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1 **Multi-scale interaction processes modulate the population response of a benthic**  
2 **species to global warming**

3

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20 Budget, mussel, habitat, biogeography, ODD

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## 23 1 ABSTRACT

24 Marine organisms are currently experiencing an unprecedented rate of climatic warming,  
25 which affects their biogeography and threatens marine ecosystem integrity. To understand  
26 how benthic species will respond to ongoing seawater warming, we assessed the relative  
27 importance of processes acting at different scales using an individual-based modelling  
28 approach. Our model integrates: (1) at the individual scale, interactions between the  
29 environment, metabolism and ontogenic transitions; (2) at the habitat scale, competition for  
30 space at settlement and mortality; and (3) at the regional scale, larval dispersal and  
31 connectivity between habitats. We focused on a coastal area in the North-East Atlantic that  
32 has experienced a significant seawater warming trend over recent decades. We built and ran a  
33 population dynamics model for the blue mussel (*Mytilus edulis*) in this area, which is a known  
34 biogeographic boundary zone. We then compared the response for a reference scenario and a  
35 RCP8.5 temperature projection for 2100. We found that (1) increase in seawater temperature  
36 would result in a decrease in average biomass associated with a change in recruitment  
37 phenology; (2) response to seawater warming is not spatially homogeneous, showing the  
38 importance of processes at the habitat scale; (3) connectivity clearly limits the consequences  
39 of warming compared with other regulation processes; and (4) larval supply does not seem to  
40 be a limiting factor regulating population biomass. The use of such generic models would  
41 therefore be very valuable for guiding and optimizing research efforts and supporting the  
42 implementation of management and conservation measures.

## 43 2 INTRODUCTION

44 In the domain of macroecology, process-based models are used to predict species invasion  
45 rate, the effect of environmental changes on species distribution, and impact of management  
46 measures on species persistence (Dormann et al., 2012). In contrast to the more popular

47 correlative models (also known as species distribution models or ecological niche  
48 models), process-based models are built based on explicitly stated mechanisms, a priori  
49 mathematical formulation and parameters with ecological meaning (Dormann et al., 2012).  
50 Kearney (2006) even judges that only models considering the mechanistic interactions  
51 between organisms and their environments can allow us to assess consequences in terms of  
52 fitness and should thus be considered as ‘niche models’. With this aim in mind, Kearney et al.  
53 (2010) highlighted the rationale of several theoretical mechanistic frameworks including  
54 Dynamic Energy Budget (DEB) theory. DEB theory explains how organisms use energy and  
55 matter throughout their life cycles. It has been widely used to simulate the life cycles of  
56 benthic organisms, and some recent studies have used it to assess the consequences of climate  
57 change for bivalves (Montalto et al., 2016; Thomas et al., 2016b; Thomas and Bacher, 2018,  
58 Steeve et al., 2018).

59 In most studies modelling the response to environmental and climatic conditions,  
60 consequences are first analysed at the individual level. However, more properties would more  
61 likely emerge by upscaling from individual to population levels (Thomas and Bacher, 2018).  
62 Modelling three bivalve species with temperature scenarios using DEB approach, we have  
63 already shown that these different benthic species would experience significant and  
64 contrasting change in population growth potential under the seawater warming conditions  
65 expected in the NE Atlantic if greenhouse gas emissions continue to increase (Thomas and  
66 Bacher, 2018). We also acknowledged that more realistic models should integrate processes  
67 regulating population density, spatial interactions (e.g., larval dispersal and competition for  
68 space) and mortality at all stages of the life cycle (e.g., ageing, starvation, predation). Such a  
69 modelling framework exists and usually combines individual growth and reproduction, larval  
70 dispersal through the hydrodynamic forces, mortality and competition for space, but the  
71 coupling among all these processes has received only a little attention (Guizien et al., 2014,

72 2012; Le Goff et al., 2017; Ménesguen et al., 2018; North et al., 2010; Opaluch et al.,  
73 2009; Puckett and Eggleston, 2016). Most often, the dispersion capacity of populations has  
74 been studied as a distinct process (Coscia et al., 2013; Davies et al., 2014; Gilg et al., 2014;  
75 Haase et al., 2012; Hubbard and Reidenbach, 2015; Kim et al., 2013; Lal et al., 2016; Laugen  
76 et al., 2015; Nicolle et al., 2013; Thomas et al., 2016; Zhang et al., 2015). For instance, Lett et  
77 al. (2010) stressed the impact of climate on the dispersal and connectivity of marine  
78 populations through changes in water circulation, earlier spawning of adults, shorter durations  
79 or the pelagic larval stage, reduced exposure of larvae to lethal temperatures, shorter larval  
80 life and increased larval swimming speed. They called for integrated biophysical models  
81 including transport, growth, behaviour, mortality and larval settlement, in an environment for  
82 which both biotic and abiotic aspects are considered.

83 Since individual traits and interactions between individuals drive the dynamics of  
84 populations, Individual-Based Models (IBM) are useful tools making it possible to study how  
85 system-level properties emerge from the behaviour of individuals and how the system affects  
86 individuals (Grimm et al., 2006). IBM represent individual organisms as entities that differ  
87 from each other and change over their life cycles (Martin et al., 2012). They are characterized  
88 by a set of state variables and attributes that change over time and interact with their abiotic  
89 environment (e.g. habitat structure or environmental drivers such as temperature) and with  
90 each other (Martin et al., 2012). The recent work by Malishev et al. (2018) illustrates how  
91 combining DEB and IBM modelling frameworks allows individual behavioural strategies to  
92 be compared among different habitat types.

93 In the present study, we used an individual-based population model of a marine benthic  
94 species to explore how interaction processes operating at different spatial scales would likely  
95 modulate the response to heat stress associated with global warming. At the individual scale,  
96 the environment (i.e. temperature, food, inorganic material), individual metabolism (i.e.

97 development, growth, reproduction efficiency) and ontogenic transition (i.e. reproductive  
98 phenology) interactions are formulated within Dynamic Energy Budget theory. At the local  
99 scale, individuals of benthic species compete for space during their settlement phase. Larval  
100 dispersal and the subsequent connectivity between habitats control the expansion of the  
101 population at the regional scale of the study area.

102 Our study focuses on the blue mussel *Mytilus edulis* in a coastal area of the North-East  
103 Atlantic, bordering the Western English Channel, Iroise Sea and Bay of Biscay to the south.  
104 This area is known as a biogeographic boundary zone, with both boreal/cold temperate and  
105 warm temperate marine faunal assemblages (Jolly et al., 2004; Southward et al., 2004). Like  
106 most marine ecosystems, this area has experienced a significant seawater warming trend over  
107 recent decades (Dye et al., 2013; L'Hévéder et al., 2017; Saulquin and Gohin, 2010). This  
108 warming is expected to continue in coming decades, with an annual mean sea surface  
109 temperature (SST) increase of 0.5°C to 2.5°C by the year 2100 depending on the  
110 representative concentration pathway (RCP) scenario (L'Hévéder et al., 2017). Some  
111 consequences of warming have already been identified, including warm water species  
112 becoming more common (Hawkins et al., 2008; Southward et al., 2004). Projections indicate  
113 that the distribution ranges of species are likely to change significantly, particularly for  
114 benthic species, which are unable to escape unfavourable conditions (Fly et al., 2015;  
115 Hawkins et al., 2009; Hilbish et al., 2012; Thomas and Bacher, 2018).

116 To predict the effect of temperature change with our integrated population model, we  
117 compared a reference scenario with the RCP8.5 climate scenario and simulated the response  
118 of populations at the regional scale of the study area. We made a detailed examination of the  
119 effect of warming on model endpoints (e.g. biomass, size structure, phenology). We also  
120 examined whether local density regulation (i.e. mortality, recruitment potential, competition  
121 for space) and connectivity would affect the response to warming.

122

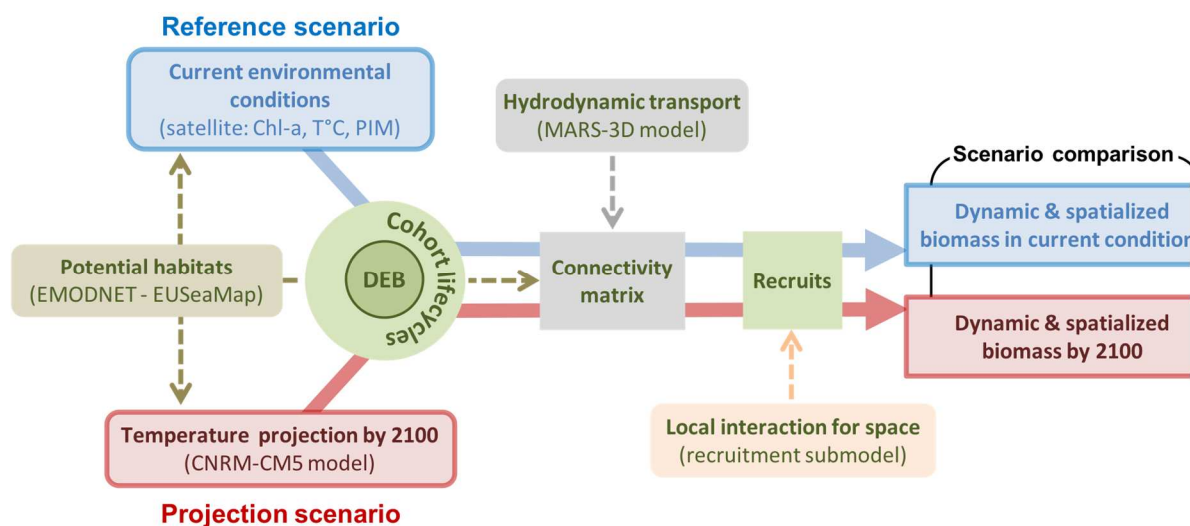
## 123 3 MATERIALS AND METHODS

### 124 3.1 Model description

125 The following sections are based on the framework of the Overview, Design concepts and  
126 Details (ODD) protocol, which is a standard way to describe an individual-based model  
127 (IBM) that makes writing and reading model descriptions more efficient, complete and easier  
128 to replicate (Grimm et al., 2010).

