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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.

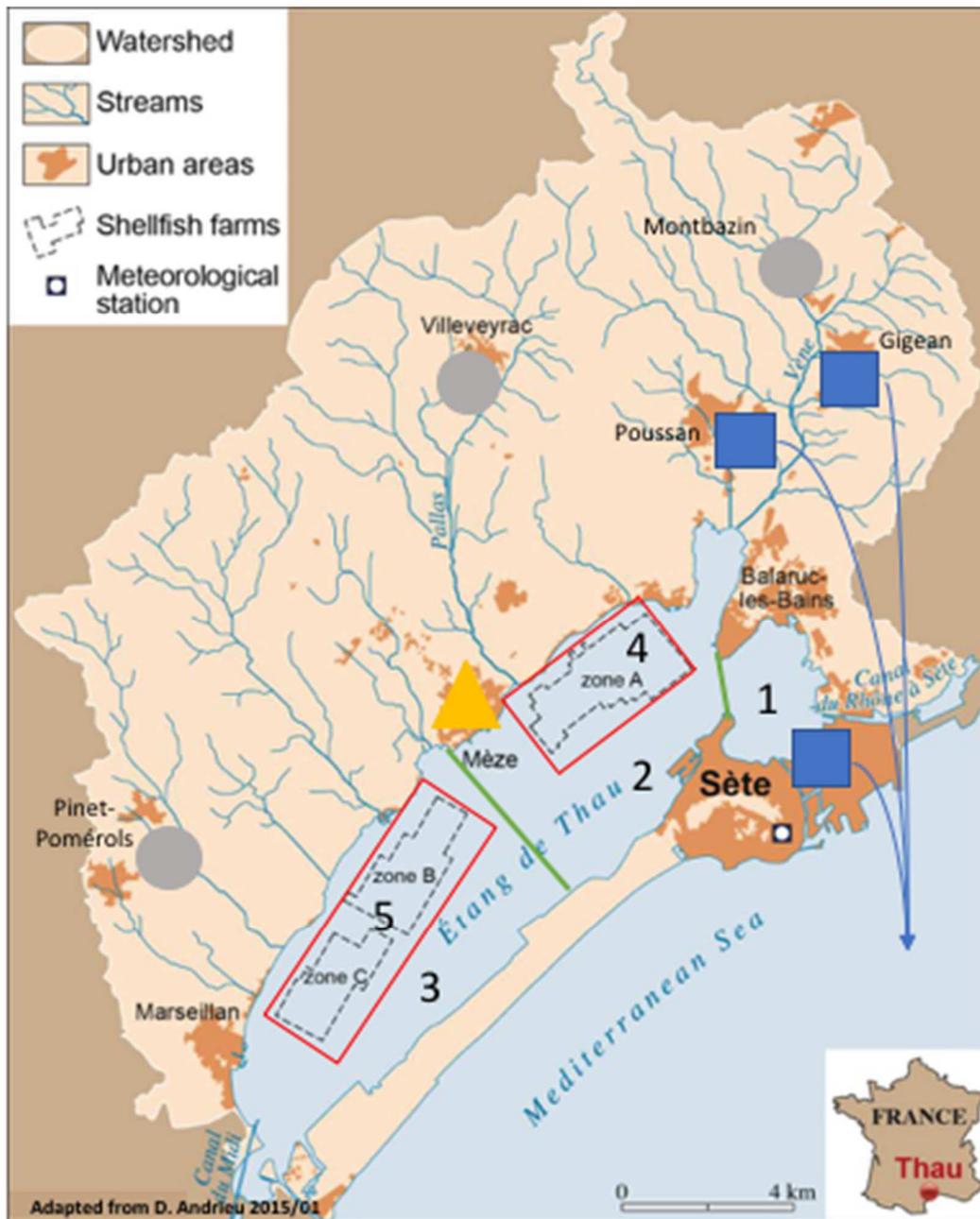
100 2 Material & Methods

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 km² (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 m². 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 m² 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 km² 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 Mm³ of

