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Mélaine Gourault, Romain Lavaud, Aude Leynaert, Laure Pecquerie, Yves-Marie Paulet, et al.. New insights into the reproductive cycle of two Great Scallop populations in Brittany (France) using a DEB modelling approach. *Journal of Sea Research (JSR)*, 2019, 143, pp.207-221. 10.1016/j.seares.2018.09.020 . hal-02324233

**HAL Id: hal-02324233**

**<https://hal.science/hal-02324233v1>**

Submitted on 15 Jun 2020

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## New insights into the reproductive cycle of two Great Scallop populations in Brittany (France) using a DEB modelling approach

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### Abstract :

The present study aimed to improve understanding of the environmental conditions influencing the reproductive cycle of the great scallop *Pecten maximus* in two locations in Brittany (France). We also evaluated potential consequences of future climate change for reproductive success in each site.

We simulated reproductive traits (spawning occurrences and synchronicity among individuals) of *P. maximus*, using an existing Dynamic Energy Budget (DEB) model. To validate and test the model, we used biological and environmental datasets available for the Bay of Brest (West Brittany, France) between 1998 and 2003. We also applied the scallop DEB model in the Bay of Saint-Brieuc (North Brittany, France) for the same period (1998–2003) to compare the reproductive cycle in different environmental conditions. In order to accurately model the *P. maximus* reproductive cycle we improved the scallop DEB model in two ways: through (1) energy acquisition, by incorporating microphytobenthos as a new food source; and (2) the reproductive process, by adding a new state variable dedicated to the gamete production. Finally, we explored the effects of two contrasting IPCC climate scenarios (RCP2.6 and RCP8.5) on the reproductive cycle of *P. maximus* in these two areas at the 2100 horizon.

In the Bay of Brest, the simulated reproductive cycle was in agreement with field observations. The model reproduced three main spawning events every year (between May and September) and asynchronicity in the timing of spawning between individuals. In the Bay of Saint-Brieuc, only two summer spawning events (in July and August) were simulated, with a higher synchronicity between individuals. Environmental conditions (temperature and food sources) were sufficient to explain this well-known geographic difference in the reproductive strategy of *P. maximus*. Regarding the forecasting approach, the model showed that, under a warm scenario (RCP8.5), autumnal spawning would be enhanced at the 2100 horizon with an increase of seawater temperature in the Bay of Brest, whatever the food source conditions. In the Bay of Saint-Brieuc, warmer temperatures may impact reproductive

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phenology through an earlier onset of spawning by 20 to 44 days depending on the year.

### Highlights

► We aimed at better understanding and quantifying the effect of environmental variables (temperature and food sources) on the reproduction variability of the Great Scallop *Pecten maximus* in Brittany. ► We improved an existing scallop-DEB model at two different levels, by adding a new food source and a more detailed reproduction module. ► We compared reproductive traits of the Great Scallop in two Brittany locations for the period 1998–2003 and we made forecasts at the 2100 horizon within a context of ocean warming. ► We evidenced two different effects of the increase of seawater temperature depending on the location: a most efficient autumnal last spawning in the Bay of Brest and an earlier onset of spawning in the Bay of Saint-Brieuc.

**Keywords** : *Pecten maximus*, DEB theory, reproduction cycle, IPCC scenarios, Bay of Brest, Bay of Saint-Brieuc

## 47 1. Introduction

48 The great scallop, *Pecten maximus* (Linnaeus, 1758) inhabits many sublittoral environments  
49 along Northeast Atlantic coasts from northern Norway to the Iberian Peninsula (Ansell et al., 1991). In  
50 France, the species is particularly abundant along the coast of northern Brittany, where it sustains one  
51 of the most important French commercial fisheries both in terms of landings and of socio-economic  
52 value (more than 300 fishing boats; ICES, 2015). The main fishing areas are located in the Bay of  
53 Brest, connected to the Iroise Sea, and in the Bay of Saint-Brieuc, open to the English Channel (Fig.  
54 1). While some of the highest scallop densities are found in the Bay of Saint-Brieuc, in part due to  
55 sustainable exploitation measures, the scallop stock in the Bay of Brest is lower and highly dependent  
56 on hatchery produced spat since 1983.

57 From a biological point of view, scallops, like most other bivalves, are filter feeders and  
58 consume phytoplankton. However, since they live settled into the surface layer of the bottom, they are  
59 also thought to use the epibenthic layer as an important food source (see review in Shumway, 1990).  
60 Concerning the reproductive cycle, *P. maximus* is a functional hermaphrodite species, it has a pelagic  
61 larval stage during approximately one month after fertilization, switching to a benthic life after  
62 metamorphosis. Its reproductive strategy is more surprising as its spawning period varies according to  
63 the geographical location of the population (see review by Gosling (2004)) There can be between one  
64 major summer spawning and more than three spawnings in the period from spring to early autumn. At  
65 a small regional scale, geographical differences can be very marked: scallops from the Bay of Brest  
66 show low inter-individual synchronism, with multiple partial spawnings from early spring to autumn  
67 and almost no resting stage, whereas the population from the Bay of St-Brieuc is almost synchronous,  
68 with one or two major spawnings over a short period (July-August), with a sexual rest stage then  
69 observed in autumn and winter (e.g. Devauchelle and Mingant, 1991; Paulet et al., 1997).

70 A major part of this phenotypic variability has been attributed to differences in environmental  
71 conditions such as food sources, temperature and photoperiod, which are known to influence  
72 gametogenesis and fecundity in marine invertebrates. For example, Claereboudt and Himmelman  
73 (1996) showed that an increase in temperature and food availability increased reproductive effort in

74 *Placopecten magellanicus*. In *P. maximus*, quantity and quality of food sources also have an impact on  
75 hatching rate (Soudant et al., 1996), and laboratory experiments showed that spring conditions (regular  
76 increase of temperature and photoperiod) favoured gonad growth, whereas winter conditions (regular  
77 decrease of temperature and daylight duration) were associated with somatic growth of the adductor  
78 muscle and digestive gland (Saout et al., 1999; Lorrain et al., 2002). More recently, Chauvaud et al.,  
79 (2012) and Lavaud et al. (2014) have proposed complementary approaches to quantitatively evaluate  
80 effects on environmental factors on growth and reproduction of scallops. However, the relative  
81 importance of these variables remains difficult to disentangle, especially under natural conditions.

82 Climate models and observations to date indicate that the Earth will warm between two (IPCC  
83 scenario RCP2.6) and six degrees Celsius (IPCC scenario RCP8.5) over the next century, depending  
84 on how fast carbon dioxide emissions increase. The ocean absorbs most of this excess heat, leading to  
85 rising seawater temperatures (e.g., IPCC, 2014; Appendix A). Increasing ocean temperatures will  
86 deeply affect marine species and ecosystems. Understanding the potential effects of climate change on  
87 the timing of life-history events such as the onset of gametogenesis, spawning, hatching and larval  
88 metamorphosis is important for benthic ecology but also for aquaculture and fisheries production. The  
89 phenology of these key life-history events has been investigated in several ecosystems and in many  
90 species (e.g., Beukema et al., 2009; Menge et al., 2009; Shephard et al., 2010; Valdizan et al., 2011;  
91 Morgan et al., 2013), although these studies often had limited spatial and/or temporal resolution.  
92 Mechanistic modelling provides a complementary tool to analyse climate effects on life-history traits,  
93 identify interactions between multiple stressors, and make predictions about future condition scenarios  
94 at a larger spatiotemporal scale. In recent decades, bivalve growth and reproduction have been  
95 successfully modelled (e.g. Bernard et al., 2011; Thomas et al., 2016; Montalto et al., 2017; Gourault  
96 et al., 2018, this issue) using mechanistic models based on Dynamic Energy Budget theory (DEB;  
97 Kooijman, 2010). This theory makes it possible to quantify the energy flows within an individual from  
98 ingestion to maintenance, growth, development, and reproduction in relation to environmental  
99 conditions.

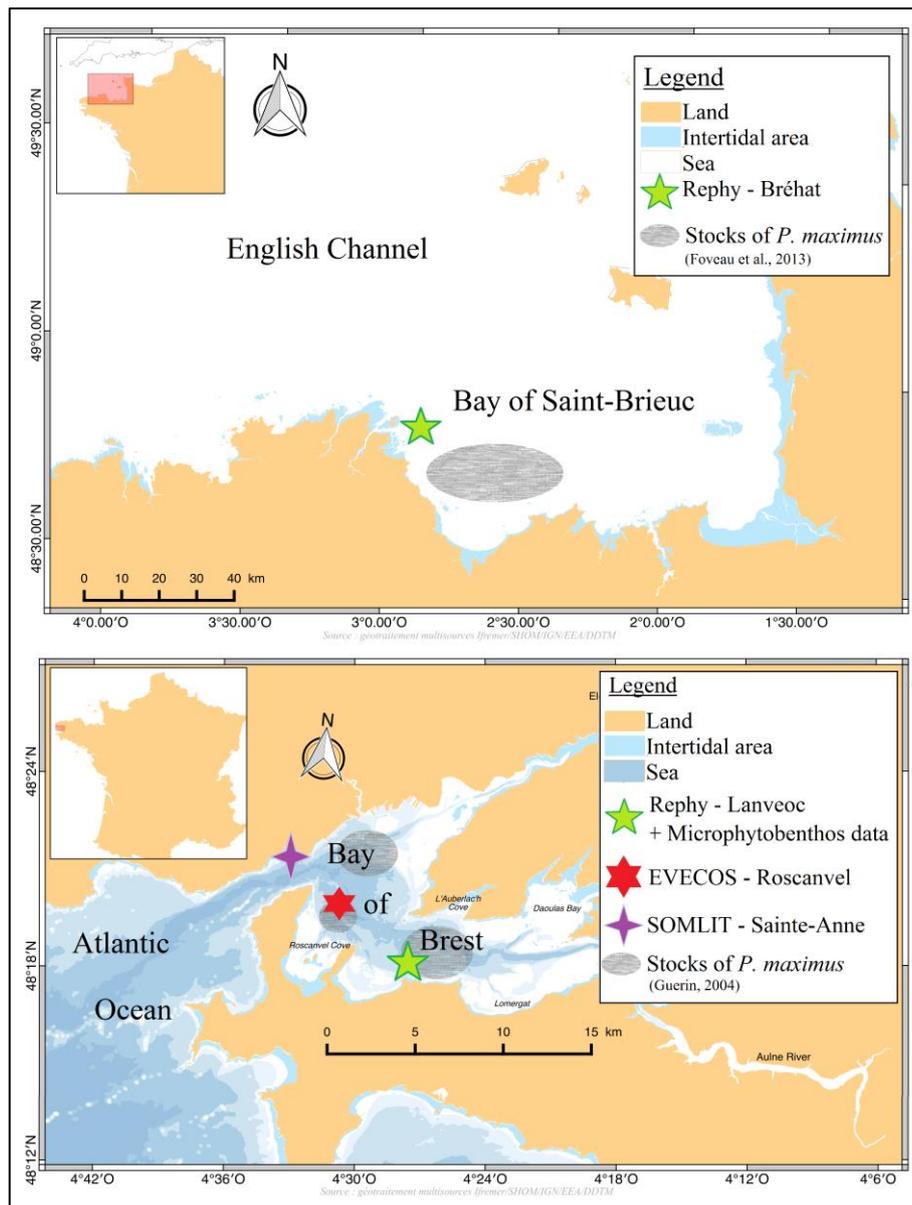
100           In this context, the present study aims to improve understanding of the environmental factors  
101 influencing the reproductive cycle of *P. maximus* using a DEB model and the potential effects of  
102 climate change on the reproductive activity of this species. Our work is based on an existing DEB  
103 model developed for the great scallop in the Bay of Brest (Lavaud et al. 2014) that we then improved  
104 by adding detail on the reproductive processes. To evaluate the ability of the model to simulate  
105 reproductive processes under various conditions, we tested it over six years in the Bay of Brest (1998–  
106 2003) and in the two main locations hosting scallop populations in Brittany: the Bay of Brest and the  
107 Bay of Saint-Brieuc. In a second step, using two IPCC climate scenarios at the 2100 horizon, we  
108 examined the potential consequences of future climate change on the reproductive activity of this  
109 emblematic species in each of the two sites.