#### 129 3.1.1 Purpose of the model

130 The purpose of the present model was to evaluate how processes associated with multi-  
131 scale interactions (from sub-individual to geographical scales) can modify the response of a  
132 bivalve species to a climate warming scenario in rocky-shore habitats along 700 km of  
133 coastline in the NE Atlantic. The model takes into account metabolic processes at the  
134 individual scale through Dynamic Energy Budget (DEB) theory (Kooijman, 2010). It includes  
135 a population dynamics module accounting for the spatial connectivity process between  
136 habitats at the regional scale of the study area and a submodel of biotic interactions  
137 (intraspecific competition for space) during the settlement phase at the local scale of habitat  
138 patches (Fig. 1; details given in the following sections). The model was implemented with an  
139 agent-based modelling platform: NetLogo 6.1.0 (<https://ccl.northwestern.edu/netlogo/>).



140

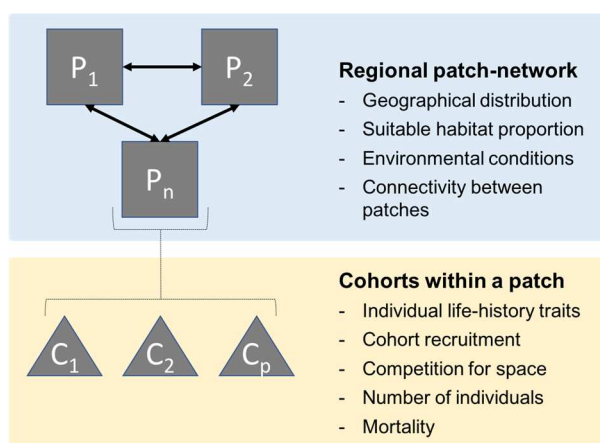
141 **Fig. 1. Conceptual diagram of the modelling strategy.** Reference and projection scenarios  
 142 of current (blue arrow) and projected (red arrow) temperatures are compared. Biomass in  
 143 potential habitats is simulated considering (1) individual metabolism with the Dynamic  
 144 Energy Budget (DEB) model, (2) modelling of multiple cohorts, and (3) spatial interactions  
 145 with connectivity at the regional scale of the study area and competition for space at the local  
 146 scale of a habitat patch. Chl-a and PIM for the projection scenario are the same as in the  
 147 reference scenario.

### 148 3.1.2 State variables and scales

149 We applied the model to the population dynamics of a single species, the blue mussel  
 150 (*Mytilus edulis*, Linnaeus, 1758). The model simulates two entities: habitat patches and  
 151 cohorts, which group individuals (Fig. 2). A regional patch network defines the geographical  
 152 distribution of potential habitats in the study area. Each patch is a square space defined by its  
 153 latitude, longitude, total area, proportion of suitable habitat for the species studied and  
 154 environmental variables which represent the living conditions of the organisms. The model  
 155 comprises a set of patches along the coasts of Brittany (France) (Fig. 3.a-b). We used the  
 156 EUSeaMap broad-scale seabed habitat map to locate habitats and define the proportion of  
 157 suitable habitat within each model patch, (<http://www.emodnet.eu/seabed-habitats>).  
 158 EUSeaMap aims to map benthic habitats of European waters and provides access to detailed  
 159 mapping of the habitats (250 m spatial resolution). Habitats are classified on the basis of  
 160 seabed substrate, biological zone and hydrodynamic energy. The choice of potential habitats



161 for mussels was based on sectors belonging to the categories 'infralittoral' and 'rock and  
 162 other hard substrata'. For our study, patches with potential mussel habitats were considered,  
 163 from the south to the north of Brittany (Fig. 3.b). All the patches are connected, allowing the  
 164 transport of larvae among patches at every spawning event (Fig. S1.b). The number of larvae  
 165 transported will depend on the number of cohorts reproducing, their reproductive efficiency,  
 166 and the connectivity level between the emitting and the receiving patches.



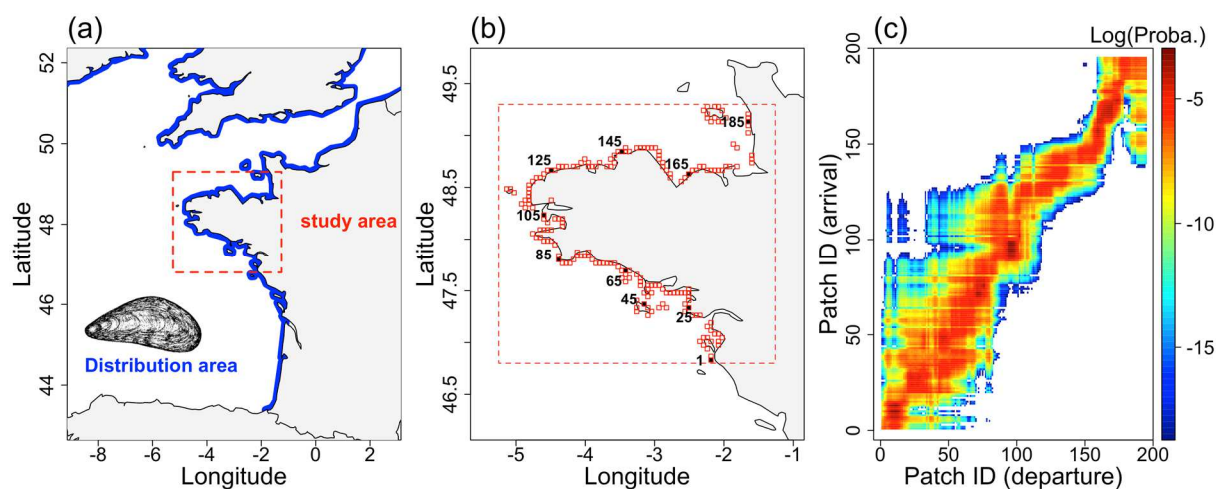
167

168 **Fig. 2. Schematic diagram of the simulated entities** in the mussel population model, indicating the  
 169 relations between network, patch and cohort and the characteristics of each.

170 A cohort represents a set of individuals recruited at the same time and consequently with  
 171 the same life history traits simulated by the DEB model (see section 3.1.4 'submodels'). A  
 172 cohort can be thought of as a super-individual (Scheffer et al., 1995) living in a patch. Each  
 173 patch can contain several cohorts and, for a given cohort, three state variables are simulated:  
 174 the number of individuals, the physical length of these individuals and their reproductive state  
 175 (i.e. gonado-somatic index, fecundity). Secondary variables, i.e. biomass, density, spatial  
 176 coverage, recruitment, etc., are computed from these state variables at the scale of the cohort.

177 The patch, is the spatial unit of the model, a  $4 \times 4 \text{ km}^2$  square corresponding to the spatial  
 178 element of the hydrodynamic model MARS3D (Lazure and Dumas, 2008) used to compute  
 179 connectivity in the present study (see section 3.3). The results (i.e. biomass, density) are

180 considered homogeneous at the scale of the model's patches and expressed in a reference  
 181 unit of  $1 \text{ m}^2$ . The model proceeds in discrete daily time steps.



182

183 **Fig. 3. Geographical information:** (a) map of the mussel distribution area (blue line along  
 184 the coast) and location of the study area, (b) location of the potential habitats in the study  
 185 area, and (c) connectivity matrix giving the connection probability between emitting (X axis)  
 186 and receiving (Y axis) habitat (Log scale).

### 187 3.1.3 Process overview and scheduling

188 A conceptual scheme of the model's processes is given in Figure S2. At each daily time  
 189 step, the individual life-history traits (growth, maturation, reproduction) of each cohort in a  
 190 given patch are simulated by the DEB model and depend on environmental forcing. If the  
 191 individuals are not mature, they remain in the juvenile phase and therefore continue to grow  
 192 and develop but cannot reproduce. A daily mortality rate is applied to integrate all the losses  
 193 occurring during juvenile and adult phases. Reproductive phenology depends on  
 194 environmental conditions and may vary greatly at the regional scale of the study area. Thus,  
 195 during the adult stage, spawning events are triggered when two thresholds are concurrently  
 196 reached: a seawater temperature and a gameto-somatic index (GSI) threshold of 35%. GSI is  
 197 defined as the mass ratio between the gametes and total dry flesh mass. Since low and high  
 198 temperatures may inhibit reproduction (Fearman and Moltschaniwskyj, 2010; Lubet, 1959;  
 199 Shpigel et al., 1992), lower and higher temperature thresholds inhibiting spawning were also

200 defined ( $TL_{spw} = 10^{\circ}C$  and  $TH_{spw} = 17^{\circ}C$ ). Outside of this range, individuals continue to  
201 grow and to acquire energy for the development of gametes.

