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

3
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26 **Abstract**

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

40
41 **Keywords:** Atlantic salmon, demo-genetic agent-based model, dispersal, eco-evolutionary
42 dynamics, metapopulation, portfolio effect, synchrony

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51 1. INTRODUCTION

52

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

62

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

74

75 Dispersal or the movement of individuals from their natal population to a different breeding
76 population, is ubiquitous in nature and is also a process that promotes species responses to
77 environmental change by spreading the risk of reproductive failure (Ronce 2007, Buoro and
78 Carlson 2014). There is growing appreciation – from both theory and empirical studies - of the
79 causes and consequences of dispersal (Clobert et al. 2009, 2012). For example, dispersal and
80 gene flow among interconnected populations can induce genotypic and demographic
81 consequences on recipient populations (Cayuela et al. 2018). This may prevent the extirpation
82 of local populations via rescue effects (see Carlson et al. 2014 for review) but also lead to “anti-
83 rescue effects” (Harding and McNamara 2002) and reduce metapopulation diversity through
84 the homogenizing effect of dispersal (Paradis et al. 1999, Lenormand 2002). Within a
85 metapopulation context (Hanski 1998), the connectivity among populations is critical because
86 it has consequences for the dynamics of local populations and the whole metapopulation. Thus,
87 we would expect eco-evolutionary dynamics of a metapopulation to differ from that of a single
88 population taken in isolation, highlighting the need to consider eco-evolutionary processes,
89 feedback loops, and the spatial structure of populations within a single, coherent framework.
90
91 More generally, the resilience of ecological systems, such as a metapopulation, relies on the
92 connectivity and the diversity of responses of its components (Elmqvist et al. 2003, Webster et
93 al. 2017). Indeed, there is growing recognition that a diverse network of populations can
94 promote overall stability of population complexes and resource flows (e.g., fishery yields,
95 Schindler et al. 2010). Ecological portfolio theory emphasizes the importance of
96 biocomplexity, or life history diversity within and among populations (Hilborn et al. 2003,
97 Abbott et al. 2017), as well as asynchronous dynamics among populations as factors
98 contributing to stability of population complexes (Schindler et al. 2010, 2015). The portfolio
99 effect has been studied extensively in imperiled and exploited salmonid species, especially for

100 Pacific salmonids (e.g., Moore et al. 2010, Carlson and Satterthwaite 2011, Anderson et al.
101 2015). However, the potential influence of dispersal among salmon populations on portfolio
102 strength has received less attention (but see Yeakel et al. 2018).

103
104 Dispersal rates are often considered low in salmonids (Schtickzelle and Quinn 2007, Birnie-
105 Gauvin et al. 2019), even though identification of dispersers (or “strayers”) and dispersal rates
106 remain difficult to assess in wild populations. For instance, Atlantic salmon (*Salmo salar*) is
107 well known for its great diversity of life-history strategies linked to phenotypic plasticity
108 (Mangel and Satterthwaite 2016, Erkinaro et al. 2019) and genetic basis of life history traits
109 (e.g., age at maturation, Barson et al. 2015, Lepais et al. 2017), but it is also commonly
110 presented as a highly philopatric species (Salmenkova 2017). Yet, evidence of dispersal
111 behavior and gene flow have been reported between several populations of Atlantic salmon
112 (e.g., Consuegra et al. 2005, see Keefer and Caudill 2014 for review), allowing recolonization
113 and expansion (Makhrov et al. 2005, Perrier et al. 2010, Pess et al. 2014). However, few studies
114 have estimated dispersal rates between wild populations of Atlantic salmon (but see Jonsson et
115 al. 1991, 2003, Consuegra et al. 2005, Jonsson and Jonsson 2017), and even fewer discuss or
116 assess the potential consequences of metapopulation functioning on conservation and
117 management of Atlantic salmon populations (but see Castellani et al. 2015, Bowlby and Gibson
118 2020). As suggested by Schtickzelle and Quinn (2007), future work should strategically
119 consider salmon dynamics from a metapopulation perspective.

120
121 Modeling approaches can overcome the difficulties associated with examining dispersal
122 consequences in nature. Among them, classical metapopulation theory, demographic, patch
123 occupancy models (Hanski 1998, 1999, Sutherland et al. 2014; Bowlby and Gibson 2020 for
124 salmonids), as well as evolutionary analytical models (Berdahl et al. 2015, Yeakel et al. 2018),

125 have advanced general concepts in metapopulation functioning and persistence. Mechanistic
126 eco-evolutionary models such as Demo-Genetic Agent-Based Models (DG-ABMs, also called
127 Eco-Genetic ABMs) provide a complementary and flexible approach for simulating the
128 complexity of a species life cycle (DeAngelis and Grimm 2014, Stillman et al. 2015) and
129 assessing the demo-genetic consequences of dispersal in a unified framework. By integrating
130 variation and interactions between individuals, as well as explicit genetic basis of traits and
131 their transmission, this approach allows life-history traits to evolve in interaction with
132 demographic effects in response to environmental and anthropogenic pressures (Dunlop et al.
133 2009, Johnston et al. 2019). Recently, several generic metapopulation DG-ABMs have
134 emerged such as Nemo (Guillaume and Rougemont 2006), SimAdapt (Rebaudo et al. 2013),
135 RangeShifter (Bocedi et al. 2014, 2021) or CDMetaPOP (Landguth et al. 2017). Several
136 specific DG-ABMs represent the complex life cycle of salmonid species (e.g., Thériault et al.
137 2008, Ayllón et al. 2016), but only two studies incorporate dispersal between populations to
138 our knowledge. Landguth et al. (2017) simulate a network of non-native Eastern Brook Trout
139 (*Salvelinus fontinalis*) populations and evaluate efficiency of fish removal management
140 strategies taking into account dispersal between patches. Lin et al. (2017) extended a single
141 population model of sockeye salmon (*Oncorhynchus nerka*) to two populations to assess the
142 consequences of dispersal on local adaptation and demography. We build on this general
143 approach, but with a focus on Atlantic salmon, to explore dispersal implications within a
144 realistic network of populations and an eco-evolutionary framework.

