

Modelling trophic flows in ecosystems to assess the efficiency of marine protected area (MPA), a case study on the coast of Sénégal

Mathieu Colléter^{a,*}, Didier Gascuel^a, Jean-Marc Ecoutin^b, Luis Tito de Morais^c

^a Université Européenne de Bretagne, UMR 985 Agrocampus Ouest, INRA « Ecologie et Santé des Ecosystèmes » (ESE), 65 rue de Saint Brieu, CS 84215, 35042 Rennes Cedex, France

^b Institut de Recherche pour le Développement (IRD), UMR LEMAR (UBO/CNRS/IRD), BP 1386 Dakar, Senegal

^c Institut de Recherche pour le Développement (IRD), UMR LEMAR (UBO/CNRS/IRD), BP 70, 29280 Plouzané, France

ARTICLE INFO

Article history:

Received 16 August 2011

Received in revised form 23 January 2012

Accepted 24 January 2012

Keywords:

Marine protected area

Ecopath

EcoTroph

Trophic network

ABSTRACT

Marine protected areas (MPAs) are now viewed as an efficient tool to fight against the global deterioration of habitats and fish populations. However their efficiency and effects on the whole trophic network are little known. Based on the Bolong de Bamboung (Sénégal) case study, the objective of this study is to assess the impact of a MPA on the entire trophic network using trophodynamic models. This estuarine small MPA is scientifically surveyed since 2003, one year before the closure of the fishery. Using the resulting dataset, we calculated time series of abundance indices and constructed two Ecopath mass-balanced models for the year 2003 (fished) and the 2006–2008 period (unfished). Using EcoTroph, an ecosystem trophic-level based model, we compared the two periods and simulated a closure of the fishery starting from 2003 to assess the effect of the MPA. We observed a rather constant total biomass, but a biomass increase by a 2.5 factor in predators and a decrease by a 1.7 factor in their preys. Simulations showed that the increase in predators was too important to only being a direct consequence of the removal of the fishing mortality and a local production. This highlighted the role of the MPA as a refuge or a foraging arena for some predator species. What's more, the decrease of the preys, corresponding to pelagic species, was very important and couldn't be explained only by an increase of the predation plus a release of the fishing pressure. This indicated other possible effects as environmental and behavioural ones, in addition of a direct MPA effect. Sensitivity testing and a comparison with another nearby similar but fished area, the Bolong de Sangako, validated the same global conclusion. We concluded that the fishing closure had direct effects but also indirect ones likely due to fish behaviour and environment, and that trophodynamic models are useful tools to analyse MPA effects on the whole trophic network.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

In the face of the global overexploitation of marine resources and the fast degradation of ecosystems integrity, many countries' governments have decided to implement an ecosystem approach to fisheries (EAF) (WSSD, 2002) and to achieve a good environmental status of marine ecosystems in 2020 (MSFD EU, 2008). In this context, developing marine protected areas (MPAs) is now viewed as an efficient way to preserve biodiversity and to protect specific habitats (Lester et al., 2009). These MPA have already shown positive effects by, for example, an increase of the fish population's mean size, biomass and density (Mosquera et al., 2000; Halpern and Warner, 2002; Gell and Roberts, 2003). However, the ability of MPAs to reduce the fishing impact on the targeted resources and on the entire trophic network is still poorly known (Murawski et al., 2005; White et al., 2010). In the present study, using the MPA of

the Bolong de Bamboung (Sénégal) as a case study, we aimed to analyse the impact of an MPA on the whole trophic network of the estuarine protected ecosystem.

Estuaries are an interface between continental and marine environments. They make the highest contribution to global food production across the globe and to the total economic value of ecosystem services (Constanza et al., 1997). The Sine-Saloum estuary (Sénégal) is inhabited by various categories of estuarine, marine and freshwater fish (Albaret, 1999) and provides most of the animal protein for the local populations (Guillard, 1998), with an average present yield of $12.5 \text{ t km}^{-2} \text{ year}^{-1}$ (Ecoutin, unpublished data). It is made up of three main affluents and many subsidiary branches called "bolongs", with a total surface area of more than 800 km^2 (Guillard, 1998). The Bolong de Bamboung is a small tributary (4.7 km^2) of the Diomboss, one of the three main branches of the estuary complex. It is monitored through scientific surveys since 2003 (Albaret, 2003) and fishing has been prohibited since 2004. Data on fish abundance were thus available before and after the MPA implementation. This constituted a reverse form of before after control impact (BACI) design (Underwood, 1992), and a very

* Corresponding author.

E-mail address: mathieu.colleter@hotmail.fr (M. Colléter).

favorable situation to assess the efficiency of the MPAs through their effects on the food web. Furthermore, there is presently only a small number of MPAs in West Africa, and this study contributes to the development of effective diagnosis on their role in the fisheries management (Gascuel and H  nichart, 2011).

