
The growth of the banded carpet shell (*Paphia rhomboïdes*) in a contrasted region, the English Channel (Western Europe): A modelling study

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Abstract:

Paphia rhomboïdes is an infaunal filter-feeding bivalve, particularly widespread and abundant in the English Channel. In order to investigate the influence of the growth-related post-settlement processes on its distribution, a spatial growth model was developed and linked to an existing ecological model of the English Channel. This model was partially parameterized on the basis of a specific ecophysiological experimental study, and calibrated with growth data collected in the "Golfe Normand-Breton" (GNB), a region of the English Channel. Compared to the actual distribution of *P. rhomboïdes*, the results suggest a strong influence of the growth-related processes on the distribution of the species: particularly, the extremely low growth obtained with the model in the Western Channel can explain the almost complete absence of the species in this area.

Keywords: *Paphia rhomboïdes*; English Channel; Growth model; Ecophysiology; Meroplanktonic invertebrates distribution

17 **1 Introduction**

18 Diversity and abundance of the benthic fauna in the English Channel has favoured the
19 development of fisheries, particularly those of shellfish: scallop, warty venus, common
20 cockle, dog cockle, banded carpet shell, surf clam (Berthou, 1983; Lemoine et al., 1988;
21 Fifas, 1991; Noël et al., 1995). It has also attracted the interest of scientists: large scientific
22 programs were carried out in the seventies (Holme, 1966; Cabioch, 1968; Cabioch and
23 Glaçon, 1975 and 1977; Gentil, 1976; Cabioch et al., 1977; Retière, 1979) to study benthos
24 distribution in the area, as well as the environmental factors controlling it.

25 Among the main listed bivalves, the banded carpet shell (*Paphia rhomboïdes*) -a subtidal
26 infaunal filter-feeding species- is particularly widespread in the English Channel and in the
27 central part, i.e., the “Golfe Normand-Breton”, where, in terms of biomass, it is one of the
28 most abundant species (Holme, 1966; Retière, 1979; Blanchard, 1982; Blanchard et al., 1983).
29 Because it is a targeted species (Berthou, 1985, 1987 and 1989; Noël et al. 1995) and
30 extensive scientific data have been collected describing its distribution, biology and ecology
31 (Holme, 1966; Cabioch, 1968; Lucas, 1969; Chassé and Glémarec, 1973; Gentil, 1976;
32 Glémarec and Bouron, 1978; Retière, 1979; Blanchard, 1982; Blanchard et al., 1983 and 1986
33 a and b; Morvan, 1987; Morin 1998), this species is of particular interest for studying the
34 distribution of meroplanktonic invertebrates in the English Channel.

35 The importance of post-recruitment processes in the spatial distribution of the benthic-
36 meroplanktonic bivalves is generally accepted (Thouzeau, 1989; Young et al., 1998; Bhaud,
37 2000). Thus, successful larval transport by currents, and even successful larval settlement on
38 the substratum, are not necessarily followed by the continuation of the life cycle and the
39 development of adulthood (Bhaud, 2000).

40 Post-recruitment structuring processes could be classified into two groups:

41 (1) Direct mortality factors, such as predation, human harvesting, or indirect mortality factors
42 such as mechanical disturbance, due to turbulence or dredging, which can be responsible for
43 an enhanced predation;

44 (2) Parameters which influence the physiological state and growth of animals (temperature,
45 food, inorganic seston, turbulence). These may influence the bivalve mortality rate, directly
46 (physiological distress) or indirectly (slow growth, smaller individuals being supposed to be
47 more vulnerable than bigger ones), and also influence the fertility of bivalves since their
48 reproductive investment depends on their size and growing conditions (Héral and Deslous-
49 Paoli, 1983; Urrutia et al., 1999; Pouvreau et al., 2000 b).

50 In the present study, we focused on the latter group of post-recruitment structuring processes
51 with an ecophysiological modelling approach.

52 Since the beginning of the 1990s, ecophysiological (or growth) models of filter-feeding
53 molluscs have become more numerous (Bensch et al., 1991; Raillard et al., 1993; Barillé,
54 1996; Kobayashi et al., 1997; Campbell and Newell, 1998; Grant and Bacher, 1998; Scholten
55 and Smaal, 1998; Pouvreau et al., 2000 a; Solidoro et al., 2000; Cardoso et al., 2001; Ren and
56 Ross, 2001; Hawkins et al., 2002). The objectives are usually to improve the aquaculture
57 techniques and management through a better understanding of processes which drive the
58 growth of the different cultivated species. To our knowledge, growth models have never been
59 used to investigate the spatial distribution of filter-feeding molluscs. In addition, a review of
60 these previously cited models bring the following observations:

61 (1) The great majority of published models are only used in a given environment with a
62 limited extension (trophic and climatic characteristics). Only a few teams have tried to
63 transpose their model to various regions (Grant et Bacher, 1998; Scholten and Smaal, 1998;
64 Ren and Ross, 2001).

65 (2) Individual growth is generally simulated during periods which range from 9 months
66 (Kobayashi et al., 1997; Grant and Bacher, 1998) to 3 years (Solidoro et al., 2000), i.e., during

67 only a part of their life. Only a few studies considered the whole life of the studied bivalve
68 (e.g., Cardoso et al., 2001).

69 (3) Most models have focussed on epibenthic species, and furthermore these species are often
70 located within the water column (on “tables” or as suspended culture on ropes hung from
71 longlines or rafts). Interest for infauna species is more recent (Solidoro et al., 2000; Cardoso
72 et al., 2001).

73 The complexity of these models depends on their objectives and the available data, but they
74 are all based on the following equation:

$$75 \quad \frac{dW}{dt} = \text{nutrition}(t) - \text{respiration}(t) - \text{reproduction}(t)$$

76 where W is the global soft bodies weight of the considered shellfish (either fresh or dry or ash free dry)

77 The soft bodies weight can be considered as a global state variable (Grant and Bacher, 1998;
78 Solidoro et al., 2000), or several compartments can be considered, such as shell (inorganic
79 and organic content), reserve compartments, gonad, which implies the formulation of transfer
80 processes between these compartments (e.g., Kobayashi et al., 1997; Cardoso et al., 2001;
81 Hawkins et al., 2002). More detailed models consider not only the weight of the different
82 flesh compartments but also their carbohydrates, lipid and protein content (e.g., Barillé,
83 1996).

84

85 In the present study, a relatively simple growth model is designed for *P. rhomboïdes*,
86 considering their whole benthic life. This model is first tested and used in the Golfe Normand-
87 Breton region, where we collected data, and then extended to the whole English Channel to
88 investigate the potential importance of the ecophysiological processes in the distribution of
89 the species.

90

90 **2 Material and method**

91 **2.1 The background model**

92 A physical box-model has been developed for the English Channel (Ménèsquen and Hoch,
93 1997) and coupled to a biogeochemical model (Hoch, 1998), using the ELISE software
94 (Ménèsquen, 1991). The physical sub-model of the Channel is divided into 71 boxes or
95 compartments (**figure 1**) with water flows between them calculated automatically from the
96 tidal residual circulation, and a 2-layer, vertical thermohaline model, linked with the
97 horizontal circulation scheme, to simulate thermal or haline stratification.

98 The biological sub-model explicitly takes into account the nitrogen, phosphorus and silicon
99 biogeochemical cycles and converts some biological variables into carbon. The pelagic
100 system is described by three phytoplanktonic compartments, and by considering the microbial
101 food web (Hoch, 1998).

