

Adapting a dynamic system model using life traits and local fishery knowledge — Application to a population of exploited marine bivalves (*Ruditapes philippinarum*) in a mesotidal coastal lagoon

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Abstract :

Effective planning and management strategies of the Manila clam (*Ruditapes philippinarum*) stock in Arcachon Bay rely on a co-management approach, involving scientific advice and the fishing industry. In order to strengthen this management process, a specific compartmental single-species model has been developed to assess different management strategies. Based upon a size structure of the population and built from the dynamic systems paradigm, the modelling involves selected environmental and fishery-related parameters for their impact on the population dynamics. Integration of newly available life traits data regarding the local population and better knowledge of the fishing activity and its control parameters have enabled a revision of the existing version including model parameters and integration of new formulations. Effect of food availability and total suspended matter on the production of newly settled juveniles, natural mortality, growth rates, and price, accounted for the bulk of the undertaken improvements. Model performance was evaluated by comparing simulation outputs to observed data from stock assessments (2003, 2006, 2008, 2010, 2012, 2014 and 2018). In addition, a sensitivity analysis regarding uncertainty on parameters related to biological and environmental aspects was carried out to provide information about parameters that influence the outputs of the model the most. In particular, this highlighted that a deeper understanding of the processes related to the reproduction phase and its control parameters on biomass should be pursued. The improvements enable the calibration of the model with parameters that are as close as possible to the specificities of the stock considered. This adaptation

permits use of the model to test various management strategies on the stock evolution and also to evaluate potential effects of environmental or market fluctuations. It encompasses ecological and socio-economic valuations of the measures of impact. As long as those objectives are shared by the different entities involved at the regional scale, communication and management decisions should be facilitated.

Highlights

► Integrating recent life traits of the local population to address its functioning. ► Consideration of multiple fishery-related factors to tackle fishing effect. ► Modeling a price effect to describe an exploitation strategy. ► Strong influence of the reproduction phase and its control parameters on biomass. ► Relevance of combining various management measures to improve the stock level.

Keywords : System dynamic model, Co-management, Population dynamic, Arcachon Bay, *Ruditapes philippinarum*

1. Introduction

Management of coastal zones is considered globally as an important issue (Pastres et al., 2001) because it implies multiple–conflicting goals involving socio-economic and ecological considerations (Freire et al., 2002). This is particularly true for areas providing bivalve resources because they frequently enable the development of flourishing activities either for fishing or farming (Canu and Solidoro, 2018; Coelho et al., 2021; Vincenzi et al., 2006). Design and implementation of adaptive management system policies are vital to conciliate socio-economic activities and long-term sustainability of the natural environment (De Leo and Levin, 1997), especially considering resources where population dynamics are particularly sensitive to environmental variations. For this purpose, models constitute useful tools for guiding management of coastal waters (Mongruel et al., 2011), including the monitoring of exploited species that generate significant income for the fishing industries in coastal zones.

To reinforce the management of exploited species, several models have been designed. These include demographic models and increasingly combined ecophysiological and economic ones (Bertolini et al., 2021; Canu et al., 2011; Ferriera et al., 2009; Grant et al., 2007; Solidoro et al., 2003; Troost et al., 2010). The first model developed for Manila clams by Bald et al. (2009) was a compartmental single-species model driven by fixed parameters, which were based upon the size structure of the population and several dynamics of the species. This modelling approach belongs to the simulation modelling category, which was built from the dynamic systems paradigm developed in the 1950s by Forrester (1973). What is more, the interactions among variables and the evolution over time of the level variables (density and abundance expressed in numbers or mass) are mathematically represented by differential equations (the model being integrated continuously in time). Six weaknesses about this model were pointed out by Bald et al. (2009). Since more ecological data on the Manila clam are now

available and on-going studies in the Arcachon Bay are completed, a revision of the first version of the model parameters can be undertaken. This new information enabled an improvement of four identified weaknesses: effect of food availability, growth rates, indirect natural predation and effect of diseases (the one remaining concern is larval transport and settlement with spatial considerations). In addition, more realistic harvesting activities and economic considerations were integrated and the lack of consideration of socio-economic drivers highlighted during working groups (involving scientists and fishermen) has also been taken into account.

In this context the present paper 1) discusses the developments implemented since the first version of the model; 2) integrates a validation and a sensitivity analysis regarding uncertainty on a selection of parameters and 3) describes the evolution of the modeled biomass under various management, environmental and economic scenarios in order to provide decision making guidance.

2. Study area and Manila clam population

2.1. Study area

Arcachon Bay is a 156 km² semi-sheltered lagoon in the southwest coast of France (Figure 1). Mostly composed of intertidal flats (110 km² within the inner lagoon which are colonized by vast *Zostera noltii* seagrass meadows), the composition of this mesotidal system ranges from mud to muddy sands. The tide is semi-diurnal and the bay is both influenced by oceanic (external neritic waters) and continental (principally from the Eyre River) inputs (Dang, 2009). The characteristics of these water masses as well as the slow renewal of water by tides (Plus et al., 2009) both influence salinity and temperature within the bay. Variations of these two parameters are important: seawater temperature ranges from 1.8 to 27.4 °C (mean value 15.4 °C) and salinity ranges from 15.4 to 35.4 (mean value 30.2) (Caill-Milly, 2012). According

to the same database, chlorophyll a concentration varies from 0.4 to 30.8 $\mu\text{g l}^{-1}$ (mean value 2.6 $\mu\text{g l}^{-1}$).

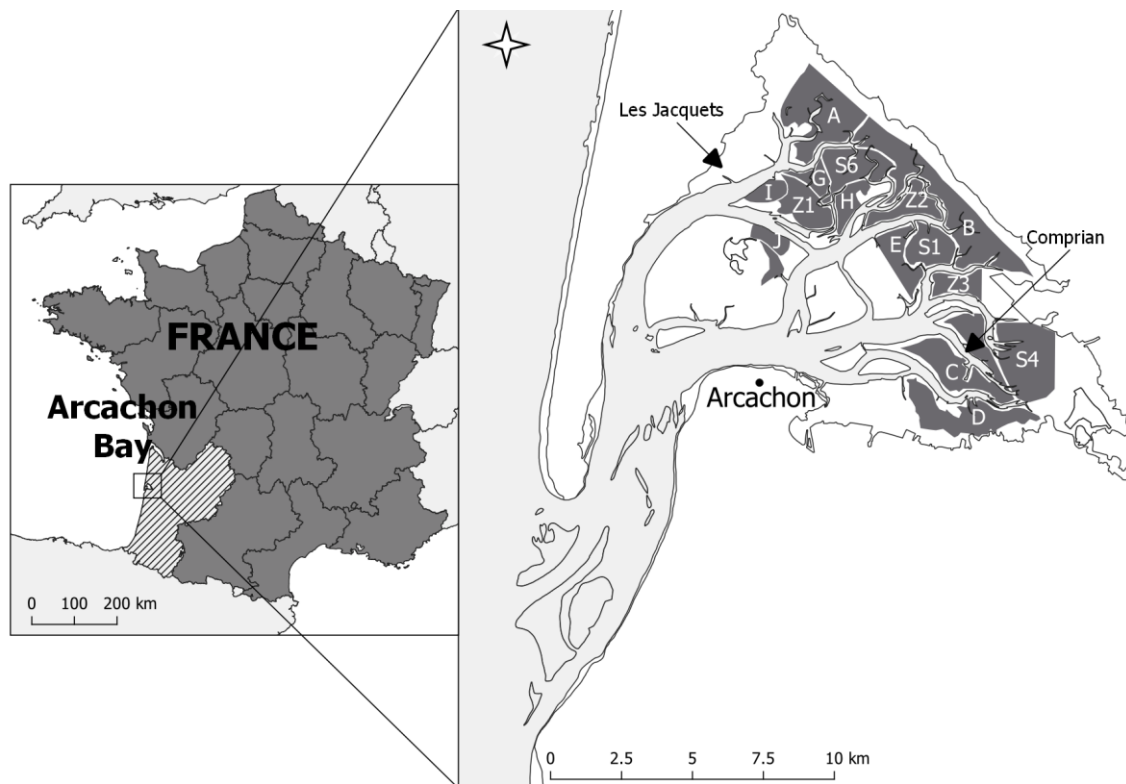


Fig. 1. Maps showing the studied site Arcachon Bay (France) (sources: ESRI, BD Carthage, Ifremer – M. Lissardy).

2.2. Species description and stock evolution

Manila clam (*Venerupis philippinarum*) is an infaunal species inhabiting various substrates such as sandy, sandy-muddy and muddy bottoms. As a suspension-feeding bivalve, its dietary regime is dominated by phytoplankton (Kanaya et al., 2005; Kasai et al., 2004; Spillman et al., 2008; Yokoyama et al., 2005). Length class differentiation within the population is determined by valve length, which is defined as the longest distance from front edge to back edge (mm). For bivalves, fecundity is age-related (Gosling, 2003) and the Manila clam sexual maturity is considered effective from the second year, corresponding to clams above 20 mm in length (Holland and Chew, 1974). Two annual spawning periods occur in Arcachon Bay: from

April to June and from August to October, which are driven by increasing seawater temperatures between 15°C and 22°C (Dang et al., 2010).

Metamorphosis and settlement occur generally after a two-to-three-week period of pelagic larval stage. Then, the spatial distribution is of an aggregative type and the limited lateral displacements of individuals are reported to reach six meters per month (Tamura, 1970 in Le Treut, 1986). Manila clam maximum lifespan is unknown (Dee Boersma et al., 2006); Gillespie et al. (1999) indicated that it rarely exceeds 10 years of age in fished populations.

Factors influencing natural mortality include natural predation (*Carcinus maenas*, *Ocenebra erinacea*, birds...), diseases (among others, Brown Muscle Disease, one of the most important) and aging. Pollution may also have an unfavorable role in the evolution of mortality (Paul-Pont, 2010).

The Manila clam resource in Arcachon Bay has been monitored through stock assessment campaigns. Surveys considering the total distribution area of Manila clam (~47 km²) began in 2003 and have been carried out as much as possible every other year since 2006 during late spring (the 2016 survey could not take place for financial reasons). Seven years of monitoring data (2003, 2006, 2008, 2010, 2012, 2014 and 2018) are currently available. These surveys provide a dataset of indicators such as abundance indices, length-frequency histograms, total abundance and biomass, fraction of juveniles (individuals measuring less than 17 mm), spawners (individuals measuring more than 25 mm) and exploitable stock (individuals measuring more than 35 mm), as well as their abundance and maps of clam densities (Sanchez et al., 2018; Caill-Milly et al., 2021). The stock assessments of these campaigns show a decrease of the population biomass until 2008, and then a recovery to a high level toward the end of the series (Figure 2).

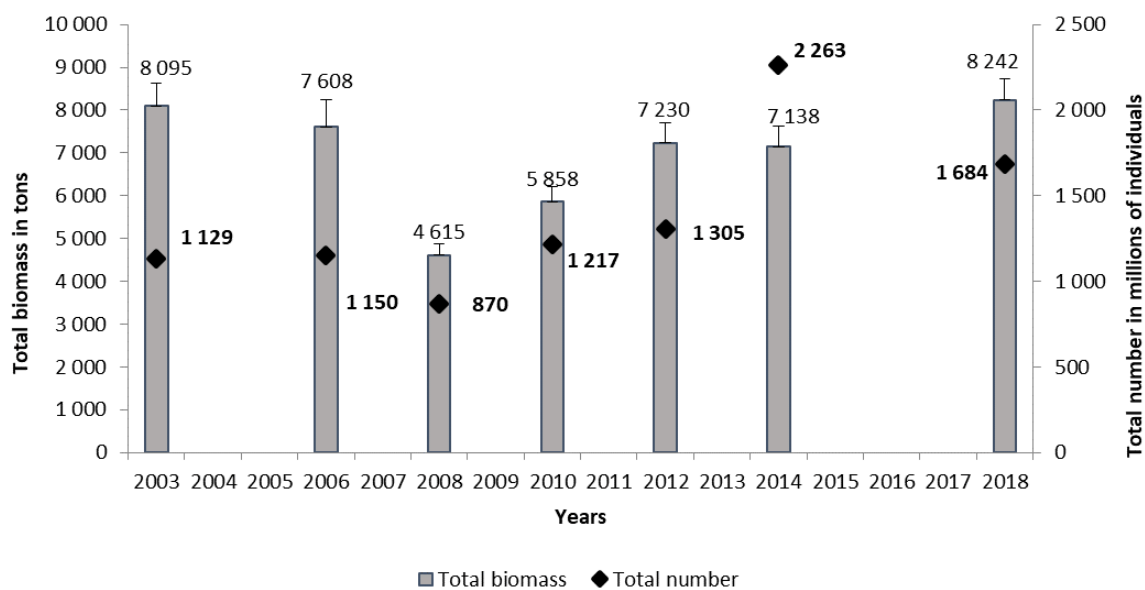


Fig. 2. Evolution since 2003 of the total biomass (with its standard deviation) and of the total numbers of Manila clams in Arcachon Bay (from Sanchez et al., 2018).

3. Fishing activity and management

Fishermen access fishing areas by boat and exploitation occurs at low tide. Clams are extracted by hand, the sediment is scraped using a small tool. Catch fishing data from national and regional databases are utilized to account for the exploitation (sources: CRTS La Rochelle, SIH Ifremer, CRPMEM Nouvelle-Aquitaine). The first catch declarations were recorded in 1992 (with 1 ton), production then grew quickly from 2001. After a peak in 2007 with 1000 tons landed, the production decreased to reach values comprised between 300 and 400 tons annually in recent years (Caill-Milly et al., 2021).

Whereas the minimum legal harvest size (40 mm prior to 2008, 35 mm since then) is set by European legislation (EC Regulation CE n°40/2008), in addition specific local legislation may be applied such as protected areas, limited fishing periods and a fixed number of licenses. They vary over time in terms of location, duration, number, allocation rules and are considered

in the next sections of this paper. The local regulations are under the responsibility of industry organisations (like Comité Régional des Pêches Maritimes et des Élevages Marins de Nouvelle-Aquitaine) and involve regional administration (Frangoudes et al., 2020).

4. Existing model structure and components

The existing model applied to Manila clam in Arcachon Bay was developed at the end of the 2000s. The model and all the simulations are performed using the object-oriented modelling framework Vensim ® DSS. This software is widely used to construct simulation models of business, scientific, environmental, and social systems. Specific dynamic models regarding exploited marine resources (by fishing and aquaculture) have been developed under various softwares such as Vensim, ExtendSim, Stella, Simile, etc. (Canu et al., 2011; Hawkins et al., 2002; Grant et al., 2007).