## 110 2. Material and Methods

### 111 2.1. Study sites

112 The Bay of Brest is a semi-enclosed coastal ecosystem located in western Brittany, France,  
113 connected to the Atlantic Ocean by a deep narrow strait. The bay itself covers an area of nearly 180  
114 km<sup>2</sup>, with an average depth of 8 m. Two rivers flow into the bay: the Elorn (watershed of 402 km<sup>2</sup>) and  
115 the Aulne (watershed of 1842 km<sup>2</sup>) (Fig. 1). Temperature and phytoplankton concentration are  
116 continuously monitored at two locations in the Bay: Lanvéoc station in the southern part of the Bay  
117 (data provided by the REPHY network - Phytoplankton and Phycotoxin monitoring Network, Ifremer,  
118 *e.g.* Belin et al., 2017) and Sainte-Anne station in the north-western part (data provided by the  
119 SOMLIT - “*Service d’Observation en Milieu Littoral*”, INSU-CNRS, Brest). Lanvéoc station (48°29'  
120 N, 04°46' W; Fig. 1) has a depth range of 6 to 9 m at lowest spring tides and a bottom composed of  
121 sandy mud, with broken shells and pebbles. Sainte-Anne station is located at the entrance to the Bay of  
122 Brest (48°21'' N, 04°33 W; Fig. 1).

123 The Bay of Saint-Brieuc is located in northern Brittany (France), 150 km from the Bay of Brest  
124 (48°32N, 02°40W; Fig. 1), in the western part of the English Channel. This bay of 800 km<sup>2</sup> harbours a  
125 large wild scallop population in its inshore shallow waters ( $\leq 30$  m). It is subject to an extreme tidal  
126 regime with a tidal range between 4 m at neap tides and nearly 13 m during spring tides. Seawater  
127 temperature and phytoplankton concentration are monitored at the Bréhat station located in the  
128 western part of the bay (Fig. 1).



129

130 Figure 1: Maps of the two study sites, the Bay of Saint-Brieuc and the Bay of Brest, showing the  
 131 position of the bimonthly great scallop monitoring area of (EVECOS) and the three environmental  
 132 monitoring sites: the REPHY stations at Lanvéoc and Bréhat and the SOMLIT station at Sainte-Anne.

## 133 2.2. Scallop biological data

134 Scallop growth and reproduction were monitored from 1998 to 2003 at Roscanvel in the west of  
 135 the Bay of Brest (48°20' N, 04°30' W; Fig. 1). This site, known to host the highest density of *P.*  
 136 *maximus* in the bay, is characterized by mixed sandy and silty sediments. It was integrated into a  
 137 multi-annual monitoring network (EVECOS database provided by the "Observatoire Marin de

138 *l'IUEM*, Brest, France"). A sample of 20 adult scallops (3 years old) was collected by dredging on a  
 139 biweekly to monthly basis in 30-m deep waters. The scallops were brought back to the laboratory  
 140 where the muscle, gonads and digestive gland were dissected out. Total wet flesh mass and total dry  
 141 flesh mass (DFM) of each organ were measured for each individual. In order to compare masses  
 142 obtained for different sized scallops, dry mass was standardized following the formula of Bayne et al.  
 143 (1987):

$$144 \quad W_r = \left(\frac{L_r}{L_m}\right)^3 W_m$$

145 where  $W_r$  is the standardized mass of an individual of standard shell height  $L_r$  and  $W_m$  is the measured  
 146 mass of an individual of measured shell height  $L_m$ . Length and mean daily shell growth rate (DSGR)  
 147 were measured according to the method proposed by Chauvaud et al. (2012) (see Lavaud et al. 2014  
 148 for more detailed information on these data).

149 Additionally, four additional *P. maximus* reproductive cycle traits were recorded through  
 150 EVECOS monitoring: the onset of gametogenesis, the number and timing of each main spawning  
 151 within the reproductive season and the reproductive investment (DFM difference before and after  
 152 spawning).

### 153 **2.3. The scallop DEB model**

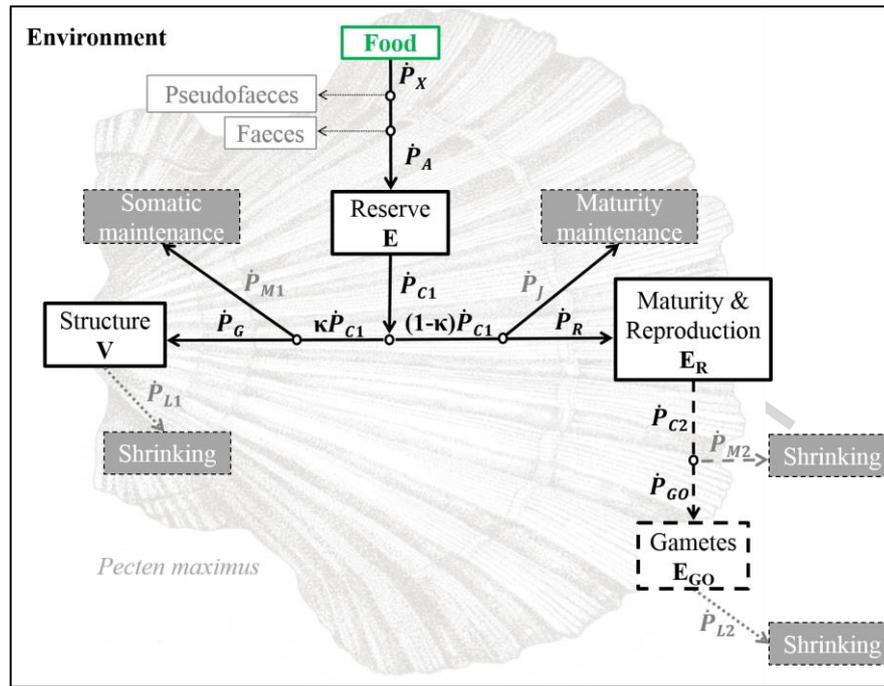
154 The scallop DEB model was derived from the standard DEB model described by Kooijman  
 155 (2010) and first applied to *P. maximus* by Lavaud et al. (2014). The DEB model is a mechanistic  
 156 model that describes the dynamics of three state variables: E, the energy in reserve, V, the volume of  
 157 structure, and  $E_R$ , the energy allocated to development and reproduction. To improve the accuracy  
 158 with which DEB models model reproductive activity, Bernard et al. (2011) refined the processes of  
 159 energy allocation to gametogenesis and resorption in the model, such that a fourth state variable,  $E_{GO}$ ,  
 160 the energy in gametes, was added to the existing scallop DEB model (Fig. 2). Briefly, the model can  
 161 be explained as follows: the reserve mobilization rate,  $\dot{p}_{C1}$ , is divided into two parts. A first constant  
 162 fraction,  $\alpha$ , is allocated to structural growth and maintenance and the remainder,  $1-\alpha$ , is allocated to  
 163 development (in juveniles), reproduction (in adults) and maturity maintenance. Energy allocation to

164 gonad construction is modelled through the gamete mobilization rate,  $\dot{p}_{C2}$ . Priority in energy allocation  
165 is always given to maintenance costs:  $\dot{p}_{M1}$  for maturity maintenance and  $\dot{p}_J$  for somatic maintenance.  
166 During starvation periods, the gametogenesis flux is re-allocated to somatic and maturity maintenance  
167 through secondary maintenance,  $\dot{p}_{M2}$ . If  $\dot{p}_{M2}$  does not provide enough energy to cover all maintenance  
168 costs, the gamete resorption rate,  $\dot{p}_{L2}$ , is activated. In case of extreme starvation, structure can be  
169 broken down at the rate  $\dot{p}_{L1}$ . The corresponding set of equations can be found in Gourault et al. (2018,  
170 this issue).

171 Regarding food assimilation, a classical scaled functional response (Holling type II) is  
172 generally calculated in the model (Kooijman, 2010), using one food source (for bivalves, this  
173 essentially consists of phytoplankton cells). However, many studies focusing on modelling the energy  
174 dynamics of filter feeders have shown the need and benefit of adding a second food source to improve  
175 the food proxy (Alunno-Bruscia et al, 2011; Bernard et al., 2011; Saraiva et al., 2011). Lavaud et al.  
176 (2014) included the Synthesizing Units (SUs) concept (Kooijman, 2010; Saraiva et al. 2011) into the  
177 scallop DEB model to consider selection of particles based on their size and/or quality. The equations  
178 for the SU concept can be found in Lavaud et al. (2014).

179 In this study we compared the previous model of Lavaud et al. (2014), hereafter referred to as  
180 “Mod-1”, with our DEB model (with the extra state variable  $E_{GO}$ ), hereafter referred to as “Mod-2”  
181 (Table 1). Two versions of the Mod-2 model were used in order to test different food sources in the  
182 model: (1) phytoplankton as a first food proxy and particulate organic matter (POM) as a second food  
183 proxy (Mod-2A) and (2) a mix of microphytobenthos and phytoplankton as a first food proxy and  
184 POM as a second food proxy (Mod-2B). All the model parameters are given in Table 2. Simulations  
185 were performed using R software (3.3.3 version).

186



187

188 Figure 2: Schema of the *P. maximus* DEB model with four state variables adapted from Bernard et  
 189 al. 2011 (Mod-2). Sources of energy to pay for somatic maintenance during prolonged starvation are  
 190 indicated by grey dotted arrows. Modifications of the standard DEB model (3 state variables; Mod-1)  
 191 are represented by dashed arrows for  $\dot{P}_{C2}$ ,  $\dot{P}_{GO}$ ,  $\dot{P}_{M2}$  and  $\dot{P}_{L2}$ .

192 Table 1: The three scallop DEB models tested in this study (<sup>a</sup> data only available for the Bay of Brest, <sup>b</sup>  
 193 data available for the Bay of Brest and Bay of Saint-Brieuc).

