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Title: A box-model of carrying capacity of the Thau lagoon in the context of ecological status regulations and sustainable shellfish cultures.

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1 Abstract:

2 The decrease of microbial and nutrient inputs from the watershed has long dominated lagoon  
3 ecosystem management objectives. Phytoplankton biomass and abundance have drastically  
4 decreased for more than a decade and *Zostera* meadow have gradually recovered, expressing  
5 lagoon ecosystem restoration such as Thau lagoon. Do the progressive achievement of the  
6 good ecological status of the Thau lagoon possibly threatens the shellfish industry in terms of  
7 production and oyster quality, by reducing the carrying capacity? To provide answers about  
8 the right balance to be achieved between conservation and exploitation, a new numerical tool  
9 was developed to help in decision-making. We hereby propose to incorporate a Dynamic  
10 Energy Budget type shellfish production model to an existing lagoon ecosystem box-model.  
11 The influence of different scenarios of nutrient inputs (related to projections of population  
12 growth or improvement of treatment plants) and shellfish stocks were tested on oyster  
13 performances (production, oyster condition index), carrying capacity of the lagoon and  
14 ecological status indices used within the EU Water Framework Directive. Model outputs  
15 demonstrated that shellfish production was mainly controlled by nutrient inputs, which  
16 depend on hydro-meteorological variability, and specifically by phosphorus and N:P ratios of  
17 nutrient inputs. Scenarios tested, however, demonstrated smaller differences of oyster  
18 production in comparison to inter-annual variability. The overall ecological status of the  
19 lagoon remained in a “good” status with acceptable lagoon-scale phytoplankton depletion,  
20 regardless of scenarios, setting the carrying capacity of this ecosystem to be sustainable.

21

22 Key words: shellfish farming, carrying capacity, stakeholder implication, nitrogen and  
23 phosphorus inputs, Water Frame Directive, ecological indicators, phytoplankton depletion,  
24 coupled Biogeochemical-DEB model.

25

## 26 1 Introduction

27 Rapid expansion of bivalve aquaculture in the last few decades with 17.1 million tons of  
28 mollusks produced worldwide (FAO, 2018) plays a key role in local socio-economic  
29 developments. FAO therefore promoted, in its recent report, a holistic and integrated  
30 ecosystem approach of aquaculture (EAA) to address management issues of sustainable  
31 aquaculture. Among the key features of this EEA framework, FAO highlighted: the wide  
32 stakeholder participation in planning and implementing; a comprehensive consideration of  
33 major components, e.g. aquaculture, socio-economics and environmental, based on “best  
34 available knowledge”; and a search for a trade-off between environment/conservation and  
35 socio-economic objectives. This rapid growing economic sector has inevitably raised  
36 questions of carrying capacity and sustainability (Nunes et al., 2003).

37 In this context, the concept of the carrying capacity is commonly used as it involves major  
38 aspects of integrated ecosystem functioning such as physics, productivity, ecology and socio-  
39 economics (McKindsey et al., 2006). Regarding cultured bivalves, this carrying capacity can  
40 be primarily defined as the biomass of a population supported permanently by a given system  
41 (Dame and Prins., 1998; Kashiwai, 1998). However, this definition has been successively  
42 extended to a maximized production without affecting growth rates (Carver and Mallet, 1990)  
43 to a maximized production of marketable cohorts (Bacher et al., 1998) and more recently to a  
44 maximized production within the frame of environmental sustainability (Smaal et al., 1997;  
45 Ferreira et al., 2008; Byron et al., 2011b; Filgueira et al., 2015). The current consensus is that  
46 production carrying capacity represents the stock that maximizes harvests while ecosystem  
47 responses or ecological carrying capacity deal with unwanted modifications of phytoplankton  
48 abundances, nutrient cycling or organic content in sediments (McKindsey et al., 2006; Grant  
49 et al., 2007; Guyondet et al., 2014;).

50 Recent research has been promoting use of mathematical models, of various complexity  
51 (Dabrowski et al., 2013), to tackle the issues of cultured shellfish management. A lot of  
52 efforts have been made in the representation of shellfish modeling from individual based  
53 (Gangnery, 2003) to mechanistic (Bourlès et al., 2009; Kooijman, 2010; Alunno-Bruscia et  
54 al., 2011) and mixed (Brigolin et al., 2009) models. These individual models are then coupled  
55 to ecosystem food web-based models that include most of the relevant biological  
56 compartments of aquatic systems (Grangeré et al., 2009; Byron et al., 2011c; Filgueira et al.,  
57 2014b). These coupled models can thus be complexified by representing exchanges with the  
58 outer world through simple renewal times (Grangeré et al., 2009), box-model (Chapelle et al.,  
59 2000; Filgueira and Grant, 2009; Raillard and Menesguen, 1994) and fully spatialized  
60 hydrodynamic models (Guyondet et al., 2010). While these models give insights into the  
61 carrying capacity of an ecosystem, it is crucial to derive other model outputs to evaluate  
62 impacts of shellfish farming on ecosystem functioning.

63 The Thau lagoon, as many other coastal Mediterranean lagoons, has been experiencing major  
64 anthropogenic pressures as it received large nutrient loadings from its watershed (La Jeunesse  
65 and Elliott, 2004; Plus et al., 2006). These nutrient inputs have been identified as the main  
66 cause of eutrophication issues or dystrophic crisis (Souchu et al., 1998; Harzallah and  
67 Chapelle, 2002). Thus, many efforts have been made to reduce nutrient loadings mainly  
68 through the installation of waste water treatment plants (WWTP) in the 1970's and their  
69 refurbishment later in the 2000's. These works have drastically reduced the amount of  
70 nutrient inputs from the watershed and successfully led to reach a current "good" ecological  
71 status of water column of the Thau lagoon according to the EU Water Framework Directive  
72 (WFD) (EC, 2000; Derolez et al, 2019). These profound changes in the lagoon inputs from  
73 the watershed have raised concerns from shellfish farmers. Oyster farming, after having taken  
74 precedence over mussel farming in the 1990s, has seen its activity largely impacted by

75 juvenile mortality phenomena from 2008 (Pernet et al., 2012) , which significantly reduced  
76 the overall annual shellfish production. Under current production conditions, long-term  
77 observations of farmed oyster performances have shown improved growth rates and condition  
78 index, probably linked to a decrease in the oyster stock, despite the decrease in phytoplankton  
79 biomass observed (Bec et al., 2018). Considering these recent and important changes in the  
80 pressures exerted on the Thau lagoon, an assessment of its ecological carrying capacity for  
81 shellfish culture is required. We hereby present a modelling work to address concerns arising  
82 from shellfish farmers and consider realistic actions combining the achievement of regulatory  
83 constraints and the sustainability of this major socio-economic activity.

84 The GAMELag model (Pete et al, *ibs*) was formerly developed for the Bages-Sigean lagoon,  
85 to produce similar ecological indicators as those used in the WFD (European Community,  
86 2000). These indicators have been established as relevant criterion to assess ecological status  
87 of a given ecosystem according to different categories from “high” to “very bad”. In addition,  
88 a dynamic energy budget (DEB) model for the Pacific oyster *Crassostrea gigas*, formerly  
89 developed on the Atlantic coast (Pouvreau et al., 2006; Bernard et al., 2011a), was  
90 parameterized for the Thau lagoon and coupled to the GAMELag model. Concomitantly to  
91 the model implementation, a major part of the presented work was realized in close  
92 partnership with shellfish growers, local and governmental management bodies and scientists.  
93 Based on this joint work, management scenarios were established on realistic working  
94 hypotheses. The objectives of this work were therefore: 1) to build a carrying capacity model  
95 and 2) to test the effects of nitrogen and phosphorus inputs and oyster stocking densities, on  
96 oyster performances (condition index, production), carrying capacity and ecological status of  
97 the Thau lagoon. This work was carried out in collaboration with managers and farmers to  
98 find the right balance between conservation and exploitation for sustainable development of  
99 shellfish farming in good ecological status coastal area.

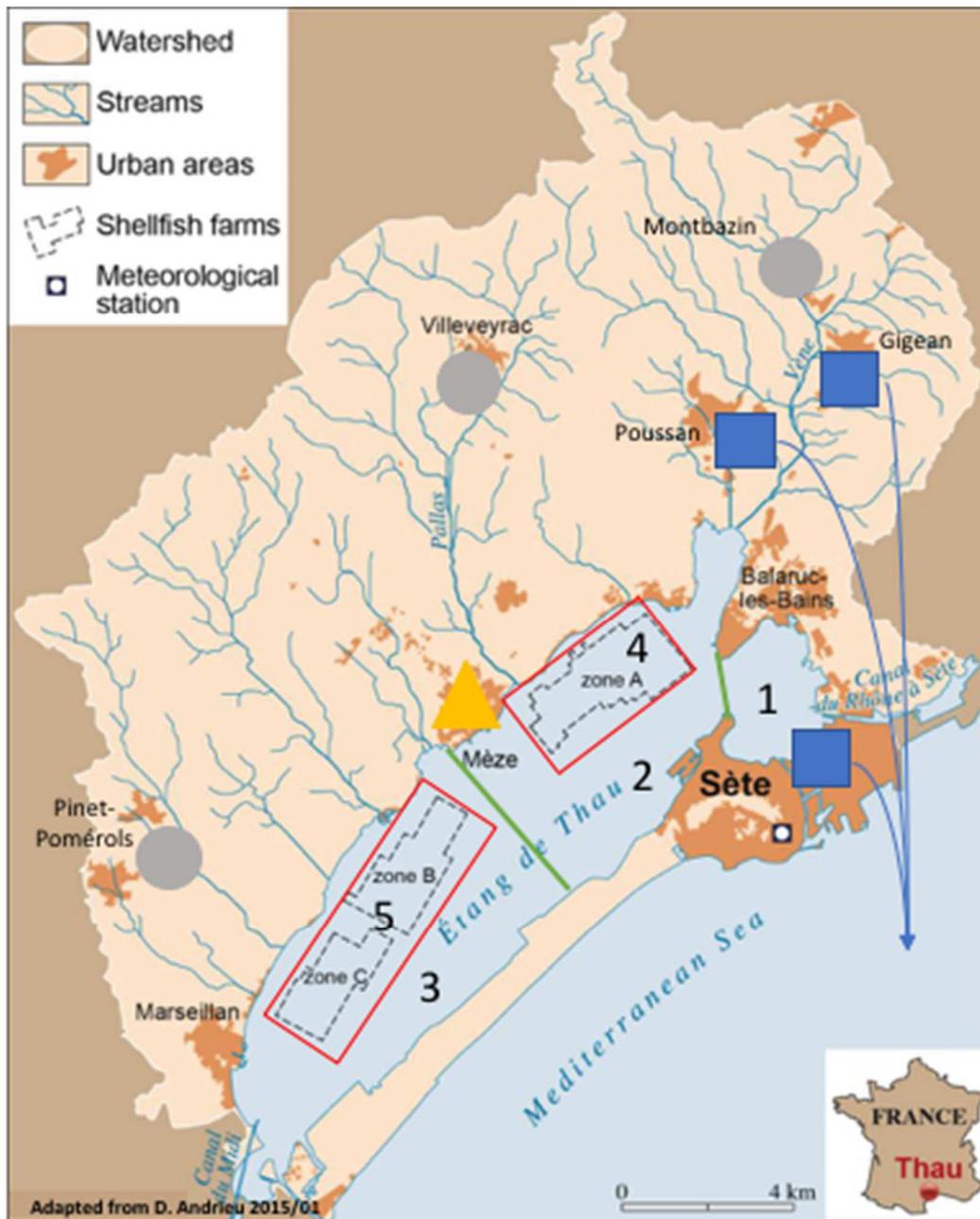
## 100 2 Material & Methods

### 101 2.1 Study site

102 Thau lagoon (Figure 1) is located on the south coast of France (43.18' - 43.28'N, 3.30' -  
103 3.45'E) and has a total area of 68 km<sup>2</sup> (19,5km long by 4.5 km width) and an average depth of  
104 4 m (Fiandrino et al., 2017). The lagoon is connected to the sea through two inlets, i.e., the  
105 Sète channel in the north (90% of sea water exchanges) and the Grau de Pisse-Saumes inlet in  
106 the south. The Sète channel is 2.4 km long with a mean cross-section of about 300 m<sup>2</sup>. The  
107 Mediterranean climate is characterised by a wide range of temperatures (5–29 °C) and  
108 salinities in the lagoon cover a range of 27–42 with a low spatial gradient (data from REPHY  
109 monitoring network; Fiandrino et al., 2017).

110 The lagoon has a narrow located between the Balaruc Point and the Barrou Point, separating  
111 the lagoon into two basins, the “Petit Etang” to the East and “Grand Etang” to the West. The  
112 Grand Etang is the location of shellfish farming activities spread over three areas at the north  
113 of this basin (20% of the lagoon surface). These shellfish farming zones, namely Bouzigues,  
114 Mèze and Marseillan (Figure 1), gather around 2800 farming structures (1250 m<sup>2</sup> and a total  
115 area of ~640 ha) harbouring growing oyster juveniles (hereafter spat) and adults (hereafter  
116 oyster) of the pacific oyster *Crassostrea gigas* (70% of the shellfish stocks) and mussel  
117 *Mytilus galloprovincialis*.