For Arcachon Bay, the processes are modelled at the bay scale (not spatialized at a finer scale) and the time frame is monthly, with the exception of temperature (daily). The model is structured into basic component parts corresponding to four interrelated so-called blocks: Production, Stock/Maturation/Mortality, Environmental parameters and Fishery (see Figure 3 and Bald et al., 2009 for details including structuration and equations of the first version). The production of juveniles (**Production block**) is controlled by the quantity of spat arriving in the system after the spawning period, the larval development and the settlement (after a pelagic phase of three weeks, Le Treut, 1986). Because those phases of the life cycle are well-known to be highly influenced by the environment [Holland and Chew (1974), Mann (1979), Ohba (1959), Park and Choi (2004), Robinson and Breese (1984) and Emmett et al. (1991)], a control block integrating environment drivers (**Environment parameters block**) acts on the Production block. In the Environment parameters block, seawater temperature was simulated using the sinusoidal function proposed by Melià et al. (2004) and adjusted to Arcachon Bay

conditions by Bald et al. (2009). In the **Stock/Maturation/Mortality** block, the Manila clam population in Arcachon Bay is divided into four sub-populations according to their length. For the population dynamics model, several authors (De Leo and Gatto, 2000; Solidoro et al., 2003) underlined the importance of length class differentiation to take into account differences in vital rates such as fertility, mortality, and respiration (Flye-Sainte-Marie et al., 2007). Therefore, they correspond to: juvenile size class (from 0 to 20 mm), adult under the minimum current harvest size class (from 21 to 34 mm) and two adult size classes above the minimum current harvest size (from 35 to 39 mm and upper 40 mm). Thereby the chosen endpoints of those classes depend on biological and exploitation considerations. The rules of evolution over time of the number of clams in each class are controlled by specific growth, natural and fishing mortality parameters and are described in detail in Bald et al. (2009). In addition, the initial condition is controlled by the production of juveniles in the first class. This compartment gives at the end the main result, which is the total biomass.

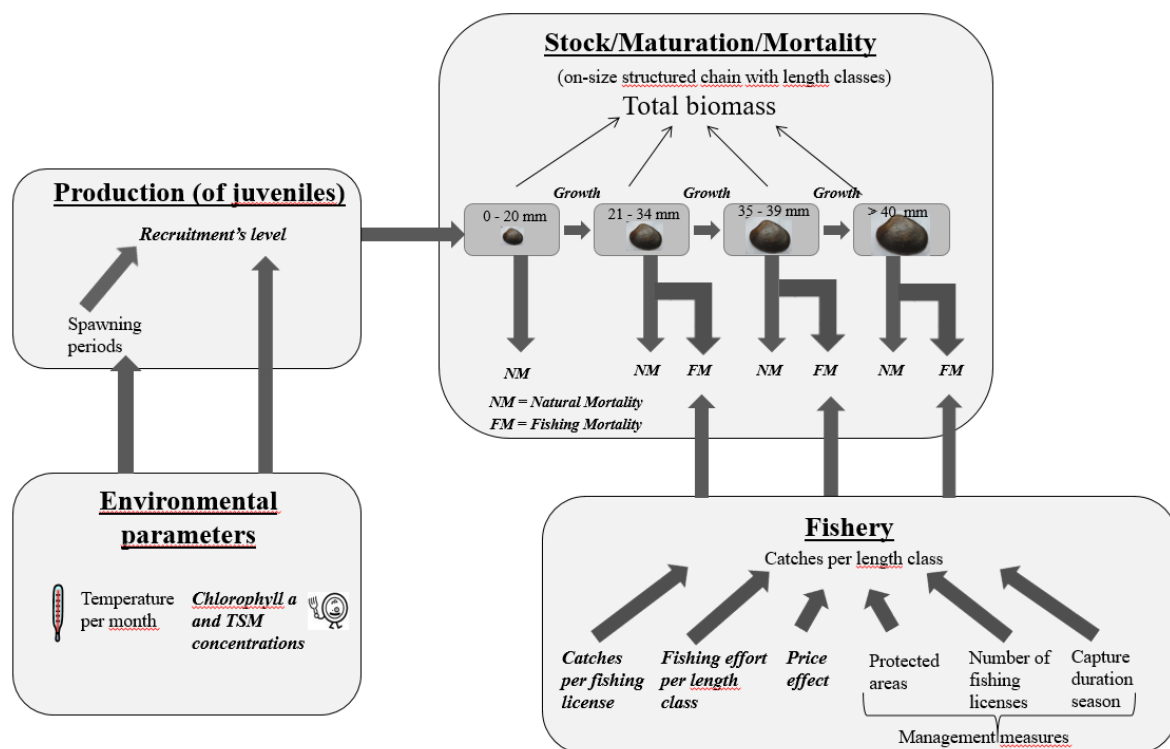


Fig. 3. Diagram of the Manila clam model illustrating the four blocks and the interactions among them. Improvements made since the first version of the model regarding blocks are in bold italics.

The **Fishery Block** includes the parameters that control the fishing mortality required for the Stock/Maturation/Mortality Block (e.g. fishing effort per clam length class, capture duration season, number of delivered fishing licenses, catches volume per license, protected area surface...). To convert the volume of catches per length class to effective per length class, a length-weight relationship for the Manila clam population was established using the 2003 survey campaign (see Appendix 1).

All the formulations of this existing model are detailed in Bald et al. (2009). Starting from this existing version, both the integration of newly and specific available life traits data, and the adjustment of the fishing activity and its control parameters allow for a revision of the model, which includes model parameters and the integration of new formulations.

5. Model revision

5.1. *Integration of real data to simulate seawater temperature*

In the first version of the model, seawater temperature T (Environment parameters block) was simulated using the sinusoidal function (Bald et al., 2009). In order to be closer to the real variations of temperature inside the Bay, this equation was replaced by real weekly temperature data coming from the ARCHYD network². Regarding the Manila clam distribution, two stations - Comprian and Les Jacquets (see Figure 1 for location) - were selected to calculate mean temperature (T_{real}) per month from 2003 to 2019. For subsequent years, the attributed value per month m is equal to the average mean over three years for a given month (T_{am}) with the

² The hydrological network of observation and monitoring dedicated to Arcachon Bay (<https://sextant.ifremer.fr/record/dde63586-6a51-4e9b-8630-b7648cda86a0/>)

addition of a parameter temperature variation (ΔT) to have the possibility to test the hypothesis of an increase or decrease of the monthly temperature.

$$T(m) = \begin{cases} T_{real}(m) & \text{from 2003 to 2019} \\ T_{am}(m) + \Delta T & \text{from 2020 to 2029} \end{cases}$$

Due to this modification, the time frame for the seawater parameter changed from daily to monthly. Using real data is considered preferable notably to work on hindcasts.

5.2. Integration of specific available life traits data

5.2.1. Recruitment (Production and environmental parameters blocks)

In the first version of the model, an iterative modeling was used to fix the recruitment level and the period of arrival of juveniles in the Stock/Maturation/Mortality block was controlled by the seawater temperature conditions (Environment parameters block) (Bald et al., 2009). Regarding Manila clam, temperature, photoperiod and food availability are the three main factors contributing to the reproduction phase (from gametogenesis to spawning) (Delgado and Pérez-Camacho, 2007; Devauchelle, 1990; Holland and Chew, 1974; Le Pennec and Benninger, 2000; Mann, 1979; Ohba, 1959; Soudant et al., 2004; Toba and Miyama, 1995). To a lesser extent, a possible effect of salinity has also been described by Park and Choi (2004) and Dang et al. (2010). For the Arcachon Bay population and using stock status indicators and environmental parameters, Caill-Milly (2012) highlighted both the importance of temperature during the reproduction phase (interaction already taken into account in the model) and the trophic conditions associated to total suspended matter (TSM) for young stages. High proportions of juveniles were related to high chlorophyll a and low TSM values.

Graphically, mean chlorophyll a concentration is the lowest in 2004 and TSM concentration is lowest in 2005. Conversely, mean chlorophyll a concentration and TSM concentration are highest in 2012 and in 2019 respectively. Regarding the trends of these two

data sets over the 2002-2019 period, they seem to display a break in the data series between 2009 and 2010 (with significant differences for TSM) (Figure 4).

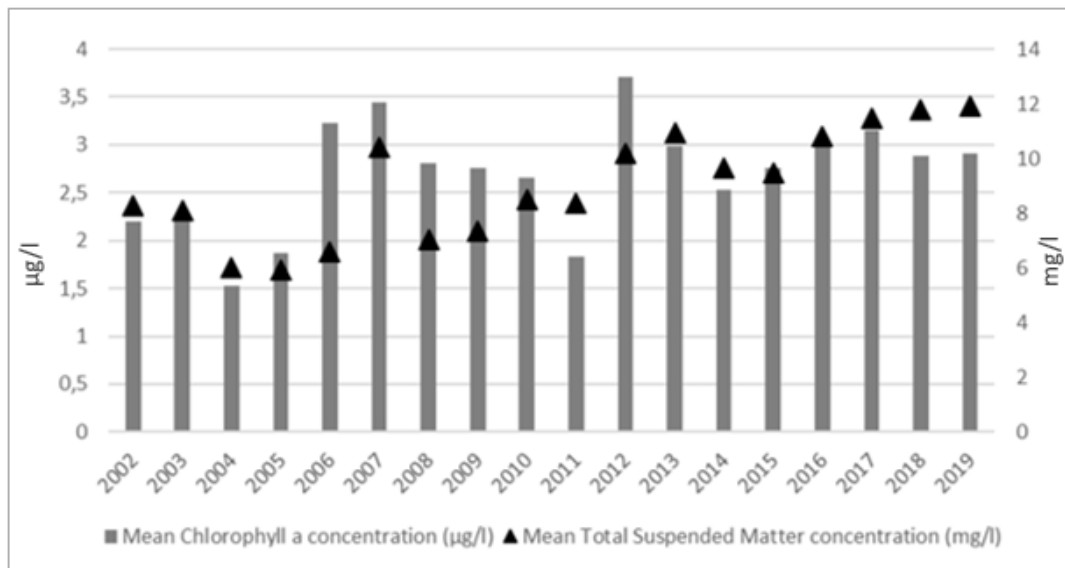


Fig. 4. Evolution of chlorophyll a and Total Suspended Matter over the 2002-2019 period.

Current understanding of the impact of these two conditions on recruitment suggests a positive effect of high chlorophyll a and low TSM. As these two factors show a break between 2009 and 2010, the recruitment level proposed by Bald et al. (2009) - *JP_m* - was modulated from 2010 using a combination of evolution rates of those two factors acting with opposite effects. To do so, chlorophyll a and TSM evolution rates were calculated between 2002-2009 and 2010-2019 and combined (considering positive effect for chlorophyll a and negative effect for TSM to estimate the $\Delta JP_m(m)$ from 2010 (Table 1).

Table 1: Applied rules to estimate the combined effects of Chlorophyll a and TSM concentrations on JPm from 2010.

Factors	Mean concentration 2002-2009	Mean concentration 2010-2019	Evolution rate between 2002-2019 and 2010- 2019	Estimated type of effect on JPm	Estimated combined effects to apply on JPm from 2010 (Δ JPm)
Chlorophyll a	2.51 μ g/l	2.84 μ g/l	13%	Positive	-25%
TSM	7.46 mg/l	10.31 mg/l	38%	Negative	

Δ JPm(*m*) is thus set at 0% between 2003 and 2009 and at -25% from 2010. As a result, from 2003 to 2009, JPm is 3.3 ind.m⁻².month⁻¹ and 2.5 ind.m⁻².month⁻¹ from 2010.

Due to this reformulation, the juvenile production per surface unit and per month JP(*m*) is:

$$JP(m) = [JPm(m) \times [1 + \Delta JPm(m)]] \times SP(m)$$

with JPm = the juvenile production per spawning month fixed by Bald et al. (2009); Δ JPm = Combined chlorophyll a and TSM effects on juveniles production and SP = Spawning occurrence for a given month.

The model now includes not only the effect of temperature (spawning triggering) but also of chlorophyll a and TSM on recruitment.

5.2.2. Growth (Stock/Maturation/Mortality block)

In the first version of the model, the growth rates were calculated following the growth model developed by Melià et al. (2004) for the Sacca di Goro Lagoon (Italy) (Bald et al., 2009).

Between 2005 and 2007, Dang et al. (2010) undertook enclosure field experiments within Arcachon Bay that allow defining the Von Bertalanffy Growth Function (VBGF) parameters related to the Bay. These ecological data led to the reassessment of realistic growth rate estimates, namely 0.361, 0.245 and 0.227 (dimensionless) for length classes 0-20, 21-34 and 35-39 mm respectively. For example, this means that each month, the number of clams entering the 21-34 mm class from the previous class (0-20 mm) is obtained by multiplying the number of clams in the 0-20 mm class from the previous month by 0.361.

5.2.3. Natural mortality (Stock/Maturation/Mortality block)

In the first version of the model, natural mortality was defined by the relationship established by Solidoro et al (2000) and Solidoro et al. (2003). It integrated sea water temperature and was based on studies on Northern Adriatic lagoons.

Also in this case, the enclosure field experiments undertaken by Dang et al. (2010) were useful to integrate more realistic values related to Arcachon to adjust the model. They allow to draw a direct assessment of this source of mortality. They were established at 6.9%, 3.9%, 1.8% and 1.2% respectively for length classes 0-20, 21-34, 35-39 and > 40 mm (deduced from Dang et al., 2010). On the same principle as for growth, this means, for example, that each month the number of clams in the 0-20 mm class that died of natural causes is obtained by multiplying the number of clams in the 0-20 mm class in the previous month by 6.9%. A feedback loop was also added from the stock variable in order to model a "trophic competition" effect on natural mortality (the rule applied is: if the stock is higher than 20000 t, natural mortality is doubled for each size class) – for equation, see Figure 5.

The updated information regarding growth and natural mortality enables describing the clam effective evolution per month m and per class i (1 to 4) and due to natural processes only as:

$$\begin{array}{ll}
\text{For } i = 1 & \\
JP(m) - Z_1(m) - G_1(m) & \text{if } S < 20000 \text{ t} \\
JP(m) - Z_1(m) \times 2 - G_1(m) & \text{else} \\
\text{For } i \geq 2 & \\
LC_{i-1}(m) \times GR_{i-1}(m) - Z_i(m) - LC_i(m) \times GR_i(m) & \text{if } S < 20000 \text{ t} \\
LC_{i-1}(m) \times GR_{i-1}(m) - Z_i(m) \times 2 - LC_i(m) \times GR_i(m) & \text{else}
\end{array}$$

5.2. Adjustment of fishing activity and its control parameters

This new work on the model was an opportunity to review some of the fishery-related parameters and to take into account other economic factors. This information includes annual fishing declarations of Manila clam within Arcachon Bay and was extracted from two complementary databases: the national statistic database of the “Système d’Informations Halieutiques” (for data between 2003 and 2008); the regional database - the “Base Pêche Aquitaine” (CRPMEM, unpublished data) (for data subsequent to 2009). Combined with the annual number of active fishing licenses (coded NFL - values in Table 2), the total annual volumes of catches declared by fishermen allow the calculation of mean catches volume per fishing license each month (coded CVL).

With respect to the fishing mortality per length class and because clams below the legal harvest size are known to be exploited (anonymous catch reports and authority controls), the fishing effort (FE) was reallocated on the whole length classes: 21-34 mm, 35-39 mm and > 40 mm length classes, which were estimated at 40%, 50% and 10 % respectively. This took into account higher fishing pressure on clams below the minimum legal size, which is more realistic.

In regard to the impact of the protected areas on catches, the Bald et al. (2009) model considered the percentage of exploitable stock and the percentage of reserve area to parametrize this variable (Dang, 2009). In the last version of the model, a reformulation was undertaken: the exploitable stock was considered using the fishing effort applied to each class above the

minimum legal size and the total applicable protected area(s) surface (expressed in m²) according to local legislation became a control variable.