	Mod-1 (Lavaud et al., 2014)	Mod-2A	Mod-2B
State variables	V, E, E <sub>R</sub>	V, E, E <sub>R</sub> , E <sub>GO</sub>	V, E, E <sub>R</sub> , E <sub>GO</sub>
X-type food	Phytoplankton <sup>b</sup>	Phytoplankton <sup>b</sup>	Phytoplankton <sup>b</sup> + Microphytobenthos <sup>a</sup>
Y-type food	POM <sup>a</sup>	POM <sup>a</sup>	POM <sup>a</sup>

194

## 195 2.4. Model calibration

196 The model was calibrated with field data observed over the 1998–2003 period in the Bay of Brest.  
 197 Model parameters (Table 2) were mostly taken from Lavaud et al. (2014), but some parameters were  
 198 recalibrated for this study. First, we set a new value for the ultimate shell length  $L_{w\infty}$  (i.e., the  
 199 maximum observed length reached in optimal condition i.e.  $f = 1$ ) at 20 cm instead of 12 cm. Some  
 200 field studies have shown that adult scallops can reach 16 cm in the most favourable conditions

201 (Mason, 1957; Chauvaud et al., 2012), so we set  $L_\infty$  above this value. According to DEB theory,  $L_\infty$  is  
 202 calculated through the following equation:

$$L_{w\infty} = f \frac{L_m}{\delta_M} = f \frac{\left( \frac{\kappa \{ \dot{p}_{Am} \}}{[ \dot{p}_M ]} \right)}{\delta_M}$$

203 where  $\{ \dot{p}_{Am} \}$  is the maximum surface specific assimilation,  $[ \dot{p}_M ]$  is the volume-specific maintenance  
 204 costs,  $\kappa$  is the allocation fraction to growth and maintenance and  $\delta_M$  is the shape coefficient. We  
 205 modified the values of  $\kappa$ ,  $\{ \dot{p}_{Am} \}$  and  $[ \dot{p}_M ]$ , while keeping  $\delta_M = 0.36$ . We estimated the values of  $\{ \dot{p}_{Am} \}$   
 206 from Strohmeier et al. (2009) and a known value of  $[ \dot{p}_M ]$  at the same reference temperature (Emmery,  
 207 2008). Therefore, we were able to recalculate  $\kappa = 0.38$ .

208 To account for variability in the initial conditions between individuals, we simulated 20  
 209 individuals in each scenario (i.e., 20 different individual growth trajectories) by setting 20 different  
 210 initial conditions of size and weight (i.e., first sampling of the year from EVECOS monitoring). Initial  
 211 values for the four state variables ( $E$ ,  $V$ ,  $E_R$  and  $E_{GO}$ ) were calculated using the equations given in  
 212 Table 3 from the measurements obtained in the first sampling of the year. Individual growth  
 213 simulations were then pooled together to compute average growth patterns and standard deviation.

214 Three parameters control spawning in our model: the gonado-somatic ratio GSI, photoperiod and  
 215 phytoplankton concentration. Threshold values for each of these three parameters were set as follows:  
 216 GSI = 15% (estimated according to biological data from EVECOS monitoring), photoperiod (Photo) =  
 217 14 hours (spawning is possible only if the daylength is above 14 h; Saout et al., 1999) and a  
 218 phytoplankton concentration threshold (Phyto) =  $2.50 \cdot 10^5$  cell  $L^{-1}$  (average value corresponding to the  
 219 beginning of a spring bloom; Paulet et al., 1997). In contrast to Lavaud et al. (2014), we calculated the  
 220 GSI as the ratio between dry gonad mass and DFM, rather than as the ratio between wet gonad weight  
 221 and cubic length. To assess the reproductive effort, individual DFM loss was estimated as the  
 222 difference between individual DFM before and after spawning. Because spawning is mostly partial in  
 223 *P. maximus*, 85% of the energy stored in  $E_{GO}$  was released as gametes at spawning and the remaining  
 224 15% was kept in the buffer for a potential subsequent spawning if environmental conditions remained

225 optimal until winter. If conditions deteriorated, energy stored in the reproduction buffer was then used  
226 for the maintenance.

227 Field studies conducted in the Bay of Saint-Brieuc in the 1980s (e.g. Paulet et al., 1988) showed  
228 that phytoplankton blooms were much lower in this bay compared with the Bay of Brest. Over the  
229 1998–2003 period, maximum phytoplankton concentrations in the Bay of Saint-Brieuc were always  
230 below the phytoplankton concentration threshold set for Bay of Brest. Therefore, we hypothesised that  
231 phytoplankton concentration might not be relevant for triggering spawning in this more oligotrophic  
232 bay. Consequently, we added a temperature criterion based on the findings of Fifas (2004), who  
233 observed a temperature threshold of 16°C for spawning in the Bay of Saint-Brieuc.

234 Table 2: List of the parameters implemented in the scallop DEB model. All rate parameters are given  
235 at  $T_1 = 15^\circ\text{C}$  (= 288.15 K).

Description	Symbol	Value	Units	Reference
<b>Biological parameters</b>				
Shape coefficient	$\delta_M$	0.36	-	Lavaud et al. (2014)
Length at puberty (reproductive maturity)	$L_p$	4	cm	Lavaud et al. (2014)
<b>Food assimilation</b>				
Radius of X-type particle	$r_X$	15	$\mu\text{m}$	Lavaud et al. (2014)
Radius of Y-type particle	$r_Y$	15	$\mu\text{m}$	Lavaud et al. (2014)
Yield of reserve on X-type particle	$y_{EX}$	0.7	-	Lavaud et al. (2014)
Yield of reserve on Y-type particle	$y_{EY}$	0.4	-	Lavaud et al. (2014)
Max. specific filtration rate of X-type particle	$\dot{F}_{Xm}$	6	$\text{J d}^{-1} \text{cm}^2$	this study
Max. specific filtration rate of Y-type particle	$\dot{F}_{Ym}$	2	$\text{J d}^{-1} \text{cm}^2$	Lavaud et al. (2014)
Mol.weight of X-type particle	$w_X$	26.95	$\text{g mol}^{-1}$	Lavaud et al. (2014)
Mol.weight of Y-type particle	$w_Y$	25.4	$\text{g mol}^{-1}$	Lavaud et al. (2014)
<b>Reserve parameters</b>				
Volume-specific maintenance costs	$[\dot{p}_M]$	24	$\text{J cm}^{-3} \text{d}^{-1}$	Emmery (2008)
Energy conductance	$\dot{v}$	0.183	$\text{cm d}^{-1}$	Van der Veer (2006)
Energy content of 1 g (dry weight) of reserve	$\rho_E$	19849	$\text{J g}^{-1}$	Lavaud et al. (2014)
Molecular weight of reserve	$w_E$	23.9	$\text{g mol}^{-1}$	Lavaud et al. (2014)
<b>Structure parameters</b>				
Volume specific cost of growth	$[E_G]$	2959	$\text{J cm}^{-3}$	Lavaud et al. (2014)
Allocation fraction to growth and maintenance	$\kappa$	0.38	-	this study
Density of structure	$d_V$	0.12	$\text{g cm}^{-3}$	Lavaud et al. (2014)
Energy content of 1 g (dry weight) of structure	$\rho_V$	19849	$\text{J g}^{-1}$	Lavaud et al. (2014)
Yield of structure tissue used for maintenance	$Y_{L1}$	1	-	Bernard et al. (2011)
<b>Reproduction parameters</b>				
Reproduction efficiency	$\kappa_{Go}$	0.70	-	this study
Density of gonad	$d_{Go}$	0.276	$\text{g cm}^{-3}$	this study
Yield of gonad tissue used for maintenance	$Y_{L2}$	1	-	Bernard et al. (2011)
Energy content of 1 g of gonad	$\rho_{Go}$	21630	$\text{J g}^{-1}$	Bernard et al. (2011)

Temperature threshold for spawning	$T_S$	16	°C	this study
Gonado-somatic index threshold for spawning	$GSI$	0.15	-	this study

**Temperature effect**

Arrhenius temperature	$T_A T_A$	8990	K	Lavaud et al. (2014)
Lower boundary tolerance range	$T_L$	273.15	K	Lavaud et al. (2014)
Arrhenius temperature for lower boundary	$T_{AL}$	50000	K	Lavaud et al. (2014)

236

237 Table 3: Initial state variables of the scallop DEB model. Values vary for each of the 20 individuals

238 simulated, according to their initial length and initial dry flesh mass.

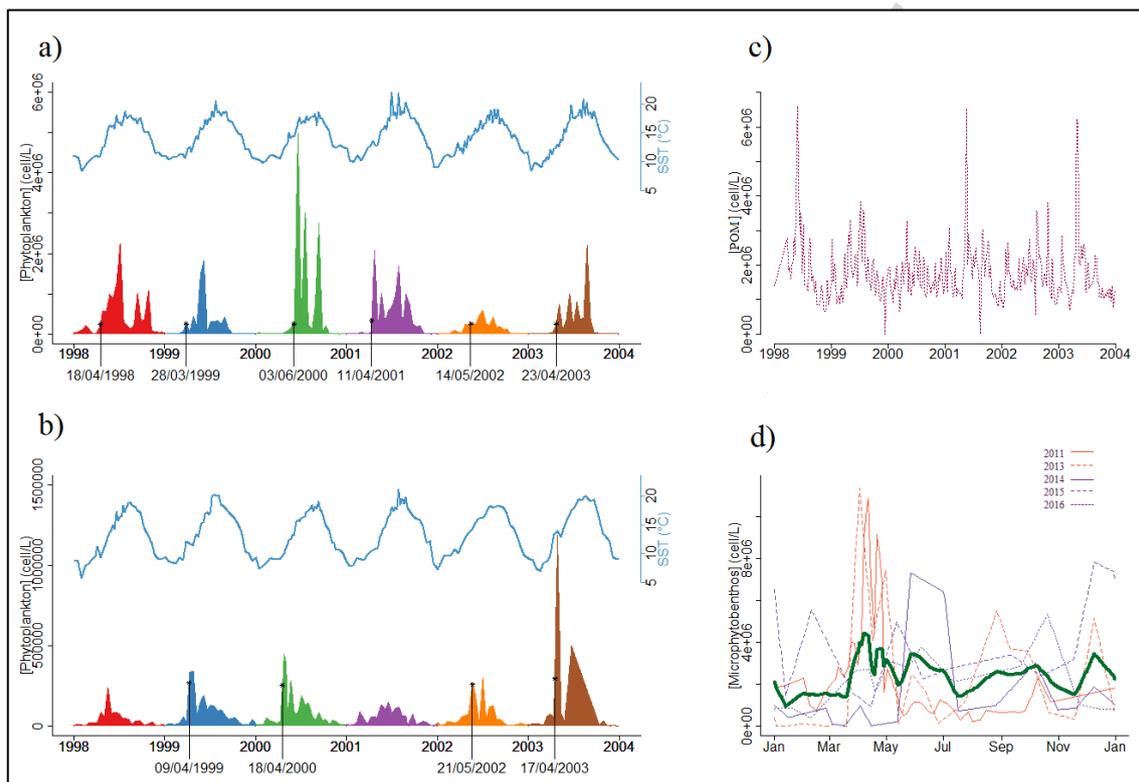
Initial conditions	Symbol	Equation	Units
Initial length	$L_0$	<i>Observed measurements in the first sampling of the year</i>	cm
Initial dry flesh mass	$W_{d0}$		g
Initial structure	$V_0$	$= (\delta_M L_0)^3$	cm <sup>3</sup>
Initial reserve	$E_0$	$= f [E_m] V_0$	J
Initial gametes	$E_{GO0}$	$= \frac{(W_{d0} \times \rho_{GO})}{\kappa_{GO}}$	J
Initial reproduction	$E_{R0}$	$= \rho_E (W_{d0} - V_0 d_V) - E_0 - E_{GO0}$	J

239

240 **2.5. Environmental forcing**241 **2.5.1. Field data**

242 The environmental variables used as forcing variables in the model are presented in Fig. 3. Three  
 243 food proxies considered as the main food sources for scallops (e.g. Lorrain et al., 2002; Marchais,  
 244 2014) were monitored for our model in the Lanvéoc area (Fig. 1.): particulate organic matter (POM,  
 245 expressed initially in mg. L<sup>-1</sup> but transformed *a posteriori* to particles L<sup>-1</sup>), phytoplankton  
 246 concentration (in cell L<sup>-1</sup>) and microphytobenthos concentration (also converted to cell L<sup>-1</sup>).  
 247 Microphytobenthos concentration was provided by the IUEM (*Institut Universitaire Européen de la*  
 248 *Mer*) observatory (Leynaert, pers. comm.). As microphytobenthos concentration was not available for  
 249 the studied period (1998–2003), we used a mean annual microphytobenthos profile that we applied for  
 250 each year from 1998 to 2003 (Fig. 3b). POM data (in mg L<sup>-1</sup>) were transformed into the number of  
 251 particles per litre considering each particle to have an average diameter of 30 µm (weight = 1.4 10<sup>-5</sup> g;  
 252 density = 1) (Lavaud et al. 2014).

