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Combining sensitivity and uncertainty analysis to evaluate the impact of management measures with ISIS–Fish: marine protected areas for the Bay of Biscay anchovy (*Engraulis encrasicolus*) fishery

Sigrid Lehuta[1, *], Stéphanie Mahévas[1], Pierre Petitgas[1] and Dominique Pelletier[2]

[1] Ifremer, rue de l'île d'Yeu BP 21105, 44311 Nantes Cedex 03, France
[2] Ifremer, Technopole de Brest-Iroise, BP 70, 29280 Plouzané, France

*: Corresponding author : S. Lehuta: tel: +33 240 374165; fax: +33 240 374075, email address : sigrid.lehuta@ifremer.fr

Abstract:

Spatio-seasonal explicit simulation models can predict the impact of spatial management measures on marine fish populations and fishing activities. As fisheries are complex systems, fisheries simulation models are often complex, with many uncertain parameters. Here, the methodology is provided to deliver fishery diagnostics within an uncertainty context using a complex simulation tool. A sensitivity analysis of the model is performed on model outputs using partial least-squares to identify the most sensitive parameters. The impact of several management measures is then simulated using a statistical simulation design taking into account the uncertainty of the selected sensitive parameters. This approach was applied to the Bay of Biscay anchovy stock using the ISIS-Fish (Integration of Spatial Information for Simulation of Fisheries) model to assess the impact of imposing marine protected areas (MPAs) conditionally on parameter uncertainty. The diagnostic appeared to be highly sensitive to the mortality of larvae and juveniles, growth, and reproduction. The uncertainty of the values of these parameters did not permit any of the simulated MPA designs to be proposed. However, according to anchovy catch and biomass, the simulations allowed the low impact of closure duration to be shown and underscored the utility of protecting such key processes as spawning.

Keywords: Bay of Biscay anchovy, marine protected area, sensitivity analysis, simulation, uncertainty analysis

Introduction

In recent decades, marine protected areas (MPAs) have been promoted as useful tools to limit the effects of fishing on an ecosystem, including biological and socio-economical aspects (Sumaila *et al*., 2000). However, a lack of tools for assessing and understanding the impacts of MPAs compromises evaluation of their possible effects (Jameson *et al*., 2002; Pomeroy *et al*., 2005). Predicting the impact of MPAs on resources and fishing activities is not easy, because fisheries are complex systems with numerous interactions at various spatial and temporal scales. Moreover, it is difficult to separate the effects of MPAs from other influencing factors, such as environmental conditions and the biology of the species. Consequently, complex spatially explicit models that incorporate MPAs are required. ISIS–Fish (Integration of Spatial Information for Simulation of FISHeries) is a flexible tool developed to simulate fishery dynamics (Mahévas and Pelletier, 2004; Pelletier and Mahévas, 2005; Pelletier et al., 2009). It permits the integration of spatial and seasonal information on population and exploitation dynamics (including economic features) of any type of fishery (particularly mixed fisheries) and allows simulation of various management scenarios accounting for fisher reactions. It is a powerful tool that can be used to obtain insight into the processes underlying the effects of MPAs on fisheries through numerical analysis of simulation results.

The potential for new fisheries management strategies needs to be evaluated in terms of their robustness to various uncertainties, using extensive simulations (Rice and Connolly, 2007). The ISIS–Fish model can handle simulations of this type, including the specifications of different management measures and statistical simulation designs built to assess rigorously the propagation of different sources of uncertainty on the model outputs.

Most fishery parameters are uncertain and fishery simulation models are characterized by a large number of parameters. For practical reasons, sensitivity analyses should be conducted before uncertainty analyses. Indeed, a sensitivity analysis identifies the parameters that influence model output and uncertainty analysis allows the uncertainty on the results to be quantified conditional to an assumed level of uncertainty on these parameters (Saltelli, 2004). Uncertainty on parameters is consequently taken into account to deliver reliable fishery diagnostics. Classically, the importance of parameter values is investigated through elasticity analyses that are carried out by assessing the impact of varying one parameter value at a time. Global sensitivity analysis advances the comprehension and exploration of the system modelled, because parameters vary simultaneously, allowing identification of interactions. Simulations are organized following an experimental design to ensure that potential interactions can be evaluated by statistical analysis of the simulation results. These methods have been used mainly in industry to optimize production planning (Kleijnen, 1998), and rarely in ecology (Cariboni *et al*., 2007) or fisheries science (but see Drouineau *et al*., 2006; Ginot *et al*., 2006). Analysis of variance (ANOVA) is often used to interpret the results of sensitivity analyses. The coefficient estimated for each parameter is considered as the sensitivity index of the parameter, but if the model output consists of several variables, ANOVA does not allow simulataneous calculation of sensitivity indices satisfactorily. Partial least squares (PLS) regression (Tenenhaus *et al*., 1995) enables these questions to be addressed and provides a robust method to analyse correlated variables.

In fisheries science, many biological parameters are often imprecisely estimated either because knowledge is incomplete (Guénette *et al*., 1998) or because parameters are estimated based on noisy data (Pelletier, 1990; Pelletier and Gros, 1991; Drouineau *et al*., 2008). These uncertainties can lead to errors in assessments of the impact if the response variables under study are sensitive to these parameter values. These errors, however, can be quantified through uncertainty analysis, in which the parameters are varied within a range defined by the associated uncertainty using a simulation design. With this type of analysis, confidence intervals associated with the model results can be produced according to the range of values observed for model outputs.

We used sensitivity and uncertainty analysis to assess the relevance and effectiveness of a MPA for the Bay of Biscay anchovy (*Engraulis encrasicolus*) fishery. The fishery is well monitored and international in nature (Uriarte *et al.*, 1996; Duhamel *et al*., 2004; Guyader *et al.*, 2005; ICES, 2006). Until 2005, it was managed by total allowable catch (TAC) shared among French and Spanish fleets, and varied between 15 000 t and 33 000 t from 2000 to 2005. However, successive recruitment failures since 2002 have led to a severe decline in the population and to closure of the fishery since summer 2005. Given the great economic importance of anchovy to French and Spanish fisheries interests, sustainable management strategies are being sought actively to allow the fishery to be reopened. In particular, the identification of essential habitats (Vaz *et al*., 2002; Petitgas and Vaz, 2005) supported ICES working group proposal for area closures as complementary measures to TAC (ICES, 2000).

In the present study, available information on the anchovy fishery for the period 2001–2003 was integrated into the ISIS–Fish model to mimic the spatial and seasonal dynamics of the fishery (ISIS–Fish model parameterization). Then a sensitivity analysis was conducted to identify the factors driving the fishery dynamics under different management measures. Finally, various MPA scenarios, including the expected reaction of fishers, were evaluated and compared using uncertainty analysis on the most sensitive parameters, to determine whether the current state of knowledge allows a reliable diagnostic on the fishery to be produced and whether the envisaged MPAs are likely to meet their objectives.