202 When spawning occurs within a habitat patch, the total number of larvae produced is  
203 calculated based on the individual fecundity and the number of individuals releasing gametes.  
204 A mortality rate is then applied to integrate all the losses occurring during the larval phase.  
205 The connectivity matrix then makes it possible to evaluate the proportion of the larvae  
206 produced that will be exported to other patches and the proportion that will remain in the  
207 starting patch (self-recruitment). The larval phase is not explicitly simulated, spawning and  
208 recruitment can occur at the same time step and new recruits all have the same initial  
209 properties. However, for the purposes of modelling, individuals recruited within a given  
210 temporal window are grouped into a single new cohort (see Section 3.1.4.2). Within each  
211 patch receiving larvae, if enough space is available, we enter into the recruitment process. A  
212 given number of recruits will settle according to the available space. Recruitment results in  
213 the creation of a new cohort, with an initial number of individuals equal to the number of  
214 recruits that can settle.

215 At each time step, the age and the number of individuals in each cohort, total number of  
216 individuals in a habitat patch and total space occupied in each patch are simultaneously  
217 updated and recorded.

### 218 **3.1.4 Submodels**

#### 219 **3.1.4.1 Dynamic Energy Budget (DEB)**

220 Dynamic Energy Budget (DEB) theory offers a quantitative framework (i.e. mass and  
221 energy) to model metabolic fluxes at the individual scale. These fluxes modulate substrate  
222 uptake and use and sustain life-history trait dynamics: growth rate, life-stage transitions,  
223 reproductive output and mortality (Kooijman, 2010). The DEB model follows the complete

224 life cycle of one individual from the embryo to juvenile and adult stages. An individual  
 225 is defined by four state variables: reserves ( $E$ , unit: J), structure ( $V$ , unit:  $\text{cm}^3$ ), maturity ( $E_H$ ,  
 226 unit: J), and reproduction ( $E_R$ , unit: J); and seven metabolic processes (unit:  $\text{J}\cdot\text{day}^{-1}$ ): ingestion  
 227 ( $\dot{p}_X$ ), assimilation ( $\dot{p}_A$ ), reserve mobilization ( $\dot{p}_C$ ), growth ( $\dot{p}_G$ ), somatic maintenance ( $\dot{p}_M$ ),  
 228 maturity maintenance ( $\dot{p}_J$ ), maturation and reproduction ( $\dot{p}_R$ ). Life-stage successions are  
 229 linked to maturity thresholds. The transition between embryo and juvenile occurs when  $E_H =$   
 230  $E_H^b$ , and the transition between juvenile and adult occurs when allocation to reproduction  
 231 occurs coupled with the cessation of maturation, when  $E_H = E_H^p$ . Somatic maintenance has  
 232 priority over growth, and maturity maintenance has priority over maturation or reproduction.  
 233 Details on DEB model equations and parameter values are given in the supplementary  
 234 materials (Table S1 and Table S2). The individual life-history traits extracted from the DEB  
 235 model were the individual physical length ( $L$ , cm), total mass ( $W$ , g) and fecundity ( $F$ , number  
 236 of eggs produced). We assumed the same parameter values for males and females. DEB  
 237 parameters for mussel were derived from the literature (Saraiva et al., 2012; Thomas and  
 238 Bacher, 2018) (Table S2).

239 Two forcing variables, temperature and food density, modulate metabolic rates and drive  
 240 individual growth and reproduction in the DEB model. When exposed to high concentrations  
 241 of suspended particulate inorganic matter (PIM), bivalves maximize organic ingestion  
 242 through pseudo-faeces production. We therefore introduced PIM concentration as a third  
 243 forcing variable, related to the ingestion functional response ( $f \in [0,1]$ ), following  
 244 Kooijman's (2006) conceptualization:

$$245 \quad f = \frac{X}{X + K(1 + \frac{Y}{K_Y})}$$

246 where  $X$  is the food density,  $Y$  the PIM concentration,  $K$  the half saturation coefficient related  
 247 to food density and  $K_Y$  the half saturation related to inorganic matter concentration. For

248 bivalve species ingestion rate, the half saturation coefficient of the functional response is  
 249 known to change as a function of the food quantity and/or quality and species physiological  
 250 flexibility (i.e. particle selection capacity) (Alunno-Bruscia et al., 2011). In the present study,  
 251 a linear relationship between the mean Chl-a concentration and the half saturation parameter  
 252 ( $K$ ) was calibrated for mussel in order to take into account feeding adaptation to local  
 253 conditions (see Thomas and Bacher, 2018, for calibration and validation steps performed on  
 254 several datasets extracted over a wide latitudinal gradient).

255 In the DEB model, seawater temperature acts on metabolic rates following the Arrhenius  
 256 function, extended over the species tolerance range, based on the idea that metabolic rates are  
 257 controlled by enzymes that are inactive beyond the optimal temperature range (Kooijman,  
 258 2010), and giving a temperature correction factor ( $T_C$ ):

$$\begin{aligned}
 259 \quad T_C &= \exp\left\{\frac{T_A}{T_1} - \frac{T_A}{T}\right\} \\
 260 \quad &\cdot \left(1 + \exp\left\{\frac{T_{AL}}{T_1} - \frac{T_{AL}}{T_L}\right\} + \exp\left\{\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_1}\right\}\right) \\
 261 \quad &\cdot \left(1 + \exp\left\{\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right\} + \exp\left\{\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}\right\}\right)^{-1}
 \end{aligned}$$

262 where  $T$  is the actual temperature,  $T_A$  the Arrhenius temperature in the tolerance range,  $T_1$  the  
 263 reference temperature (20°C) for which  $T_C = 1$ ,  $T_L$  and  $T_H$  are the lower and higher boundaries  
 264 of the optimal tolerance range and  $T_{AL}$  and  $T_{AH}$  the Arrhenius temperatures beyond the lower  
 265 and higher boundaries, respectively.

#### 266 3.1.4.2 Recruitment submodel

267 At the local scale of a patch, the settlement submodel makes it possible to integrate  
 268 interactions between new individuals at the time of attachment to the substrate: settlement of  
 269 new recruits is only possible if there is sufficient space. If the space is limited, only a limited

270 number of individuals settle and recruit, while the others die. If there is no space, there is  
 271 no settlement and all individuals die. The settlement submodel integrates the spatial  
 272 connectivity, which allows the inclusion of spatial interactions between patches.

273 The recruitment submodel is based on the work of Roughgarden et al. (1985). It also  
 274 incorporates the connectivity process that allows a spatially explicit approach and integration  
 275 of spatial interactions between habitat patches. Recruitment therefore involves (1) evaluating  
 276 the number of larvae produced, (2) integrating the connectivity process, and (3) integrating  
 277 small-scale spatial interactions (intra-specific competition for space). These processes are  
 278 defined in the following sections below.

### 279 Larval production

280 When a spawning event occurs, at time ( $t$ ), the number of eggs produced in a patch  $i$   
 281 ( $O_i(t)$ , # number of eggs) is the cumulative number of eggs produced by the  $n$  cohorts:

$$282 \quad O_i(t) = \sum_{c=1}^n SR F_{ci} N_{ci}(t)$$

283 where  $SR$  corresponds to the population sex ratio,  $F_{ci}$  the number of eggs produced by an  
 284 individual of the cohort  $c$  in patch  $i$ , and  $N_{ci}(t)$  the number of individuals within the cohort  $c$   
 285 in patch  $i$  at time ( $t$ ). We considered an  $SR$  of 50%, which corresponds to the mean proportion  
 286 in natural populations (Yasuoka and Yusa, 2016; Yusa et al., 2013). The produced egg  
 287 number is then adjusted by a mortality rate ( $m$ ), including the overall mortality during the  
 288 larval phase (i.e. fertilization success ( $FS$ ) and daily mortality rate ( $M_{larvae}$ ) associated with the  
 289 pelagic larval duration ( $PLD$ )). This rate is assumed to be constant and spatially uniform. The  
 290 total number of potential recruits produced in a patch  $i$  at time  $t$  ( $l_i(t)$ , # larvae) is:

$$291 \quad l_i(t) = O_i(t) m \text{ with } m = FS e^{-M_{larvae} PLD}$$

### 292 Spatial connectivity

293 The connectivity process allows the number of larvae coming from a given habitat  
 294 patch to be quantified. These will then be distributed within the connected habitat patches  
 295 through the larval dispersal process. The connectivity matrix synthesizes the rate of  
 296 connection between every emitting habitat patch and all the others, including itself (self-  
 297 recruitment). The total number of larvae received by a given patch  $j$  at time  $t$  ( $L_j(t)$ , # larvae)  
 298 corresponds to the sum of the larvae produced in the  $k$  patches connected with  $j$ , multiplied by  
 299 the connectivity rate between  $j$  and each of the  $k$  patches ( $C_{ij}$ , %):

$$300 \quad L_j(t) = \sum_{i=1}^k l_i(t) C_{ij}$$

301 where  $C_{ij}$  is the connectivity rate between patches  $i$  and  $j$ .

