and number of days), a weight (W), a body length (L), a fat reserve (Fat), a location (in river, reach or at sea), a binary maturation indicator ($Mature$), a binary smoltification indicator (Sm), a number of returns from the sea ($Nret$), their origin (river and sea region), an intrinsic metabolism influencing the growth rate in river (pG) and at sea ($pGsea$), a proportion of growth attributed to fat reserves ($pPercF$, see section 6.2.7.4) and a genetic material coding (see section 6.2.7.3) for the growth potential, dispersal and maturation thresholds ($pFmid$ see section 6.2.7.7). Fish also record their dates of emergence, of maturation, departure from river, return to river and reproduction.

Redds are created by one mother salmon only during reproduction events in winter

(within a reproduction time window). Redds store identity and genetic material of the mother and different fathers, and the number of fertilized eggs. They also record the cumulative daily water temperature which will influence the date of emergence of the offspring in spring/summer. Then they disappear after producing new fish in the following summer.

Fry siblings are created from Redds at emergence. They correspond to the total of emerging individuals from two parents, i.e., there are as many fry as there are fathers who fertilized the eggs. They stored the identity and genetic material of the two parents. Fry siblings share the same genotype while their phenotype of heritable traits can differ due to recombination and environmental variance. To limit computational time and because fry suffer high mortality during the first weeks after emergence, they are not yet individualized. But fry siblings are also affected by survival, growth and maturation decisions during summer. The surviving fry will be recruited as individual fish at the end of the summer period (*Summer_End_Doy*, Table 6.5).

The model environment is described through its spatial component including rivers (subdivided into reaches separated by weirs) and sea regions (see scales section below), and an environmental component through daily time series of water temperature data, water flows and growing conditions in sea regions (see section 6.2.6).

States

Table 6.4 in supplementary materials describes the entities and their different attributes that can be static or dynamic.

Temporal and spatial scales

The basic time step for all individual processes is daily, with processes happening every day of the year (e.g., growth, survival) and other only during a specific day or time window (e.g., maturation and migration decisions, see Fig. 6.10). Simulation can be run for multiple years to generate multiple generations of the focal species.

While MetaIBASAM is designed to simulate a network of populations by dividing them into several parallel IBASAM processes, this new version of IBASAM is now spatially explicit and can simulate complex watersheds (several rivers and/or interconnected basins) and several marine regions. Rivers are divided into reaches separated by weir (passable or not). Each reach, river and sea region have a specific ID and can be characterized by different carrying capacity and spatial variation of environmental conditions (e.g., water temperature). Note that, the first reach of a

given river is considered as the estuary. An estuary can be shared by multiple rivers. No reproduction can occur in the estuary. As the initial version of Ibasam, the size of the simulated population was scaled to the wetted area of the river expressed in m² of riffle and rapid equivalent area.

6.2.3 Process overview and scheduling

The model is developed to simulate the life-cycle of migratory salmonid species. It is structured in 9 submodels corresponding to life cycle events and processes : 1) reproduction and redd creation, 2) emergence from the redd, 3) genetic coding and transmission, 4) growth, 5) survival, 6) smoltification, 7) sexual maturation, 8) migration and 9) Fishing.

Every day processes are applied depending on location (rivers or sea regions), individuals status (e.g., juvenile vs anadromous, mature), and time (season, time windows). A summary of the processes and submodels is presented below and in Figure 6.1.

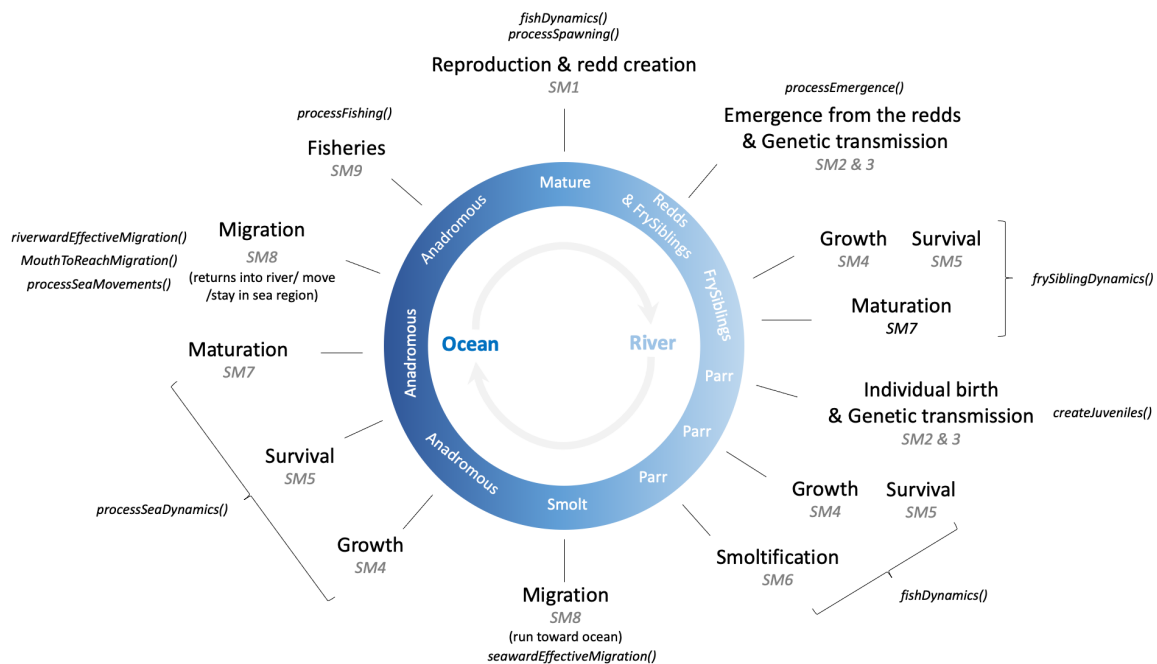


Figure 6.1: Life cycle, submodels (SM) and processes (in italics) of the model.

In rivers:

- *processSpawning* (SM1) : reproduction, sexual selection, and redds creation by mature fish;
- *processEmergence* (SM2): emergence of fry, survival, frysiblings creation and genetic transmission (SM3);
- *processRiverDynamics*: growth (SM4), survival (SM5) and maturation (SM7) for fry siblings (*frySiblingDynamics*) and for individualized fish (*fishDynamics*);
- *createJuveniles* (SM3): individualization of frysiblings to fish.
- *seawardMigrationDecision* : smoltification (SM6);
- *seawardEffectiveMigration* (SM8): Effective migration of smolts during spring (*seawardEffectiveMigrationWindow*), choose each day which fish migrate among the fish which decided to migrate last summer (smolt);
- *mouthToReachMigration* (SM8): Once the fish has returned to the river mouth, first move to another reach;
- *processFishing*: fishing of anadromous returning to river (SM9);

At sea:

- *processSeaDynamics*: growth (SM4), survival (SM5) and sexual maturation (SM7);
- *riverwardEffectiveMigration* (SM8): If the fish are ready to migrate back to river (i.e. mature), they choose which river (philopatry or dispersal) and go to its mouth (estuary).
- *processSeaMovements* (SM8): If the fish is not ready to migrate back to river (i.e. not mature), it changes of sea region or stays in the last.

6.2.4 Design concepts

Objectives and Learning do not apply to the IBASAM model.

- *Basic principles:* The model integrates eco-evolutionary processes, i.e., the interaction between the environment (e.g., temperature effects on survival), demographic processes (e.g., density-dependence, interaction between individuals) and genetics (genetic basis of traits). Processes display at the reach scale within rivers that are interconnected by a dispersal process, and in sea regions for anadromous individuals. Processes run at the daily scale so the phenology of life histories can be monitored.
- *Emergence:* All individual life histories (growth, survival, maturation, smoltification, reproduction) are emerging from a mechanistic description combined with environmental variables, interactions with other individuals, demographic dynamics and genetic structures themselves emerging from individual life histories, i.e. via an eco-evolutionary feedback (see 2).
- *Adaptation:* Maturation decisions and growth potential are adaptive traits which influence individual fitness. They are characterized by a genetic basis (via thresholds) and environmental influence (via environmental cue) favoring adaptative phenotypic plasticity. Smoltification decision is purely plastic and depend only on body size.
- *Prediction:* Individuals use a prediction of their fat reserves during a maturation window to trigger the maturation decision.
- *Sensing:* No sensing mechanisms are explicitly implemented but individuals know their individual/ state variables (e.g., fat reserves) and environment (e.g., river or sea) which drive their life history decisions.
- *Interaction:* Individuals directly interact together during the reproduction and sexual selection process. Indirect interactions via density-dependence effects also occur during competition for shared resources which drive growth and survival.
- *Stochasticity:* Stochasticity emerges from environmental variability in space and time and the random draw of individual probabilities within several processes.
- *Collectives:* At emergence, collectives of frysiblings are created for each pair of parents. Before individualization at the end of summer, all members from each frysiblings share the same genotypes and phenotypes, so that only one average individual representing the siblings undergo growth, survival, and maturation decision.

- *Observation*: All individual traits are recorded at specific time steps (e.g., day 91 and 274 on the julian day calendar of each year) defined at initialization by the user.

6.2.5 Initialization

At initialization, spatial structure, i.e., numbers of rivers and sea regions, locations, reaches and weirs, have to be provided. For each reach, we also provide the wetted area, i.e., riffle and rapid equivalent area (RA in m²) potentially used by salmonids, as well as the module of flow conditions (in m³.s⁻¹), and the fishing rates (for 1SW and MSW individuals, Table 6.2). The genetic architecture also have to be provided (Table 6.3). Mean and variance of traits, heritabilities, alleles frequencies (here set to 0.5), dominance effects (here set to 0), and loci effects are necessary to determine the genetic map. The time windows of life cycle processes (maturation, migration, reproduction) have to be defined, as well as all the populations parameters needed in the submodels (see Table 6.5).

At the beginning of each simulation (*initialDoy*, Table 6.5) a virtual population is created per river with individuals from each individual life stages (parr, smolt, anadromous). Each individual's state variable was initialized by drawing from probability distributions describing their variability (see Table 6.6), and their genotype created to meet average, variance and allele frequency's values of phenotypic traits defined by the user. Collectives (Redds and Fry siblings) are not created at initialization.

All these prerequisites have to be provided in a single file (*IbaParameters*), created via R scripts which will be made available once the model will be finished.

6.2.6 Input data

Two input data files are used in the model: *river climate* and *sea climate*. River climate data consists of daily time series of water temperature (degree-Celsius) and water flows (m³.s⁻¹) for each reach (Table 6.1). Sea climate data consists of daily time series of growing conditions (a variable synthesizing marine environment effects on growth, see section 6.2.7.4) for each sea region. These datasets can be generated, e.g., to simulate scenarios of climate change, or following time-series from observations.

An input data file is also used to define the spatial structure of rivers, indicating reach length and width, position, average flow rate, and fishing rates (Table 6.2).

Table 6.1: Example of data file for river climate. With doy: day of the year (julian day), river : river id, reach: reach id, flow: flow rate (m³.s-1) and temp: water temperature (°C).

year	doy	river	reach	flow	temp
1970	1	1	1	2.39	3.72
1970	2	1	1	2.25	2.84
1970	3	1	1	2.21	2.53
...
1970	1	1	2	2.32	4.02
1970	2	1	2	2.15	2.99
1970	3	1	2	2.11	2.33

Table 6.2: Example of data file for rivers spatial structure. With FR-1SW and FR-MSW the fishing rates of 1SW and MSW individuals.

ID	fatherID	riverID	Area	module	length	width	FR-1SW	FR-MSW
1	1	1	0	0	1000	10	0.5	0.5
2	2	1	100000	4	825	3.5	0.07	0.12
3	3	1	129000	4	500	3.5	0.07	0.12
1	1	2	0	0	120	40	0.5	0.5
2	2	2	150	5	825	10	0.07	0.12
3	2	2	150	5	825	10	0.07	0.12

The genetic architecture of traits is also indicated at initialization in a separated input file (Table 6.3).

Table 6.3: Genetic parameters to provide at initialization.

Trait	μ	CV_P	nloci	nbAllele	h^2	α
matThresholdMaleParr	1.25	0.1	20	2	0.4	0
matThresholdFemaleParr	40	0.12	20	2	0.4	0
matThresholdMaleAnadromous	40	0.8	20	2	0.4	0
matThresholdFemaleAnadromous	85	0.8	20	2	0.4	0
smoltThresholdMale	89	0.1	10	2	0.4	0
smoltThresholdFemale	89	0.1	10	2	0.4	0
riverGrowthPotential	1	0.2	20	2	0.2	0
seaGrowthPotential	1	0.2	20	2	0.2	0
dispersalPropensity	1.4	0.1	20	2	0.2	0

6.2.7 Submodels

IBASAM consists of 9 submodels representing fundamental biological processes.

6.2.7.1 Reproduction and redd creation (SM1)

Reproduction and sexual selection

Reproduction and sexual selection: What's new?

- Spatial scale: per reach instead of river
- Temporal scale: determination of female reproduction date before sexual selection

The reproduction process follows the same procedure as described in (Piou and Prévost, 2012), except that reproduction occurs at reach level (instead of the river, but not in the estuary) during a specific time window (given in julian days as initial parameters by *reproductionWindow*, see Table 6.5 and Fig. 6.2).

At the first day of the reproduction window, sexually mature individuals are pooled in three groups: females (*femalesCandidateForReproduction*, hereafter FC), anadromous males (*anadromousMales*, AM) and mature parr (*precociousMales*, PM). Then, a date of reproduction $DateRepro_i$ was randomly set for each AF according to a Weibull distribution of parameters *shapeDR* and *scaleDR* (Table 6.5) added to the first Julian day of the reproduction window. If a date greater than the reproduction window is selected, the last day of the reproduction window is used. Note that males are considered available for breeding on the first day of the reproduction window.

Each FC was attributed randomly a potential number of AM as potential mates according to a Poisson distribution of parameter *MeanNanadromousMales* (see Table 6.5). FC were sorted along their weight (W) and were attributed in order N_{males_i} specific AM depending on the availability and the relative weight of these AM and the potential number of AM just drawn. If for an AF_i the number of available AM was lower than the potential number of AM then all the available AM were attributed to i . Otherwise, AMs were successively and randomly picked among the available AM with for each of these AM j a probability to be selected following:

$$P[selected|W_j] = \frac{W_j}{\sum_{l=1}^{\infty} W_l} \quad (6.1)$$

where l was an AM among the available ones. Once attributed to an AF, the

weight and Fat of the selected AM were updated by subtracting $LossFatReproAM$ (6.5). The availability of any AM was then re-evaluated and turned to non-available if its updated Fat was lower or equal to 0. AM are thus able to spawn with another female during the same day and the same spawning season, depending on the remaining reserves and post-reproduction mortality. After all AF were attributed their respective AM, each AF obtained a random number $Nparrs_i$ of MP according to a Poisson distribution of parameter $MeanNParrs$ (Table 6.5). $Nparrs_i$ MP were then picked randomly at equal individual probabilities as long as they were available to each AF_i in order of their $DateRepro$.

The MP attributed to an AF was reduced in weight and Fat by a fixed value $LossFatReproParr$ (Table 6.5). Instead of the AM, each MP was dead if its Fat was lower or equal to 0. This structure of female ranking and male attribution to females represented (i) an advantage in reproductive success for larger females through higher availability of AM if they are limited (Fleming et al., 1997), (ii) sexual selection for large AM by females (Fleming, 1996, 1998), (iii) a decreasing availability of MP as the reproductive season unfold and (iv) no sexual selection among the MPs.

Redd creation

After males attribution to females, each AF produced a redd with a date of creation set to $DateRepro$ (see above). A mean egg weight ($EggW_i$) was attributed to the redd depending on the mother i weight following:

$$EggW_i = \frac{\exp(aWegg \times \log(W_i) + bWegg)}{10000} \quad (6.2)$$

where $aWegg$ and $bWegg$ were population parameters (Table 6.5). A number of eggs ($Neggs_i$) was then computed by (Jonsson et al., 1996):

$$Neggs_i = \exp(aNegg \times \log(W_i) + bWegg) \quad (6.3)$$

where $aNegg$ and $bNegg$ were population parameters (Table 6.5). This construction of egg weight and number variability among females represent the documented trade-off on these traits at the individual level (Jonsson et al., 1996).

After this redd creation, the given female i was reduced in Fat by a fixed value $LossFatReproFemale$ weighted by the total egg weight ($EggW_i \times Neggs_i$). In our case, $LossFatReproFemale$ was set to 1, assuming no extra metabolic losses. For a given redd i , each selected father fertilized only a proportion of the $Neggs_i$ eggs. For

an AM j of a redd i the number fertilized ($NFertilized_{j,i}$) depended on the weight regulated competition with all other selected males:

$$NFertilized_{j,i} = \frac{W_j^{aFert}}{\sum_s^{allmales_i} W_s^{aFert}} \times Neggs_i \quad (6.4)$$

where $allmales_i$ represented all the selected male contributing to the redd and $aFert$ (Table 6.5) was a parameter adjusting the competitive advantage due to weight among males (Fleming et al., 1997; Fleming, 1998). Each parr k was attributed an identical fraction of fertilized eggs irrespective of its size because recent works (Jones and Hutchings, 2002; Grimardias et al., 2010a,b) indicated that the individual fertilization proportions of MP was not primarily size-dependent, as some earlier controlled experiments suggested (Thomaz et al., 1997). Thus, the number of eggs fertilized by each parr k for the redd i ($NFertilizedParrs_i$) was:

$$NFertilizedParrs_i = \frac{\sum_k^{Nparrs_i} W_k^{aFert}}{\sum_s^{allmales_i} W_s^{aFert}} \times \frac{Neggs_i}{Nparrs_i} \quad (6.5)$$

Post-reproduction mortality

Anadromous individuals that participated in reproduction had a mortality probability of $ReproMortalityFemale$ for females and $ReproMortalityMale$ for males (Table 6.5) to account for their very high survival cost of reproduction. These mortalities were set to represent the very low second returns rates in French rivers such as the Scorff and the slight advantage of females (Fleming, 1996). The surviving individuals (usually named kelts) were sent back at the first sea region directly after reproduction for females (to avoid multiple reproduction during the spawning season) and at the end of the reproductive window for males (multiple reproductive events within a season possible). The cost of reproduction for MP was considered in the survival attributed afterward (see section 6.2.7.5).