Material and methods

ISIS–Fish model parameterization for the anchovy fishery

The dynamics in the ISIS–Fish model are based on a monthly computation of fishing mortality by area. This fishing mortality is the result of spatio-temporal interaction between population abundance resulting from the population submodel and fishing effort provided by the exploitation and management submodels (Pelletier and Mahévas, 2005). A brief description of the model is presented in Appendix 1.

Our parameterization of the anchovy fishery was aimed at reproducing the fishery dynamics described below. The anchovy population is length–age structured, fish changing length class every month during their 15 first months, then every year. Maximum and minimum lengths for each class were deduced from a von Bertalanffy growth function and weight from the length (L) –weight (W)

relationship $W(\mathrm{cl}) = 0.004184069L(\mathrm{cl})^{3.200812}$, derived from the results of two surveys (the Juvaga and PelGas surveys of 2000–2005). In that equation, the term “(cl)” refers to “class”. Mortality was assessed using data from surveys (for adults) and from a Pareto function for anchovy younger than 1 year (Lo *et al.*, 1995, Pertierra *et al.*, 1997; Table 1). Area-specific mortality during the first month (larval stage) is defined using survival success predicted by the hydrological larval-dispersal model of Allain *et al.* (2007b; Table 1). Population areas, in which the population is assumed to be homogeneously distributed, were identified according to spatial and seasonal distributions by length class observed during spring scientific surveys and deduced from commercial fishing effort distribution in autumn (PelGas and Evohe surveys of 2000–2005; Vaz *et al.*, 2002; Figure 1). Although seasonal changes in distribution pattern are probably the result of multidirectional movements of fish between identified population areas, we assumed unidirectional migrations from the northern to the southern area in spring, and the reverse in autumn (Table 2). Neither emigration nor immigration was assumed. Time and location of spawning according to length were defined based on the hypothesis that spawning duration is determined by the length at the beginning of the spawning season; the longer a fish is, the longer the period it can spawn (PP, pers. obs.). In addition, as observed at sea, fish begin to spawn later in the Rochebonne area, supposedly because of temperature (Allain *et al.*, 2007a; Table 3). For the classes of fish that spawn in the area *z*pop in month t, the number of eggs is derived from the product: Number of eggs $(z\mathrm{pop}, t) = \sum_{\mathrm{cl}} N(\mathrm{cl}, z\mathrm{pop}, t) \times W(\mathrm{cl}) \times \mathrm{fec}$, where *N* is the number of fish and *W* denotes the weight. Fecundity, fec, per month is assumed to be 3500 eggs per gramme of female (Motos, 1996). The ogive obtained mimics the observed pattern (PP, pers. comm.). Fish accessibility by age was obtained by fitting the model to landings data using an optimization algorithm (Table 1). The fishing activity model was based on descriptions of the fleets, metiers, and strategies. Fleets are sets of vessels sharing the same technical characteristics and attached to the same harbour. Métiers are defined at the scale of a fishing operation by the use of a particular gear to target a set of species in a particular area (Biseau, 1998; ICES, 2005). Fleets are named after the gear they use and their harbour of origin. Parameters relative to fleets and métiers were computed based on data extracted from the French fishery information system (SIH) for French fleets, and from data and information on expertise provided by the Basque Spanish Institute of the Sea (AZTI) for Spanish fleets (Table 4). The number of vessels in the fleet was computed as the mean number of vessels per fleet fishing anchovy each year between 2001 and 2003. Métiers targeting anchovy are identified by their catch profile (Vermard *et al.*, 2008). They are designated according to their area of practice (Figure 2a, b). Target factor is computed as the mean percentage of anchovy in the landings per métier trip per month. Effort was standardized between gears (pair trawl, Spanish seine, and French seine) using standardization factors. They were the values of the gear effect in a log-linear model applied to logbook data assuming that log(cpue) is a function of gear and month (Table 5; cpue is the catch per unit effort). According to fishing experts, no selectivity applies to anchovy. The minimum length of anchovy in the catch is 9 cm (ICES, 2006; Table 5). Strategy is the succession of métiers practiced in the year by a fleet, and is characterized by the proportion of time spent on each métier per month, computed as the percentage of time spent on the métier relative to the potential time spent at sea ($\mathrm{h}_{\text{métier}}$/h at $\mathrm{sea}_{\text{month}}$; Table 4). The Spanish Païta métier catches small anchovy (aged either 1 or 0, depending on the month) live for tuna fishing, but no effort or catch has been reported for this métier in recent years, so areas and annual catch per vessel were determined by experts and assumed to be constant (Table 4).

Description of management measures

Two different types of measure are proposed to regulate fishing activity on anchovy. The stock was historically managed through annual TACs set at a fixed level independent of advice from 1979 to 2004, but since 2005, ICES has advised a zero TAC. However, discussions during meetings with fishers led to the belief that a 6000 t TAC would be the minimum consistent with economic sustainability of the fleet, so a TAC of 6000 t was tested in this work.

Two MPA designs aimed at protecting juveniles and allowing the largest possible part of the recruiting year class to spawn were tested (Figure 3, Table 6). Vaz *et al.* (2002) showed that in the Bay of Biscay, anchovy population dynamics and especially recruitment success are very dependent on certain coastal areas, representing essential habitats (Petitgas and Vaz, 2005). In 1999, ICES recommended closure to pelagic fishing of an essential habitat area (ICES, 2000) located in front of the Gironde river plume (MPA1 on Figure 3), for the entire spawning period (April–June). Protecting that area was expected to favour egg production and to ensure minimum recruitment even in unfavourable years. In addition, we assessed the consequences of a second spatial and seasonal closure (MPA2 on Figure 3) from September to November, an area located along the coast south of 46°N where juveniles concentrate when they first become available to fishing. Such a closure would be intended to maximize the chances of juveniles surviving until they had reproduced. Both designs cover all the métiers targeting anchovy.

Fisher reactions to management measures were coded as decision rules. As soon as a management measure is applied, fishers change their allocation of fishing effort. When the TAC is reached, fishers are assumed to change métiers at the next time-step, and to reallocate effort to métiers that do not target anchovy. Here this corresponds to stopping fishing until the end of the year. In the case of a MPA, fishers who were fishing in a closed area reallocate their effort. If the closure does not include their entire métier zone, effort is reallocated to the part of the métier zone not included in the closure. Otherwise, if the whole métier zone is closed, effort is reallocated outside the MPA where most of the fishing effort was deployed during that month. Finally, if there is no other métier area available at that time, fishers stop fishing for the time-step.