128 freshwater (about 50% of total flow, ranging from 3.1 to 24.7 Mm³ 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

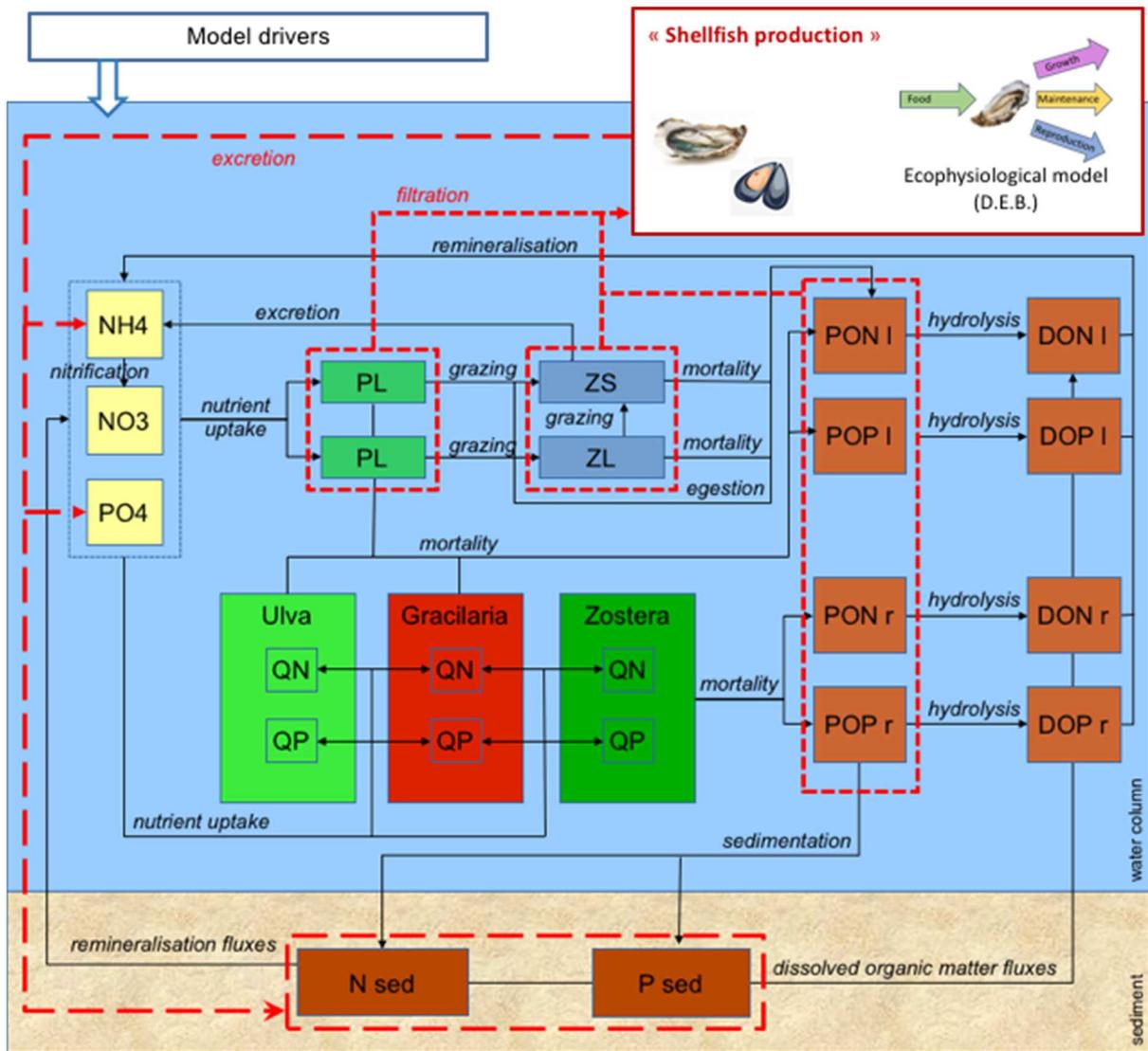
136 2.2 Carrying capacity model

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 α_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 μ_{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/). Thus, the chemical potential of the food,