145
146 Our ultimate goal is to shed light on the potential implications of dispersal on the portfolio
147 effect and eco-evolutionary dynamics in Atlantic salmon. To do so, we extended a demo-
148 genetic agent-based model of Atlantic salmon (IBASAM, Piou and Prévost 2012) to a
149 metapopulation context. The original IBASAM model was developed to evaluate eco-

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

163

164 **2. MODEL DESCRIPTION: MetaIBASAM, A SPATIALLY STRUCTURED**
165 **VERSION OF IBASAM**
166

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

180
181 MetaIBASAM aims to simulate a network of interconnected Atlantic salmon populations and
182 to explore the consequences of dispersal at demographic, phenotypic, and genotypic levels in
183 a unique and coherent framework. This simulation tool is a demo-genetic agent-based model
184 representing explicitly the life cycle of the species, individual life histories from birth to death,
185 reproduction, and transmission of individual traits to successive generations. The full
186 description of IBASAM is available from earlier studies (Piou and Prévost 2012, 2013, Piou et
187 al. 2015), but we present the key features, model improvements (i.e., growth potential

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

190

191 2.1. Key features of IBASAM

192 2.1.1. Modeling the life cycle of Atlantic salmon at the individual scale

193

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

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

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

215 2.1.2. Density and environment effects on life-history traits

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

223 2.1.3. Heritable traits and selective pressures

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

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

241 2.2. Model improvements: a genetic basis of growth and a growth – survival trade-off

242 While growth depends mainly on environmental conditions encountered by individuals, we
243 introduced a genetic basis for the growth potential parameter as suggested by Gjerde et al.
244 (1994). However, preliminary analysis showed that including a genetic basis to growth
245 potential led to its evolution toward higher values, resulting in larger individuals over time (see
246 Supporting information 1). Indeed, because sea survival and reproductive success depend
247 positively on size and growth (Piou and Prévost 2012), natural and sexual selection tend to
248 favor larger individuals with higher growth potential. To limit this directional selection and
249 represent mortality costs of rapid growth as reported in experimental studies (Bochdansky et
250 al. 2005, Biro et al. 2006), we implemented a growth–survival trade-off in river (Fig. 1,
251 Supporting information 1; survival at sea is size-dependent). Combined with the size-
252 dependent survival at sea and reproductive success, the growth-survival trade-off induces a
253 stabilizing selection for growth and size and an optimal fitness value of growth potential (Fig.
254 2 A), ensuring stable size distributions in a neutral context (without selection, Supporting
255 information 1).

256 2.3. Dispersal modeling: extending IBASAM into a metapopulation context

257
258 MetaIBASAM considers the connectivity between populations by implementing a dispersal
259 process, i.e., adults can disperse toward other rivers of the system during their breeding

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

268
 269 At the time of adult riverward migration, dispersing individuals are randomly selected from
 270 their population of origin j with a probability to disperse P_j , independently from their individual
 271 characteristics (Equation 1). The probability P_j is function of a constant philopatry rate (noted
 272 h), i.e., without variation between populations, fixed at initialization. Then, for the subset of
 273 dispersing individuals, the recipient population j' is determined by sampling into a multinomial
 274 distribution of parameter $p_{jj'}$, which is the probability to disperse from the population j to the
 275 population j' .

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

276
 277 With P_j the total dispersal rate of the population j and h the philopatry rate.

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

282 2012), which maximizes the connectivity between close populations while still allowing some
 283 flow of individuals between distant rivers (long-distance dispersal, Equation 2). Because the
 284 attractiveness of rivers for anadromous salmonids can vary as a function of the population size,
 285 likely because of chemical attraction to congeners, collective behavior, and/or the influence of
 286 river discharge (Jonsson et al. 2003, Berdahl et al. 2016; see Keefer and Caudill 2014 for
 287 review), we weigh the distance kernel by a parameter g_j , the relative size of the destination
 288 population with other populations, to represent its attractiveness (Equation 3). The larger the
 289 populations, the more attractive they are to dispersing individuals.

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

$$\text{with } g_{j'} = \frac{\log_{10}(A_{j'})}{\sum_{A_1}^{A_{npop}} \log_{10}(A_j)} \quad (3)$$

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

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

299 2.4. Model parameterization and outputs

300

301 MetaIBASAM consists of a set of IBASAM sessions - with one session simulating one
302 population - running in parallel and exchanging information about the dispersers (e.g.,
303 phenotypic, genetic values, and genotypes). Similar to IBASAM, MetaIBASAM was
304 parameterized in a pattern-oriented modeling framework (Grimm et al. 2005) using values
305 extracted from the literature and empirical studies (see Piou and Prévost 2012, and Supporting
306 information 2), and adjusted using a long-term monitoring program of the salmon population
307 in the Scorff River (Brittany, France). We adjusted the parameters of the growth-survival trade-
308 off (see Supporting information 1 and 2) to ensure that abundances and size at different life
309 stages are within the range of observed values on the Scorff River. All other parameters of each
310 population are kept identical to the IBASAM version (Piou and Prévost 2012), except for
311 survival rates at different life stages and a temperature-survival related parameter (dr) that have
312 been adjusted (Supporting information 2) to updated environmental conditions (see section
313 3.1). The parameter b of dispersal kernel was adjusted to limit dispersal under 50km for at least
314 80% of dispersers individuals, as suggested by Jonsson et al. (2003) and Keefer and Caudill
315 (2014). Daily water temperature, water discharge, marine growth conditions, and exploitation
316 are the main environmental and anthropogenic factors affecting individuals in the model (Fig.
317 1).

318
319 IBASAM is coded in C++ language, and an R package named MetaIBASAM has been
320 developed (<https://github.com/Ibasam/MetaIBASAM>). Each IBASAM can be parametrized by
321 users to represent a unique population with its own demographic (area, distance), phenotypic,
322 genetic (initial distribution), environmental (water temperature, discharge), and anthropogenic
323 (exploitation rate) characteristics. One simulation of MetaIBASAM returns all information on
324 individuals (e.g., unique ID, population of origin, current population, body size, genetic values)
325 and nests (e.g., ID of parents, number of eggs) two times per year for each population.