Sensitivity analysis

Global sensitivity analysis is normally conducted by varying the values of model parameters around their reference value with a given amplitude, traditionally ±20% (De Castro *et al*., 2001; Elkalay *et al*., 2003). The impact of these variations on one or several response variables is then assessed. Performing a sensitivity analysis requires (i) definition of input "factors" and their modalities (values), (ii) choice of response variables to be considered, (iii) use of an appropriate simulation design, and (iv) definition of the statistical model to be applied to analyse the response variables. Each of these is discussed further below.

(i) The sensitivity analysis consisted of varying both the model and the management measure parameters. There were too many parameters in ISIS–Fish to assess the impact of each parameter separately on the response variables, so a group-screening method was used to group and hence to reduce the number of factors (Kleijnen, 1986; Drouineau *et al*., 2006). Parameters in a group were assumed *a priori* to impact the response variables in the same direction. Each group was then considered as a single "factor". In our case, ten groups were defined, related to growth (gro), fecundity (fec), larval and juvenile mortality (Jmo), corresponding to the first 15 classes (from birth up to the end of first spawning), adult mortality (Amo), migration (mig), accessibility (*q*), standardization factors for gears (SF_{std}), target factor for métiers on anchovy (targetF), selectivity (sel), and effort (eff). Table 7 describes these groups further. The levels of factors within groups were defined by variations of ±20% around the reference value of the parameters, all parameters in a group simultaneously taking one of these two values, e.g. +20%. The response corresponded to the joint effect of changing all parameters of the group, and if no significant response was detected, it was concluded that none of the parameters of the group had a significant effect on the response variables. The main hypothesis underlying this approach is that there are no interaction effects between parameters inside a group. As management actions influence the dynamics of the system, the sensitivity analysis was carried out conditional on management measures, which were considered in the simulation design as additional factors. Significant interactions between parameters and management measures indicate changes in the system dynamics induced by the management measure. Two management measures were investigated in the sensitivity analysis, TAC regulation (a 6000 t TAC fixed for all years), and a MPA (MPA1 from April to June) that aims to protect spawning fish. For both measures, the two modalities tested were either implementing or not implementing the measure.

(ii) The choice of response variables was guided by the wish to assess effects at different time-scales. Anchovy being a short-lived species (~3 years), the response variables considered were the biomass at the end of the fifth and the eighth year of simulation, and the annual catches of the fifth year and the eighth year of simulation.

(iii) A fractional factorial design of resolution *V* (256 simulations) is generally recommended to organize the sensitivity analysis for factors (here parameter groups) with two modalities (Kleijnen, 1986). It consists of selecting a set of experiments among the 2^p (*p* being the number of factors) possible experiments sufficient to assess the sensitivity to factors, including first-order interactions (Droesbeke *et al.*, 1997).

(iv) Sensitivity indices (SIs) were assessed by the fit of a meta-model to response variables. As we wanted to compute SIs for all four response variables simultaneously, a PLS regression (Wold *et al.*, 1983) was used. Variable Importance in Projection (VIP) measures the importance of a factor in explaining all response variables, so VIPs were computed for each factor and used as sensitivity indices. Factors with a high VIP are those to which the model is the most sensitive. It is generally agreed that VIPs are significant when >1 (Tenenhaus, 1998). For more detail on PLS and VIP formulae, see Appendix 2.

MPA evaluation with uncertainty

After the sensitivity analysis, the next step was to evaluate the impact of various MPA designs on the fishery. For this purpose, the response variables obtained for each design were compared with those from a baseline simulation, i.e. without any regulation on fishing. Biomass represented population health, and catches were taken to be a proxy for economic consequence. Several MPA types were simulated, characterized by their location, period, and duration of the closure: to investigate the impact of closure duration, closures were taken to last from 1 to 3 months. The period of closure depended on the MPA location: April–June for MPA1, and September–November for MPA2. This results in 12 MPA designs (Tables 8 and 9).

As the values of the three most sensitive parameters identified in the previous step (early life mortality, growth, and fecundity) were uncertain, simulations were coupled with an uncertainty analysis on these three parameters, assuming an uncertainty of 20% around their reference values. The range of uncertainty is difficult to evaluate, particularly for natural mortality during early life, but 20% variation was considered to be realistic according to literature estimates. Indeed, egg mortality, the determining point of the mortality curve, was estimated by ICES (2006) as 0.266 (*CV* 0.4), by Pertierra *et al*. (1997) as 0.565 (*CV* 0.36), and by Lo *et al*. (1995) for *E. mordax* in California as 0.231 (*CV* 0.36). Three values were considered for each uncertainty parameter, corresponding to its reference value (considered the most plausible value, see Tables 1–5), the reference value +20%, and the reference value –20%. Simulations were organized in a full factorial design to provide confidence intervals conditional on each MPA design.

Simulation set-up

Simulations were run for eight years. Population abundance at the beginning of the simulations was extracted from the 2001 evaluations of ICES working group report (ICES, 2006; Table 10). We implemented management rules from the first to the last year of simulation.

Results

Sensitivity analysis

Depending on the response variable considered, the metamodel using PLS regression explained 81–99% of the variability of the four output variables with the two first components (Table 11). Here, the first and second components explained the main part of the variability in output. The four output variables projected on the positive part of the first component, both catch variables on the positive part of the second component, and biomass variables on the negative part. The first component correlated negatively with larval and juvenile mortality, along with its interactions with fecundity and growth. The first component was positively correlated with growth and fecundity, and their interaction. It explained a large part of output variability, particularly the biomass after five years of simulation. The second component explained most of the variability in the catches of the fifth year. It was correlated negatively with TAC and positively with the interactions between migration coefficients and the standardization factors between gears.

VIPs were computed using the first two components, and significant ones are shown in Figure 4. Considering only the main effects, the most sensitive parameters were the values for larval and juvenile natural mortality, growth rate, and fecundity rate. In contrast, VIP values associated with adult mortality, migration, and accessibility were not significant, nor were those related to standardization factors, target factors, selectivity coefficients, and fishing effort. All interactions between the three factors with high VIP, early mortality, growth, and fecundity, were significant, as were those between accessibility and fishing effort (q×eff), and between migration coefficients and standardization factors (mig×$\mathrm{SF}_{\mathrm{std}}$). The strength of these interactions should be considered carefully, however, because interaction coefficients only provide an average estimate of the effects of the different levels of the factors combined. However, the strength does indicate that the effects of these factors can only be assessed conditionally with respect to other factor values.

The results depended on management scenarios, but the VIP corresponding to a MPA was low, indicating that the impact of the MPA implementation on the response variables was not significant. Further, interactions between MPA and parameter factors were weak. However, TAC implementation induced significant changes in biomass and catches, evidenced by the high value of the VIP of the TAC factor (Figure 4). In addition, the sensitive parameter factors described above were influential in interactions with the TAC factor, meaning that the magnitude of their impact varied when a TAC was implemented. Inversely, TAC effects depended on the value of the sensitive parameters. The VIPs of these interactions were smaller or equal to those of the principal effects for each factor, but because each parameter was involved in cyclic interaction, it was difficult to predict the resultant direction of the impact.