### 302 **Competition for space**

303 Occupancy of the substrata by sessile organisms can be represented by a 2-D physical area  
 304 of each individual. Competition for space occurs at the time of recruitment. New recruits will  
 305 only be able to settle if enough space is available to accommodate them. This available area is  
 306 a function of the occupancy rate by all the individuals already recruited. It evolves over time  
 307 depending on individuals' growth and mortality and the arrival of new recruits. The physical  
 308 surface area occupied by an individual ( $b$ , m<sup>2</sup>) is a function of individual height ( $h$ , cm) and  
 309 width ( $l$ , cm). The allometric equation for calculating the individual basal area is written:

$$310 \quad b(t) = h(t) l(t)$$

$$311 \quad \text{where } h(t) = \frac{L(t)}{\alpha} \text{ and } l(t) = \frac{L(t)}{\beta}$$

312 with allometric parameters  $\alpha$  and  $\beta$  linking individual height and width to the physical length  
 313  $L$  (Alunno-Bruscia et al., 2001). This relation is needed because the DEB model only gives

314 the physical length. The cumulative surface area occupied by all individuals within a  
 315 patch  $i$  ( $B_i$ , m<sup>2</sup>) is the sum of the space inhabited by all individuals of the  $n$  cohorts:

$$316 \quad B_i(t) = \sum_{c=1}^n b_{ci}(t) N_{ci}(t)$$

317 where  $b_{ci}(t)$  is the individual surface coverage for cohort  $c$  in patch  $i$  at time  $t$ , and  $N_{ci}(t)$  is  
 318 the total number of individuals within the cohort  $c$  in patch  $i$ , at time  $t$ . The available area for  
 319 recruitment in patch  $i$  ( $F_i(t)$ ) is then obtained from:

$$320 \quad F_i(t) = A_i - B_i(t)$$

321 where  $A_i$  is the habitat area in patch  $i$ , scaled at 1 m<sup>2</sup>.

322 Finally, the number of recruits will depend on the area of habitat needed by a single recruit  
 323 ( $b_0$ , m<sup>2</sup>), which then makes it possible to calculate the number of recruits per available surface  
 324 unit ( $s$ , ind.m<sup>-2</sup>) and to calculate the number  $Q$  of recruits that can be fixed at time  $(t + 1)$ , per  
 325 unit of space:

$$326 \quad s = \frac{1}{b_0}$$

$$327 \quad Q_i(t + 1) = sF_i(t)$$

328 Within a habitat patch, spawning events occurring at the same time step are considered  
 329 together to generate a single new cohort per patch. Thus, individuals recruited within a 22-day  
 330 interval, which is the mean pelagic larval duration for mussel (Sprung, 1984), are grouped  
 331 into a single new cohort.

#### 332 3.1.4.3 Changes in population abundance and biomass

#### 333 **Mortality after settlement**



334 The number of individuals in a given cohort  $c$  and patch  $i$  at time  $t$  ( $N_{ci}(t)$ ) is defined  
 335 as follow:

$$336 \quad N_{ci}(t) = N_{ci}(0) e^{(-M a_{ci}(t))} = Q_{ci} e^{(-M(t-t_{ci}(0)))}$$

337 where  $Q_{ci}$  is the initial number of recruits for a given cohort  $c$  in patch  $i$ ,  $M$  the daily mortality  
 338 rate after settlement,  $a_{ci}(t)$  the age of the cohort  $c$  in patch  $i$  at time  $t$ , and  $t_{ci}(0)$  the time step  
 339 when the cohort was created in patch  $i$ . A cohort disappears when its age ( $a_c(t)$ , days) reaches  
 340 the lifespan of the species ( $a_d$ , days; Table S2). In the model, lifespan is assumed to be both  
 341 constant and spatially homogeneous.

### 342 **Mussel biomass**

343 Cumulative biomass in every patch  $i$  at time ( $t$ ) ( $Biom_i(t)$ ) is computed as follows:

$$344 \quad Biom_i(t) = \sum_{c=1}^n N_{ci}(t) W_{ci}(t)$$

345 where  $W_{ci}(t)$  is the individual mass for individuals in cohort  $c$  of patch  $i$  at time ( $t$ ).

### 346 **3.2 Input data**

347 The DEB model is computed using daily time series of water surface temperature (SST),  
 348 chlorophyll-a concentration (Chl-a) and particulate inorganic matter (PIM) concentration.  
 349 Daily Chl-a and PIM concentration time series from 2000 to 2014 were obtained from ocean  
 350 colour remote-sensing using merged SeaWiFS, MODIS and MERIS data processed using a  
 351 regional algorithm specifically designed for the coastal waters of the Bay of Biscay (Gohin et  
 352 al., 2002; Saulquin et al., 2011). The daily sea surface temperature (SST) was obtained from  
 353 remote-sensing products from the Advanced Very High Resolution Radiometer (AVHRR)  
 354 over 2000–2008 and from the Group for High Resolution Sea Surface Temperature  
 355 (GHRSSST) initiative over 2009–2014 (Martin et al., 2012). Input datasets are imported in

356 NetLogo as tables, each row corresponding to one time-step and each column to a patch.  
357 Time series of the individual functional response and temperatures in every patch for the  
358 reference and projection scenarios are given in Figure S3a-b.

359 Following the work by Thomas and Bacher (2018), two temperature scenarios were  
360 considered and compared in this study: 1) a reference (R) scenario, consisting of current  
361 temperature conditions, based on the 2000–2015 period following the above description from  
362 satellite information; and 2) a projection (P) scenario, consisting of predicted thermal  
363 conditions at the end of the 21<sup>st</sup> century, based on the 2085–2100 period. For the latter, we  
364 chose the well documented and most severe scenario, known as the ‘business as usual’  
365 Representative Concentration Pathway scenario RCP8.5 (i.e. the rising radiative forcing  
366 pathway leading to 8.5 W.m<sup>-2</sup> by 2100), which assumes that greenhouse gas emissions will  
367 continue to rise throughout the remainder of the 21<sup>st</sup> century (van Vuuren et al., 2011). For  
368 every location, time series of Sea Surface Temperature (SST) were extracted from the  
369 CNRM-CM5 climate model outputs (from the French National Centre for Meteorological  
370 Research's Coupled Model Intercomparison Project 5 (CMIP5) archive ([https://esgf-  
371 node.llnl.gov](https://esgf-node.llnl.gov)), following the nearest neighbour strategy. This model demonstrated its ability  
372 to correctly simulate the mean present-day SST seasonal cycle in the considered area with a  
373 higher ocean resolution (1° x 1°) and more realistic topography and coastline geometry than  
374 other climate models (L'Hévéder et al., 2017). SST from the climate model was available  
375 with daily frequency. There is significant uncertainty in the projections of phytoplankton  
376 production by climate models. Furthermore, Thomas and Bacher (2018) showed that these  
377 projections would have a limited effect on population growth performance. Our projection  
378 simulations therefore used the same Chl-a time series as the reference scenario. Response of  
379 mussel populations along the latitudinal gradient was then studied by comparing the mean  
380 biomass per unit area between the two temperature scenarios.

381 The connectivity matrix is an array with as many rows as columns, corresponding to  
382 the number of patches in the model (Fig. 3.c). Each cell in the table contains a connection rate  
383 between a emitting patch (column) and a receiving patch (line). The connectivity matrix was  
384 derived from simulations performed by a hydrodynamic model (MARS3D) that simulates the  
385 evolution of the concentrations of a tracer emitted in each potential habitat mesh square and  
386 dispersed over a period of 22 days. The emitted particles were considered to be passive, with  
387 no vertical migration behaviour considered. The mesh size of the hydrodynamic model is 4 x  
388 4 km. Computing the connectivity matrix for several decades was not possible. Connectivity  
389 simulations were thus performed monthly for a given year to represent the mean conditions  
390 encountered over a long period and maintain realistic forcing. The year 2005 was chosen after  
391 an analysis of wind conditions over 10 years, which showed that this year was the closest to  
392 the climatology of this area.

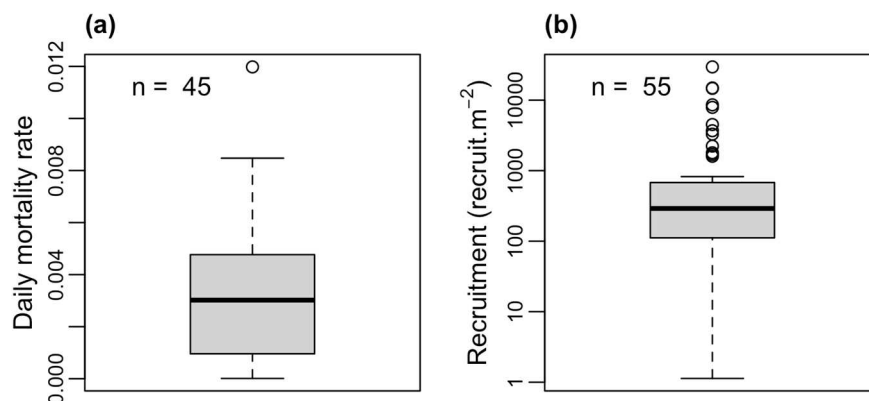
### 393 **3.3 Initialization**

394 At the initial time step, one single cohort with 50 ind.m<sup>-2</sup> is created in every patch. All  
395 individuals are similar and considered to be at the post-metamorphosis stage. Time series of  
396 simulated biomass in every patch are given in Figure S3c for the reference and projection  
397 scenarios, with identification of the spin-up and analysed periods. A spin-up time of three  
398 years is long enough for the emergence of a stable pattern of abundance and biomass at the  
399 scale of the study area and was applied before analysing the model results over a period of 15  
400 years.

### 401 **3.4 Model calibration and performance evaluation**

402 A set of data was extracted from the literature (Table S3) for the calibration of two  
403 parameters: the post-settlement mortality rate ( $M$ ) and the number of recruits per available  
404 surface unit ( $s$ ) (Fig. 4). The median was chosen because of the asymmetrical dispersion of

405 the data. Model performances were then evaluated with these values, with regard to the  
 406 simulated mussel density, space coverage, number of recruits 10 months post-settlement and  
 407 mussel size distribution. Due to the uncertainty associated with these density control  
 408 parameters, we performed a sensitivity analysis on them (see next section).