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

3.1. Scenario and parameterization

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

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

358
359 Simulations were initialized for each population using a random draw of individuals
360 corresponding to 25% of rivers production area A_j only to limit the computing time without
361 loss of generality. Phenotypic and genetic values were sampled using the same distributions
362 implemented in IBASAM (see Piou and Prévost 2012). Since generation time for this species
363 is approximately 2.5 years in French populations, we simulated each dispersal scenario and
364 population network over 50 years, which is sufficient time to detect any changes in the
365 population dynamics and evolution of life-history traits. For each dispersal scenario, we
366 simulated 100 replicates with a 10-year burn-in period. We ran the simulation using R version
367 3.6.3 and the package MetaIbasam version 0.0.6. Code and R scripts are freely available at
368 <https://github.com/Ibasam/Portfolio>.

369

370 3.2. Simulations outcomes analysis

371 3.2.1. Network spatial structure

372

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

375 demography (growth rate) and immigrants rates, we classified each population as sink, neutral,
376 or source based on the ratio of incoming individuals (immigrants) to outgoing individuals
377 (emigrants) in the sea-adult returns. We considered populations with a ratio above one as *sinks*,
378 those with a ratio below one as *sources*, whereas the *neutral* populations have a ratio near one.
379
380 Regardless of the fixed dispersal rate, source-sink dynamics within a network of fifteen
381 populations emerged from the model due to asymmetric dispersal that was driven by
382 differences in population size and spatial structure (Fig. 3 A and B). For example, larger
383 populations generated more emigrants, and more isolated populations received less immigrants
384 but “sent” the same proportion of emigrants. The ratio between immigrants and emigrants was
385 highly variable between populations, as well as the proportion of immigrants, which ranged
386 from 4% to 27% for dispersal rates of 10%. But the source-sink dynamics among populations
387 within the network remained similar between dispersal scenarios or over time (Fig. 3 A).

389 3.2.2. Demographic consequences of dispersal: population network stability, 390 synchrony, and persistence

391
392 For each dispersal scenario and simulation, we measured the stability and diversity of the
393 network using the portfolio effect and synchrony metrics. The portfolio effect (hereafter PE) is
394 a metric measuring the stabilizing effect of population diversity on metapopulation dynamics
395 (Schindler et al. 2010), by comparing the measured metapopulation variance over the time
396 series to the theoretical variance expected if the metapopulation was considered as a unique
397 population. To do so, we used the mean-variance method from the R package *ecofolio*
398 (Anderson et al. 2013). Using this approach, if this ratio equals 1, it means that the network is
399 as stable as expected if it was a single population. If the ratio exceeds 1, it suggests evidence

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

403
 404 The synchrony index ϕ_x , reflecting the degree of population synchrony in their demographic
 405 evolution over time, was measured as the ratio between the detrended network variance σ_x^2 and
 406 the squared sum of populations detrended standard deviation σ_{x_i} (adapted from Loreau and de
 407 Mazancourt 2008, Equation 4). This index is expressed between 0 (asynchrony) and 1
 408 (synchrony).

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

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

415
 416 Our analyses revealed a non-linear relationship between dispersal and stability of the
 417 population network, resulting in an optimal portfolio effect for dispersal rates around 20%, i.e.,
 418 80% of a population returning to its natal site (Fig. 4 A). With strict philopatry (i.e., no
 419 dispersal), the PE was on average above 1, meaning that the population network was more
 420 stable than expected if it was the sum of the local populations. Indeed, the dynamics of all
 421 populations were stable and asynchronous ($\phi \sim 0.1$; Fig. 4 B). Between dispersal rates of 0%

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

428
429 At the local population level, dispersal tended to decrease the coefficient of variation of the
430 abundance of adult returns, suggesting a stabilizing effect of dispersal on population dynamics
431 (Fig. 4 C). Dispersal rates also reduced the extinction risk of small and sink populations,
432 whereas the extinction risk of other populations appeared insensitive to dispersal (Fig. 4 D).
433 Altogether, these results suggest a demographic rescue of populations by dispersal, especially
434 for those behaving as sink populations.

436 3.2.3. Intra- and interpopulation phenotypic and genotypic diversity

437
438 Our results showed that dispersal per se can induce phenotypic diversity between populations.
439 Indeed, we observed a slight decrease of median juvenile and adult size with dispersal for sink
440 populations and an increase in source populations, which might have consequences on life-
441 history tactics illustrated by shifts in the age at sea maturation (Fig. 5, A, B, D). Note that we
442 assessed phenotypic changes on philopatric individuals only, to test the consequences of
443 dispersal on each population's trait distribution without the direct influence of immigrants. As
444 immigrants do not differ from philopatric adults in terms of size and growth potential at
445 initialization, this unexpected result could be explained by density-dependent effects on river
446 growth. Indeed, dispersal increased juveniles density in sink populations (due to higher

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

451

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

456

457 **4. DISCUSSION**

458

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

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

478

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

481

482 Our study emphasizes a non-linear relationship between dispersal rates and the stability of the
483 metapopulation, resulting in an optimal portfolio effect for dispersal rates around 20% with the
484 particular parameterization of our model. Using a network of two populations, Yeakel et al.
485 (2018) also found non-linear effects of dispersal on metapopulation robustness (PE) and
486 identified two optimums (strongest PE, called alternative stable state regimes in their paper) at
487 levels of dispersal below 10% and 30% of the population respectively. Interestingly, the
488 optimal dispersal rate that we report is consistent with the few empirical studies reporting
489 dispersal rates in Atlantic salmon (Jonsson et al. 2003, Jonsson and Jonsson 1991, 2017, Keefer
490 and Caudill 2014). However, it is important to note that it might depend on the adjustment of
491 the dispersal kernel parameter and reported rates in the literature are highly variable and likely
492 biased (e.g., site/year dependence, low sample size, hatchery influence; Jonsson et al. 2003,
493 Consuegra et al. 2005, Jonsson and Jonsson 2017, Keefer and Caudill 2014). When the
494 dispersal rate was below 20% in our model, dispersal had a stabilizing effect on population
495 dynamics and fostered the demographic rescue of small, sink populations by increasing
496 population size and/or limiting demographic stochasticity. Using a theoretical two-patch