253 Weekly bottom temperatures were measured at Sainte-Anne from 1998 until 2003 by the SOMLIT  
 254 monitoring network (Fig. 3a). Phytoplankton data and surface seawater temperature in the Bay of  
 255 Saint-Brieuc from 1998 to 2003 were available from the REPHY monitoring network (Fig. 3c). All  
 256 these environmental measurements were linearly interpolated to fit the daily time step of the  
 257 simulations.



258  
 259 Figure 3: Environmental forcing from 1998 to 2003 in (a,c,d) the Bay of Brest (Lanvéoc station)  
 260 and (b) Bay of Saint-Brieuc (Saint-Pol station) used for the DEB model simulations. (a,b)  
 261 phytoplankton concentration (one colour per year; cell/L) and seawater surface temperature (SST, light  
 262 blue line; °C). The dates on x-axis indicate the time, each year, when the phytoplankton concentration  
 263 threshold for spawning was reached ( $2.5010^5$  cell/L). (c) Particulate Organic Matter concentration  
 264 (POM, magenta line; cell/L) measured in the Bay of Brest. (d) Microphytobenthos concentration  
 265 measured in 2011 and from 2013 to 2016 in the Bay of Brest. Mean microphytobenthos concentration  
 266 is shown by a green line.

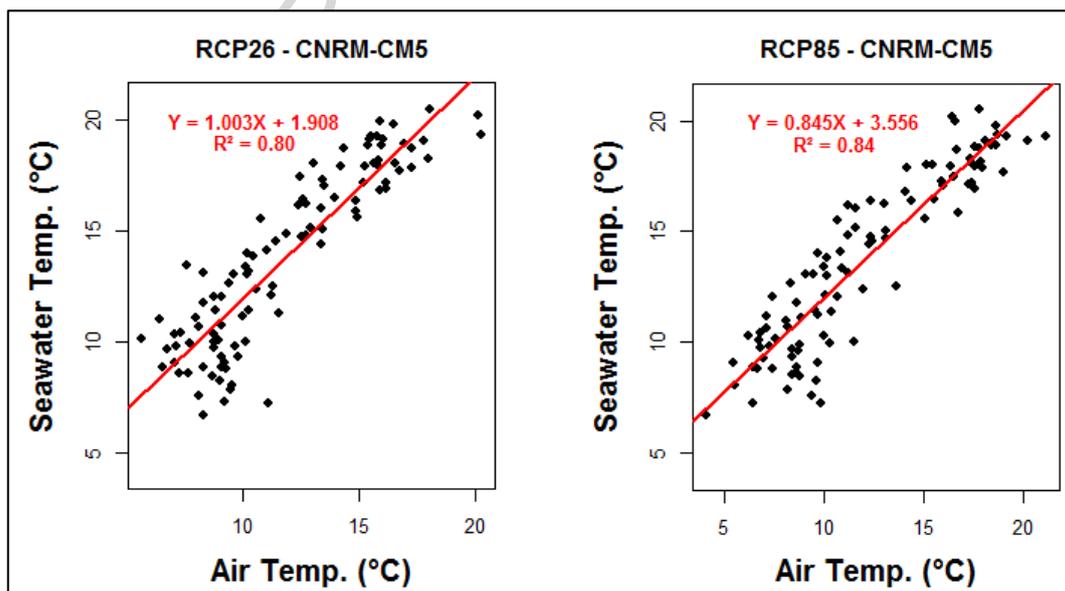
### 267 2.5.2. Climatic scenarios and forecasting approach

268 In order to study the potential effect of climate change on the reproductive cycle of *P.*  
 269 *maximus*, we used monthly time series of predicted atmospheric temperature ( $T_{Atm}$ ) from the RCP2.6  
 270 (i.e., an increase of 0.3 to 1.7°C) and RCP8.5 scenarios (a drastic increase of 2.6 to 4.8°C) from 2040  
 271 to 2100 (IPCC Representative Concentration Pathways, Appendix A). For each scenario, we converted  
 272  $T_{Atm}$  into SST by using linear regressions according to the following equation:

$$SST = a \times T_{Atm} + b$$

273 where  $a$  is a coefficient that estimates the determination coefficient,  $b$  is a coefficient that represents  
 274 the intercept (Fig. 4). To the best of our knowledge, no phytoplankton models or projections are  
 275 currently available for our sites. Therefore, we used the previously recorded time series of  
 276 phytoplankton, POM and microphytobenthos in the Bay of Brest from 1988 to 2003 (see previous  
 277 paragraph) as potential conditions in future scenarios (letters A to F were used to refer to the  
 278 phytoplankton concentrations observed from 1998 to 2003, respectively).

279 We analysed patterns in reproductive activity in the simulations performed under the RCP2.6 and  
 280 RCP8.5 scenarios. In each case,  $6 \times 20 = 120$  individual trajectories were simulated, with initial  
 281 conditions corresponding to initial L and DFM of a representative set of individuals sampled during  
 282 the 6-year monitoring program (see Scallop data in the results section).



283

284 Fig 4: Relations between monthly air temperature from the RCP scenarios and monthly seawater  
285 temperature in the Bay of Brest (from 2006 to 2014): on the left, monthly air temperatures on monthly  
286 seawater temperature under the RCP2.6 scenario with the CNRM-CM5 model; on the right, monthly  
287 air temperatures on monthly seawater temperature under the RCP8.5 scenario with the CNRM-CM5  
288 model.

## 289 2.6. Statistical analysis

290 To evaluate the best fit, mean simulations for each model (Mod-1, Mod-2A and Mod-2B) and  
291 mean observed data were compared using a Taylor diagram. This diagram provides a statistical  
292 summary of the agreement between a reference (observed data) and modelling results (Taylor, 2001).  
293 Three statistical measures are presented in the Taylor diagram: the centred root mean square (RMS)  
294 difference, normalized standard deviation, and Pearson's correlation coefficient. All statistical  
295 analyses were conducted in R version 3.3.3 (R Core Team, 2017).

## 296 3. Results

### 297 3.1. Contrasted environmental forcing conditions in the two study sites

298 Between 1998 and 2003, sea surface temperatures (SST) in the Bay of Brest reached a minimum  
299 of 8.3°C in February 1998 and a maximum of 22.1°C in July 2001 (Fig 3a). The overall annual mean  
300 was  $14.0 \pm 0.3^\circ\text{C}$ . The warmest year was 2001, with a yearly mean temperature of 14.5°C. This year  
301 also had the warmest summer, with a mean temperature of 18.4°C. The coldest year was 1998, with a  
302 yearly mean temperature of 13.7°C. The coldest summer was 2000, with a mean temperature of  
303 16.9°C. Phytoplankton concentration from 1998 to 2003 averaged 328,000 cell/L per year, with an  
304 intra-annual SD of 135,000 cell/L. Phytoplankton concentration showed a seasonal pattern, with  
305 maximum values in spring and summer and minimum values in winter (Fig 3a). The magnitude and  
306 timing of spring and summer blooms showed high inter-annual variability. For example, the spring  
307 bloom reached 5,000,000 cell/L in 2000, but the maximum phytoplankton concentration recorded in  
308 2002 was 600,000 cell/L. The bloom onset date also differed among years. The first bloom observed  
309 in 2000 (30,000 cell/L) occurred on 20 January, while it was observed on 25 February in 1998  
310 (206,000 cell/L).

311 The POM concentration showed similar patterns over the study period (Fig. 3a). However, larger  
312 peaks were observed in 1998, 2001 and 2003, at about 6,460,000 particles  $\text{L}^{-1}$ , compared with lower  
313 values of 3,640,000 particles  $\text{L}^{-1}$  in 1999, 2000 and 2002.

314 Microphytobenthos concentration showed two seasonal trends (Fig. 3b). The first pattern was  
315 observed in 2011 and 2013 with a large peak in spring and two smaller peaks in autumn and winter.  
316 The second pattern, observed in 2014, 2015, and 2016, showed a peak in early summer and two  
317 smaller ones in autumn and winter. The smallest number of microphytobenthic species ( $n = 22$ ) were  
318 identified in 2011 and a maximum of 67 species were identified in 2016. For the rest of the study, we  
319 used a mean profile of microphytobenthos computed by taking the average of all these observations  
320 (Fig. 3d).

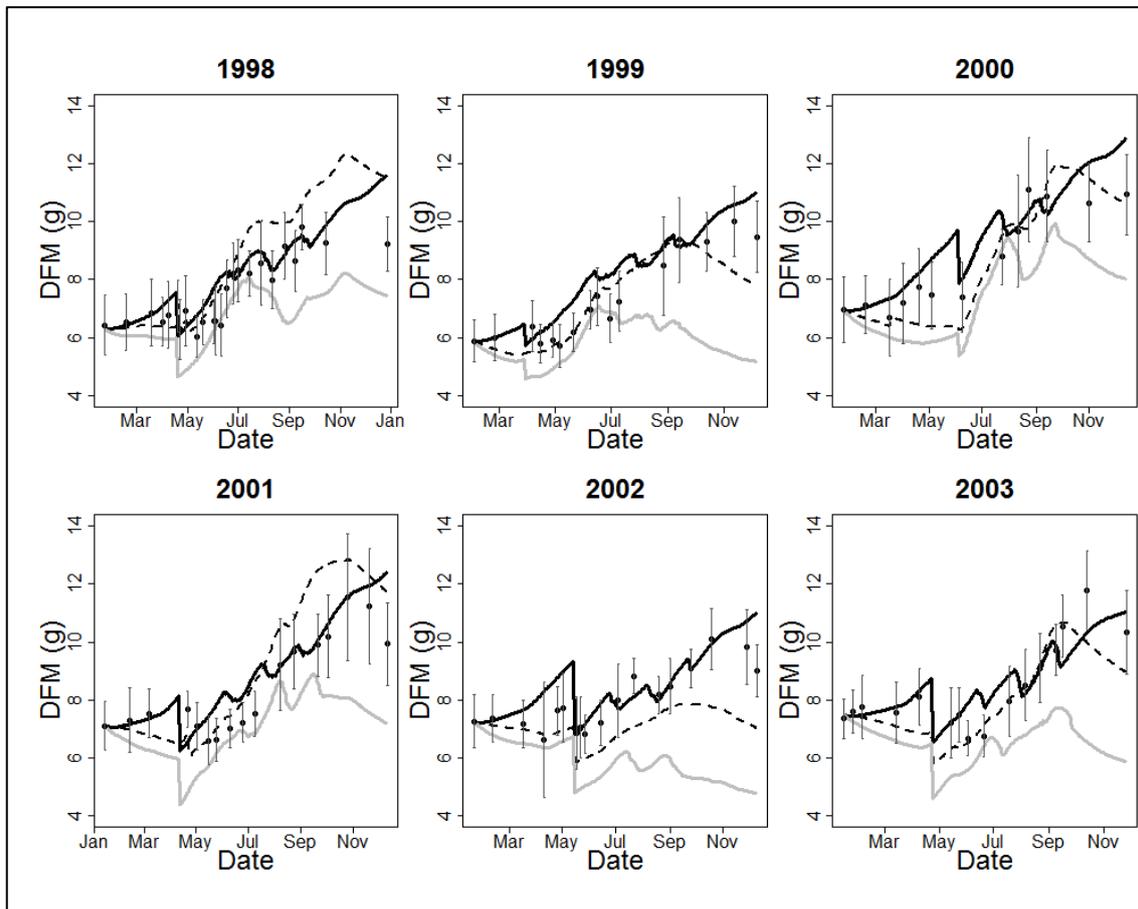
321 In the Bay of Saint-Brieuc, SST fluctuated between a minimum of 5.8°C in February 1998 and a  
322 maximum of 21.2°C in July 2001 (Fig. 3b), thus showing a greater range of variation than the Bay of  
323 Brest. The average SST was  $12.6 \pm 0.5^\circ\text{C}$ . The warmest year was 2003 with a mean temperature of  
324 13.6°C. This year also had the warmest summer with a mean temperature of 18.4°C. As in the Bay of  
325 Brest, the coldest year was 1998, with a mean temperature of 12.6°C, and 2000 was the coldest  
326 summer, with a mean temperature of 16.5°C.