To clarify the meaning of these interactions, we broke down some of the simulations further: it appeared that when the mortality of larvae and juveniles was high, anchovy biomass remained lower than the TAC tested (6000 t), so TAC regulation was not a constraint on fishing activity. This management measure consequently had no effect on the fishery at high values of natural mortality.

MPA impacts

The uncertainty analysis showed that anchovy population dynamics were determined mainly by early stage natural mortality (not shown), so forecasts will remain weakly accurate until knowledge of that biological process can be improved. Despite this, the analysis revealed that whatever the combination of values for uncertain parameters, the diagnostic relating to MPA design was seldom modified. We can therefore consider the relative efficiency of MPA designs in the scenarios with all parameters fixed at their reference values (Figure 5). In that case, the baseline simulation (without management) led to a rapid decrease in population numbers.

Whatever the design, the population still decreased, and the gain in biomass resulting from MPA implementation was small compared with the loss attributable to fishing mortality. Depending on the design (MPA1 or MPA2, and their period of application), management did not always benefit anchovy biomass compared with the baseline scenario (Figure 5). The MPA1 effect should be distinguished from MPA2. Indeed, in simulations where MPA1 was closed, the final biomass improved and was positively related to closure duration. In contrast, biomass was lower than without management and decreased with closure duration for MPA2, although the closed area was larger. Moreover, closing MPA1 in May was as efficient as closing it in April and May, despite the different duration. In that case, the performance of a MPA in terms of biomass was more related to season (month) and location than to duration or surface area of closure. Catches improved in any case, but significantly more so with MPA1. Short- and long-term effects of management were clear. Indeed, closure in autumn increased catches initially, but led to lower levels of biomass. Consequently, after eight years, closure was no more beneficial for fishers than the baseline scenario. On the contrary, with MPA1, a positive influence on biomass with the longest closures resulted in better catches after eight years. Finally, in the long term and whatever the hypothesis on parameter values, establishment of MPA1 in May and June was most beneficial in terms of anchovy biomass and catch.

Discussion

The flexibility of the ISIS–Fish tool allowed integration of spatial and non-spatial information at different levels of complexity in simulating various aspects of anchovy fishery dynamics under the most realistic conditions. The exercise allowed us, on the one hand, to take account of the large quantity of spatially disaggregated information available for the population, and on the other hand, to identify the uncertainties and knowledge gaps for the fishery and the stock. For instance, comparing simulated with observed catch-at-age, we clearly capture the seasonal pattern in catches, but interannual variability was not always reproduced. However, the parameterization was considered satisfactory enough to address the issue of expected MPA impacts on the anchovy fishery.

The sensitivity analysis revealed great dependence of the simulation results on the values of some of the biological parameters. An absolute diagnostic can only be provided if the values of these influential parameters were determined accurately. Currently, biological knowledge does not allow for this, so the impact of management options could only be analysed in relative rather than absolute terms in respect of biomass and catch.

From a biological perspective, the results of the sensitivity analysis confirmed the *a priori* notion that the driving processes of the fishery were early life growth and mortality, and spawning, as expected for a short-lived species. The same parameters were identified as sensitive for the ISIS–Fish model applied by Drouineau *et al.* (2006) to the mixed hake–*Nephrops* fishery in the Bay of Biscay. The parameter values varied naturally from year to year, and the sensitivity analysis showed that the variations likely affected management efficiency. Therefore, it would seem crucial to obtain more accurate information on the early life history of anchovy to improve both the estimates and the understanding of the fluctuations in these vital rates. Natural mortality appeared to have a greater impact than fishing mortality, but fishing mortality worsened the outcome under unfavourable conditions (high accessibility, changes in spatial distribution of 1-year-old fish), jeopardizing population viability.

The results of the sensitivity analysis could also be interpreted directly in terms of management. The significant interaction between accessibility and fishing effort, for instance, indicates that under favourable conditions for accessibility, regulation of the fishery by fishing effort restriction might be valuable.

TAC levels significantly impacted anchovy biomass. However, as the significance of the interactions between TAC and critical biological and fishing parameters showed, the management efficiency of a TAC depended strongly on the values of those parameters. For instance, a TAC was useless when natural mortality was high, demonstrating the limits to the classical use of a TAC and favouring adaptive management such as setting a TAC proportional to recruitment. However, this measure cannot yet be applied in an annual management cycle because of the difficulty of predicting recruitment, and would instead require seasonal management (Fréon *et al.*, 2005). However, in the context of a fluctuating environment and great uncertainty surrounding population parameters, a precautionary approach suggests that the efficiency of management options should not be conditioned on parameter values. As stressed by Kell *et al.* (2007), it is seldom possible to predict the response of fish populations to management with any degree of accuracy, but it is possible to evaluate which strategies on average works best, i.e. which management option is most robust. A fixed TAC value, although constraining compared with historical catch levels, does not appear to be the most precautionary measure. Inversely, the results of MPA simulations showed only a limited positive effect compared with scenarios without a MPA, but did prove to be robust to parameter uncertainties.

Sensitivity analysis confirmed (i) the importance of fecundity for population growth, supporting proposals to protect spawning, and (ii) the high impact of early mortality, supporting the need to better understand the interplay between fishing and natural mortality on juveniles to assess their cumulative effects. Therefore, it seems that the proposed MPA could be considered as appropriate for the population. Another notable result is that the measures described here could potentially benefit fishers in the long term. Although some designs appeared to be more effective than others, MPA effects were still limited and not significant because of the overall uncertainties surrounding some of the parameters. It could be that MPAs need more time to restore a population effectively or that fishing pressure is anyway too high to allow sustainable exploitation of the population without effort restriction. Nevertheless, the results of the simulations did advance other explanations and directions to improve MPA design. A first explanation relies on the way the design of the MPAs was chosen: period and location were chosen according to biological processes and the presence of fish, and did not account for the dynamics of fishing activity. In particular, even if April is the key month for spawning, it is a month of limited activity by the French fleet because of a bilateral agreement with Spain, and the MPA covered only a small portion of the Spanish fishing area. Consequently, MPA effects on fisheries were generally weak, although weak or negative effects can also result from effort being transferred to other areas, underscoring the importance of accounting for fisher response to management.

Another explanation is provided by the model structure. Actually, one of the hypotheses of the model is that whatever the overlapping surface between a métier area and a population area, the whole population of the latter is accessible to the métier. Given this hypothesis, if the area of closure does not totally overlap with the population area and if the métier still operates in the rest of the population area, the whole population is still accessible to fishing, resulting in a weaker effect of the MPA. It could also explain why migration rates were not significant in the sensitivity analysis despite being described as a determinant parameter for MPA evaluation (Babcock *et al.*, 2005). This modelling hypothesis is reasonable when considering the high mobility of fish inside a population area, at a monthly scale. However, it is not certain whether it is relevant for a pelagic population at these spatial and temporal scales. It could be added as an extra hypothesis to explore future versions of the model. Finally, it is acknowledged that MPAs are less effective as a tool to restore biomass rather than as one to protect key processes under occasionally bad conditions (Sumaila *et al.*, 2000), so MPA results might be more significant in the case of unfavourable environmental conditions.