409

410 **Fig. 4. Observed (a) mortality rate and (b) recruitment density** used for the model  
 411 calibration step. Medians were used for model parameterization:  $M = 0.003 \text{ d}^{-1}$ ;  $s = 290$   
 412  $\text{recruits.m}^{-2}$ .

### 413 3.5 Sensitivity analysis

414 A first step, in order to evaluate stability and potential edge effects, was to assess the effect  
 415 of the spatial model fit on the results. Three zoom levels were compared, corresponding to  
 416 three spatial coverages, with differences between biomass variations related to temperature  
 417 scenario computed between each pair of zooms. A description of these preliminary results is  
 418 given in the supplementary material (Fig. S4, Fig. S5 and associated text), and led us to  
 419 choose one zoom level as the study area for the subsequent analyses.

420 A set of sensitivity analyses was then conducted to assess the effect of interaction  
 421 processes occurring at different spatial scales on the response to the temperature scenarios.  
 422 We tested the effect of the connectivity, which represents interactions occurring at the  
 423 regional scale of the study area and the effect of larval and adult mortality and recruitment  
 424 potential, which are related to processes occurring at the local scale of habitat patches.

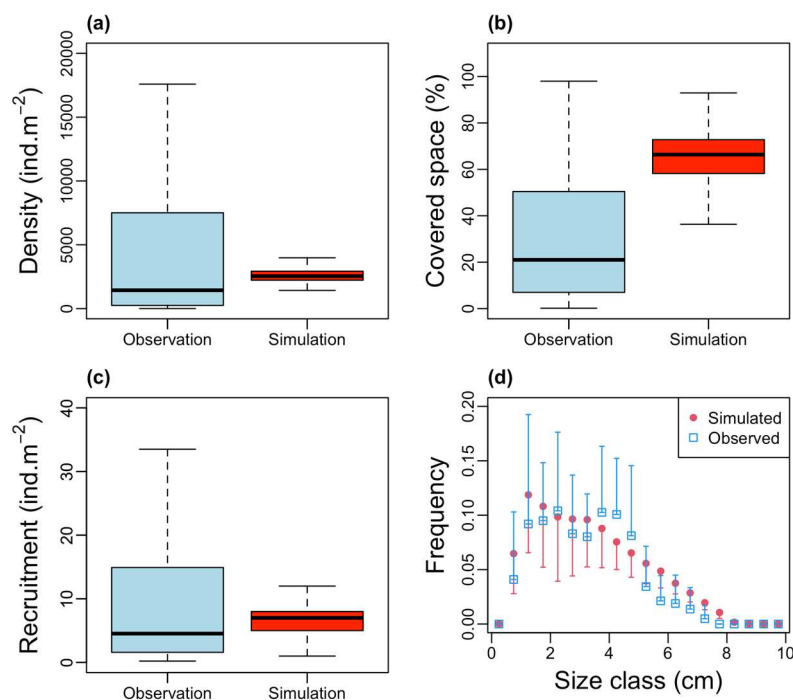
425 For the connectivity scenarios, the results obtained with a reference connectivity  
426 scenario (i.e. monthly connectivity, PLD = 22 days) were compared with a scenario without  
427 connectivity, under which there was only self-recruitment, considered to be average and  
428 uniform over the whole area, corresponding to the average value of the connectivity matrix  
429 diagonal. Since temperature has the effect of shortening the duration of the pelagic larval  
430 phase, we tested a connectivity scenario with a PLD of 19 days, which reduced the dispersal  
431 potential and larval mortality. Finally, in order to assess the impact of seasonal variability in  
432 connectivity patterns associated with the reproductive phenology (i.e. seasonality of the  
433 spawning events), we compared the baseline scenario with year-averaged connectivity  
434 scenarios in each habitat for each PLD (i.e. 19 and 22 days).

435 For the sensitivity analysis of mortality and recruitment potential, we applied factors of  $\pm$   
436 10% and  $\pm$  50% to the mean values of larval mortality ( $m$ ), adult daily mortality rate ( $M$ ) and  
437 number of recruits per unit area ( $s$ ). We ran simulations for both temperature scenarios and  
438 compared the responses to temperature changes obtained with the modified parameter values  
439 with the results obtained with the mean values.

440 In every patch and at each time step, simulated values were output and stored in the form  
441 of .CSV files for (1) individual life history traits (size, weight, gonado-somatic index,  
442 spawning efficiency) for each cohort, (2) population structure (density per cohort,  
443 recruitment), and (3) habitat cover rates in all patches. All these outputs were used to perform  
444 post-treatment with R software (R Development Core Team, 2012).

445 **4 RESULTS**446 **4.1 Model performance evaluation**

447 Our simulated mean densities, coverage rates and recruitment observed 10 months after  
 448 fixation (Fig. 5.a-b-c) are not significantly different from the observations (t-test,  $p < 0.05$ ).  
 449 The simulated mean size distribution at the patch scale matches the mean size distribution  
 450 produced by a set of observations (Fig. 5.d). The variance measured in the observations is  
 451 well reproduced by the simulated monthly profiles, which show the evolution of mussel sizes  
 452 distribution over the year as a result of recruitment, growth and mortality processes.  
 453 Simulated maximum lengths around 8 cm are consistent with observed data, although the 4  
 454 cm class appears underestimated and the 6 cm class overestimated by the model.

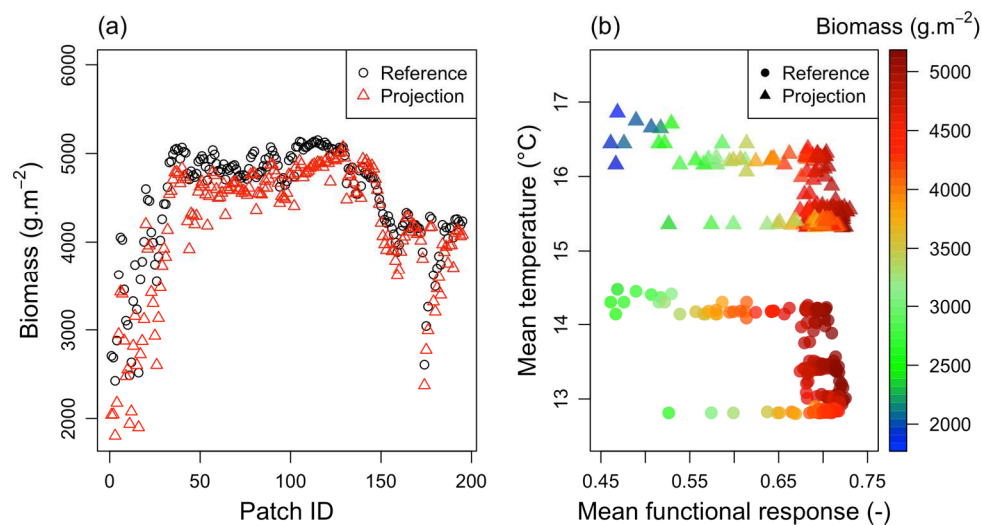


455

456 **Fig. 5. Comparisons of the IBM predictions with data from the literature.** (a) Observed density ( $n = 71$ ), (b) covered area ( $n = 37$ ) and (c) recruitment density after 10 months ( $n = 53$ ). No significant  
 457 differences were found between observations and simulations (Student test,  $p < 0.05$ ). (d) Individual  
 458 size (i.e. length) distributions: observations refer to a set of published data (mean  $\pm$  STD; see Table  
 459 S3) and simulations to the monthly average distributions for all patches, error bars represent the  
 460 monthly variability (i.e. STD; half of error bars are drawn for readability).  
 461

## 462 4.2 Effects of seawater warming conditions

463 Under reference temperature conditions, simulated biomasses differ along the latitudinal  
 464 gradient (Fig. 6.a). Lower biomasses are simulated in southern areas and range from 2425  
 465  $\text{g}\cdot\text{m}^{-2}$  to more than 5150  $\text{g}\cdot\text{m}^{-2}$  close to patch 110. In the projection scenario, the geographical  
 466 pattern of simulated biomass remains identical to that of the reference scenario, with a  
 467 decrease in absolute values south of patch 125: min/max = 1805/5070  $\text{g}\cdot\text{m}^{-2}$ . Biomasses  
 468 plotted in temperature-food space can be viewed as the realized population niche (Fig. 6.b).  
 469 Large differences were simulated along the food gradient, with a positive and significant  
 470 relationship (linear regression:  $R^2 = 0.73$ ;  $p < 0.001$ ), accounting for over 110% of variation.  
 471 Response across the thermal range appears lower, with variations related to warming reaching  
 472 -27%.