118



119  
 120 Figure 1. Map of the Thau lagoon and its watershed. WWTP are located by symbols and distinguish  
 121 WWTP releasing to the sea (squares), using normal abatements (circles) or maximum abatements  
 122 (triangle). Hydrodynamic frontiers are represented by green lines separating three basins (numbered 1  
 123 to 3) and shellfish farming area are located by the two red boxes (numbered 4 and 5).

124  
 125 The watershed spreads mainly northward from the lagoon over an area of 280 km<sup>2</sup> and is  
 126 drained by several rivers with intermittent flows. The main tributary (the Vène River) is  
 127 connected to the Crique de l'Angle area and brings an annual average of 15.1 Mm<sup>3</sup> of

128 freshwater (about 50% of total flow, ranging from 3.1 to 24.7 Mm<sup>3</sup> between 2009 and 2016).  
129 The population in this watershed amounts to 126604 inhabitants (French National Institute of  
130 Statistics and Economical Studies, Insee, 2015) over 14 main cities equipped with waste  
131 water treatment plants (WWTP). Five of these towns, Sète, Poussan, Bouzigues, Gigan and  
132 Balaruc (Figure 1) are connected to the Sète WWTP which discards effluents 7 km offshore  
133 in the Mediterranean Sea. The four other cities, Montbazin, Villeveyrac, Mèze-Loupian and  
134 Pinet-Pomerols have their own WWTP releasing effluents into the Thau lagoon.

135

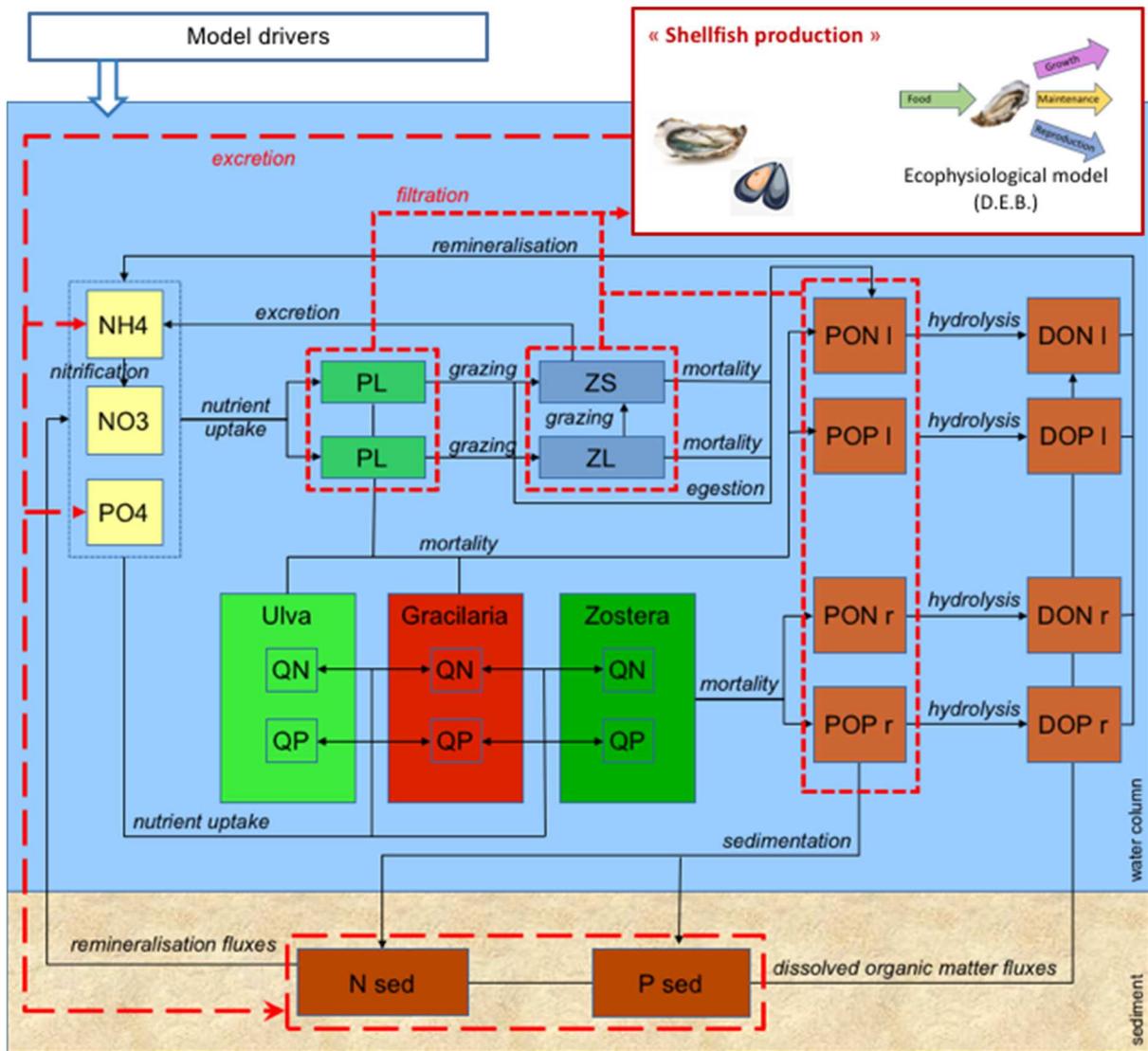
## 136 2.2 Carrying capacity model

137 The GAMELag model (Pete et al, *ibs*) was formerly developed for management purposes  
138 with regards to water quality assessment under the WFD. GAMELag works on the principle  
139 of a box-model, where the lagoon is represented by basins, physically homogeneous, in which  
140 the stocks of the different biological compartments are simulated as well as the fluxes of  
141 matter (nitrogen N and phosphorus P) connecting these compartments (Figure 2). The lagoon  
142 was separated into three main boxes (green boxes, Fig. 1): “Petit Etang” (box 1), East of  
143 “Grand Etang” and West of “Grand Etang” (box 2 and 3, respectively on Fig. 1). In order to  
144 simplify the model and to be able to compare it with available observations, the Mèze and  
145 Marseillan shellfish farming zones were gathered to form box 5, whereas Bouzigues shellfish  
146 farming zone formed box 4 (red boxes, Fig. 1).

147 The hydrodynamic exchanges between box 1 and the Mediterranean Sea and between two  
148 adjacent physical boxes are simulated following formalism defined by Gordon et al, 1996  
149 based on daily net residual volumes and mixing volumes. While net residual volumes are state  
150 variables of the hydrodynamic module of the GAMELag model, daily time series of mixing  
151 volumes at frontiers of physical boxes have to be defined as forcing dataset. The  
152 hydrodynamic exchanges between box 4 and physical box 1 and between box 5 and physical

153 box 2 only depend on mixing volume, there is no net residual volumes between these boxes.  
154 Mixing volume takes into account wind mixing (mainly inside the lagoon) and tide-driven  
155 exchange (between lagoon and the sea). These mixing volumes are therefore varying in time.  
156 A 3-dimensional hydrodynamic Model for Application at Regional Scale (MARS-3D) was  
157 used to compute daily time series of mixing volumes (Lagarde et al., 2019; Lazure and  
158 Dumas, 2008). Descriptions of the MARS3D model applied on Thau lagoon and the forcing  
159 dataset necessary for simulating water bodies circulation are provided in Fiandrino et al.  
160 (2017). Same atmospheric (wind, air temperature, incident radiation) and hydrological (daily  
161 average river water fluxes ( $\text{m}^3 \cdot \text{s}^{-1}$ ) from the watershed) are used to force MARS-3D and  
162 GAMELag models. Specific dataset were used (sea level elevation in Sete Channel) to force  
163 MARS-3D model at the open boundary condition for the simulated period.

164



165

166 Figure 2. Conceptual scheme of the GAMELag-Conch model representing biological compartments  
 167 (boxes) and processes (black arrows) within the water column (blue area) and sediment (brown area).

168 The oyster ecophysiological model is linked to the biogeochemical cycles (red boxes) through  
 169 filtration and excretion processes (red arrows).

170

171 In order to model the growth of an average oyster individual in the shellfish production areas  
 172 of the Thau Lagoon, a coupling of the GAMELag and DEB oyster model was carried out to  
 173 form “GAMELag-Conch” model. It involves the integration of the DEB model into the  
 174 biogeochemical model. The dynamic energy budget of *C. gigas* model is based on the DEB

175 theory (Kooijman, 2009) and adapted to the Pacific oyster in the Atlantic under various  
 176 versions, 3 state variables (Pouvreau et al., 2006) or 4 state variables (Bernard et al., 2011b).  
 177 The dynamics in time of the different energy fluxes are described by a system of differential  
 178 equations (see suppl. Mat. Tables S1) and associated processes (Pouvreau et al., 2006;  
 179 Bernard et al., 2011b;). Within the frame of this work, the model was adapted and  
 180 parameterised for the Thau lagoon with additional parameters related to rearing schemes (see  
 181 suppl. Mat., Table S2).

182 The DEB model operates on energy flows (in joules) allocated to different functions within  
 183 the individual (reserve, maintenance, growth and reproduction). Among these energy costs,  
 184 some imply a dissipation of energy, which must be translated into excretion of matter to  
 185 maintain steady mass balances within the GAMELag-Conch model. The oyster food resource  
 186 in terms of nitrogen and phosphorus ( $X_N$  and  $X_P$ ) is assumed to be a mix of various available  
 187 particles in the water column (e.g. state variables of the biogeochemical model) and is defined  
 188 as:

$$189 \quad X_N = \alpha_{PS}PS + \alpha_{PL}PL + \alpha_{ZS}ZS + \alpha_{ZL}ZL + \alpha_{PON}PON \quad \text{Eq. 1}$$

190 and

$$191 \quad X_P = \frac{\alpha_{PS}PS + \alpha_{PL}PL}{NP_{phyto}} + \frac{\alpha_{ZS}ZS + \alpha_{ZL}ZL}{NP_{zoo}} + \alpha_{POP}POP \quad \text{Eq. 2}$$

192 where PS, PL, ZS and ZL are small and large phytoplankton and small and large zooplankton  
 193 and PON the sum of labile and refractory particulate organic nitrogen. Each of these food  
 194 resources is weighted by a preference coefficient  $\alpha_i$  with  $i = PS, PL, ZS, ZL, PON$  or  $POP$ .  
 195 The oyster food resource is expressed in phosphorus using N to P stoichiometry of  
 196 phytoplankton and zooplankton, ( $NP_{phyto}$  and  $NP_{zoo}$ ), whereas POP is the sum of labile and  
 197 refractory particulate organic phosphorus. Hence, the stoichiometry of food resources is  
 198 expressed as

$$199 \quad NP_X = \frac{X_N}{X_P} \quad \text{Eq. 3}$$

200 The food resource and dissipated DEB energy fluxes were translated respectively from mmol  
201 N (or P) to Joules and from Joules to mmol N (or P) using conversion factors (see suppl. Mat.,  
202 Table S2).

203 In the DEB model, some of the available energy is lost. First, there is the amount of material  
204 ingested but not assimilated by the oyster, which is expressed in the DEB model by the  
205 excretion of feces and pseudo-feces (joules per unit of time). This part of the non-assimilated  
206 food either reached the sea bed to fuel sediment stock of N and P or was remineralised into  
207 inorganic nitrogen and phosphorus in the water column. Once assimilated, the energy is  
208 allocated into the compartments of the DEB model (structures, reserves and reproduction). In  
209 order to maintain balanced stoichiometry in the DEB model, excretion is required and is  
210 simulated according to the stoichiometry of the ingested material. Thus, the ratio N: P of the  
211 resource ( $NP_X$ ) is compared to the ratio N:P of the oyster ( $NP_O$ ). When this  $NP_X$  is greater  
212 than the  $NP_O$ , the regeneration of material is in the form of ammonium in the model. On the  
213 contrary, when the  $NP_X$  is lower than the  $NP_O$ , the regeneration was assumed to be in the form  
214 of orthophosphate. In this way, even if the stoichiometry of the resource is variable, the  
215 individual rejects a quantity of N or P to maintain a balanced stoichiometry. This system of  
216 regeneration of post-assimilation material provides available mineral forms of N and P in the  
217 water column. The maintenance costs ( $\dot{p}_M + \dot{p}_J$ ) (Eq. 4), growth costs ( $\dot{p}_G (E_G - d_V \times$   
218  $\mu_V) / E_G$ ) (Eq. 5) and gamete production costs ( $\dot{p}_G (E_{GG0} - d_{G0} \times \mu_{G0}) / E_{GG0}$ ) (Eq. 6)  
219 were also added to the amounts of regenerated matter as they correspond to dissipated energy  
220 (see suppl. Mat., Table S3). In the GAMELag-Conch model, these energy costs were  
221 converted into  $NH_4^+$  or  $PO_4^{3-}$  with conversion factors  $C_{oyster}$  and  $\mu_{EN}$  (energy yield of  
222 reserves). These conversion factors are based on the available data on the chemical potential  
223 of the different compartments of the oyster (Add-my-pet portal:  
224 [https://www.bio.vu.nl/thb/deb/deblab/add\\_my\\_pet/](https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/)). Thus, the chemical potential of the food,

225 once converted to  $\text{J mmol}^{-1} \text{N}$ , gives a conversion factor,  $C_{\text{oyster}}$ , of  $3250 \text{ J mmol}^{-1} \text{N}$ . The  
226  $C_{\text{oyster}}$  conversion factor affects energy related to ingested but non-assimilated matter (feces  
227 and pseudo-feces) and the energy related to predation on the different compartments  
228 composing oyster food (ie, small and large phytoplankton, small and large zooplankton and  
229 particulate organic matter). The second conversion factor,  $\mu_{\text{EN}}$ , is obtained by deriving the  
230 chemical potential of bivalve reserves with the nitrogen (or phosphorus) content of the  
231 organic matter that makes up these reserves. The factor thus obtained is  $3667 \text{ J mmol}^{-1} \text{N}$ . In  
232 general, these conversion factors vary between  $2400$  and  $3700 \text{ J mmol}^{-1} \text{N}$  depending on  
233 whether food, structure or reserves are considered as N or P content (Platt and Irwin, 1973;  
234 Grangeré et al., 2009).