102 **2.2 The growth model**

103 2.2.1 Growth data

104 2.2.1.1 Life growth curves

105 Individuals of *P. rhomboïdes* were collected in the different areas of the “Golfe Normand-
106 Breton” (GNB, **figure 1**) during four cruises: BENTHOMONT I and II (April 2002),
107 BIVALVES I and II (May 2002) (Savina, 2004). The number of individuals obtained in each
108 compartment depended on the sampling effort and density of the species (**table 1**).

109 All animals were aged, by counting the annual growth bands on their shell (Berthou et al.,
110 1986) and shell length measured to the nearest mm. In three compartments of the GNB,
111 randomly selected animals were weighed. They were washed gently with freshwater; and the
112 soft bodies were separated from the shell, and weighted to the nearest mg, after drying at
113 80°C for 24 h. and combusting at 450°C for 4 h. The relationship (**figure 2**) between shell
114 length and ash free dry weight (AFDW) was used to convert the shell length of all sampled

115 bivalves into AFDW of soft bodies (assuming that the data obtained during the two cruises
116 and in the different compartments can be pooled together). For each compartment, these data
117 were used to build a growth curve (AFDW vs. age), assuming that the obtained
118 “instantaneous” growth curves is similar to the “historic” ones (i.e., obtained by measuring
119 the growth of one cohort during several years). For each age, the mean AFDW values are
120 assumed to correspond to the weight on the 29/04, average sampling date.

121 2.2.1.2 Annual growth curves

122 A shellfish factory (CELTARMOR) located in the “Baie de Saint-Brieuc” (coast of
123 compartment A, **figure 1**) produces shelled and frozen banded carpet shells. Only animals
124 fished in Compartment A are treated in this factory. A mean production output is calculated
125 every month which corresponds to the ratio: total weight of frozen soft bodies/total fresh
126 weight (shell and soft bodies, Brezellec personal communication, 2002). In the same manner,
127 Morvan (1987) calculated an individual condition index of *P. rhomboïdes* from a station
128 located in the compartment E (**figure 1**) over a two year period, which corresponds to the
129 ratio dry weight of soft bodies/total dry weight (soft bodies and shell).

130 Assuming that the shell weight does not vary too much during a year, these indices give fairly
131 good indications about the intra-annual soft-bodies weight variations of the shellfish.

132 2.2.2 Ecophysiological experiments

133 An ecophysiological study of *P. rhomboïdes* was conducted during September-October 2002
134 in the IFREMER station of Argenton, to obtain the mean values of clearance, absorption and
135 respiration rates of this species. These parameters were studied in the mean ranges of
136 temperature and chlorophyll concentrations that can be found in the GNB; only the
137 temperature minimum condition was not applied because of technical problems. All these
138 results are available in Savina and Pouvreau (2004).

139 2.2.3 The growth model

140 The ash free dry weight (AFDW) of soft body (mg) was the only state variable finally
141 considered. Equations of the growth model and parameter values are shown respectively in
142 **tables 2** and **3**. A conceptual diagram is also presented in **figure 3**.

143 Ecophysiological experiments showed that the filtration rate of *P. rhomboïdes* is mainly
144 controlled by the particulate organic matter (POM) concentration in the investigated range of
145 temperature (Savina and Pouvreau, 2004). The parameters of the filtration rate equation (**table**
146 **2 (1)**), obtained with a phytoplankton cocktail (the concentration of which was expressed in
147 $\mu\text{g l}^{-1}$ chl. a), were converted in order to use this equation with a food concentration expressed
148 in mg l^{-1} dry weight of POM (**table 4**). It was assumed that the measured clearance rate was
149 equivalent to the filtration rate (see Savina and Pouvreau, 2004).

150 Due to the limited range of temperature investigated in our experiments and to its
151 demonstrated influence on physiological rate, the influence of temperature on the filtration
152 rate was considered in the model, using the formulation suggested in Gouletquer et al (1989).

153 Food selection processes were not considered in the model. The ingestion rate was calculated
154 directly with the filtration rate and the food concentration in the filtered sea water (**table 2**
155 **(2)**). In the same manner, the excretion processes were neglected, and a simple absorption rate
156 (instead of an assimilation rate) was used for the Scope for Growth (ie: the energy available to
157 grow, once the respiration and reproduction losses have been deduced from the gain due to
158 nutrition) calculations. To reflect the limited capacity of an organism to produce biomass (ie:
159 to create tissues) even in optimal trophic conditions, a maximum daily absorption rate was
160 introduced (**table 2 (3)**). Metabolic requirements can be divided into two categories: the basal
161 metabolic rate which represents the metabolic rate of a non-feeding animal, and the routine
162 metabolic rate, which include the additional requirements associated with e.g., feeding and
163 digestion (Bayne et al., 1989). The respiration rate is also influenced by environmental
164 parameters, mainly temperature (Winter, 1979; Shumway and Koehn, 1982; Bernard, 1983;
165 Riva and Massé, 1983; Bodoy et al., 1986; Laing et al., 1987; Le Gall and Raillard, 1988;

166 Gouletquer et al., 1989). Though we did not find any significant influence of the temperature
167 on the respiration rate of *P. rhomboïdes* in the investigated range of temperature, again we
168 found more reasonable to consider it. The respiration rate measurements of *P. rhomboïdes*
169 (Savina and Pouvreau, 2004) were therefore re-considered, as a function of temperature and
170 absorption rate (which represents an indicator of the feeding activity; Bayne et al., 1989).
171 Here also, we considered the formulation suggested in Gouletquer et al. (1989) (**table 2 (4)**).
172 As only the global AFDW of soft bodies is considered in this model, reproduction consists of
173 a simple weight loss during the presumed spawning period (**table 2 (5)**). The reproductive
174 effort (proportion of SFG devoted to the reproduction) of bivalve species is considered as
175 increasing with age or with the body weight (Héral et Deslous-Paoli, 1983; Urrutia et al.,
176 1999; Pouvreau et al., 2000 b). Here, the weight loss corresponding to the spawn is calculated
177 from the reached weight at the beginning of the spawning period, and the reproductive effort
178 is an asymptotic function based on Pouvreau et al. (2000 b).
179 Considering the numerous results of the measurements done on several bivalve species
180 (review in Pouvreau et al., 1999 and Savina and Pouvreau, 2004 for example) and the
181 geometric considerations about the influence of size of an organism on its physiological rate
182 (West et al., 1997; Kooijman, 2000), the allometric coefficients were set to 2/3 for the
183 filtration rate, and 3/4 for the respiration rate.

184 2.2.4 Environmental data

185 Food and temperature data used in the growth model were obtained with the biogeochemical
186 model of Hoch (1998). Two types of food were considered among the different pelagic state
187 variables: diatoms and detrital particulate organic matter. They were expressed in the
188 biogeochemical model in $\mu\text{g l}^{-1} \text{ N}$ and $\mu\text{g l}^{-1} \text{ C}$ respectively; and were converted into mg dry
189 matter of POM (**table 5**). We assumed that the filtration and ingestion behaviour of *P.*
190 *rhomboïdes* is the same with natural organic seston than it has been with pure phytoplankton
191 mixture during the experiments (on the basis of which the relationship food-filtration rate was
192 established, Savina and Pouvreau, 2004).

193 The treatment of satellite SeaWiFs pictures of the whole Channel (around 25 pictures per year
194 from 1999 to 2001) with the OC5 algorithm (Gohin et al., 2002) allowed the calculation of
195 an annual average concentration of suspended inorganic matter (or suspended sediment) in
196 each compartment. Considering the important vertical mixing in the GNB, these averages
197 were considered as correct indicators of the sediment load in bottom water.