In addition, a price effect was included as a control parameter of the fishing activity. This aims to fill a gap in the model regarding socio-economic drivers which was picked up on by stakeholders. Following interviews with professionals, the applied rules follow a linear response of catches to any price increase from a reference price (*Pref*) fixed at 3.5 euros per kilogram (considered by fishermen as a mean selling price for Manila clam from Arcachon Bay). In other words, if the difference between the effective price (*Pr*) and the reference price (*Pref*) is one euro, the catches increase by 10%; if the difference is two euros, the catches increase by 20% and so on.

All this updated information mentioned above led to the reformulation of the temporal fishing catches evolution per month *m* and per class *i* (1 to 4) denoted $FM(m) \times Capt_i(m)$, which was expressed in effective per surface unit each month (ind.m⁻².month⁻¹), according to the following equations:

$$FM(m) = \begin{cases} 1 & \text{if } OFM \leq m \leq OFM + CDS \\ 0 & \text{else} \end{cases}$$

with *FM* = Fishing Month, *OFM* = Open Fishing Month (month number), *CDS* = Capture Duration Season (in month).

$$Capt_i(m) = \begin{cases} \frac{NFL(m) \times CVL(m) \times 10^6 \times FE_i(m)}{ABS \times MW_i} \times \frac{ABS - PAS(m)}{ABS} \times \left[1 + \frac{Pr(m) - Pref}{10} \right] & \text{if } Pr(m) > Pref \\ \frac{NFL(m) \times CVL(m) \times 10^6 \times FE_i(m)}{ABS \times MW_i} \times \frac{ABS - PAS(m)}{ABS} & \text{else} \end{cases}$$

with *NFL* = Number of Fishing Licenses each month, *CVL* = Catches Volume per fishing License each month (t), *FE_i* = Fishing Effort allocated for class *i* each month (in %), *ABS* = Arcachon Bay Surface (m²), *PAS* = Protected Area Surface each month (m²), *MW_i* = Mean

Weight for class i (g), Pr = Effective price each month (€. kg^{-1}), Pr_{ref} = Reference price fixed at 3.5 euros per kg^{-1} . The first fraction of the last equation reported the catch as a function of the number of licenses, the catch per license and the mortality of the class considered in Arcachon Bay. The second fraction accounts for the fishing reserve effect. When the selling price was greater than 3.5 €. kg^{-1} , the third fraction reflected a price effect with a linear response.

Equation formulations for each process [including those not modified from the Bald et al. (2009) version and their parametrization are presented in detail in Figure 5 and Table 2. Figure 5 distinguishes the known parameters or fixed by the user from those estimated by equations within the model. Table 2 provides details regarding the latest parametrization. The output variable is the total biomass (S) since it constitutes the current indicator shared between scientists and managers to discuss the responses of the system to different scenarios.

Environment and Production of juveniles blocks

$T(m)$: Temperature at month m
 $\Delta T(m)$: Temperature variation
 T_{smin} , T_{smax} : temperature for spawning
 $JPm(m)$: Juveniles Production per spawning month fixed by Bald et al. (2009)
 $\Delta JPm(m)$: Combined chlorophyll a and TSM effects

$SP(m)$: Spawning occurrence for a given month
 $JP(m)$: Juvenile Production per surface unit and per month

$$SP(m) = \begin{cases} 1 & \text{if } T_{smin} < T(m) + \Delta T(m) < T_{smax}(m) \\ 0 & \text{else} \end{cases}$$

$$JP(m) = [JPm(m) \times [1 + \Delta JPm(m)]] \times SP(m)$$

Stock/Maturation/Mortality block

$Z_i(m)$: Natural mortality evolution per surface unit and per month for a generic i^{th} length class
 $M_i(m)$: Effective per surface unit of the 1st class length having died per month
 $G_i(m)$: Effective per surface unit of the 1st length class having grown to achieve the next length class in a month
 $GR_i(m)$: Growth rate of the i^{th} length class per month

$M_i(m)$: Mortality evolution per surface unit and per month for a generic i^{th} length class
 $LC_i(m)$: Clam effective evolution per surface unit and per month for a i^{th} length class

$$M_i(m) = \begin{cases} Z_i(m) + FE_i(m) \times FM(m) \times Capt_i(m) & \text{For } i = 1 \text{ to } 4 \\ Z_i(m) \times 2 + FE_i(m) \times FM(m) \times Capt_i(m) & \text{else} \end{cases} \quad \text{if } S < 20000 \text{ t}$$

$$LC_i(m) = \begin{cases} JP(m) - M_i(m) - G_i(m) & \text{For } i = 1 \\ LC_{i-1}(m) \times GR_{i-1}(m) - M_i(m) - LC_i(m) \times GR_i(m) & \text{For } i \geq 2 \end{cases}$$

Fishery block

OFM : Opening Fishing Month
 CDS : Capture Duration Season (month)
 $NFL(m)$: Number of Fishing Licenses
 $CVL(m)$: Catches Volume per fishing License each month
 $FE_i(m)$: Fishing Effort expressed in percentage of the total fishing effort all length class considered applied to class 1 to 4 each month
 ABS : Arcachon Bay Surface (m^2)
 MW_i : Mean Weight of the i^{th} length class (g)
 $PAS(m)$: Protected Area Surface
 $Pr(m)$: Selling price
 $Pref$: Reference price

$FM(m)$: Fishing Month
 $Capt_i(m)$: Fishing catches evolution expressed in effective per surface unit and per month for a generic i^{th} length class

$$FM(m) = \begin{cases} 1 & \text{if } OFM \leq m \leq OFM + CDS(m) \\ 0 & \text{else} \end{cases}$$

$$= \begin{cases} \frac{NFL(m) \times CVL(m) \times 10^6 \times FE_i(m)}{ABS \times MW_i} \times \frac{Capt_i(m)}{ABS - PAS(m)} \times \left[1 + \frac{Pr(m) - Pref}{10} \right] & \text{if } Pr(m) > Pref \\ \frac{NFL(m) \times CVL(m) \times 10^6 \times FE_i(m)}{ABS \times MW_i} \times \frac{ABS - PAS(m)}{ABS} & \text{else} \end{cases}$$

$S(m)$: Total biomass

$$S(m) = \sum_{i=1}^4 LC_i(m) \times MW_i \times ABS$$

1

2 **Fig. 5.** Equation formulations for each process from the starting point S (biomass) - in blue: known parameters or fixed by the user; in green: estimated by the
 3 model.

4 **Table 2:** Fixed or known parameters used for the parametrization of the differential equations.

Blocks	Parameter sets (units)	Values of parametrization	References
Environment and Production (of juveniles)	T: temperature per month (°C) Defined by f, h and g: coefficients of the sea water temperature with f : half of the maximum temperature variation h: phase g: mean annual temperature	From 2003 to 2019: real data From 2020: moving average over three years calculated on each month	ARCHYD network on two stations (Comprian and Les Jacquets)
	ΔT: temperature variation (°C)	From 2003 to 2019: 0 From 2020: see part 7 for retained values according to scenarios	Parameter added to simulate environmental scenario from 2020.
	Tsmin: minimum temperature for spawning (°C)	15	Literature (Beninger and Lucas, 1984; Rodríguez-Moscoso et al., 1992; Solidoro et al., 2003)
	Tsmax: maximum temperature for spawning (°C)	22	Literature (Rodríguez-Moscoso et al., 1992; Solidoro et al., 2003)
	JPm: juveniles production per spawning month (ind m ⁻² month ⁻¹) fixed by Bald et al. (2009)	3.3	Bald et al., 2009
	ΔJPm: Combined chlorophyll a and TSM effects on juveniles production (%)	From 2003 to 2009: 0 From 2010 to 2019: -25 From 2020: see part 7 for retained values according to scenarios	Caill-Milly (2012), ARCHYD network on two stations (Comprian and Les Jacquets)
Stock/Maturation/ Mortality/Fishery	ABS: Arcachon Bay Surface (m ²)	46,4 x 10 ⁶	Bald et al., 2009

Stock/Maturation/Mortality	GR ₁ to GR ₄ : growth rates of length class 1 to 4 (dimensionless)	[0-20]: 0.361 [21 – 34]: 0.245 [35 – 39]: 0.227 > 40: /	Assessed from enclosure field experiments undertaken by Dang et al (2010)
	MW ₁ to MW ₄ : mean weight of length class 1 to 4 (g)	[0-20]: 0.992 [21 – 34]: 6.624 [35 – 39]: 11.662 > 40: 18.288	Calculated using relation length-weight (see Appendix 1)
	Z ₁ to Z ₄ : natural mortality evolution per surface unit for class 1 to 4 (%)	[0-20]: 6.9 [21 – 34]: 3.9 [35 – 39]: 1.8 > 40: 1.16	Assessed from enclosure field experiments undertaken by Dang et al (2010)
Fishery	FE ₁ to FE ₄ : fishing effort expressed in percentage of the total fishing effort all length class considered applied to class 1 to 4 (%)	[0-20]: 0 [21 – 34]: 0.4 [35 – 39]: 0.5 > 40: 0.1	Estimated from anonymous catches reports and authority controls
	OFM: opening fishing month	July	From Bald et al., 2009
	CDS: capture duration season	2003: 6 2004 to 2008: 12 2009 to 2012: 10.3 2013 to 2019: 12	Local regulation (Sanchez et al., 2018 ; Caill-Milly et al., 2021)
	NFL: number of fishing licenses	2003 to 2008: 70 2009: 66 2010: 57 2011: 57 2012: 60 2013: 55 2014: 56 2015: 52 2016: 44 2017: 49 2018: 47 2019: 46	Local regulation (Caill-Milly et al., 2021)

PAS: protected area surface (x 10 ⁶ m ²)	2003 to 2005: 2.37 2006 to 2007: 0.96 2008: 9.10 2009 to 2012: 4.3 2013: 4.3 and 5.4 2014: 5.4 and 0 2015: 0 and 9.6 2016: 0, 9.6 and 4.9 2017 to 2019: 4.9	Local regulation (Sanchez et al., 2018 ; Caill-Milly et al., 2021)
Pr: Effective price (€.kg ⁻¹)	From 2003 to 2019: 3.5	Based on interviews with fishermen
Pref: Reference price (€.kg ⁻¹)	3.5	Based on interviews with fishermen
CVL: catches volume per fishing license each month (t.month ⁻¹)	2003: 0.47 2004: 0.67 2005: 0.46 2006: 1.06 2007: 1.22 2008: 0.85 2009: 0.82 2010: 0.73 2011: 0.90 2012: 0.68 2013: 0.75 2014: 0.51 2015: 0.50 2016: 0.64 2017: 0.75 2018: 0.88 2019: 0.74	Calculated from fishermen declarations (SIH, unpublished data and CRPMEM, unpublished data; Sanchez et al., 2018; Caill-Milly et al., 2021).

6. Validation and sensitivity analysis

6.1. Goodness of fit of the model

The first available dataset on size distribution of the population within the bay (Caill-Milly et al., 2003) determines the initial time of the model and is available for July 2003. Starting from this date, the model was calibrated with the aforementioned recent population, ecological and fishery data. This “historical” reconstitution ended in December 2019. It traced the stock evolution before testing new management strategies.

Model validation was performed on this hindcast using the subsequent stock assessments (2003, 2006, 2008, 2010, 2012, 2014 and 2018). Those observed data (learning samples) were compared to the predicted data given by the model. The model efficiency, which is the calibration step, was evaluated by the percentage of deviation between observed and predicted data sets. The criterion of a maximum deviation percentage (set to 10 %) was retained according to previous works (Bald et al., 2006, 2009). The model output for the July 2003 to December 2019 period is illustrated in Figure 6 and presents a first period characterized by a global decrease of the total biomass up to 4,883 tons mid-2008 and a second period displaying a recovery of the stock (with a maximum at 9,188 tons early 2018). At the end of the period, the total biomass is around 8,000 tons.

For this historical reconstitution, the model outputs fits quite well with the real data since the percentage of deviation (in absolute terms) between observed and predicted data were respectively 4% in 2003, 10% in 2006, 11% in 2008, 3% in 2010, 6% in 2012, 1% in 2014 and 3% in 2018 (Figure 6) (average of the absolute values of this percentage equal to 5.3%). Those values meet the criterion of a maximum deviation percentage set at 10% except for 2008 with 11%.

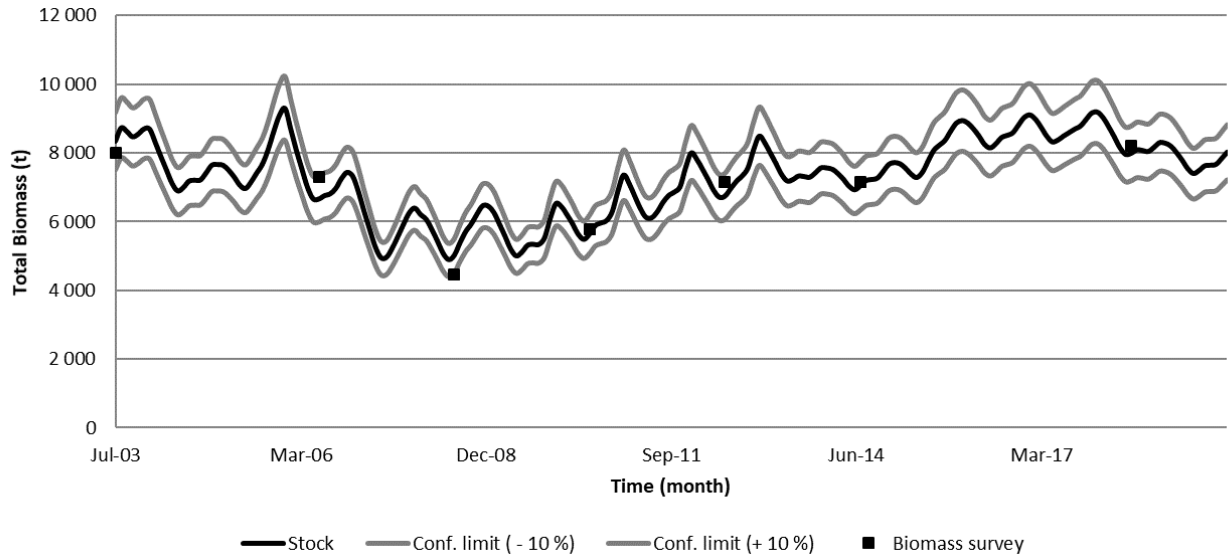


Fig. 6. Total biomass (in t) simulated between July 2003 and December 2019 (“historical” reconstitution).

6.2. Model sensitivity

6.2.1. Retained methodology

Parameters of system dynamics models are subject to uncertainty, which propagates throughout the model, and lead to variability of its outputs. In this context, sensitivity analysis can provide an answer to various issues such as improvement of the model formulation including simplification by eliminating non-essential components, model robustness assessment, identification of the parameters that have the greatest influence of chosen target variables, etc. (Banos-Gonzalez et al., 2018; Norton, 2015; Pianosi and Wagener, 2018). In this paper, the effect of variations in assumed information on the model output is considered. It enables identification of the most influential parameters.