We used trophodynamics models to analyse the following questions: how did the MPA impact the biomass of the fishery-targeted species? How was this impact reflected on the other biological compartments via the trophic network? And how did all of this modify the general characteristics of the ecosystem?

By modelling the trophic interactions inside the MPA, the software and model Ecopath with Ecosim (EwE) (Christensen and Walters, 2004; Christensen et al., 2005) seemed to be relevant for the evaluation of the reserve effects. A reference Ecopath mass-balance model was built for the year 2003, synthesizing data available on the entire trophic network (see Coll  ter, 2010). We estimated 2003–2009 time series of abundance for each Ecopath group using a delta GLM-based approach. A mean Ecopath model for the 2006–2008 period was so derived from the reference one. We used EcoTroph (a new plug-in of the EwE software; Gascuel et al., 2009) to simulate the closure of the fishery back in 2003. Results were compared to the 2006–2008 model to determine if changes resulted only from a direct MPA effect, linked to the removal of the fishing mortalities. Finally, an Ecopath model was built for the Sangako, a tributary similar to the Bolong de Bamboung but still heavily fished. It allowed us to compare these two ecosystems in order to determine the importance of the fishery closure as a driver of biomass changes.

2. Materials and methods

2.1. Presentation of the MPA and the scientific surveys

The Bolong de Bamboung is a salted water channel, a small branch of the Diomboss, one of the three affluents of the Sine-Saloum estuary (Fig. 1). This estuary is characterized by an inverse salinity gradient (range 36–140) (Pag  s and Citeau, 1990), and so a stressful environment structuring fish populations and assemblage (Panfili et al., 2006). However this ecosystem has one of the highest species richness compared to the other West African estuaries, the deficit of species of continental origin being compensated by the presence of a large number of strictly marine species (Baran, 2000). The MPA covers an area of 6.8 km² including 4.7 km² of intertidal bottoms. The bolong himself measures 15 km length, is 50–500 m width and 0–15 m deep (Albaret, 2003). It is around 15 km far from the coast, with a mean salinity of 39.3 allowing the presence of both estuarine and marine species.

Since 2003, scientific surveys were conducted three times a year, corresponding to the three different seasons (dry cool, dry hot and wet seasons). The same 12 sampling stations were collected using a purse seine ($L = 250$ m, $H = 20$ m, 14 mm mesh size, sampled surface $S = 4973.6$ m²) during each survey. In 2008, the scientific monitoring enlarged with the survey of another bolong 7 km far from the MPA, the Bolong de Sangako (Fig. 1). It is still fished but assumed to be similar to the Bamboung in term of ecological functioning and order of surface (3.4 km²). It has a mean salinity of 39.1 in 2008–2009. Only 6 stations on the 12 are still sampled in the MPA and six new in the Sangako ever since. These surveys were realized by a local team of fishermen without targeting any shelters or fish schools, but were done at the specific GPS locations of the stations (Albaret and Simier, 2005).

During the surveys, abiotic data were collected for each station, season and year: salinity, temperature, conductivity, turbidity and tide conditions. The yields for each survey station were sorted by species, measured, weighed and the degree of maturity was

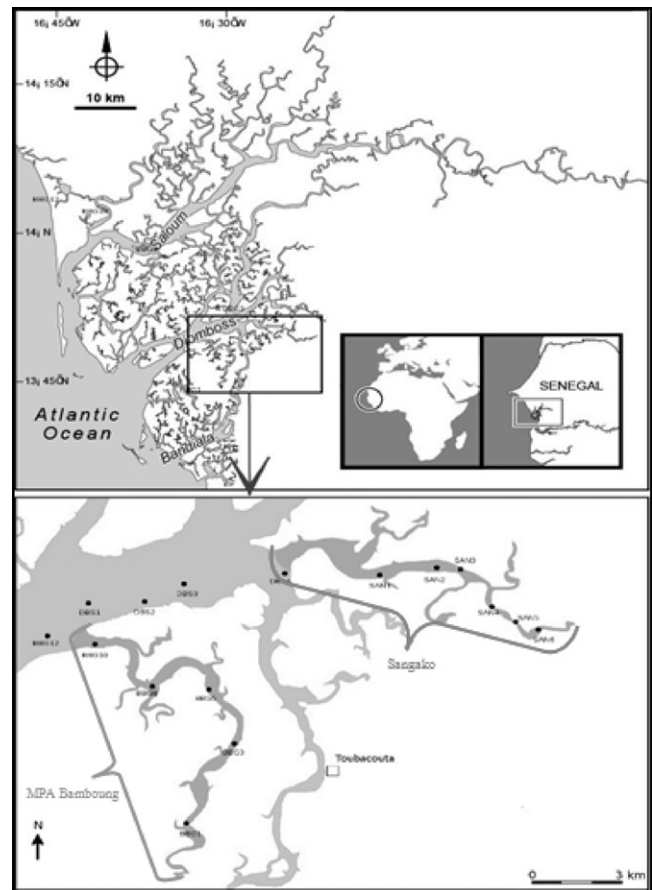


Fig. 1. Location of the Bolong de Bamboung MPA and the Bolong Sangako. Points denote the sampling stations in 2008.