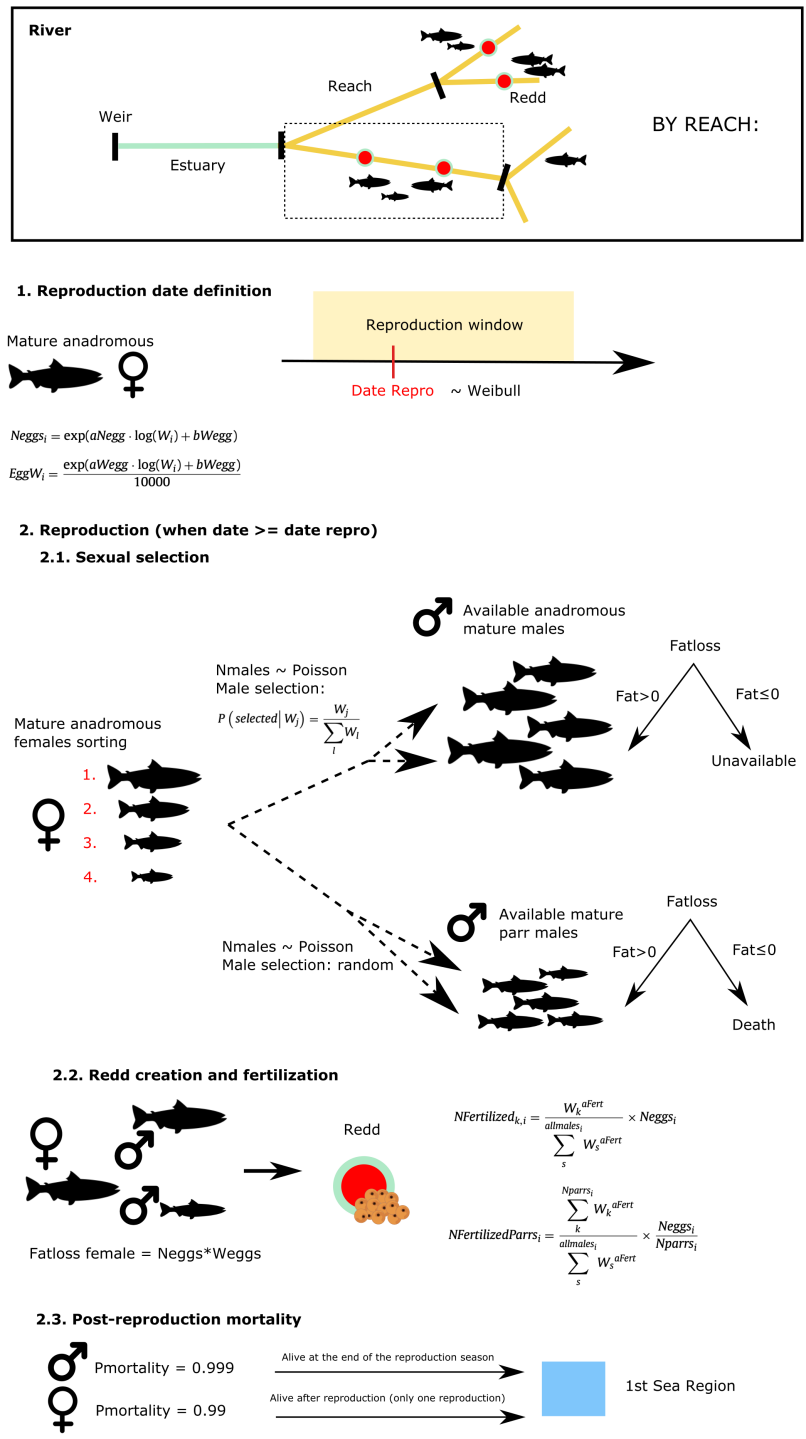


Figure 6.2: Reproduction, sexual selection and redd creation.

6.2.7.2 Emergence from the redds and individual birth (SM2)

Emergence and individualization: what's new?

- Spatial scale: environmental conditions effects at the redd scale and density effects at the reach scale
- Temporal scale: density effects at the daily scale (accounting for the other redds and the already hatched fry in the reach)
- Emerging individuals are not directly individualized and rather emerging as siblings with common initial weight and size

Emergence of frySiblings

For each redd, a date of emergence of the alevins from the gravel of their redd ($DateEmergence_i$) was computed depending on the cumulated daily water temperatures during winter. A degree day (DD) threshold for emergence, $DDEmerge_i$, was chosen from a uniform distribution between $DDEmergeMin$ and $DDEmergeMax$ (Table 6.5). $DateEmergence_i$ was then chosen as the day on which the sum of $T(d)$ (the water temperature for day d) commencing on $DateReprod_i$ exceeded $DDEmerge_i$. In each redd, egg mortality was influenced by reach temperature, flow and a global reach density effect (Fig. 6.3). Thus a survival rate component integrating the temperature effect ($tSurvival_i$) until emergence was computed as:

$$tSurvival_{i,d} = aR \times (T(d) + bR) \times (1 - \exp(cR \times (T(d) - dR))) \quad (6.6)$$

where aR , bR , cR and dR were population parameters (Table 6.5) adjusted to experimental observation of mortality of salmon eggs depending on temperature (Peterson et al., 1977; Gunnes, 1979; Brännäs, 1988). To represent the catastrophic effects of extreme floods and/or droughts during the under-gravel embryo-larval phase, a survival rate component integrating flow effect ($fSurvival_i$) was drawn from a Beta distribution for each redd i :

$$fSurvival_{i,d} \sim Beta \left(aF; aF \times bF \times \max \left(1; \frac{I(flow(d) < cFi \times Module_g)}{I(flow(d) > cFi \times Module_g)} \right) \right) \quad (6.7)$$

where aF and bF were population parameters (Table 6.5) that allows the Beta

distribution to simulate very high or very low survival. The probability to have a low survival was increased by the number of days the $flow(d)$ was below or above critical levels (cFi and cFs respectively, Table 6.5, $Module_g$ the module of the flow at the reach level). Here $I(condition)$ was an indicator function returning 1 when condition is true and 0 otherwise.

Then, the day of emergence, a total number of hatching fry in the redd ($Nhatch_i$) is calculated following:

$$Nhatch_i = Neggs_i \times tSurvival_i \times fSurvival_i \quad (6.8)$$

A density-dependent survival rate affecting all hatching fry of a reach g only at the day of their emergence is then computed using a Beverton-Holt relationship (Beverton and Holt, 1957):

$$gSurvival_g = \min \left(1; \frac{NfryMax}{\frac{NfryTot_g}{S_g} + \frac{1}{aBH} \times NfryMax} \right) \quad (6.9)$$

where aBH and $NfryMax$ are population parameters (Table 6.5), $NfryTot_g$ the cumulated number of hatching fry and parr0+ of the reach g at the day of emergence, and S_g the habitat area of the reach g . Thus, for each redd i the number of offspring of father k ($Noffspring_{k,i}$) was computed as:

$$Noffspring_{k,i} = Nfertilized_{k,i} \times gSurvival_g \times tSurvival_i \times fSurvival_i \quad (6.10)$$

The new emerging individuals of a redd were initialized in the reach at their emergence date as $frySiblings$ (Fig. 6.3). With a sex-ratio of 1:1, female and male frysiblings from a same father were assigned a unique emerging weight Wm_i , drawn from a normal distribution around the mean egg weight of the redd ($EggW_i$) and a fixed variability $sdWm$ (Table 6.5). The Fat was set to 0 and the L computed according to the W-L relationship (see section 6.2.7.4). The genetic material for each frySibling was a recombination of its parents' (see section 6.2.7.3).

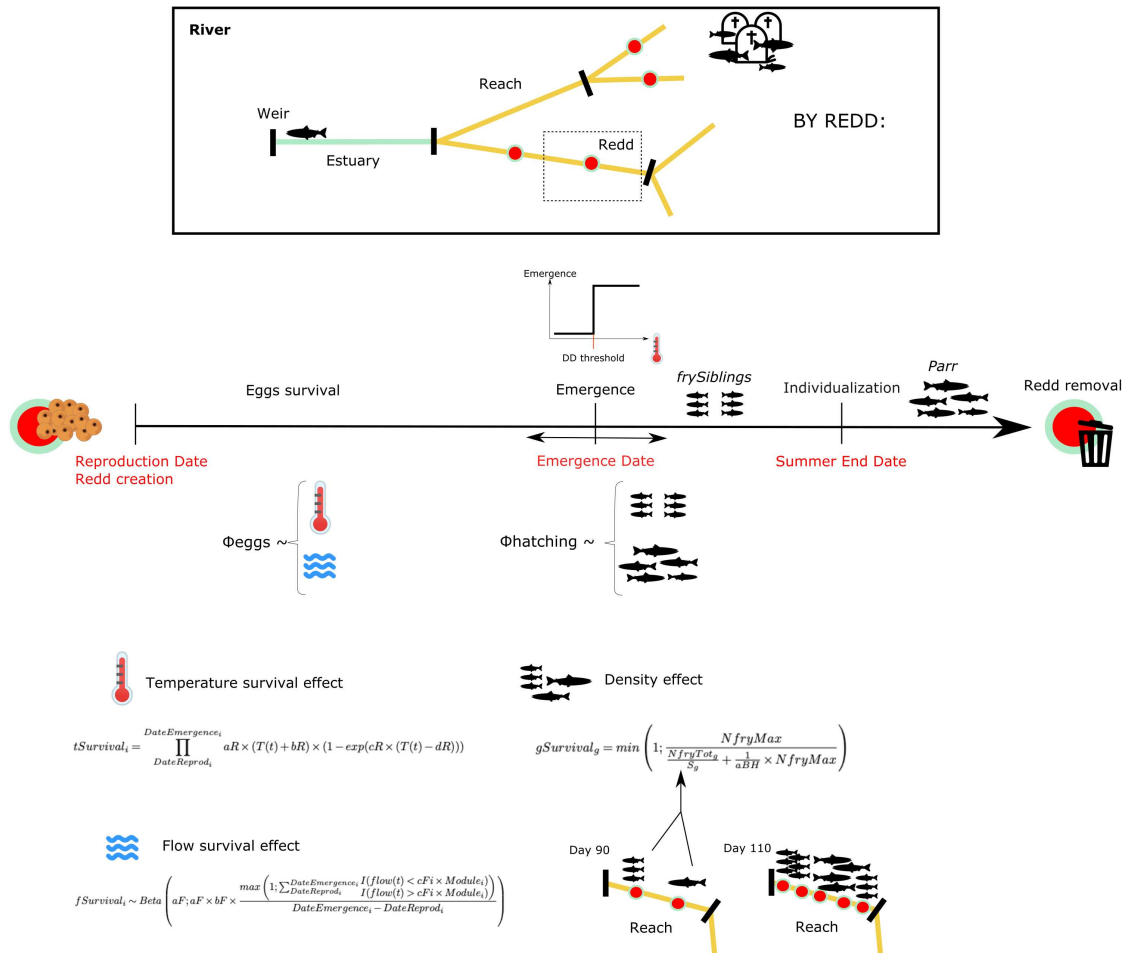


Figure 6.3: Emergence and individualization process.

Individualization

FrySiblings are then individualized into juvenile fish after experiencing growth, survival, and precocious maturation decision (see section 6.2.7.7) at the end of the summer period (*Summer – end – day*, defined as a population parameter, Table 6.5, Fig. 6.3). The genotype and phenotypic expression of others genetic traits are computed at this time and is different across individuals from a same sibling due to genetic recombination and environmental variance.

6.2.7.3 Genetic coding and transmission (SM3)

Genetic coding and transmission: what's new?

- Support a wide range of genetic architecture from a highly polygenic architecture (i.e. many loci with small effects) to a single major locus with or without polygenic background;
- Method to calculate genetic value of trait based on additive allele effects;
- The effects of the loci can differ;
- Dominance effects of alleles are implemented;

Individual traits can be genetically coded and heritable. They are supported by a genetic architecture which is a combination of a quantitative genetic framework with a Mendelian inheritance system (Fig. 6.4). Specifically, the phenotypic expression of a given trait results from the additive effects of its genetic and environmental components ($P = G + E$), with the genotypic value being under a multi-locus bi-allelic control with independent/unlinked loci. Indeed, we do not consider interactions between loci (e.g. epistasis and pleiotropy) in the model but we take into account interactions within loci (i.e. dominance effects). To determine the phenotypic and genetic values of the traits at initialization, we assume that the populations are at Hardy-Weinberg equilibrium and the populations mate randomly (no inbreeding).

Modeling Quantitative Trait Inheritance

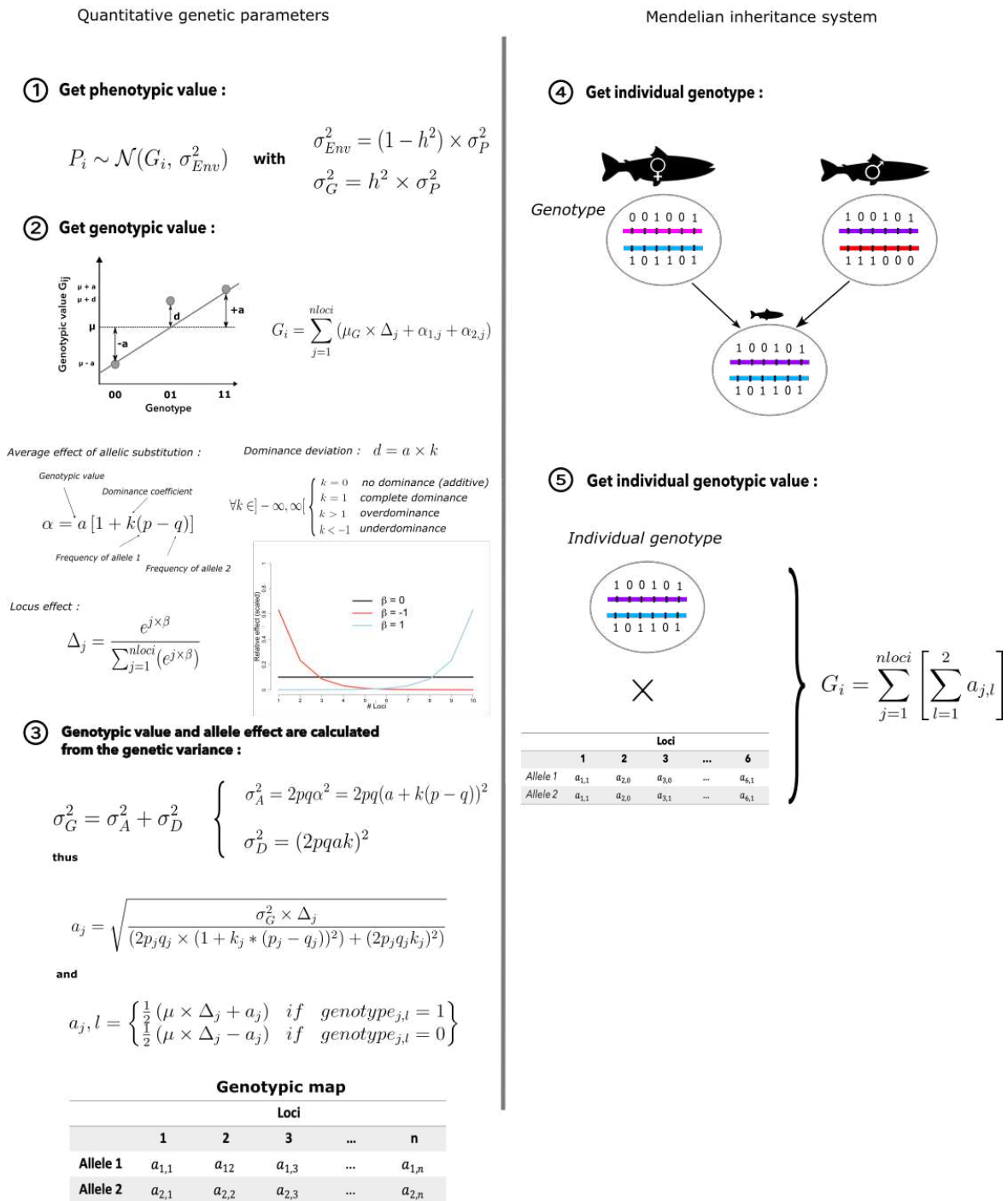


Figure 6.4: Genetic coding and transmission.

Quantitative genetic framework

In IBASAM, individual phenotypic value (P_i) of a given trait is sample in a normal distribution around the genotypic value G_i and with an environmental variance (σ_{Env}^2) as:

$$P_i \sim \mathcal{N}(G_i, \sigma_{Env}^2) \quad (6.11)$$

The genetic and environmental variances are calculated from the total phenotypic variance σ_P^2 and the heritability h^2 :

$$\sigma_{Env}^2 = (1 - h^2) \times \sigma_P^2 \quad (6.12)$$

and

$$\sigma_G^2 = h^2 \times \sigma_P^2 \quad (6.13)$$

Given our initial assumptions (no between loci interactions and random mating), we assume that the genotypic value of an individual i for a given trait G_i is the additive combination of genotypic values of all loci:

$$G_i = \sum_{j=1}^{nloci} \left[\sum_{l=1}^2 \left(\frac{\mu_{g,j} + a_j \times (1 + k_{j,l})}{2} \right) \right] \quad (6.14)$$

with

$$\mu_{g,j} = \mu_G \times \Delta_j \quad (6.15)$$

where $\mu_{g,j}$ is the mean genetic effect at locus j , μ_G the population mean of the phenotypic trait, number of loci $nloci$, allele effects $a_{j,l}$ and dominance coefficient $k_{j,l}$ (with $d = a \times k$) at each locus l . The parameter k specifies the degree of dominance of the favourable allele over the unfavourable/recessive allele. By default $k = 0$, i.e., no dominance is considered but incomplete dominance ($k < 1$), complete dominance ($k = 1$) or over-dominance ($k > 1$) can also be specify at initialization.

Because loci can differ in their influence on genetic value, the average effect of each locus Δ_j is calculated using an exponential distribution :

$$LocusEffect_j = e^{j \times \beta} \quad (6.16)$$

and rescaled:

$$\Delta_j = \frac{LocusEffect_j}{\sum_{j=1}^n LocusEffect_{1:J}} \quad (6.17)$$

The parameter β control the degree of influence of each locus. When $\beta = 0$ all locus carry the same effect on trait (Fig. 6.4). With α decreasing (negative exponential), the first loci tend to have larger effects while many locus carry small effects. Thus, by controlling the number of locus and the parameter α for each trait, IBASAM can support a wide range of genetic architecture from a highly polygenic architecture (i.e. many loci with small effects) to a single major locus with or without polygenic background (i.e. a locus with large effect associated with or without many small effects locus).

Mendelian inheritance system

Thus, to assess the genetic value of an heritable trait G_i in IBASAM, one need to determine the allele effects $a_{j,k}$ and individual genotype associated to the trait. Following Fisher's seminal work on genetics and evolution of complex traits, the genetic variance of a gene (e.g. one bi-allelic locus) σ_G^2 is the sum of the additive genetic variance σ_A^2 and the dominance variance σ_D^2 which depends on the average allele effect α of substituting allele, the frequencies of the two alleles p and q respectively, and the dominance effect d :

$$\sigma_A^2 = 2pq\alpha^2 \quad (6.18)$$

and

$$\sigma_D^2 = (2pqd)^2 \quad (6.19)$$

with

$$\alpha = a[1 + k(p - q)^2] \quad (6.20)$$

Assuming that the genotypes are in Hardy–Weinberg equilibrium, we can determine

the averaged effect of allele α_j of the locus j :

$$\alpha_j = \sqrt{\frac{\sigma_G^2 \times \Delta_j}{(2 \times p_j \times q_j \times (1 + k_j * (p_j - q_j))^2) + (2 \times p_j \times q_j \times k_j)^2}} \quad (6.21)$$

where σ_G^2 is the genetic variance of the trait weighted by the locus-scaled effect Δ_j . The parameters p and q are the frequencies of dominant and recessive alleles 1 and 2 respectively at each locus j , and d_j is the locus-specific dominance value. Note that, when dominance is present, additive variance is an asymmetric function of allele frequencies. Thus, alleles frequencies can influence strongly the genetic value of the trait.