327 Phytoplankton concentrations were maximal in spring and summer and minimal in winter (Fig  
328 3b). The annual phytoplankton concentration from 1998 to 2003 averaged  $40,764 \pm 4,990 \text{ cell L}^{-1}$ .  
329 Bloom intensities were lower than in the Bay of Brest, but the magnitude and timing appeared quite  
330 different from year to year. For example, the 2003 spring bloom peaked at  $1,187,000 \text{ cell L}^{-1}$ , while  
331 only reaching  $150,000 \text{ cell L}^{-1}$  in 2001. The earliest first bloom was observed in 1999, on April 1  
332 ( $114,000 \text{ cell L}^{-1}$ ), while the latest was observed in 2001, on May 14 ( $103,000 \text{ cell L}^{-1}$ ).

### 333 3.2. Comparing the DEB models

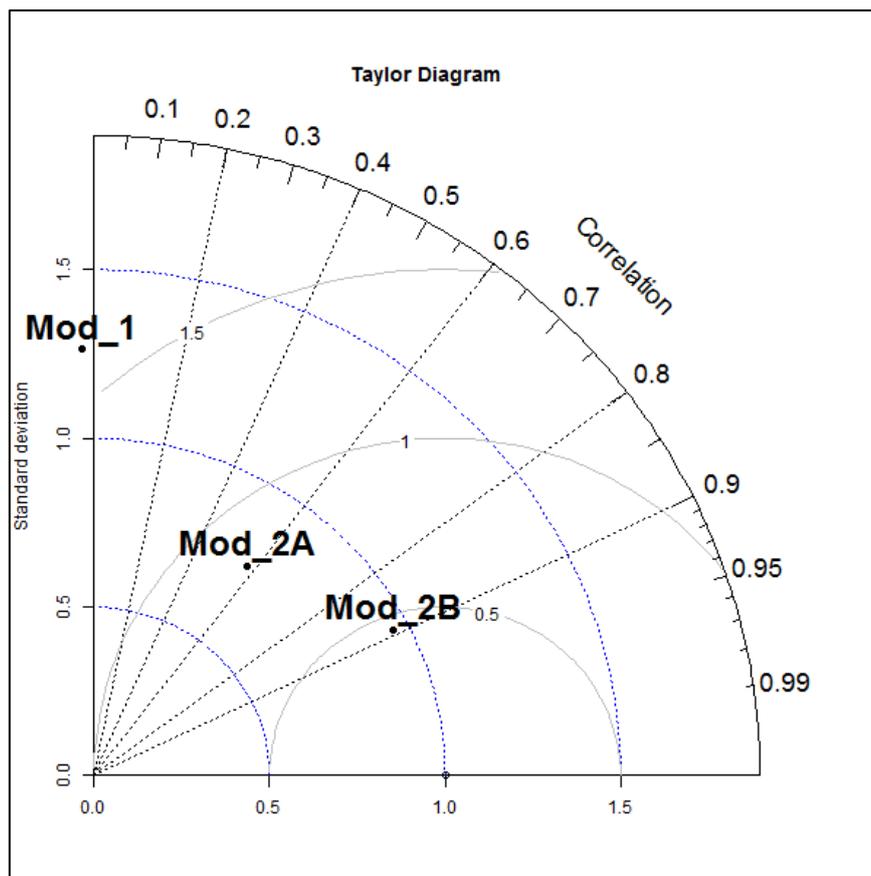
334 Simulations of dry flesh mass using model Mod-2A fitted the observations better than simulations  
335 from Mod-1 (Fig. 5). The addition of the fourth state variable  $E_{G_0}$  seemed to improve prediction of  
336 spawning events. Spawning events can be identified on each curve by a sharp decline in DFM. The  
337 spawning period was more pronounced using Mod-2A than with Mod-1. For example, under Mod-1,  
338 the first spawning occurred on May 11 in 1999 whereas it appeared March 28 under Mod-2A.  
339 However, neither model successfully reproduced the observed increase in DFM from March to May.  
340 On average, the difference between observed and simulated DFM values from January to May was  $\pm$   
341  $0.39 \text{ g}$  under Mod-1 and  $\pm 0.95 \text{ g}$  under Mod-2A. DFM modelled using Mod-2B was more accurate  
342 and the increase of DFM in spring fitted the observed data well ( $\pm 0.09 \text{ g}$  of difference). Similarly to  
343 Mod-2A, the spawning period was longer and more realistic than when using Mod-1. The addition of  
344 microphytobenthos to phytoplankton for *P. maximus* food intake allowed a better simulation of growth  
345 and reproductive activity, especially in the spring. For all years, model Mod-2B gave the best fit  
346 between observations and simulations of growth, with a mean correlation coefficient up to 0.9 and a

347 normalized standard deviation close to 1 (Fig. 6). Therefore, for the remaining part of this study, we  
 348 exclusively used model Mod-2B.



349

350 Figure 5: Mean observed ( $\pm$  SD,  $N = 20$ , black dots) and simulated ( $N = 20$ ) dry flesh mass (DFM)  
 351 of 3-year-old scallops in the Bay of Brest between 1998 and 2003, using Mod-1 (dotted black line),  
 352 Mod-2A (full grey line) and Mod-2B (full black line).



353

354 Figure 6: Taylor diagram presenting the normalized standard deviation, Pearson's correlation  
 355 coefficient and centred root mean squared difference (grey line) between simulated and observed dry  
 356 flesh mass. The average of the 6 years simulated with each model is shown by a black dot.

### 357 3.2. Simulation of reproductive activity

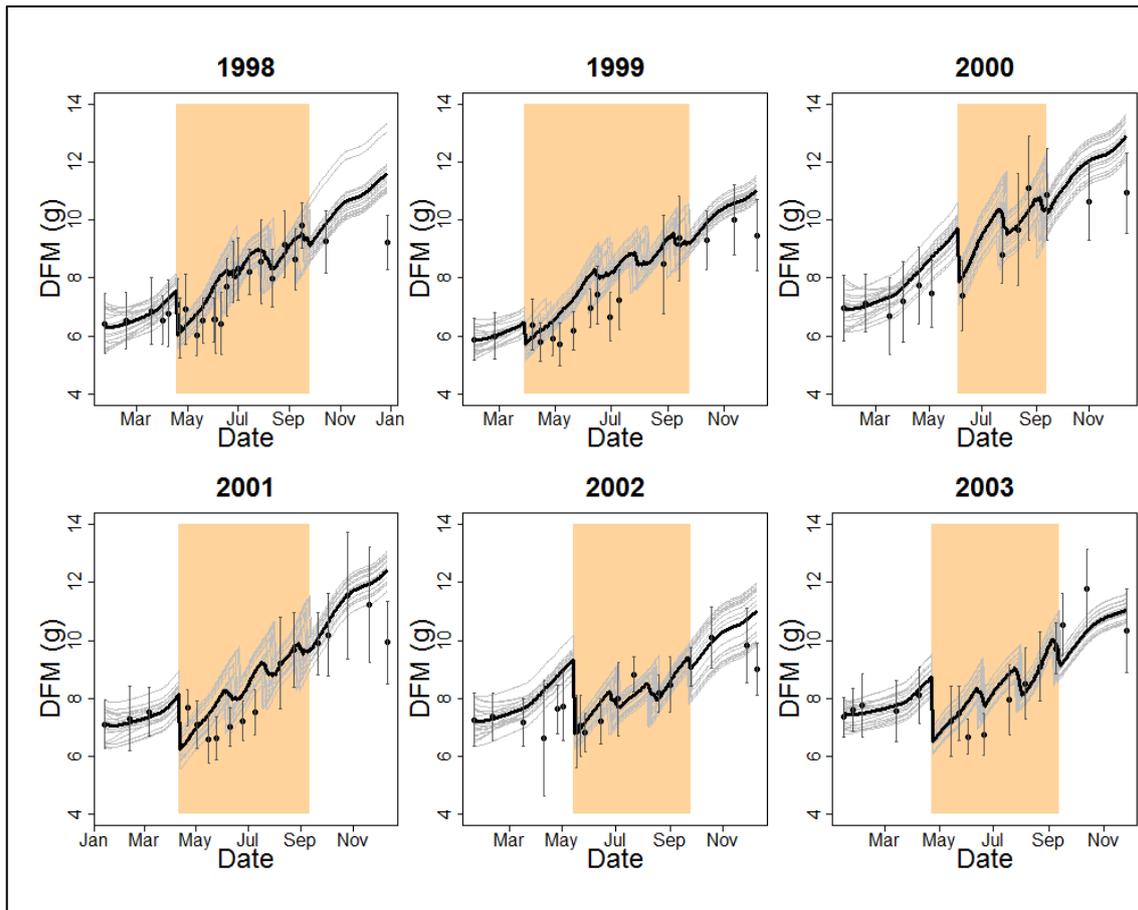
358 Simulations of individual DFM using Mod-2B in the two study areas highlighted three major  
 359 trends in scallop reproductive activity. Firstly, the number of spawning events per reproductive season  
 360 varies between years (Fig. 7). At least four spawning events were simulated for almost all individuals  
 361 in the Bay of Brest except in 2000, when there were only three major spawning events. This could be  
 362 because the phytoplankton threshold for spawning was only reached in June this year and the summer  
 363 seawater temperatures were colder (Fig. 3).

364 Secondly, the spawning period lasted from early spring to early autumn, corresponding to a wide  
 365 period of 4 to 6 months depending on the year. This temporal window was shorter in 2000 and 2002  
 366 (around 100 days) compared with 1998 and 1999 (above 150 days; Fig. 7). The interval between

367 spawning events (i.e. time for gametogenesis) ranged from 25 to 50 days. In the literature, spawning in  
368 *P. maximus* in the Bay of Brest was reported to span over a 6-month period with intervals of 20 to 50  
369 days (Paulet et al., 1995). Our simulations are in full agreement with these field observations, showing  
370 the ability of the model to accurately simulate energy allocation to reproduction and spawning events  
371 in *P. maximus*.

372 The third observed pattern was asynchronicity between individuals, observed every year following  
373 the first synchronous spawning (except in 1999 when asynchronicity was also observed for the first  
374 spawning event). For instance, in 2003 spawning occurred in all individuals within 8 days while in  
375 1999 it took 29 and 26 days for all the individuals to spawn during the first and fourth spawning  
376 events, respectively.

377 In comparison with results obtained for the Bay of Brest, only two clear spawning events were  
378 observed in the Bay of Saint-Brieuc (Fig. 8). Furthermore, in 2000, only 22% of individuals spawned  
379 twice. The spawning period was much shorter (~50 days) and only occurred in summer. The first  
380 spawning event was mainly synchronous between individuals, except in 1999. In contrast, the second  
381 spawning event was mainly asynchronous but the temporal window did not exceed 15 days.