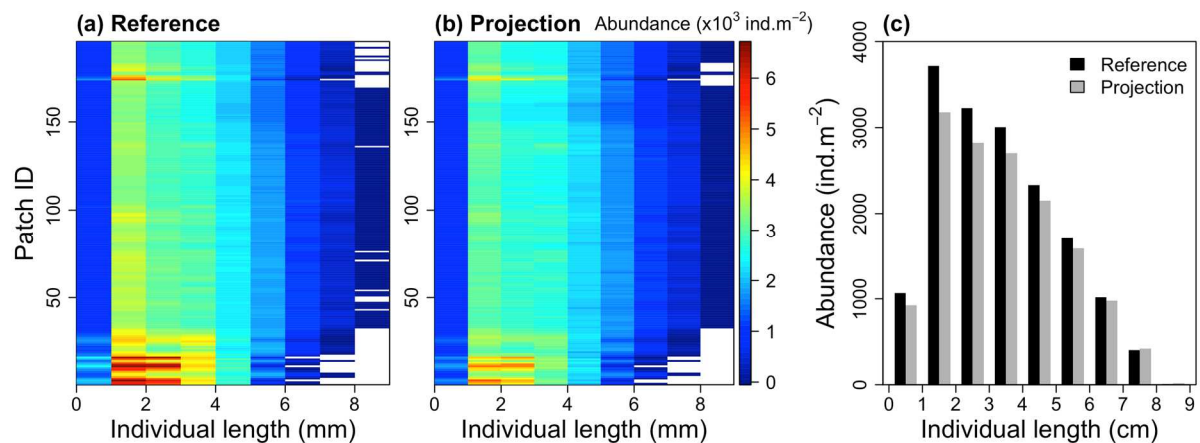


473

474 **Fig. 6. Simulated biomass in reference and projection scenarios:** (a) mean biomass simulated in  
 475 every patch (patches are ordered from south to north of the study area) and (b) mean biomass  
 476 simulated in every patch as a function of mean temperature and individual functional response (i.e.,  
 477 food effect) for the two temperature scenarios.

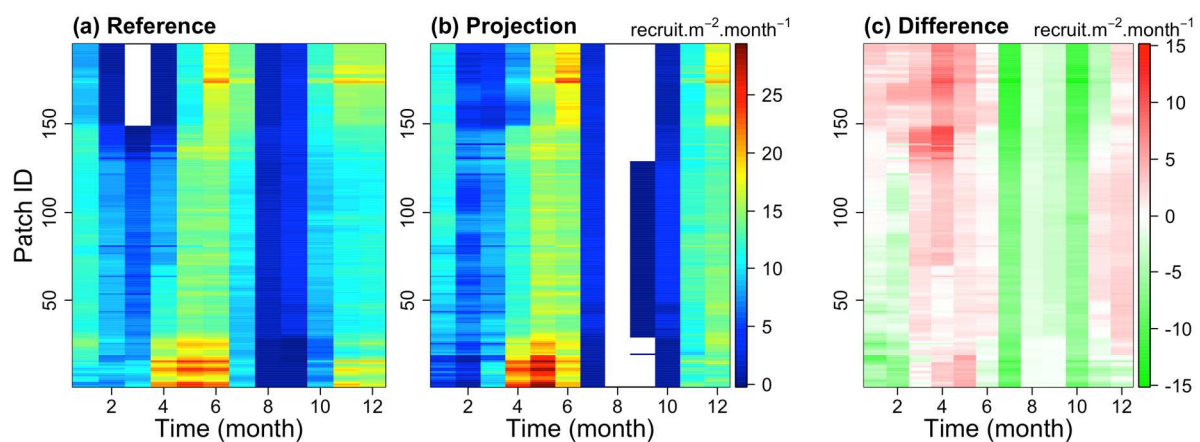
478 The mussel size distribution is modified by the seawater warming projection scenario (Fig.  
 479 7). Abundance of small individuals is significantly lower throughout the study area. This  
 480 difference results in a mean individual length of 3.37 cm in the projection scenario compared  
 481 with 3.29 cm in the reference scenario. This change in size structure is accompanied by a

482 clear change in reproductive phenology (Fig. 8). A total halt in recruitment is simulated  
 483 during the summer period throughout the study area. This phenomenon is associated with the  
 484 upper temperature threshold applied for reproduction. Conversely, the effect of the lower  
 485 threshold seems to be noticeable in the northern part of the study area (patch > 125), with an  
 486 activation of recruitment during winter, which is not observed in the reference scenario. The  
 487 overall average recruitment rate is thus significantly reduced from 9.3 to 8.2 recruits.m<sup>-2</sup>.  
 488 month<sup>-1</sup> between the reference and projection scenarios, respectively. The patches in the  
 489 south of the study area appear to be the most heavily penalized by decreased recruitment.



490  
 491 **Fig. 7. Size frequency simulated over the studied area in the reference and projection scenarios:**  
 492 (a) monthly mean size frequency (expressed as abundance) in every patch in the reference scenario,  
 493 (b) monthly mean size frequency (expressed as abundance) in every patch in the projection scenario  
 494 and (c) monthly mean abundance, averaged over the studied area for the two scenarios.

495



496  
 497 **Fig. 8. Seasonal recruitment simulated over the studied area in the reference and projection**  
 498 **scenarios:** (a) monthly mean number of recruits in every patch in the reference scenario, (b) monthly

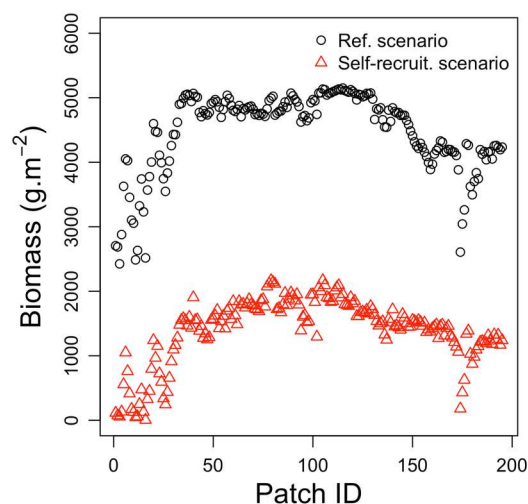


499 mean number of recruits in every patch in the projection scenario and (c) difference in mean  
 500 number of recruits between the two scenarios (projection - reference) in every patch.

### 501 4.3 Sensitivity analysis

#### 502 4.3.1 Connectivity effect

503 As previously described, simulated biomasses with the reference scenario (i.e. current  
 504 temperature, monthly connectivity, PLD = 22 days, average mortality and recruitment  
 505 potential) show geographical heterogeneity, with lower biomasses in the south of the study  
 506 area (Fig. 9). Biomasses stabilize in the centre of the study area (patch ID > 40), before  
 507 decreasing again in the north of the area (patch ID > 150). When connectivity between  
 508 patches is removed and only self-recruitment is considered, this general pattern of biomass  
 509 variation is maintained, but biomasses are significantly lower. Average biomass decreases  
 510 from  $4480 \pm 620$  to  $1401 \pm 510$   $\text{g.m}^{-2}$ , corresponding to a mean decline of 69%. Habitats in  
 511 the south of the area can show biomasses very close to 0  $\text{g.m}^{-2}$  (min = 5  $\text{g.m}^{-2}$ ).

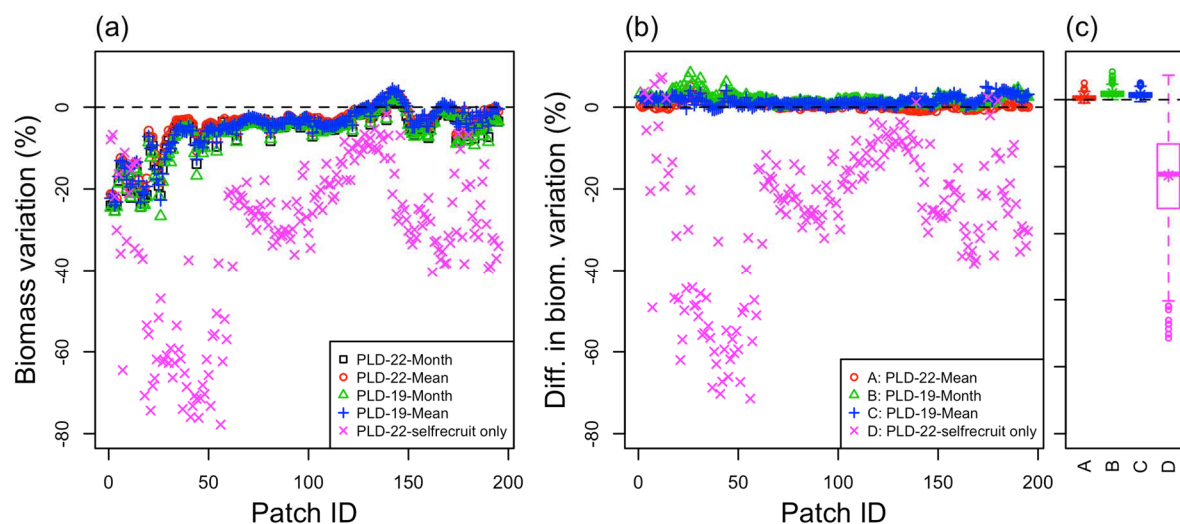


512

513 **Fig. 9. Effect of population connectivity on simulated mussel biomass:** biomass simulated in every  
 514 habitat for the reference temperature scenario and with connectivity (ref.) or self-recruitment only.  
 515 Data are averaged over the simulated period (15 years).

516 Beyond the direct effect on biomass, the simulations highlight that connectivity also  
 517 mitigates the effect of the seawater warming scenario. If connectivity is removed and there is

518 only self-recruitment, the decrease in biomass in the projection scenario is enhanced. On  
 519 average, there is 22% lower biomass compared with the baseline simulation with monthly  
 520 connectivity (Fig. 10.b-c). The other connectivity scenarios show that there is a limited effect  
 521 of PLD and seasonal variation on biomass patterns. The three scenarios associated with PLD  
 522 equal to 19 days and year-averaged connectivity tend to slightly limit the effect of warming  
 523 by limiting biomass decline. Simulations show that the response has a spatial structure, with  
 524 higher sensitivity in the south (patches 20 to 60) (Fig. 10.b). A possible edge effect appears at  
 525 the extreme southern end of the study area, with results converging between the scenarios  
 526 with and without connectivity.