235

### 236 2.3 Oyster seeding scheme in the model

237 Seeding scheme, as the introduction in farming structures of spat and oysters, is rather  
238 complex in the Thau lagoon and mainly depends on environmental conditions, contamination  
239 risks time frame or market dynamics. Two main periods for seeding were extracted from the  
240 monograph results (Cepalmar, 2016) indicating that, according to growth durations, most  
241 spats (6 to 8 mm) were mainly reared on lanterns or pearl nets and introduced between July  
242 and August (47% reared over the summer) for a period of 6 to 8 months. In addition, this  
243 study indicated that oysters (15 to 20 mm) were introduced within the early months of the  
244 year (53% in January and February) for a duration of 12 to 14 months to reach marketable-  
245 size oyster. Therefore, in order to simplify this seeding time schedule for the GAMELag-  
246 Conch model, we assumed a common seeding scheme where oysters were introduced on the  
247 first of February and harvested in mid-December. Regarding to spat seeding, the first of July  
248 was used in the model to start growth of spats for a duration of 7 months. In February,  
249 remaining spats from year  $n$  were then used to seed oysters in year  $n+1$ . The total abundances

250 were  $532.1 \cdot 10^6$  and  $235.7 \cdot 10^6$  individuals for spats and oysters respectively for the entire  
251 farming zone (box 4 + box 5, Figure 1). Mortality rates were also extracted from the  
252 monograph with values of 38.2% ( $10.5 \cdot 10^{-4} \text{ d}^{-1}$ ) during the pre-growing phase and 32.5%  
253 ( $8.9 \cdot 10^{-4} \text{ d}^{-1}$ ) during the growing phase (Cepralmar, 2016). Seeding densities were then used  
254 to simulate stocking densities over the growing period as follows:

$$255 \quad \frac{dOyster}{dt} = Seeding_{Oyster} - Oyster \times mortality_{Oyster} \quad \text{Eq. 7}$$

256 And

$$257 \quad \frac{dSpat}{dt} = Seeding_{Spat} - Spat \times mortality_{Spat} \quad \text{Eq. 8}$$

258 Where  $Seeding_{Oyster}$  and  $Seeding_{Spat}$  are densities of oysters and spats introduced as  
259 described above. The number of individuals introduced was extracted from the monograph  
260 (Cepralmar, 2016) and extrapolated to the farming zones with data from local authorities  
261 (DDTM, 2014), which represented an average exploitation of 70% of growing structures.  
262 Length (L) and dry flesh matter (DFM) were calculated at harvest for each simulated year.  
263 Annual oyster production was estimated from total weight (derived from DFM, equation 16,  
264 Table S1 in suppl. Material) and the number of living individuals simulated at harvest. Oyster  
265 condition index (CI, %) was estimated from model outputs by using the ratio of DFM (g) over  
266 Length (cm).

267

#### 268 2.4 Reference simulation

269 The baseline simulation (e.g. “Reference”, scenario n°1, Table 1) used in this study  
270 represented the current conditions of the Thau lagoon functioning. This baseline simulation  
271 was used to evaluate model skills (see section 2.5). This simulation covered the period from  
272 2014 to 2016 and was carried out with the hydro-meteorological conditions of these three  
273 years including precipitation, contributions of the natural catchment and contributions from

274 WWTP, based on the data of self-monitoring recorded at the entrance of the WWTP (data  
 275 from SMBT).

276 Table 1. Summary of scenarios tested with reference simulation, watershed nutrient inputs and  
 277 shellfish densities described according to their characteristics.

<i>Type of scenario</i>	<i>Scenario number</i>	<i>Characteristic</i>	<i>Observation – management interest</i>	<i>Name of scenario in figures</i>
<b>Reference</b>	1	Current stocking densities, WWTP outputs estimated from current average abatements	Use as a standard for comparing scenarios	Ref
<b>Watershed inputs</b>	2	Maximum yield on N& P for all WWTP ( $\geq 90\%$ on both N & P)	Correspond to the scheme for water management (SAGE)	Max. yield
	3	Normal yield on N & P for all WWTP (75% N, 60% P)	Classification off « sensitive zone » to eutrophication	Nal yield
	4	Projection of an increase in the number of inhabitants in the territory	Correspond to the comprehensive territorial occupation scheme (SCOT) predicting a 23% increase of the population in the Thau watershed by 2030	SCOT
	5	Partial release of water and nutrients from the Sète WWTP into the lagoon	Operating strategy of Sète WWTP	Sète
<b>Shellfish farming</b>	6	Seeding to the maximum of the growing structure capacity according to the « structure scheme (DDTM)	Evaluation of the effect of the maximum capacity of breeding structures on the lagoon ecosystem and oyster production and performances	Max. dens.

278  
 279 Hydrological conditions of the simulated years were contrasted in terms of total rainfall and  
 280 associated trophic contributions. The year 2015, defined as a dry year (-255 mm compared to  
 281 1970-2016 average), showed low natural hydrological contributions with inputs of 0.77 t of P  
 282 and 12.7 t of N, whereas the years 2014 and 2016, with more intense rainfall events (+70 mm  
 283 and -55 mm compared to 1970-2016 average), brought natural nutrient loadings to a  
 284 respective estimate of 5 and 5.6 t of P and 86.6 t and 98 t of N. During wet years,  
 285 anthropogenic inputs from WWTP amounted for 18% of N loading against 55% for P inputs.  
 286 Total inputs from the watershed (natural and anthropogenic) reached 109.2, 39.4 and 113.8  
 287 tons of N and 10.1, 6.1 and 10.2 t of P for the three simulated years. For the year 2015,  
 288 WWTP discharges constituted the main source of N (62%) and P (90%) inputs, whereas for

289 the wet years 2014 and 2016, WWTP inputs accounted for up to 20% of total nutrient  
290 loadings. The initialization of the biological compartments takes into account the most recent  
291 observations in order to get as close as possible to the current conditions in the simulations.  
292 Concerning the initialization of shellfish culture, data from the Cépralmar monograph  
293 (Cépralmar, 2016) were used for livestock densities in the Bouzigues and Mèze-Marseillan  
294 areas (see section Oyster seeding scheme in the model). The extrapolation of these survey  
295 results to both production areas was based on the data provided by local authorities (DDTM,  
296 2014) with 2632 tables in concession of which 382 were not active. The estimate of the  
297 structures hosting pre-growth (spats) and growth (adults) was conducted using data from the  
298 monograph (Cépralmar 2016) extrapolated to the 2250 tables in operation on each of the two  
299 areas. This baseline scenario is referred as “Ref” in table 1 (scenario n°1, Table 1).

300

### 301 2.5 Model skills evaluation & model computation

302 The Willmott index of agreement (Willmott, 1981),  $d$ , was used to evaluate the performance.

303 This metric is a standardized measure of the degree of model prediction error and varies

304 between 0 and 1. A value of 1 indicates a perfect match, and 0 indicates no agreement at all.

305 This index of agreement was used to evaluate model skills on salinity, Chl *a* concentration as

306 well as shell length (cm) and tissue dry weight (g) of cultured oysters. Available observations

307 for these variables were compared to simulations for the two shellfish farming zones (Figure

308 1, box 4 and 5). The GAMELag-Conch model was implemented in R (R Core Team, 2017),

309 using the deSolve package (Soetaert et al., 2010) for differential equation solving (time step: 1

310 day).

311

### 312 2.6 Description of scenarios

313 Scenarios of different nutrient inputs and shellfish culture strategies were determined in close  
314 interactions with shellfish farmers (Mediterranean shellfish committee, CRCM), managers  
315 (the Thau basin organization, SMBT; the Centre for studies of lagoon and maritime activities,  
316 CEPRALMAR; the French water agency, AERM&C; Departmental Direction of Territories  
317 and Sea DDTM) and scientists (MARBEC). These scenarios were built on realistic  
318 management hypotheses, established during participative meetings and are based on two main  
319 axes: 1) scenarios related to trophic contributions from the watershed and associated  
320 management measures and 2) scenarios related to shellfish production and they are  
321 summarized in Table 1.

322 The anthropogenic contributions of the watershed were tested according to different scenarios  
323 corresponding to different management hypotheses around the watershed of Thau (Scenario 2  
324 to 5, Table 1). The yields of the WWTPs are constrained by the environment that receives the  
325 discharges and come within the context of the Regional Plan for Water Management (SDAGE  
326 Rhône-Méditerranée) and the local Water Management Scheme (SAGE) applied to the Thau  
327 lagoon territory. When these receiving water bodies carry a risk of eutrophication, they are  
328 classified as sensitive to eutrophication according to European regulation (EC, 1991). In the  
329 context of "sensitive zones", the European legislation (EC, 1991) requires WWTP to treat at  
330 least 80% of phosphorus and 70 to 80% of nitrogen for cities with more than 10 000  
331 inhabitant equivalents (IE). For smaller municipalities, these obligations vary and may be  
332 higher depending on the case. Thau lagoon was classified as a "sensitive zone" in 2004  
333 according to European recommendations (EC, 2004). On these provisions, it was concluded  
334 to test initially two scenarios declining these treatments of WWTP to: 1) maximum yield  
335 (scenario 2: Max. yield) with abatements greater than 90% for nitrogen and phosphorus; 2)  
336 normal yield (scenario 3: Nal yield) corresponding to reductions of 75% and 60% respectively  
337 for nitrogen and phosphorus. It should be noted that only the Mèze lagoon-based treatment

338 plant currently offers yields comparable to the high abatements required by the "sensitive  
339 zone" classification (> 90%).

340 In direct relation with the environmental management constraints, the territorial occupation  
341 scheme (SCOT) and, in particular, the demographic projections of this SCOT, were evaluated  
342 in this study. Indeed, an increase in population (estimated at 23% at 2030 horizon) directly  
343 leads to increased WWTP effluents (wastewater discharges) and, consequently,  
344 recommendations to anticipate these evolutions must be incorporated into a management  
345 policy of the territory. This scenario (Scenario 4, "SCOT" Table 1) aimed at estimating the  
346 impact of the population increase on the Thau catchment area by 2030 in terms of nitrogen  
347 and phosphorus inputs to the lagoon, as well as its impact on ecological status and shellfish  
348 cultures in the Thau lagoon. Current yields of WWTPs were then applied to these estimated  
349 quantities of nitrogen and phosphorus to provide quantities entering the lagoon.

350 The following scenario (scenario 5; "Sète", Table 1) corresponded to potential management  
351 leverage for freshwater and nutrient inputs (N & P) to the lagoon through an operating  
352 strategy of the Sète WWTP. This scenario addressed the question of the evaluation of the  
353 impact of discharges in the Sète channels and hence in the lagoon, in anticipation of important  
354 modernization works on the WWTP. The Sète WWTP currently has its outfall in the sea but  
355 could release discharges to the Sète channels in case of heavy rains. This scenario examined  
356 the effect of an additional 69.5, 72.9 and 84.7 tons of nitrogen in 2014, 2015 and 2016  
357 respectively. In terms of phosphorus, additional quantities were estimated at 3.7, 3.1 and 3.6  
358 tons for the same years respectively.

359 The scenario of different oyster stocking densities tested in this study corresponded to seeding  
360 conditions for which all the growing structures would be filled with oysters at the maximum  
361 densities allowed by the structure scheme (DDTM, 2014). In comparison to reference seeding  
362 conditions (see section Oyster seeding scheme in the model), abundances were increased by a

363 factor 2 for spats (e.g.  $501 \cdot 10^6$  and  $546 \cdot 10^6$  individuals for box 4 (Bouzigues) and box 5  
364 (Mèze-Marseillan), respectively) and by a factor 1.3 for oysters (e.g.  $158.7 \cdot 10^6$  and  $129.9 \cdot 10^6$   
365 individuals for box 4 and box 5, respectively).

366

## 367 2.7 Data treatment and scenario realization

368 Prior to the simulations of these different scenarios, a first step was the WWTP data  
369 processing to force the GAMELag-Conch model. Work to recover volumes and  
370 concentrations of global nitrogen (NGL) and global phosphorus (PGL) at the inlets of the  
371 WWTPs was performed based on data from SANDRE (portal:  
372 <http://www.sandre.eaufrance.fr>). These data were used to establish: 1) yield matrices, for each  
373 WWTP located on the Thau watershed, and 2) matrices of fractions of the different forms of  
374 nitrogen and phosphorus for each of the WWTP, to allow the transformation of total nitrogen  
375 and total phosphorus after treatment into their different inorganic and organic fractions  
376 necessary to force the model.