With our application, we have proposed a methodology to identify the most important parameters of the model. Management option efficiency compared with baseline simulation and its limitations have also been shown. There are some limitations of the method, however. First, an experimental design that can assess each parameter effect separately rather than as group effects, in particular for parameters dependent on length classes (mortality and fecundity), would permit more-precise determination of the stages that subsequently govern the population. Additionally, the greater number of parameters in some groups than in others (for instance groups that contain parameters by length class, such as mortality) may bias the perception of the importance of groups. Furthermore, some interactions could have been neglected, because parameters for each group were probably correlated.

VIPs were effective in measuring factor importance, but there is currently no method to test their significance. Moreover, the absolute direction of the effects depends on the output considered, and is difficult to solve because of the numerous interactions. On the other hand, diagnostic plots on PLS results (not displayed) showed evidence of a weak non-linear relationship between factors and responses that could explain the importance of the interactions. We believe that assuming linearity would not significantly impact the results. However, a non-linear meta-model and a design allowing for more than two modalities per factor may improve the output.

The choice of the parameters tested is also crucial. Here, we only studied sensitivity to parameter values, and did not investigate sensitivity to model specification. Actually, alternative hypotheses concerning the relationships between stock size and egg production, and the effects of larval and juvenile mortality, migration seasons, and initial numbers needs to be explored and included in the sensitivity analysis. A fixed percentage variation of a parameter value was easily implemented for continuous parameters such as fecundity, but is not relevant for discrete parameters or those such as length, which are fixed according to a growth function.

Finally, a single scenario of fisher reaction to a MPA was considered, although this aspect is very uncertain and generally presumed to be highly relevant (Apostolaki *et al.*, 2002; Smith and Wilen, 2003; Babcock *et al.*, 2005). The MPA2 results showed possible negative impacts of a MPA when effort is reallocated to areas where the fishing pressure is already intense. Additionally, neither the exploration of new areas nor the concentration of effort at the boundaries of the MPA shown by some authors (Murawski *et al.*, 2005) to be important was considered here. We assumed that when all fishing areas are closed, fishers stopped fishing. Data on how effort is reallocated to other species should also be integrated so as to be able to evaluate the ecosystem effects of MPA implementation and TAC regulations in a broader context. Investigations of such phenomena would require the model to describe also the dynamics of other target species and fisheries. Until this issue is clarified, e.g. through interviews with fishers, by extrapolation of fishing effort, or through the use of discrete-choice models that take account of economic conditions, we believe that fisher response scenarios should be added as a factor in the experimental design (Smith and Wilen, 2003; Vermard *et al.*, 2008).

Finally, it should be noted that the results of the sensitivity analysis obviously depend on the outputs considered. These outputs need to be selected in relation to the questions posed. As the main management objectives are presumed to be biomass restoration along with catch maximization, we chose biomass and catch to assess management impact and to report on performance. However, considering biomass and catch has, *inter alia*, the consequence of adding more weight to adult abundance than to juvenile abundance in the diagnostic, even if the simulation durations of five and eight years allow the impact to be observed on second and third generations of fish. However, the consideration of other outputs accounting for time or spatial variations could provide further insights beyond the specified objectives of the MPA, and could help to describe processes underlying the management impact. Relevant indicators of MPA effects could be identified. Guénette *et al*. (1998), for instance, explained that the benefits from MPAs came from the increase in biomass and individual size, resulting in adult migration and/or larval dispersal that would replenish fishing grounds. Moereover, this can result in unexpected side-effects (e.g. Murawski *et al*., 2005, showed reallocation of fishing effort around the MPA), rather than focusing only on the objectives to be achieved (see Pelletier *et al*., 2005, and Clua *et al*., 2005, for a description of fishery indicators in the context of coral reef fisheries). Future development of the simulation tool will allow these questions to be explored further, and hopefully the proposed methodology will allow the most relevant indicators of a MPA impact on the anchovy fishery to be identified.

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Appendix 1

ISIS–Fish model

The model equations are described in Mahévas and Pelletier (2004) and Pelletier *et al*. (2009) and major features used for the anchovy application are briefly presented here. The ISIS–Fish model is a deterministic dynamic simulation model. It is time-discrete with a monthly time-step. Processes are described at a seasonal scale (group of months), during which spatial distribution of abundance and effort in a population is assumed to be fixed. Seasonal patterns and biological processes are assumed to remain unchanged across years. From the chronology of processes, the evolution of population abundance between time t and time t+1 can be written as

$$N(t+1) = \mathrm{SR}(t)(R(t) + D^{\mathrm{mig}}_{\mathrm{season}} CC_{\mathrm{season}} N(t)), \qquad \text{(A1)}$$

SR(t) being the diagonal matrix of survival rates at time t, $N(t)$ the length-class- and area-specific abundance matrix of a given population in month t, and $R(t)$ is the recruitment vector, for anchovy corresponding to the number of eggs spawned per population area. $D^{\mathrm{mig}}_{\mathrm{season}}$ is the migration matrix and CC_{season} is the matrix depicting the proportion of fish of length class i growing to length class j at the beginning of each month of the season. Change of class, migrations, spawning, and recruitment are assumed to occur instantaneously, and following this chronology, at the beginning of the time-step, whereas natural and fishing mortality influence population abundance throughout each time-step. Survival rates follow the classical exponential decay model widely used in fisheries models, so that the survival rate sr of class cl at time t in population area z is

$$\mathrm{sr}(\mathrm{cl}, z, t) = \exp\left[-\left(F(\mathrm{cl}, z, t) + \frac{M(\mathrm{cl})}{12}\right)\right], \qquad \text{(A2)}$$

where $F(\mathrm{cl},z,t)$ and $M(\mathrm{cl})$, respectively, denote the instantaneous fishing mortality rate expressed per month (see below for the fishing mortality computation based on fishing time), and the instantaneous natural mortality rate expressed per year.