Source: Bertrand Gaspard.

analysed. Some stomach contents were collected too. Information related to the quality of the seine fishing was also compiled: the respect of the GPS position, the rightness of the seine placement and the escapes occurring.

2.2. Estimation of yearly abundance indices

In order to determine abundance indices (AI) for the trophic groups defined in our Ecopath model (see below Section 2.3), we used a GLM-based “delta approach” (Stefansson, 1996). This method allows the treatment of zero-inflated data, which was our case for the survey yields data. The species constituting the Ecopath trophic groups were not caught at each station, season and year. The estimated AI was the product of two models, a probability of presence ($AI^{0/1}$) and an estimated abundance index for the positive values (AI^+) (Eq. (1)):

$$AI = AI^{0/1} \times AI^+ \quad (1)$$

The model consisted of a binomial distribution for the presence/absence (0 for the absence, 1 for the presence) and a lognormal distribution for the positive yields (Le Pape et al., 2003).

We selected explicative variables containing the highest part of the data variance to apply this method in a statistically parsimonious way. Conducting linear regressions, we found that the factors year (from 2003 to 2009), season (dry cool season from November to March, dry hot season from April to June and wet season from July to October) and sector (corresponding to the gathering of the 12 stations into three physically homogenous areas) properly expressed the environmental variations visible through the abiotic data. We

calculated Ecopath groups catch data in each station for all the sectors, seasons and years by summing their respective species catches (in grams of wet weight). We predicted the AI (Eq. (1)) using the GLM fitted on the survey yields data. We tested two modelling choices applied on this catch data for each model of the GLM-based “delta approach”:

- The reference choice: we forced the year factor as the first one tested and retained it when the p -value was inferior or equal to 0.5. The other factors and the cross effects were also considered and retained when significant at 95%. Using this method we calculated yearly AI reflecting the most likely possible changes, and so rejected the equality of the biomass across the year as an acceptable estimation of the real situation.
- The second choice: only factors whose effects were significant at a 95% level were considered. We also tested cross effects and retained them when significant. This hypothesis enabled us to calculate the minimum year effect on the biomass, by retaining only the highly significant changes.

The reference choice was used to estimate yearly AI for each group of fishes over the 2003–2009 period. The other calculation choice was considered in sensitivity analysis.

The estimation of total biomasses B_{tot} (in tons of wet weight) all over the Bamboung was calculated using a surface area rate, $S_{\text{Bamboung}}/S_{\text{Seine}}$, and a catchability coefficient of the seine, q , initially assumed equal to 0.5 but varying for certain groups (see below Section 2.3) (Eq. (2)):

$$B_{\text{tot}} = \frac{(AI \times 10^{-6} \times [S_{\text{Bamboung}}/S_{\text{Seine}}])}{q} \quad (2)$$

We decided to test the robustness of our AI estimations and access the differences observed between 2003 and 2006–2008 (see below Section 2.3). We constructed 1000 bootstrap replicates of the survey yields data (Efron and Tibshirani, 1993), and applied the method mentioned above. We calculated the 2003 AI and the mean AI for the 2006–2008 period for each bootstrap data set using the GLMs fitted on original data. We then performed a mean analysis to compare the 1000 AI for 2003 and the 1000 obtained for the 2006–2008 period. We used two sided Wilcoxon non parametric tests (Wilcoxon, 1945; Bauer, 1972): the null hypothesis was that the distributions of the 2003 AI and 2006–2008 AI differed by a location shift equal to 0 and the alternative is that they differ by some other location shift.

2.3. Construction of a 2003 mass-balance Ecopath model

The trophic structure of the Bolong de Bamboung ecosystem network was analysed by applying the EwE modelling software (ver. 5.1; [Christensen and Walters, 2004; Christensen et al., 2005]). The ecosystem was so described in terms of trophic groups and flows connecting them. These groups represented biological components pooled together according to similarities of species trophic properties and distribution.

The Ecopath model assumes the trophic network to be in a steady state during the studied period, and consequently a mass-balance where the production of the group is equal to the sum of all predations, non-predatory losses, exports, biomass accumulations and catches (see Eq. (3)).

For each group, the Ecopath software solves the two balancing equations (Eqs. (3) and (4)) (Christensen et al., 2005):

$$B_i \times \left(\frac{P}{B}\right)_i = \sum_{j=1}^N B_j \times \left(\frac{Q}{B}\right)_j \times DC_{ji} + \left(\frac{P}{B}\right)_i \times B_i \times (1 - EE_i) + Y_i + EX_i + BA_i \quad (3)$$

$$Q_i = P_i + R_i + GS_i \times Q_i \quad (4)$$

where N is the number of groups in the model, B the biomass, P/B the production rate, Q/B the consumption rate, DC_{ji} the diet matrix representing the fraction of prey i in the diet of predator j , EX the net export, BA the biomass accumulation, Y the catches, EE the ecotrophic efficiency, i.e. the fraction of production which is used in the system, R the respiration, P the production, Q the consumption, GS the fraction of unassimilated consumption because of egestion and excretion. The quantity $(1 - EE) \times P/B$ is the “other mortality” M_0 unexplained by the model.