382

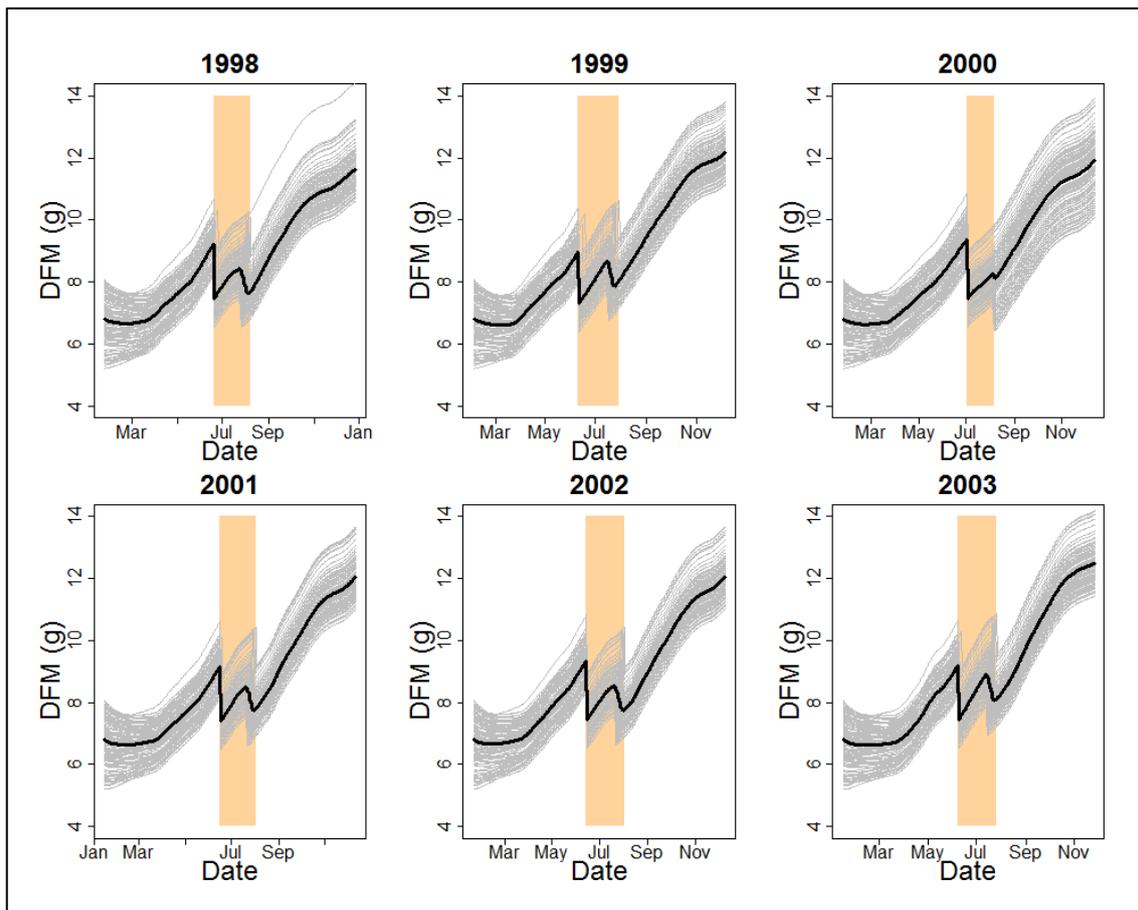
383 Figure 7: Mean observed ( $\pm$  SD,  $N = 20$ , black dots) and simulated ( $N = 20$ , thick black line) dry

384 flesh mass (DFM) of 3-year-old scallops in the Bay of Brest between 1998 and 2003 using Mod-2B.

385 Individual growth trajectories of the 20 scallops simulated are indicated by grey lines. The orange area

386 shows the spawning period.

387



388

389 Figure 8: Individual (grey lines) and mean simulated ( $N = 120$ , thick black line) dry flesh mass  
 390 (DFM) of 3-year-old scallops in the Bay of Saint-Brieuc in 1998–2003 using Mod-2B. The orange  
 391 area shows the spawning period.

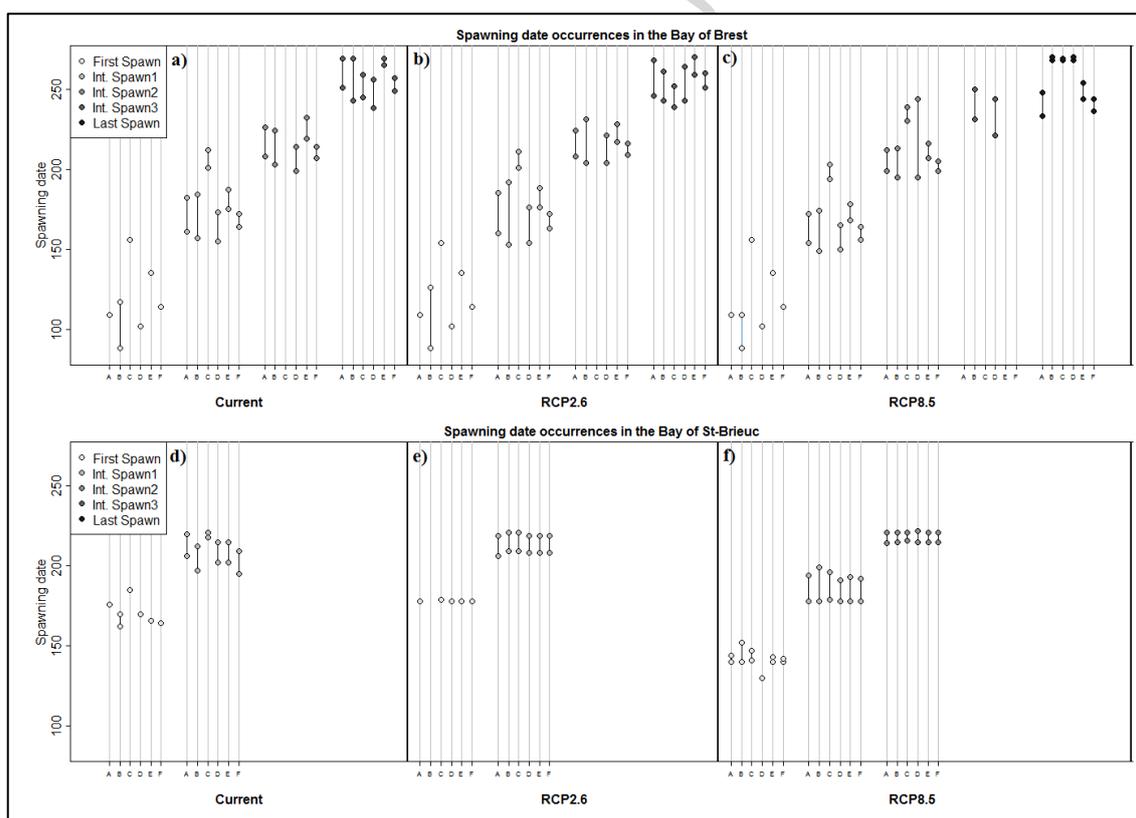
### 392 3.3. Simulating reproductive activity of *P. maximus* in a warming ocean

393 In order to evaluate the impacts of climate change on the reproduction of *P. maximus* off the coast  
 394 of Brittany, we simulated DFM in two extreme cases: the RCP2.6 scenario (an increase of 0.3 to  
 395 1.7°C) and the RCP8.5 scenario (a drastic increase of 2.6 to 4.8°C) and six phytoplankton conditions  
 396 (scenarios A to F).

397 In the Bay of Brest, under the RCP2.6 scenario, spawning dates were similar to current  
 398 observations and no change in the individual spawning strategies were observed (Fig. 9a-b). Under the  
 399 RCP8.5 scenario, we observed a decrease of the interval between spawning events after the first one  
 400 except with phytoplankton regime D during the third spawning event (Fig. 9a-c). The second and third  
 401 spawnings occurred 5 and 10 days earlier, respectively, under phytoplankton regimes C and E, and the

402 fourth spawning occurred 20 days earlier under phytoplankton regimes B, D and F. Finally, more  
 403 spawning occurred in autumn with a higher number of individuals spawning four to five times.

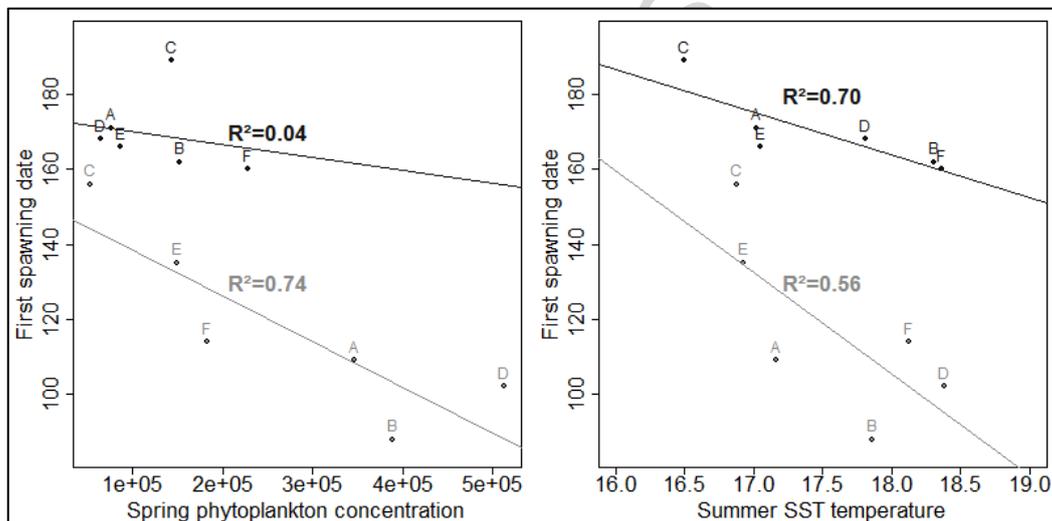
404 Spawning events were less frequent in the Bay of Saint-Brieuc than in the Bay of Brest in both  
 405 temperature scenarios. Under the RCP2.6 scenario, two spawning events were observed as in the  
 406 simulation of the current situation (Fig. 9d-e). In contrast, under RCP8.5 scenario, a third spawning  
 407 event appeared every year (Fig. 9f). Moreover, spawning occurred 30 to 48 days earlier depending on  
 408 the phytoplankton scenario. The spawning period was slightly shorter under the RCP2.6 scenario  
 409 (around 40 days), while it was longer under the RCP8.5 scenario, reaching 80 days. Furthermore,  
 410 asynchronicity between individuals was only observed under the RCP8.5 scenario, especially during  
 411 the second spawning event.



412  
 413 Figure 9: Simulated spawning date (Int. = Intermediate) in the Bay of Brest (a to c) and Bay of  
 414 Saint-Brieuc (d to f) under three temperature scenarios (current, RCP2.6 and RCP8.5) and six  
 415 phytoplankton regimes (A to F, corresponding to conditions in years 1998 to 2003). The lines between

416 two points represent the asynchronicity between individuals with the first and last spawning date  
 417 within a population.