In this context, uncertainty of the control parameters used in the model were considered; they are related to biological and environmental aspects. For each parameter, an arbitrarily selected range of 25% variation around the default parameter value was applied (Banos-Gonzalez et al., 2018), unless available assessment of uncertainty was already available. This

was the case for natural mortality, spawning minimum and maximum temperature, mean length weight. For natural mortality, the standard deviation of calculated values established from Dang (2009) was employed as the uncertainty measure (± 3.3 , ± 1.5 and $\pm 1.1\%$ for the 0-20 mm, 20-35 mm and 35-40 mm length classes respectively). In the case of spawning minimum and maximum temperature, few works established a threshold (Delgado and Pérez-Camacho, 2007; Holland and Chew, 1974; Mann, 1979; Obha, 1959; Toba and Miyama, 1995), which challenged us to consider a possible difference of $\pm 0.5^\circ\text{C}$. For mean length weight, the standard deviation calculated by Bald et al. (2009) was used as the uncertainty measure (± 0.67 , ± 0.21 , ± 0.41 and $\pm 1.12\%$ for the 0-20 mm, 20-35 mm, 35-39 mm and above 40 mm length classes respectively) (Table 3).

Table 3. Parameters' uncertainty applied in the model to assess the sensitivity analysis using Monte Carlo simulations.

Parameters	Uncertainty applied	Percentage of variation around the default parameter value
Natural mortality evolution (%)	0-20 mm: ± 3.3	48%
	21-34 mm: ± 1.5	38%
	35-40 mm: ± 1.1	61%
	> 40 mm : ± 0.3	25%
Spawning minimum temperature ($^\circ\text{C}$)	± 0.5	7%
Spawning maximum temperature ($^\circ\text{C}$)	± 0.5	5%
Mean length weight (g)	0-20 mm: ± 0.670	68%
	21-34 mm: ± 0.210	3%
	35-40m: ± 0.410	3%
	> 40 mm: ± 1.120	6%
Growth rates of the length (dimensionless)	0-20 mm: ± 0.090	25%
	21-34 mm: ± 0.061	25%
	35-40 mm: ± 0.057	25%
Juveniles production per spawning month (ind month^{-1})	± 0.6	25%

On a first step, each parameter was studied separately to test for the variability of the estimated biomass (S) using thousand Monte Carlo simulations (Univariate Sensitivity Analysis) with a random uniform distribution of probability. This approach corresponded to the One-Factor-At-A-Time analysis where the initial values of the parameters were modified in a

range that account for ecological reality or in a range of +/- 25%. For December 2029, a sensitivity index (Banos-Gonzalez et al., 2018) was calculated for each parameter.

$$Sensi_i = \left(\frac{SMax - SMin}{SVal} \right) \div \left(\frac{PMax - PMin}{PVal} \right) \times 100$$

where $Sensi_i$ represents the sensitivity index of the biomass in relation to the parameter i ; $SMax$ and $SMin$ are the maximum and minimum values, respectively, of the biomass at time December 2029; $SVal$ represents the status quo model value of the biomass at time December 2029; $PMax$ and $PMin$ represent the maximum and minimum values of the i th parameter, respectively; and $PVal$ is the status quo model value of the j th parameter.

The sensitivity index values are visualized on an ordered bar chart (Pianosi et al., 2016). Using this index, the parameters can be classified into five categories: insensitive ($Si = 0\%$), low sensitivity ($Si < 10\%$), moderate sensitivity ($10\% < Si < 50\%$), high sensitivity ($50\% < Si < 100\%$), and very high sensitivity ($Si > 100\%$). In addition, confidence bounds of the biomass were plotted for the variation of each parameter. In relation to the corresponding relative variation of the input parameter, the index and the graphical representation provided information about the parameters, which influenced the system the most.

In a second step, the sensitive parameters ($Si > 50\%$) were considered together (general sensitivity analysis) to quantify the effects of their simultaneous variations on the biomass. In this case, one thousand Monte Carlo simulations were generated with Latin Hypercube sampling. For this, it is common practice to constrain the parameter variations to acceptable ranges in order to have realistic levels (Banos-Gonzalez et al., 2018). In the absence of additional information, the percentages of variation were here identical to those of step one. With Latin Hypercube sampling, the full range of each parameter was thus explored using a reasonable number of runs (Banos-Gonzalez et al., 2018) and provided sufficient information about the distribution in the outcome (Ford and Flynn, 2005). It can be efficient in order to

reveal non-linearities, principally if one or two parameters dominate (Manache and Melching, 2008).

A variation coefficient (VC) (Banos-Gonzalez et al., 2018) of the biomass shown by the Monte Carlo simulations was calculated for December 2029.

$$VC = \left(\frac{SMax95 - SMin95}{\bar{S}} \right) \times 100$$

where VC is the relative variation of the biomass (S) with respect to its mean value using 95% confidence bounds; $SMax95$ and $SMin95$ are the maximum and minimum values of the biomass in December 2029, using the 95% confidence bound; and \bar{S} is the mean value of biomass.

This coefficient was set in one of the three following categories: low response ($VC < 50\%$), moderate response ($50\% < VC < 100\%$) and high response ($VC > 100\%$).

For the two steps, Monte Carlo simulation is appropriate since the model may generate interactions between factors or have non-linear outputs as stated by Lesnoff et al. (2012). The time-frame has two parts: from July 2003 to December 2019 – historical reconstitution; from January 2020 to December 2029 – projection with historical trends of environmental data and application of the same management measures as for 2019.

6.2.2. Sensitivity analysis results

For the control parameters tested, the values of the sensitivity index are comprised between 1 and 399%, which means that the model is from low sensitive to high sensitive regarding those parameters. The highest indexes are obtained with parameters regarding or influencing young stages of the population: spawning maximum temperature, recruitment and spawning minimum temperature (Figure 7). The following are related to mean length weight 21-34 mm, mean length weight above 40 mm and to a lesser extent natural mortality above 40 mm. The lowest indexes are related to mean length weight for 0-20 mm to natural mortality of 35-40 mm, to growth rate 21-34 mm and to natural mortality 21-34 mm.

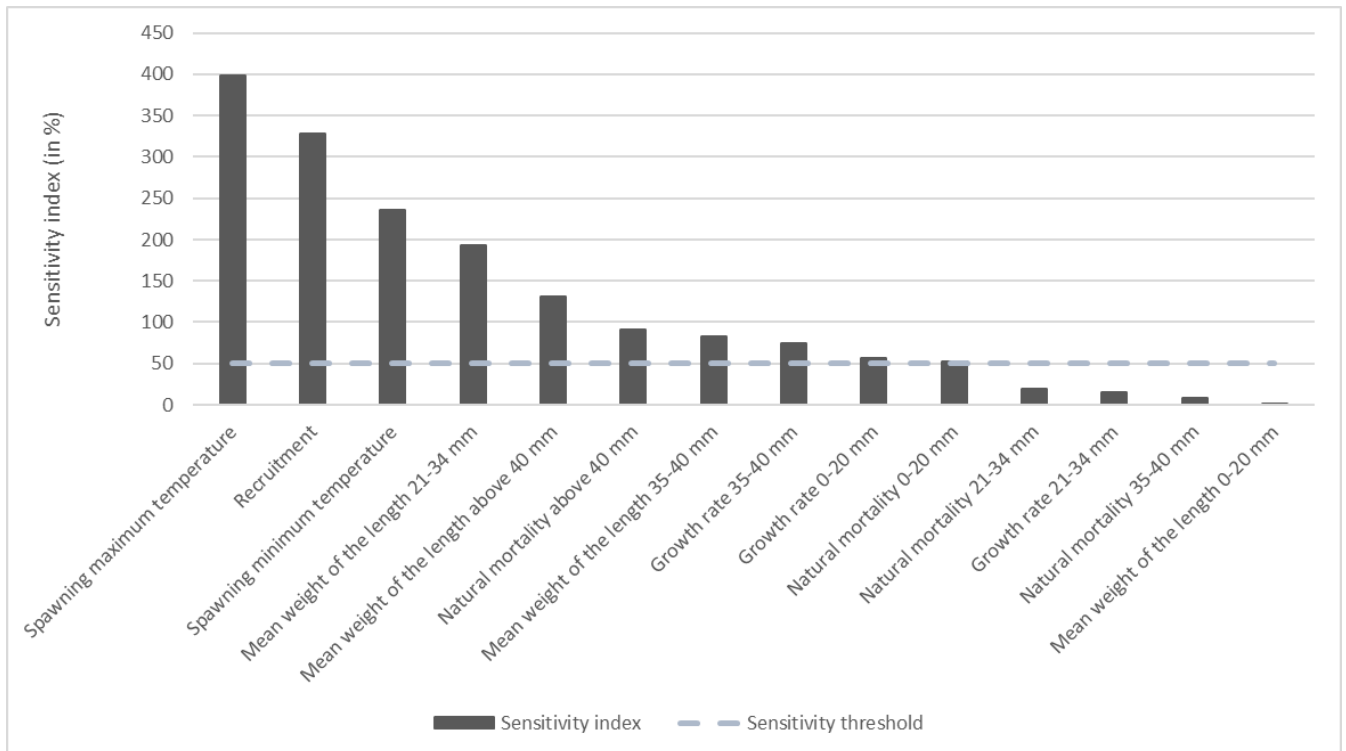


Fig. 7. Value of the sensitivity index for the control parameters used as input factors.

Ten out of fourteen parameters are associated to the sensitive index. The confidence bounds of the biomass according to their respective variation are plotted for each of those parameters (Appendix 2).

Those ten parameters were used to run one thousand Monte Carlo simulations with Latin Hypercube sampling. The variation coefficient is 173%, which means that the model displays a high response of the biomass to those parameters.

7. Application of various scenarios

7.1. Simulations of several management strategies

Since the outcome of the model was to be used as a decision-making tool, case studies were defined to observe the simulated evolution of the total biomass according to various

strategies relying on different types of measures (reducing fishing effort, technical measures and limitation of catches) (Table 4).

Forecasts from January 2020 to December 2029 resulting from the introduction of different management options were undertaken. The eight scenarios **related to management strategies** and retained for this paper were the following:

- Scenario 1 (status quo) corresponded to maintenance of the management measures in similar levels than those applied in 2019 ($CVL = 0.74 \text{ t month}^{-1} \text{ license}^{-1}$, $CDS = 12 \text{ months}$, $PAS = 4.9 \times 10^6 \text{ m}^2$, $NFL = 46$);
- Scenario 2 doubled the protected area surface, the other parameters remaining the same as for status quo ($CVL = 0.74 \text{ t month}^{-1} \text{ license}^{-1}$, $CDS = 12 \text{ months}$, $PAS = 9.8 \times 10^6 \text{ m}^2$, $NFL = 46$);
- Scenario 3 reduced the fishing period (equivalent to one day per week off) ($CVL = 0.74 \text{ t month}^{-1} \text{ license}^{-1}$, $CDS = 10.3 \text{ months}$, $PAS = 4.9 \times 10^6 \text{ m}^2$, $NFL = 46$);
- Scenario 4 simulated a decrease of the number of fishing licenses ($CVL = 0.74 \text{ t month}^{-1} \text{ license}^{-1}$, $CDS = 12 \text{ months}$, $PAS = 4.9 \times 10^6 \text{ m}^2$, $NFL = 40$);
- Scenario 5 simulated a decrease of the catches per fishing licenses ($CVL = 0.6 \text{ t month}^{-1} \text{ license}^{-1}$, $CDS = 12 \text{ months}$, $PAS = 4.9 \times 10^6 \text{ m}^2$, $NFL = 46$);
- Scenario 6 combined three measures – slight decrease of the catches per fishing licenses, decrease of the capture duration season and increase of the protected area surface ($CVL = 0.70 \text{ t month}^{-1} \text{ license}^{-1}$, $CDS = 11 \text{ months}$, $PAS = 7.35 \times 10^6 \text{ m}^2$, $NFL = 46$);
- Scenario 7 also combined three measures – slight decrease of the catches per fishing licenses, decrease of the capture duration season and of the number of fishing licenses ($CVL = 0.70 \text{ t month}^{-1} \text{ license}^{-1}$, $CDS = 11 \text{ months}$, $PAS = 4.9 \times 10^6 \text{ m}^2$, $NFL = 40$);

- Finally, Scenario 8 combined two measures – decrease of the catches per fishing license and decrease of the capture duration season ($CVL = 0.60 \text{ t month}^{-1} \text{ license}^{-1}$, $CDS = 10.3 \text{ months}$, $PAS = 4.9 \times 10^6 \text{ m}^2$, $NFL = 46$).

When a parameter was not listed above, it means that the applied value was the same as for the last year of the “historical” reconstitution.

To undertake comparisons between these management scenarios, evolution of the total biomass trend was compared between the chosen scenarios and the continuation of the active management measures in 2019 (Scenario 1 - status quo) (Table 4).

Table 4. Description of the eight tested management scenarios integrated in the model from 2020 to 2029. Relative differences of each management measure applied in Scenarios 2 to 8 are compared to Scenario 1 (status quo) management measure values using the following codification = no changes, ↗ increase comprised between 1 and 10%, ↗↗ increase (strictly) superior to 10%, ↘ decrease comprised between 1 and 10%, ↘↘ decrease (strictly) superior to 10%.

Key: NFL = number of fishing licenses, CVL = catches volume by license ($\text{t month}^{-1} \text{ license}^{-1}$), CSD = capture season duration (month), PAS = Protected area surface ($\times 10^6 \text{ m}^2$).

	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 5	Scenario 6	Scenario 7	Scenario 8
Types of measures differing from status quo	/	Technical measures,	Technical measures	Reducing fishing effort	Limitation of catches	Limitation of catches, technical measures	Limitation of catches, technical measures, reducing fishing effort	Limitation of catches, technical measures
NFL	46	=	=	↘↘	=	=	↘	=
CVL	0.74	=	=	=	↘↘	↘	↘	↘↘
CDS	12	=	↘↘	=	=	↘	↘	↘↘
PAS	4.9	↗↗	=	=	=	↗↗	=	=

The total biomass according to the eight management strategies (from January 2020 to December 2029) displayed in any case an improvement in the stock level. The results were summarized in the two following categories (single measures and multiple measures, see Table 5):

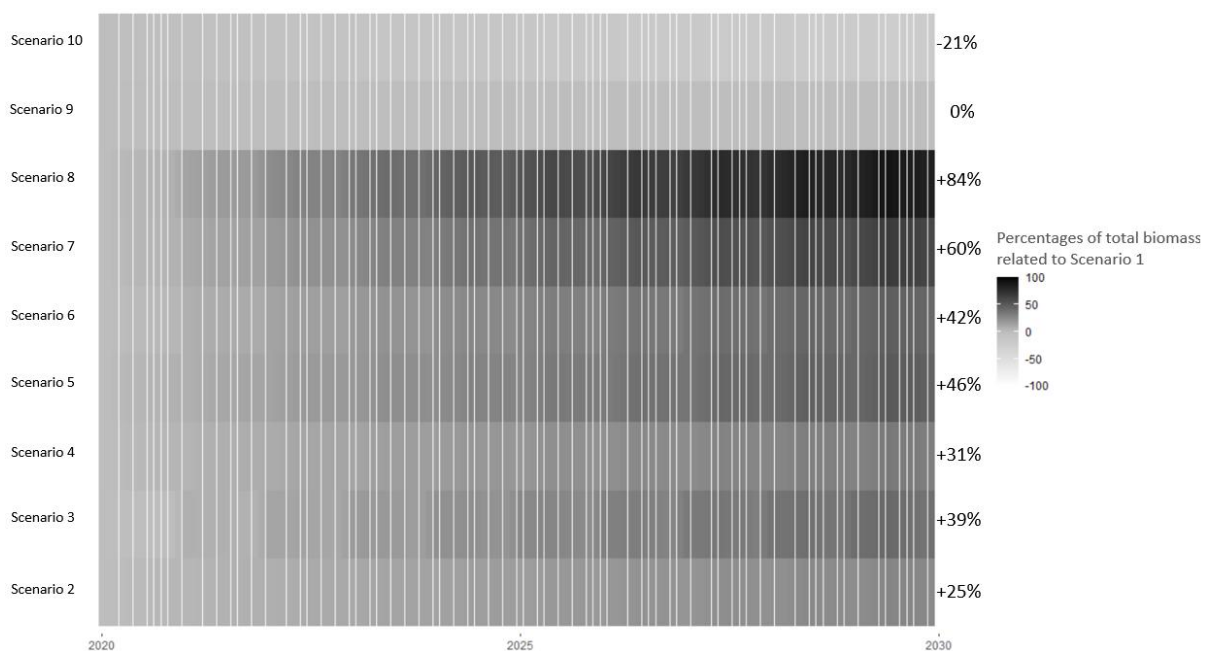
- Among the single measures, the gain between the scenarios 2 to 5 and scenario 1 (status quo) is comprised between 25% and 46% at the end of 2029. The lowest gain

is obtained with technical measures (*PAS*); the highest gain is obtained with the limitation of catches (*CVL*);

- Among the multiple measures, the gain between the scenarios 6 to 8 and scenario 1 (status quo) is comprised between 42% and 84% at the end 2029. The highest gain is obtained with the limitation of catches (*CVL*) combined with technical measures (*CDS*).