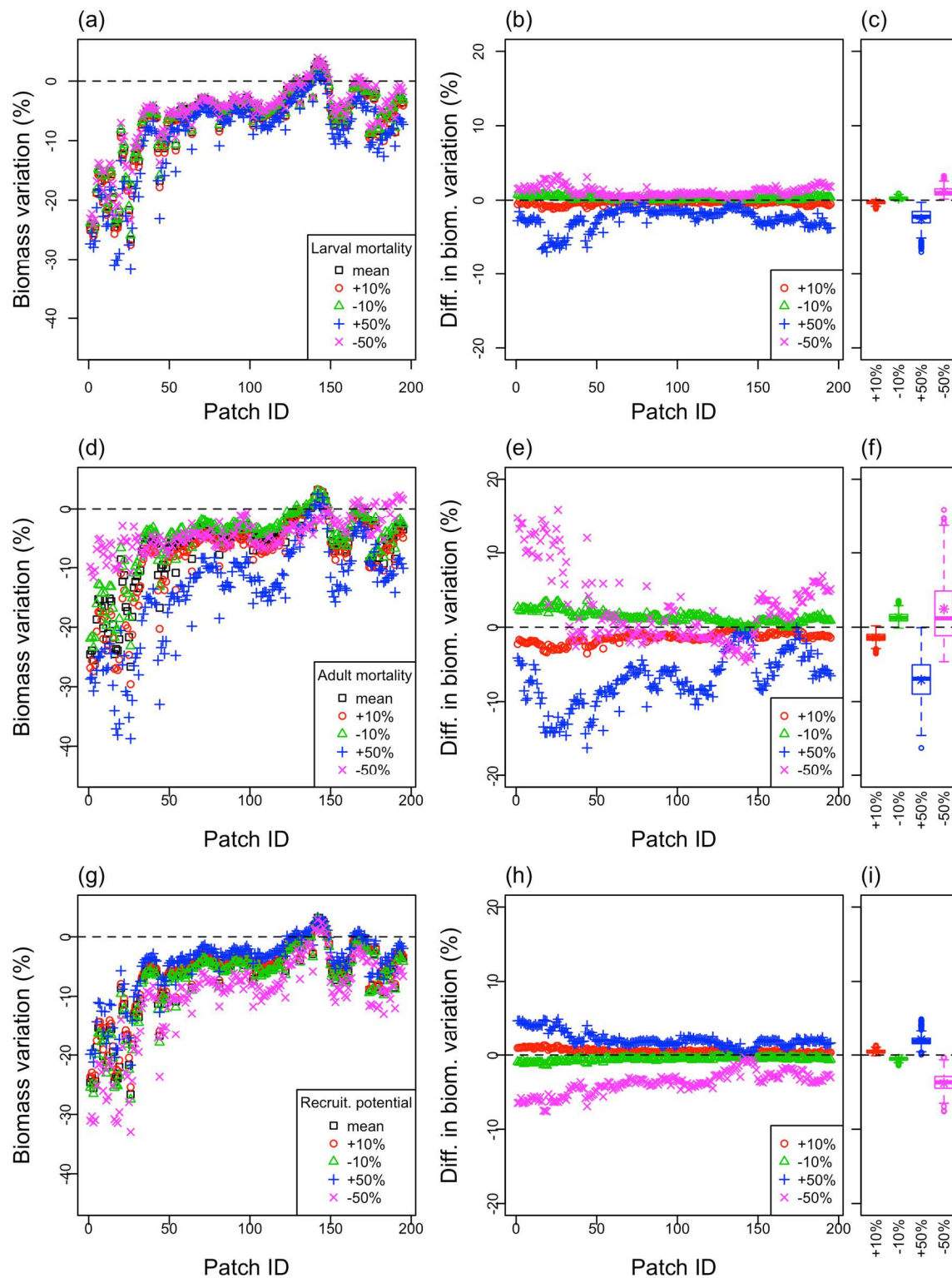
527

528 **Fig. 10. Effect of habitat connectivity on mussel response to seawater warming scenario**  
 529 **(RCP8.5):** (a) difference in simulated biomass between the reference (R) and projection (P)  
 530 temperature scenarios ( $100 \times (P - R) / R$ , %) in each patch and for each connectivity scenario, (b)  
 531 difference in biomass variation between the realistic connectivity scenario ('PLD-22-Month') and the  
 532 others, and (c) boxplot of the differences results, summarizing panel (b) for each connectivity  
 533 scenario.

#### 534 4.3.2 Mortality and recruitment effects

535 Whatever the scenario regarding mortality or recruitment potential, the response to the  
 536 projection scenario shows the same pattern, with a decrease in simulated biomass in most of  
 537 the habitats studied (Fig. 11.a, d, g). In a similar way to the reference model (monthly  
 538 connectivity; PLD = 22 days; mean mortality and recruitment potential), the decrease in

539 biomass is greater in the south of the study area. The effect of the mortality and  
540 recruitment potential scenarios on response to warming is relatively limited and differences  
541 with the reference model do not exceed 6% on average. However, this modulation is spatially  
542 heterogeneous. Southern habitats are systematically more sensitive and show larger  
543 differences from the reference model. The modulation is also non-symmetrical depending on  
544 whether the factor under consideration is increased or decreased. Increases in larval or post-  
545 larval mortality and decreases in recruitment potential have a greater effect on response to  
546 warming than decreases in these parameters.



547

548 **Fig. 11. Response to seawater warming scenario as a function of (a-c) larval mortality, (d-f)**  
 549 **adult mortality and (g-i) recruitment potential.** For each process tested, the three panels correspond  
 550 to: (a, d, g) change (%) in simulated biomass between the reference (R) and projection (P) temperature  
 551 scenarios ( $100 \times (P - R) / R$ ), in each patch; (b, e, h) difference in biomass variation between the  
 552 realistic scenario (here 'Mean') and the others; and (c, f, i) boxplots of the differences results,  
 553 summarizing the second panel for each scenario.

## 554 **5 DISCUSSION**

### 555 **5.1 Results highlights**

556 Our results confirm the poleward latitudinal shift of a species distribution range resulting  
557 from global warming (Jones and Cheung, 2015; Jones et al., 2010). With the RCP8.5  
558 scenario, our simulation showed a decrease in biomass ranging from -27% in the south to 0%  
559 in the north of the study area, under the most realistic modelling conditions. We found that  
560 this decrease is related to a change in recruitment success and shift in reproduction  
561 phenology. This confirms previous results on the importance of reproductive phenology in the  
562 response of bivalve species to seawater warming (Thomas et al., 2016; Thomas and Bacher,  
563 2018). The consequences of such an evolution are numerous for fishery and aquaculture  
564 activities (e.g. reduction in individual growth, standing stock biomass and recruitment  
565 success), but also for the balance of ecosystems (e.g. benthic-pelagic coupling, biodiversity  
566 associated with reef building, food web equilibrium). Our modelling approach is generic and  
567 is therefore applicable to many species with a benthic-pelagic life cycle. This would make it  
568 possible to evaluate consequences at the ecosystem scale, particularly by assessing the effects  
569 on material flows (biomasses, filtration rates, biodeposition, etc.) and food webs (impact on  
570 biodiversity at the local scale).

571 Previous studies did not account for the process of connectivity between populations or  
572 density regulation processes at the local scale of mussel patches (i.e. competition for space),  
573 which allow a realistic representation of biomass dynamics. In the present work, we modelled  
574 these processes of regulation and spatialization, allowing a relevant representation of  
575 population densities and size structures, comparable to data available in the literature. Our  
576 results highlight four major findings: (1) the temperatures projected by the RCP8.5 climate  
577 scenario to 2100 imply a decrease in average biomass and a shift in reproductive phenology,

578 (2) the modulation response to temperature change is not spatially homogeneous,  
579 showing the importance of the processes implemented at the local scale, (3) the connectivity  
580 process clearly limits the consequences of seawater warming compared to other regulation  
581 processes, and (4) the larval supply does not seem to be a limiting element and only slightly  
582 modulates the response to temperature change. We will next examine the assumptions and  
583 implications of our results.

## 584 **5.2 Importance of local-scale processes: habitat definition**

585 The ecological niche concept locates species in the optimal zone of the environmental  
586 space that regulates their biomass. By considering temperature and food (here modulated by  
587 the density of inorganic particles), we have shown that the heterogeneity of trophic conditions  
588 is a key element that explains a large part of the simulated biomass variability. Nearly 110%  
589 biomass variation was simulated between the most contrasting habitats in our baseline  
590 scenario along the trophic gradient, compared with a maximum of -27% along the thermal  
591 gradient. However, our approach does not consider the complexity of the thermal conditions  
592 that may exist at a small scale. This has already been well demonstrated in rocky intertidal  
593 habitats, notably through the concept of a mosaic of thermal environments (Helmuth et al.,  
594 2002). Since our study area was not located at the extreme limit of the species range, we  
595 considered that the temperatures used should reflect average conditions and that the  
596 physiological extremes were not reached. However, this assumption highlights the importance  
597 of considering the processes prevailing at a small scale that modulate both physiological  
598 performances and biotic interactions.