497 metapopulation model, Hill et al. (2002) also demonstrated that dispersal rates between 0% and
498 20% increased the time before extinction two-to four-fold, and a recent Population Viability
499 Analysis revealed the benefit of population connectivity for persistence of diadromous fishes
500 more generally under high productivity scenarios (Bowlby and Gibson 2020). However, we
501 found that the positive effects of dispersal on metapopulation stability are overcome by
502 increased synchronization of population dynamics with higher dispersal rates (>20%), which
503 could increase the metapopulation risk of collapse (Carlson and Satterthwaite 2011). The “anti-
504 rescue” effects (Harding and McNamara 2002) associated with higher dispersal rates have been
505 demonstrated both theoretically and empirically on patterns of synchrony (Paradis et al. 1999,
506 Yeakel et al. 2018), but also on genetic homogenization (Tinnert and Forsman 2017), and
507 reduced local adaptation (Schiffers et al. 2013).

508

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

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

528

529 **Model significance, limits, and perspectives**

530

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

547
548 However, despite the model complexity, some processes are still represented in an overly
549 simplified manner, especially the *causes* of dispersal. Like other models focused on salmonids
550 (see Table 1), we simulated dispersal as a random individual process, with a probability of
551 dispersing that was constant in space and time, and limited to a fixed expansion range. Yet, it
552 has been shown in several species and also suggested for salmonids that dispersal depends on
553 individuals traits (e.g., sex-biased dispersal, Li and Kokko 2019, genetic basis, Saastamoinen
554 et al. 2018) or populations characteristics (e.g., density-dependent dispersal, Berdahl et al.
555 2016). These features might modify the intensity and direction of flow of individuals and the
556 consequences of our dispersal scenarios, because dispersal could evolve towards dispersal rates
557 which optimize the portfolio effect. For example, Berdahl et al. (2015) tested a model including
558 joint evolution of dispersal and local adaptation and showed that dispersal should evolve
559 towards lower values in the context of heterogeneous populations environments. Additionally,
560 we did not represent explicitly the consequences (e.g., costs) of dispersal, such as additional
561 mortality or reduced reproductive success (Moblely et al. 2019). However, this is limited by the
562 lack of knowledge on processes and mechanisms of dispersal in salmonids (but see Jonsson et
563 al. 2003 for Atlantic salmon and Bett et al. 2017 for Pacific salmon). Thus, there is considerable
564 room for improvement in our model, and below we highlight some potential research avenues
565 and ideas that could be addressed by MetaIBASAM and any other demo-genetic ABM of
566 salmonid metapopulation, based on burgeoning theoretical and empirical research on causes
567 and implications of dispersal.

568
569 *1/ We need more studies to understand dispersal mechanisms and their consequences on eco-*
570 *evolutionary dynamics of metapopulations.*

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

582

583 *2/ We need to evaluate how diversity between and within populations may shape an adaptation*
584 *network fostering response to environmental changes.*

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

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

597

598 *3/ We need to assess the interplay between diversity and dispersal by considering spatial*
599 *structure and local adaptation.*

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

616

617 *4/ We need to consider the implications of spatially structured populations for management.*

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

620 Prior work has warned about the danger of ignoring spatial structure and connectivity of
621 populations (Cooper and Mangel 1999), but few studies have compared different management
622 strategies while also considering the spatial structure of populations (but see Tufto and Hindar
623 2003, Moore et al. 2021). While mixed-stock fisheries explicitly consider variation in
624 productivity among harvested stocks, rarely is connectivity considered. Our preliminary results
625 suggest that any alteration in a source population could affect demography and phenotypic
626 traits of surrounding populations. Moreover, selective exploitation within spatially structured
627 populations could drive complex evolutionary trajectories in the whole network – whether local
628 populations are exploited or not - because selective exploitation can induce evolution of life
629 history traits (Piou et al. 2015, Ayllón et al. 2018).

630

631 **Conclusions**

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

643

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652

653 **COMPETING INTERESTS STATEMENT**

654 The authors declare there are no competing interests.

655

656 **AUTHORS' CONTRIBUTIONS STATEMENT**

657 AL: conceptualization, methodology, formal analysis, writing (original draft, review and
658 editing), MB: conceptualization, methodology, writing (review and editing), SMC:
659 conceptualization, writing (review and editing), FH: methodology, CP: methodology, JP:
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661

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666

667 **DATA AVAILABILITY STATEMENT**

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

670 obtained via the ORE-DiaPFC observatory and can be accessible on <https://github.com/ORE->
671 [DiaPFC/Abondance/tree/master/Scorff](https://github.com/ORE-DiaPFC/Abondance/tree/master/Scorff), and on demand, respectively.