377 In a first step, the input data of WWTP undergoes a reduction corresponding to the scenario  
378 tested (see abatements, Table 1) and in a second step, the output concentrations thus estimated  
379 are fractionated according to the different forms of nitrogen and phosphorus for the  
380 corresponding WWTP. This procedure allowed for multiple different yield matrices (or input  
381 augmentations as per SCOT projections) applied to the same starting NGL and PGL datasets.  
382 This method was applied for all scenarios with three matrices of yields covering current  
383 treatment, maximum treatment and normal treatment (see sections on Reference and scenarios  
384 description).

385

## 386 2.8 Carrying capacity evaluation

387 As mentioned in the introduction, the targeted carrying capacity lies in the equilibrium  
388 between an optimised harvest without negative effects on ecological functioning. The dame  
389 index and phytoplankton depletion index were then used where the former provides a bulk  
390 information on ecosystem functioning and allows comparison between different ecosystems.  
391 Whereas the depletion index linked more finely cultured bivalves to its resource.

### 392 *2.8.1 Dame index*

393 The Dame index was calculated from the characteristic times of the lagoon (Dame and Prins.,  
394 1998). These characteristic times included: i) the lagoon renewal time (RT: time required to  
395 renew the entire lagoon volume) which is a hydrodynamic feature, ii) the phytoplankton  
396 renewal time (PPT: equivalent to the ratio of the average phytoplankton biomass to average  
397 gross primary production); and finally, iii) the clearance time (CT: time required for the total  
398 stock of shellfish to filter the lagoon volume).

399 The renewal time (RT) was calculated for the whole lagoon using the volumes entering the  
400 lagoon by the Sète channel:

$$401 \quad RT = \frac{V_{lagune}}{\overline{V}_{in}} \quad \text{Eq. 9}$$

402 Where  $V_{lagune}$  and  $\overline{V}_{in}$  were the volumes of the lagoon ( $m^3$ ) and mean annual incoming  
403 volume ( $m^3 d^{-1}$ ), respectively. This formulation gave renewal times of 48.6, 48.4 and 48.8  
404 days for the years 2014, 2015 and 2016 respectively. These RT values were in agreement with  
405 the field observations reported by Fiandrino et al. (2012) where  $RT \sim 50$  days.

406 The phytoplankton renewal time (PPT) was obtained by the ratio of the annual mean  
407 phytoplankton biomass (estimated from the Chl *a* concentration expressed in  $mmol N m^{-3}$ ) on  
408 the mean daily gross primary production (estimated from the phytoplankton growth calculated  
409 by the model and expressed in  $mmol N m^{-3} d^{-1}$ ).

410 The clearance time (CT), time required for cultured oysters to filter the volume of the lagoon,  
411 was calculated taking into account the oyster filtration rate according to the formulation of  
412 Bougrier et al. (1995):

$$413 \text{ Filtration rate} = 4,825 - (0,013 \times (T_{\circ C} - 18,954)^2) \times DFM^{0,439} \quad \text{Eq. 10}$$

414 Where  $T_{\circ C}$  was the temperature in degrees Celsius and DFM the dry weight (g) at harvest.

415 The filtration rate was expressed in  $L \text{ ind}^{-1} \text{ h}^{-1}$ . The clearance time CT was expressed by

416 comparing the filtered volume with the average volume of the lagoon:

$$417 \text{ Clearance time} = \frac{Vol_{lagoon}}{\text{filtration rate} \times \text{nb of individuals} \times 24 / 1000} \quad \text{Eq. 11}$$

418 where the filtration rate was extrapolated to the number of cultured individuals for a day and

419 expressed in  $m^3 \text{ d}^{-1}$  and  $Vol_{lagoon}$  ( $m^3$ ) to give a clearance time in days.

420 All these characteristic times were expressed in days and their ratios (CT:RT and CT:PPT)

421 potentially inform on the capacity of the lagoon to support or not a sustainable shellfish

422 production. The CT:RT ratio indicated whether filter feeders and its resources were controlled

423 by exchanges with the sea or by internal (including inputs from the watershed) availability of

424 nutrients. The CT:PPT ratio expressed directly the link between the resource and the shellfish

425 culture, where a ratio of 1 would indicate that all phytoplankton primary production was

426 consumed by filter feeders in culture and would therefore be a critical value.

### 427 2.8.2 Lagoon-scale phytoplankton depletion index

428 At the scale of the lagoon area, a phytoplankton depletion index (Filgueira et al., 2014a) was

429 calculated to determine the impact of shellfish farming on its main resource. This index

430 compared the average phytoplankton biomass in farming areas (box 4 and 5, Figure 1) with

431 the phytoplankton biomass produced outside these zones (off-table: boxes 1, 2 and 3; Figure

432 1). Negative values indicated a depletion in nutritive resource, whereas positive values

433 indicated sufficient resource for the growth of bivalves.

434 
$$\text{Lagoon - scale depletion index} = \frac{[\text{Chla}]_{\text{farms}}}{[\text{Chla}]_{\text{off-table}}} \times 100 - 100 \quad \text{Eq. 12}$$

435 This formula compared the daily average Chl *a* concentration of all shellfish growing areas  
436 (box 4 and 5, Figure 1) with the daily average Chl *a* concentration for all off-table areas  
437 (boxes 1, 2 and 3, Figure 1).

438 This index may be gauged against the natural variability of the phytoplankton biomass to  
439 evaluate the sustainability of the shellfish farming activity (Grant and Filgueira, 2011). This  
440 lagoon-scale depletion index is asymmetrical and a value of -100% indicates a complete  
441 depletion, whereas enrichment has no upper limit. For this reason, the median annual values  
442 of this index were preferred to mean values and were used to compare the scenarios.

443

## 444 2.9 Ecological indicators and ecological status

445 The compartments of the model relative to the dissolved organic and inorganic matter were  
446 used to estimate summer nutrient concentrations. 90<sup>th</sup> percentiles (p90) were calculated from  
447 the 92 daily values obtained from June 1<sup>st</sup> to August 31<sup>st</sup> for each simulated year, of dissolved  
448 inorganic nitrogen (DIN= NO<sub>3</sub><sup>-</sup> + NH<sub>4</sub><sup>+</sup>), dissolved inorganic phosphorus (DIP), total nitrogen  
449 (TN: dissolved and particulate inorganic and organic nitrogen as well as the two "small" and  
450 "large" phytoplankton compartments) and total phosphorus (TP: inorganic phosphorus and  
451 dissolved and particulate organic and phytoplankton compartments expressed as phosphorus  
452 using the Redfield (1963) N:P ratio of 16). These four variables DIN, DIP, TN and TP,  
453 represented estimates of the WFD indicators measured for the diagnosis of the ecological  
454 status of lagoon water bodies (Derolez et al., 2013). These simulated indicators were used to  
455 compare the "Reference" scenario with actual observations and the influence of the different  
456 scenarios tested on the ecological status. The model also estimated Chlorophyll *a*  
457 concentration in the water column using the "small" and "large" phytoplankton variables.  
458 These two state variables were expressed in mmol N m<sup>-3</sup> in the model and converted to µg

459 Chl *a* l<sup>-1</sup> using a conversion factor of 1 (Parsons et al., 1961). The summer averages obtained  
460 from the simulations were used as an indicator of the phytoplankton biomass as in the WFD  
461 diagnosis. Finally, the TN to TP ratio was used as an indicator of nitrogen and phosphorus  
462 balance within the system.

463

## 464 2.10 Statistical analyses

465 Data did not fulfilled tests for both normality and homosedasticity and non-parametric,  
466 Kruskal-Wallis, was therefore used for statistical analysis. Correlations were determined  
467 following Spearman correlation coefficient,  $\rho$ . Statistical analyses were considered  
468 significant with p-value < 0.01. Principal component analysis (PCA) was performed on model  
469 outputs presented in this work. All statistical analyses were performed using the R software  
470 (R Core Team, 2017).

471

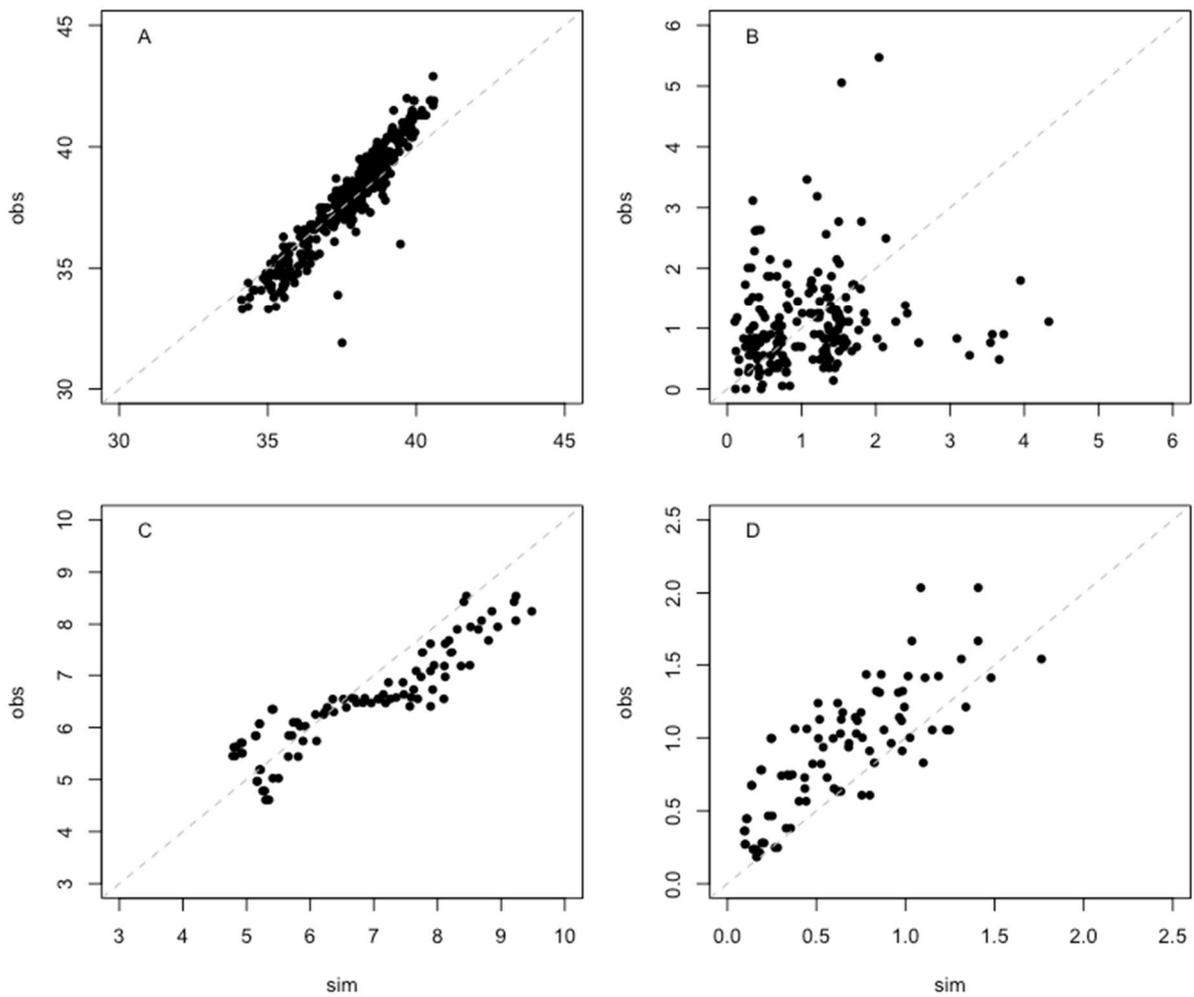
## 472 3 Results

### 473 3.1 Model skills

474 Model skills evaluation was based on model outputs of the “Reference” scenario representing  
475 current situation. The GAMELag-Conch model satisfactorily simulated observations of  
476 salinity (Figure 3-A) for both shellfish farming zones with a Willmott index “d” of 0.96  
477 (linear regression  $r^2 = 0.91$ ). This agreement between observed and simulated values  
478 prevailed the good representation of the lagoon hydrodynamics when described by 3 physical  
479 boxes (see “Carrying capacity model” description”).

480 Similar to salinity, model outputs were correctly correlated with the observed length (Figure  
481 3-C) and dry weight (Figure 3-D) of oysters, with Willmott index of 0.69 ( $r^2 = 0.77$ ) and 0.76  
482 ( $r^2 = 0.76$ ) respectively.

483



484

485 Figure 3. Biplots of simulated vs. observed salinity (A), Chl *a* concentration ( $\mu\text{g l}^{-1}$ , B), oysters shell  
 486 length *L* (cm, C) and oyster dry weight (g, D) extracted from model outputs within the two shellfish  
 487 farming zones (box 4 and 5).

488

489 A poorer Willmott index was found for the Chl *a* variable at  $d=0.46$  ( $r^2 = 0.03$ ). The  
 490 comparison of observations against simulations indicated that simulated Chl *a* concentrations  
 491 were within the range of observations for concentrations lower than  $2.5 \mu\text{g Chl } a \cdot \text{L}^{-1}$ .  
 492 However, the model could not capture the timing of extreme values (peaks), which explained  
 493 the mismatch on Figure 3-B for high Chl *a* concentrations.