225 once converted to $\text{J mmol}^{-1} \text{N}$, gives a conversion factor, C_{oyster} , of $3250 \text{ J mmol}^{-1} \text{N}$. The
226 C_{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, μ_{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 spats 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>
Reference	1	Current stocking densities, WWTP outputs estimated from current average abatements	Use as a standard for comparing scenarios	Ref
Watershed inputs	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
Shellfish farming	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:

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

402 Where V_{lagune} and \bar{V}_{in} were the volumes of the lagoon (m^3) and mean annual incoming
403 volume ($\text{m}^3 \text{d}^{-1}$), 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 $\text{mmol N m}^{-3} \text{d}^{-1}$).

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. 90th percentiles (p90) were calculated from
447 the 92 daily values obtained from June 1st to August 31st for each simulated year, of dissolved
448 inorganic nitrogen (DIN= NO₃⁻ + NH₄⁺), 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⁻³ in the model and converted to µg

459 Chl *a* l⁻¹ 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 homoscedasticity and non-parametric,
466 Kruskal-Wallis, was therefore used for statistical analysis. Correlations were determined
467 following Spearman correlation coefficient, ρ . 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

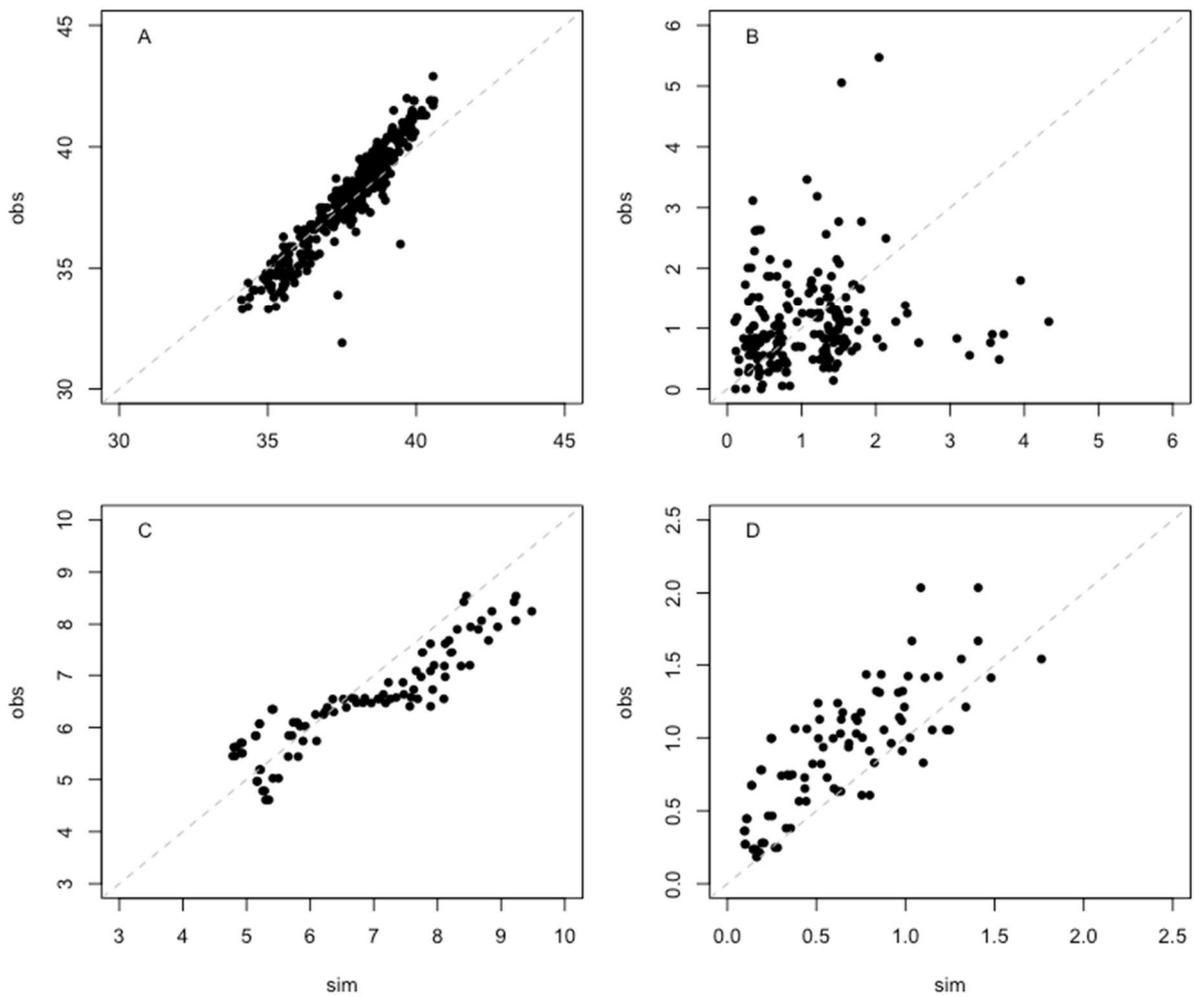
472 3 Results

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 $2.5 \mu\text{g Chl } a.L^{-1}$.
 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.

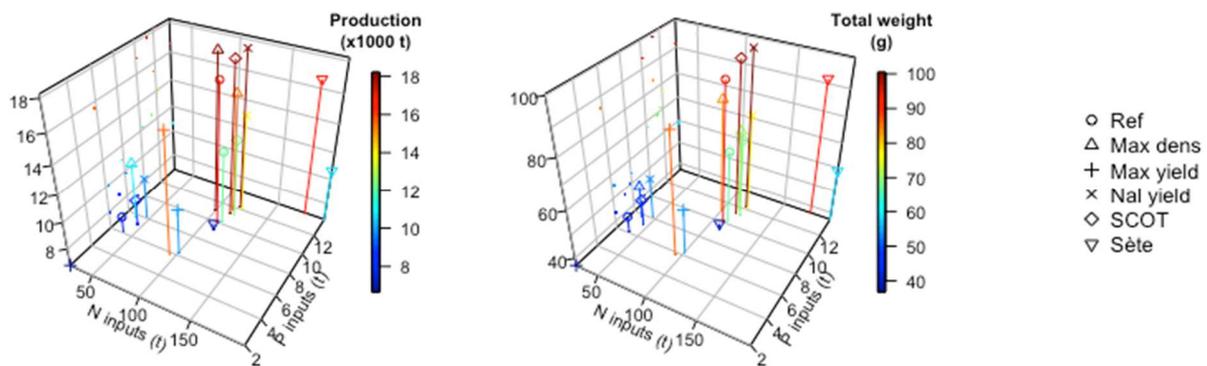
520 Table 2. Summary of simulations inputs and outputs for the three years (2014-2015-2016) and the six scenarios tested.

	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 ^a [NID-PID-TN-TP-CHLA-TN:TP] Summer – P90 – (µM)	RT (days)	CT (days)	PPT (days)	Median lagoon-scale depletion index (%)
Reference												
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
Max. yield												
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
Normal yield												
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
SCOT												
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
Sète												
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
Max density												
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

^a: ecological status based on 90th 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.