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

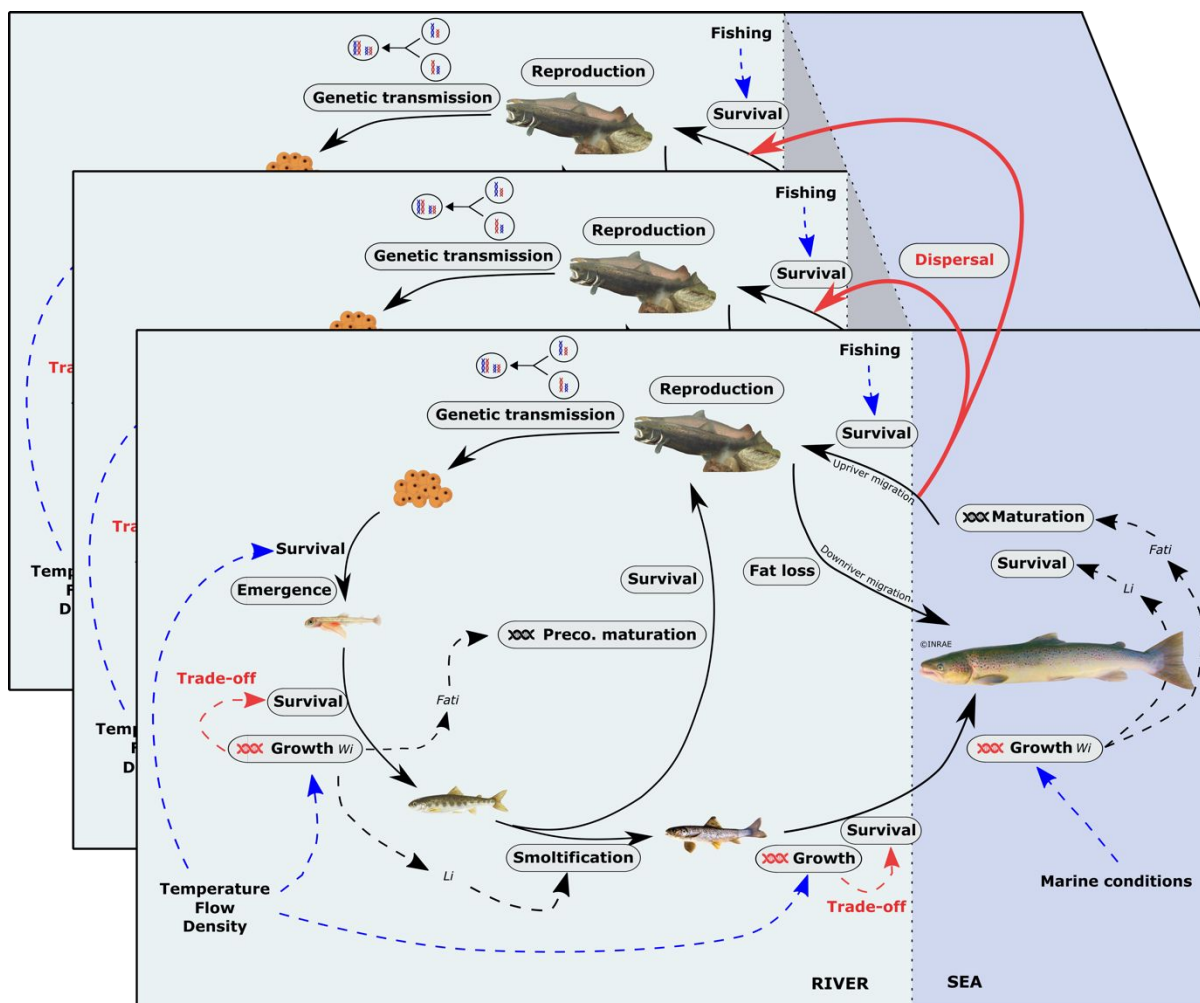
References	Model type	Species	Dispersal/Connectivity	Eco-evolutionary dynamics	Key mechanistic processes
Bowlby and Gibson 2020, Fullerton et al. 2011	Population dynamics models, graph theory	Salmonids	-Explicit SS: multiple populations, size and distance -Em: fixed emigration rate -Im: distance dispersal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

(extension from IBASAM,
Piou and Prévost 2012).

-Im: dispersal kernel (distance
and attractivity)

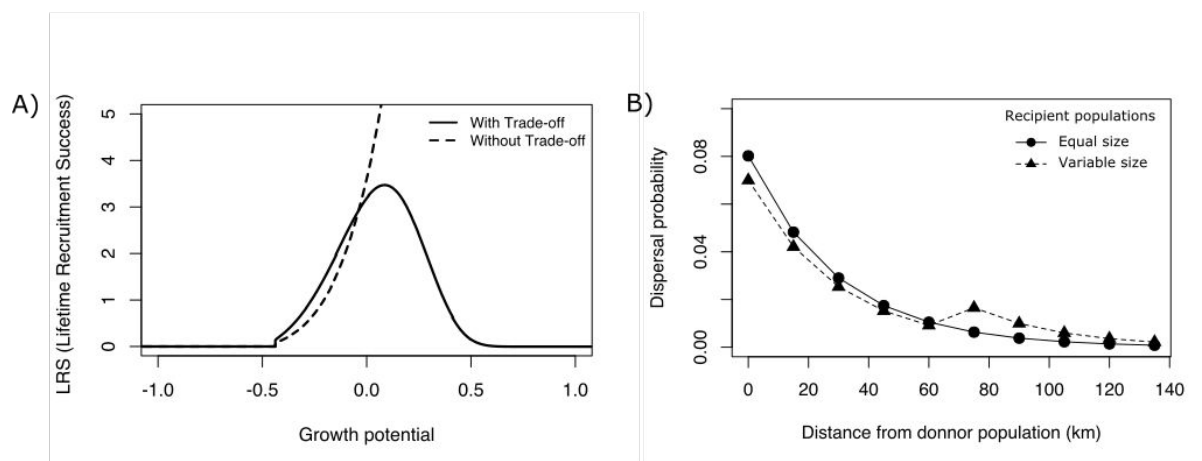
-Emerging fitness
from fitness-related
traits

-Survival ~ temperature,
flow, density, growth
potential, size
-Maturation (precocious
and at sea) ~ energetic
reserves and genetic
thresholds
-Size dependent
migration
-Sexual selection