494

495 3.2 Nutrients inputs and shellfish performances

496 For the three simulated years and all the scenarios, annual nutrient inputs varied from 25.5 to  
497 198.6 tons of nitrogen and from 1.8 to 13.8 tons of phosphorus (Table 2). These ranges  
498 included lower and higher values of nutrient inputs than that of the Reference scenario (39.4  
499 to 111.5 t of N and 6.1 to 10.2 t of P, Table 2). Results presented in Fig. 4 and Table 2  
500 highlighted the significant variability of oyster performances (weight and production)  
501 according to years and scenarios of nutrient inputs. The variability of oyster production as  
502 well as total weight of oyster, was mainly controlled by the hydrometeorology, with oyster  
503 production being 1.8-2.3 times higher during rainy years than dry years whatever the tested  
504 scenario (Table 2). Total weight of oysters at harvest varied between 36.6 to 100.5 g (Table 2)  
505 according to scenarios and simulated years. Similar to production, total weight was  
506 significantly higher in wet years than dry years (Kruskal-Wallis,  $p < 0.05$ ), although no  
507 significant differences were found between scenarios. In comparison to the current situation  
508 (Reference), higher oyster productions were simulated with normal waste water treatment  
509 plant efficiency (Normal Yield:  $\square 75\%$  N,  $\square 60\%$  P) with an additional 1700 t produced during  
510 dry years corresponding to an increase in production of 25%. This increase was less important  
511 during wet years (940-1200 t, +5-7%). By contrast, maximum WWTP efficiency (Max yield  
512  $\square 90\%$  N & P) induced a mean decrease of 1598 t, corresponding to a decrease of 12% in  
513 comparison with mean reference production. The foreseen increase in population (SCOT  
514 scenario) induced a mean increase in oyster production of 5%. Finally, in the Sète scenario,  
515 oyster production was not enhanced and recorded 875 t less than reference production (Table  
516 2), while nitrogen and phosphorus inputs were significantly higher than reference (1.8-2.8  
517 times more N and 1.3-1.5 more P). Scenario of oyster stocking density to its authorized  
518 maximum (by the French regulation body) triggered a mean increase of oyster productions by  
519 7% at the expenses of thinner oysters with a lower condition index.

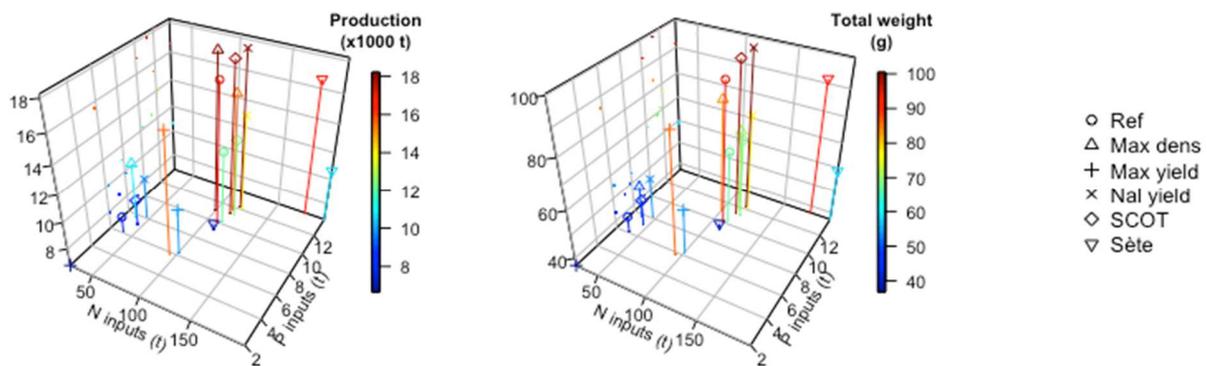
520 Table 2. Summary of simulations inputs and outputs for the three years (2014-2015-2016) and the six scenarios tested.

	Annual N inputs (t)	Annual P inputs (t)	Inputs N:P molar ratio	Production at harvest (tons)	Length at harvest (cm)	Total weight at harvest (g)	Condition index at harvest (%)	Ecological status <sup>a</sup> [NID-PID-TN-TP-CHLA-TN:TP] Summer – P90 – (µM)	RT (days)	CT (days)	PPT (days)	Median lagoon-scale depletion index (%)
<b>Reference</b>												
2014	109.2	10.1	23.9	16977	9.5	93.7	17.5	[0.31-0.50-16.00-1.29-1.68-13.52]	48.6	17.4	6.3	-14.1
2015	39.4	6.1	14.3	7896	8.0	43.6	9.7	[0.49-0.45-20.35-1.39-3.57-18.52]	48.4	20.1	7.1	-12.8
2016	113.8	10.2	24.7	12208	8.8	67.4	13.6	[0.34-0.46-18.56-1.35-3.43-16.65]	48.8	18.2	7.4	-14.0
Mean ± sd	87.5 ± 41.7	8.8 ± 2.3	21.0 ± 5.8	12360 ± 4542	8.8 ± 0.8	68.2 ± 25.1	13.6 ± 3.9	[0.38-0.47-18.30-1.34-2.89-16.23]	48.6 ± 0.2	18.6 ± 1.4	6.9 ± 0.6	-13.6 ± 0.7
<b>Max. yield</b>												
2014	93.9	5.8	35.7	15606	9.4	86.2	16.3	[0.31-0.41-15.64-1.19-1.70-14.56]	48.6	17.3	6.0	-14.2
2015	25.5	2.0	28.8	6669	7.5	36.8	8.7	[0.50-0.48-21.15-1.48-3.90-18.88]	48.4	19.8	7.2	-12.4
2016	100.2	6.3	35.5	10011	8.3	55.2	11.8	[0.34-0.47-19.18-1.40-3.62-17.82]	48.8	18.0	7.4	-13.7
Mean ± sd	73.2 ± 41.4	4.7 ± 2.4	33.3 ± 3.9	10762 ± 4515	8.4 ± 0.9	59.4 ± 25.0	12.3 ± 3.8	[0.38-0.46-18.65-1.35-3.07-17.09]	48.6 ± 0.2	18.4 ± 1.3	6.9 ± 0.7	-13.4 ± 0.9
<b>Normal yield</b>												
2014	118.6	12.3	21.4	18194	9.6	100.5	18.7	[0.31-0.54-16.27-1.35-1.68-13.19]	48.6	17.4	6.6	-14.0
2015	46.4	8.1	12.7	9838	8.4	54.3	11.6	[0.49-0.40-19.43-1.30-3.14-18.59]	48.4	20.6	7.1	-13.3
2016	20.8	12.2	22.0	13909	9.2	76.8	14.9	[0.32-0.42-17.73-1.27-3.15-16.65]	48.8	18.4	7.5	-14.2
Mean ± sd	95.3 ± 42.3	10.8 ± 2.4	18.7 ± 5.2	13981 ± 4178	9.0 ± 0.6	77.2 ± 23.0	15.0 ± 3.6	[0.37-0.45-17.81-1.30-2.66-16.14]	48.6 ± 0.2	18.8 ± 1.7	7.1 ± 0.5	-13.8 ± 0.5
<b>SCOT</b>												
2014	114.8	11.2	22.6	17894	9.6	98.8	18.4	[0.31-0.52-16.14-1.32-1.67-13.32]	48.6	17.4	6.4	-14.0
2015	44.6	7.2	13.7	8610	8.2	47.5	10.3	[0.50-0.43-19.97-1.35-3.41-18.58]	48.4	20.3	7.1	-13.0
2016	118.9	12.2	23.3	12571	9.0	69.4	13.8	[0.33-0.45-18.35-1.32-3.27-16.61]	48.8	18.3	7.4	-14.2
Mean ± sd	92.8 ± 41.7	9.9 ± 2.3	19.9 ± 5.4	13025 ± 4658	8.9 ± 0.7	71.9 ± 25.7	14.2 ± 4.0	[0.38-0.47-18.15-1.33-2.79-16.17]	48.6 ± 0.2	18.7 ± 1.5	7.0 ± 0.5	-13.7 ± 0.6
<b>Sète</b>												
2014	178.7	13.8	28.7	16616	9.5	91.8	17.1	[0.31-0.48-16.84-1.30-1.68-14.13]	48.7	17.3	5.9	-14.2
2015	112.3	9.2	26.9	7184	7.8	39.7	9.1	[0.51-0.50-22.35-1.52-3.91-18.92]	48.5	20.0	6.8	-12.6
2016	198.6	13.6	31.7	10654	8.5	58.8	12.4	[0.34-0.50-20.71-1.47-3.68-18.14]	48.9	18.0	7.2	-13.8
Mean ± sd	163.2 ± 45.2	12.3 ± 2.6	29.1 ± 2.4	11485 ± 4770	8.6 ± 0.9	63.4 ± 26.4	12.9 ± 4.0	[0.39-0.49-19.97-1.43-3.09-17.06]	48.7 ± 0.2	18.5 ± 1.3	6.6 ± 0.6	-13.6 ± 0.8
<b>Max density</b>												
2014	109.2	10.1	23.9	18735	9.3	85.8	16.5	[0.31-0.52-16.00-1.31-1.87-13.46]	48.6	14.1	6.0	-15.1
2015	39.4	6.1	14.3	7976	7.8	36.6	8.3	[0.44-0.48-20.57-1.44-3.69-18.41]	48.4	16.1	6.8	-13.4
2016	113.8	10.2	24.7	12936	8.5	59.2	12.5	[0.34-0.54-19.16-1.47-3.56-16.57]	48.8	14.8	7.1	-14.5
Mean ± sd	87.5 ± 41.7	8.8 ± 2.3	21.0 ± 5.8	13216 ± 5385	8.5 ± 0.7	60.6 ± 24.7	12.4 ± 4.1	[0.38-0.43-17.00-1.24-2.35-16.07]	48.6 ± 0.2	15.0 ± 1.0	6.7 ± 0.6	-14.3 ± 0.9

<sup>a</sup>: ecological status based on 90<sup>th</sup> percentile on indicators: NID, PID, TN, TP and Chla. Color code gives the class of these indicators: “High” (blue), “Good” (green), “Average” (yellow), “Bad” (orange) and “very bad” (red).

521 To conclude oyster production, the comparison of scenarios showed that only “Sète” (n°5)  
 522 and “Max. yield” (n°2) scenarios induced lower oyster production than “Reference” scenario  
 523 exhibiting a decrease of 8 and 16 % respectively. All other scenarios that involved increased  
 524 nutrient inputs, “Nal yield” (n°3) and “SCOT” (n°4), presented higher oyster production  
 525 levels with sensibly higher shell length and total weight (Table 2). On the contrary, if scenario  
 526 “Max. dens.” (n° 6) rendered higher oyster production than “Reference” scenario, no increase  
 527 of length or total weight of individuals was apparent. Oyster condition index (CI) was used as  
 528 a proxy for the health of oysters and was significantly lower in 2015 (Kruskal-Wallis,  $p <$   
 529 0.05) with no differences between scenarios.

530 When discriminating dry and wet years, according to the different nitrogen and phosphorus  
 531 inputs simulated, one can note on Figure 4 that oyster production values were maximized for  
 532 a mass ratio N:P of the watershed contributions around 8.3 (that is, about 100 t N for 12 t P or  
 533 a molar ratio of 18.4; Figure 4).



534  
 535 Figure 4. 3D scatter plot of production ( $10^3$  t) and total weight (g) of oysters as function of N and P  
 536 inputs (t) according to scenarios and years (see legend inset).

537  
 538 This seemingly optimal N:P ratio was obtained for the scenarios varying nutrient loadings  
 539 "Nal yield" (n°3), "SCOT" (n°4) and “Reference” during" wet years (2014 & 2016) but not  
 540 during 2015 (Table 2) where N:P ratio was 6.6.