Assuming there is no export and no biomass accumulation, and the catches Y are known, only three of the four parameters B , P/B , Q/B and EE have to be set initially for each group. The remaining parameter can be calculated by the software.

The Ecopath model included all the ecosystem biological components using 31 trophic groups. For the fish groups, all the species appearing in the survey were pooled into groups using the trophic category resuming the diet (from the database Pechexp [Simier et al., 2003]; see Table A1) and the trophic level (TL) (from Fishbase [Froese and Pauly, 2010]). Two other parameters were used to pool more precisely the different species: the asymptotic length calculated using the maximum length observed in the Bamboung (Froese and Binohlan, 2000), and the ecological category defined by Albaret (1999). This last parameter summarized the abundance, the bioecological life cycle and the euryhalinity degree (Albaret, 1999; see Table A1). The model comprised 20 groups of fishes spanning from sharks to tilapias plus a group of small benthic feeders, representing 71 different sampled species. Two more groups were also constructed for the dolphins, and the seabirds (Reynaud, unpublished data). Regarding the invertebrates, the lack of information coming from the surveys (too wide meshes enabling the capture of this compartment) constrained us to use 5 groups already defined in previous Ecopath models build for the entire Sine-Saloum estuary (Villanueva, 2004; Vignot, 2007): shrimps, crabs, macrobenthos, meiobenthos and zooplankton. We also kept the groups phytoplankton, microphytobenthos as primary producers and the detritus.

Input biomasses were expressed and standardized as annual averages in tons of wet weight per km^2 coming from the estimated AI (Eq. (2)). When not available (invertebrates, small benthic feeders, and primary producers), EE was set according to expert knowledge, previous Ecopath models (Villanueva, 2004; Vignot, 2007) and the needs of the 2006–2008 model (see below Section 2.4). We let the model estimate the biomass corresponding to the needs of the ecosystem (Table 1). The production and consumption rates of the fish groups were estimated using empirical formula. P/B was assumed to be equal to the total mortality Z (Allen, 1971) with $Z = M + F$, where F is the fishing mortality and M the natural mortality calculated using the Gislason formula (Gislason et al., 2008) (details in Table 1). Q/B was calculated using an empirical equation (Palomares and Pauly, 1998). The biomass of the group seabirds was estimated using a counting made in the Senegal delta (Tr  ca, 1996) and a list of 266 species present in the Saloum (Reynaud, unpublished data).

Diet matrix (see Table A2) was constructed using data from previous models made on the Sine-Saloum (Villanueva, 2004; Vignot, 2007) and from different sources for specific groups (Longhurst, 1957; Rabarison-Andriamirado and Caveriviere, 1989; Sene, 1997; Pauly, 2002; Thiaw, 2005; Sylla and Diop, 2006; Villanueva et al., 2006).

No surveys were available to evaluate the catch in 2003. We so formulated a reference hypothesis on the fishing mortality F to calculate yields entered in the model: $F = 0.2$ assuming total yield equal to around 2.5 t km^{-2} , 1/5 of the yield observed in the Sine-Saloum (Ecoutin, unpublished data). We also considered extreme values

Table 1

Basic inputs and estimated outputs (bold) for the trophic groups considered in the 2003 reference model of the Bolong de Bamboung MPA. (TL: trophic level; B: biomass; P/B: production–biomass ratio; Q/B: consumption–biomass ratio; EE: ecotrophic efficiency; P/Q: production–consumption ratio; and Y: yield.)