198

198 **3 Results**

199 **3.1 The growth of *P. rhomboïdes* in the GNB**

200 The examination of the environmental parameters (**figure 4**) distinguishes two zones in the
201 Golfe Normand-Breton (GNB): (1) an “oceanic” zone with clear, relatively poor resources
202 water, and a weak thermal seasonal contrast (compartments A, B, C and D); and (2) a
203 “coastal” zone with higher concentrations of food and suspended sediment and a higher
204 seasonal contrast (compartments E, F, G and H).

205 The growth model was used first without considering suspended sediment concentration
206 influence on the total absorption rate. The absorption efficiency of detrital particulate organic
207 matter and the reproduction parameters were calibrated in the region providing the most
208 complete data set, i.e., the compartment A (Bay of Saint-Brieuc). The agreement between the
209 observed and predicted AFDW is correct for the compartment A, B, C and D (**figure 5**), but
210 the model largely overestimates the growth in the other compartments (E, F, G and H).

211 The suspended sediment concentrations in the compartments E, F, G and H (**figure 4**) are
212 significantly higher than in the first set of compartments (where the model gives good
213 results). Therefore, we tried to improve the model considering the influence of this parameter
214 on the nutrition processes in a simple manner. For each of the 4 compartments concerned (E,
215 F, G and H), a correction factor of the total absorption efficiency (F_{pim}) was calibrated, in
216 order to obtain the best fit between the observed and predicted AFDW.

217 Then the values found for F_{pim} for each compartment were plotted as a function of the
218 suspended sediment concentration (**figure 6**). A linear relationship clearly appears ($R^2=74\%$),
219 which confirms that this environmental parameter is important to be considered. Thus, this
220 correction factor was included into the model as it is shown in **table 2(3)**. The results of this
221 new version of the model are shown in **figure 7** and **5**. The agreement between the observed
222 and predicted AFDW is now correct for all the compartments (except for some points in the
223 compartments E and F, but there the data could be doubtful).

224 Assuming that the shell weight is constant, the mean production output of the shellfish factory
225 as well as the condition index both described in the materials and methods section give a good
226 idea of the change in the mean AFDW of an animal. We compared these indices to the
227 predicted annual change in the ASDW of a 5 years old animal, with a shell growth assumed to
228 be negligible (**figure 8**). In the compartment A, the observed and predicted periods of both
229 maximum weight and decrease of the weight at the end of summer coincide. However, the
230 model predicts a later and shorter period of growth than the observed one. In compartment E,
231 the predicted and observed annual evolutions of the animal weight are similar, but there is a
232 time lag about 80 days.

233 **Figure 9** compared to **figure 4** shows that the simulated growth of *P. rhomboïdes* in the
234 different compartments is the result of the antagonistic actions of food and suspended
235 sediment concentrations. The higher growth is observed in the “continental” compartments G,
236 H and E but also in the “oceanic” compartment A, where the absence of suspended sediment
237 compensates the relatively poor food resources. Nevertheless, the lowest growth corresponds
238 to poor “oceanic” compartment (B and C).

239 **3.2 Results of the growth model in the English Channel**

240 Six categories of compartments can be considered (**figure 10**): (1) a first one where the
241 AFDW of soft bodies goes to 0 very rapidly i.e., where the growth of juveniles is not possible;
242 (2) a second one where the AFDW of soft bodies is maintained between 5 and 200 mg
243 without any real growth; and (3) finally 4 regions where growth is possible.

244 **Figures 10** and **11** show the relationship between the growth capabilities of the species and its
245 real occurrence (dredging data from Cabioch, personal communication, 2002). The proportion
246 of boxes where *P. rhomboïdes* is present clearly increases from the first to the last growth
247 group.

248 The differences of growth between the two annual cohorts are of variable importance
249 depending on the regions (and therefore on the growth capabilities of the individuals), but
250 vanish everywhere for 7 years (or more) old individuals (**figure 10**).

251 **4 Conclusion and Discussion**

252 4.1.1 The growth model development

253 This model was built with a global mechanistic approach; the main ecophysiological
254 processes were considered (nutrition, digestion, respiration, reproduction), as well as the main
255 environmental parameters known to have an influence on these processes in the marine
256 subtidal environment (temperature, food and inorganic seston concentrations). Some of the
257 processes formulation and parameter values were based on measurements (Savina and
258 Pouvreau, 2004) or literature data. Nevertheless, detailed information and parameter values
259 were not available for all processes, and it did not appear necessary to design a too much
260 detailed model for this study because of the considered spatial scale, and of the availability of
261 the data.

262 The feeding behaviour and digestion efficiency of different infaunal bivalve species facing to
263 different qualities and quantities of seston (e.g., organic/inorganic matter proportion, organic
264 matter concentration, living/non living organic matter) have been intensively studied
265 (Widdows, 1978; Winter, 1979; Fiala-Medioni et al., 1983; Bayne et al., 1989; Gouilletquer et
266 al., 1989; Barillé, 1996; Barillé et al., 1997; Defosse and Hawkins, 1997; Dolmer, 2000;
267 Riisgard et al., 2003), most concerned with much more turbid and productive environments
268 than most of the English Channel; while one of the main results of the cited studies is that the
269 feeding behaviour and digestion efficiency of bivalves highly depend on the species and on
270 the environmental conditions in their usual habitat. No specific study about *P. rhomboïdes*
271 behaviour has occurred. Moreover, the spatial resolution of our model and the food and
272 turbidity dataset that we used did not allow us to consider such detailed processes (food
273 selection, pseudo-faeces production, variations in digestion time and/or efficiency). As a
274 consequence, we considered the nutrition processes in a simple manner, and only added a
275 level of regulation (influence of the inorganic matter concentration) on the basis of the results
276 obtained with the previous version.

277 Although they were not necessary to obtain satisfying results in the GNB, some processes
278 were included in the model for application to the whole English Channel, in order to address
279 the broader range of environmental parameter values:

280 (1) the regulation of the filtration rate by temperature, which is more likely to be the limiting
281 factor for nutrition in rich environments such as estuaries, while food concentration is clearly
282 the limiting factor in the GNB.

283 (2) the introduction of a daily growth rate limitation, which reflects the limited capacity of an
284 organism to produce biomass (ie: to create tissues) even in optimal trophic conditions.

285 These two processes were formulated and parameterised in order not to affect the results in
286 the GNB.

287 4.1.2 The growth model results and its application on the distribution of *P. rhomboïdes*

288 The obtained model simulates a realistic behaviour of shellfish weight: the alternation of
289 weight gain (in summer) and loss (in winter) year after year, with a positive annual budget
290 during the first period and a balanced one after (examples of experimental data in the
291 following papers: Bacher and Gouilletquer, 1989; Scholten and Smaal, 1998; Urrutia et al,
292 1999; Ren and Ross, 2001).

293 Unfortunately, we do not have any data about the growth of this species outside of the GNB.

294 Given the demonstrated plasticity of molluscs (Hadfield and Strathmann, 1996; Kooijman,
295 2000), we consider our results in the whole English Channel as reasonable. However, we
296 expected that the high turbidity in the “Bay of Seine” would have prevented such an
297 important growth of *P. rhomboïdes* (black area in **figure 10**). The turbidity data that we used,
298 the calibrated function absorption rate-turbidity and the simple function of growth limitation
299 are probably too simple to allow a real investigation of the growth in really turbid and rich
300 environments such as the “Bay of Seine”.

301 In spite of this remaining weakness, the obtained results provide a fruitful explanation to the
302 observed distribution of the species in the Channel:

303 (1) Growth is impossible in the 1st category (**figure 10**) and therefore survival too, whatever
304 the input of larvae and their settlement conditions.

305 (2) In the 2nd category, the initial weight is maintained, but without proper growth. The
306 mortality rate of the eventually settled individuals is therefore considered to be very
307 important, and if there are survivors, they do not reach a weight sufficient to enable
308 reproduction. The population can therefore be maintained only by the input of allochthonous
309 larvae. This corresponds to the concept of sterile population proposed by Bhaud (2000).