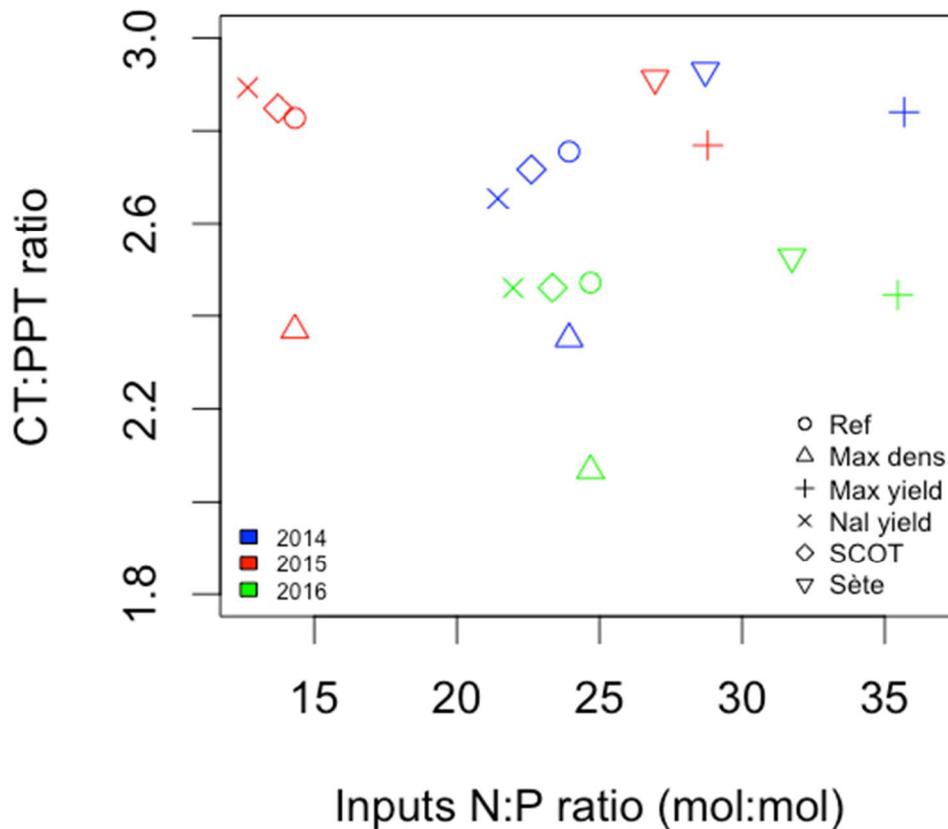
541 In fact, the nitrogen inputs according to the different scenarios during the dry year (2015)
542 varied from 25% to 50% of those during the two wet years (2014 and 2016) with the largest
543 difference between dry and wet years recorded for the “Max. yield” scenario (Table 2). For
544 phosphorus, 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.

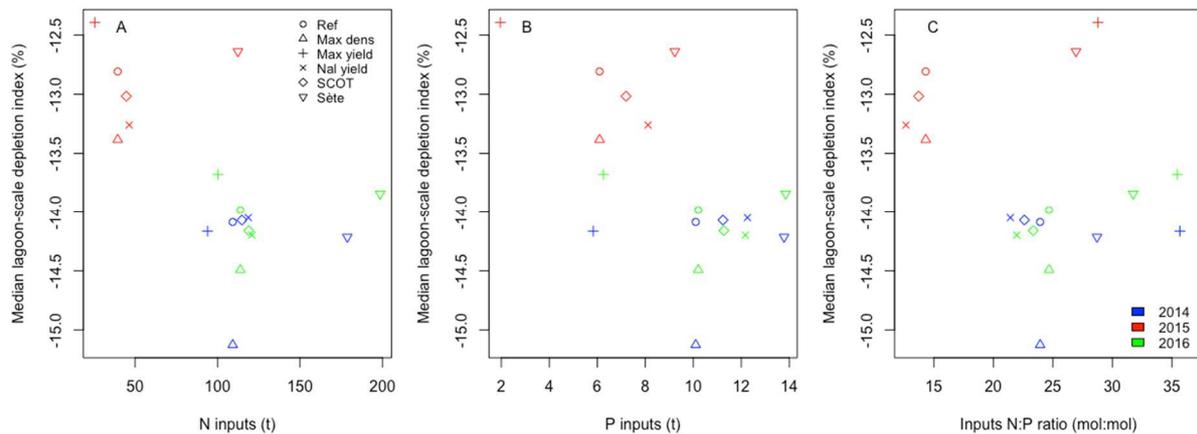


567
568 Figure 5. Clearance time to phytoplankton renewal time ratio as a function of inputs N:P molar ratios
569 plotted for the 3 simulated years and all scenarios (see legend inset).