These results highlighted the relevance of combining selected management measures to improve the stock level.

Table 5. Relative differences expressed in percentages between the total biomass estimated for each Scenario [Scenarios 2 to 8 (management strategies); Scenarios 9 to 10 (potential effects of environmental or market modifications)] and the total biomass estimated for Scenario 1 (status quo) from January 2020 to December 2029. The gains or losses at the end of 2029 are displayed on the right of the table.



7.2. Simulations of environmental and market modifications

Two other scenarios were defined to consider the **potential effects of environmental or market modifications** to the stock evolution in addition to *status quo* management measures. For these scenarios, the management measures applied were the same as those selected for Scenario 1 (*status quo*) on which the additional hypotheses were applied from 2020:

- Scenario 9 simulated an increase of the seawater temperature. To define this augmentation, the last report of the GIECC (IPCC, 2019) was used. Considering the projected change in sea surface temperature between the recent past (1986–2005) and the near term (2031–2050) under scenario RCP8.5, an increase of 0.04°C per year was tested. It was applied to all the months of the same year. This value is consistent with regional forecasts given by Chust et al. (2014) for the Bay of Biscay for the end of the century. This modification was applied between 2020 and 2029;
- Scenario 10 considered the increase of the selling price from 3.5 euros per kg to 4.5 euros per kg. As mentioned above, this resulted in an increase in catches of 10%.

Regarding scenario 9 (slight increase of temperature applied in addition to *status quo* management measures), the total biomass exhibited the same evolution as for the status quo scenario (Table 5). Over the period 2020-2029, the number of months favorable to the realization of spawning was not modified. When modelling is continued with the same assumption (+ 0.04°C per year), a change is observed in 2037. All other things being equal, at the end of 2040, the biomass would be 24% higher than with scenario 1 (Appendix 3).

For scenario 10, the simulated price per kilo increase results in a gradual decrease in the total biomass over the period 2020-2029 (Table 5). At the end of the period, the difference reaches -21% compared to the level obtained for the status quo.

8. Discussion and conclusion

Considering the initial assumptions listed in Bald et al. (2009), major developments and improvements have been undertaken. Those recent improvements are in bold italics in Figure 3.

Integration of specific available life traits data

The parameterization of Bald et al.'s (2009) model relied mainly on different bibliographic sources related to population dynamics of the Manila clam (Beninger and Lucas, 1984; Melià et al., 2004; Rodríguez-MoscOSO et al., 1992; Solidoro et al., 2000, 2003) together with data related to Arcachon Bay (Caill-Milly et al., 2003 and G. Trut, unpublished data). Recent ecological data available at the bay scale led to the revision of the previous model's assumptions.

First, environmental drivers on key processes of the population dynamics have been reinforced thanks to integration of real data or to new formulations. This evolution mainly regarded the reproduction phase. Until now this phase, which is one of the key processes of population dynamics (Flye-Saint-Marie, 2007) was only controlled by seawater temperature. A preliminary modulation relying on food availability expressed by chlorophyll a levels and on total suspended matter concentrations was undertaken. Measurement of photosynthetic pigment water concentration remains relatively easy to acquire and appears to be the most common indicator used for food availability (*e.g.* Shibata et al., 1999). Unlike the older stages (Flye-Sainte-Marie et al., 2003), we have not identified any work questioning the validity of this descriptor as an adequate substitute for food availability in young Manila clams. Nevertheless, it is always interesting to consider other trophic resource proxies when available. In the case of Arcachon, the evolution of the monthly average of phytoplankton abundance also showed a change consistent with the hypothesis adopted for this work [Phytoplankton and Phycotoxin

Monitoring Network (REPHY, Ifremer), unpublished data]. In those conditions, the retained formulation corresponded to a more realistic hypothesis since those modelled environmental parameters (temperature, food supply and total suspended matter) are well known for influencing the reproductive phase (Delgado and Pérez-Camacho, 2007; Devauchelle, 1990; Holland and Chew, 1974; Le Pennec and Benninger, 2000; Mann, 1979; Ohba, 1959; Soudant et al., 2004; Toba and Miyama, 1995) or described as driving factors for Arcachon Bay (Caill-Milly, 2012). However, the applied modulation does not take into account the observation of a phenomenal number of juveniles in 2014 (Sanchez et al., 2014). Moreover, the sensitivity analysis highlighted that the target variable – the biomass – was very sensitive to the uncertainty of the parameter recruitment. Such results advocate for deeper analysis of the processes related to the younger stages including data collection efforts as recommended by Sterman (2000). This encourages the implementation of a monitoring of the number of clam larvae just as it is already practiced for the intra-basin oysters but for the moment not carried out on Manila clam for lack of means. In the meanwhile, as long as such an episode remains exceptional and the current conditions on chlorophyll a and TSM do not exhibit major changes, the applied rules should be maintained.

A second important process for population dynamics, *i.e.* growth, could also have been determined by this integration of specific environmental drivers. The reason is that numerous authors agree with the main role played by the temperature on *Venerupis species* (Beiras et al., 1994; Fan et al., 2007; Laing et al., 1987; Toba, 1987 in Nakamura et al., 2002), but also food supply (Maître-Allain, 1982; Yamamoto et al., 1956) and even duration of immersion (Gouilletquer et al., 1987). Nevertheless, two reasons led to the application of minor changes in the formulation of the growth process. First, the highlighted interrelations between the studied stock status and temperature did not consider growth but mainly the reproductive phase (Caill-Milly et al., 2012). Secondly, the possible effects involved (directly and indirectly via the link

between temperature and trophic resources) were highly complex and the current constitution of the model did not allow their consideration. Numerous references have already addressed the problem of model complexity (Costanza and Sklar, 1985; Håkanson, 1999; Jørgensen, 1988) since the right balance must be struck between simplicity and complexity. On one hand, a simplistic model may not account for important ecological processes and may reduce descriptive and realistic model properties (Cetin, 2007). On the other hand, a highly complex model may reduce predictive accuracy, be difficult to run, and produce a high number of errors (Håkanson, 1999; Tsang, 1991). High dependence on assumptions, parameter values, and environmental forcing functions was also mentioned by Murray and Parslow (1999). It was assumed that ecological processes involved in the growth phase were insufficiently controlled.

With respect to growth and natural mortality, the previous formulations relied on growth model developed for the Sacca di Goro Lagoon (Italy) (Bald et al., 2009) or on an empirical equation proposed by Solidoro et al. (2000, 2003) for Northern Adriatic lagoons. Direct assessments of growth and of this source of mortality were drawn from enclosure field experiments undertaken by Dang et al. (2010) within Arcachon Bay between December 2005 and November 2007. In addition to being reliable data for the considered stock, their variations with age (related to mean size) were coherent with the models proposed by Caddy (1991) and Appeldoorn (1988) notably to reproduce mortality at age. Moreover, those values were used to account for the natural predation of Manila clams, which was considered to be important in Arcachon Bay (Robert and Deltreil, unpublished results). They also included the effect of diseases.

Regarding ecological processes not treated until now, future improvements could mainly concern the question of linkage between the stock and the recruitment. The current biomass surveys led every two years indicated high variability of the recruitment levels at the bay scale (Sanchez et al., 2018) that was in accordance with the work undertaken by Tezuka et

al. (2012). Nevertheless, they did not allow the validation of any intraspecific stock/recruitment relationship for the investigated population. To identify this relationship for coastal species, Freire and García-Allut (2000) reported the importance of scale considerations or the occurrence of low stock levels to be detected. Moreover, processes involved are complicated because a stronger effect of interspecific stock-recruitment relationship can also occur as demonstrated for *Donax hanleyanus* by Defeo (1998). In the absence of evidence, recruitment fluctuations in response to environmental parameters were deemed much stronger than those linked to density-dependent mechanisms (intra and interspecific). If this hypothesis were to be revised, the model structure would allow, for example in considering fertility rates according to size classes, since reproductive effort and fecundity are age-related (Gosling, 2003). For the lagoon of Venice, Solidoro et al. (2003) considered that each parental class (minimum length required 18 mm) enabled the successful implantation of one hundred juveniles. For Arcachon Bay, a first approach could be undertaken by using the age-related gonadal production established by Urrutia et al. (1999) for *Venerupis decussatus*.

Adjustment of the realized fishing activity and its control parameters

Reformulations of the monthly catches volume per fishing license using data from two databases (“Système d’Informations Halieutiques” and “Base Pêche Aquitaine”) was integrated, and is considered as the most reliable parameter for professional fishing activities. In addition, the fishing effort according to the different length classes was reallocated based on more realistic field information. Those improvements permitted a reformulation of the temporal fishing catches evolution expressed in effective per surface unit for each length class (units in $\text{m}^{-2} \text{month}^{-1}$). The fishery block was also amended by a first option to simulate a price effect on the fishing strategies. Socio-economic objectives are generally poorly defined so a price-effect has been recently integrated into the model to enrich it and to take into account human behavior. Such relationships could be more precisely established as well as the relationship between

biomass availability, effort and profitability of the fishery. For instance, it would be interesting to introduce modification of *CVL* level in response to strong decrease of total biomass. As well, a reflection on the desired breakdown of the licenses between full time and part time activities could be set.

In addition, the current fishing activity modelled within the model remained the commercial one. Manila clams are also caught by recreational fishermen, but their impact is considered negligible in comparison to commercial fishing (FMPAA, unpublished results). Under those conditions, it did not seem useful to include this factor in the modeled parameters.

Performance of the model, sensitivity and used framework

The adequacy of the model with regards to reality was considered by using the acceptable limit of deviation percentage between observed and predicted data sets (Bald et al., 2006, 2009). The obtained average of the absolute values of the deviation percentage (considering years 2003, 2006, 2008, 2010, 2012, 2014 and 2018) is equal to 5.3%. This level reflects a slightly better performance than that described by Bald et al (2009) and over a larger number of years. In the future, it would be worth considering the model performance with new indices of performance, such as those implemented by Anastácio et al. (2009) for *Scrobicularia plana*. The implementation of the Loague and Green's modeling efficiency (EF) would also provide an overall indication of the goodness of fit (Mayer and Butler, 1993). EF is a dimensionless statistic based on the coefficient of determination and directly compares predictions with real-world observations.

This paper proposed a first sensibility analysis of biological and environmental control parameters. The temperature conditions related to spawning periods and recruitment appear to give the highest sensitivity for determining the total biomass. This highlights the importance of selecting the right parameters that control the number of recruits on the modelled dynamics. A

first modulation according to Chlorophyll a and TSM concentrations was undertaken for this work. It is clearly an area for future work to improve the model.

The sensitivity analysis was mainly local and to a lesser extent global. It remains an elementary sensitivity analysis realized with the available module in Vensim (Faivre et al., 2013). Another avenue for improvement in this work would be to fully implement the method proposed by Pianosi et al. (2016) by implementing the packages for GSUA³. Another possible avenue would be to extend the sensitivity analysis to resource exploitation parameters. The improvement of the model was conducted step by step and the formulations both reinforced environmental and socio-economic considerations within the model. Cumulative effects of those drivers could therefore be considered (Scenarios 9 to 10). Although limitations on the modeling of biological processes were identified by the sensitivity analysis. Bearing these limitations in mind, we are convinced that this model remains reliable to investigate different management strategies under current environmental conditions but is not well suited to consider strong environmental shifts such as those considered in the worst climate change case scenarios.

For the accompaniment of a co-management approach for this local exploited stock

From the start, the model specifically intended to strengthen the management of the stock by enabling a robust and well-informed decision-making process based on science. This tool was used for the first time in 2008-2009. The simulations were presented and discussed in the framework of working groups (associating scientists, fishermen and administration representatives) (Caill-Milly et al., 2021). When the results of the last stock assessment campaign will be presented to professionals, the model can again be used to support management decision-making. The different management scenarios tested with this last version

³ <https://www.safetoolbox.info/info-and-documentation/>

of the model should help in this context in the coming months. The results argue for the choice of a management strategy involving several management measures as opposed to one strong measure modification. Such combinations are part of the arsenal of measures that are implemented on Manila clam resource in other European coastal systems (Coelho et al., 2021). Different combinations are possible and additional ones may stem from discussion. The acceptability dimension will have to be considered in this context.

Most of the existing management models dealing with clams necessitate the assessment of a large number of parameters (Cossarini et al., 2009; Pastres et al., 2001; Solidoro et al., 2000). Conversely, our present model necessitates fewer parameters and relies on a “system dynamic” approach implemented to understand and conceptualize the complex system regarding both the surrounding environment and human activity (Costanza and Ruth, 1998).

Similar approaches based on models were conducted *inter alia* on the gooseneck barnacle (Bald et al., 2006) and the Peruvian scallop (Ortiz et al., 2002). In our situation, its implementation complemented the existing collaborations between scientists and fishermen, who have both conducted field surveys since 2003. This type of functioning is in line with the directions of Oregon’s Development Fisheries Program (see Harte et al., 2008) because it aims at incorporating design of science and management plans for small-scale fisheries. Integration of different kinds of operational management measures and institutional structures for governance was highlighted by Defeo (2011) as a key issue in successful management of sandy beach fisheries. This approach is considered by the coastal Galician fisheries (Freire and García-Allut, 2000; Freire et al., 2002) and has been applied in Southeast Asia coastal fisheries since the 1960s (Pomeroy, 1995). Management of numerous other local French resources such as bivalves (Manila clam, scallop, mussel ...), crustaceans (spiny lobster) or algae, mainly in Brittany and in Normandy (Picault et al., 2014; D’Hardivillé and Bouché, 2018; ICES, 2018) rely on close collaborations between scientists and commercial industries; however, none of

them has used such a dynamic model before. In our case this approach has proven its effectiveness in selecting management measures for the sustainability of the neonatural resource, however the environment and design of the software should be enhanced in order to be used more systematically. Indeed, it is very difficult to change tack midway through a period and currently lacks an interface, which can also easily be used by managers (Caill-Milly et al., 2021). Moreover, the license restricts the use of the software in an easily accessible web-type form (Elsawah et al., 2017). Recent publications (Garcia, 2021a and Garcia, 2021b) should make it possible to solve some of the aforementioned points in the near future.