The overall fishing mortality endured by a class of population cl in area z during month t is calculated by summing over strategies (str) and (métiers) met:

$$F(\mathrm{cl}, z, t) = \sum_{\text{strategies}} \sum_{\text{métiers}} F(\mathrm{str},\ \mathrm{met},\ \mathrm{cl}, z, t) \tag{A3}$$

Fishing mortality is based on fishing effort. It is assumed that fishing mortality induced by a métier depends only on fishing time in the métier area and the population area z:

$$F(\mathrm{str}, \mathrm{met}, \mathrm{cl}, z, t) = \mathrm{Sel}(\mathrm{gear}, \mathrm{cl}) \times q(\mathrm{cl}, \mathrm{season}) \times \mathrm{Target}F(\mathrm{met}, \mathrm{cl}, \mathrm{season}) \times \mathrm{StdEffort}(\mathrm{str}, \mathrm{met}, z, t)\ , \tag{A4}$$

Sel being the selectivity of the gear, q the accessibility, and Target$F$ the target factor. Fishing time is converted to standardized fishing effort, accounting for the gear used by the métier using $\mathrm{SF}_{\mathrm{std}}$ the standardization factor between gears:

$$\mathrm{StdEffort}(\mathrm{str}, \mathrm{met}, t) = \mathrm{SF}_{\mathrm{std}}(\mathrm{gear}) \times \mathrm{FishingTime}(\mathrm{str}, \mathrm{met}, t)\,. \tag{A5}$$

Appendix 2

PLS method

The term PLS refers to partial least squares regression on latent structures (Tenenhaus *et al.*, 1995). It is a sequential method that may be seen as an extension of principal component analysis to a regression used to explain a set of response variables Y by another set of predictor variables X. It consists of building a sequence of couples (t_p, u_p) p in 1, ... h of linear combinations t_p of the X variables and u_p of the Y variables, with the constraint to maximize their covariance (max[cov(t_p, u_p)$_{p=1,\dots h}$]). At each step, Y is projected on t_p, which is called a component (Appendix Figure 1). Interpretation of PLS results relies on two coefficients: the weight coefficient $w_{x,p}$ measuring the weight of the predictor variable x, in the building of component t_p, the coefficient c_p of the linear regression of the variables of Y on the component t_p. The number of components that need to be searched for is determined by cross validation using the root mean squared error of prediction (RMSEP). This criterion does not necessarily decrease when adding new components, because the smaller it is, the better the model fit. When the number h of couples of latent variables (defining axes) is selected, the redundancy Rd(Y; t_p … t_h), part of the variance of Y explained by the h first latent variables, gives a measure of the goodness of fit. For each predictor x, Variable Importance in Projection (VIPx) is the sum over each component p of the weight coefficients ($w_{x,p}$) of the predictor on the component, weighted by the redundancy Rd(Y; t_p) explained by the component (Tenenhaus *et al.*, 1995). The VIP of the predictor variable x using the first h components t_h is given by

$$\mathrm{VIP}_{xh} = \sqrt{\ } (n / \mathrm{Rd}(Y; t_1, t_2, \dots, t_h) \textstyle\sum_{i=1}^{h} w_{xi}{}^{2} \times \mathrm{Rd}(Y; t_i)) \tag{A6}$$

where Rd(Y; t_p) is the variance of Y explained by the component t_p, and n is the number of factors. In the present case, X variables are the factors and Y variables are the response variables.

As the direction of impact could be different depending on the variable considered, this direction could be investigated graphically by plotting weighting coefficients and projections of response variables on PLS components. Factors can be projected on the baseline going from the response variable of interest to the origin. The distance from the origin to the projection of the factor is proportional to the influence of the factor on the response variable. As for PCA, observation may also be plotted on the latent variables to be considered in groups.

Figure legends

Figure 1. Anchovy population areas as defined in the model deduced from survey results. The different shaded areas correspond to the habitats identified for anchovy: horizontal dotted lines correspond to area North, horizontal lines to area Gironde; upward hachured area : Rochebonne; bolded upward hachured area: Landes coastal; bolded downward hachured area: Landes offshore. The box corresponds to the recruitment area.

Figure 2. Fishing areas defined from a map of fishing effort. (a) Fishing areas of French pair-trawlers. Horizontal dotted lines corresponds to area North, horizontal lines to area Gironde; upward hachured area : Rochebonne; bolded downward hachured area: Landes. (b) Fishing areas for purse-seiners. Shaded areas are those of French purse seiners: horizontal dotted lines corresponds to area Brittany, horizontal lines to area Gironde; bolded downward hachured area: Landes. Boxes correspond to Spanish purse seiners fishing areas: thin line surrounded the area South corner and bolded line the area Cantabria.

Figure 3. Map of the study area with the two marine protected areas evaluated in the study, MPA1 delimited by a continuous line, and MPA2 by a dotted line.

Figure 4. Significant variable importance in projection (VIP), used as sensitivity indices of the entire set of output variables to inputs of the model (Jmo, mortality of the first 15classes; gro, length class boundaries; mig, migration coefficients; SF_{std}, standardization factors for gears; fec, fecundity rates; *q*, accessibility; eff, effort, the symbol * indicates interaction between the two parameters).

Figure 5. Results of MPA evaluation with the parameters fixed at their reference values. The ratio is provided for biomass (left panels) and catch (right panels) after five years (top panels) and eight years (bottom panels) of simulation for the various management scenarios (identified by their period of closure) over the corresponding results for the reference scenario, i.e. without regulation. Results are presented according to the duration of closure (*x*-axis). Note the difference in the scales of the *y*-axes.

Table 1. Length–age group characterization by age, maximum length, annual mortality rate, and accessibility coefficient.

Group number	Age when entering group (months)	Maximum length (cm)	Natural mortality rate (per area for group 0) (year^{-1})	Accessibility *q*, calibrated (month^{-1})
0	0	2.00	Rochebonne: 87.14 Landes Coastal: 87.75 Landes Offshore: 88.3 Gironde: 87.5	8.2582×10^{-6}
1	1	4.00	15.5	
2	2	7.67	9.2	
3	3	8.76	6.6	
4	4	9.75	5.1	
5	5	10.65	4.2	
6	6	11.45	3.5	
7	7	12.17	3.1	
8	8	12.83	2.7	
9	9	13.41	2.4	
10	10	13.90	2.2	
11	11	14.40	2.0	
12	12	14.85	1.9	0.0024
13	13	15.24	1.7	
14	14	15.59	1.6	
15	15	17.39	1.5	
16	27	18.37	1.4	
17	39	18.65	1.5	

Table 2. Migration coefficients between population areas by month and length group.

Month and departure area	Percentage of fish that migrate by age		Arrival area
January	Small age 1	Big age 1 (>13 cm)	
Recruitment area (recruits)	38	18	Gironde
	34	38	Rochebonne
	13	13	Landes Coastal
	15	31	Landes Offshore
March	Age 2+		
North	18		Gironde
	38		Rochebonne
	13		Landes Coastal
	31		Landes Offshore
August	Age 2+		
Gironde Rochebonne Landes coast Landes offshore	65		North
September	Age 1		
Gironde Rochebonne Landes coast Landes offshore	65		North

Table 3. Time and location of spawning according to fish length.