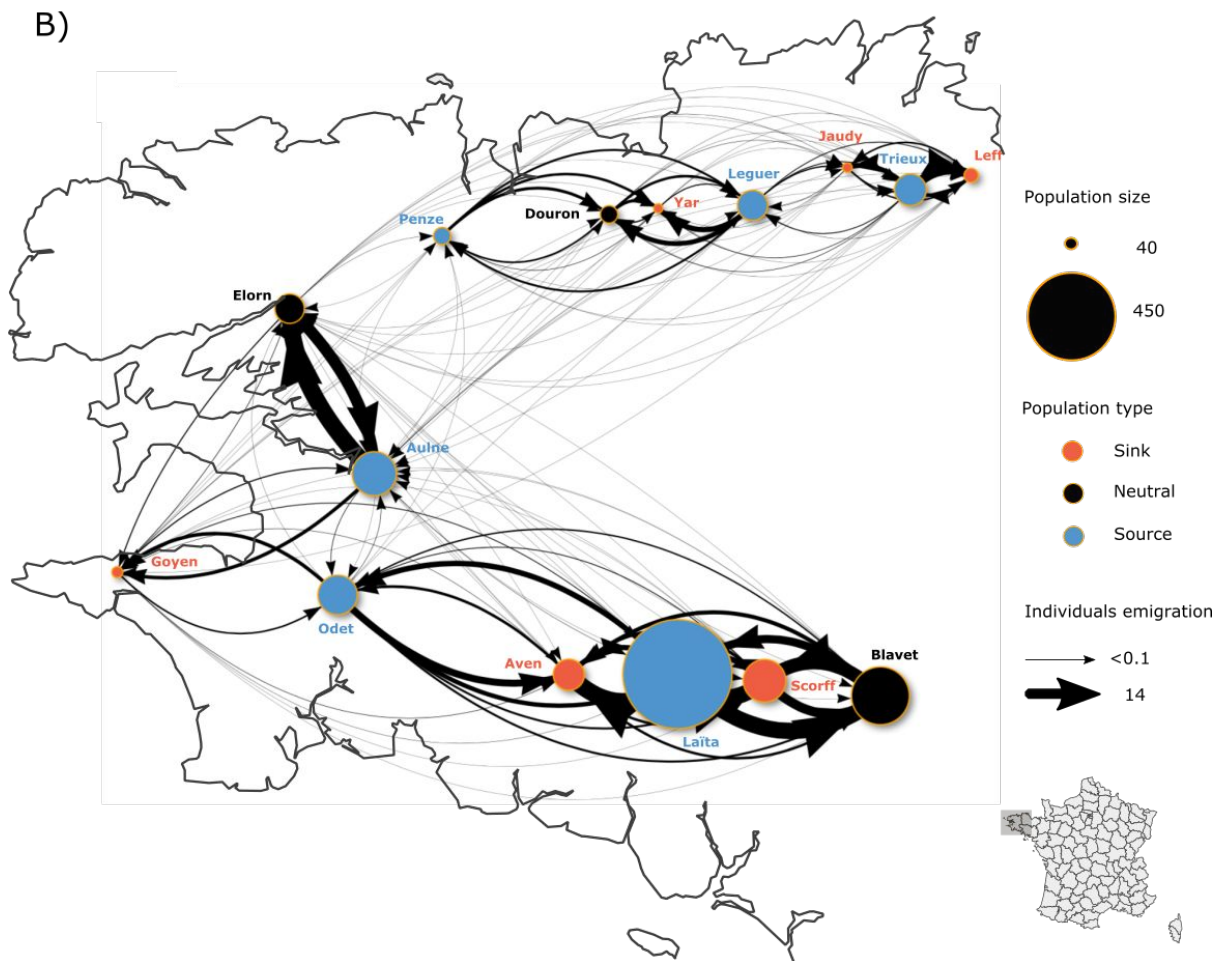
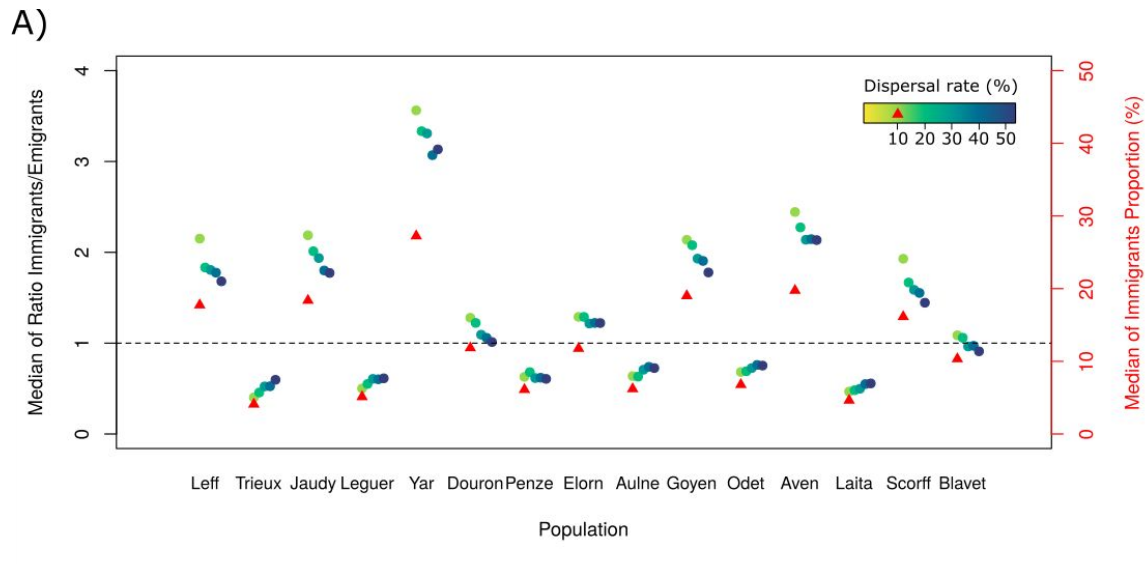
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2 **Fig. 1:** Conceptual framework of the MetaIBASAM model, adapted from Piou and Prévost
 3 2012. Processes at individual levels are highlighted in grey, where the DNA icon indicates
 4 heritable traits linked to these processes (maturation thresholds and growth potential). The
 5 dashed arrows represent the influence of both environmental and anthropogenic factors (in
 6 blue), or the influence of state variables of individuals (in italics). New additions from
 7 IBASAM, the dispersal process, growth potential heritability and growth-survival trade-off,
 8 are identified in red. Each big rectangle represents a population, exchanging individuals with
 9 neighboring populations via dispersal.