The locus-specific genetic value is then the sum of the two allele-specific genetic value (a_j, l) (under bi-allelic control) with a_j, l determined from the mean of the trait weighted by the locus-scaled effect, the averaged allele genetic value a_j and individual genotypes at locus j :

$$a_j, l = \begin{cases} \mu \times \Delta_j + a_j \times (1 + d_j) & \text{if } genotype_{j,l} = 1 \\ \mu \times \Delta_j - a_j \times (1 + d_j) & \text{if } genotype_{j,l} = 0 \end{cases} \quad (6.22)$$

The individual genotypes (*genotype*) consist of a sequence of 0 (unfavourable) or 1 (favourable) for each allele at each locus.

Initialization of genetic traits

To describe a trait with this structure it is necessary to provide a population mean μ , the variance of the phenotypic value (σ_P^2) (or alternatively the coefficient of variation CV_P) and a heritability value (h^2) at start. The number of loci *nloci*, the degree of influence of each locus α , allele frequencies p and dominance effects d at each locus are also population parameters provided at initialization. A genetic map is then build from these parameters for each heritable traits.

The number of loci (*nloci*) was set arbitrarily to 20 for the present version of IBASAM to avoid the potential of rapid genetic drift by random fixation of alleles in the population. At initialization, the individual genotypes are generated from a Dirichlet distribution, whose parameters control the allele frequencies at each locus and for each traits (here, $p=0.5$). Note that modifying allele frequencies allows to generate variation across populations in genetic traits. Then, for a newly born individual, its genotype derived from the genotype of the parents by simulating the processes of

meiosis and fertilisation using the Genetics library in Capsis.

Due to the high number of loci and the few number of generations simulated (generally <100) we considered that mutation was unimportant and did not implement it. However, natural selection and genetic drift were two potential evolution forces on these genetically coded traits.

In the current version of IBASAM, only threshold values for maturation, growth potential and dispersal were considered genetically coded and heritable. Four respective set of genetically coded maturation thresholds were implemented corresponding to male parr, female parr, anadromous males and anadromous females. These values were transformed respectively to phenotypic expression of the genetic maturation thresholds. By separating genetic thresholds for male and female, one can easily implement major locus effect with polygenic background and sex-dependent dominance on maturation as observed by [Barson et al. \(2015\)](#), [Sinclair-Waters et al. \(2020\)](#), and [Mobley et al. \(2021\)](#).

6.2.7.4 Growth (SM4)

Growth: what's new?

- Growth potential with genetic basis
- Growth of frysiblings and fish
- Competition at the reach scale

Growth was considered primarily to be a weight (W) increase process implemented differently according to location (in river or at sea, Fig. 6.5). For riverine growth of frysiblings or parr individuals, IBASAM used the [Ratkowsky et al. \(1983\)](#) model adjusted to *S. salar* by [Forseth et al. \(2001\)](#) to consider the temperature effect (ΩT_d°). A density-dependent effect ($DensEffect_d$) was also added to this growth function to represent scramble competition often described in salmonid juveniles populations (e.g., [Grant and Kramer, 1990](#); [Imre et al., 2005, 2010](#)). Inter-individual variation in growth rates and seasonal variation in activity depending on life-history was also considered ($activity_i$). The resulting growth function for an individual i on a day d in a reach g was:

$$W_{i,d+1,g} = (W_{i,d,g}^b + b \times \Omega(T_{d,g}^\circ) \times activity_i \times DensEffect_{d,g}/100)^{1/b} \quad (6.23)$$

where b was an allometric parameter for the relation between specific growth rate and W estimated at 0.31 for *S. salar* (Elliott and Hurley, 1995). The temperature effect on growth was computed by:

$$\Omega(T_{d,g}^{\circ}) = \max(0; dr \times (T(d, g) - T_{lr}) \times (1 - \exp(gr \times (T(d, g) - T_{ur})))) \quad (6.24)$$

where d was the day, g the reach, and T_{lr} , T_{up} , dr and gr were population parameters (see Forseth et al., 2001 for details, and Table 6.5 for values). We assumed that scramble competition was only important during summer time steps when growth is highest. During these time steps the density effect was computed as:

$$DensEffect_{d,g} = \frac{1}{1 + \beta dens \times ED_{d,g} \times IWUH_{d,g}} \quad (6.25)$$

where $IWUH_{d,g}$ was an effect of reach flow on competition, $ED_{d,g}$ was the effective density (sensu Post et al., 1999; Imre et al., 2005) of all fry/siblings or parr individuals in the reach g at day d and $\beta dens$ was a population parameter (Table 6.5).

$$ED_{d,g} = \frac{\sum_{i,g}^{N_g} L_{i,g}^2}{S_g \times 10^6} \quad (6.26)$$

where $L_{i,g}$ is the forklength of a fish (or fry/siblings) i in a reach g and S_g the habitat area of the reach in m².

Flow influence on this density effect was introduced as an availability index ($IWUH$) of weighted usable habitat (Capra et al., 1995):

$$IWUH_{d,g} = \max(1; \frac{cFgi \times Module_g}{flow(d, g)}) \quad (6.27)$$

where $cFgi$ was the minimum critical flow level below which density-dependent effects were reinforced (Table 6.5). Activity level of each individual i was depending on its own intrinsic metabolism (pG_i) and its condition and season following:

$$activity_i = pG_i \times activity_{state} \quad (6.28)$$

where $activity_{state}$ was a value depending on the status of the individual and the season. It was always 1 for summer time steps. For winter time steps, it took $activity_{smolt1}$ if i was going to be a 1 yr old smolt in the following spring, $activity_{smoltN}$ if i was going to be an older smolt in the following spring and $activity_{winter}$ if i was

in another state (Table 6.5 for all values). Anadromous individuals back in the river stop feeding when entering into freshwater hence their growth was considered as null in IBASAM.

For oceanic growth, weight increase was following a Gompertz function (close to a von Bertalanffy growth for L) computed for each day d as:

$$W_{i,d+1} = W_{i,d} + \left(Kg \times W_{i,d} \times \log \left(pGsea_i \times \frac{Wmax}{W_{i,d}} \right) \times NoiseSea_d \right) \quad (6.29)$$

where Kg and $Wmax$ were population parameters (Table 6.5), $pGsea_i$ was an individual parameter representing growth capacity and $NoiseSea_d$ was a daily environmental condition for growth at sea which depends on the sea region. For each individual i , whatever its location, a portion of W growth was allocated to Fat reserves:

$$Fat_{i,d+1} = Fat_{i,d} + (W_{i,d+1} - W_{i,d}) \times aPercF_i \quad (6.30)$$

where $aPercF_i$ was an individual parameter calculated as:

$$aPercF_i = pPercF_i + matPercF(Mat_i, sex_i) \quad (6.31)$$

where $pPercF_i$ was a state variable (see state variable Table 6.4) and $matPercF(Mat, sex_j)$ was a function returning 0 if the individual was not mature and returning $matPercF_{males}$ or $matPercF_{females}$ if the individual was a maturing male or female respectively (Table 6.5). Several studies observed a difference in fat content for maturing and non-maturing individuals (Rowe and Thorpe, 1990; Rowe et al., 1991; Simpson, 1992; Dębowski et al., 1999) as well as sexual differences in gonadosomatic indexes (Jonsson et al., 1997). We adjusted the corresponding parameters $pPercF_m$, $matPercF_{males}$ or $matPercF_{females}$ accordingly (see Table 6.5). Body lengths of individuals were adjusted after the growth process following the equation:

$$L_{i,d+1} = \max \left(L_{i,d}; \exp \left(lwa_{stage} + lwb_{stage} \times \log \left(\frac{W_{i,d+1} - Fat_{i,d+1}}{1 - pPercF_m} \right) \right) \right) \quad (6.32)$$

where lwa_{stage} and lwb_{stage} were population parameters of log-log W-L relationships and were equal to lwa_{parr} and lwb_{parr} respectively if the individual had not decided to smolt or lwa_{sea} and lwb_{sea} otherwise (see Table 6.5 for all values). The $pPercF_m$ (Table 6.5) was a population parameter corresponding to the mean population percentage of growth allocated to fat reserves (corresponding to the mean

of $pPercF$). This construction assured that depending on life history chosen by the individuals, they could be of different length for identical weight and, in particular, maturing individuals would spend more energy in building fat reserves than on increasing their length.

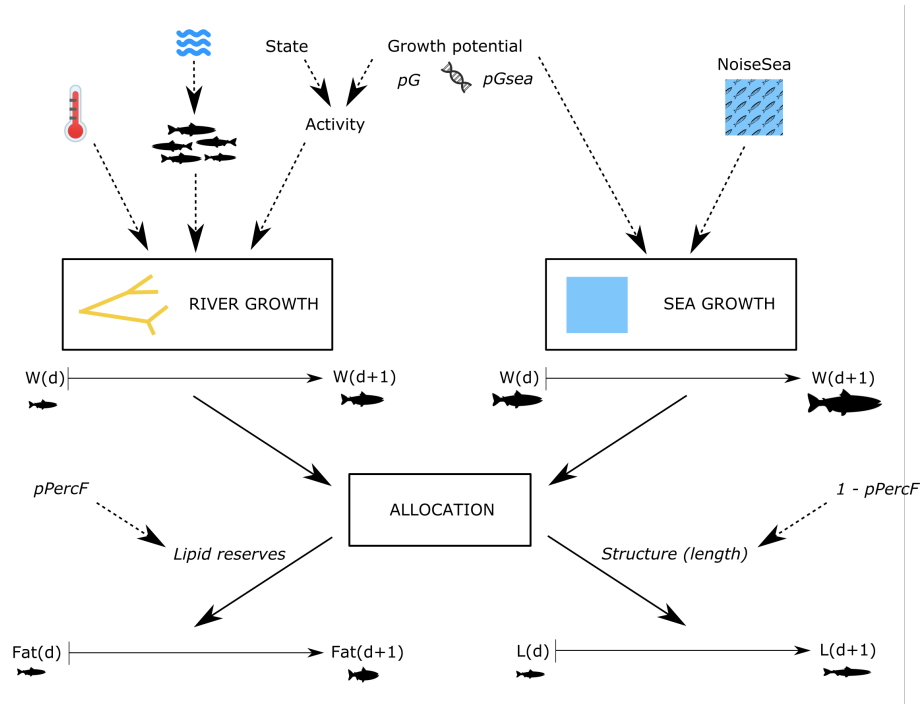


Figure 6.5: River growth, sea growth, and allocation processes.

6.2.7.5 Survival (SM5)

Survival: what's new?

- Survival rates adjusted (new values)
- Trade-off between survival and growth
- Survival of fry/siblings and fish
- Daily survival probability so densities are evolving daily (density-dependent)

In river, the daily survival probability ($Sp_{i,d}$) of an individual i at day d , depending on its age and maturing status, is mitigated by its phenotypic growth potential (in log

scale pG_i) through a growth-survival trade-off coefficient ($CoeffSurvRIV_i$) according to the Equation 6.33, 6.34, and 6.35.

$$Sp_{i,d} = Sp_{i,d}^{status} \times CoeffSurvRIV_i \quad (6.33)$$

Where $Sp_{i,d}^{status}$ can take one of the population parameters survival values as function of the individual i status at day d (Piou and Prévost, 2012).

$$CoeffSurvRIV_i = \frac{\exp(-kappaRIV \times pGres_i^{sigRIV}) - \exp(-kappaRIV)}{1 - \exp(-kappaRIV)} \quad (6.34)$$

$$with pGres_i = \min(1, \frac{\exp(pG_i)}{maxRIV}) \quad (6.35)$$

Where $maxRIV$, $sigRIV$ and $kappaRIV$ are populations parameters. Since the literature regarding growth-survival trade-offs is limited (but see Bochsansky et al., 2005; Biro et al., 2006), the values of these parameters (Table 6.5) were adjusted based on anadromous returns number and size distributions monitored on the Scorff river that were used for calibrating IBASAM (Piou and Prévost, 2012).

Consequences on life-history traits evolution

Implementing the growth-survival trade-off in river limited the evolution of growth potential genetic value and adult size towards high values, as showed by MetaIBASAM simulations on the Scorff river only (without dispersal) with and without the trade-off (Fig. 6.6).

At sea, survival of anadromous individuals has been showed to be strongly related to their size (Salminen, 1997; Gregory et al., 2019), thus sea survival is mainly size dependant in our model. However, a growth-survival trade-off at sea is also implemented and mitigate sea survival. For each day d a daily survival probability ($Sp_{i,d}$) was computed as (Mangel, 1994):

$$Sp_{i,d} = (1 - \alpha S \times \frac{L_{i,d}}{\exp(lwa)} \frac{\beta S}{lwb})^{1/30} \times CoeffSurvSEA_i \quad (6.36)$$

where αS and βS (Table 6.5) were population parameters.

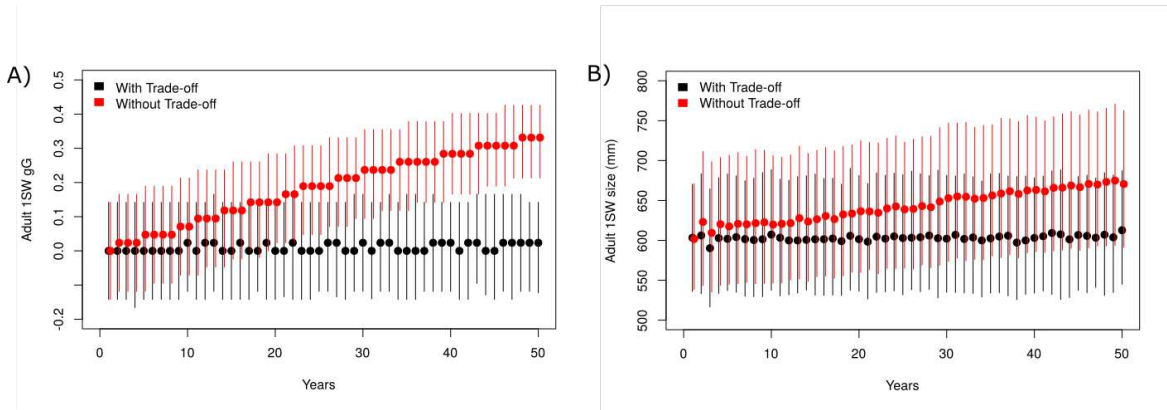


Figure 6.6: Temporal evolution of (A) growth potential genotypic value (in log scale) and (B) 1SW adult size in 10 simulations of one population (Scorff) with (black) and without (red) growth-survival trade-off implemented in the model.

with

$$CoeffSurvSEA_i = \frac{\exp(-kappaSEA \times pGseares_i^{sigSEA}) - \exp(-kappaSEA)}{1 - \exp(-kappaSEA)} \quad (6.37)$$

with

$$pGseares_i = \min(1, \frac{\exp(pGsea_i)}{maxSEA}) \quad (6.38)$$

Where $maxSEA$, $sigSEA$ and $kappaSEA$ are populations parameters. In our case, the values of these parameters (Table 6.5) were set so there is no growth-survival at sea ($CoeffsurvSEA=1$).

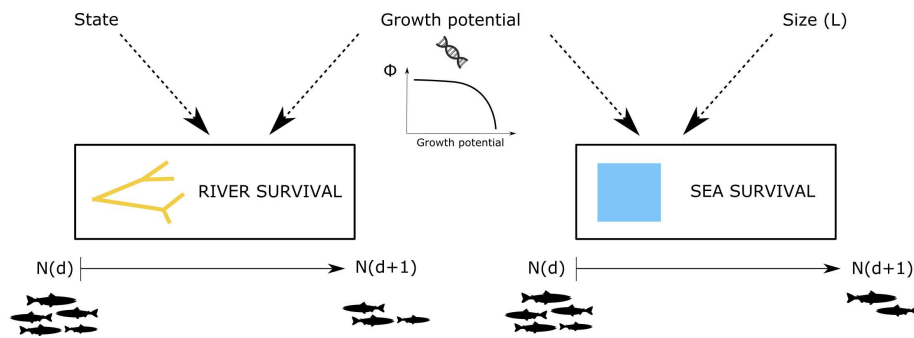


Figure 6.7: Process of survival in river and sea.

6.2.7.6 Smoltification (SM6)

Smoltification: what's new?

- Window for migration decision (here last day of summer) and for effective migration (spring)
- By default, plastic decision based on body size but genetic basis of smoltification threshold also implemented

Individual parr need to undergo a smoltification process to be able to leave the river the following spring. It is well documented that this physiological, behavioural and morphological process is a function of individual growth (Thorpe, 1977) and that it is initiated much earlier than actually visible (see reviews of McCormick and Saunders, 1987; McCormick et al., 1998). It was therefore opted for a initiation time at the end of summer (*seawardMigrationDecisionWindow*, according to Debes et al., 2020, Table 6.5) with an actual seaward migration during the following spring (as in Thorpe et al., 1998, see section 6.2.7.8). We used the probabilistic reaction norm depending on body length and adjusted by Buoro et al. (2010) on the Scorff to simulate this process. An individual parr i becomes a future smolt following the relation:

$$\text{logit}(P(Sm_i = 1)) = aSm \times (L_i - LmidSm) \quad (6.39)$$

where aSm and $LmidSm$ (Table 6.5) were population parameters and Sm_i was the binary indicator state variable. The inter-individual variation for an identical L was considered in the probabilistic aspect of this implementation.

6.2.7.7 Maturation (SM7)

Maturation: what's new?

- Earlier time window for anadromous maturation decision (in summer) according to Tréhin et al. (2021)
- More variability in timing of decision for precocious maturation depending on emergence date

Maturation is considered as an underlying process of energy allocation of individuals. We adopted the conceptual framework of maturation decision proposed by Thorpe et al. (1998) based on a time window evaluation of the rate of

change in lipid content and a comparison of a projected lipid content at a given time horizon with a threshold (Fig. 6.8). This approach was implemented in IBASAM and considers genetic variability of maturation thresholds (Piché et al., 2008). For an individual i , the binary indicator Mat_i was set to 1 when a $ProjectedFatTheory_i$ was above the phenotypic expression $pFmid_i$ of the genetically coded threshold of maturation $gFmid_i$. The $ProjectedFatTheory_i$ was calculated as a linear projection of Fat_i at the end of the maturation projection time window, but the decision of maturation is taken at the end of the evaluation time window. For sexual maturation of parr (precocious maturation), the evaluation time window is set at the frySiblings stage after emergence (between $emergenceDate$ and $emergenceDate+nDaysWindowRiverMaturation$) and the projection time window is set at the end of summer ($nDaysProjectionRiverMaturation$, Table 6.5) according to Thorpe et al. (1998). For anadromous individuals, the evaluation time window is now set at summer according to Tréhin et al. (2021) ($riverwardMigrationDecisionWindow$) with a projection set to the following spring ($nDaysProjectionSeaMaturation$, Table 6.5). As explained in SM3, the maturation thresholds $pFmid$ used for an individual was depending on sex and location (i.e., river vs ocean).