Such developments are in accordance with the four main uses of a model as reported by del Granado (2007): increasing the human understanding of the considered system; communicating visually, making predictions and supporting decision-making. This last use was also described by other authors (Felleman, 1999; Hannon and Ruth, 1994; Shenk and Franklin, 2001). Opening science to society becomes a significant subject at a national level since a dedicated charter was revised and signed at the end of 2020 by eight French institutes (public establishments for research, expertise and /or risk assessment in the fields of health and the environment) (Caill-Milly et al., 2021). Regarding the improvements of the model identified, this recent context militates for a rapid interface development to be more easily shared with and used by managers.

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References

- Anastácio, P.M., Verdelhos, C.T., Marques, J.C., Pardal, M. A., 2009. A validated population-dynamics model for *Scrobicularia plana* (Mollusca, Bivalvia) in a south-western European estuary. Mar. Freshwater Res. 60, 404–416, www.publish.csiro.au/journals/mfr
- [Appeldoorn, R.S., 1988. Ontogenetic changes in natural mortality rate of queen conch, *Strombus gigas* L. in southwest Puerto Rico. Bull. Mar. Sci. 42, 159–165.](#)
- Bald, J., Borja, A., Muxika, I., 2006. A system dynamics model for the management of the gooseneck barnacle (*Pollicipes pollicipes*) in the marine reserve of Gaztelugatxe (Northern Spain). Ecol. Model. 194, 306-315, <http://dx.doi.org/10.1016/j.ecolmodel.2005.10.024>
- Bald, J., Siquin, A., Borja, A., Caill-Milly, N., Duclerc, B., Dang, C., de Montaudouin, X., 2009. A system dynamics model for the management of the Manila clam, *Ruditapes philippinarum* (Adams and Reeve, 1850) in the Bay of Arcachon (France). Ecol. Model 220, 2828–2837.
- Banos-Gonzalez, I., Martínez-Fernández, J., Esteve-Selma M.-Á., Esteve-Guirao, P., 2018. Sensitivity Analysis in Socio-Ecological Models as a Tool in Environmental Policy for Sustainability. Sustainability 10, 2928, doi:10.3390/su10082928
- Beiras, R., Camacho, A.P., Albentosa, M., 1994. Influence of temperature on the physiology of growth in *Ruditapes decussatus* (L.) larvae. J. Shellfish Res. 13(1), 77-83.
- Beninger, P., Lucas, A., 1984. Seasonal variation in condition, reproductive activity and gross biochemical composition of two species of adult clam reared in a common habitat *Tapes decussatus* (L) (Jefreys) and *Tapes philippinarum* (Adams and Reeve). J. Exp. Mar. Biol. Ecol. 79, 19-37.
- Bertolini, C., Bernardini, I, Brigolin, D., Matozzo, V., Milan, M., Pastres, R., 2021. A bioenergetic model to address carbon sequestration potential of shellfish farming: example from *Ruditapes*

philippinarum in the Venice lagoon. ICES J. Mar. Sci., fsab099,
<https://doi.org/10.1093/icesjms/fsab099>

Caddy, J.F., 1991. Death rates and time intervals: is there an alternative to the constant natural mortality axiom? Rev. Fish Biol. Fisheries 1, 109–138.

Caill-Milly, N., 2012. Relationships between stock status and its exploitation via comprehension and formalization of socio-ecosystems interactions. Application to Manila clam (*Venerupis philippinarum*) population of Arcachon Bay. PhD Thesis, Université de Pau et des Pays de l'Adour (UPPA).

Caill-Milly, N., de Casamajor, M.N., Lissardy, M., Sanchez, F., Morandea, G., 2003. Évaluation du stock de Palourdes du bassin d'Arcachon – Campagne 2003. Rapport Ifremer, DRV/RH/LHA.

Caill-Milly, N., Bru, N., Mahé, K., Borie, C., D'Amico, F., 2012. Shell Shape Analysis and Spatial Allometry Patterns of Manila Clam (*Ruditapes philippinarum*) in a Mesotidal Coastal Lagoon. J. Mar. Biol., 2012(ID 281206), 1-11. Publisher's official version: <https://doi.org/10.1155/2012/281206>,

Caill-Milly, N., Sanchez, F., Lissardy, M., De Montaudouin, X., Bru, N., Kermorvant, C., Ganthu, F., 2021. Drawing lessons from a pluridisciplinary approach associating stakeholders for a better management of a bivalve population (French Atlantic coast)? Estuar. Coast. Shelf Sci. 251, 107194 (12p.). <https://doi.org/10.1016/j.ecss.2021.107194>

Canu, D.M., Campostrini, P., Riva, S.D., Pastres, R., Pizzo, L. Rossetto, Solidoro, C., 2011. Addressing Sustainability of clam farming in the Venice Lagoon. Ecol. Soc. 16, No. 3, 26.

Canu, D.M., Solidoro, C., 2018. Clam harvesting in the Venice Lagoon. In Global change in Marine Systems. Integrating natural, social and governing responses. Edited by P. Guillotreau, A. Bundy

- and R. I. Perry. *Routledge Studies in Environment, Culture and Society*. pp. 121-134. Routledge, New York. ISBN: 978-1-138-05922-1 (hbk) ISBN: 978-1-315-16376-5 (ebk).
- Cetin, L.T., 2007. SALMO-00: A process-based Simulation Library for Lake Ecosystems, PhD thesis, University of Adelaide, Australia.
- Chust, G., Allen, J. I., Bopp, L., Schrum, C., Holt, J., Tsiaras, K., Zavatarelli, M., Chifflet, M., Cannaby, H., Dadou, I., Daewel, U., Wakelin, S. L., Machu, E., Pushpadas, D., Butenschon, M., Artioli, Y., Petihakis, G., Smith, C., Garçon, V., Goubanova, K., Le Vu, B., Fach, B. A., Salihoglu, B., Clementi, E., Irigoien, X., Biomass changes and trophic amplification of plankton in a warmer ocean. *Global Change Biology*, 2014, vol. 20, pp. 2124-2139.
- Coelho, P., Carvalho, F., Goulding, T.A., Chainho, P. and Guerreiro, J, 2021. Management Models of the Manila Clam (*Ruditapes philippinarum*) Fisheries in Invaded European Coastal Systems. *Front. Mar. Sci.* 8:685307. doi: 10.3389/fmars.2021.68530.
- Cossarini, G., Lermusiaux, P.F.J., Solidoro, C., 2009. Lagoon of Venice ecosystem: Seasonal dynamics and environmental guidance with uncertainty analyses and errorsubspace data assimilation. *J. Geophys. Res.* 114, C06026. doi:10.1029/2008JC005080.
- Costanza, R., Sklar, F.H., 1985. Articulation, accuracy and effectiveness of mathematical models: a review of freshwater wetland applications. *Ecol. Model.* 27, 45–68.
- Costanza, R., Ruth, M., 1998. Using Dynamic Modeling to Scope Environmental Problems and Build Consensus. *Environ. Manage.* 22(2), 183-195.
- Dang, C., 2009. Dynamique des populations de palourdes japonaises (*Ruditapes philippinarum*) dans le bassin d'Arcachon, conséquences sur la gestion des populations exploitées. PhD thesis, University of Bordeaux I, France.

- Dang, C., de Montaudouin, X., Gam, M., Bru, N., Paroissin, C., Caill-Milly, N., 2010. The Manila clam population in Arcachon Bay (SW France): can it be kept sustainable? *J. Sea Res.* 63, 108-118.
- Dee Boersma, P., Reichard, S.H., Van Buren, A.N. (editors), 2006. *Invasive species in the Pacific Northwest*.
- Defeo, O., 1998. Testing hypotheses on recruitment, growth, and mortality in exploited bivalves: an experimental perspective. In *Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management* Edited by G.S. Jamieson and A. Campbell. *Can. Spec. Publ. Fish. Aquat. Sci.* 125, 257-264.
- Defeo, O., 2011. Sandy beach fisheries as complex social-ecological systems: emerging paradigms for research, management and governance. *Proceeding of the Fifth International Symposium on Sandy Beaches*, 19th- 23rd October 2009, Rabat, Morocco. Editor Bayed A., *Travaux de l'Institut Scientifique, Rabat, série générale* 6, 111-112.
- De Leo, G.A., Gatto, M., 2000. A stochastic bioeconomic analysis of silver eel fisheries. *Ecol. Appl.* 11(1), 281-294.
- De Leo, G.A., Levin, S., 1997. The multifaceted aspects of ecosystem integrity. *Conserv. Ecol.* 1, 1-3.
- Delgado, M., Pérez-Camacho, A., 2007. Influence of temperature on gonadal development of *Ruditapes philippinarum* (Adams and Reeve, 1850) with special reference to ingested food and energy balance. *Aquaculture* 264(1-4), 398-407.
- Del Granado, S.M., 2007. *The Use of Computer Models in Collaborative Decision-making in the Great Lakes: Two Case Studies*. State University of New York College of Environmental Science and Forestry. Environmental Science, ProQuest.

- Devauchelle, N., 1990. Sexual development and maturity of *Tapes philippinarum*, in: *Tapes philippinarum*, Biologia e Sperimentazione, E.S.A.V. (Ed.), E.S.A.V., Treviso; 49-58.
- D'Hardivillé, C., Bouché, L., 2018. Campagne d'évaluation du stock de palourdes du Golfe du Morbihan : 11, 12, 13 et 16 avril 2018. Rapport Ifremer LTBH Lorient et CDPMEM du Morbihan, 60 p.
- Elsawah, S., Pierce, S. A., Hamilton, S. H., Van Delden, H., Haase, D., Elmahdi, A., Jakeman, A. J., 2017. An overview of the system dynamics process for integrated modelling of socio-ecological systems: Lessons on good modelling practice from five case studies. *Environ Model Softw* 93, 27-145, DOI:10.1016/j.envsoft.2017.03.001.
- Emmett, R.L., Hinton, S.A., Stone, S.L., Monaco, M.E., 1991. Distribution and abundance of fishes and invertebrates in west coast estuaries, Volume II: Species life history summaries. ELMR Rep. No. 8 NOAA/NOS Strategic Environmental Assessments Division, Rockville, MD.
- Faivre, R., Iooss, B., Mahévas, S., Makowski, D., Monod, H., 2013. Analyse de sensibilité et exploration de modèles : Application aux sciences de la nature et de l'environnement. Editions Quae, 352 p., 2013, Collection Savoir-Faire, 978-2-7592-1906-3. {hal-01173750}
- Fan, D., Zhang, A., Yang, Z., Sun, X., 2007. Observations on shell growth and morphology of bivalve *Ruditapes philippinarum*. *Chinese J. Oceanology Limnology* 25(3), 322-329.
- Felleman, J., 1999. Internet Facilitated Open Modeling: A Critical Policy Framework. *Policy Stud. Rev.* 16(3/4), 193-219.
- Ferreira, J.G., Sequeira, A., Hawkins, A.J.S., Newton, A., Nickell, T.D., Pastres, R., Forte, J., Bodoy, A., Bricker, S.B., 2009. Analysis of coastal and offshore aquaculture: Application of the FARM model to multiple systems and shellfish species. *Aquaculture* 289, 32-41.

- Flye-Sainte-Marie, J., Ford, S.E., Hofmann, E., Jean, F., Klinck, J., Paillard, C., Powell, E., 2003. Development of an individual, energy-balance based, growth model for the Manila clam (*Ruditapes philippinarum*). National Shellfisheries Association Annual Meeting, New Orleans, J. Shellfish Res. 22(1), 354.
- Flye-Sainte-Marie, J., Jean, F., Paillard, C., Ford, S., Powell, E.N., Hoffmann, E., Klinck, J., 2007. Ecophysiological dynamic model of individual growth of *Ruditapes philippinarum*. Aquaculture 266, 130-143.
- Ford, A., Flynn, H., 2005. Statistical screening of system dynamic models. Syst. Dyn. Rev. J. Syst. Dyn. Soc. 21, 273–303.
- Forrester, J.W., 1973. Confidence in Models of Social Behavior – With Emphasis on System Dynamics Group, Sloan School of Management, MIT.
- Frangouides K., Bellanger, M., Curtil, O., Guyader, O., 2020. Small-Scale Fisheries in France: Activities and Governance Issues. In Small-Scale Fisheries in France: Activities and Governance Issues. In: Pascual-Fernández J., Pita C., Bavinck M. (eds) Small-Scale Fisheries in Europe: Status, Resilience and Governance. MARE Publication Series, vol 23. Springer, Cham. doi.org/10.1007/978-3-030-37371-9.
- Freire, J., García-Allut, A., 2000. Socioeconomic and biological causes of management failures in European artisanal fisheries: the case of Galicia (NW Spain). Mar. Policy 24, 375-384.
- Freire, J., Bernárdez, C., Corgos, A., Fernández, L., González-Gurriarán, E., Sampedro, M.P., Verísimo, P., 2002. Management strategies for sustainable invertebrate fisheries in coastal ecosystems of Galicia (NW Spain). Aquat. Ecol. 36, 41–50.
- García, J., M., 2021a. Modelos basados en agentes I: Introducción práctica al análisis del comportamiento de sistemas complejos. Independent editor. ISBN-13: 979-8565201819.

- Garcia, J., M., 2021b. Modelos basados en agentes II: Acciones, Cohortes y Análisis de Resultados. Aplicado a la gestión de empresas y organización de la producción. Independent editor. ISBN-13: 979-8590094301.
- Gillespie, G.E., Norgard, T.C., Scurrah, F.E., 1999. Review of the Area 7 Manila Clam Fishery. Fisheries and Oceans Canada/Canadian Stock Assessment Secretariat Research Documents 99/197, 71 pp.
- Gosling, E., 2003. Bivalve Molluscs – Biology, Ecology and Culture. Fishing News Books.
- Gouletquer, P., Lombas, I., Prou, J., 1987. Influence du temps d’immersion sur l’activité reproductrice et sur la croissance de la palourde japonaise *Ruditapes philippinarum* et l’huître japonaise *Crassostrea gigas*. *Haliotis* 16, 453–462.
- Grant, J., Curran, K.J., Guyondet, T.L., Tita, G., Bacher, C., Koutitonsky, V., Dowd, M., 2007. A box model of carrying capacity for suspended mussel aquaculture in Lagune de la Grande-Entrée, Iles-de-la-Madeleine, Quebec. *Ecol. Model.* 200, 193-206.
- Håkanson, L., 1999. On the principles and factors determining the predictive success of ecosystem models, with a focus on lake eutrophication models. *Ecol. Model.* 121, 139-160.
- Hannon, B., Ruth, M., 1994. *Dynamic modeling*, Springer-Verlag.
- Harte, M., Endreny, P., Sylvia G., Munro Mann, H., 2008. Developing under utilized fisheries: Oregon’s developmental fisheries program. *Mar. Policy* 32, 643-652.
- Harte, M., Endreny, P., Sylvia G., Munro Mann, H., 2008. Developing underutilized fisheries: Oregon’s developmental fisheries program. *Mar. Policy* 32, 643-652.
- Hawkins, A.J.S., Duarte, P., Fang, J.G., Pascoe, P.L., Zhang, J.H., Zhang, X.L., Zhu, M.Y., 2002. A functional model of responsive suspension-feeding and growth in bivalve shellfish, configured and

- validated for the scallop *Chlamys farreri* during culture in China. J. Exp. Mar. Biol. Ecol. 281 (1–2), 13–40.
- Holland, D.A., Chew, K.K., 1974. Reproductive cycle of the Manila clam (*Venerupis japonica*) from Hood Canal, Washington. Proc. Natl. Shellfish Ass. 64, 53-58.
- ICES, 2018. Report of the Scallop Assessment Working Group (WGScallop). 10-12 October 2018 York, UK. CIEM, Ref. ICES CM 2018/EPDSG: 13, 54 p.
- IPCC, 2019: IPCC Special Report on the Ocean and Cryosphere in a Changing Climate [Pörtner, H.-O., Roberts, D.C., Masson-Delmotte, V., Zhai, P., Tignor, M., Poloczanska, E., Mintenbeck, K., Alegría, A., Nicolai, M., Okem, A., Petzold, J., Rama, B., Weyer, N.M. (eds.)]. In press.
- Jørgensen S.E., 1988. Modelling Eutrophication of Shallow Lakes, in: Mitsch, W.J., Straskraba, M., Jørgensen, S.E (eds.), Wetland Modelling. Elsevier Science Publications, Amsterdam, pp. 177-189.
- Kanaya, G., Nobata, E., Toya, T., Kikuchi, E., 2005. Effects of different feeding habits of three bivalve species on sediment characteristics and benthic diatom abundance. Mar Ecol.-Prog. Ser. 299, 67-78.
- Kasai, A., Horie, H., Sakamoto, W., 2004. Selection of food sources by *Ruditapes philippinarum* and *Macra veneriformis* (Bivalva: Mollusca) determined from stable isotope analysis. Fisheries Sci. 70, 11–20.
- Laing, I., Utting, S.D., Kilada, R.W.S., 1987. Interactive effect of diet and temperature on the growth of juvenile clams. J. Exp. Mar. Biol. Ecol. 113, 23-28.
- Lesnoff, M., Corniaux, C., Hiernaux, P., 2012. Sensitivity analysis of the recovery dynamics of a cattle population following drought in the Sahel region. Ecol. Model. 232, 28–39.