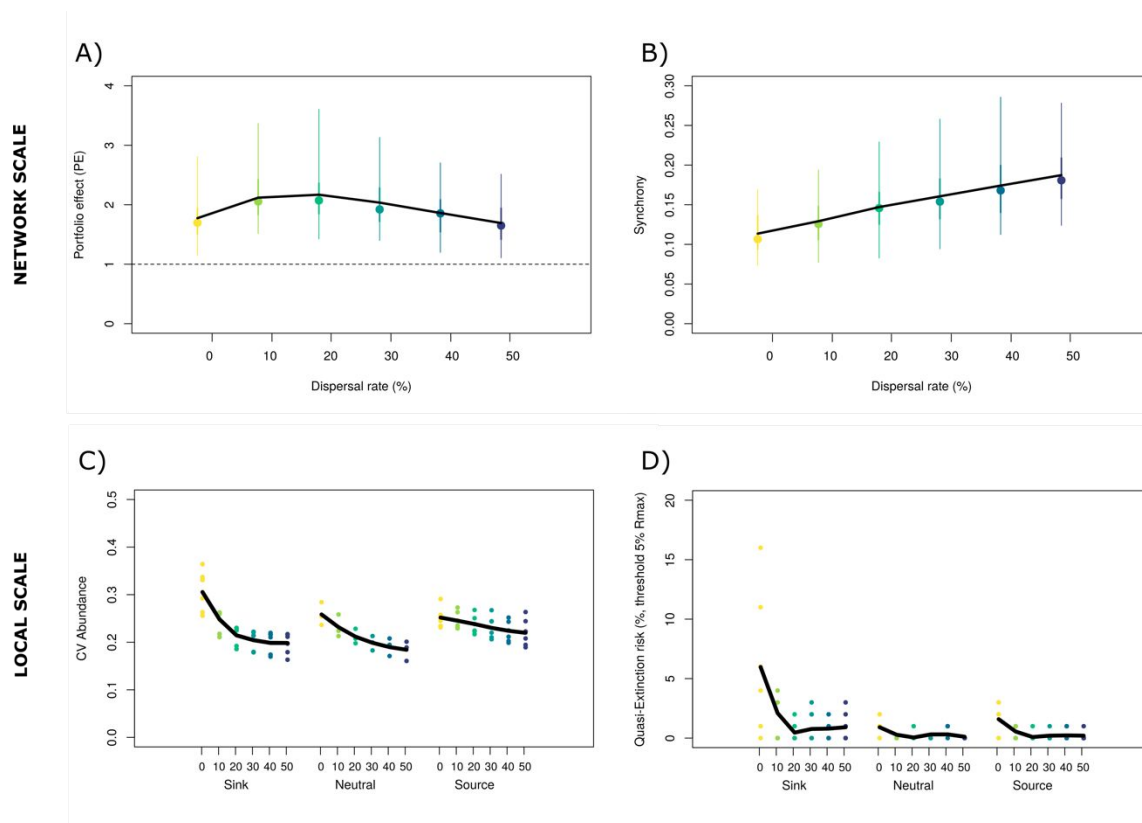
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2 **Fig. 2:** Additions into MetaIBASAM from IBASAM. In A), theoretical optimal value of
 3 phenotypic growth potential (in log scale) based on mean individual Lifetime Recruitment
 4 Success (measured as the mean egg number per female; see processes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



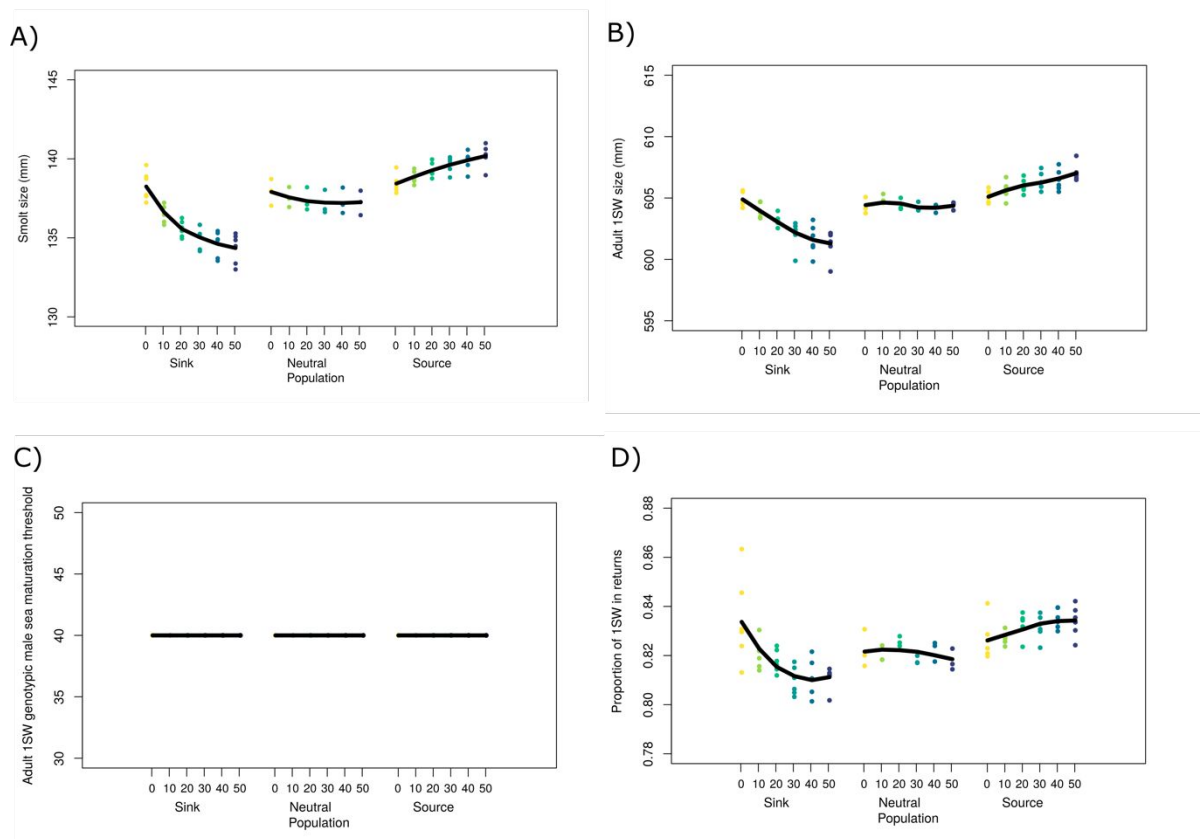
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 2 **Fig. 3:** A) In points, median over simulations of the ratio between immigrants and emigrants
 3 number of the 5 last years for each population and dispersal scenario. In red triangle, median
 4 over simulations of the proportion of immigrants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