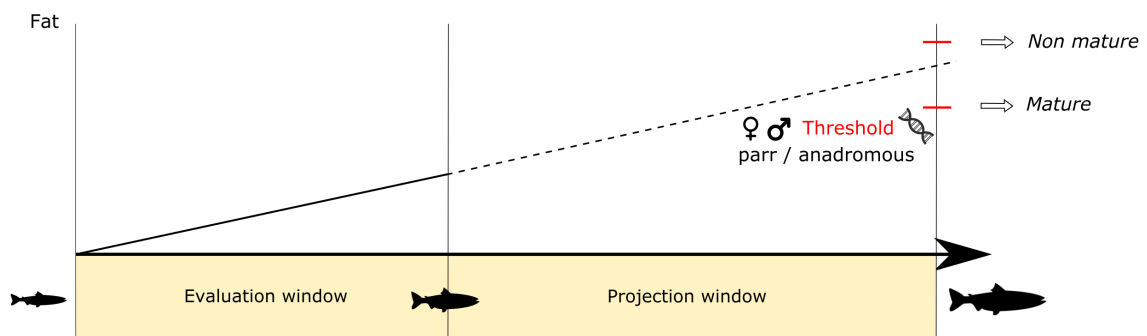


Figure 6.8: Maturation process.

6.2.7.8 Migrations (SM8)

Migrations: what's new?

- Time window for seaward effective migration (spring) with a daily migration decision of fish which decided to migrate last summer (smolts)
- Riverward migration: dispersal process, estuary, and reach choice
- Movement between sea regions

Our model considers two migration phases (Fig. 6.9): seaward migration of smolts and riverward migration of anadromous fish. The effective migration takes place long after the decision to migrate was made (smoltification in the river and maturation at sea) and therefore the effective migration depends on the status of individuals, i.e. *smolt* and *mature* respectively.

Seaward migration

First, the seaward migration occurs during a seaward time window (*seawardEffectiveMigrationWindow*) in spring that is defined as population parameters (see Table 6.5). Each day, the individuals called *smolts* can initiate their migration according to a random sampling in a Bernoulli distribution following a probability *pSeawardMigration*. Then, the migrating smolts are sent to the first sea region. Smolts that have not migrated by the last day of the window are sent directly to the first sea region. They change their status and become *anadromous*.

Riverward migration and dispersal

After maturation decision of anadromous, i.e. the individual status is *mature*, each mature anadromous check every day if it is ready to migrate to the river from its sea region (*isReadyForRiverwardMigration*). This process depends on a number of days which varies according to the age of maturation (*riverwardMigrationTime_{oneSeaWinter}* and *riverwardMigrationTime_{multipleSeaWinters}* are population parameters), i.e. if the fish has been mature for X days. If the fish is not ready to migrate back to river (not *mature*) by the end of the *riverwardMigrationDecisionWindow*, it changes sea region or stays in the last via the sea movement process (*processSeaMovements*).

For fish ready to migrate back to the river, they must choose between returning to

their natal river (also called *homing*) or disperse to another river following a dispersal process. Here, we decompose the process into two steps: 1) decision to disperse or not, and 2) for the dispersers, choice of the recipient population (river).

First, at the time of adult riverward migration, the decision of an individual to disperse is based on an individual parameter $aDisp_i$ (Equation 6.40) which can be fixed or variable as function of individual or population features (e.g., genetic basis, age at maturation, population density).

$$\text{logit}(P(Disp_i = 1)) = aDisp_i \quad (6.40)$$

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' . The probability $p_{j,j'}$ is based on a dispersal kernel that depends on distance from the natal river estuary ($D_{j,j'}$) and the attractiveness of the recipient population (see Nathan et al., 2012 for review). We use the Laplace distribution, a leptokurtic distribution commonly used for fish (Pépin et al., 2012), which maximizes the connectivity between close populations while still allowing some flow of individuals between distant rivers (long-distance dispersal, Equation 6.41). 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 6.42). The larger the populations, the more attractive they are to dispersing individuals.

$$p_{j,j'}(D_{j,j'}, b) = g_{j'} \times \frac{1}{2b} \times \exp\left(-\frac{D_{j,j'}}{b}\right) \quad (6.41)$$

$$\text{with } g_{j'} = \frac{\log_{10}(N_{j'})}{\sum_{j'=1}^n \log_{10}(N_{j'})} \quad (6.42)$$

With b the mean dispersal distance in the metapopulation and $N_{j'}$ the number of returning adults (philopatric) to the river j' .

Finally, the fish (dispersers and no dispersers) is moved to the mouth of the selected river (estuary).

Movement within the river (mouthToReachMigration)

Once the fish has come back in the river mouth, it stays for one day only and then move randomly toward one of the reach of the river (except the river mouth).

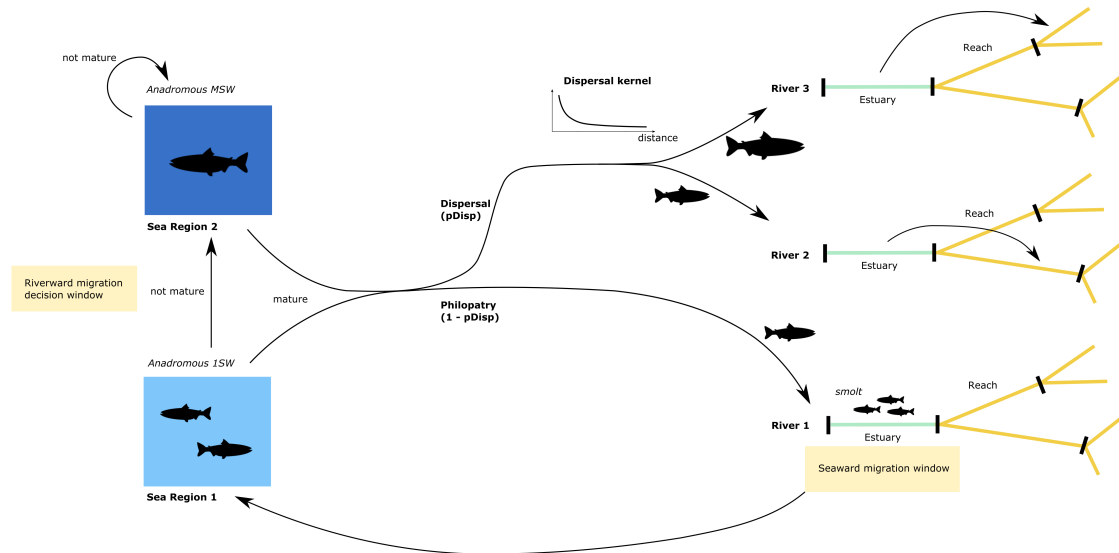


Figure 6.9: Migration processes.

6.2.7.9 Fishing (SM9)

Fishing: what's new?

- Fishing rates variation between estuary and reaches, in addition to variation between age at maturation
- Commercial fisheries applied for one day in estuary
- Angling applied during one day or a time window after all anadromous are back in river

Fishing is now at the reach scale, allowing the implementation of various rates or selective pressures of fishing depending on the spatial location of fish. For instance, commercial fishing in estuary can now be separated from angling in upper river reaches. Fishing rates can still be differentiated between life histories such as 1SW and MSW. Fishing rates have to be provided by reach at initialization.

Commercial fishing is applied during one day when fish migrate through the estuary, while angling can be applied during a time window or a single day.

6.3 DISCUSSION

6.3.1 Model structure and innovations

This new version of our modeling approach thus addresses the gaps identified in Introduction. First, the spatial resolution, at the reach level, enables to work at multiple spatial scale, from within river variation of habitats, to metapopulation structure. Also, the spatial explicit construction of basins allow real time transfer of information between populations (e.g., of density), which was not possible with the previous version of the model because several processes ran in parallel. Second, the daily temporal scale of the model and time windows structure of processes provides flexibility to simulate different salmonid life cycle and to study phenological traits. Third, the flexible genetic architecture open up new perspectives on the evolution of life history traits, and more flexibility on dispersal mechanisms is also possible. Finally, code and libraries sharing is possible with a community of modelers on the Capsis software, and an interface facilitates the use of the model by managers and the parameterization of the model for various contexts (e.g., different spatial structures) or different species. In our case, the model is being parameterized based on Atlantic salmon and the Scorff population because of the amount of data available, but may be easily adapted to other populations or species.

6.3.2 Perspectives

However, perspectives of improvement of this new version may already be envisaged, as indicated by the lens icon on the figure 6.10.

6.3.2.1 Reproduction and sexual selection

Jonsson and Jonsson (2009) indicated potential variability in spawning time arising from plastic response, e.g. from temperature dependent gonad development, or from adaptive response resulting from a significant heritability of spawning time (*Stewart et al., 2002*). In the model, a genetic basis for the date of reproduction, or an effect of the water temperature, could be reasonably implemented.

Regarding sexual selection, instead of being fixed, the number of males chosen by the female could be influenced by the real density of fish available in the reach to better represent the probability to find a partner. This process could particularly influence reproduction success in small or imperiled populations where spawners density might be low.

6.3.2.2 Emergence

The timing of emergence is also an important phenological trait which may have a genetic basis and may be under stabilizing selection (Einum and Fleming, 2000; Carlson and Seamons, 2008). In the model, a genetic basis for the temperature threshold determining the date of emergence could be implemented.

6.3.2.3 Smoltification and seaward migration

In the model, the smoltification decision is based on a probabilistic reaction norm depending on body length. Thériault et al. (2008) also represented a migration reaction norm in their model of brook charr, describing an individual probability of migrating to the sea as function of the age and body length. However, four inherited parameters modulated these effects, assuming a genetic basis of migration. This is in line with a significant body of literature suggesting a governance of migration phenotype by strong genetic effects, interacting with phenotypic (body size) and environmental effects (in Atlantic salmon, Debes et al., 2020, in rainbow trout, Hecht et al., 2013, 2014). However, this genetic basis of migration could be strongly related to that of individual growth potential (Debes et al., 2020), which already have a genetic basis in the model. Kelson et al. (2020) also suggested an indirect genetic basis of migration in rainbow trout mediated by physiological traits such as growth rate. The option of adding a genetic basis to smoltification thus remains an open question.

Once the smoltification process is engaged, the effective migration towards the sea occurs the following spring at a date which is defined within a time window according to an individual probability fixed. However, a genetic, phenotypic and environmental influence on the migration timing of smolts have been reported in the literature. Local adaptation of migration timing have for example been reported in two populations of Atlantic salmon (Stewart et al., 2006). Body size, rather than age, also seems to be a driver of migration timing differences, as well as energetic status (brown trout, Bohlin et al., 1996; Birnie-Gauvin et al., 2021). Environmental conditions, i.e. the temperature and water level, explained a significant part of variation in

migration timing of brown trout (Bohlin et al., 1993), Chinook (Sykes et al., 2009) and Atlantic salmon (Jonsson and Ruud-Hansen, 1985) smolts. Considering the factors influencing migration timing is particularly important because variation in migration patterns could reinforce the portfolio effect and the stability of species facing changing environment (Carr-Harris et al., 2018; Schindler, 2019). Allowing more phenological diversity in our modelling approach is now feasible and might opens up new perspectives of theoretical work in a context of climate change.

6.3.2.4 In river movements

The study of in river movements is now possible with the new model version, giving opportunity to explore the consequences of individual variation in spawning or growth areas. For example, Hendry et al. (2001a) provided evidence that individual condition may influence the choice of breeding location in sockeye salmon, which may affect reproductive success. Bouchard et al. (2018) also showed strong aggregation of A. salmon nests, likely resulting from an ideal distribution of females, and this spatial distribution diminished the variability of population recruitment. Evaluating the demographic, genetic and evolutionary (life history traits diversity) consequences of the spawning reach for returning adults (e.g., natal reach vs ideal free distribution), or the growth reach for juveniles (e.g., function of the density) may constitute a future avenue of research with our modelling approach.

6.3.2.5 Energy allocation

The structure of DEB (Dynamic Energy Budget) theory is such that there is a splitting of individual energy between reserves and structures, which are key features driving fitness related life history strategies, such as migration (depending on body size) and maturation (depending on fat reserves, Kooijman and Kooijman, 2010). In the current version of the model, a fixed parameter drives this trade-off of energy allocation. Yet, seasonal energy allocation likely has a genetic basis (Schultz and Conover, 1997), and energy allocation might constitute a key individual trait under selection, which might evolve in response to evolutionary changes in acquisition strategies. Adding a genetic basis to this trait, such as in the DG ABM of Ivan and Höök (2015), might be relevant to study the response of species and life history diversity to environmental change.

6.4 SUPPLEMENTARY MATERIALS

Table 6.4: Entities and variables of the model.

Entities	Variable name	Variable type and units	Meaning
	<i>id</i>	numeric, static	Unique identifier
	<i>female</i>	boolean, static	Sex
	<i>state</i>	nominal, dynamic	Life history state (parr, smolt, anadromous)
	<i>age – days</i>	numeric, dynamic	Age in days
	<i>forklength</i>	numeric, dynamic, mm	Body size
	<i>weight</i>	numeric, dynamic, gram	Mass
	<i>fat</i>	numeric, dynamic	Fat reserves
	<i>pPercF</i>	numeric, static	Fat allocation parameter
Fish	<i>fatAtBeginRiverMaturation,</i> <i>fatAtBeginSeaMaturation</i>	numeric, static	Fat reserves before maturation decision
	<i>emergenceDate</i>	date, static	Date of emergence
	<i>maturationDate</i>	date, static	Date of maturation
	<i>departureDate</i>	date, static	Date of seaward migration
	<i>returnDate</i>	date, static	Date of riverward migration
	<i>reproduced</i>	boolean, dynamic	Reproduction indicator
	<i>spawningCount</i>	numeric, dynamic, count	Number of reproduction events
	<i>iteroparous</i>	boolean, dynamic	Indicator of iteroparity
	<i>nEggsForReproduction</i>	numeric, dynamic, count	Number of eggs of mature female
	<i>mId, pId</i>	numeric, static	Parents identifiers
	<i>genotype</i>	vector, static	Genotype

Continued on the next page

Entities	Variable name	Variable type and units	Meaning
	<i>maturatationThresholdMaleParr</i> , – <i>FemaleParr</i> , – <i>MaleAnadromous</i> , – <i>FemaleAnadromous</i> , <i>smoltificationThresholdMale</i> , – <i>Female</i> , <i>riverGrowthPotential</i> (pG), <i>seaGrowthPotential</i> (pGsea)	numeric, static	Phenotypic values of genetic traits
	<i>birthRiverId</i> , <i>birthReachId</i>	numeric, static	Identifiers of river and reach of birth
	<i>atSea</i>	boolean, dynamic	Location (sea/ river)
	<i>seaRegionId</i>	numeric, dynamic	Location (which sea region)
	<i>lastNumberOfSeaWinters</i>	numeric, dynamic, count	Number of winter at sea during the last migration
	<i>durationInSea</i>	numeric, dynamic	Total number of winters at sea
	<i>durationInRiverAsParr</i>	numeric, dynamic	Number of years in river for juveniles
FrySibling	<i>id</i>	numeric, static	Unique identifier
	<i>female</i>	boolean, static	Sex
	<i>number</i>	numeric, dynamic	Number of frysiblings
	<i>age – days</i>	numeric, dynamic	Age in days
	<i>forklength</i>	numeric, dynamic, mm	Body size
	<i>weight</i>	numeric, dynamic, gram	Mass
	<i>fat</i>	numeric, dynamic	Fat reserves
	<i>pPercF</i>	numeric, static	Fat allocation parameter
	<i>emergenceDate</i>	date, static	Date of emergence
	<i>maturatationDate</i>	date, static	Date of maturatation
	<i>genotype</i>	vector, static	Genotype

Continued on the next page

Entities	Variable name	Variable type and units	Meaning
	<i>maturityThresholdMaleParr,</i> <i>–FemaleParr,</i> <i>riverGrowthPotential</i>	numeric, static	Phenotypic values of genetic traits
Redds	<i>mId</i>	numeric, static	Unique identifier (of the female)
	<i>eggNumber</i>	numeric, dynamic, count	Number of fertilized eggs
	<i>pContribution</i>	matrix, static	pId and fertilized number of eggs of fathers
	<i>DDemerge</i>	numeric, static	Emergence temperature threshold
	<i>cumulatedWaterTemperature</i>	numeric, static, Celsius	Cumulated water temperature from redd creation
	<i>wEggs</i>	numeric, static, gram	Mean egg weight

Table 6.5: IBASAM parameter descriptions and selected values required in the submodels.