599 Here, we defined the potential habitat as rocky intertidal areas, which were derived from  
600 the products of the European EMODNET Seabed Habitats project (Thomas and Bacher,  
601 2018). In our model, we hypothesized that colonization of this habitat by mussels would take

602 place depending on two conditions: i) local food concentration must support mussel  
603 individual growth and reproduction, and ii) connectivity between habitats and self-recruitment  
604 within a given habitat would maintain the recruitment of individuals high enough to  
605 compensate for the mortality of new recruits, juveniles and adult mussels. All our modelled  
606 patches match these conditions. We also accounted for the competition for space using a  
607 simple rule linking space availability to the size and density of mussels already present in a  
608 patch. Simulations showed that all the space was eventually occupied, and we found that  
609 differences between patches and temporal variability of mussel density merely resulted from  
610 growth differences due to local food concentration. Therefore, the predicted mussel density  
611 and biomass can be seen as proxies of the actual values, and the results interpreted in terms of  
612 the relative differences between scenarios.

613 More realistic predictions of mussel biomass would require i) a better estimation of the  
614 area of potential habitat within each patch and ii) to determine the local factors that limit the  
615 occupation of potential habitat (i.e. realized habitat). The spatial resolution of the EMODNET  
616 layers we used to identify the different type of habitats may be not sufficient to represent  
617 coastal intertidal habitats, though we do not know of any work addressing this issue. Spatial  
618 resolution is an issue addressed in Species Distribution Modelling, and some authors have  
619 shown that it has an effect on model performance (Lowen et al., 2016). Gomes et al. (2018)  
620 recently presented the advantages of aerial photography for investigating large-scale patterns  
621 of mussel distribution in intertidal mud and sand flats. They pointed out the lack of studies  
622 quantifying mussel distribution on rocky shores and demonstrated how the use of aerial  
623 photography with a drone helps us to understand mussel distribution in such habitats.  
624 Through the combination of image analysis and habitat suitability model at a high spatial  
625 resolution, they mapped the density, mean size and reproductive effort of *Mytilus*  
626 *galloprovincialis* along the Portuguese rocky intertidal coastline. Density ranged from 0 to

627 6500 ind.m<sup>-2</sup>, which compares well with the values we found with our model. Mussel  
628 coverage (ratio mussels/rocky substrate) varied between 0.4 % up to 60% depending on  
629 location. They also found a significant relationship between wave exposure and the density  
630 and distribution of mussel populations and argued that wave action forces intertidal organisms  
631 to adapt and withstand the dynamics of water motion. Physical drivers would explain, at least  
632 partly, the distribution of mussel populations, and Gomes et al. (2018) concluded that  
633 location-specific predictions can be used in metapopulation models. Considering the effect of  
634 physical drivers in addition to the bioenergetics of organisms and the connectivity between  
635 patches would, therefore improve the quantitative predictions of our models. The  
636 development of habitat observation tools (e.g. high-resolution photogrammetry) combined  
637 with tools for modelling (e.g. microclimate conditions, Kearney et al., 2020) offer promising  
638 prospects in this context (Choi et al., 2019).

### 639 **5.3 The two sides to larval supply: larval production and connectivity**

640 'Supply-side ecology' recognizes that variable larval input is a key factor determining the  
641 size of local adult populations (Hughes et al., 2000). However, as Hughes et al. (2000) point  
642 out, the spatial scale at which adult stocks and recruitment are coupled is unknown for most  
643 marine organisms. By decoupling these two processes, our results highlight the lower effect  
644 of larval supply relative to the connectivity potential. A variation of  $\pm 50\%$  in larval mortality,  
645 which could be associated with a significant decrease in reproductive efficiency, modulates  
646 the response to the projection scenario by less than  $\pm 5\%$ , compared with the  $-22\%$  simulated  
647 by our 'self-recruitment' scenario. The comparison between the 'self-recruitment' and  
648 reference (with connectivity) scenarios also showed that the response of mussel biomass to  
649 temperature change was more sensitive to connectivity than to any other factor we tested (Fig.



650 S6). Mussel biomass would also be reduced by 70% if self-recruitment was the only  
651 process of population renewal.

652 Our simulations also give an idea of the dispersal capacity and dispersion range of mussel  
653 populations. Additional simulations (Fig. S7) indicate that the southernmost mussel  
654 population in this study would need 13 years to reach the most northern set of patches and  
655 that mussels never propagate from north to south, reflecting the asymmetry in the  
656 connectivity matrix and breakpoints associated with environmental conditions limiting  
657 sufficient reproductive capacity. Ayata et al. (2010) simulated connectivity in the same region  
658 and also showed that the Ushant Sea, which lies between the western English Channel and  
659 northeast Bay of Biscay, likely acts as a partly permeable one-way barrier. However, there is  
660 very little quantitative information on spatial dispersion of mussel propagules, and most  
661 observations, calculations or hypotheses give values between a few kilometres up to 100 km.  
662 In their modelling of mussel dispersion along the French Atlantic coast, Wetthey et al. (2011)  
663 assumed that the spatial scale of dispersal was 25 km and argued that this value is typical of  
664 the dispersal ranges of intertidal species with planktonic larvae. In South Africa, McQuaid  
665 and Phillips (2000) found that the dispersal radius would maintain 90% of the intertidal  
666 mussel *Mytilus galloprovincialis* population within an area of 5 km, while the maximum  
667 effective dispersal of mussel larvae in this area would be less than 100 km. Gilg et al. (2007)  
668 found exchanges of *M. edulis* and *M. galloprovincialis* larvae possible over distances >100  
669 km though barriers to dispersal could occur at some locations. For another mussel species,  
670 model projections made by Gilg et al. (2014) suggested that dispersal distance could exceed  
671 100 km. Carsons et al. (2010) identified larval source populations of mussels species and  
672 found dispersal distances around 35 km. These examples show that, for intertidal species like  
673 mussels, hydrodynamics control the spread of populations and should be investigated in more  
674 detail. Following the work of Nicolle et al. (2017) and Ménesguen et al. (2018) on other

675 benthic species, it would be interesting to extend our calculation to a larger set of  
676 patches extending to the north of the English Channel and to assess the kernel and barriers to  
677 dispersion at a larger spatial scale.

#### 678 **5.4 Larval behaviour and phase duration**

679 We assumed that the pelagic phase duration was spatially homogeneous and constant in a  
680 given scenario, and that the larvae were transported passively, with no swimming behaviour.  
681 Testing the effect of pelagic larval phase duration showed that changes of biomass in response  
682 to temperature change were not very sensitive to this parameter.

683 We have not found any similar studies addressing the effect of larval swimming on mussel  
684 larvae dispersion and metapopulation connectivity. Other authors made different assumptions  
685 depending on the species of interest, modelling scope or available information, and  
686 conclusions on the need for incorporating behaviour do not converge. McQuaid and Philipps  
687 (2000) estimated that passive transport was sufficient to explain the abundances of larvae in  
688 their region of interest. Kim et al. (2013) found that physical forcing showed a greater  
689 influence on the loss of *C. virginica* larvae than did behaviour. but North et al. (2008) found  
690 that behaviour had significant consequences for dispersal distances, transport success, and the  
691 degree of connectivity between subpopulations. Hubbard and Reidenbach (2015) follow the  
692 same line, concluding that changes in swimming behaviour due to turbulence influence the  
693 probability of settling of *C. virginica* on suitable substrate. This apparent contradiction  
694 regarding the need, or lack thereof, to account for larval behaviour, can be explained by  
695 sources of variability considered and the hypotheses tested. In our model, we emphasized  
696 multiple spawnings within mussel populations, due to local differences in individual growth  
697 and reproduction. Emissions of larvae at different times of the year would generate new  
698 cohorts of individuals with different life histories and spawning events. This cascade effect

699 yields a large variability of life history traits within each population and contributes to  
700 the variability of larval transport.

## 701 **5.5 Conclusion**

702 The effect of a climate warming scenario, currently considered to be the most severe of the  
703 projections, appears to be strongly modulated by processes occurring at multiple scales. At  
704 the local scale, food availability remains a major factor structuring biomass, and neither  
705 ontogenic mortality nor recruitment potential seem to strongly modulate the response. At the  
706 study area scale, the connectivity between populations mitigates the consequences of warming  
707 by limiting the loss of biomass locally. These results are made in a restricted biogeographic  
708 transition zone. The same approach would merit being established over the entire range of the  
709 species to assess whether this observation remains homogeneous. The generic nature of the  
710 approach developed will also make it possible to compare the response of other species.

711 Our model is constructed of solid elements, based on well-established theories and  
712 processes. It produces results that have demonstrated their realism and robustness to  
713 sensitivity analysis. We need, however, to know more about the realized habitat in order to  
714 have a more quantitative approach of realized niche. Connectivity appears to be a determining  
715 factor, and patterns of population connectivity could be strongly modified by local processes  
716 limiting the occupation of potential habitats. The next step in the implementation of such a  
717 population dynamics modelling approach would be to have a more realistic representation of  
718 the realized habitat, in order to get as close as possible to the true connectivity (*sensu* Watson  
719 et al., 2010).

720 Identifying and prioritizing the processes likely to modulate the multi-scale response of  
721 species to climate change is a key element in predicting the dynamics of marine ecosystems in  
722 a context of increasing pressures such as seawater warming, hypoxia events, acidification,

723 overexploitation, pollution, etc. As biological responses, socio-economic and  
724 administrative aspects are not spatially homogeneous (Barillé et al., 2020), the integration of  
725 spatial processes into a spatially explicit modelling (SEM) strategy appears to be the decisive  
726 difference from spatially implicit models (SIMs), which are more oriented towards theoretical  
727 issues (DeAngelis and Yurek, 2017). The use of such models, with a generic approach, would  
728 make it possible to provide scientific support to guide and optimize research efforts, e.g.  
729 define key field observations, experimentation and operational modelling strategies, and  
730 support the implementation of management and conservation measures.

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