418 Last, we found two significant relationships, between the date of the first spawning event and  
 419 spring phytoplankton concentrations on one hand and summer SST (mean value) on the other (Fig.  
 420 10). The date of the first spawning event was significantly inversely correlated with summer SST in  
 421 the Bay of Saint-Brieuc (Fig. 10, linear regression:  $r^2 = 0.70$ ,  $p < 0.05$ , slope =  $- 11 \text{ d } ^\circ\text{C}^{-1}$ ). In the Bay  
 422 of Brest, the date of the first spawning event was significantly inversely correlated with the spring  
 423 phytoplankton bloom concentration (Fig. 10, linear regression:  $r^2 = 0.74$ ,  $p < 0.05$ , slope =  $- 1.22 \cdot 10^{-4} \text{ d}$   
 424  $\text{cell L}^{-1}$ ).



425

426 Figure 10: Relationships between environmental conditions (left: spring phytoplankton  
 427 concentration; right: summer SST temperature) and the first spawning date in the Bay of Brest (grey)  
 428 and in Bay of Saint-Brieuc (black) for the six phytoplankton regimes (A to F).

429

## 4. Discussion

430

431 The main objective of this study was to quantify the influence of environmental variables  
432 (temperature and food sources) on the reproductive processes of the great scallop, *P. maximus*, and  
433 explore the potential impacts of climate change on its dynamics. We improved an existing scallop  
434 DEB model developed by Lavaud et al. (2014) by detailing the reproductive processes and by adding  
435 microphytobenthos as a new food source.

436 In order to improve the DEB model for *P. maximus*, a fourth state variable was added to describe  
437 the fixation of energy in gametes, as done by Bernard et al. (2011) for the Pacific oyster, *Crassostrea*  
438 *gigas*. Furthermore, the maximum possible shell length was assumed to be 20 cm rather than the  
439 previous assumption of 12 cm, since studies have shown that adult scallops can reach 16 cm in the  
440 most favourable conditions (Mason, 1957; Chauvaud et al., 2012) and thus the ultimate length would  
441 presumably be above 16 cm. This led to the recalculation of three model parameters:  $\{p_{Am}\}$ ,  $[p_M]$  and  
442  $\kappa$ . The new values obtained are different from the previous version in Lavaud et al. (2014), particularly  
443  $\kappa$ . The previous value, fixed at 0.86, was high compared with other bivalve species. For instance, the  $\kappa$   
444 value for *Crassostrea gigas* is around 0.45. Considering that, in some environments, *P. maximus* could  
445 spawn more than three times within the same reproductive season and that its gonad represents more  
446 than 30 % of the whole flesh weight at maturity, it seems logical that this species would have a high  
447 energy allocation ratio (and thus a low value for  $\kappa$ ) similarly to *C. gigas*. Considering this, the new  
448 value calculated here is probably more consistent with the reproductive capacity of *P. maximus*. These  
449 changes do not fundamentally alter the dynamics of the model, but allow more spawning events and  
450 higher fecundity than other versions of the model. Of course, further testing in other locations with  
451 contrasted forcing conditions as well as with younger age-classes would also be needed to fully  
452 validate this updated version of the scallop DEB model.

453 Another improvement made in the current model concerns trophic resources. Microphytobenthos  
454 was added as a new source of food for scallops. Previously, Lavaud et al. (2014) demonstrated that  
455 POM constitutes an additional food source allowing scallops to compensate phytoplankton limitation.  
456 In addition, our study suggests that microphytobenthos would probably also be a valuable source of

457 food that could sustain energy acquisition, especially in spring. For the moment, the taxonomic  
458 composition of each food source is not detailed in the model, but several studies have shown  
459 relationships between specific phytoplankton species and life history traits of the great scallop in  
460 Brittany. For example, Chauvaud et al. (1998, 2001) showed, in the Bay of Brest, that growth and food  
461 intake of *P. maximus* were dependent on phytoplankton taxonomic composition and concentration.  
462 The related growth cessation depended on massive sedimentation of diatom blooms or toxic  
463 dinoflagellate blooms. For example, *P. maximus* food intake and growth were highest when  
464 *Cerataulina pelagica* blooms occurred and lowest during *Gymnodinium nagasakiense* blooms. In  
465 addition, Lorrain et al. (2000) demonstrated that large bottom concentrations of chlorophyll-*a*,  
466 following diatom blooms, could have a negative effect on the ingestion or respiration of *P. maximus*  
467 juveniles, either by gill clogging or by oxygen depletion at the water-sediment interface associated  
468 with the degradation of organic matter. The current version of the DEB model does not take into  
469 account these specific effects which are linked to the type of food that is available. However the  
470 current model provides the basis for taking them into consideration in future studies.

471 One major difficulty with a modelling approach is to obtain a sufficient dataset to calibrate, test  
472 and validate a numerical model. When using a bioenergetics model, this implies monitoring growth  
473 and reproduction of marine organisms and their surrounding environmental data, at the same place and  
474 ideally over a long period (many years) to evaluate temporal phenotypic variability. In our study, the  
475 Bay of Brest sampling sites (St Anne, Roscanvel, Lanvéoc) are not closed off from each other but are  
476 instead located in a very well mixed area within the Bay of Brest (Salomon and Breton, 1991) where  
477 scallops are the most abundant. So we can suppose that environmental data are sufficiently  
478 representative of conditions encountered by scallops. In the Bay of Saint Brieuc, there is no growth  
479 monitoring of scallops and there are too many gaps in the environmental data to apply the model in a  
480 satisfactory manner. Our approach is therefore limited but it offers a first application of the model to  
481 this new environment and constitutes a stepping-stone for further development of the modelling  
482 approach for this bay.

483 Other limitations of our model that should be mentioned are its systematic overestimation of  
484 growth during the autumnal period and an insufficient integration of inter-individual variability. The  
485 systematic tendency to overestimate growth could be due to a change in the physiology of scallops at  
486 the end of the reproductive season and period leading into winter. Specific ecophysiological  
487 experiments should be developed to address this question and improve the model. For the moment, we  
488 have applied an individual-based modelling strategy by introducing variability between individuals  
489 through the initial condition values. To account for more variability in physiological traits, similar  
490 studies, e.g. Thomas et al. (2015) and Bacher and Gangnery (2006) used specific model  
491 parameterization of the ingestion function for each individual. For instance,  $X_k$  values were allocated  
492 to each individual following a Gaussian distribution. It would now be interesting to adapt a similar  
493 approach to the scallop DEB model.

494 Quantitative modelling of reproductive processes (preliminary storage phase, gametogenesis,  
495 spawning and/or resorption) is not easy as these processes are typically species-specific. There are no  
496 general rules on how to handle reproductive activity in DEB theory, especially regarding reproduction  
497 buffer dynamics. Bernard et al. (2011) introduced a fourth state variable in order to improve modelling  
498 of reproduction dynamics in the Pacific oyster, *Crassostrea gigas*. Numerous marine organisms from  
499 temperate waters spawn once or twice at a relatively fixed time each year (Gosling, 2004). For *P.*  
500 *maximus*, however, reproductive activity is more complex, with asynchronous spawning during a  
501 highly variable reproductive window. For this preliminary approach, however, we made the  
502 assumption that the mechanisms governing reproductive activity would be quite similar among  
503 bivalves and thus between oysters and scallops.

504 The reproductive cycle of *P. maximus* has been studied extensively in many places (e.g. Magnesen  
505 and Christophersen, 2008). Concerning our studied area, contrasting patterns were shown between the  
506 Bay of Brest and Bay of Saint-Brieuc (Paulet et al., 1995). Scallops in the Bay of Brest usually spawn  
507 between April and October, with a massive first spawning in April followed by a second maturation  
508 phase until July characterized by one or several smaller spawning events. A third summer maturation  
509 phase leads to a last major spawning event during August (Paulet et al., 1995). A late spawning event

510 may be observed in autumn, but only in a few individuals (Saout et al., 2000). In the Bay of Brest, this  
511 seasonal cycle varies strongly between individuals, resulting in a lack of synchronism (Paulet et al.,  
512 1995). The results from our simulations, obtained over six years in the Bay of Brest, correspond fairly  
513 well to this description. More precisely, the model was able to partly simulate the observed  
514 asynchronicity between individuals, and the mechanisms implemented to trigger spawning appeared to  
515 be sufficiently relevant to simulate the onset of the first spawning, the temporal spawning window,  
516 and the number of spawning events (Fig. 6).

517 In the Bay of Saint-Brieuc, scallops only spawn from June until mid-August (Paulet et al., 1988;  
518 Paulet, 1990). Moreover, the seasonal cycle is known to be similar between individuals, showing a  
519 higher synchronism in this area than in the Bay of Brest (Paulet et al., 1988). Of course, the  
520 application of our model in the Bay of Saint-Brieuc is only a first attempt and suffers from a lack of  
521 forcing data. Nevertheless, it seems that the current version of the model was able to reproduce the  
522 different patterns of the reproductive cycle of *P. maximus* observed in this area. This tends to confirm  
523 that the environmental factors used here are the main key-drivers of reproduction processes of *P.*  
524 *maximus*.

525 Despite its limitations, our modelling study suggests that differences in the timing of spawning  
526 events might be explained mainly by environmental differences in food and temperature. Among  
527 invertebrates, there is much evidence for the influence of exogenous factors (e.g. temperature, food  
528 and photoperiod) on the progress of gametogenesis and for regulation by endogenous rhythms on  
529 which environmental signals may act as synchronizers (e.g. Mat et al., 2014). Many environmental  
530 variables trigger such regulation but, most often, temperature and food availability (Franco et al.,  
531 2015; Ubertini et al., 2017) are considered to be the key factors. This is the case for bivalves,  
532 particularly pectinids (Lavaud et al. 2014). Scallops are sublittoral, epifaunal and active suspension-  
533 feeding bivalves that rely on suspended detrital material, phytoplankton and microphytobenthos as  
534 their main food sources (Robert et al., 1994; Chauvaud et al., 2001). Saout et al. (1999) showed that,  
535 in *P. maximus*, a simultaneous increase of temperature and photoperiod enhanced gonad growth when  
536 food is not limiting. However, it was still not clear which of these two factors is the more influential.

537 Our results obtained in the Bay of Brest show that, within a temporal photoperiod window, spawning  
538 is mainly triggered mainly by phytoplankton blooms once the GSI threshold is reached. In this  
539 eutrophic area, temperature might play a secondary role in terms of triggering spawning. For instance,  
540 in 2000 and 2002, the first bloom of the year was late compared with the other years (June 3 and May  
541 14, respectively; Fig. 3). Accordingly, for both years, the model simulated a later occurrence of first  
542 spawning (June 4 and May 15, respectively; Fig. 7) that fitted well with field observations. By  
543 comparison, blooms of phytoplankton in the Bay of Saint-Brieuc were much lower than those  
544 observed in the Bay of Brest and presumably not a source of stress. Values were always below the  
545 threshold for triggering spawning. In this new environment, phytoplankton blooms were presumably  
546 not the trigger for spawning. Based on previous studies, we basically used a temperature threshold in  
547 this environment (Fifas, 2004) and the simulations obtained were in accordance with spawning  
548 processes observed in this bay.