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).

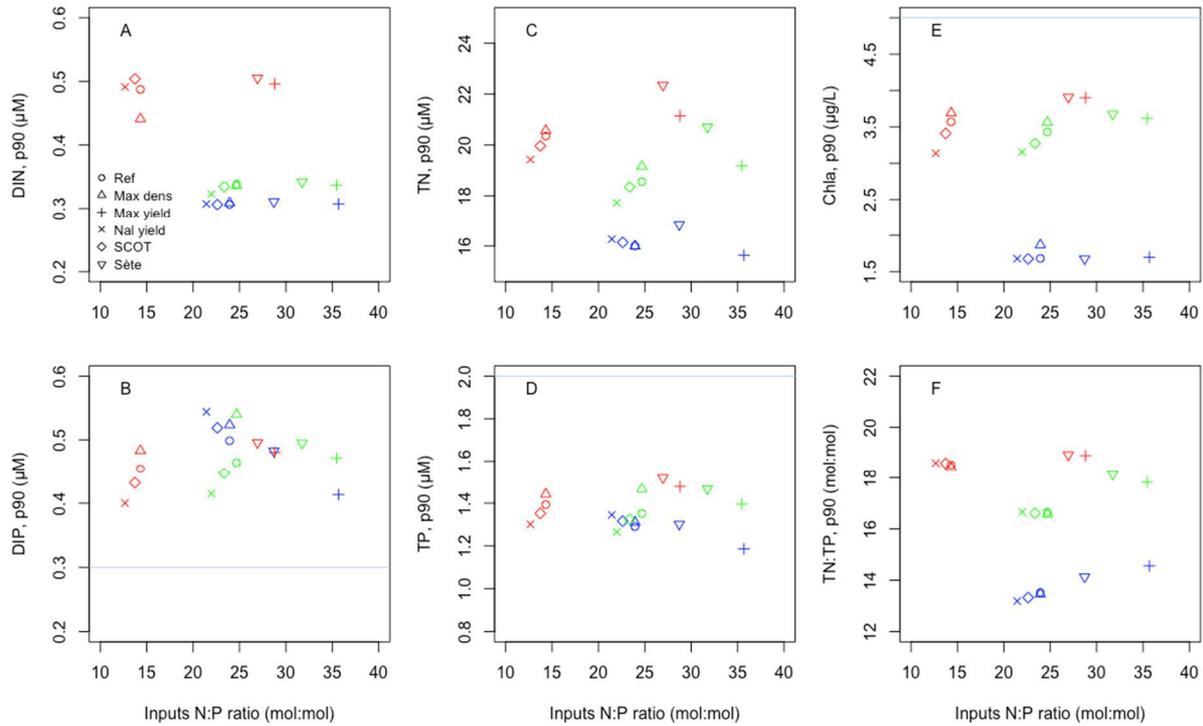


587
 588 Figure 6. Median lagoon-scale depletion index expressed as a function of N inputs (A), P inputs (B)
 589 and inputs N:P molar ratio (C).

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.