- Le Pennec, M., Benninger, P.G., 2000. Reproductive characteristics and strategies of reducing-system bivalves. *Comp. Biochem. Phys.* 126, 1-16.
- Le Treut, Y., 1986. La palourde. Anatomie - Biologie - Elevage - Pêche - Consommation -Inspection sanitaire. PhD thesis, Ecole Nationale Vétérinaire, University of Nantes, France.
- Maître-Allain, T., 1982. Influence du milieu sur la croissance de deux palourdes, *Ruditapes decussatus* et *Ruditapes philippinarum*, dans l'étang de Thau (Hérault). *Vie Marine* 4, 11–20.
- Manache, G., Melching, C. S., 2008. Identification of reliable regression- and correlation-based sensitivity measures for importance ranking of water-quality model parameters. *Environ Model Softw* 23, 549-562.
- Mann, R., 1979. The effect of temperature on growth, physiology, and gametogenesis in the Manila clam *Tapes philippinarum* (Adams & Reeves, 1850). *J. Exp. Mar. Biol. Ecol.* 38, 121–133.
- Mayer, D.G., Butler, D.G., 1993. Statistical validation. *Ecol. Model.* 68, 21–32. doi:10.1016/0304-3800(93)90105-2.
- Melià, P., De Leo, G.A., Gatto, M., 2004. Density and temperature dependence of vital rates in the Manila clam *Tapes philippinarum*: a stochastic demographic model. *Mar. Ecol. Prog. Ser.* 272, 153–164.
- Mongruel, R., Prou, J., Balle-Beganton, J., Lample, M., Vanhoutte-Brunier, A., Rethoret, H., Pérez Agúndez, J., Vernier, F., Bordenave, P., Bacher, C., 2011. Modeling soft institutional change and the improvement of freshwater governance in the coastal zone. *Ecol. Soc.*, 16(4), 15. doi.org/10.5751/ES-04294-160415.
- Murray A.G., Parslow, J.S., 1999. The analysis of alternative formulations in a simple model of a coastal ecosystem. *Ecol. Model.* 119, 149-166.

- Nakamura, Y., Hagino, M., Hiwatari, T., Iijima, A., Kohata, K., Furota, T., 2002. Growth of the Manila clam, *Ruditapes philippinarum* in Sanbanse, the shallow coastal area in Tokyo Bay. *Fisheries Sci.* 68, 1309–1316.
- Norton, J., 2015. Introductory Overview - An introduction to sensitivity assessment of simulation models. *Environ Model Softw* 69, 166-174. <https://doi.org/10.1016/j.envsoft.2015.03.020>.
- Ohba, S., 1959. Ecological studies in the natural population of a clam, *Tapes japonica*, with special reference to seasonal variations in the size and structure of the population and to individual growth. *Biol. J. Okayama University* 5, 13-42.
- Ortiz, M., Wolff, M., Mendo, J., 2002. Qualitative modelling for the development of a sustainable management strategy for the Peruvian scallop *Argopecten purpuratus* (Lamarck 1819). *Aquat. Conserv.* 12, Issue 3, 273–287.
- Park, K.I., Choi, K.S., 2004. Application of enzyme-linked immunosorbent assay for studying of reproduction in the Manila clam *Ruditapes philippinarum* (Mollusca: Bivalvia) I. Quantifying eggs. *Aquaculture* 241, 667–687.
- Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D., Dejak, C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system. *Ecol. Model.* 138, 231-245.
- Paul-Pont, I., 2010. Sensibilité et adaptation de populations de bivalves marins soumis à des stress multiples : infestation parasitaire, contamination microbienne et pollution métallique. PhD thesis, University of Bordeaux I, France.
- Pianosi, F. Beven, K., Freer, J., Hall, J. W., Rougier, J., Stephenson, D. B., Wagener, T., 2016. Sensitivity analysis of environmental models: A systematic review with practical workflow. *Environ Model Softw* 79, pp 214-232.

- Pianosi, F., Wagener, T., 2018. Distribution-based sensitivity analysis from a generic input-output sample. *Environ Model Softw* 108, 197-207. <https://doi.org/10.1016/j.envsoft.2018.07.019>.
- Picault, D., Lesueur, M., Noel, J., Lepetit, A., Nys, C., Pellan, C., Trougan, M., Rezgani, W., Souidi, S., 2014. Inshore fisheries and governance (France). The case of the commercially harvested mussel fishery of eastern Cotentin (Lower Normandy). Study report. GIFS Project. Action 1. Les publications du Pôle halieutique AGROCAMPUS OUEST, (23), 32p.
- Pomeroy, R.S., 1995. Community-based and co-management institutions for sustainable coastal fisheries management in Southeast Asia. *Ocean Coast. Manage.* 27 (3), 143-162.
- Plus, M., Dumas, F., Stanisière, J.Y., Maurer, D., 2009. Hydrodynamic characterization of the Arcachon Bay, using model-derived descriptors. *Cont. Shelf Res.* 29, 1008-1013.
- Robinson, A.M., Breese, W.P., 1984. Gonadal development and hatchery rearing techniques for the Manila clam, *Tapes philippinarum* (Adams & Reeve). *J. Shellfish Res.* 4, 161-163.
- Rodriguez-Morosco, E., Pazo, J.P., Garcia, A., Fernandez-Cortes, F., 1992. Reproductive cycle of Manila clam, *Ruditapes philippinarum* (Adams & Reeve 1850) in Ria of Vigo (NW Spain). *Sci. Marina* 56, 61-67.
- Sanchez, F., Caill-Milly, N., Lissardy, M., Bru, N., 2014. Campagne d'évaluation de stock de palourdes du bassin d'Arcachon. Année 2014. RBE/HGS/LRHA 14-003. <https://archimer.ifremer.fr/doc/00233/34383/>
- Sanchez, F., Caill-Milly, N., Lissardy, M., 2018. Campagne d'évaluation du stock de palourdes du bassin d'Arcachon. Année 2018. Rapport Ifremer R.ODE/LITTORAL/LER AR 18.015. <https://archimer.ifremer.fr/doc/00477/58897/>

- Shenk, T.M., Franklin, A.B., 2001. Modelling in Natural Management: Development, Interpretation, and Application. Island Press. Washington, D.C.
- Shibata, T., Toba, M., Sakai, M., Kaneko, A., 1999. Availability of photo-pigment as an index of productivity in the culture ground of Japanese little neck clam *Ruditapes philippinarum*. B Chiba Prefecture Fishery Exp. Station 55, 67-72.
- Solidoro, C., Pastres, R., Melaku Canu, D., Pellizzato, M., Rossi, R., 2000. Modelling the growth of *Tapes philippinarum* in northern adriatic lagoons. Mar. Ecol. Prog. Ser. 199, 137–148.
- Solidoro, C., D. Melaku Canu, Rossi, R., 2003. Ecological and economic considerations on fishing and rearing of *Tapes philippinarum* in the lagoon of Venice. Ecol. Model. 170 (2-3), 303-318.
[http://dx.doi.org/10.1016/S0304-3800\(03\)00235-7](http://dx.doi.org/10.1016/S0304-3800(03)00235-7)
- Soudant, P., Paillard, C., Choquet, G., Lambert, C., Reid, H.I., Marhic, A., Donaghy, L., Birkbeck, T.H., 2004. Impact of season and rearing site on the physiological and immunological parameters of the Manila clam *Venerupis* (= *Tapes*, = *Ruditapes*) *philippinarum*. Aquaculture 229(1-4), 401-418.
- Spillman, C.M., Hamilton, D.P., Hipsey, M.R., Imberger, J., 2008. A spatially resolved model of seasonal variations in phytoplankton and clam (*Tapes philippinarum*) biomass in Barbamarco Lagoon, Italy. Estuar. Coast. Shelf S. 79(2), 187-203.
- Sterman, J., 2000. Business Dynamics: Systems Thinking and Modeling for a Complex World. Boston: Irwin/McGraw-Hill.
- Tamura, T., 1970. Marine aquaculture; translated from Japanese (2nd edition 1966) by M.I. Watanake. Nat. Science Foundation, Washington D.C.
- Tezuka, N., Kamimura, S., Hamaguchi, M., Saito, H., Iwano, H., Egashira, J., Fukuda, Y., Tawaratsumida, T., Nagamoto, A., Nakagawa, K., 2012. Settlement, mortality and growth of the asari clam

- (*Ruditapes philippinarum*) for a collapsed population on a tidal flat in Nakatsu, Japan. J. Sea Res. 69, 23–35.
- Toba, M., 1987. *Ruditapes philippinarum*: growth of larvae and juveniles artificially fertilized. B Chiba Prefecture Fishery Exp. Station 45, 41–48.
- Toba, M., Miyama, Y., 1995. Influence of temperature on the sexual maturation in Manila clam *Ruditapes philippinarum*. Suisanzoshoku 43, 305-314.
- Troost, T. A., Wijsman J. W. M., Saraiva, S., Freitas, V., 2010. Modelling shellfish growth with dynamic energy budget models: an application for cockles and mussels in the Oosterschelde (southwest Netherlands). Phil. Trans. R. Soc. B (2010) 365, 3567–3577. doi:10.1098/rstb.2010.0074
- Tsang, C., 1991. The modelling process and model validation. Ground Water 29, 825-831.
- Urrutia, M.B., Ibarrola, I., Iglesias, J.I.P., Navarro, E., 1999. Energetics of growth and reproduction in a high-tidal population of the clam *Ruditapes decussatus* from Urdabai Estuary (Basque Country, N. Spain), J. Sea Res. 42, 35-48.
- Vincenzi, S., Caramori, G., Rossi, R., De Leo, G.A., 2006. A GIS-based habitat suitability model for commercial yield estimation of *Tapes philippinarum* in a Mediterranean coastal lagoon (Sacca di Goro, Italy). Ecol. Model. 193, 90-104.
- Yamamoto, K., Iwata, F., 1956. Studies on the bivalve, *Venerupis japonica*, in Akkeshi Lake II. growth rate and biological minimum size. B Hokkaido Regional Fisheries Res. Laboratory 14, 57–62.
- Yokoyama, H., Tamaki, A., Koyama, K., Ishihi, Y., Shimoda, K., Harada, K., 2005. Isotopic evidence for phytoplankton as a major food source for macrobenthos on an intertidal sandflat in Ariake Sound, Japan. Mar. Ecol. Prog. Ser. 304, 101–116.

Figure captions

1. Maps showing the studied site Arcachon Bay (France) (sources: ESRI, BD Carthage, Ifremer – M. Lissardy).
2. Evolution since 2003 of the total biomass (with its standard deviation) and of the total numbers of Manila clams in Arcachon Bay (from Sanchez et al., 2018).
3. Diagram of the Manila clam model illustrating the four blocks and the interactions among them. Improvements made since the first version of the model regarding blocks are in bold italics.
4. Evolution of chlorophyll a and Total Suspended Matter over the 2002-2019 period.
5. Equation formulations for each process from the starting point S (biomass).
6. Total biomass (t) simulated between July 2003 and December 2019 (“historical” reconstitution).
7. Value of the sensitivity index for the control parameters used as input factors.

Appendix 1

Introduction

To be able to estimate abundance of clams for a given biomass, a length-weight relationship is mandatory. Because variability exists among sites (Caill-Milly et al., 2012) - mainly due to environmental conditions - a relationship for Manila clam (*Ruditapes philippinarum*) population of the Arcachon Bay was established.

Materials

Clams were collected during the survey campaign of 2003. This campaign aims to assess the Manila clam stock within the Arcachon Bay and occurred in June-July 2003 (Caill-Milly et al., 2003). 14 strata located at intertidal level (excluding channels) (Figure 1) were investigated for a total of 450 sampling stations. Sediments core of 0.25 m² (0.5 m x 0.5 m) on a 0.2 m depth were sampled with a Hamon grab (Figure 2) at the high tide and filtered onboard with running water over a set of three sieves with 2, 1 and 0.5 cm mesh size.

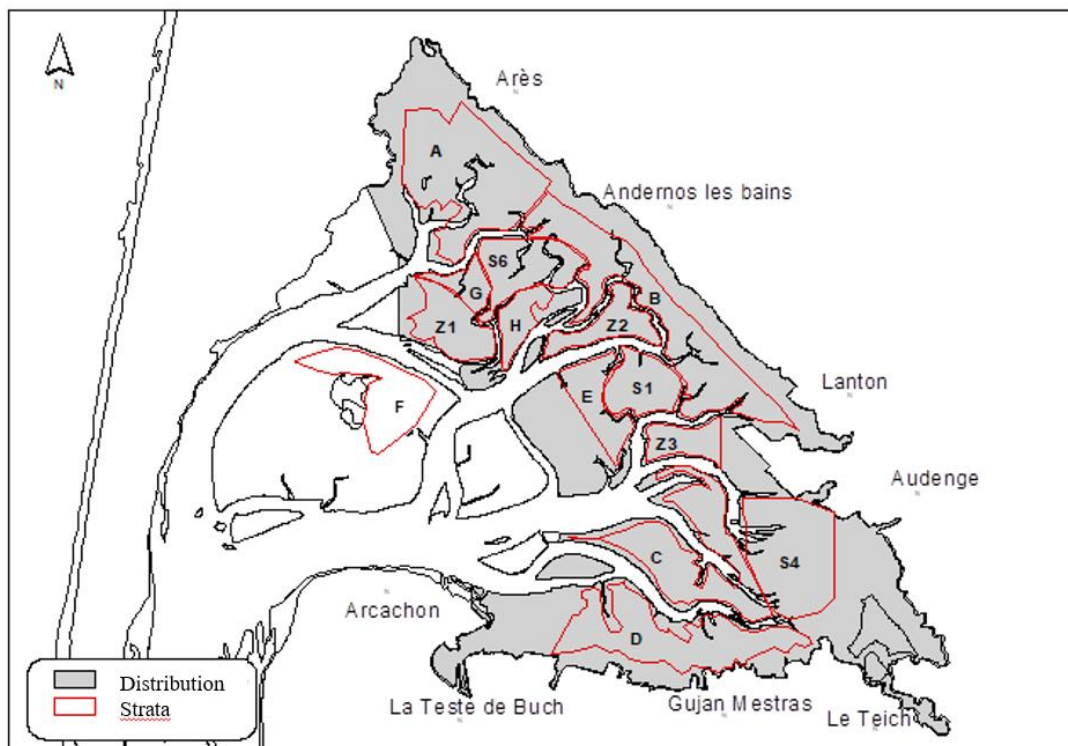


Figure 1: Strata investigated during the survey campaign of 2003.