Submodel	Parameter type	Parameter name	Value	Remarks
SM1	Time window for reproduction	<i>reproductionWindow</i>	[322,5]	-
	Mean number of anadromous and parr males fertilizing the eggs of 1 female	<i>MeanNMales</i> , <i>MeanNParrs</i>	3, 10	Observations from the Nivelle River, Southwest France Adjusted
	Fat reserves lost after anadromous, parr males and females reproduction participation (g)	<i>LossFatReproAM</i> , <i>LossFatReproParr</i> , <i>LossFatReproFemale</i>	73, 3, 1	Adjusted
	Weibull distribution parameters for date of reproduction	<i>shapeDR</i> , <i>scaleDR</i>	3.598, 38.24	Adjusted from the Nivelle River
	Parameters for mean egg weight calculation from female weight	<i>aWegg</i> , <i>bWegg</i>	0.168, 5.68	—
	Parameters for number of eggs calculation from female weight	<i>aNegg</i> , <i>bNegg</i>	0.86, 1.63	—
	Weight importance parameter for males participation in fertilization	<i>aFert</i>	0.5	Adjusted to obtain 40% of parr fertilization with mean size and numbers from Scorff
	Mortality rates post-reproduction	<i>ReproMortalityFemale</i> , <i>ReproMortalityMale</i>	0.99, 0.999	—

Continued on the next page

Submodel	Parameter type	Parameter name	Value	Remarks
SM2	Degree-days necessary from fertilization to emergence	$DDmergeMin, DDmergeMax$	880, 920	Prouzet and Gaignon (1982)
	Parameters to relate water temperature to egg survival	aRt, bRt, cRt, dRt	0.00019346, 5161.93, 0.608211, 19.055	Adjusted to observations from Peterson et al. (1977), Gunnes (1979) and Brännäs (1988).
	Parameters to relate water flow to egg survival	aF, bF	0.01, 100	Adjusted to Scorff data.
	Critical flow influencing on egg survival	cFi, cFs	0.1, 7	Adjusted to Scorff data and selected most optimistic values
	Beverton-Holt stock-recruitment asymptote and slope	$NfryMax, aBH$	3.21/m ² , 1	Estimated from Scorff data
	Coefficient of variation of weight distributions at emergence	$sdWm$	0.034	Fleming et al. (1996), Assume an identical variation for emerging weight than eggs weight
	Mean and standard deviation at population level of individual capacity to store growth into fat reserves pPercF	$pPercFm, pPercFsd$	0.12, 0.01	Rowe et al. (1991), Dêbowski et al. (1999)

Continued on the next page

Submodel	Parameter type	Parameter name	Value	Remarks
SM4	Minimal, maximal and parameter regulating the optimum temperature for growth	T_{lr}, T_{up}, gr	6.0, 24.5, 0.208	Forseth et al. (2001)
	Growth speed according to temperature	dr	0.5	Adjusted (chapter 3)
	Density-dependent growth regulating parameter	β_{dens}	142.7	Adjusted to Scorff data
	Critical flow reinforcing density-dependent effect on growth	cF_{gi}	0.2	Adjusted to Scorff data and selected most optimistic values
	Winter activity of young of the year future smolt, future smolt of more than a year and other parr	$activity_{smolt1}$, $activity_{smoltN}$, $activity_{winter}$	0.725, 0.188, 0.1	Adjusted to Scorff data
	Parameters for the Gompertz growth function at sea	Kg, W_{max}	3.057074E3, 8500	Adjusted
	Supplementary percentage of growth allocated to fat reserves during maturation phases for males and females	$matPercF_{males}$, $matPercF_{females}$	0.04, 0.18	Adjusted

Continued on the next page

Submodel	Parameter type	Parameter name	Value	Remarks
	Log-log weight-length relationships parameters for parr or smolt and anadromous individuals	$lwa_{parr}, lwb_{parr}; lwa_{sea}, lwb_{sea}$	3.804, 0.32; 3.82568, 0.333779	lwa_{parr} and lwb_{parr} adjusted to W-L data from parr of the Scorff river. lwa_{sea} and lwb_{sea} adjusted to Vibert (1950) data (for a wider range).
SM5	Daily survival probability depending on stage of individuals	$Sp0+, Sp1, Sp1Mat, Sp1Smolt, SpMat, SpN, SpAnad$	0.9866210015, 0.9934226796, 0.98879532375, 0.9987858846, 0.9931621596, 0.9997455, 1	Adjusted on Scorff data for SpN
	Parameters for length dependent survival at sea	$\alpha S, \beta S$	2.533333, -0.524	Adjusted
	Maximum growth rate in river and sea	$maxRIV, maxSEA$	5, 50	adjusted to Scorff
	Shape of the river trade-off function	$sigRIV, kappaRIV$	3.7, 0.001	adjusted to Scorff
	Shape of the sea trade-off function	$sigSEA, kappaSEA$	100, 0.001	adjusted to Scorff
SM6	Time window for smoltification decision	$seawardMigration-DecisionWindow$	[274,274]	-
	Population level smoltification reaction norm parameters	$LmidSm, aSm$	89.03333, 0.15	Buoro et al. (2010)
SM7	Time window for sexual maturation for parr	$nDaysWindow-RiverMaturation, nDaysProjection-RiverMaturation$	61, 122	Thorpe et al. (1998)

Continued on the next page

Submodel	Parameter type	Parameter name	Value	Remarks
	Time window for sexual maturation for anadromous	<i>riverwardMigration-DecisionWindow, nDaysProjection-SeaMaturation</i>	[274,321], 135	Tréhin et al. (2021)
SM8	Time window for seaward migration of smolts in spring	<i>seawardEffective-MigrationWindow</i>	[91,120]	Adjusted on Scorff
	Probability to migrate to sea, i.e. departure (daily)	<i>pSeawardMigration</i>	0.9	Adjusted on Scorff
	Numbers of days before riverward migration	<i>riverwardMigration-TimeOneSeaWinter, riverwardMigration-TimeMultipleSeaWinters</i>	254, 134	Adjusted on Scorff
	Parameters for Laplace kernel	μ	0.0	Adjusted so that >80% of migrants disperse into the first 50km, Keefer and Caudill (2014)
	Mean dispersal distance (dispersal kernel parameters)	b	29.5	Adjusted so that >80% of migrants disperse into the first 50km, Keefer and Caudill (2014)
Other	Date of end of summer	<i>Summer – end – day</i>	274	-
	Initial date (year and julian day) for simulation	<i>initialYear, initialDoy</i>	1995, 267	-

Table 6.6: IBASAM parameter descriptions and selected values for individuals initialization.

Life stage	N	Wm (sd)	Fatm (sd)	FemaleProb	MatureProb
Parr 0+	10740	8 (1)	1.25 (0.2)	0.5	0.05
Parr 1+	500	7.7 (1.8)	0.64 (0.28)	0.5	0
1SW	651	2500 (500)	370 (100)	0.467	1
MSW	40	4560 (760)	590 (110)	0.81	1

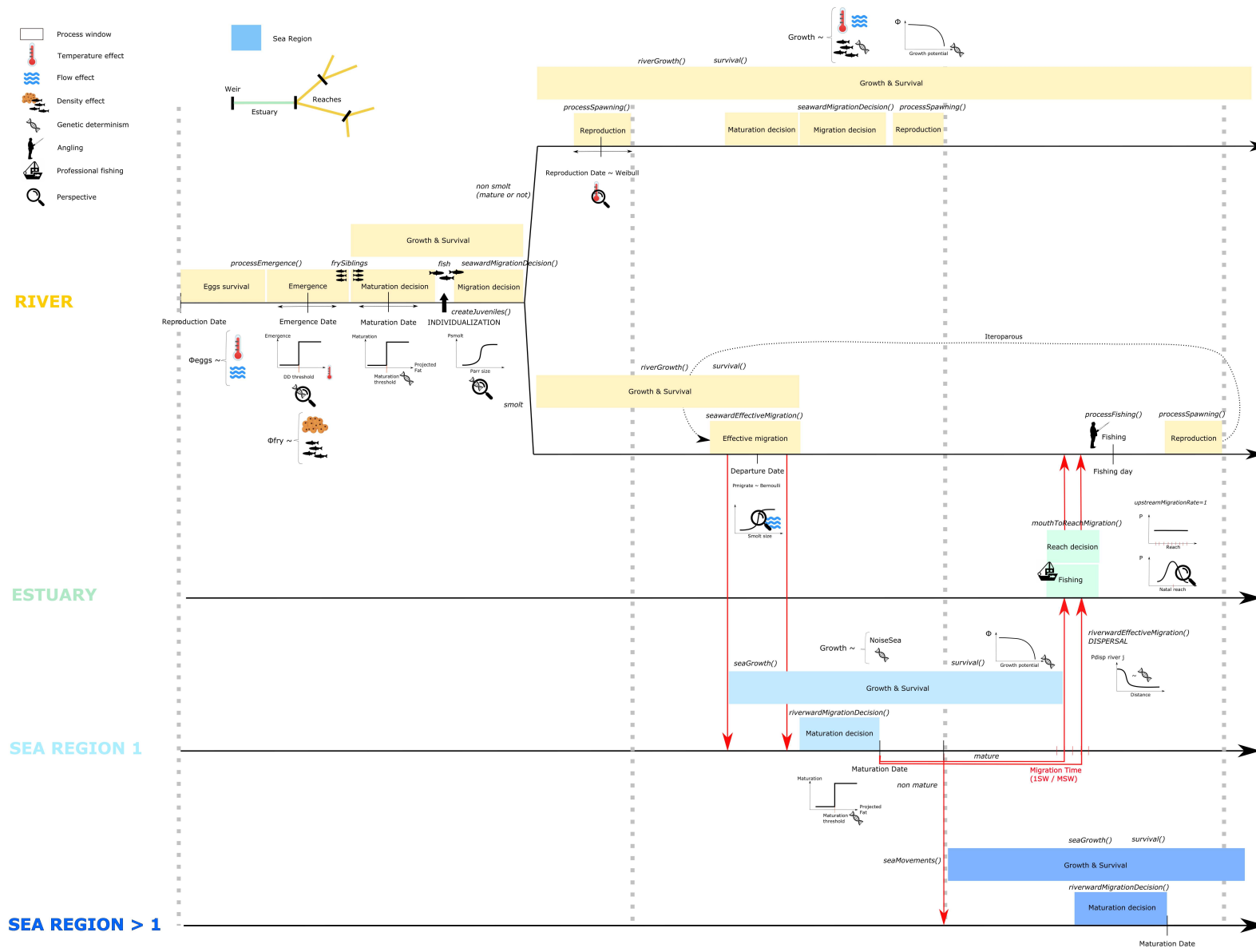


Figure 6.10: Global scheme of the spatial and temporal framework of the model processes.

6.5 CHAPTER HIGHLIGHTS

This chapter aimed at presenting the newest version of our modelling approach which addresses some gaps identified with the version that we used in this thesis. I also briefly presented some perspectives of improvements which may be based on the recent literature. The main lessons of this chapter are the following:

Chapter 6 highlights

- The new version of the model is now available on an interactive, shared platform, with an end user interface that can be easily used by managers;
- Flexibility in the spatial and temporal scale is now included;
- The genetic architecture is also more flexible;
- Perspectives of improvements of several processes may already be identified.

General discussion

My thesis aimed to i) improve our understanding of eco-evolutionary dynamics in metapopulations, and to ii) demonstrate implications of dispersal for Atlantic salmon adaptation, persistence and management. These two main objectives addressed the four main gaps identified by this thesis, which were i) a lack of knowledge on the influence of spatial structure on populations eco-evolutionary dynamics and ii) adaptation networks, iii) the implications of dispersal for management of metapopulations, and iv) particularly in the case of salmonids for which dispersal is often overlooked. Using a modelling approach, this thesis explored these four main issues within three main chapters (chapters 3, 4, and 5).

I will first discuss the main findings of my thesis and their implications in relation to the two main objectives and the different gaps identified. Then, I will discuss the benefits and limits of the modelling approach applied. Finally, I will introduce potential perspectives for future research following this thesis, before to mention what is also a PhD to me and to conclude.

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7.1 MAIN RESULTS AND IMPLICATIONS

7.1.1 Metapopulation eco-evolutionary dynamics

This thesis builds on a large body of literature focusing on metapopulation theory and dynamics (Hanski, 1999; Hanski and Gaggiotti, 2004b), and adds more evidence on the complexity of interacting demographic and evolutionary consequences of connectivity (Fig. 7.2).

Demographic dynamics

First, with a parsimonious design of metapopulation structure without genetic diversity among populations, my work isolates the consequences of dispersal on both local populations and metapopulation demographic dynamics. At the local scale, dispersal provided demographic rescue of some populations (defined as "sink" in this thesis; chapter 3). In the context of exploited populations (chapter 5), immigration from protected source populations provided compensation of exploitation in sink populations, conferring an advantage to this strategy relatively to the protection of sink populations, and particularly for high dispersal rates (30%).

At the metapopulation scale, chapter 3 emphasizes a non-linear relationship between dispersal rates and the stability of the metapopulation. Yeakel et al. (2018) also found non-linear effects of dispersal on the stability of a network but for two populations of pink salmon only. With the particular parameterization of our model applied to Atlantic salmon, I show a dispersal optimum around 20% favoring the stability of the metapopulation (i.e., portfolio effect). Note that Wang et al. (2015) showed that the stabilizing and synchronizing effects of dispersal cancelled each other in a metapopulation model of homogeneous populations.

Interestingly, the optimal dispersal rate emerging from our modelling approach is consistent with the averaged emigration rate of 14.4% estimated on wild populations of Atlantic salmon, although based on a small number of studies (chapter 1). However, it likely depends on the dispersal kernel, the spatial structure of the network, and local populations dynamics and diversity. For instance, a portfolio effect of 1.05 and a regional synchrony of 0.63 (perso. com. Bouchard) have been estimated by Bouchard et al. (2022) on adult returns of 18 populations of Atlantic salmon from Brittany. The differences with values emerging from our model (chapter 3) might be explained because our simulations did not consider environmental covariation between populations. Yet, environmental conditions are known to synchronize the dynamics

of populations, via the Moran effect (Moran, 1953; Bouchard et al., 2022). Thus, an optimum of dispersal is expected to emerge from metapopulation functioning but it may be context dependent.

Evolutionary dynamics

Along with demographic consequences, connectivity also influences the phenotypic and genotypic distributions of local populations. In a homogeneous network, chapter 3 isolated plastic responses of individual size and life history strategies to density changes induced by immigration and emigration patterns, which generated phenotypic diversity among populations. This is not surprising since salmonids are highly plastic species characterized by several life histories. For example, plastic response of age at migration and maturation to changes of river growth conditions have been showed in Pacific salmon (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 Prévost, 2013). However, dispersal-induced changes of phenotypes have rarely been isolated to my knowledge.

Although populations did not show inbreeding depression in our simulations, chapters 3 and 4 also support the genetic rescue effect (i.e., increased genetic variance within populations) provided by movement of individuals among populations. The greater genetic variance provided by dispersal could potentially favor a better response of populations to an uncertain future with variable selective pressures in space and time (Jump et al., 2009).

The evolutionary response of populations within a network to perturbations (chapter 4) and selective pressures (exploitation, chapter 5) on a ecological time scale was also assessed in this thesis. Chapter 4 particularly highlighted the evolutionary rescue effect of dispersal, since adaptation of local populations was fostered by increased dispersal rates when combined with genetic diversity among the network. These results support the adaptation network theory, where diversity, combined with connectivity, provides ecological and evolutionary options to local populations (Webster et al., 2017). However, this is particularly true when there is no divergent selection among populations, and where the homogenizing effect of dispersal rather favors than impedes adaptation of local populations. Chapter 5 showcased evolutionary response of life history traits, such as growth and age at maturation, to increased exploitation. However, connectivity did not appear as a constraining or facilitating factor of adaptive response to exploitation, at least in the configuration

evaluated.

Spatial structure

My thesis highlighted the crucial influence of spatial structure of interconnected populations on the eco-evolutionary consequences of dispersal. In chapter 3, the demographic and plastic responses to dispersal depended on whether the populations were sink or source, which in this work, was strongly driven by the spatial structure (e.g., carrying capacity and distance between populations) of the metapopulation. In chapter 5, differential demographic and evolutionary response to exploitation emerged depending on the exploitation strategy (i.e., exploitation on sink or source), although it is difficult to disentangle interacting direct effects of immigrants, indirect effects of density changes, and differential adaptive response of local populations. One could nevertheless assume that various spatial structures of networks would lead to different consequences of exploitation.

Chapter 4 explicitly evaluated the effect of spatial structure on evolutionary dynamics and identified several components as potential drivers of evolutionary trajectories of populations. First, the spatial structure of genetic diversity, e.g. gradual vs random, is interacting with dispersal patterns to provide more or less opportunities for adaptation to local populations. Second, the spatial configuration of populations (distance and carrying capacities) modulates their evolutionary trajectories, with key populations (e.g., large, or highly productive, and highly connected) having a major influence on relatively smaller populations. Conversely, more isolated populations might be less influenced by dispersal patterns. Importantly, this was particularly true in our case because emigration intensity was scaled by carrying capacity of populations, and the dispersal kernel was strongly related to the distance between populations. These conclusions may thus be highly dependent on the dispersal kernel and dispersal process (e.g., attractivity towards large populations, long distance dispersal, negative density-dependent emigration).

7.1.2 Implications of dispersal for Atlantic salmon dynamics and management

This thesis provided insight into the implications of the metapopulation functioning for the management of Atlantic salmon populations (Fig. 7.2).

Atlantic salmon populations are not isolated systems

First, chapters 3, 4 and 5 all demonstrated that dispersal and metapopulation structure influence the stability, persistence, and adaptive response of local populations of Atlantic salmon to perturbations and exploitation. According to our results, any alteration in a source population could affect the demography, genotypic and phenotypic traits of surrounding populations via multiple and complex pathways (e.g., density effects, evolutionary response). Active management practices favoring the productivity and connectivity of a river, such as dam erasure, could also benefit interconnected adjacent populations. Therefore, I advocate that when studying or managing the dynamics of a population, one should consider that its dynamics may be influenced by dispersal from surrounding populations and *vice versa*. Prior work already warned about the danger of ignoring spatial structure and connectivity of populations (Cooper and Mangel, 1999; Ying et al., 2011), but it remains rarely considered into management decisions. For example, even if mixed-stock fisheries explicitly consider variation in productivity among harvested stocks, connectivity is rarely considered.

Encouraging knowledge on dispersal rates and metapopulation structure

Chapters 4 and 5 emphasized that a good knowledge of the network is mandatory to ensure conservation success. For example, according to chapter 4, some key populations might significantly drive the dynamics of others and favor their adaptation. Depending on their adaptive potential, it might be relevant to protect them or not in order to favor adaptation of a larger part of the network. Thus, identifying key populations based on their influence on eco-evolutionary dynamics of the metapopulation (e.g., adaptive value, higher genetic diversity) could enhance adaptation and conservation success. Also, a good knowledge of the diversity *among* populations, in addition to *within* populations diversity, could also target management actions towards highly diverse areas or promote diversity where it is limited. Chapter 5 also emphasizes a potential interest in identifying source/sink dynamics to protect source populations from exploitation rather than protecting the sink. This strategy may seem counter-intuitive for managers because there is a tendency to protect populations that are considered "at risk", such as those with smaller population sizes. Ultimately, a good knowledge of dispersal rates and patterns appears crucial, since they largely interact with the spatial structure (chapter 4) and exploitation strategies (chapter 5) to determine eco-evolutionary dynamics of the metapopulation and the

portfolio effect (chapter 3). Altogether, this encourages empirical work dedicated to acquiring a better knowledge of the spatial genetic structure and configuration of the network, as well as dispersal patterns connecting populations.

Conservation according to the portfolio approach

However, the challenges described in chapter 2 of evaluating dispersal rates and metapopulation structure in nature make it unlikely to have an ideal knowledge of a system to manage. Applying management strategies based on limited estimations of dispersal patterns and population structure might be risky and lead to unsuccessful conservation actions. For example, protecting a population which has little effective influence on the network, or protecting a maladapted population instead of a population with high adaptive potential, might result from a misidentification of dispersal patterns and genetic diversity. Moreover, even if extensive knowledge would be ideally available on a system, the temporal variability of metapopulation dynamics may compromise the success of a conservation strategy in the long term. Thus, as pointed out in chapters 4 and 5, a safer strategy addressing these challenges and risks might be to spread conservation effort over a diversity of populations.