310 (3) Our third and fourth categories of populations are distinguished by their growth rates
311 during the first 4 or 5 years: it can influence the mortality rate, considering that the smaller
312 individuals are more vulnerable (predation, mechanical disturbance, lack of metabolic
313 reserves ...). It can also influence the age of first maturity, since the energetic investment in
314 the reproduction depends on the size of the bivalve (Héral et Deslous-Paoli, 1983; Urrutia et
315 al., 1999; Pouvreau et al., 2000 b). These groups are also distinguished by the adult weight
316 that they finally reach, which have consequences on the reproduction too.

317 (4) The simulated differences of growth between the two annual cohorts during the growth
318 period are consistent with the observations made in the “Golfe Normand-Breton” (Blanchard
319 et al, 1986 a). During the first year, the first recruited cohort has more time to grow before the
320 winter period than the second one, which increases its survival chances (Thouzeau and Lehay,
321 1988); the first cohorts keep an advantage during a few years.

322 The proportion of boxes where *P. rhomboïdes* is present clearly increases from the first to the
323 next-to-last growth group (**figure 10**-central map; the last group is not considered due to the
324 problems detailed before), which suggests the importance – at this scale – of the post-
325 recruitment growth-related processes in the distribution of this species, through action on
326 survival rate and fecundity. Particularly, the extremely low growth obtained in the Western
327 Channel can explain the almost complete absence of the species in this area.

328 Contrasting with the high growth potential provided by our growth model, and hence the
329 favourable conditions of population settlement, *P. rhomboïdes* is actually absent from the

330 “Bay of Seine” (black area in **figure 10**). This can be due to growth-related mortality in
331 relation with the high turbidity, and in this case, our model failed to explain it, but it could
332 also be due to other factors not considered here (settlement of post-larvae in instable muddy
333 substrates, gill clogging, high predation or competition with more adapted species). In all
334 cases, the growth modelling in highly rich and turbid environment must be improved.
335 This model was then included in a global population dynamic model of *P. rhomboïdes*, which
336 will be presented in another article.

337 **5 Acknowledgements**

338 This work was supported by IFREMER and Région Bretagne funding. Thanks to L. Cabioch
339 for his unpublished data about the distribution of *P. rhomboïdes* in the English Channel, and
340 to F. Gohin for his help in processing the satellite SeaWiFS images for turbidity assessment.
341 The authors are also grateful to Rich Little as well as some anonymous reviewers who made
342 useful comments and corrections.

343

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553 **Tables**

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555 Table 1: Number of individual measurements of *Paphia rhomboïdes* coming from the cruises BIVALVES and
 556 BENTHOMONT 2002. The third column gives the number of animals whose age and shell length are known,
 557 and the fourth one gives the number of animals whose age, shell length and AFDW of soft bodies are known.

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compartment	total number of sampled animal	age- shell length	age-shell length- AFDW
A	1595	1595	170
B	33	33	0
C	30	30	0
D	84	84	0
E	106	106	33
F	239	239	95
G	141	141	0
H	298	298	0

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Table 2: Equations of the growth model

1) Filtration rate (L d ⁻¹):	5) Weight loss due to reproduction (mg d ⁻¹ DW):
$FR = fa \times e^{-\frac{fb}{POM}} \times \left[fc \times (T - fd)^{fe} \times e^{-ff \times (T - fd)} \right] \times \left(\frac{W}{1000} \right)^{b1} \times 24$	if $t = t_b$ and $W \geq W_{threshold}$
2) Ingestion rate (mg d ⁻¹ DW):	$reprod = \frac{pa}{pb + pc \times e^{pd \times W}}$
$IR_{phy} = FR \times PHY$	if $t_b \leq t \leq t_e$
$IR_{det} = FR \times DET$	$reprod_{day} = \frac{reprod \times W_{t_b}}{t_e - t_b}$
3) Absorption rate (mg d ⁻¹ DW):	either $reprod_{day} = 0$
$AR_{phy} = IR_{phy} \times AE_{phy}$	6) Scope for Growth (mg d ⁻¹):
$AR_{det} = IR_{det} \times AE_{det}$	$\frac{dW}{dt} = AR_{final} - R_{tot} - reprod_{day}$
$AR_{tot} = (AR_{phy} + AR_{det}) \times F_{pim}$	
with:	
$F_{pim} = ma - mb \times PIM$ if $PIM \geq 2$	
$F_{pim} = 0$ either	
As also:	
$AR_{max} = SAR_{max} \times W^{b1}$	
Finally:	
$AR_{final} = \min(AR_{tot}, AR_{max})$	
4) Respiration rate (mg d ⁻¹ DW):	
$RM = ra \times (T - rb)^{rc} \times e^{rd \times (T - rb)}$	
$RA = activ \times AR_{tot}$	
$R_{tot} = (RM + RA) \times W^{b2}$	

W : AFDW of soft body (mg)
PHY: phytoplankton concentration (mg L⁻¹ DW)
DET: detrital particulate organic matter (mg L⁻¹ DW)
PIM: particulate inorganic suspended matter (mg L⁻¹)

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Table 3: Parameters of the growth model

Parameter	Comments	Unit	Value	references
fa	parameters of the filtration rate – food concentration relationship	L h ⁻¹	2.18	Converted from Savina and Pouvreau (2004)
fb		mg L ⁻¹ MS	0.1152	
fc	Parameters of the filtration rate – temperature relationship	mg j ⁻¹ (°C) ⁻¹ DW	0.000158	Calibrated (considering that the effect of T° in the GNB range was null)
fd		°C	2.4876	
fe		dimensionless	6.1583	
ff	allometric coefficient for anabolism	(°C) ⁻¹	0.5392	see the text
b1		dimensionless	2/3	
AE _{phy}	absorption efficiency for phytoplankton	dimensionless	0.897	Savina and Pouvreau (2004)
AE _{det}	absorption efficiency for detrital particulate organic matter	dimensionless	0.41	calibration
ma	calibrated parameters for total absorption rate as a function of PIM concentration	dimensionless	1.157	see the text
mb		L mg ⁻¹	0.095	
SAR _{max}	Maximum standard absorption rate	mg d ⁻¹ DW	13.8	Calibrated (maximal absorption rate recorded in the GNB)
ra	calibrated parameters for maintenance respiration rate as a function of temperature	mg dj ⁻¹ (°C) ⁻¹ MS	0.003	Calculated from available data in Savina and Pouvreau 2004
rb		°C	0.1	
rc	proportion of absorbed energy respired to support nutrition activity	dimensionless	3.88	See the text
rd		(°C) ⁻¹	-0.2	
activ	allometric coefficient for catabolism	dimensionless	0.17	
b2	limits of the spawning period	dimensionless	0.75	Calculated from Morvan, 1987
t _b		julian day	152	
t _e	minimum weight for reproduction	mg	273	
W _{threshold}	parameters for the weight loss due to reproduction as a function of soft body weight	dimensionless	200	calibration
pa		dimensionless	0.5	
pb	dimensionless	1		
pc	dimensionless	80		
pd	weight	mg ⁻¹ PSSC	-0.01	

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569 Table 4: Conversion factors used to calculate the POM concentrations from chlorophyll concentrations of the
 570 cocktail of algae used during ecophysiological experiments; from Brown, 1991.
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Species	pg cell ⁻¹ chl a	pg cell ⁻¹ MS
<i>Chaetoceros calcitrans</i>	average: 0.485	average: 31.75
<i>Skeletonema costatum</i>		
<i>Isochrysis aff. galbana</i>	0.29	269
<i>Tetraselmis chui</i>	3.83	29.7
Average	1.535	110.15