Figure 2: Implementation of the Hamon grab.

The samples were rinsed and sieved on two sorting tables consisting of three sieves of 20, 10 and 5 mm square mesh. All the Manila clams were sorted and brought to the laboratory in order to be measured and weighted with respective accuracies of almost 1.10^{-2} millimeter and 1.10^{-2} gram. The two considered parameters were:

- Length (L), defined as the longest distance from front edge to back edge (mm);
- Weight of the whole clam (W) including flesh and shell (mg).

Individuals with broken shells were not considered for the relation between length and weight.

The relationship used to describe the relationship between L and W is of the power type:

$$W = a L^b$$

where W represents the total fresh weight in mg and L the length in mm, a and b being the coefficients of the relationship. The coefficients a and b are determined by a logarithmic transformation of the function:

$\log W = \log a + b \log L$, with b the slope of the regression line and a the intercept.

Results

A total of 4 398 clams were measured and weight. Their length ranged from 5.79 mm to max 44.90 mm.

The analyses performed assume the normality of the residuals. This condition is considered satisfied.

The relationship between the two parameters L and W are displayed in figure 3 (with and without logarithmic transformation). The adjusted equation in its exponential form is $W = 0,2162 L^{3,049}$ with $R^2=0,948$ ($n = 4\ 398$).

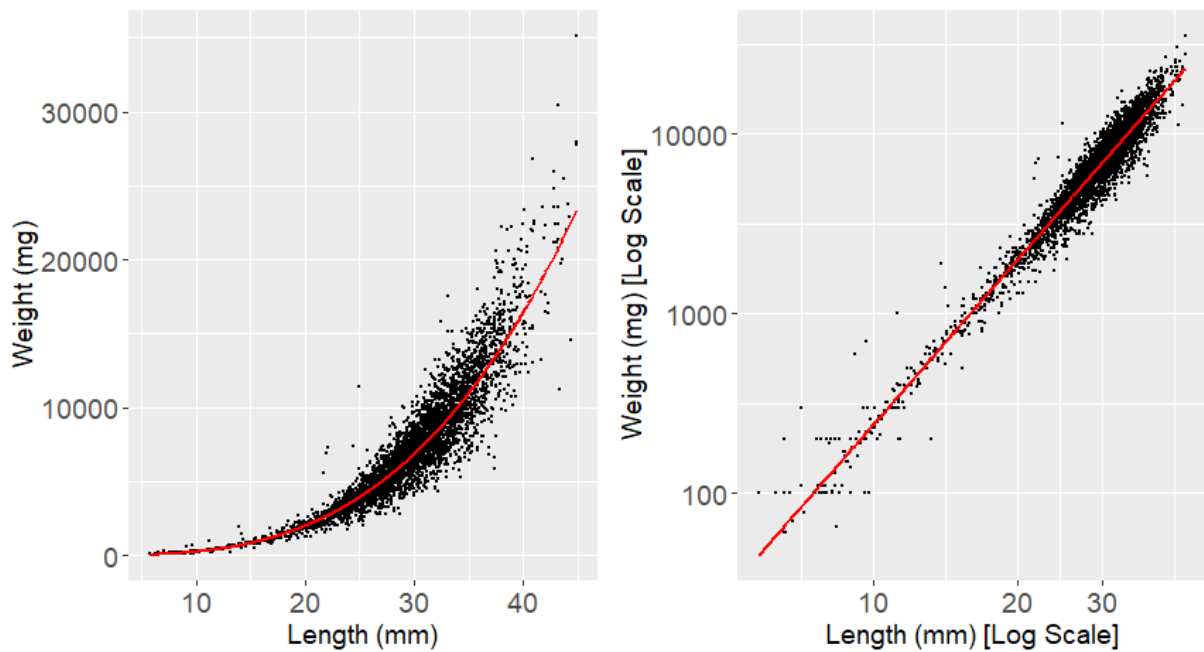
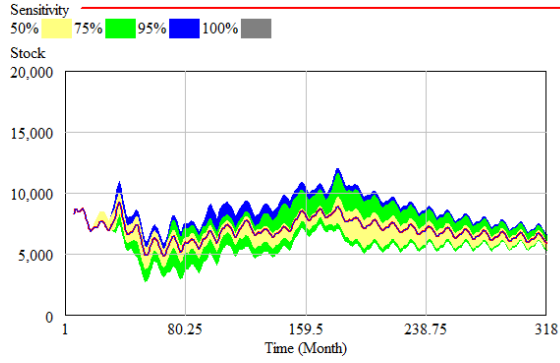


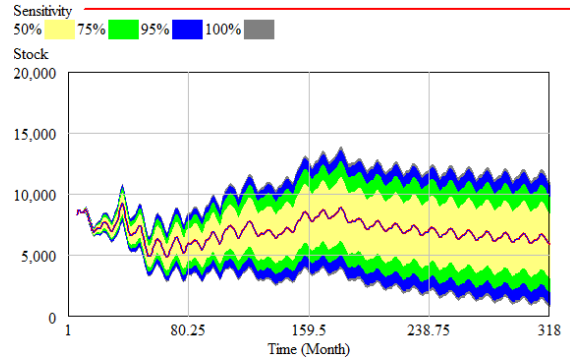
Figure 3: Size-fresh weight relationship of Manila clams in the Arcachon Basin in 2003 (length L in mm; fresh weight W in mg; $n = 4398$). Measurements were made in May-June.

This relationship allows to estimate a theoretical weight for any individual whose size is known.

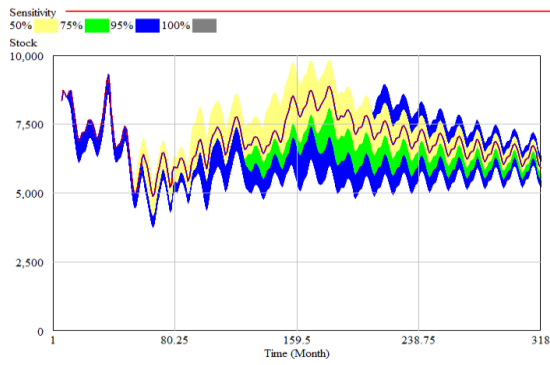
Appendix 2



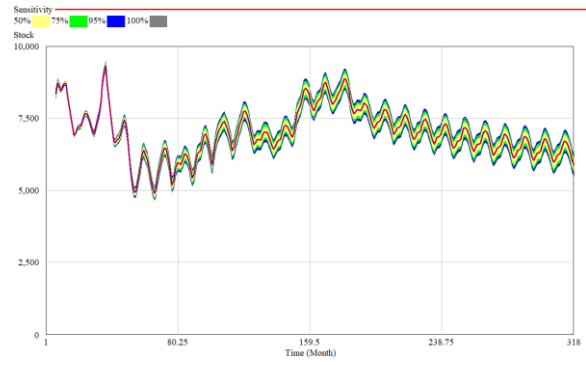
a)



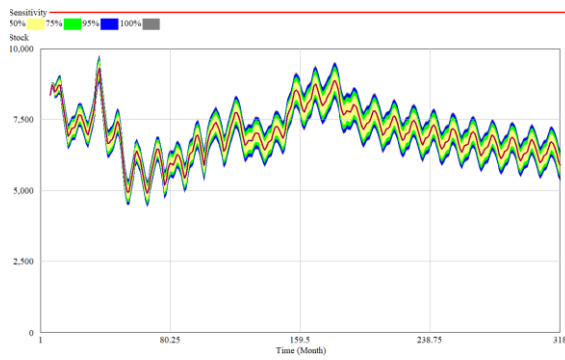
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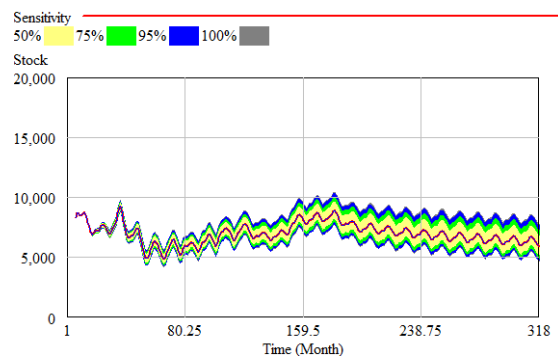
c)



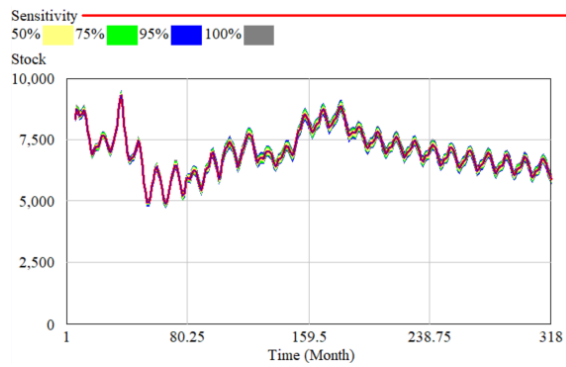
d)



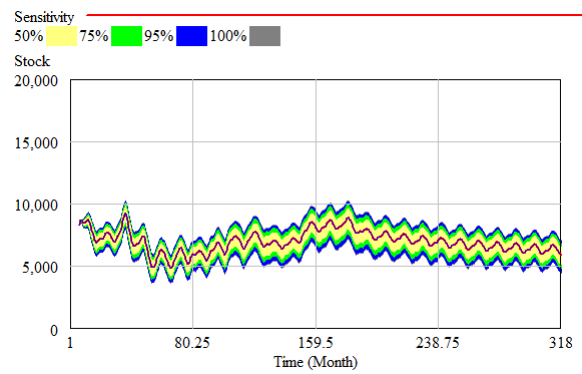
e)



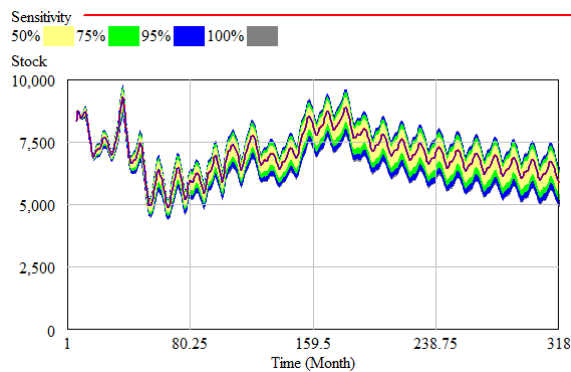
f)



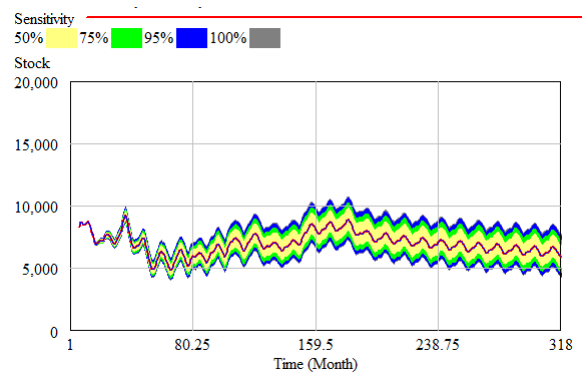
g)



h)



i)



j)

Figure 1: Confidence bounds for the biomass for the 1000 Monte Carlo simulations with application of uncertainty on control parameters associated to sensitive index – a) spawning maximum temperature; b) recruitment; c) spawning minimum temperature; d) mean weight of the length 21-34 mm; e) mean weight of the length above 40 mm; f) natural mortality above 40 mm; g) mean weight of the length 35-40 mm; h) growth rate 35-40 mm; i) growth rate 0-20 mm; j) natural mortality 0-20 mm.

The widest confidence bounds is observed for recruitment and then for spawning maximum temperature, spawning minimum temperature, natural mortality 0-20 mm, natural mortality above 40 mm and growth rate 35-40 mm. The narrower ones for mean weight of the length 21-34 mm and mean weight of the length 35-40 mm. The results obtained here for the wide confidence bounds are in line with those relating to the sensitivity index, *i.e.* an importance of parameters regarding or influencing young stages of the population. They differ a bit concerning the mean weight of the length 21-34 mm.

Appendix 3

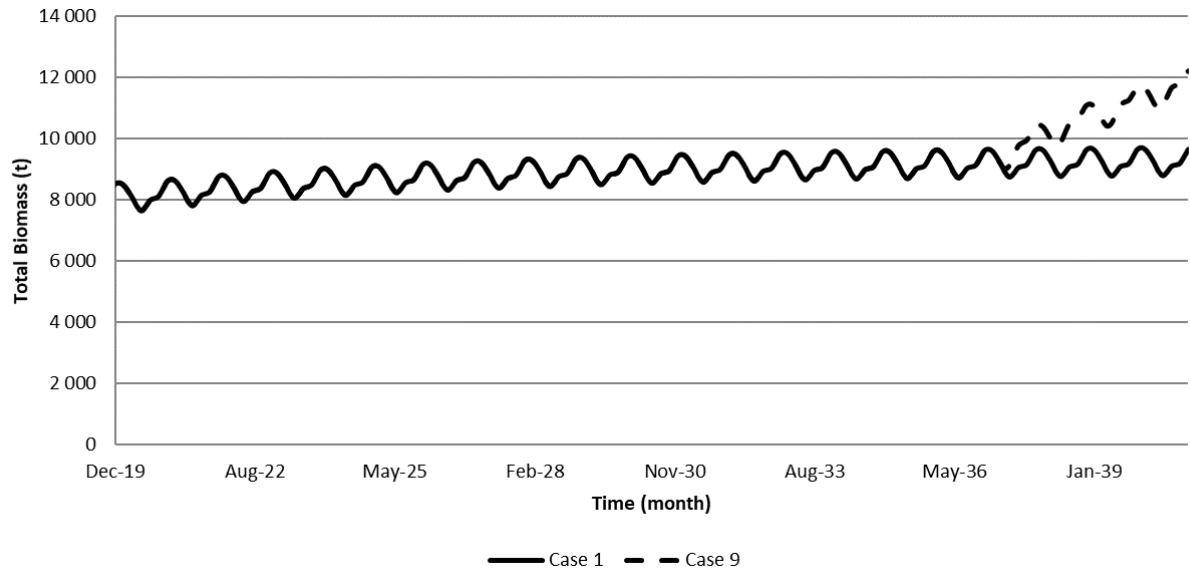


Figure 1: Total biomass (t) forecasts obtained for Scenario 1 and 9 between January 2020 and December 2040.