In addition, in the face of uncertain future changes and selective pressures, conserving populations diversity according to the portfolio approach would provide opportunities for adaptation to the network. Chapter 4 suggests that favoring adaptation network would help populations resilience to perturbations, by conserving diversity within and among populations and by favoring connectivity between habitats. This conservation approach gains mounting attention and evidence, in particular for the conservation of salmonids and corals in the context of climate change (Moore et al., 2021; Moore and Schindler, 2022; Colton et al., 2022). Anderson et al. (2015) advocates for preserving all the process promoting a diversity of thermal tolerance in salmon populations, such as genetic diversity of habitat heterogeneity. As Walsworth et al. (2019) for coral reefs, I advocate that considering the evolutionary capacity of interconnected salmonid populations might change the recommendations for conservation actions, for instance shifting from protecting thermal refugia to habitat diversity. I suggest for local (e.g., fishermen, migrating species protection association), regional (e.g., COGEPOMI), national (e.g., OFB) and international (e.g., CIEM) stakeholders that conservation strategies should consider the portfolio approach for managing salmon by focusing on a large scale (e.g., watersheds or region), favoring diversity of habitats (e.g., limiting habitat destruction and homogenization) and

connectivity (e.g., removing dams).

Managing for diversity could also imply active management of gene flow between populations, for instance when habitat connectivity is not high enough to provide sufficient genetic diversity within populations. In the case of populations with low diversity, controlled translocation of individuals between populations could increase genetic variation and help populations to alleviate inbreeding depression in the short term, and to provide evolutionary options to future environment in the long term. However, particular attention must be paid to avoid complete homogenization of the populations. [Fitzpatrick et al. \(2020\)](#) documented genetic rescue in small populations of Trinidadian guppies and suggested assisted gene flow may be an effective conservation strategy, as well as other studies on salmonids (e.g., [Pregler et al., 2018](#); [Kazyak et al., 2022](#)).

7.2 DISCUSSION OF OUR MODELLING APPROACH

This thesis provided key insight into all the above-mentioned aspects of metapopulation functioning and their implications for management of Atlantic salmon. This was made possible using a single and coherent modelling approach I am discussing below.

7.2.1 DG-ABMs, a great but challenging potential for metapopulation research

Across the chapters 2, 3, 4, and 5, my work emphasized the potential of demographic agent based models (DG-ABMs) to investigate eco-evolutionary dynamics within metapopulations. First, simulations constitute a framework for studies at a larger spatial and temporal scale than empirical studies, although long-term monitoring programs provide increasing spatially and temporally extended data. Second, as discussed in chapter 2, such process-based modelling approach allow the emergence of individual fitness and the resulting population and evolutionary dynamics, interacting within feedback loops. This emergence of observed patterns from multiple interacting processes (e.g., plasticity and genetic adaptation, chapter 3, 5) makes their interpretation more complex but more robust than if it was based on strong *a priori* assumptions. Third, the key benefit of using modelling approaches to evaluate implications of dispersal for management without threatening species or habitats by human intervention was illustrated by all the chapters.

However, developing and using such modelling approaches remains challenging. During their development, one has to identify which level of complexity is required for the precise aim of use, but it also largely depends on the knowledge available on the species. With the complexity of interacting processes, the parameterization and calibration of the model can also be tedious. Ultimately, the development and calibration of a model often result from a trade-off between generality and realism. For instance in this thesis, the model is based on the knowledge and data from the salmon metapopulation of Brittany, but it is not used to accurately represent and predict its dynamics. Instead, I used this model as a prospective tool informing knowledge on metapopulation dynamics and their implications for management. Indeed, I am in line with [Holt \(1990\)](#) who stated that "There is almost no species for which we know enough relevant ecology, physiology and genetics to predict its evolutionary response to climate change". But this still raises questions about the generality of model findings. We require realism (e.g., in processes or spatial structure) in our model to get closer to the complexity of species functioning or spatial dynamics, which may bring out unexpected patterns, but it is difficult to assess to which extent results based on a case study can be generalized. This is a concern I had throughout my thesis. I would say that the observed trends and patterns, e.g. between contrasting scenarios, can be generalized, but the observed values or levels of changes should change between systems or species.

Another issue related to this trade-off between generality and realism is the technical applicability of the model to other systems or other species. Since DG-ABMs offer the opportunity to explicitly represent the life cycle of species, they are often designed for one or few species and may hardly be transferred to others. In this thesis, focusing on Atlantic salmon was motivated in many ways (chapter 1), but there is considerable interest in applying the same questions to other species facing similar issues. For instance, there is a striking parallel between the challenges faced by Atlantic salmon in France and Pacific salmon in California ([Herbold et al., 2018](#)), being both at the southern edge of their distribution area and strongly impacted by climate change and exploitation.

Efforts can be undertaken to increase flexibility of models for other systems and species; the new version of IBASAM, presented in chapter 6, provides more flexibility in the parameters and time schedule of the processes integrated, enabling its adaptation to other salmonids. More flexibility on the spatial structure will also allow its application to different systems (e.g., dendritic). This version is still underway, with calibration and sensitivity analysis to be done, but perspectives of improvements have

already been identified (see chapter 6), often related to the findings of recent empirical work.

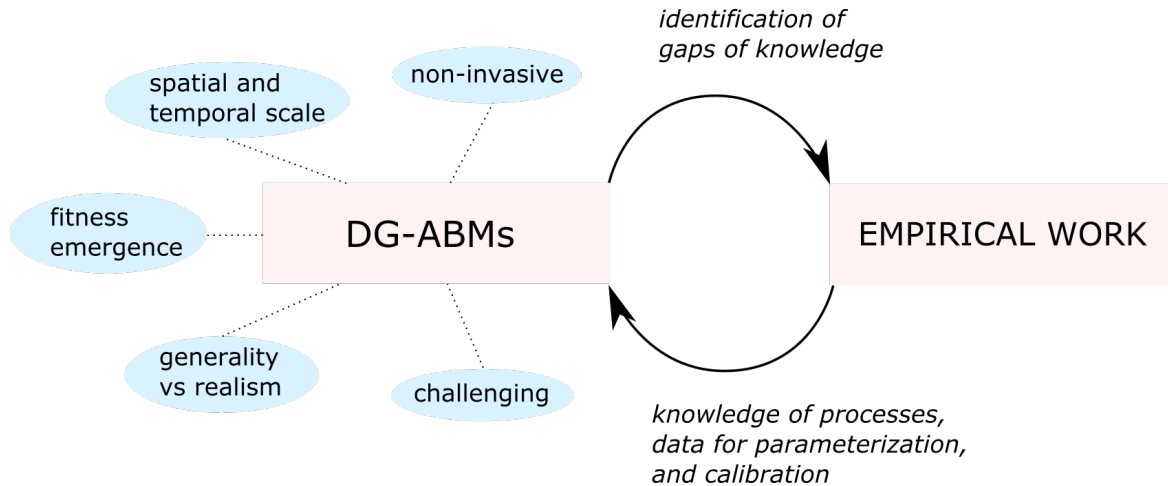


Figure 7.1: Feedback loop between DG-ABMs and empirical work.

7.2.2 Interaction between modelling and empirical work

Indeed, there is a strong interaction between modelling approaches and empirical work, that can be described with a loop (Fig. 7.1). Models are based on the knowledge provided by experimental and field work studies, which describe the main processes of species functioning, and are constantly updated with the most recent literature. In turn, models can provide insights into gaps of knowledge and identify factors that deserve more attention, motivating further empirical studies (Cordoleani et al., 2020).

For example, this thesis emphasized the importance of dispersal rate and spatial structure on the portfolio effect, evolutionary dynamics, and effects of exploitation. This may contribute to motivate empirical work on dispersal patterns in Brittany. A new tagging antenna, located on the Blavet river which shares an estuary with the Scorff river, identified several returning adults that were tagged as juveniles in the Scorff river, and preliminary genetic analyses suggest the Scorff population could be a source of many dispersing individuals (perso. com. Buoro). This is particularly interesting regarding our results, which indicated the Scorff as a potential sink population. It raises question about our definition of source/sink population based on the ratio immigrants /emigrants, which is largely driven by the spatial configuration of the network, rather than the intrinsic population growth rate (see Pulliam, 1988). This also supports a previous discussion of the risk of misidentifying

populations contributions and focusing conservation actions on them (section 7.1.2). It is therefore necessary to deepen these new genetic analyses and/or to extend tagging antenna to better identify the metapopulation structure of Brittany. Through the long-term monitoring program deployed on the Scorff, there are also opportunities to estimate the emigration rate, for instance by comparing the proportion of tagged smolts to the proportion of returning tagged adults (considering there is no differential mortality due to tagging).

7.3 PERSPECTIVES

This work constitutes a first step in the evaluation of the implications of metapopulation functioning on adaptation and management of Atlantic salmon populations. With parsimonious simulation designs, it shows certain limitations stated in the different chapters. It must therefore be pursued by future research for which some directions are discussed here (Fig. 7.2). These could be investigated via the new version of the model presented in chapter 6.

7.3.1 Dispersal mechanisms

I simulated dispersal as a random individual process, with a probability to disperse constant in space and time. Yet, evidence of spatial and temporal variation in dispersal in many taxa suggest that dispersal is likely not random (both for emigration and immigration, [Conradt et al., 2000](#); [Edelaar and Bolnick, 2012](#)) and may be condition and context dependent (chapter 1). On salmonids, several studies suggested sex-biased (brook trout, [Hutchings and Gerber, 2002](#); brook charr, [Fraser et al., 2004](#); chinook, [Hamann and Kennedy, 2012](#)) and life history dependent (Atlantic salmon, [Jonsson et al., 2003](#); sockeye, [Lin et al., 2008](#)) emigration. Density also have been identified as a potential driver of dispersal patterns; a collective navigation hypothesis has been proposed to explain patterns of high philopatry for large population size (Atlantic salmon, [Jonsson et al., 2003](#); sockeye, [Westley et al., 2015](#); [Berdahl et al., 2016, 2017](#)). A lower reproductive success of immigrants relatively to philopatric individuals has also been demonstrated in several studies (chum, [Tallman and Healey, 1994](#); sockeye, [Peterson et al., 2014](#); Atlantic, [Dionne et al., 2008](#); [Mobley et al., 2019](#)), although there is few information if this is due to pre- or/and post-zygotic isolation (mate choice or offspring survival). A genetic basis of dispersal has also been suggested for salmonids ([Keefer and Caudill, 2014](#) for review, in Atlantic salmon, [Jonsson and Jonsson, 2017](#)).

Integrating these mechanisms of dispersal might strongly impact eco-evolutionary dynamics. For instance, introducing explicit cost and lower fitness of dispersers might buffer the consequences of dispersal observed in the different chapters. Considering phenotypic-dependent emigration might also influence phenotypic and genotypic patterns, while negative density-dependent dispersal (collective behavior) could accelerate the decline of small populations. [Yeakel et al. \(2018\)](#) illustrated that the relationship between dispersal rate and metapopulation robustness may depend on the strength of collective behavior. Importantly, adding a genetic basis to dispersal might lead to unexpected emerging patterns of dispersal. According to chapter 3, selection should favor dispersal rates around 20% in a context of homogeneous populations. According to chapter 4, high dispersal rates could be selected to foster adaptation after a perturbation when there is no divergent selection among populations. More complex patterns of dispersal evolution could emerge when applying spatialized management strategies (chapter 5), where exploitation might select for dispersal in exploited populations and conservation might select against dispersal in protected populations such as showcased by [Poethke et al. \(2011\)](#). Therefore, further work evaluating the influence of dispersal mechanisms, and in particular dispersal evolution, might reevaluate the results of the thesis.

7.3.2 Climate change

Here, the adaptation and persistence of Atlantic salmon metapopulation was evaluated in a i) neutral context (chapter 3), ii) after a perturbation (chapter 4), and iii) facing exploitation (chapter 5). Yet, climate change is also a particularly pressing threat for species like salmonids, and evaluating its impact and implications for management is mandatory.

Relative effects of climate change and dispersal on synchrony

First, I suggest to focus on the synchronizing effect of climate change, which can be compared to the relative synchronizing effect of dispersal in the context of spatially structured populations. Indeed, chapter 3 highlighted the synchronizing effect of dispersal. But numerous studies suggested that the Moran effect, i.e. the synchrony of environmental conditions, might play an important role ([Ranta et al., 1999](#); [Koenig, 2002](#)). Climate change has the potential to synchronize selection regimes in spatially structured populations ([Kahilainen et al., 2018](#)) as it drives environmental temporal trends at a large scale ([Post and Forchhammer, 2002, 2004](#); [Parmesan and Yohe,](#)

2003; Shestakova et al., 2016; Hansen et al., 2020; Fisogni et al., 2022), as well as the overlooked simultaneous occurrence of frequent extreme events (Hansen et al., 2013).

This large body of literature raises concern about salmonids stability, whose complex life cycle could increase the probability for synchronizing factors at different life stages or rather mitigate these effects. Bellmore et al. (2022) showed that climate change induced homogenization of flow regimes across a watershed (initially fed by glacier, snowpack or rain), synchronizing resource phenologies and growth opportunities for juvenile salmonids with potential consequences for life history expression and stability. Bouchard et al. (2022) also identified a Moran effect of summer low flow on the synchrony of Atlantic salmon juveniles, while Olmos et al. (2020) identified a response of salmon populations to common sea climate changes impacting marine survival. Thus, it would be interesting to evaluate with our modelling approach if climate change would increase the synchrony of populations and reduce the stability of the network, and if different levels of diversity and asynchrony among populations might buffer this effect.

Adaptation network

Besides its synchronizing effect, climate change also has impacts on river and sea survival which threatens salmonids species (Jonsson and Jonsson, 2009; Crozier et al., 2021; Warkentin et al., 2022). Climate change is also a selective pressure which can have evolutionary consequences on life history traits (e.g., Reed et al., 2011a; Piou and Prévost, 2013, Nadeau and Urban, 2019 for review). However, these evolutionary responses are often investigated at the population scale. In chapter 4, we analysed the adaptive capacity of a network of populations after a temporary perturbation, which may strongly differ from a directional and gradual change induced by climate change. Building on the work of Penaluna et al. (2015), Fullerton (2016), Walsworth et al. (2019), and McManus et al. (2021b), evaluating the adaptive capacity of interconnected and diversified populations of Atlantic salmon facing climate change is thus a central question, and the theory of adaptation network could be particularly interesting to examine in this context.

How dispersal will evolve with climate change is also a hot topic (Travis et al., 2013). Empirical work suggested increased gene flow between neighboring populations of Atlantic salmon with increasing temperatures and lower discharges (Valiente et al., 2010), while a theoretical study found that high rates of climate change can select for increased dispersal distances (Boeye et al., 2013). Integrating a genetic basis of

dispersal to assess climate change impacts is therefore another avenue of study with our modelling approach.

7.3.3 Spatial structure

My work highlighted the importance of spatial structure (e.g., carrying capacity and distance between populations) on eco-evolutionary dynamics of populations. This motivates further work evaluating more contrasted structures, such as dendritic (e.g., the Adour system) vs coastal rivers (e.g., the Brittany system). Several hypothesis could be tested around the spatial structure of metapopulations.

First, an interesting area of study would be to compare the level of environmental and population diversity resulting from contrasted spatial structure. [Paz-Vinas and Blanchet \(2015\)](#) and [Thomaz et al. \(2016\)](#) found higher genetic diversity and differentiation related to a dendritic landscape, while [Altermatt and Fronhofer \(2018\)](#) found more variable population densities in dendritic networks than in linear networks. The complexity of the network (branching prevalence) was also showed to influence population synchrony ([Yeakel et al., 2014](#); [Larsen et al., 2021](#)). The case of the Adour system, where Atlantic salmon populations are present, is particularly interesting to compare with the Brittany metapopulation. Indeed, its geological and hydrological context, with a combination of rivers fed from rainfall and snow-melt water, might generate higher diversity of population dynamics than the Brittany system composed of coastal rivers (see [Bellmore et al., 2022](#)). Assuming differences of biocomplexity between the two systems, evaluating differential response to climate change could be relevant.

Second, our modelling approach provides opportunity to examine if different spatial structures lead to evolution of contrasted dispersal rates via kin selection; indeed, dispersal evolution was showed to emerge from kin structure in similar DG-ABM models ([Poethke et al., 2007](#); [Fronhofer and Altermatt, 2017](#)). However, dispersal evolution might be strongly related to the cost of dispersal, to the size of populations (stronger effect of kin competition in small populations), and these studies were applied for simple life cycles with non-overlapping generations. One can wonder if this effect is still visible in the case of overlapping generations such as in Atlantic salmon and what conditions are necessary for this effect to emerge. An interesting case could be a comparison of emerging dispersal rates between Atlantic salmon and Pink salmon (*Oncorhynchus gorbuscha*), a species whose generations are non overlapping and which shows particularly high rates of dispersal while extending its distribution

range (Sandlund et al., 2019).

Third, one could also investigate the influence of spatial structure on the consequences of dispersal. For example, in dendritic networks, populations closer to the estuary might be more influenced by dispersal compared to populations in headwaters, if dispersers show a spatial distribution closer to the river mouth than philopatric individuals. A study to which I contributed depicted a decrease in the immigration rate of anadromous brown trout with distance to river mouth in three different rivers using genetic assignment of individuals to populations (see Appendix A, Chat et al., 2022). Besides, this study also suggests that estimates of dispersal rates from field studies must be interpreted with caution since locations of sampling sites might strongly determine estimations.

7.3.4 Genetic architecture

In this thesis, fitness related traits with an underlying genetic basis were maturation thresholds and growth potential. Evaluating the evolution of other life history traits under selection by including a genetic basis constitutes another perspective of work. In particular, phenological traits, such as spawning timing, or traits related to thermal tolerance, might evolve in response to climate change, and adaptive alleles might spread within adaptation networks via dispersal. A comparison of the evolution of these traits and the adaptation of populations to climate change could be carried out between different scenarios of spatial structures (e.g., driving connectivity), dispersal (e.g., with or without a genetic basis), and initial biocomplexity (e.g., homogeneous network of Brittany vs heterogeneous network of Adour system).

The flexibility in the genetic architecture of the new version of our modelling approach presented in chapter 6 also opens up new perspective of work on the influence of genetic architecture on the evolution of life history traits within a metapopulation context. Indeed, there is mounting evidence of the presence of a single major locus influencing age at maturation in salmonids (Barson et al., 2015; Sinclair-Waters et al., 2020), and this genetic architecture, relatively to polygenic basis of traits, is expected in populations connected by gene flow according to (Savolainen et al., 2013). Moreover, Kardos and Luikart (2021) showed theoretically that polygenic trait architectures conferred higher evolutionary potential and population viability than genetic architectures with large-effect loci. Therefore, an improved understanding of the influence of genetic architecture within metapopulations on the evolution of fitness-related traits has important implications for our understanding of adaptation and for

the conservation of natural populations (Waples et al., 2022). Regarding management, the loss of large-effect adaptive alleles and thereby adaptive phenotypes (Thompson et al., 2019) might be more likely than if there are polygenic; evolutionary rescue via immigration might be crucial in this case, and conservation of connectivity and regions with adaptive potential would be mandatory.