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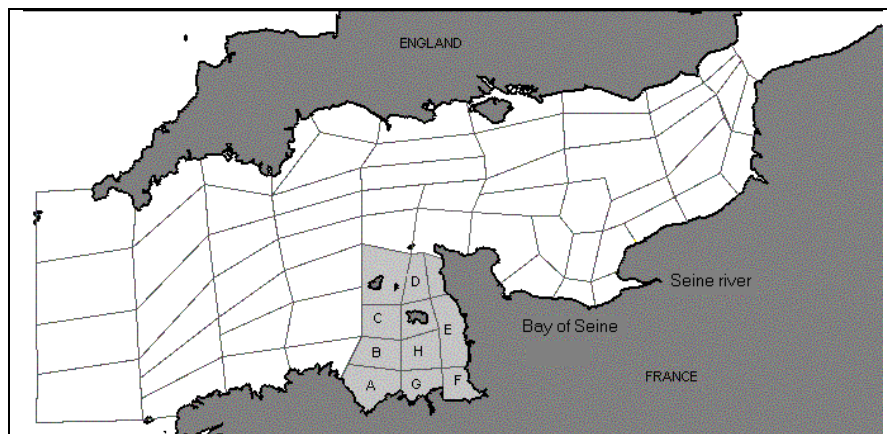
573 Table 5: Conversion factors used to calculate the POM concentrations corresponding to the N and C
574 concentrations of diatoms and detrital particulate organic matter respectively, given by the biogeochemical
575 model (Hoch, 1998).
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Ratios	Values	References
$\mu\text{g chl a} / \mu\text{mol phytoplanktonic N}$	1	Aminot et al, 1997
$\text{mg C} / \mu\text{g phytoplanktonic chl a}$	6	Eppley et al, 1971
$\text{mg C} / \text{mg dry weight of living organic matter}$	0.25	Le Fèvre Lehoërff et al, 1993
$\text{mg C} / \text{mg dry weight of detrital matter}$	0.38	Soletchnik et al, 1996

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580 **Figures**

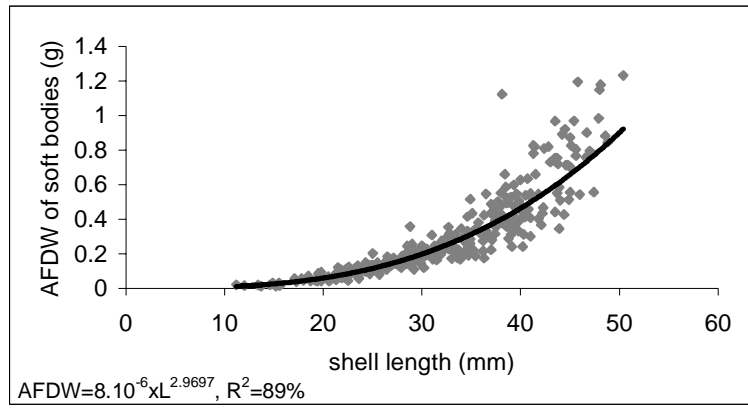
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Figure 1: The English Channel and the ecological box model design. The light grey area is the “Golfe Normand-Breton” (GNB).

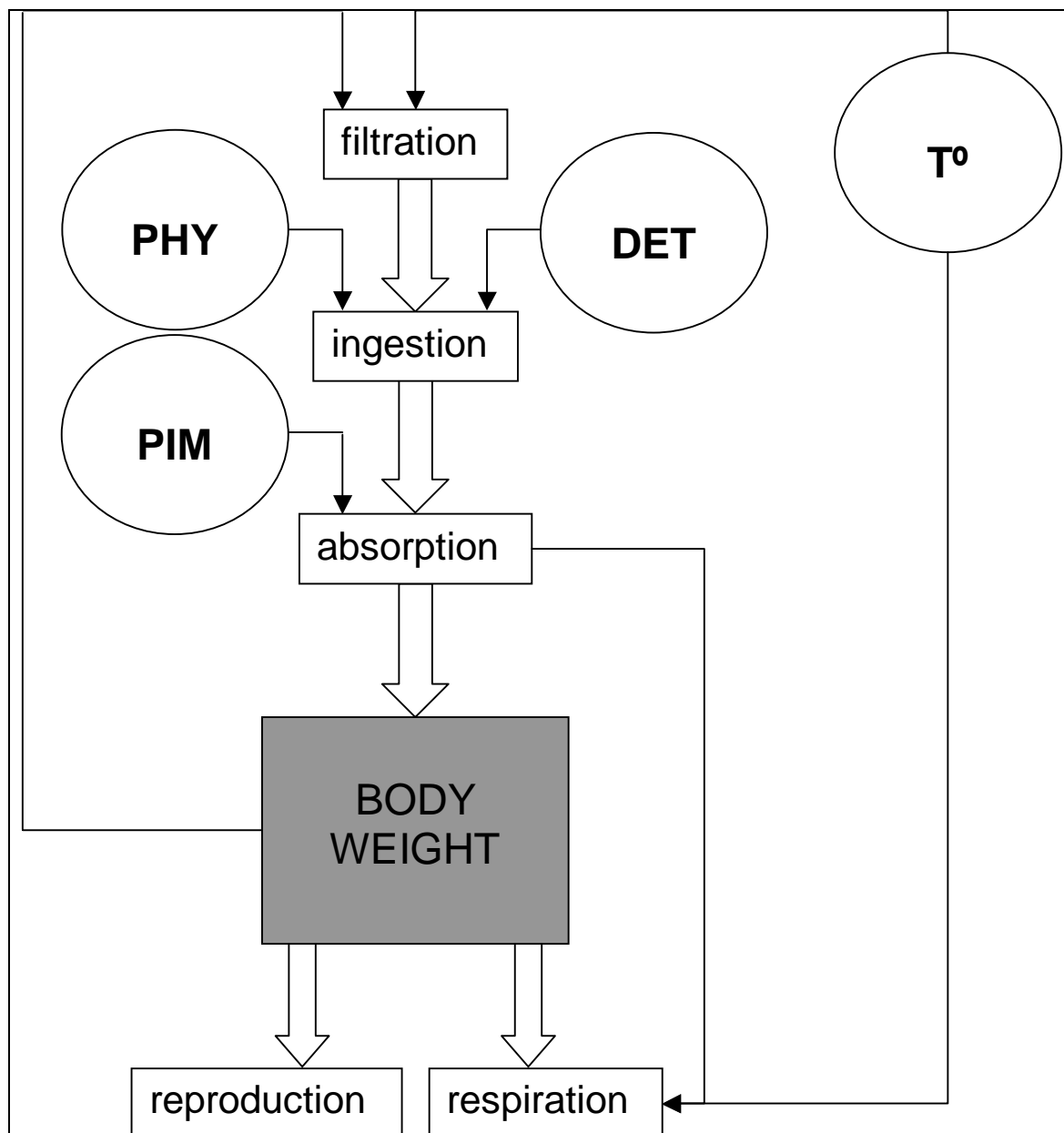
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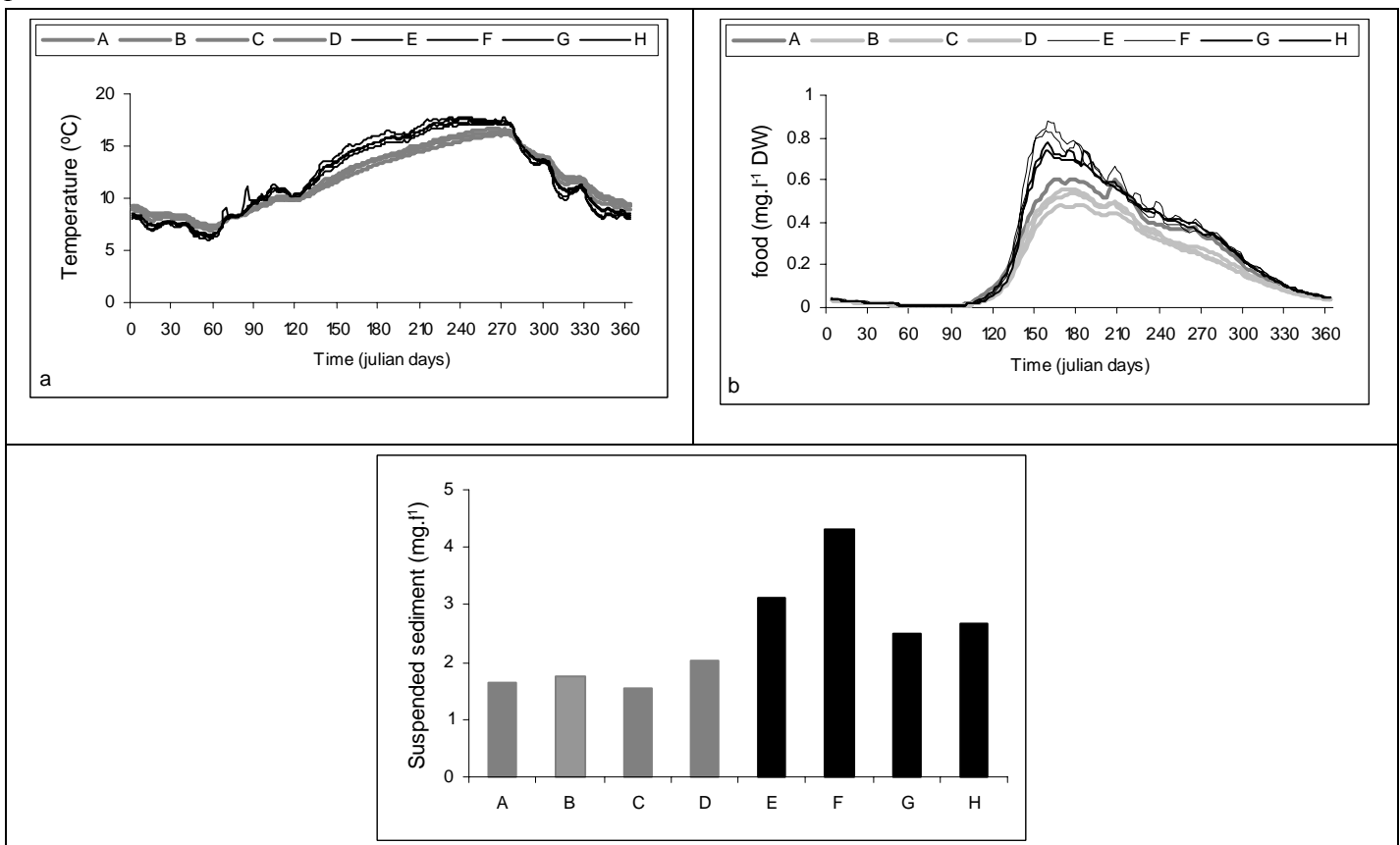
Figure 2: Relationship between shell length and AFDW of soft bodies of the 298 weighted animals.