Month	**Gironde / Landes**	**Rochebonne**
April	Yes	No
May	Yes	Yes
June	Yes for fish >14.9 cm	Yes
July	Yes for fish >15.6 cm	Yes for fish >14.9cm
August	No	Yes for fish >15.6cm

Table 4. Parameters relative to fleets, metiers, and strategies, with the number of vessels in each fleet indicated in parenthesis. Métiers are designated according to their area of practice and characterized by a target factor (target*F*) depending on season and the proportion (prop) of time spent on it per month.

Fleet (number of fishing units)	**Métier targeting anchovy**		**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
French pair-trawlers (36)	Rochebonne	prop	0.029 5	0.013 9	0.008 5	0	0.000 8	0.044 3	0.040 5	0.024 3	0.022 3	0.011 2	0.023 4	0.001 0
		target*F*	0.98											
	Gironde	prop	0.011 4	0.024 3	0.012 0	0	0	0.014 2	0.000 8	0.003 5	0.009 3	0.003 8	0.001 8	0
		target*F*	0.98											
	Landes	prop	0	0.000 1	0.000 1	0	0.001 4	0.039 9	0.003 5	0.000 3	0	0	0	0
		target*F*	0.98											
	North	prop	0.004 4	0.000 3	0.001 5	0	0	0.001 3	0.038 4	0.090 6	0.077 4	0.072 0	0.037 4	0.000 5
		target*F*	0.98											
Purse-seiners Basque Country (10)	Landes	prop	0	0	0	0.012 1	0.047 0	0.049 3	0.028 4	0.010 9	0.005 4	0	0	0
		target*F*	0			0.881		0.8	0.72	0.93		0		
	Gironde	prop	0	0	0	0	0	0	0.002 8	0.001 3	0.001 0	0	0	0
		target*F*	0						0.77	0.67	0.73	0		
Purse-seiners Brittany (9)	Brittany	prop	0	0	0	0	0	0	0	0.003 7	0.014 9	0.009 1	0.001 7	0
		target*F*	0							0.56		0.38	0.51	0
Spanish purse-seiners (167)	Landes	prop	0	0	0	0.464 1	0	0	0	0	0	0	0	0
		target*F*	0			0.52	0							
	South corner	prop	0	0	0	0	0.820 7	0.552 9	0	0	0	0	0	0
		target*F*	0				0.57		0					
	Cantabria	prop	0.032 7	0.027 0	0.278 2	0	0	0	0.180 7	0.115 8	0.140 0	0.015 3	0.189 9	0.085 4
		target*F*	0.07			0			0.07					
Spanish purse-seiners, Païta (107 vessels harvesting 2 t each every two weeks for live bait)	Gironde		0	0	0	0	0	Age 1		Age 1/big age 0	0	0	0	0
	South of 46°		0	0	0	0	0	0	0	0	Age 0		0	0

Table 5. Standardization factors for each gear and minimum length of catch.

Gear	Standardization factor (SF_{std})	Minimum length of catch
French purse-seine	1	
Spanish purse-seine	0.0686	9 cm
Trawl	0.8	

Table 6. Characteristics of the two MPA designs evaluated. MPA1 aims to protect fish during the spawning season, and MPA2 aims to protect juvenile fish during their period.

MPA1	MPA 2
Area: Gironde river plume (44°30′–46°N; 1°00’–2°30′W) Spawning period April–June	Area: coast south (43–46°N; 1–2°W) Recruitment period September–November

Table 7. Description of the groups of factors defined for the sensitivity analysis, with the name of the group, the abbreviation used to design it, its nature, the number of the parameters inside the group, and reference values.

Group name	Abbreviation	Parameters covered	Number	Reference values for parameters
Growth	gro	Minimum and maximum length for each class	18	Table 1, maximum length
Fecundity	fec	Fecundity rate of each mature length class	10	3 500 eggs g dry weight^{-1}
Larval and juvenile mortality	Jmo	Mortality rate of each length class (0–14) corresponding to young fish before the end of first spawning	15	Table 1, natural mortality rate
Adult mortality	Amo	Mortality rates for age 1 to age 3 fish (length classes 15–17)	3	Table 1, natural mortality rate
Migration	mig	Migration coefficients of recruits (length classes 5–9) from recruitment area to the areas Gironde, Landes, and Rochebonne in January	20	Table 3, first line
Accessibility	*q*	Accessibility coefficient of each length class	18	Table 1, accessibility
Standardization factors for gears	SF_{std}		3	Table 4
Target factor of the métiers on anchovy	target*F*	One per métier and season of practice	24	Table 5
Selectivity	sel	Minimum length of catch with each gear, three parameters	3	Table 4
Effort	eff	Total fishing time per month per strategy	48	Days in the month minus 8 d of inactivity

Table 8. Designs (4 factors) to evaluate the effect of MPAs. For each, the duration was changed from 1 to 3 months, and for each duration, every combination of consecutive months was evaluated (see Table 4). Designs also account for uncertainty on groups of sensitivity parameters (early mortality, growth, and fecundity), a range of ±20% uncertainty having been considered around the mean value.

Factor	Level
MPA design	No MPA
MPA1	Duration (1, 2, or 3 months)
MPA2	Period (consecutive months of closure)
Sensitive parameter(s)	
Early mortality	
Growth	High, +20% /Mean / Low, –20%
Fecundity	

Table 9. Descriptions of the MPAs. The duration was changed from 1 to 3 months, and for each duration, every combinations of consecutive months was evaluated.

	Period	
Duration	MPA 1	MPA 2
1 month	April, May, June	September, October, November
2 months	April-May, May-June	September-October, October-November
3 months	April-June	September-November

Table 10. Initial numbers by area and length class used in the simulations (modified from ICES, 2006).

Length class	Recruits	Rochebonne	Landes coastal	Landes offshore	Gironde	North
5	705 650 000	0	0	0	0	0
6	1 218 850 000	0	0	0	0	0
7	1 218 850 000	0	0	0	0	0
8	2 052 800 000	0	0	0	0	0
9	1 154 700 000	0	0	0	0	0
15	0	186 473 000	71 298 500	170 019 500	98 721 000	1 018 550 000
16	0	18 683 000	7 143 500	17 034 500	9 891 000	102 050 000
17	0	7 735 000	2 957 500	7 052 500	4 095 000	42 250 000

Table 11. Outcomes of the PLS regression model. For each variable included in the analysis (Biomass 5 and Biomass 8 refer to biomass at the end of the fifth and eighth years of simulation; Catch 5 and Catch 8 refer to cumulative catches for the fifth and eighth years of simulation), and the cumulative percentage of variance of each output variable explained by the components of the model.