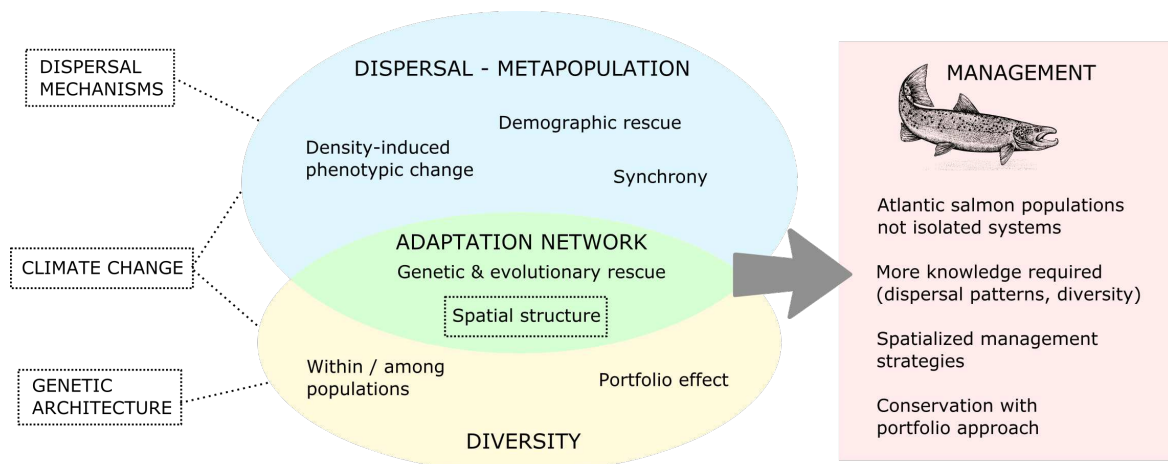


Figure 7.2: Diagram of the conclusions and perspectives (dotted boxes) of the thesis.

7.4 WHAT ALSO IS A PHD

Ultimately, I would like to wrap up this general discussion of my dissertation with personal thoughts on what a PhD can also be and what was my experience, hoping it may motivate further students. In my opinion, a PhD is an opportunity to lead a project, almost full-time, with a relatively large freedom, and to develop by your own (and often with the help of your supervisors) the skills of the research process (keeping up with the (sometimes overwhelming) literature, designing experiments, analysing (sometimes weird) results, identifying perspectives, redesigning experiments). But in my opinion, besides these research aspects, a PhD also offers time for various opportunities: in my case, it gave me the opportunity to apply for travel grants (Fulbright), to visit another lab, to present my work in multiple conferences (although most of them were virtual), to supervise an internship, to teach at the university, and last but not least, to organize an international conference (Fig. 7.3). These different activities took a significant part of my time but were very rewarding experiences and I believe introduced me to the many components of a researcher's work.



Figure 7.3: Poster of the NoWPaS 2022 held in France.

7.5 CONCLUDING REMARKS

I believe my work contributed to improve our understanding of the demographic and evolutionary consequences of dispersal, showcased the importance of spatial structure of populations, and emphasized potential implications for Atlantic salmon management. In particular, Atlantic salmon populations should not be considered as isolated systems, and their conservation would benefit from more knowledge on their spatial structure and dispersal patterns, and from considering the portfolio approach. My thesis also identified gaps of knowledge and opens up new perspectives of work, particularly focusing on evaluating metapopulation response to climate change by explicitly considering dispersal mechanisms, spatial structure of populations, and genetic architecture of traits. I also hope to have demonstrated the potential of our modelling approach, which is in constant evolution following advances in empirical work, and I hope it motivates further work on the topic.

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Appendices

APPENDIX A

Sea trout straying rate decreases as
distance from river mouth increases

Sea trout (*Salmo trutta*) straying rate decreases as distance from river mouth increases

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Abstract

For both conservation and management purposes, it is important to identify the natal origin of migratory individuals entering a river, particularly in genetically spatially structured species like brown trout (*Salmo trutta*) where the migrant ecotype (called sea trout) can originate from different populations. Nonetheless, little attention has been paid to the spatial distribution of non-local fish at the level of an entire river catchment. The objective of the study was to quantify the proportion of non-local sea trout entering a river catchment (*i.e.*, straying rate) and estimate the spatial extent of their upstream migration. Here, the authors considered dispersal in three distinct rivers, taking advantage of 10 sampling sites. Sea trout, either trapped or rod-caught, were genotyped and genetically assigned to their source populations using appropriate baselines. Based on 1437 sea trout fish classified as local or non-local, the authors empirically demonstrate that straying rate declines in each river as distance from the coast increases in a non-linear fashion. Straying rate exceeds 50% near the mouth, and then decreases gradually to reach <10% 40–50 km inland. A similar spatial pattern is found in the three rivers investigated suggesting an underlying common behaviour of non-local sea trout. The data and results presented here suggest that straying in is far more constrained spatially than first expected. The majority of non-local sea trout were found within the first 25 km of the estuary in the three rivers investigated.

KEYWORDS

anadromy, brown trout, dispersal, genetic assignment, microsatellite, migratory fish, straying, trapping

1 | INTRODUCTION

It is well known, as early as the 17th century (Nall, 1930), that the great majority of salmonid species that survive at sea return to fresh water as adults to spawn at their natal site (philopatry or homing). It was predicted that, at the end of their marine homeward migration (a) returning fish migrate along the coast in an attempt to locate their natal river; (b) cross plumes of water with distinct olfactory cues; (c) undertake upstream migration as soon as they detect imprinted familiar odours (*e.g.*, Johnsen and Hasler, 1980); (d) possibly decide to move downstream if they have investigated the wrong river or the wrong tributary (Keefer *et al.*, 2008); and (e) finally, swim upstream

and reach their natal site (homing) to spawn. Nonetheless, in the past decades, a growing number of studies demonstrated that a variable proportion of salmonids disperse (or stray) to new spawning sites upon returning from their marine migration (*e.g.*, Ford *et al.*, 2015; Keefer & Caudill, 2014; Santaquiteria *et al.*, 2016; Tallman & Healey, 1994). Straying, a term commonly used in the salmonid literature to refer to dispersal, is typically defined as adult migration and reproduction – completed or even attempted – at non-natal sites (*e.g.*, Keefer & Caudill, 2014). Homing (*i.e.*, philopatry) and its counterpart straying are both ecologically and evolutionarily important. Homing maximizes the reproductive success of individuals in the case of a stable and favourable environment, whereas straying allows the

long-term persistence of populations and species faced with dramatically changing environments. There is considerable variation in straying among species and rivers, although the reasons are far from being fully elucidated (Quinn, 2018). As this author rightly pointed out (p. 118), “Straying is common enough to be important but rare enough that it is difficult to study.”

Dispersal issues can be addressed from two distinct perspectives depending on whether one is considering the donor population (*i.e.*, emigration) or the recipient population (*i.e.*, immigration). The so-called straying out refers to sea trout originating from one given river (donor population) being found in non-natal rivers (Quinn, 2018). In contrast, “straying in” focuses on non-local sea trout found in one given river (recipient population). In *Salmo trutta*, both “straying out” (*e.g.*, Fournel *et al.*, 1990; Jonsson *et al.*, 2018; Pratten & Shearer, 1983; Skrochowska, 1969) and “straying in” (King *et al.*, 2016; Masson *et al.*, 2018) have been documented. Here, the authors take advantage of the natural dispersal events previously observed in two distinct areas of the natural distribution range of sea trout (the Bay of Biscay and the English Channel) to further study “straying in” behaviour by focusing on within-catchment variation, a spatial scale still explored very little. They then tried to distinguish between two competing, but nonexclusive, hypotheses regarding the straying data collected.

Throughout this article, the authors have used the terms “straying rate” to refer to the proportion of fish in a sea trout run entering a non-natal river and “stray” as a synonym of non-local fish, whether it is an effective disperser or not.

The authors first hypothesized that the proportion of individuals that stray into a river is characteristic of that river, at least on ecological time scales. Here, the river must be taken in the broad sense of the term, that includes both environmental (*e.g.*, river location, river size, river mouth, river network) and biological (*e.g.*, brown trout population size, population propensity for anadromy) factors. As pointed out by Keefer and Caudill in their review (2014), straying is not spatially random. First, sea trout itself seems unevenly distributed along the Atlantic coast, with some rivers famous for their sea trout populations and well known by the fishermen, whereas others are not. Second, even if some individuals undertake a long and distant marine migration, most of them stay at sea in the vicinity of their natal river mouth (Berg & Berg, 1987; Skrochowska, 1969), so that straying is more likely to occur between neighbouring rivers (Pratten & Shearer, 1983). Third, marine environment plays an important role in sea trout dispersal, either promoting dispersal or acting as a physical barrier to connectivity (Quéméré *et al.*, 2016). It thus makes sense to consider the river as a key factor. In this first candidate model for predicting straying, the proportion of strays was assumed constant or nearly constant at any place within the dendritic river system. An alternative and slightly complex model, which better acknowledged increased information on sea trout movement and behaviour, was also hypothesized. Salmonids are known to use chemical cues to identify their home rivers (*e.g.*, Hasler *et al.*, 1978). To do so, fish need to enter freshwater upstream enough to detect freshwater local cues (either in the estuary, in the main stem or further upstream in a tributary) before deciding to stay or leave the river system. Non-local fish are

thus likely to be more frequent in the downstream part of the river than upstream. The authors then hypothesized that straying rate declines inland as the distance from the coastline increases.

The objective of the study was to identify key features possibly associated with “straying in” and to classify their respective contributions. This study focused on two parameters, the river and the distance to the mouth following the course of the river. Although the river is often invoked as a key factor in the metapopulation theory applied to salmonids (*e.g.*, Schtickzelle & Quinn, 2007), the distance from the coast has, to the author’s knowledge, never been examined statistically as a quantitative explanatory variable of “straying in.”

2 | MATERIALS AND METHODS

2.1 | Samples

Two data sets from the literature were used. They fulfilled the requirements to assess the spatial pattern of sea trout straying at a catchment scale, *i.e.*, a monitoring of sea trout populations at multiple collection sites along the rivers (allowing an assessment of the effect of distance from the river mouth) and the genetic assignment of their individuals to their putative source population. The first data set was from southwest France, an area located south of the brown trout distribution range, and previously described in Masson *et al.* (2018). In this study, 615 sea trout were sampled throughout at least one annual upstream migration period between 2002 and 2013 at seven fish traps (Uxondoa, Olha, Chopolo, Halsou, Sorde-l’Abbaye, Puyoo, Baigts) on the Adour and Nivelle, two rivers draining into the south-eastern corner of the Bay of Biscay (Figure 1a). These samples were collected following the national regulations of the country. The second data set was compiled in more northerly waters by King *et al.* (2016). The authors retrieved data concerning 921 sea trout collected between 2010 and 2014 in the Tamar and Tavy, two rivers of south-west England sharing the same estuary and flowing into the English Channel (Figure 1b). This increased the total number of sites studied to three, one being obtained at a fish trap and the two others being rod-caught fish samples provided by anglers. Two rod-caught sea trout samples, from Lynher and Lower Tamar, were ignored because of insufficient spatial information. In the end, this amounted to three rivers and 10 sampling sites.

The aim was to study sea trout dispersal in well-established populations living in a somewhat favourable environment. The three rivers investigated, *i.e.*, Adour, Nivelle (Bay of Biscay, France) and Tamar (English Channel, UK), have been subject to monitoring programmes for a long time (Nivelle and Tamar being two “Index Rivers” in their respective countries) and fulfil the requirements.

2.2 | Spatial consideration

For the modelling analysis, the authors considered that rivers sharing the same estuary belonged to the same river system (the river system Adour encompassing River Adour and River Nive, and the river system Tamar encompassing River Tamar and River Tavy). It makes sense

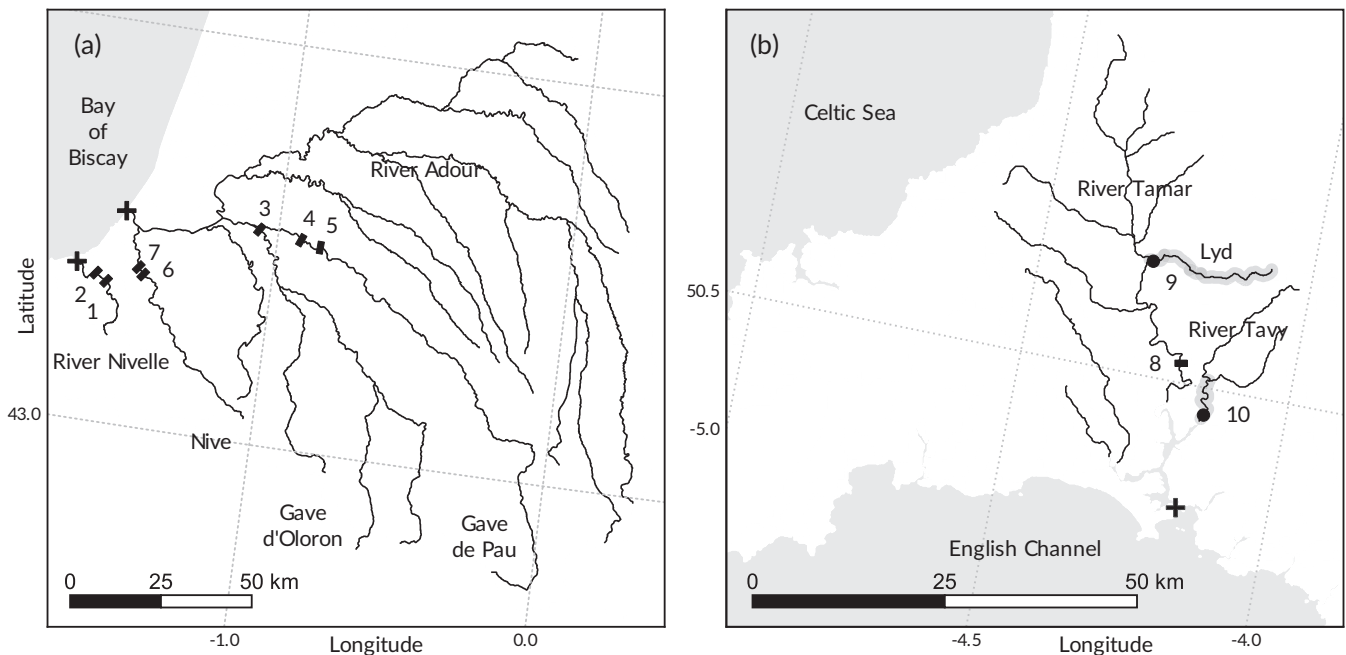


FIGURE 1 Geographical locations of the three rivers considered in this study. (a) River Nivelles and River Adour in France flowing westwards into the Bay of Biscay (data from Masson *et al.*, 2018). (b) River Tamar in the UK flowing southwards into the English Channel (data from King *et al.*, 2016). Numbers (1–10) indicate the 10 sampling sites considered in the present study. Black rectangles (1–8) illustrate the position of the eight trapping devices (1: Olha, 2: Uxondoa, 3: Sorde-l'Abbaye, 4: Puyoo, 5: Baigts-de-Bearn, 6: Halsou, 7: Chopolo, 8: Gunnislake Dam). River segments highlighted in grey are the places where rod-caught sea trout were sampled (9: Lyd tributary of the River Tamar and 10: River Tavy between Lopwell Dam and the confluence of the main river and the Walkham tributary). A black point on the map illustrates the downstream end of these two recreational rod fisheries. A cross indicates the mouth of the river/estuary used to calculate distances (km). Spatial coordinates (grid lines) are expressed in decimal degrees using EPSG:4326. Source of GIS data: CCM River and Catchment Database, © European Commission - JRC, 2007 (Vogt *et al.*, 2007)

from a biological viewpoint because the common estuary is a mandatory passage way for sea trout wanting to reach the upper part of the rivers sharing the estuary. It also makes sense from a historical viewpoint because what are considered today as distinct rivers were, a couple of 1000 years ago, distinct sub-catchments of a larger river due to deglaciation and increasing sea level.

For sea trout caught in a trap, the authors estimated the distance in kilometres from the trap downstream to the mouth of the river/estuary, *i.e.*, Adour ($43^{\circ} 31' 45.95''$ N, $1^{\circ} 31' 23.15''$ W), Nivelles ($43^{\circ} 23' 17.66''$ N, $1^{\circ} 40' 11.31''$ W) and Tamar ($50^{\circ} 21' 23.86''$ N, $4^{\circ} 10' 1.47''$ W), following the course of the river. Similarly, for sea trout caught in the recreational rod fisheries on a particular stretch of a river (King *et al.*, 2016), they measured the distance from the downstream end of the stretch to the mouth of the estuary. For the River Tamar, the stretch was delimited downstream by the confluence of the main river and its tributary, the Lyd. For the River Tavy, rod-caught fish were all caught upstream of the tidal limit (Lopwell Dam), the upper limit being the confluence of the main river and the River Walkham.

2.3 | Sea trout individual assignment

Both data sets were initially used to study homing/straying behaviour of sea trout (King *et al.*, 2016; Masson *et al.*, 2018), and the authors used genetic tools together with a baseline to estimate the stock

composition of sea trout runs. For the French rivers, they proceeded to an individual assignment. Sea trout individuals entering fresh water, whatever the duration of their marine sojourn, and provided that they were successfully genotyped for at least 9 of the 10 microsatellite loci considered, were probabilistically assigned to a putative source population (see Supporting Information no. 1 pdf and Figures S1–S5). The migration behaviour of each sea trout individual (homing vs. straying) was then deduced. If the inferred population was the one in which the sea trout had been trapped, they deduced that it was a local trout (homing behaviour). Otherwise, they deduced that it was a stray (straying behaviour). The straying rate at each trapping site was calculated accordingly. For the English river, the genetic assignment was described in King *et al.* (2016). In both cases, the assignment of resident fish (distinct from the baseline and considered of known origin) to the correct river/group of origin was >87%, showing that the baseline samples were representative of the subpopulations considered (Supporting Information no. 2). Correct assignment was also high for the simulated data sets (150–200 simulated genotypes from each river), ranging from 95% to 99%.

2.4 | Straying rate calculation

For the French rivers, the authors decided to include in their calculation of straying rate only those individuals whose assignment

probability exceeded 80% in order not to inflate the number of (wrong) strays. For those individuals, the designated population was thus at least four times more likely than any other source population of the baseline. In this way, they reduced the risk of including individuals of hybrid, complex or uncertain origin in their calculation of straying rate and conversely increased the chance of including individuals of “pure” origin, either local (=non-migrants) or non-local (=first-generation migrants).

For the English rivers (King *et al.*, 2016), homing rates were retrieved from Appendix 2b (considering $N = 765$ sea trout trapped at Gunnislake) and 2d (considering sea trout caught in the recreational rod fisheries on the Rivers Lyd and Tavy, respectively $N = 82$ and $N = 74$) considering assignment to river of origin. The straying rates used in the present study were then calculated by subtracting the homing rates from 100%.