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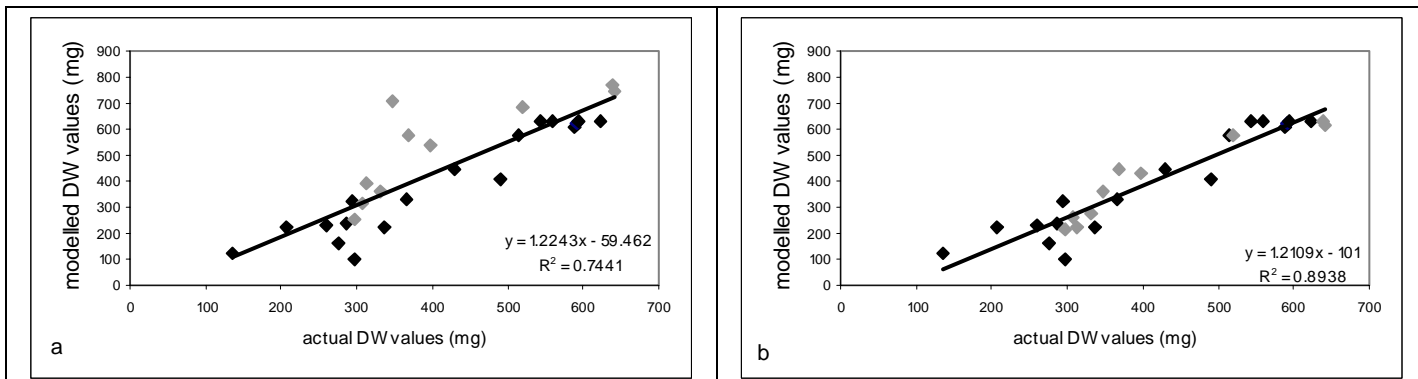
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Figure 3: Conceptual diagram of the growth model. Circles represent the environmental variables: phytoplankton (PHY), detrital particulate organic matter (DET) and particulate inorganic matter (PIM) concentrations, and the temperature (T°). White rectangles represent the processes and the grey rectangle corresponds to the state variable.