| | Group name | TL | B (t km ^{−2}) | P/B (per year) | Q/B (per year) | EE | P/Q | Y |
|----|----------------------|-------------|-------------------------|--------------------|---------------------|--------------------|--------------|---------------------|
| 1 | Sharks | 4.07 | 0.001 ^a | 0.329 ^d | 4.991 ⁱ | 0.609 | 0.066 | 0.0002 ^l |
| 2 | Dolphins | 3.73 | 0.000475 ^a | 0.07 ^e | 12.12 ^e | 0.000 | 0.006 | 0 |
| 3 | Birds | 3.41 | 0.0024 ^b | 0.5 ^f | 79.5 ^f | 0.000 | 0.006 | 0 |
| 4 | Rays | 3.23 | 0.09 ^c | 0.515 ^d | 3.391 ⁱ | 0.531 | 0.152 | 0.018 ^l |
| 5 | Croakers | 3.56 | 0.089 ^c | 0.551 ^g | 7.169 ^j | 0.695 | 0.077 | 0.0178 ^l |
| 6 | Barracudas | 3.64 | 0.264 ^c | 0.49 ^d | 6.182 ⁱ | 0.434 | 0.079 | 0.0528 ^l |
| 7 | Giant Threadfin | 3.56 | 0.15 ^c | 0.521 ^d | 6.535 ^j | 0.490 | 0.080 | 0.03 ^l |
| 8 | Snappers | 3.32 | 0.034 ^c | 0.529 ^d | 9.887 ⁱ | 0.766 | 0.054 | 0.0068 ^l |
| 9 | Puffer | 3.34 | 0.045 ^c | 0.509 ^d | 6.134 ^j | 0.910 | 0.083 | 0.009 ^l |
| 10 | Biglip grunt | 3.19 | 0.081 ^c | 0.69 ^d | 10.626 ^j | 0.677 | 0.065 | 0.0162 ^l |
| 11 | Pompano | 3.3 | 0.113 ^c | 0.517 ^d | 6.412 ^j | 0.668 | 0.081 | 0.0226 ^l |
| 12 | Jacks | 3.4 | 0.034 ^c | 0.787 ^d | 17.487 ⁱ | 0.838 | 0.045 | 0.0068 ^l |
| 13 | Sea catfishes | 3.39 | 0.361 ^c | 0.512 ^d | 9.739 ^j | 0.646 | 0.053 | 0.0722 ^l |
| 14 | Ladyfish | 3.48 | 0.118 ^c | 0.588 ^d | 10.293 ^j | 0.693 | 0.057 | 0.0236 ^l |
| 15 | African moony | 3.17 | 0.04 ^c | 0.999 ^d | 18.269 ^j | 0.874 | 0.055 | 0.008 ^l |
| 16 | Tonguesole | 3.26 | 0.102 ^c | 0.502 ^d | 6.513 ^j | 0.749 | 0.077 | 0.0204 ^l |
| 17 | Sardinella | 2.75 | 0.441 ^c | 0.839 ^d | 18.119 ^j | 0.817 | 0.046 | 0.0882 ^l |
| 18 | Mojarra | 3.03 | 0.33 ^c | 0.792 ^d | 13.636 ^j | 0.811 | 0.058 | 0.066 ^l |
| 19 | Bonga | 2.57 | 4.044 ^c | 0.743 ^d | 28.978 ^j | 0.730 | 0.026 | 0.809 ^l |
| 20 | Mulletts | 2.67 | 2.454 ^c | 0.709 ^d | 28.479 ^j | 0.471 | 0.025 | 0.491 ^l |
| 21 | Grunts | 3.18 | 0.141 ^c | 0.673 ^d | 9.712 ^j | 0.617 | 0.069 | 0.0282 ^l |
| 22 | Tilapias | 2.03 | 0.202 ^c | 0.737 ^d | 33.926 ^j | 0.518 | 0.022 | 0.0404 ^l |
| 23 | Small Benthicfeeders | 2.35 | 0.69 | 1.997 ^g | 19.887 ^g | 0.28 ^j | 0.100 | 0 |
| 24 | Shrimps | 2.53 | 3.16 | 4.605 ^h | 22 ^h | 0.405 ^j | 0.209 | 0.632 ^l |
| 25 | Crabs | 2.74 | 3.99 | 2.5 ^h | 8.5 ^h | 0.26 ^j | 0.294 | 0 |
| 26 | Macrobenthos | 2 | 59.56 | 1.2 ^h | 10 ^h | 0.8 ^a | 0.120 | 0 |
| 27 | Meiobenthos | 2.12 | 8.29 | 4 ^h | 50 ^h | 0.8 ^a | 0.080 | 0 |
| 28 | Zooplankton | 2.05 | 4.55 | 50 ^h | 150 ^h | 0.8 ^a | 0.333 | 0 |
| 29 | Phytoplankton | 1 | 14.43 | 138 ^h | – | 0.5 ^k | – | 0 |
| 30 | Microphytobenthos | 1 | 27.97 | 15 ^h | – | 0.5 ^k | – | 0 |
| 31 | Detritus | 1 | 1.00 | – | – | 0.323 | – | 0 |

^a Set under expert advice (Tito de Moraes, pers.comm.).

^b Calculated using birds counting (Tr  ca, 1996; Reynaud, pers. comm.).

^c Calculated using the estimated AI.

^d $P/B = Z + F + M$ (Allen, 1971) with $F = 0.2$ and M calculated using the Gislason formula (Gislason et al., 2008) (details of calculation in Coll  ter (2010)).

^e Gascuel et al. (2009).

^f Calculated using a broad set of data.

^g Villanueva et al. (2006).

^h Villanueva (2004).

^j Calculated using empirical equation (Palomares and Pauly, 1998).

ⁱ Set to obtain an $EE = 0.8$ in the 2006–2008 model (fixed biomass).

^k Vignot (2007).

^l Calculated with $F = 0.2$, $Y = F \times B$.

of $F = 0.1$ (low fishing effort) and $F = 0.4$ (high fishing effort) based on expert advice for the sensitivity analysis (Ecoutin, unpublished data).