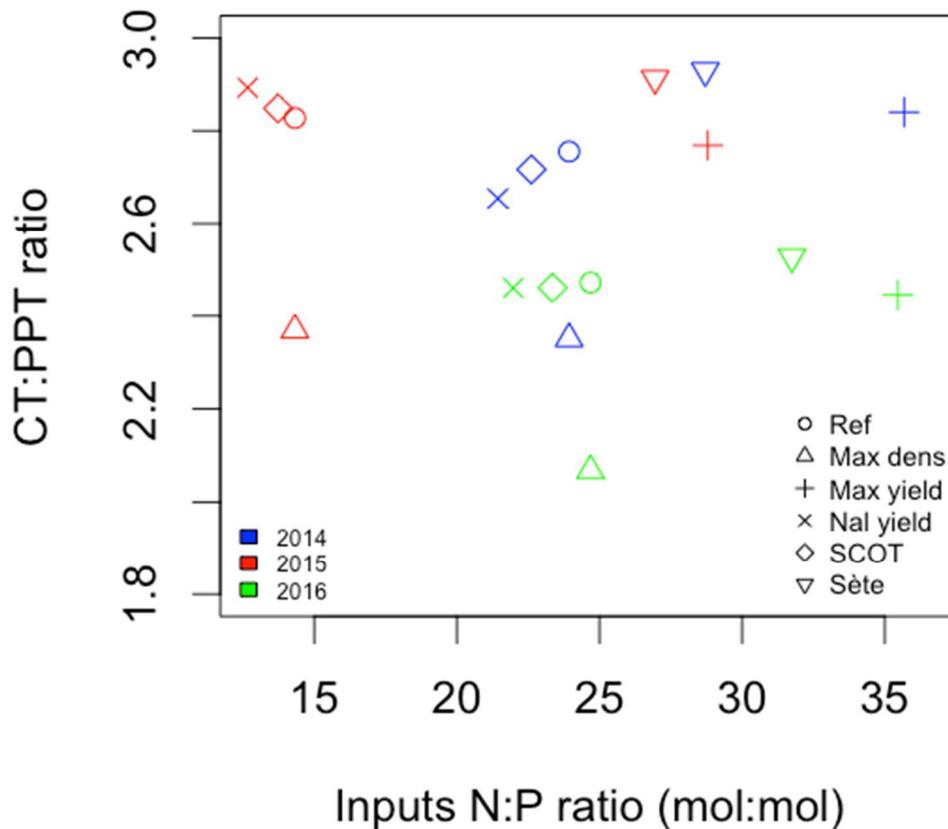
541 In fact, the nitrogen inputs according to the different scenarios during the dry year (2015)  
542 varied from 25% to 50% of those during the two wet years (2014 and 2016) with the largest  
543 difference between dry and wet years recorded for the “Max. yield” scenario (Table 2). For  
544 phosphorus, the variability of the contributions according to the hydrometeorology was less  
545 marked. Nevertheless, inputs of phosphorus in the dry year were 1.5 to 3 times lower than for  
546 wet years. This difference between wet and dry years was also largely marked by a significant  
547 modification of the contribution of the WWTP to the total inputs of the watershed reaching  
548 89% on average in a dry year. Nitrogen to phosphorus mass ratios of inputs varied from 4.6 to  
549 16.0 (10-35 mol:mol) depending on the year and scenario and encompassed the optimal 8.3  
550 N:P value linked to the highest oyster productions obtained in our simulations.

551

### 552 3.3 Carrying capacity

553 While renewal time (RT) seemed constant and corresponded to 48.6 days (Table 2),  
554 phytoplankton biomass renewal time (PPT) and clearance time (CT) varied according to  
555 scenarios with minimal and maximal means observed for “Max density” and “Normal yield”  
556 scenarios respectively (Table 2). The CT:RT ratio remained constant regardless of the nutrient  
557 loading scenario (mean of 0.38) and was lower as part of the “Max density” scenario (mean  
558 0.30), indicating that water renewal times exceeded clearance times. The CT:PPT ratios  
559 ranged from 2.06 to 2.93 with minimal mean observed at “Max density” (Table 2, Figure 5),  
560 indicating that shellfish culture pressure on phytoplankton was not critical, because clearance  
561 time was of 34% to 50% of phytoplankton production potential. In other words, the renewal  
562 time of phytoplankton production in the Thau lagoon was systematically twice as fast as the  
563 time required for oysters to filter all the phytoplankton biomass produced. This “Max.  
564 density” scenario led to the lowest CT:PPT ratios with values of 2.13, 2.45 and 1.98 for 2014,

565 2015 and 2016 respectively, revealing a stronger pressure of shellfish farming on its  
566 phytoplankton resources than the other scenarios.

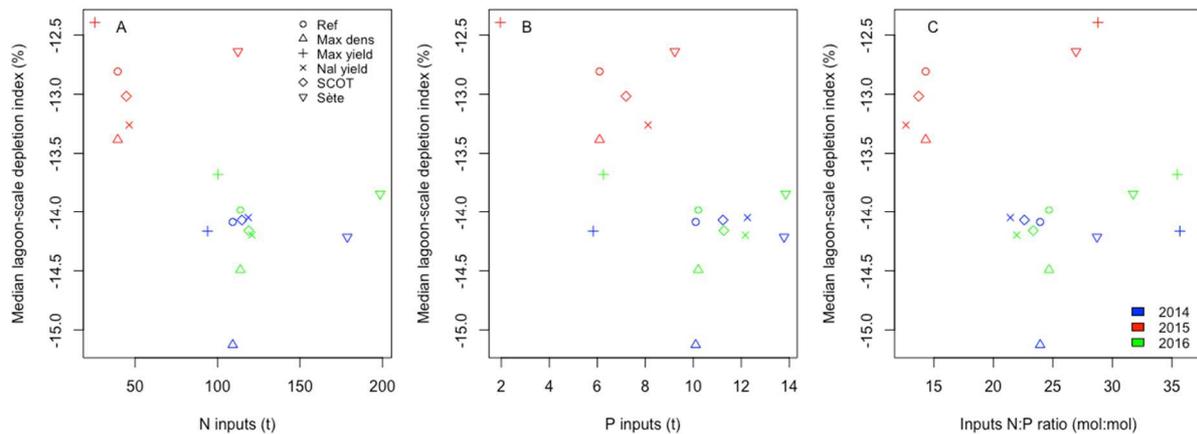


567  
568 Figure 5. Clearance time to phytoplankton renewal time ratio as a function of inputs N:P molar ratios  
569 plotted for the 3 simulated years and all scenarios (see legend inset).

570  
571 This pressure was accompanied by the lowest lagoon-scale phytoplankton depletion index  
572 over these three simulated years (Table 2). The CT:RT and CT:PPT ratios showed no  
573 significant correlation with N:P ratio of catchment inputs.

574 For the "Reference" scenario presented (Figure 6), the median value of this index varied  
575 between -14% and -13% indicating that the lagoon was in slight depletion conditions but may  
576 support shellfish production. The median lagoon-scale depletion indices appeared consistently  
577 negative, regardless of the scenario tested (Figure 6-A, B & C). Overall median lagoon-scale

578 depletion indices varied between -12.3 and -15.1% depending on the year and scenarios  
 579 tested, but they did not show a clear trend depending on the amount of nitrogen or phosphorus  
 580 brought by the watershed (Figure 6- A and B). The range of values of the median depletion  
 581 index was bounded by the scenarios "Max. density" and "Max. yield". The difference between  
 582 simulated years was the main contrast between these median values of the depletion index  
 583 (Kruskal-Wallis, p-value <0.01). Figure 6-C showed these median depletion indices as a  
 584 function of the N:P ratios of the catchment contributions and the values of these indices  
 585 decreased with decreasing N:P ratio of watershed inputs in 2015 and 2016 (Spearman  
 586 correlation coefficient of -0.83 and -0.94, respectively).

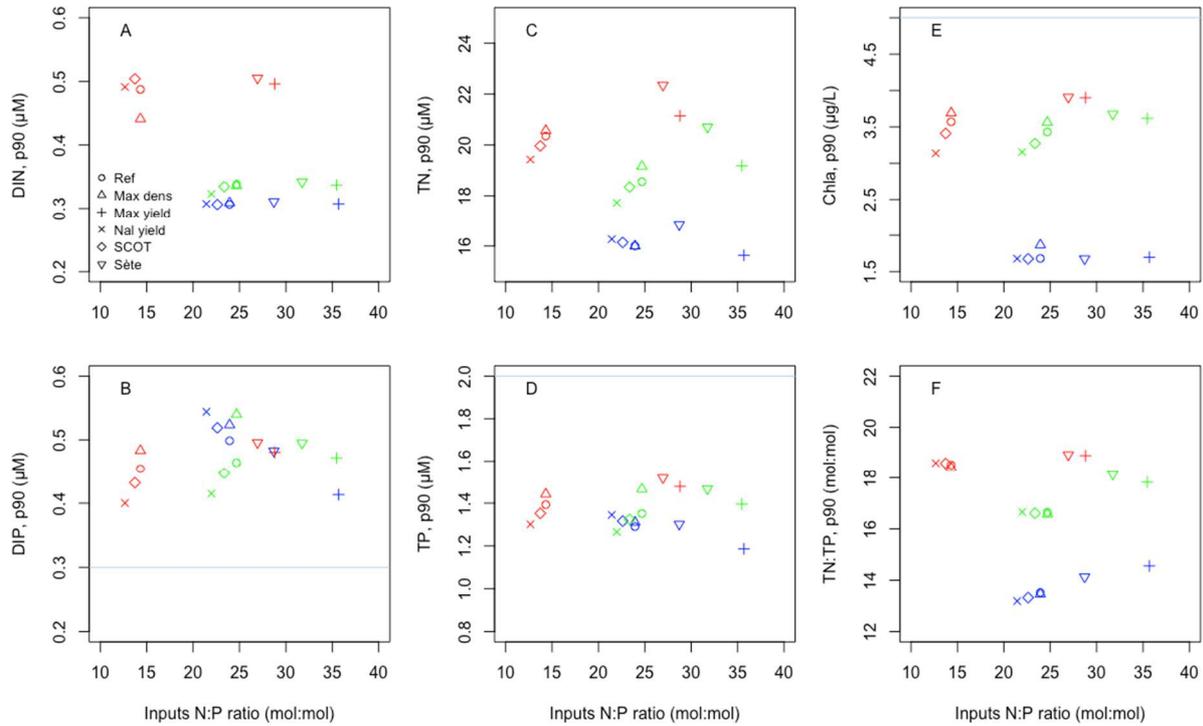


587  
 588 Figure 6. Median lagoon-scale depletion index expressed as a function of N inputs (A), P inputs (B)  
 589 and inputs N:P molar ratio (C).

590  
 591 **3.4 Ecological Status**

592 Although carrying capacity can be assessed through different indices, ecological status of the  
 593 lagoon must be regarded as another major characteristic depending on nutrient loadings or  
 594 shellfish culture practices. The p90 summer concentrations of DIN, DIP, TN and TP, derived  
 595 from the "Reference" simulations (Figure 7-A, B & C) were consistent with the  
 596 concentrations observed in the water column of Thau lagoon in the context of the 2011-2016  
 597 WFD diagnosis (concentrations measured: 0.2, 0.2, 22.2, 0.9  $\mu\text{mol.l}^{-1}$  respectively) (Derolez

598 et al., 2017). DIN p90 were significantly higher (Kruskal-Wallis, p-value < 0.001) in 2015  
 599 (mean = 0.49) than in 2014 and 2016 (mean: 0.31 and 0.33, respectively), regardless of the  
 600 scenario tested.

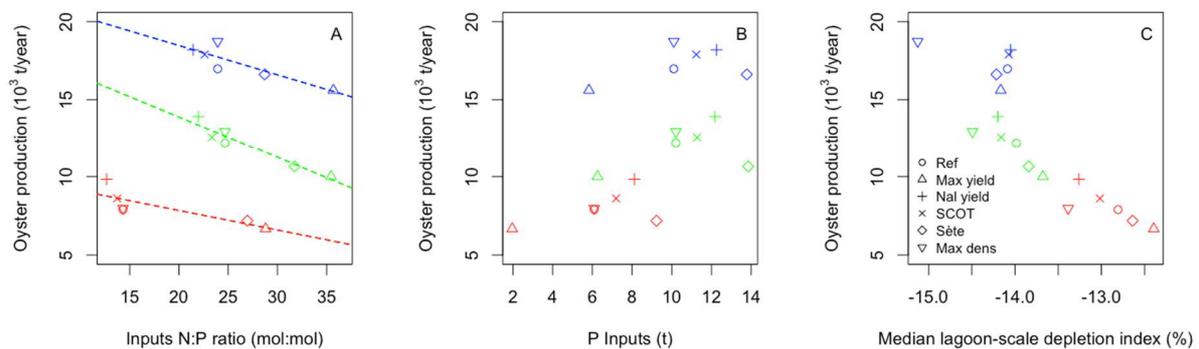


601  
 602 Figure 7. 90<sup>th</sup> percentiles for DIN (A), DIP (B), TN (C), TP (D), Chl *a* (E) and TN:TP ratio (F) as a  
 603 function of inputs N:P molar ratio for all scenarios (see legend in Figure A inset). Colors correspond  
 604 to simulated years (2014: blue, 2015: red, 2016: green). High/Good ecological status thresholds  
 605 according to WFD are represented by blue lines for DIP, TP and Chl *a*. These thresholds were not  
 606 visible for DIN (2 µM) and TN (50 µM).

607  
 608 TN p90 were contrasted between years with significant differences recorded between 2014  
 609 and the two other years 2015 and 2016 (Kruskal-Wallis, p-value < 0.001). Finally, Chl *a* p90  
 610 were found significantly lower (Kruskal-Wallis, p-value < 0.001) in 2014 (mean = 1.71 µg.l<sup>-1</sup>)  
 611 than 2015 and 2016 (mean = 3.60 and 3.45 µg.l<sup>-1</sup>, respectively).

612 However, the model seemed to underestimate TN values (17.6 and 20.4 µmol.l<sup>-1</sup> for the  
 613 "Reference" scenario, n=92 and all scenarios, n=552, respectively). Nitrogen and Phosphorus  
 614 inputs, associated with the different scenarios, did not seem to affect the ecological diagnosis

615 of the water column based on nutrient indicators as none of these scenarios triggered a  
 616 modification of ecological status classes. These simulated indicators gave p90 values in  
 617 agreement with the "High" status fixed by WFD (MEDDE, 2015), in accordance with the  
 618 High status evaluated by 2011-2016 WFD diagnosis. Only simulated DIP concentrations were  
 619 classified in the "good" ecological status for all scenarios (Table 2). Shellfish production at  
 620 harvest, for all scenarios, decreased significantly for a given year when the N:P ratio of  
 621 catchment contributions increased (Figure 8-A). These relationships have a Spearman  
 622 correlation coefficient of -0.75, -0.98 and -0.90 for years 2014, 2015 and 2016 respectively  
 623 (p-value <0.05 for the three relationships) although no significant relationship has been  
 624 established between shellfish production and nitrogen inputs or phosphorus inputs  
 625 independently.