2.5 | Logistic regression

The authors examined the effects of the two aforementioned key features, the river (categorical variable) and the distance to the mouth of the river (continuous variable), on straying using logistic regression (“glm” function in R with a binomial error distribution and a logit link function, detailed in Supporting Information no. 3). Their response variable was binary (they classified sea trout individuals as local or disperser). They began by fitting a saturated model (seven parameters), considering the river of destination and the distance from the sea as the main factors with their interaction as well as the square of the aforementioned distance. They further adopted a stepwise model simplification using Chi deletion tests to obtain the minimal adequate model. During model simplification, a variable was retained in the model only if it caused a significant increase in deviance when it was removed. The authors also compared the saturated model and the

nested models using AIC (Sakamoto *et al.*, 1986). In the end, they assessed goodness-of-fit and verified assumptions of the minimal adequate model using a half-normal plot of residuals and made interpolations using the “polyroot” function in R.

3 | RESULTS

3.1 | Sea trout individual assignment (River Adour and River Nivelle)

Among the 644 sea trout, 25 fish were not assigned due to genotyping failure or incomplete genotype (<9 microsatellite loci). A group of 546 fish exhibited an assignment probability above 80%. Among those that were considered as confidently assigned (above the probability threshold of 80%), 3 fish were assigned to Atlantic salmon (*Salmo salar* L. 1758), 23 to hatcheries and 73 to rivers outside the focal area (4 from Dordogne-Garonne, a river system located further north, and 69 from Spanish coastal streams further south). The present study focusing on the migration behaviour of wild sea trout, Atlantic salmon and domestic fish were no longer considered in the subsequent analyses. In addition, four fish assigned to Dordogne-Garonne and caught in Gave de Pau were discarded because their classification as stray was dubious (details in Supporting Information no. 4).

3.2 | Straying rate calculation

In the end, the total number of sea trout that could be confidently relied on to do statistics and modelling reached 1437 with 516 from France and 921 from the UK. The number of sea trout varied substantially depending on both the river (94, 422 and 921, respectively for Nivelle, Adour and Tamar) and the sampling site (ranging from 9 to

TABLE 1 Details of sea trout (*Salmo trutta*) runs studied and number/proportion of fish exhibiting homing/straying behaviour (deduced from their genetic assignment)

Sampling site	Site no. ^a	River	Subcatchment	Distance (km)	n_1 homing	n_2 straying	Total ($n_1 + n_2$)	Straying proportion ($n_2/n_1 + n_2$)
Uxondoa (ROE71472 ^b)	2	Nivelle	Nivelle	12	27	56	83	0.67
Olha (ROE71479 ^b)	1	Nivelle	Nivelle	18	8	3	11	0.27
Chopolo (ROE99511 ^b)	7	Adour	Nive	22	8	24	32	0.75
Halsou (ROE99512 ^b)	6	Adour	Nive	25	4	5	9	0.56
Sorde-l'Abbaye (ROE90134 ^b)	3	Adour	Gave d'Oloron	44	252	15	267	0.06
Puyoo (ROE99309 ^b)	4	Adour	Gave de Pau	58	34	2	36	0.06
Baigts-de-Bearn (ROE44851 ^b)	5	Adour	Gave de Pau	67	73	5	78	0.06
Lower Tavy	10	Tamar	Tavy	15	20	54	74	0.73
Gunnislake Dam	8	Tamar	Tamar	31	650	115	765	0.15
Upper Tamar	9	Tamar	Lyd	57	78	4	82	0.05

^aThe site No. used in Figure 1.

^bThe ROE code in brackets refers to the French National Data Reference Centre for Water (<https://www.sandre.eaufrance.fr/>).

267 for French rivers and from 74 to 765 for Tamar). The traps were spread inland at a distance ranging from 12 to 67 km from the sea. The highest straying rates, 75% and 73%, respectively, were observed within 25 km from the coast, whereas the two lowest rates, 6% and 5%, were observed more than 44 km inland (Table 1).

3.3 | Logistic regression

Whatever the procedure used (model simplification by stepwise deletion at 5% level or delta AIC <2), the minimal adequate model only included additive effects. The interaction between the river and the distance from the sea was not significant, meaning the slope of the relationship between straying frequency and distance from the seafront did not depend on the river considered. The minimal model contained just five parameters, which were all significantly different from zero. Unlike the slope, the intercept differed among rivers. As illustrated in Figure 2, straying rate and distance from the sea front

negatively correlated, as evidenced by the non-zero (negative) coefficient associated with distance. The minimal adequate model explained slightly more than 44% of the deviance in straying rate, the proportion of non-local fish in a sea trout run caught at any point along a river depended on the distance separating this point to the seafront (nearly 40% of the deviance explained) rather than on the river itself (nearly 5% of the deviance explained). Plotting the fitted curves with their 95% C.I. through the scatterplot illustrated the fit of the minimal adequate model (Figure 2). The pattern was roughly common in all three rivers with curves being asymptotic to nearly zero as the distance from the sea exceeded 50 km and shifted to the right for Tamar and Adour compared to Nivelle. The predicted distances at which 50% of the sea trout run were of non-natal origin ranged from 15 (Nivelle) to 24 km (Adour) (Supporting Information no. 4). Nevertheless, it was impossible to model the curve properly close to the coast (<10 km) due to the absence of trapping devices so downstream and, consequently, the lack of empirical data. At the opposite end of the spectrum, the authors' best model became inappropriate because straying rate is not supposed to increase as it did due to the quadratic term.

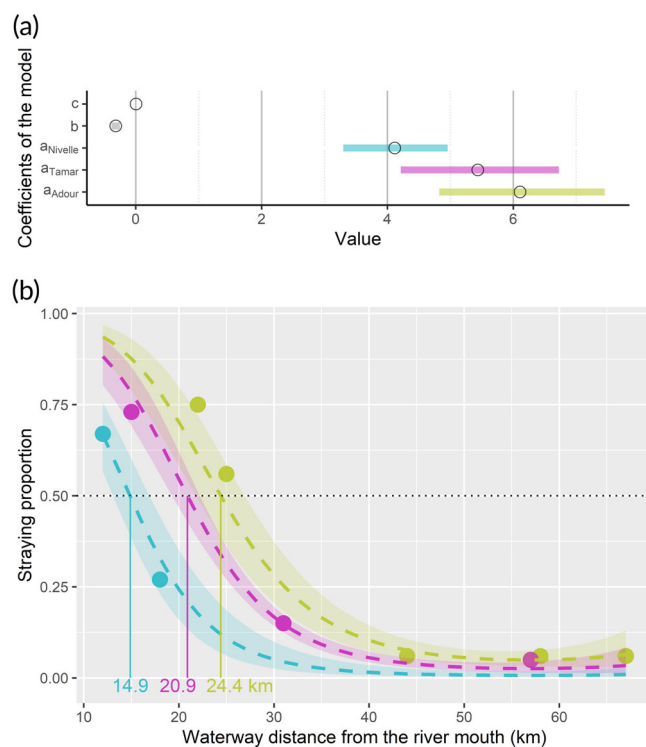


FIGURE 2 Best candidate generalized linear model, which included significant differences by river and as a function of distance, but with no significant interaction between river and distance. Three rivers from two geographically distant areas of the sea trout natural range have been considered, namely Adour and Nivelle flowing into the Bay of Biscay and Tamar flowing into the English Channel. (a) Value and 95% C.I. for the five parameters of the best candidate model. (b) The straying rate (y) on the vertical axis along the river course, with distance from the river mouth (x) indicated on the horizontal axis. Dotted lines are fitted model results from the best candidate linear model with colour-shaded regions representing the 95% C.I. The curves were fitted by $y = \exp(a_i + bx + cx^2) (1 + \exp(a_i + bx + cx^2))^{-1}$ with $a_{Adour} = 6.1088$, $a_{Tamar} = 5.4348$, $a_{Nivelle} = 4.1163$, $b = -0.3186$ and $c = 0.0028$. ● Adour, ● Nivelle and ● Tamar

4 | DISCUSSION

There are few places, if any, where one can observe migratory fish in their wild aquatic environment (Fausch *et al.*, 2002; Ryman *et al.*, 1995). That is the reason why, in the present days, monitoring activities on salmonid rivers, such as trapping, counters or video recording, are mainly based on purpose-built facilities. Such monitoring devices provide an invaluable tool for evaluating the numbers of fish recorded migrating either upstream or downstream. But installing such a device along the course of one river is largely the result of a compromise between the needs (population monitoring, research topics), the possibilities in terms of sites to be equipped (*e.g.*, mill, weir, dam, waterfall), and financial consideration. Subsequently, only a few monitoring devices, sometimes just a single or even none at all, exist along a migratory fish river leading at best to spotty records and reports. Quantifying fish abundance and tracking fish movements at the river basin scale are then challenging. This may explain why modelling straying at spatial river scale had rarely, if ever, been attempted before.

Here, to mitigate the paucity and the uneven coverage of the available data at one river scale, the authors aggregated data from 10 sea trout samples caught in three distinct river systems (Nivelle, Adour and Tamar) draining in two distinct basins of the Atlantic Ocean (the Bay of Biscay and the English Channel). By chance, the trapping devices in these three monitored rivers are located at various distances from the river mouth (from 12 to 67 km), leading to a great variation in straying rate from one device to another (ranging from 0.05 to 0.75), and enabling the authors to properly model spatial pattern of straying behaviour at a finer scale than usual. It should be noted that a genetic miss-assignment alone cannot account for the variation in straying rates observed between sites as the fraction of fish incorrectly assigned is moderate in the three target rivers and did

not exceed 9% and 5% depending on the tests performed by the authors, respectively, on empirical and simulated data sets. They then empirically demonstrated that straying rate and distance from the sea front negatively correlated, although in a non-linear manner. As they intuitively expected, the proportion of non-local sea trout entering a river depended on the river considered. More surprisingly, the decrease in straying rate along the river course did not depend on which river catchment was considered. Total sea trout abundance gradually decreases along a river course as distance from the sea increases due to the dendritic spatial structure of a river network. The cost of inland migration due to fishing mortality, migratory obstacles and altitude (Bohlin *et al.* 2001), to name but a few, also contributes to that decrease. But here, the authors showed that non-local sea trout abundance decreased at a more dramatic rate than total sea trout abundance in the three rivers investigated, suggesting a common behaviour underlying sea trout straying in fresh water. For the three rivers investigated, the fitted distances at which local and non-local fish proportions equalled did not exceed 25 km inland. Beyond 40 km, they empirically observed that straying rate decreased dramatically below 10% in all three rivers.

The overall sea trout sample used for the present study was large (approximately 1400), collected in two geographically distant populations of both the northern and the southern parts of the range (c. 800 km from one another), and genetically assigned by two distinct teams of researchers. This provides considerable support to the authors' statistical model. Based on sea trout runs from well-established populations, the model is, however, not expected to fit in other situations such as a post-glacial recolonization of virgin rivers with runs entirely composed of strays, to name but one. Nor is it supposed to accurately reflect the reality of the straying process near the river mouth (at least in the first 10 km) because no such empirical data were available at the time of this study. In all these cases, additional data are required to verify the accuracy of the model and to make any necessary adjustments.

These results shed new light on the poorly understood and under-explored spatial distribution of sea trout in fresh water and highlighted the considerable variation in straying rate that can be found within a catchment (*i.e.*, between sampling sites). Accordingly, the authors believe that it will help resolve some of the conflicting conclusions found in the literature regarding genetic differentiation between anadromous and freshwater resident brown trout, *e.g.*, Skaala and Naevdal (1989) vs. Hindar *et al.* (1991), and, more interestingly, avoid some sampling bias and help stratify sampling in future empirical studies on sea trout.

The reasons why so many sea trout enter non-natal rivers, why straying is so common throughout the species range and why straying appears spatially constrained at a river catchment level remain unclear, however. In the Bay of Biscay, sea trout populations enter Nivelle and Adour rivers in spring, months before spawning that takes place in late autumn under these latitudes. The authors hypothesize that this premature migration is a consequence of the fish having to avoid marine stressful conditions in summer due to the combination of high temperature and high salinity. Estuarine waters could

represent a refuge for sea trout facing osmoregulatory stress in marine waters. Such a hypothesis has already been invoked in northern latitudes where suboptimal temperatures and salinities prevail in winter (*e.g.*, Larsen *et al.*, 2008; Thomsen *et al.*, 2007). Sea trout spend more than half of their time in the uppermost 2 m of the water column (Rikardsen *et al.*, 2007), an area prone to temperature elevation in summer and temperature decrease in winter. Indeed, as recently demonstrated by Legrand *et al.* (2021), sea surface temperature plays a significant role in the timing of sea trout return migration in French Atlantic rivers. The estuaries of Adour, Nivelle and Tamar are under tidal influence with marine water flooding up to a few 10 of kilometres, *e.g.*, 15–20 km inland for River Adour (Goni-Urriza *et al.*, 2007; Sharif *et al.*, 2014). The river entry of non-local sea trout and their aggregation in the lower catchment are possibly related to the salinity gradient prevailing in estuary (King *et al.*, 2016; Masson *et al.*, 2018). Stressful marine conditions are also expected to drive local sea trout premature upstream migration, but unlike non-local sea trout, local sea trout migrate further inland driven by their homing behaviour.

It is, however, not known whether strays breed or not in the non-native rivers they enter. As a long time elapsed between upstream migration peaks and spawning, strays may move downstream in search of their natal river when sea surface temperature drops to ultimately reach their natal river before the start of the spawning season. To the authors' knowledge, there is no empirical evidence in the literature to support this hypothesis. Unfortunately, providing additional evidence of such allegation in the context of the present study was not possible because trapping devices used for sampling migratory fish were built to intercept upstream but not downstream migrating fish. Nonetheless, the fact that straying behaviour results in limited or no contemporary gene flow among established populations occupying distinct river systems, as demonstrated in salmonids (Santaquiteria *et al.*, 2016; Tallman & Healey, 2011) including sea trout (Masson *et al.*, 2018), adds further weight to this hypothesis.

In conclusion, estimating dispersal from an overall straying rate per river or tributary using a sample or a complete census of the sea trout run has been done for a long time in numerous rivers. In the light of the present results, extreme caution must be exercised when interpreting such data and comparing such figures among rivers or tributaries, because the sampling site, or more accurately its location relative to the river mouth, is of prime importance and far more important than the river/tributary itself. The spatial scale of dispersal movements is one of the key aspects to understand the genetic structuring of anadromous fishes and the functioning of their populations. The data and results presented here suggest that straying in is far more constrained spatially than first expected.

From a conservation perspective, local and non-local sea trout show different patterns of estuary use during upstream migration. The most notable result of this study was the quick decrease in the proportion of non-local sea trout with the distance to the sea. Accordingly, if reproduction events of non-local sea trout indeed occur, they are likely to occur in the lower catchment. Estuary, floodplain and lower tributaries are then supposed to be key habitats for restoring,

maintaining or promoting gene exchange between brown trout resident populations. This information is particularly relevant to restoration actions and will help managers adopt and implement biologically sound management strategies. The knowledge of spatial distribution of sea trout by origin within a catchment thus provides a valuable aid for the managers in their strategies to conserve or restore particular stocks. For instance, it becomes theoretically possible to decide which stock to preserve and which one to target by delineating the fishing areas.

AUTHOR CONTRIBUTIONS

J.C. and O.L. acquired the funds and designed the study. J.C. performed *in silico* genetic analyses under the supervision of O.L. J.C. performed statistical analyses and wrote the manuscript with contributions from O.L. and A.L. All three authors contributed to revisions and approved the final version of the manuscript.

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CONFLICTS OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY OF STATEMENT

Raw data used to draw the conclusions of the present study are from two previously published papers. Additional information concerning *in silico* genetic and statistical analyses could be found in the Supplementary Materials deposited in the INRAE external data repository available upon acceptance of the article.

ETHICAL CONSIDERATIONS

INRA UMR ECOBIOP ISC ECP (<https://doi.org/10.15454/1.5572402068944548E12>), INRA UE 1036 U3E (<https://doi.org/10.15454/1.5573930653786494E12>), ONEMA, French Federations and local associations of Angling (departments 40, 64 and 65), Parc Naturel des Landes de Gascogne, Parc National des Pyrénées, ECOGEA, fish farms and Gestion Ambiental de Navarra have contributed to Adour and Nivelle sample collections. Each of the field campaigns was granted by the competent national authorities (Direction Départementale des Territoires et de la Mer under the supervision of the Préfet Départemental for France and Director del Servicio de Conservación de la Biodiversidad for Navarra). For Tamar sample collection, details are provided in the original paper of King *et al.* (2016).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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Abstract

In a context of rapid environmental changes and anthropogenic pressures, there is an urgent need to better understand the responses of species and to provide recommendations on how we can manage and conciliate human activities with the functioning of ecosystems. However, there is often a mismatch between the scale of species functioning, threats, and management actions. In particular, even if dispersal is a ubiquitous trait in organisms, implications of connectivity and spatial structure for adaptation, persistence, and management of populations are still poorly appreciated for numerous species. This is the case of Atlantic salmon (*Salmo salar*), for which eco-evolutionary dynamics, exploitation and management of populations are rarely considered within a metapopulation perspective. Yet, growing evidence shows individuals and gene flow among populations of salmon. Motivated by this context, this thesis aims to use an innovative multi-scale approach, from genes to metapopulation, to 1) better understand the capacities of adaptation and persistence of exploited populations of Atlantic salmon and 2) explore management practices that would meet both objectives of conservation and exploitation. Using a spatially explicit demo-genetic agent-based model, I simulated a network of interconnected populations of Atlantic salmon based on the metapopulation of Brittany. Through several scenarios, I explored the influence of a gradient of dispersal rates, various spatial genetic structures, the spatial configuration of populations, and spatial management strategies on the demographic (e.g., stability, persistence) and eco-evolutionary (e.g., life history traits, genetic diversity) dynamics of interconnected and exploited local populations. This thesis highlighted a non-linear relationship between dispersal rates and the stability of the metapopulation, resulting in an optimal portfolio effect for dispersal rates around 20% in a homogeneous network. At local population scale, I demonstrated phenotypic changes induced by density-dependent effects modulated by dispersal, as well as an increase in genetic diversity within populations. Simulations also showed adaptation of local populations was fostered by dispersal between initially diverse populations, providing general support for the adaptation network theory. However, the spatial configuration of populations also played an important role in their evolutionary trajectories by modulating dispersal patterns. Ultimately, this thesis showcased a slight benefit from a spatialized management strategy protecting source populations from exploitation, especially for high dispersal rates. Contrasted and complex evolutionary consequences emerged from the different management strategies in interaction with dispersal. I conclude that it is critical to account for complex interactions between dispersal, eco-evolutionary processes, and spatial structure of populations to better understand and manage Atlantic salmon response to environmental change and anthropogenic pressures. This thesis also encourages empirical knowledge about dispersal rates and metapopulation structure of this species, and advocates for conservation actions according to the portfolio and adaptation network approach, protecting connectivity and biocomplexity in the face of uncertainty. My thesis opens up further perspective of work and illustrates the potential of our modelling approach as a prospecting tool for theoretical and applied research on metapopulations.

Keywords: dispersal, spatial structure, adaptation network, management, Atlantic salmon, exploitation, model, demo-genetic, portfolio effect