Parameter	First component	Second component
Catch 5	65.8	20.6 (86.5)
Biomass 5	86.7	12.4 (99.2)
Catch 8	65.6	15.5 (81.0)
Biomass 8	82.8	15.5 (98.4)

Figure 1

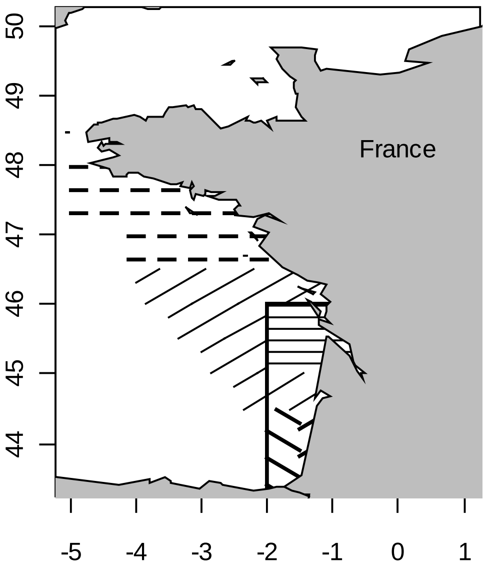


Figure 2

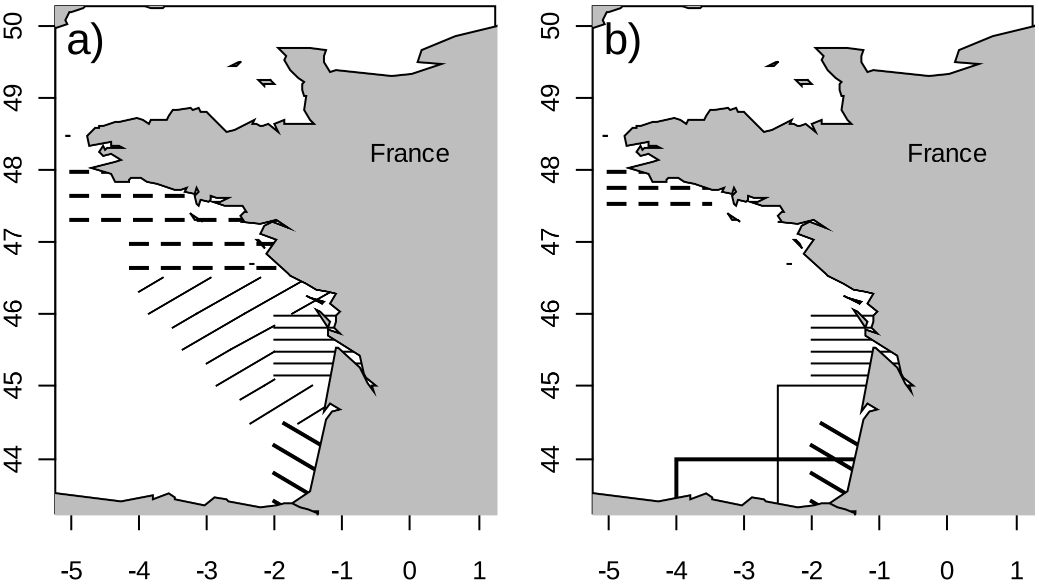


Figure 3

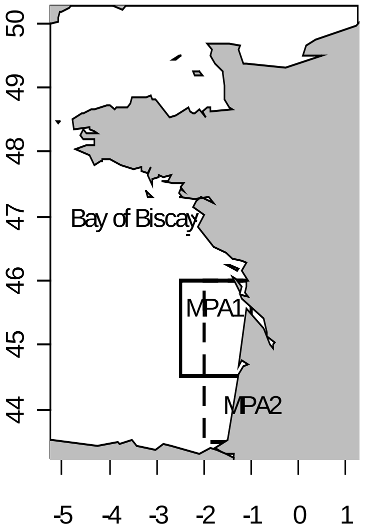


Figure 4

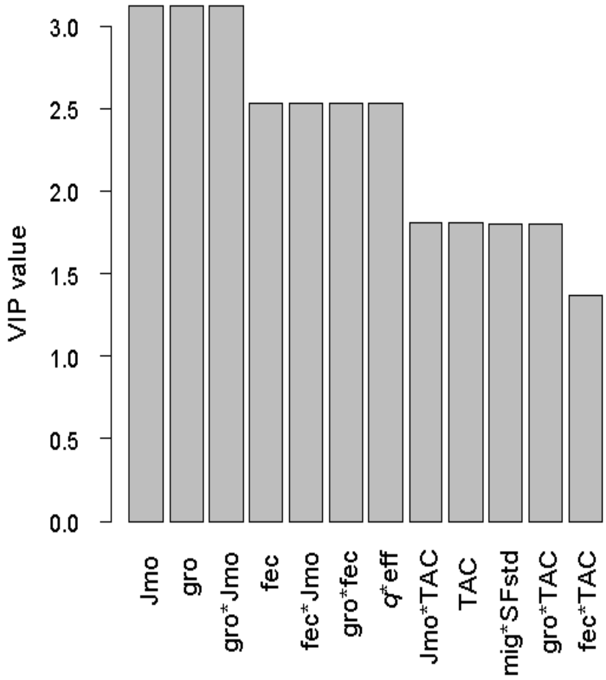
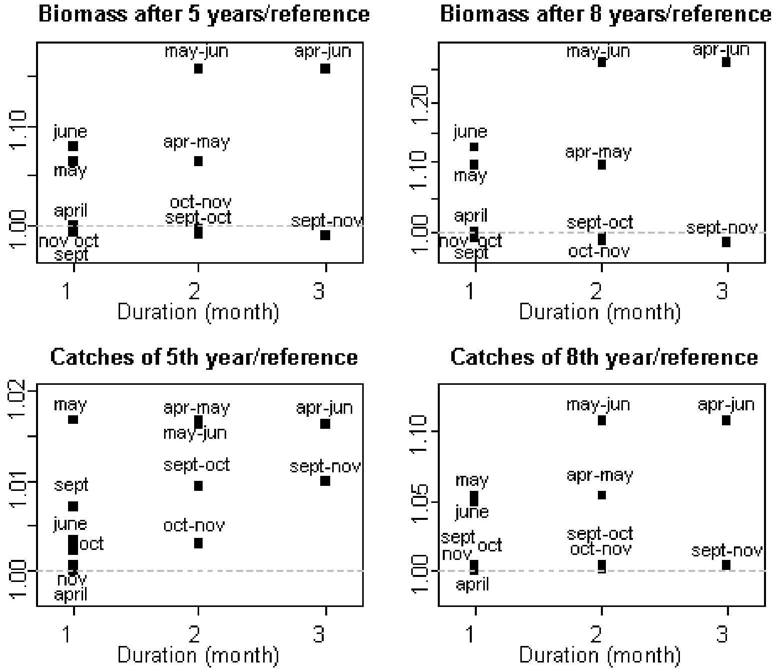


Figure 5


Biomass after 5 years/reference

Biomass after 8 years/reference

Catches of 5th year/reference

Catches of 8th year/reference