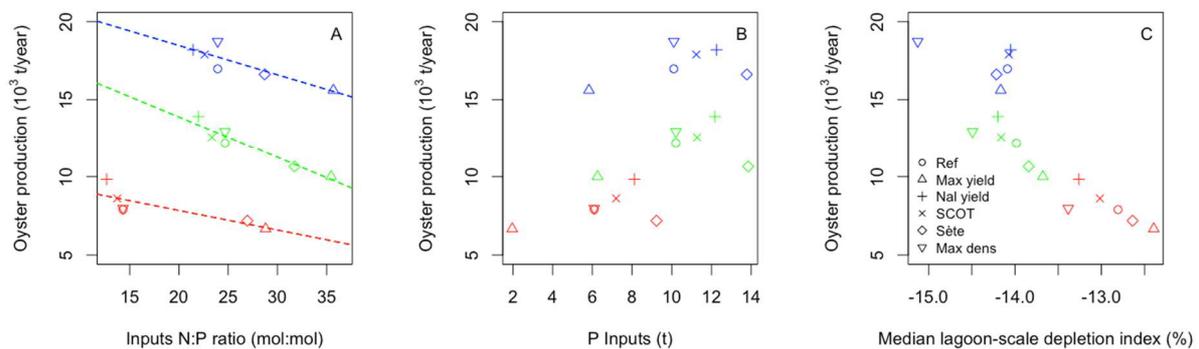


601
 602 Figure 7. 90th percentiles for DIN (A), DIP (B), TN (C), TP (D), Chl *a* (E) and TN:TP ratio (F) as a
 603 function of inputs N:P molar ratio for all scenarios (see legend in Figure A inset). Colors correspond
 604 to simulated years (2014: blue, 2015: red, 2016: green). High/Good ecological 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⁻¹)
 611 than 2015 and 2016 (mean = 3.60 and 3.45 µg.l⁻¹, respectively).

612 However, the model seemed to underestimate TN values (17.6 and 20.4 µmol.l⁻¹ 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

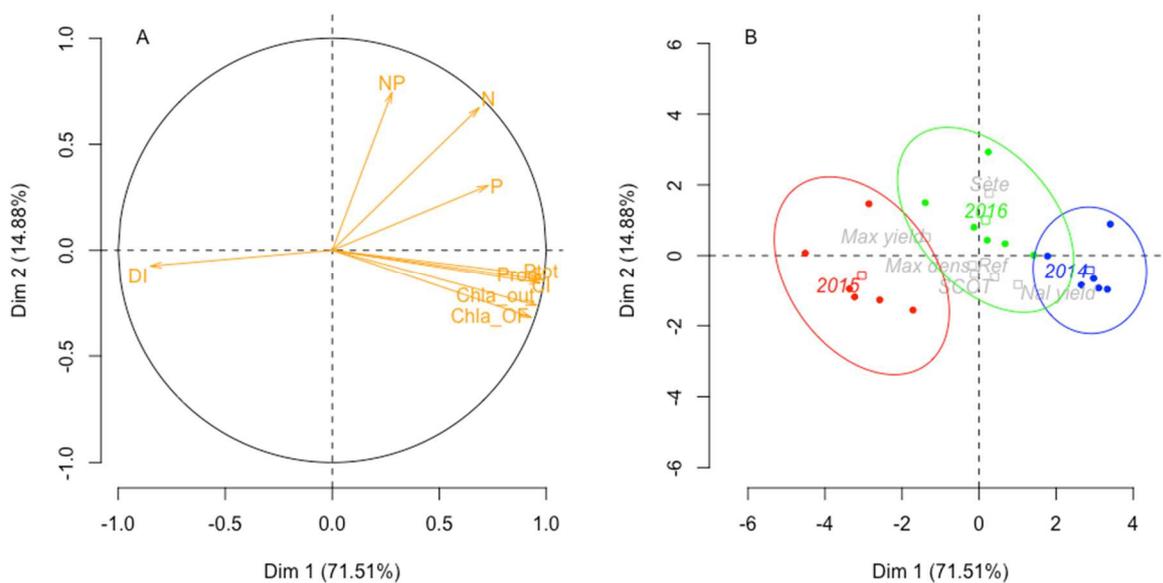
805 The results obtained in this modeling work of the Thau lagoon seemed to indicate a control of
806 the system by the nitrogen and phosphorus inputs from the watershed and more precisely by
807 the N:P ratio of these inputs. When the inputs related to the various scenarios are detailed, it
808 appeared 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 μM against 0.1 μM). At the same time, even though the
873 concentrations of 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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947 Philian Retif, AERMC: Anahi Barrera, Anais Giraud).

948

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