549 In the last part of this study, we explored the potential consequences of climate change for the  
550 reproductive activity of *P. maximus* in northern Brittany. Predicting the temperature of the future  
551 atmosphere and oceans has been a focus of research for a few decades now. The evolution of food  
552 supply to organisms, which in the ocean starts with phytoplankton, is comparatively less well  
553 understood or predictable. Although the reliability of ocean primary production models is continually  
554 improving, predicting the future is challenging (Gradinger et al., 2009; Lavoie et al., 2017) for coastal  
555 environments. In this context, we believe that our approach, consisting of transposing current food  
556 availability time series to future scenarios, is valuable because it allows a greater degree of complexity  
557 in predictions as it provides realistic estimates of inter-annual variability. This approach could be  
558 complemented by simulations under enhanced phytoplankton productivity, as predicted by recent  
559 modelling (Jensen et al., 2017). Only the most extreme scenario (RCP8.5) revealed contrasting  
560 predictions with the current one. While distinct reproductive cycles are currently observed between the  
561 Bay of Brest and the Bay of Saint-Brieuc, it seems that future environmental conditions would  
562 generally extend the spawning period, with an additional spawning event predicted in both locations.  
563 However, contrasted impacts also emerged when comparing simulations obtained for the two bays. An

564 increase in seawater temperature advanced the onset of spawning by 20 to 44 days in the Bay of Saint-  
565 Briec, irrespective of the phytoplankton scenario, while the spawning timeline in the Bay of Brest  
566 was unchanged. Warmer temperatures might also lead to better recruitment. Shephard et al. (2010)  
567 found that the mean annual recruitment of young scallops in the Isle of Man was positively related to  
568 spring water temperature. Adult gonads were also larger, indicating higher egg production during  
569 warmer years. Our simulations led to similar conclusions, showing that an increase in seawater  
570 temperature combined with adequate food supply could well enhance scallop recruitment by: (1)  
571 increasing the spawning window in late summer and (2) advancing the onset of spawning in spring in  
572 the Bay of Saint-Briec.

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573 **Acknowledgements**

574 A grant from *Région Bretagne* and the University of Western Brittany (UBO) supported MG  
575 during her PhD work. The authors are grateful to the IUEM staff of the EVECOS networks, the  
576 IFREMER staff of the REPHY network and the staff of the SOMLIT network, through which all the  
577 field data were gathered. We also thank Helen McCombie-Boudry of the Translation Bureau of the  
578 University of Western Brittany for improving the English of this manuscript.

579

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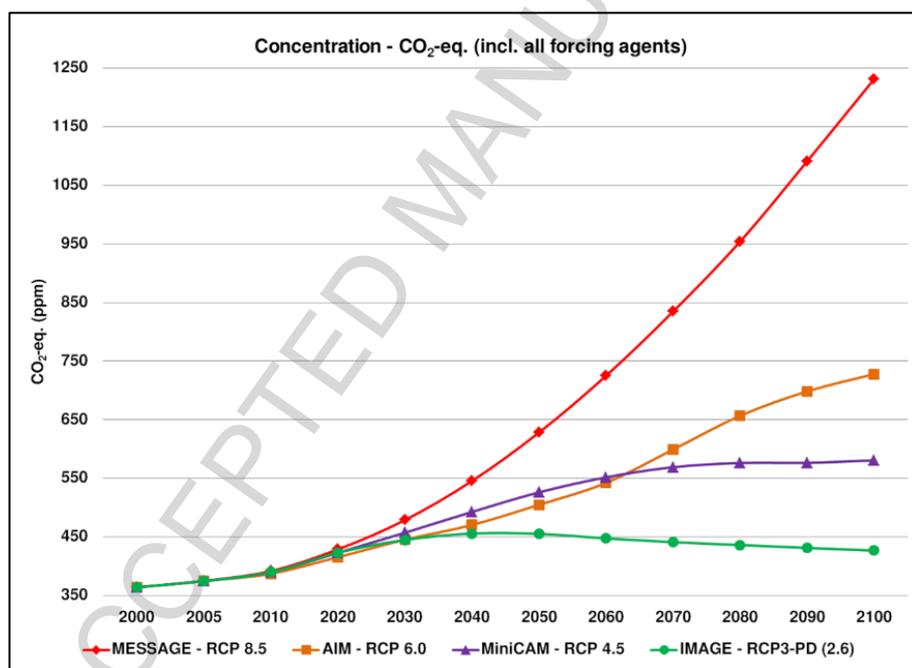
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732

733 **Appendix**

734 **Appendix A:** Details on climatic projections models used and additional figures (Fig. A.1 and A.2)  
 735 and tables (Table A.1 and A.2).

736 In this study we used temperature scenarios resulting from Representative Concentration Pathways  
 737 (RCP) models, the latest generation of scenarios that provide inputs to climate models. The purpose of  
 738 using scenarios is not to predict the future, but to explore both the scientific and real-world  
 739 implications of different plausible futures (van Vuuren et al., 2011). The IPCC authors chose four  
 740 carbon dioxide (CO<sub>2</sub>) emission trajectories to focus on and labeled them based on how much heating  
 741 they would result in at the end of the century: 2.6, 4.5, 6 and 8.5 watts per square meter (W m<sup>-2</sup>). Fig.  
 742 A.1 shows the annual CO<sub>2</sub> emissions (in billions of tons of carbon) until 2100 for each of the RCPs.



743  
 744 Fig. A.1: Emissions of annual CO<sub>2</sub> across the RCPs. The RCP2.6 scenario (IMAGE-RCP3-PD(2.6))  
 745 and the RCP8.5 scenario (MESSAGE-RCP8.5) represent extreme situations: RCP2.6 is the most  
 746 optimistic and RCP8.5 is the most drastic warming. Source: IPCC Fifth Assessment Report (2014).

747 In the 2.6 W m<sup>-2</sup> scenario (RCP2.6), greenhouse-gas emissions drop to zero by about 2070, and  
 748 then continuing to fall, so that the world's emissions would become negative — actually withdrawing  
 749 greenhouse gases from the air and locking them away — for decades. This pushes the bounds of what

750 is plausible through mitigation, some experts say. At the high end, in the  $8.5 \text{ W m}^{-2}$  scenario  
 751 (RCP8.5),  $\text{CO}_2$  levels would soar beyond 1,300 parts per million by the end of the century and  
 752 continue to rise rapidly (Table A.1).

753 Table A.1: Description of  $\text{CO}_2$  emissions scenarios used by IPCC authors (van Vuuren et al., 2011).

Scenario	Description
RCP8.5	Rising radiative forcing pathway leading to $8.5 \text{ W m}^2$ ( $\sim 1370 \text{ ppm CO}_2 \text{ eq}$ ) by 2100.
RCP6	Stabilization without overshoot pathway to $6 \text{ W m}^2$ ( $\sim 850 \text{ ppm CO}_2 \text{ eq}$ ) at stabilization after 2100.
RCP4.5	Stabilization without overshoot pathway to $4.5 \text{ W m}^2$ ( $\sim 650 \text{ ppm CO}_2 \text{ eq}$ ) at stabilization after 2100.
RCP2.6	Peak in radiative forcing at $\sim 3 \text{ W m}^2$ ( $\sim 490 \text{ ppm CO}_2 \text{ eq}$ ) before 2100 and then decline (the selected pathway declines to $2.6 \text{ W m}^2$ by 2100).

754 Atmospheric temperature data were obtained from the CERFACS modeling center. For each  
 755 scenario (RCP2.6 and RCP8.5) 14 models were available ([http://cmip-  
 756 pcmdi.llnl.gov/cmip5/availability.html](http://cmip-pcmdi.llnl.gov/cmip5/availability.html); Table A.2). To know which model was the most comparable  
 757 to our historical temperature data in the Bay of Brest and the Bay of Saint Briec, we used the diagram  
 758 of Taylor (Fig. A.2) in order to compare monthly air temperature since 1960 to nowadays in our bays  
 759 with monthly air temperature from the 14 models during the same period. Among the 14 models, the  
 760 CNRM-CM5 model was the best (Fig. A.2).

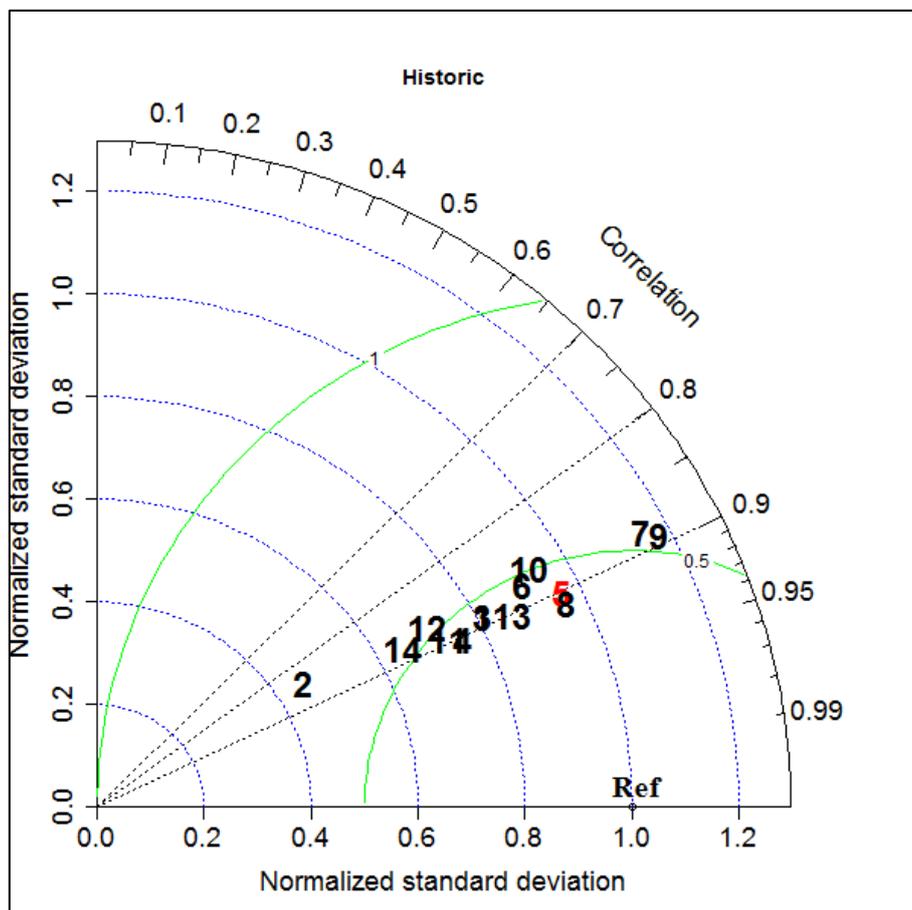
761 Table A.2: Description of the 14 models available for the study.

Modeling Center	Model	N°	Institution
BCC	BCC-CSM1.1	1	Beijing Climate Center
CCCma	CanESM2	2	Canadian Centre for Climate Modelling and Analysis
NCAR	CCSM4	3	National Center for Atmospheric Research
NSF-DOE-NCAR	CESM1(CAM5)	4	National Science Foundation, Department of Energy, National Center for Atmospheric Research
CNRM-CERFACS	CNRM-CM5	5	Centre National de Recherches Météorologiques / Centre Européen de Recherche et Formation Avancées en Calcul Scientifique
LASG-IAP	FGOALS-g2	6	LASG, Institute of Atmospheric Physics
NOAA GFDL	GFDL-CM3	7	Geophysical Fluid Dynamics Laboratory
INPE	HadGEM2-ES	8	Instituto Nacional de Pesquisas Espaciais
IPSL	IPSL-CM5A-LR	9	Institut Pierre-Simon Laplace
	IPSL-CM5A-MR	10	
MPI-M	MPI-ESM-LR	11	Max Planck Institute for Meteorology

	MPI-ESM-MR	12	
MRI	MRI-CGCM3	13	Meteorological Research Institute
NCC	NorESM1-M	14	Norwegian Climate Centre

762

763



764

765 Fig. A.2: Taylor diagram giving the Pearson's correlation coefficient, the centered root mean squared  
 766 difference and the normalized standard deviation between historical air temperature observed in the  
 767 Bay of Brest since 1960 (Ref) and air temperature predicted by 14 different models (see Table above;  
 768 N°1 to N°14).

769