The input of the initial data ended in an unbalanced model. The biomasses of five fish groups were adjusted considering that their catchability, q , initially set equal to 0.5 was not reflecting the actual situation. q was changed assuming lower values for mullets ($q = 0.4$, escape from the seine), mojarra ($q = 0.3$, escape from the seine), tilapias and tonguesole ($q = 0.2$, tilapias hiding in the mangroves and tonguesole, flatfishes, not easy to capture with a seine), and higher values for sea catfishes ($q = 0.7$, low swimming fish, easy to capture). A manual adjustment was preferred to automatic routines for the diet matrix (e.g. Kavanagh et al., 2004), since this balancing procedure itself gave us a better understanding of the structure of the network. These changes were made according to general knowledge on species biology and using a broad set of diet compositions, differing from a study to another aiming to obtain the best possible “picture” of the ecosystem network.

Relative impacts of each group on all others in the system were quantified using the mixed trophic impact (MTI) analysis (Ulanowicz and Puccia, 1990). They were used to highlight the expected effect of a fishery removal on the top predators and their preys. The MTI values corresponded to the effect of a relative catch augmentation of 1 unit.

2.4. Analysis of the MPA effect building of a mean Ecopath model for the years 2006–2008

From the 2003 Ecopath model, we derived a new Ecopath model representing the mean trophic functioning of the Bolong de Bamboung over the 2006–2008 period, two years after the closure of the fishery (see Table A3). We kept the general structure of the 2003 model using the same trophic groups and calculation for the input parameters. Fish biomasses changed using the estimated AI calculated from 2003 to 2008. We calculated mean values over the 2006–2008 period. P/B also changed. In the majority of the Ecopath models, this value is calculated under the Allen assumption $P/B = Z$ and so $P/B = M$ in a MPA case ($F = 0$). But a part of the production previously taken by the fishery is supposed to remain in the trophic network and also be predated in a MPA case. This led to a new sensitivity testing of the Ecopath models with three hypotheses for the P/B value:

- H_01 : an upholding of the 2003 P/B value assumed to be a biological characteristic of species independent of fishing or abundance. In such a case, steady state can be observed only if the decrease in the fishing mortality is assumed to be compensated by an increase in the natural mortality, mainly due to an increase in predators’ abundance.

- H₀2: a change in the P/B value considering the Allen assumption (Allen, 1971): $P/B = Z = M$ ($F = 0$). In such a case, M is assumed to be a biological characteristic of the species or groups independently of predators' abundances. Changes occurring in the fishing mortality of a group induce changes in its productivity P/B . In other words, like in a surplus production single-species model, a compensation effect does exist within the group allowing to maintain equilibrium ($P/B = Z$)
- H₀3 is the reference hypothesis. The P/B value is calculated using the "top-down equation" (Eq. (5)) proposed by (Gascuel et al., 2009). The P/B ratio of a group (considered as a prey) is:

$$(P/B)_{2008} = [(P/B)_{2003} - F_{2003}] \times \left[1 + \alpha \frac{\sum_{\text{pred } i} [(B_{2008} - B_{2003}) \times M_{2003}]}{\sum_{\text{pred } i} B_{2003} \times M_{2003}} \right] \quad (5)$$

where P/B is the production rate and F the fishing mortality of the (prey) group, B the biomass of predator, M the natural mortality applied by predators on the prey group, and α the top-down parameter defining the intensity of the top-down control that affects the prey groups. More precisely, α is a coefficient expressing the fraction of the natural mortality which depends on predator abundance; it may vary from 0 (no top-down control) to 1 (the natural mortality M is proportional to predators' abundance). Thus the ratio in the right part of the equation is a measure of the relative changes occurring in the biomass of all predators groups.

This reference hypothesis took into account two effects: changes occurring in the group productivity P/B in response to varying fishing pressure (i.e. intra-group regulation according to F), and changes in P/B according to predators' abundance (affecting an α fraction of the natural mortality). This last effect implies a top-down effect of predators on their preys. It was also used in the next step of our analysis, a MPA simulation on the Bannong using the EcoTroph model.

We had no biomass data for the invertebrates and primary producers in 2006–2008 like in 2003. Starting with given EE for these prey groups, the 2003 Ecopath model calculated the biomass required to feed predators. As a result, changing fish abundance in the 2006–2008 model with fixed EE s would let to artefactual results indicating the MPA may increase the primary or secondary production or biomass. We thus maintained the biomass of all invertebrates and primary producers unchanged between 2003 and 2006–2008 (i.e. assuming a constant primary and secondary production) and so estimated new EE s in the 2006–08 model according to the new abundance of predators' groups. Nevertheless, this reasoning may not hold when the top-down effect of predators on preys is considered, using H₀3. The following procedure was used in that case:

- The 2006–2008 ecotrophic efficiencies EE s were estimated for all invertebrates and primary producers based on biomass assumed to be unchanged between 2003 and 2006–2008, using H₀1.
- Using these EE s, biomasses were re-estimated for all groups, based on H₀3 (i.e. adding to H₀1 the top-down effect on preys' groups).