626  
 627 Figure 8. Oyster production as a function of (A) inputs N:P ratio, (B) phosphorus inputs and (C)  
 628 median lagoon-scale depletion index for the three years (2014: blue, 2015: red, 2016: green) and all  
 629 scenarios (see legend inset).  
 630 In addition, production was negatively correlated with the median lagoon-scale depletion  
 631 index, but this relationship was not linear for a given year (Fig. 8-B).  
 632 The "Max. Dens." Scenario (n°6) had the lowest median depletion index (Figure 8-B)  
 633 indicating that it had more impact on phytoplankton biomass than scenarios with comparable  
 634 production outputs (ie "Nal Yield", scenario n°3). On the other hand, the "Max. yield" (n°2)  
 635 and "Sète" (n°5) scenarios gave the highest median depletion indexes but at the expense of

636 lower oyster productions. The comparison of nitrogen and phosphorus quantities added to the  
637 lagoon in each of the three simulated years showed the role of the hydro-meteorology on  
638 oyster production.

639

#### 640 4 Discussion

641 The GAMELag-Conch model was developed to address the questions related to the  
642 management of the Thau lagoon ecosystem with regards to the issues of shellfish production  
643 and ecological status regulations. Scenarios tested were developed from realistic management  
644 hypotheses. These hypotheses included leverages on the quantities of nitrogen and  
645 phosphorus potentially available through waste water treatment plant management or on the  
646 quantities of cultured filter feeders introduced in farming zones.

647

#### 648 4.1 Scenarios and oyster performances

649 All scenarios tested in this study were based on achievable management objectives. In this  
650 respect, little difference was highlighted from oyster performance model outputs when  
651 comparing scenarios. Although, nutrient loadings, in terms of nitrogen and phosphorus, were  
652 varying with these different scenarios, the highest increase in oyster production was recorded  
653 at +25% (“Normal yield” scenario) in 2015 in comparison to “Reference”. This specific case  
654 corresponded to the modification of the Mèze WWTP efficiency, going from maximum to  
655 normal abatements, and a very dry year (2015, - 200 mm) where WWTP effluents were the  
656 main contributors to nutrient loadings (+7 t N and +2 t P). To a lesser extent, “SCOT” and  
657 “Max. density” scenarios also demonstrated an increase in oyster production but limited to +3  
658 to +9% and +1 to +10%, respectively. The effect of increased nutrient loadings, mainly  
659 nitrogen, on the production of cultured filter feeders has already been reported in modelling  
660 studies (Ferreira et al., 2007; Guyondet et al., 2014; Rose et al., 2015). On the opposite,

661 reducing nutrient loadings from the watershed (scenario “Max yield” in this study) through  
662 the improvement of waste water treatment efficiency triggered a loss in production between -  
663 8% and -18% compared to our “Reference” scenario further indicating this dependence of  
664 oyster farming on nutrient supply of the Thau system. However, the variation in nutrient  
665 loadings quantity may not solely explain the response of cultured oyster as large addition of  
666 nitrogen (+171%) in the “Sète” scenario rendered lower oyster production than “Reference” (-  
667 2% to -13%). This effect is probably linked to the joint influence of nitrogen and phosphorus  
668 additions, the location of these inputs and the response of the biological compartments and is  
669 further discussed below. In terms of oyster performances, scenarios associated with increased  
670 nutrient loadings demonstrated that oysters marginally gained in length, quality (condition  
671 index) and total weight at harvest but remained in the same market grade (66-85 g; according  
672 to the French 6 grades weight where n°5: 30-45g, n°4: 46-65g, n°3:66-85g, n°2: 86-110g, n°1:  
673 111-150g and n°0: over 151g ). However, a reduction of, as well as unbalanced, nutrient  
674 loadings, produced smaller oysters and a modification of the market grade (46-65 g) with  
675 potential repercussion on economic aspects (Ferreira et al., 2007). Finally, “Max. density”  
676 scenario demonstrated higher oyster production but at the expenses of thinner oysters with  
677 lower condition index. This scenario highlighted the density effect where an increased  
678 abundance triggered a competition for the resources yielding smaller individuals (Gangnery et  
679 al., 2001; Gangnery, 2003; Filgueira et al., 2014b).

680 The scenarios tested here have revealed differences in terms of oyster performances and  
681 productions, however, major contrasts were brought by interannual variability where dry  
682 against wet years triggered the largest variations in nutrient loadings. Consequently, oyster  
683 productions were significantly lower in years presenting evident rainfall deficit. Oyster  
684 lengths, total weight and condition index were also significantly affected with smaller, lighter  
685 and lower quality during dry years. Nevertheless, oyster production and performances

686 evaluated through this modelling work shall be replaced within the context of ecological  
687 status and ecological carrying capacity to better assess overall functioning of the ecosystem  
688 (Byron et al., 2011b; Higgins et al., 2011).

689

#### 690 4.2 Trophic carrying capacity and ecological status

691 One of the objectives of this work was to assess the carrying capacity of the Thau lagoon  
692 regarding to shellfish farming within the frame of WFD regulation. The Thau lagoon, as any  
693 other shellfish farming sites, is characterized by complex dynamics of interacting biological  
694 and physical processes. Within these systems, filter feeding activity may deeply modify the  
695 energy fluxes as they clear large volume of water including suspended particles (Dowd, 2003;  
696 Filgueira et al., 2014a).

697 To evaluate the capability of an ecosystem to support various uses, it is important to compare  
698 phytoplankton production, phytoplankton biomass, lagoon hydrodynamics as well as shellfish  
699 culture pressure to truly highlight the limits of the ecosystem. A first approach using these  
700 different aspects of the functioning of the ecosystem is the Dame index (Dame and Prins.,  
701 1998). This index relates the characteristic times RT (renewal time), CT (clearance time) and  
702 PPT (phytoplankton biomass renewal time) of the Thau lagoon. The CT:RT ratio indicates  
703 whether filter feeders and its resources are controlled by exchanges with the sea or by internal  
704 (including inputs from the watershed) availability of nutrients. The GAMELag-Conh model  
705 was able to simulate oyster productions along with indicators of the ecological status,  
706 depletion index and characteristic times (CT, RT, PPT) comparatively with different scenarios  
707 of nutrient inputs and shellfish cultures. The relationships between oyster production and the  
708 carrying capacity of the lagoon was evaluated with regards to the Dame index, particularly the  
709 CT:PPT ratio, and the lagoon-scale phytoplankton depletion index. Both markers  
710 demonstrated a top-down control of filter feeders on phytoplankton population. In this study,

711 simulated clearance and water renewal times, CT and RT, indicated that hydrodynamic  
712 exchanges with the far field (outside the lagoon) were not efficient enough to drive the filter  
713 feeder resources. Therefore, phytoplankton dynamic or its bottom-up control, would rather be  
714 driven by nutrients coming from the watershed. In comparison, the Marennes-Oléron site  
715 (Bacher, 1989; Dame and Prins., 1998; Raillard and Menesguen, 1994) showed slower  
716 phytoplankton biomass renewal times and much faster filtration capacity resulting in a system  
717 that did appear to be largely under pressure (Marennes-Oléron CT:PPT = 0.27) despite a more  
718 efficient hydrodynamics than in the Thau lagoon (Marennes-Oléron RT = 7.1). The simulated  
719 values of the CT:PPT ratio suggested that the consumption of phytoplankton biomass by  
720 farmed oysters was constrained between 34 and 50%, leaving half, or more, of the  
721 phytoplankton stock available for other trophic levels. Trousselier & Deslous-Paoli (2001)  
722 had also concluded that Thau lagoon was productive in the 1990s, with shellfish harvested  
723 production representing about 3% of primary production. Dame and Prins (1998) postulated  
724 that successful shellfish population occur when RT is less than 40 days and PPT below 4  
725 days. If characteristic times calculated for the Thau lagoon are longer than these  
726 recommended times, shellfish cultures have prospered in the Thau lagoon and its carrying  
727 capacity did not seem to be threatened. Both ratios, CT:RT and CT:PPT, expressed the state  
728 of the carrying capacity of the lagoon by comparing the characteristic times of physics,  
729 phytoplankton, and shellfish in culture (Table 2). However, they do not consider the presence  
730 of nutritive resources other than phytoplankton such as zooplankton or particulate organic  
731 matter. The model outputs indicated that oyster production is related to the input N:P molar  
732 ratio with production increasing with decreasing N:P ratios. These linear relationships were  
733 contrasted between years, highlighting the strong influence of the hydrological regime and  
734 hence the quantities of nitrogen and phosphorus entering the lagoon. These first relationships  
735 were bounded by the maximum WWTP yield and normal WWTP yield scenarios as they

736 provided the highest and lowest input N:P molar ratio, respectively. This also revealed that, if  
737 filter feeder production might be increased by decreasing the N:P ratio of inputs, the amount  
738 of nutrients coming from the watershed, most probably phosphorus, would limit the  
739 maximum levels of production to be reached. The shellfish productions were also increasing  
740 with decreasing lagoon-scale depletion index indicating that more production would trigger  
741 higher depletion of the Thau system. Once again, the most apparent contrast was linked to the  
742 different simulated years where higher nutrient loadings generated higher shellfish  
743 productions and hence an increased pressure on its phytoplankton resource. N:P ratio of  
744 loadings, however, was similar in 2014 and 2016, whereas phytoplankton summer biomass  
745 was similar in 2015 and 2015. Therefore, higher oyster production and subsequent increased  
746 filter feeder pressure could not only be explained by nutrient loadings. Annual mean  
747 temperature anomaly, compared to the 1970-2016 mean (15.3°C) was +1.5°C, +1.4°C and  
748 +1.1°C for 2014, 2015 and 2016 respectively. In previous modelling studies (Filgueira et al.,  
749 2016), increased temperature has been identified as a key factor in enhancing grazer activity  
750 through higher metabolism with concomitant higher pressure on phytoplankton. The highest  
751 oyster production simulated in 2014 would be in agreement with highest annual average  
752 temperature recorded in 2014 for the Thau lagoon. In addition, 2015 was associated with low  
753 nutrient inputs, which resulted in low oyster performances, even if temperature anomaly was  
754 similar to 2014. In this second relationship (e.g. oyster production against depletion index),  
755 oyster production was bounded by the maximum oyster densities and the maximum WWTP  
756 yield scenarios. The use of maximum allowed stocking densities generated the highest  
757 depletion in agreement with the density effect (Chapelle et al., 2000; Grant et al., 2007;  
758 Grangeré et al., 2010).

759 The increase in the quantities of seeded shellfish did not lead to significantly higher harvests  
760 compared to the “Reference” scenario (1 to 10%). Moreover, the shellfish thus produced were

761 smaller, probably because of the competition for the nutritive resource between growing  
762 individuals. This scenario also exhibited the lowest CT:PPT ratios indicating a noticeable  
763 pressure of farmed oysters on their phytoplankton resource. Accordingly, highest depletion  
764 was recorded when increasing stocking densities, which corroborates this impact on  
765 phytoplankton stock. However, Chl *a* concentrations, used in the ecological status evaluation,  
766 were not lower in the presence of higher densities of filter feeders than with the other  
767 scenarios. This might be explained either by the fact that: 1) energy stocks of filter feeders  
768 during the summer are allocated to spawning rather than nutrition (e.g. filtration), or 2) the  
769 increase in cultured bivalve density may have a positive feedback effect on phytoplankton  
770 outside growing structures through more excretion of inorganic nutrients (Filgueira et al.,  
771 2014b; Kellogg et al., 2014).

772 It is important to note that shellfish farming activities occupy about 20% of the Thau lagoon  
773 area (~ 30% by volume) which is probably a criterion of its durability. In agreement with the  
774 occupational state of the Thau lagoon, Byron et al (2011b) reported, using the Ecopath model  
775 on the Narragansett bay, another example of a low-intensity of shellfish cultures where  
776 carrying capacity is not reached due to high nutrient loadings and primary productivity. These  
777 authors evaluated that if shellfish cultures density remained at current levels, the growing area  
778 might theoretically be extended up to 26% of the bay area without exceeding the ecological  
779 carrying capacity. On the contrary, the study by Filgueira et al. (2014), concerning a bay  
780 occupied at 80% in volume by the mussel farms, showed a strong impact on the  
781 phytoplankton resource, where the median bay-scale depletion index (-34.2%) was below the  
782 sustainable threshold calculated from natural variability of Chl *a* concentration (-27.5%). This  
783 shellfish farming pressure was also reported, to a lesser extent, in Saint Peter's Bay  
784 (Guyondet et al, 2015), where only the central part of the bay exhibited depletion for a total  
785 farmed area of 40%.