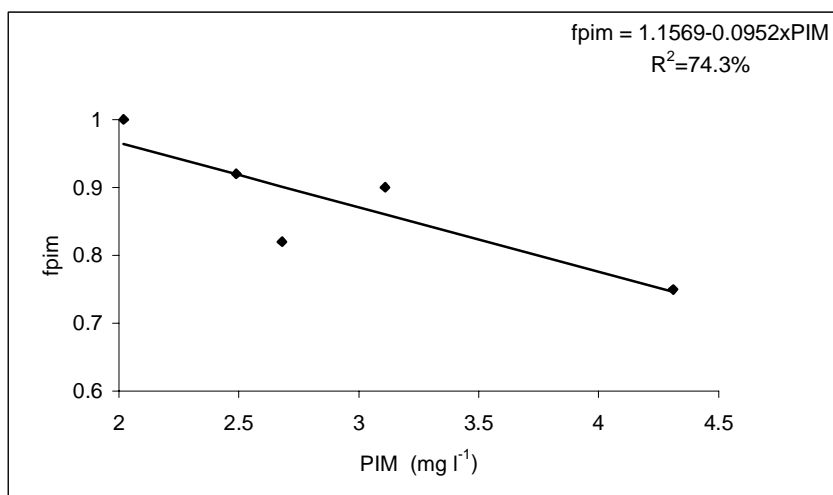
602 **Figure 4: Environmental conditions in different compartments of the GNB; (a) Temperature, (b) Food**
 603 **concentration i.e. diatoms and detrital particulate organic matter and (c) annual average concentration of**
 604 **suspended sediment. The food and temperature datasets are outputs from the physical model, whereas the**
 605 **suspended sediment data set was calculated from satellite data (see 2.2.4)**
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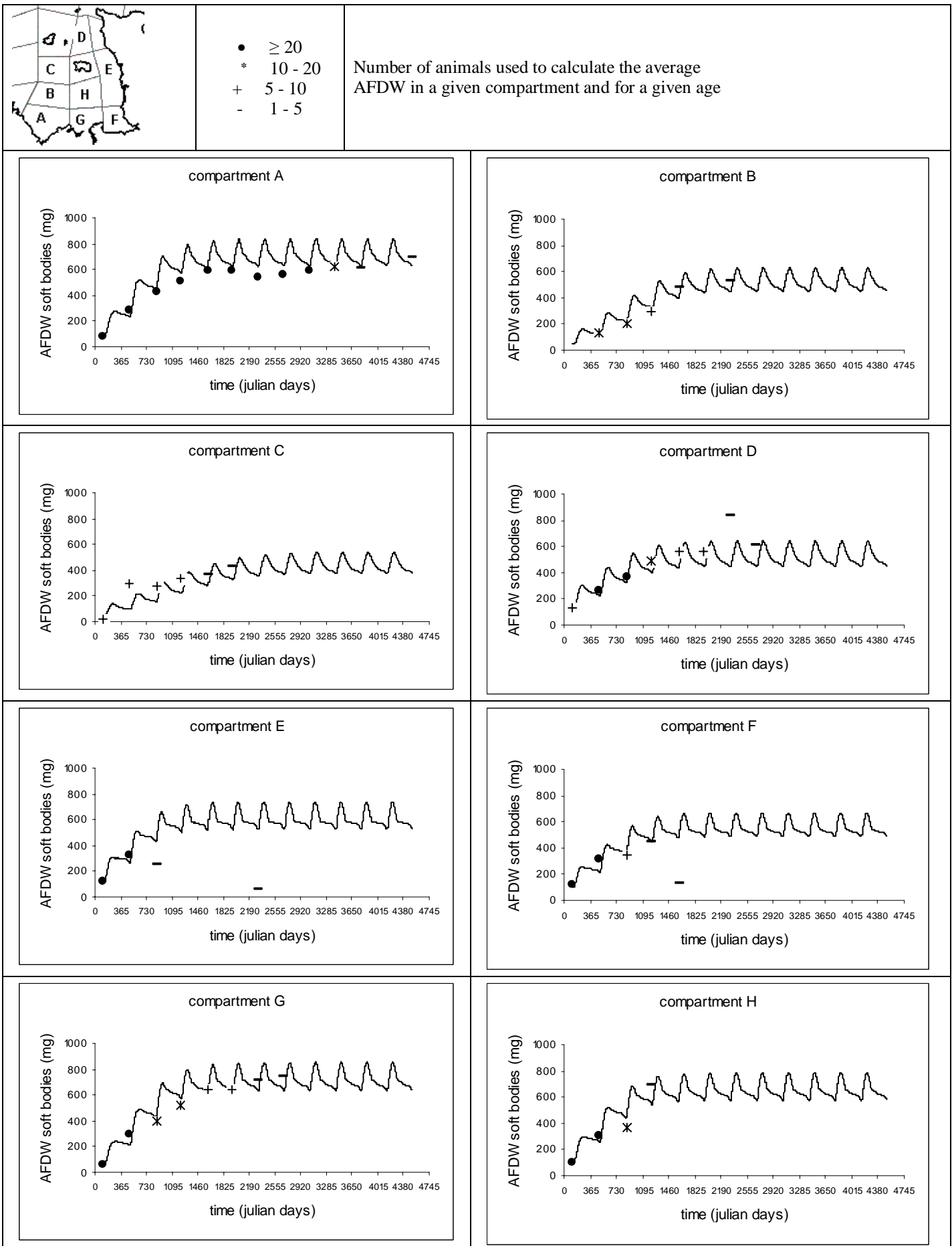
610 **Figure 5: Correlation between the average weight measured for each compartment and age class and the**
611 **corresponding model result (a) for the first version of the model (ie: without suspended sediment**
612 **influence), and (b) the second version of the model (ie: with suspended sediment influence). In both cases,**
613 **the grey points correspond to the compartment with significant concentration of suspended sediment. The**
614 **weight (per age class and compartment) based on less than 5 data were not considered.**
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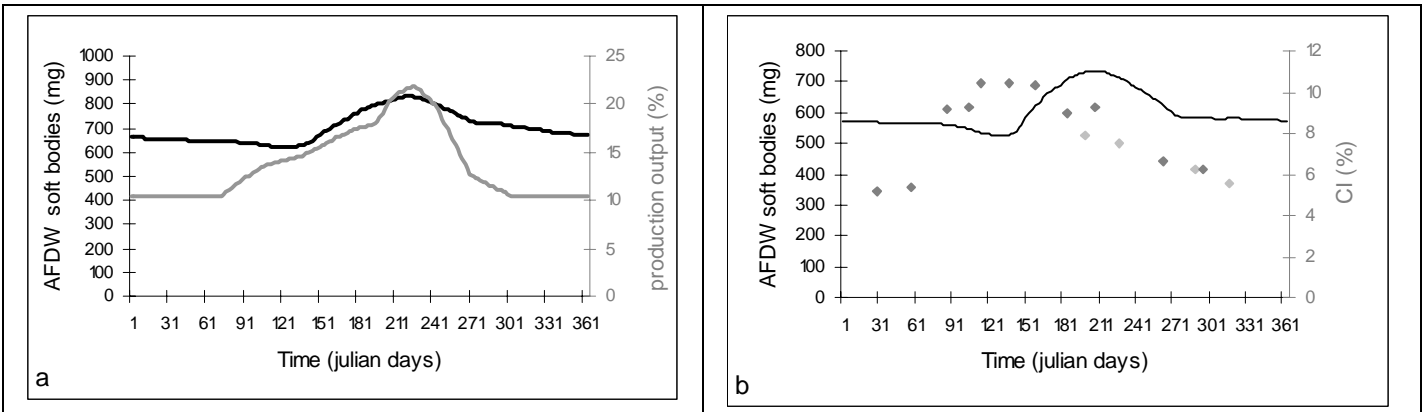
619 **Figure 6: Calibration of the correcting factor of total absorption as a function of suspended sediment**
620 **concentration. Dots represent the values of fpim calibrated for each compartment, and the line a linear**
621 **function adjusted to these results, to be used in the second version of the model.**
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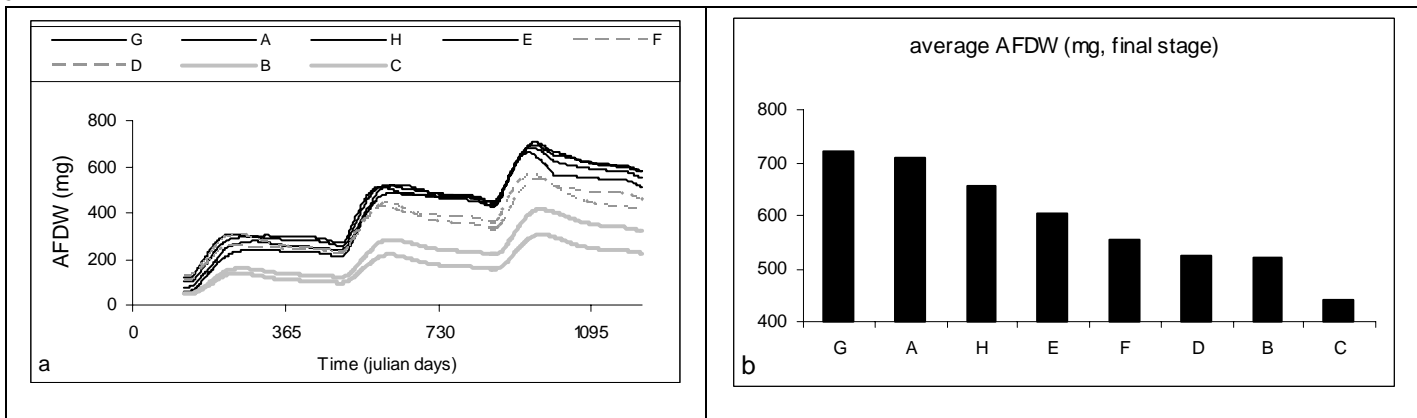
658 **Figure 7: Results of the second set of simulations (with the influence of suspended sediment concentrations**
 659 **on nutrition processes) for the different compartments of the GNB, compared to the observed ASFW. The**
 660 **runs start from the 29/04, to match the sampling dates (see 2.2.1.1)**
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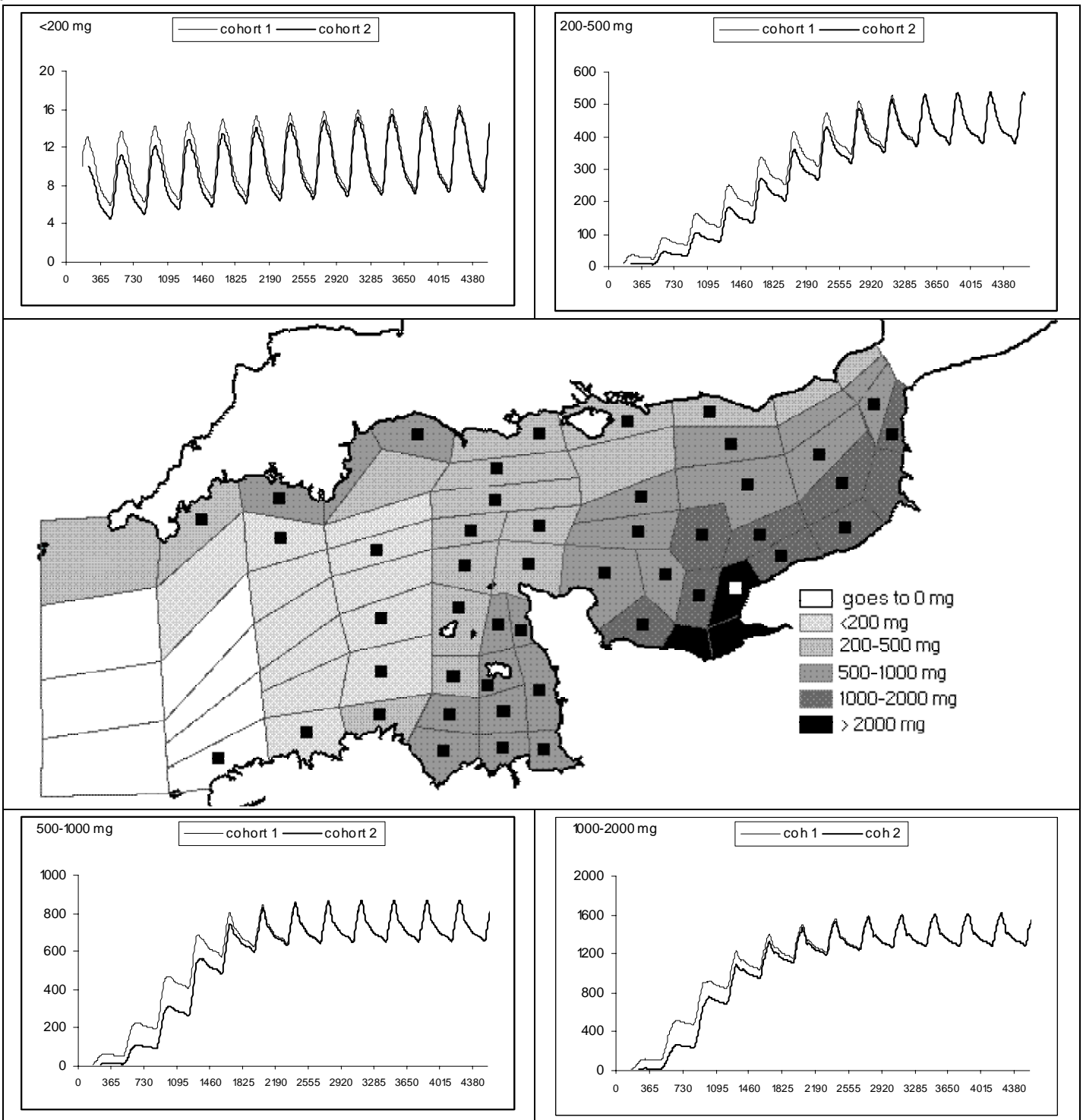