We also calculated Ecopath ecosystem indices and compared the 2003 and 2006–2008 models. The calculated total system throughput (TST) is the sum of all flows in a system. It represents the "size of the entire system in terms of flow" (Ulanowicz, 1986). The ratio of net system primary production to total respiration is a system maturity index (Odum, 1969). Values of this ratio near 1 indicate an ecosystem approaching maturity (Christensen et al., 2005). The system omnivory index (SOI) is computed as the average omnivory

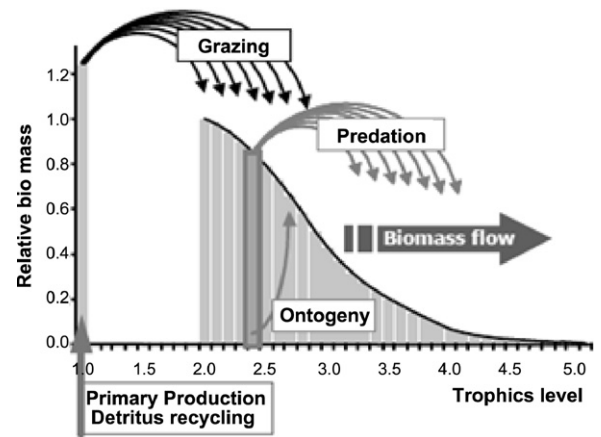


Fig. 2. Diagram of the trophic functioning of an ecosystem: theoretical distribution of the biomass by trophic level and trophic transfer processes, given an arbitrary input of biomass (fixed equal to 1 for TL = 2) (Gascuel and Pauly, 2009).

index of all consumers weighted by the logarithm of each consumer's food intake (Christensen et al., 2005). The connectance index (CI), a system maturity index, is the ratio of the number of actual links to the number of theoretically possible links between groups (Odum, 1969; Christensen et al., 2005). Energy and matter recycling is an important process within ecosystems (Odum, 1969). The Finn's cycling index (FCI) is the fraction of the TST that is recycled (Finn, 1976) and quantifies one of Odum's 24 properties of system maturity. This is similar to the predatory cycling index, which is calculated by excluding the cycling through detritus. The overhead reflects the energy in reserve of an ecosystem (Monaco and Ulanowicz, 1997).

2.5. Analysis of the MPA effect using EcoTroph

EcoTroph (ET) is a modelling software recently incorporated to the Ecopath plugins (Gascuel, 2005; Gascuel and Pauly, 2009). The first key idea of ET is that it deals with the continuous distribution of the biomass in an ecosystem as a function of continuous TL. The biomass enters the foodweb at TL 1, generated by the photosynthetic activity of primary producers, or recycled from the detritus by the microbial loop (Fig. 2). Then, at TLs > 2, the biomass is distributed along a continuum of values of TL, the diet variability of the various consumers usually resulting in all fractional TLs being filled. The second key feature of ET is that the trophic functioning of marine ecosystems is modeled as a continuous flow of biomass surging up the foodweb, from lower to higher TLs, through predation and ontogenic processes. Based on the traditional equations of fluid dynamics, the density of biomass at TL τ under steady-state conditions is expressed as (Eq. (6)):

$$D(\tau) = \frac{\Phi(\tau)}{K(\tau)} \quad (6)$$

where $\Phi(\tau)$ is the biomass flow, which refers to the amount of biomass that moves up the foodweb through TL τ (expressed in tons per year), and $K(\tau)$ is the speed of flow, which quantifies the velocity of biomass transfers in the foodweb (expressed as the number of TLs crossed per year). As natural losses occur during trophic transfers (through non-predation mortality, respiration, and excretion), the biomass flow $\Phi(\tau)$ is a decreasing function. Adding to this negative natural trend, exploitation by fisheries can be considered a diversion of one part of the trophic flow (Eq. (7)):

$$\Phi(\tau + \Delta\tau) = \Phi(\tau) \exp[-(\mu_\tau + \varphi_\tau) \Delta\tau] \quad (7)$$