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



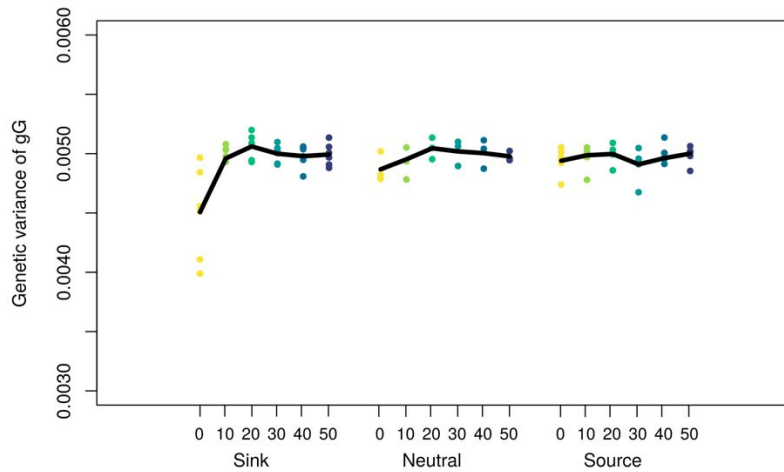
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 2 **Fig. 4:** Distribution (median, 95% confidence interval) over simulations of the detrended
 3 metapopulation PE (A) and synchrony (B) metrics for each scenario of dispersal. Median over
 4 simulations of local populations CV of detrended returns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

9



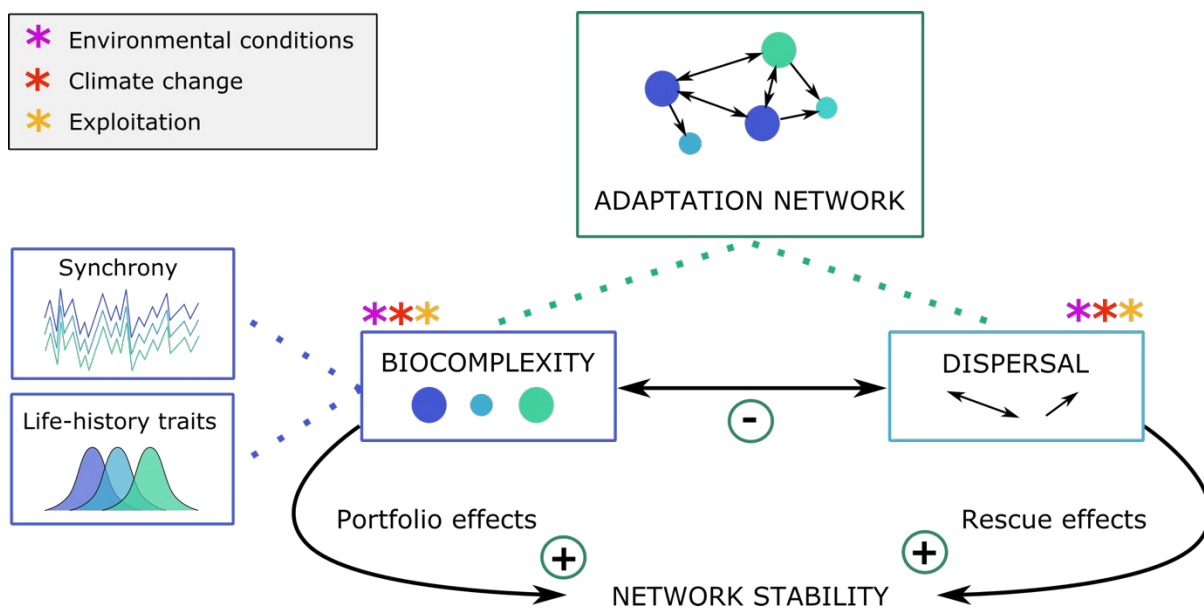
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 2 **Fig. 5:** Median over simulations of populations last 5 years median smolt size (A), philopatric
 3 adult 1SW size (B), philopatric adult 1SW genotypic value of male sea maturation threshold
 4 (C), and proportion of 1SW in philopatric adult returns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

8



1

2 **Fig. 6:** Median over simulations of populations last 5 years genetic variance (of philopatric
 3 1SW genotypic growth potential), for each scenario of dispersal. Each point is a population,
 4 categorized by its type (sink/source/neutral), and a local regression is added to represent a
 5 global trend as a function of dispersal rates and category of populations (sink/source/neutral).



1
 2 **Fig. 7:** Theoretical framework of the adaptation network theory. Both biocomplexity (e.g. trait
 3 diversity, populations synchrony) and dispersal can foster network stability through portfolio
 4 and rescue effects. The homogenizing effect of dispersal and divergent effect of local
 5 adaptation on populations can also induce negative feedbacks between biocomplexity and
 6 dispersal. Examples of promising future directions with MetaIBASAM are identified by
 7 asterisks. In particular, how various environmental conditions, climate change, and exploitation
 8 management affect network stability are questions that could be addressed in this framework.