786 The simulated ecological indicators were chosen to correspond to the observations used in the  
787 WFD diagnosis (EC, 2000). Regardless of scenarios or simulated years, these ecological  
788 indicators fell into the “high” ecological status class. Only, simulated DIP concentrations  
789 exceeded the “high” to “good” threshold ( $0.3 \mu\text{M}$ ), hence placing the ecological status of the  
790 lagoon into the “good” conditions for the water column chemistry. The comparison of  
791 simulated years or scenarios showed significant differences for DIN between dry and wet  
792 years with higher concentrations recorded during the dry year (2015) and for Chl *a* where  
793 concentrations in 2015 and 2016 were found higher than in 2014. The main concluding  
794 remarks on this ecological status evaluation is that scenarios tested in this study did not  
795 altered the ecological status of the lagoon. In addition to this fulfilling “high” ecological  
796 status, weak phytoplankton depletion and the moderate pressure of cultured oysters on their  
797 resources, the current oyster production (“Ref”, scenario n°1), oscillating between 7900 and  
798 17000 tons, would therefore be sustainable and not conflicting with EU regulation nor are  
799 opposed to the important efforts made to reduce nutrient inputs from the watershed. Indeed,  
800 ecological carrying capacity appears as a major component in the evaluation of the whole  
801 ecosystem functioning and should be carefully considered at the same level as ecological  
802 status.

803

#### 804 4.3 Control of lagoon phytoplankton and shellfish productivity

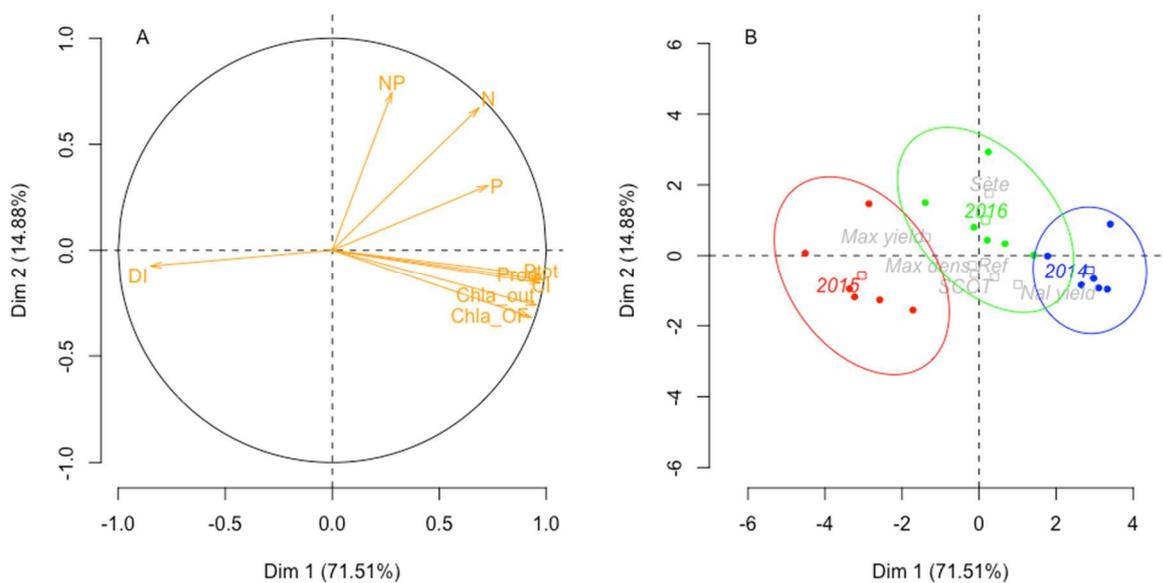
805 The results obtained in this modeling work of the Thau lagoon seemed to indicate a control of  
806 the system by the nitrogen and phosphorus inputs from the watershed and more precisely by  
807 the N:P ratio of these inputs. When the inputs related to the various scenarios are detailed, it  
808 appeared that if the N inputs from the watershed covered a wide range of values (25.5 to  
809 198.6 tons), the variability of phosphorus inputs was much smaller (1.8 to 13.8 tons). The  
810 variability of N and P inputs related to the hydrometeorological regime seemed the main

811 driver for the variability of shellfish production. Increases of 57% and 27% in N and P inputs  
812 during wet years led to a 36% increase in predicted oyster production.

813 By replacing shellfish production at harvest in the context of nitrogen and phosphorus inputs  
814 for all scenarios and the three simulated years, an optimum of the N:P inputs molar ratio  
815 appeared (~ 18.4) around which the oyster productions seemed to be maximized (in 2014 and  
816 2016, wet years). Current loadings (“Reference”), both natural and anthropogenic, are just  
817 over 100 tons of nitrogen in wet years (2014, 2016) for a phosphorus input of about 10 tons,  
818 bringing the N:P molar ratio above 22. To obtain a molar ratio of inputs around 18.4, it would  
819 therefore be necessary to bring an additional 2.5 tons of P into the system (ie 12.5 tons of P in  
820 total). Phosphorus appeared to be insufficient and therefore limiting if one considers these  
821 current contributions of nitrogen. The "Sète" scenario (n° 5) confirmed the hypothesis of a  
822 phosphorus-controlled system, where a misleading excess of nitrogen (~ +100 tons) did not  
823 help to achieve higher production because this scenario increased the phosphorus deficit in  
824 the system. Although more P was brought to the lagoon, oyster production did decrease in  
825 comparison with “reference” scenario. The “Sète” scenario tested the response of the  
826 ecosystem to excess N and P loading from a WWTP. In the current situation, this WWTP  
827 releases its wastewater into the sea. This scenario involved the release of waste waters into  
828 box 1 (“Petit étang”) of the model. Box 1 is the box connected with the sea, hence part of  
829 these inputs is exchanged with the sea, the other part reached box 2 then box 3 where cultured  
830 areas are located. In the “Sète” scenario, the model shows that sediment has accumulated  
831 more N (times 2.5) and has released less P (times 0.4) in box 1 than the “Reference”. Along  
832 with the sediment compartment, macroalgae, notably *Ulva* and *Gracilaria*, yielded higher  
833 biomasses (times 2 and times 1.5 for *Ulva* and *Gracilaria* respectively) than in the reference  
834 scenario. This may indicate that macrophytes enter a competition for nutrients in box 1. N &  
835 P in sediment and macroalgae did not show marked differences in all other boxes of the

836 model. Nevertheless, this would indicate that box 1 was the first to respond to these additional  
 837 inputs. Remaining nitrogen and phosphorus were then exchanged with the sea and with box 2  
 838 and further up. Macrophytes competing for nutrient resources and a greater accumulation of  
 839 matter may have led to a lower P availability in boxes 2 and 3 including farming areas (boxes  
 840 4 and 5) and hence lower oyster production.

841 N inputs (N), P inputs (P) and N:P ratio of inputs (NP) were used in a PCA analysis (Figure 9)  
 842 along with shellfish culture performances variables such as production (Prod), total weight at  
 843 harvest (P\_tot) or condition index (CI) and ecosystem functioning variables as chlorophyll *a*  
 844 concentration in and out oyster farming zones (Chla\_OF and Chla\_out, respectively) or the  
 845 lagoon-scale phytoplankton depletion index (DI). Phosphorus inputs were strongly correlated  
 846 with shellfish performances (first axis, 71.51% of variance explained) and chlorophyll *a*  
 847 concentrations, suggesting a key role of phosphorus in controlling both phytoplankton and  
 848 oyster production.



849  
 850 Figure 9. PCA analysis (A) of model outputs including nitrogen inputs (N), phosphorus inputs (P),  
 851 inputs N:P ratio (NP), oyster production (Prod), oyster total weight (P\_tot), condition index (CI), Chl *a*  
 852 concentration in (Chla\_OF) and outside (Chla\_out) oyster farms and the median lagoon-scale  
 853 phytoplankton depletion index (DI). Supplementary qualitative variables (B) representing simulated

854 years with coloured 95% confidence interval ellipses (individuals: dots and barycentre: square) and  
855 scenarios (named grey squares).

856

857 The phosphorus inputs were inversely correlated with the depletion index, indicating also a  
858 role in regulating the carrying capacity of the Thau lagoon. Nitrogen to phosphorus ratio of  
859 inputs, and to a lesser extent nitrogen inputs, explained the second dimension of this PCA  
860 analysis (14.88% of variance explained; Figure 9-A) suggesting that, if phosphorus may  
861 control production levels importantly, the balance between nitrogen and phosphorus in  
862 loadings carried from the watershed had a major importance in the efficiency of the Thau  
863 ecosystem and hence on its trophic carrying capacity. Supplementary variables, as simulated  
864 years and simulated scenarios, once placed in this PCA (Figure 9-B), demonstrated the major  
865 importance of contrasted hydrological conditions as suggested above, whereas the variability  
866 linked to the scenarios tested in this study exhibited less difference between scenarios with no  
867 clear pattern.

868 Deslous-Paoli et al. (1998) reported this control of shellfish production by phosphorus in the  
869 1990s, where the oyster stocking density was around 25 to 30 000 tons of shellfish and for an  
870 annual production exceeding 15 000 tons (against 9200 to 9500 tons currently reported by  
871 shellfish farmers). This study also reported phosphate concentrations in water 40 times higher  
872 than the current concentrations (4  $\mu\text{M}$  against 0.1  $\mu\text{M}$ ). At the same time, even though the  
873 concentrations of  $\text{PO}_4^{3-}$  in water have been decreasing since the 1970s, the significant  
874 expansion of oyster farming during this period (from 1400 to 2440 tables in 20 years) would  
875 have reduced the risk of eutrophication by removing about 30%, according to the authors, of  
876 this readily available phosphorus from the Thau lagoon. At present, the decrease in  
877 phosphorus inputs from the watershed and, consequently, the concentrations in the water  
878 column, is mainly attributed to the major efforts made on the waste water treatment systems  
879 (Derolez et al., 2013; La Jeunesse, 2001; Souchu et al., 2010). Depending on the year, the

880 contribution of anthropogenic inputs from WWTP varies importantly to supply up to 90% of  
881 total inputs in dry years. The N:P molar ratio of these anthropogenic inputs (~5; 2009-2016  
882 average, data not shown) is much lower than that of natural inputs (~40; 2009-2016 average,  
883 data not shown), thus placing the lagoon in nitrogen limiting conditions in those years, the  
884 main source of current phosphorus inputs coming from the WWTPs.

885

## 886 5 Conclusions

887 The GAMELag-Conch model, developed to answer the problem of reconciling resource  
888 exploitation through shellfish culture and regulatory constraints, allowed an evaluation of the  
889 ecosystem carrying capacity of the Thau lagoon and the simulation of various scenarios waste  
890 water treatment management and shellfish farming strategies. To the best of our knowledge,  
891 there are no existing model taking into account both nitrogen and phosphorus inputs within  
892 the frame of carrying capacity assessment and most carrying capacity models are based solely  
893 on nitrogen (Dowd, 2003; Byron et al., 2011c; Chapelle et al., 2000; Filgueira et al., 2014a;  
894 Guyondet et al., 2014) or biomass data sets (Jiang and Gibbs, 2005). Under current  
895 conditions, the carrying capacity of the Thau Lagoon does not appear to be limiting. The  
896 interannual variability introduced by the differences in weather conditions strongly affects  
897 shellfish farming in terms of production and shellfish performances rather than did the  
898 contrast between the different tested scenarios. The productivity of the ecosystem seemed to  
899 depend mainly on watershed inputs in which inputs from WWTPs had a predominant role in  
900 dry years. Shellfish production was more specifically controlled by phosphorus as revealed by  
901 unbalanced N:P ratio in loadings. The trophic resource being sufficient, the oyster control on  
902 the phytoplankton was not excessive and depended on the stock density of cultured bivalves  
903 or additional phosphorus brought to the lagoon. The use of high stocking densities should be  
904 prohibited because if they generated higher production than current conditions, at the

905 expenses of thinner oysters with low condition index. Finally, the ecological status did not  
906 appear to be threatened with regard to the current shellfish pressure. This model thus appeared  
907 as a suitable tool for management perspectives. Another strength and recommended approach  
908 (Byron et al., 2011a) of this work resides in the implication of shellfish farmers, stakeholders,  
909 local and governmental management bodies as well as scientists to implement realistically  
910 based scenarios in the search for an equilibrium between shellfish production and ecological  
911 status regulation.

912 However, important caveats must be given here as this paper reports a global evaluation of the  
913 carrying capacity through the use of characteristic times or depletion index that might vary in  
914 time and space (Dame and Prins., 1998; Guyondet et al., 2014). Further work is necessary to  
915 alleviate this time varying control of the carrying capacity where characteristic times or even  
916 depletion index are used to identify seasonal effects and sensitive periods to be confronted to  
917 shellfish production, performances and potential ecological impacts. This ongoing work shall  
918 help management of shellfish culture practices in this context of maintaining “good”  
919 ecological status. A perspective use of this numerical tool resides in a theoretical approach  
920 that would involve large variations of nutrient loadings to seek for tipping points where  
921 depletion or ecological indicators may drastically change with strong impacts on the whole  
922 ecosystem functioning. Short term development of this tool would address the question of  
923 anoxic crisis, which had sporadically occurred in the Thau lagoon when temperature increases  
924 and weather conditions are calm. These anoxic crises have led to dramatic loss of cultured  
925 bivalves hence temporarily damaging ecological conditions of the lagoon. Further  
926 developments of this management tool should address questions related to climate change,  
927 where the frequency and-or the intensity of meteorological events, such as temperature  
928 increase or the modification of rainfall regimes should be considered concomitantly with

929 increase in population, in turn increasing watershed loadings, subsequent refit of WWTP and  
930 sustainability of uses in the Thau lagoon.

931

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