666 **Figure 8: Daily time course of 5 years old individual weight over a one year period (black line, a:**
667 **compartment A; b: compartment E), compared with local values of two weight indices (a: the grey line**
668 **represents the mean production output of a shellfish factory %; b: the light grey points correspond to the**
669 **condition index for 1984, and the dark grey points correspond to the condition index for 1985; see the**
670 **text).**
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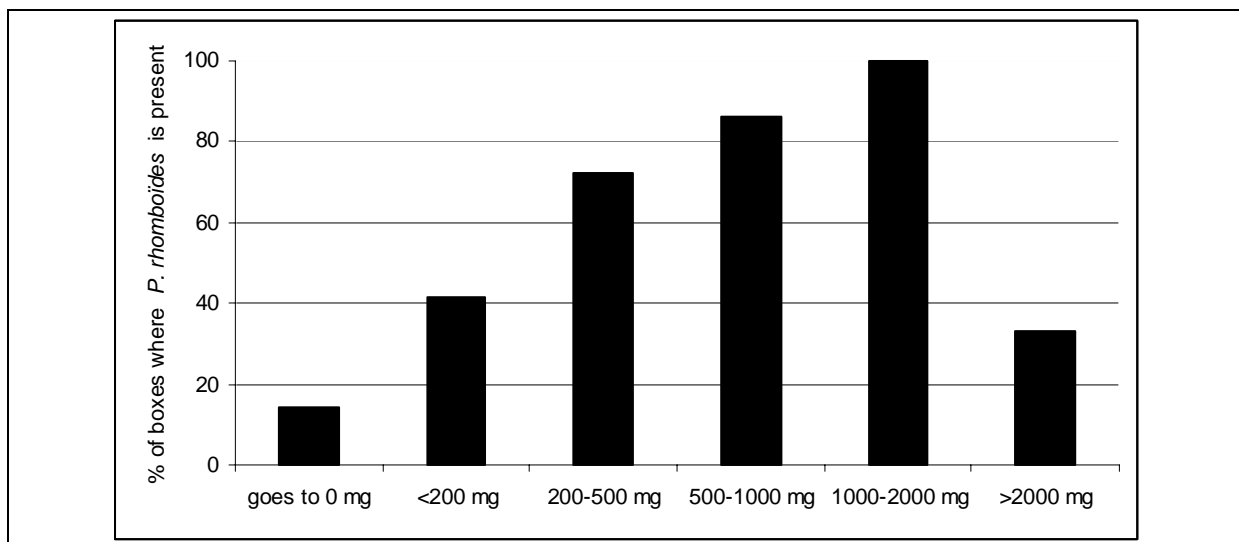


677 **Figure 9: Comparison of the results of the growth model in the different compartments (see figure 1) for**
678 **the first 3 years of life (1-4 yrs, a) and for the final adult weight (mean of the 9-12 yrs, b).**
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680 **Figure 10: Results of the growth model obtained in the whole English Channel area. Graphics: life course**
 681 **of the individual weight (mg AFDW of soft bodies); time is expressed in Julian days. Central map:**
 682 **classification of the different areas of the English Channel into growth categories, on the basis of the**
 683 **asymptotic individual weight. The squares (black or white) show the compartments where *P. rhomboïdes***
 684 **is present (compilation of Cabioch, Glaçon and Rétière data: Cabioch, pers. comm.)**
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698 **Figure 11: Proportion of boxes where *P. rhomboïdes* is present for each weight categories identified from**
699 **the model results (central map of figure 9, asymptotic individual weight).**
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