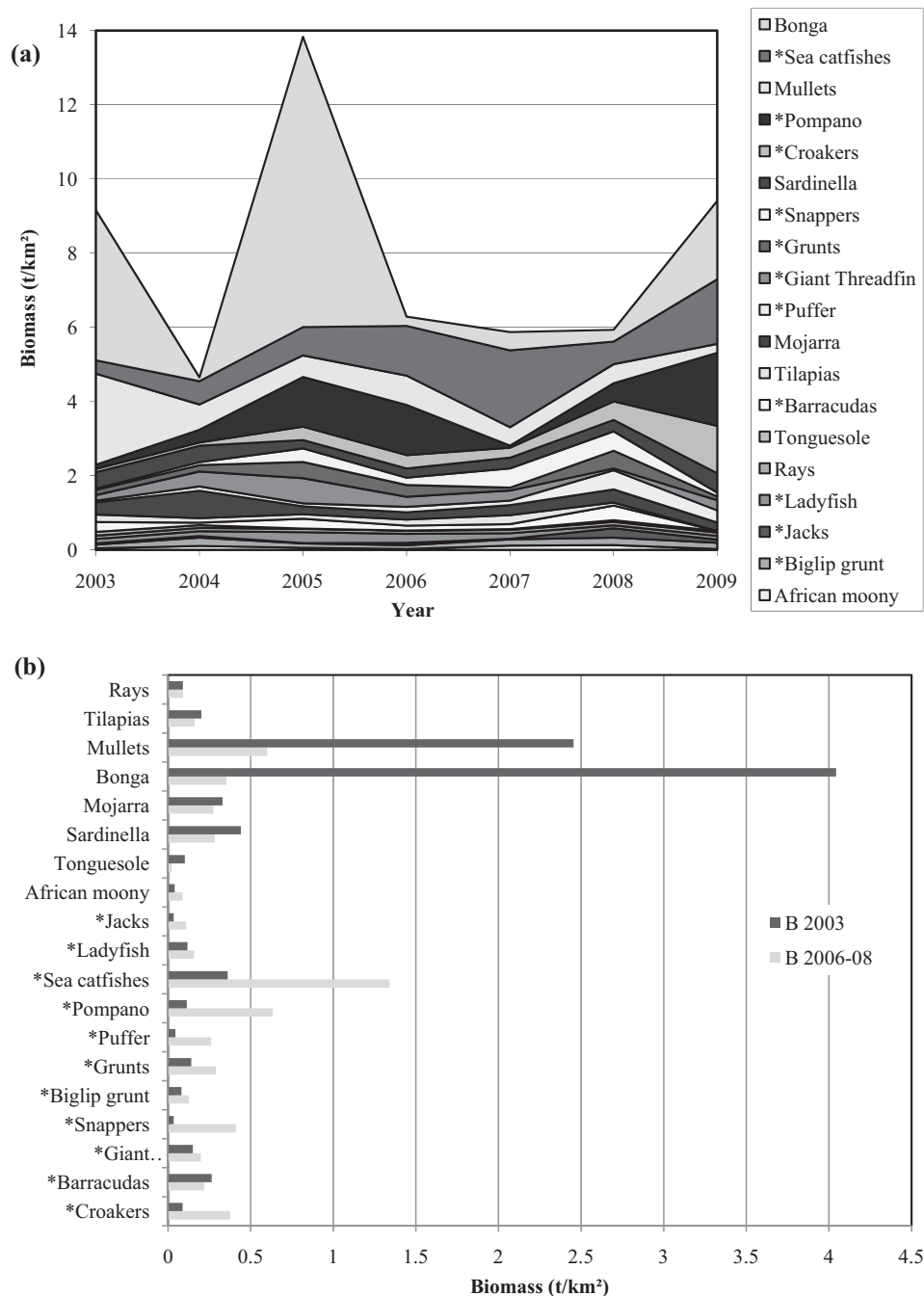


Fig. 3. (a) Stacked area chart of the biomass time series from 2003 to 2009 for the Ecopath fish groups. The groups with a star (*) correspond to the “predators”. (b) Bar chart of the estimated biomass for the Ecopath fish groups in 2003 and 2006–08. The groups with a star (*) correspond to the “predators”.

where μ_τ is the mean rate of natural loss of biomass flow within the trophic class, and φ_τ is the mean rate of loss of biomass flow attributable to fishing (Gascuel and Pauly, 2009).

We used two ET tools based on these key ideas, ET-Transpose and ET-Diagnosis. The first one enabled us to create trophic spectra, a graphical representation of the Ecopath parameters along the trophic level (described in detail in [Gascuel et al., 2009]). We compared the biomass, catch and production trophic spectra (BTS, CTS and PTS) from the 2003 and 2006–2008 Ecopath models. We performed a sensitivity analysis considering the two methods used to estimate the AI and the different hypotheses made on F and P/B. We then used the new version of ET-Diagnosis based on two distinct kinetics, for the whole ecosystem biomass and for the accessible

biomass to fishery only (Gascuel et al., 2011). It allows the simulation of various fishing impacts on the trophic spectra, relying on a few elementary and robust assumptions (Gascuel et al., 2009, 2011; Gasche et al., 2012). Using the 2003 model as a base, we simulated a partial or total closure of the fishery with different effort multipliers (mF) ranging from $mF=0$ (total closure) to $mF=1$ (unchanged fishery). We then compared these simulations to the observed trophic spectra from the 2006–2008 Ecopath model. Our aim was to detect if the observed changes could be related to a direct MPA effect, simulated by setting to 0 the fishing mortalities in the ET model. A sensitivity testing was also conducted over the top-down control parameter α used in the calculation of the P/B (H_03) and consequently in the biomass flow equation (see Gascuel et al., 2009).

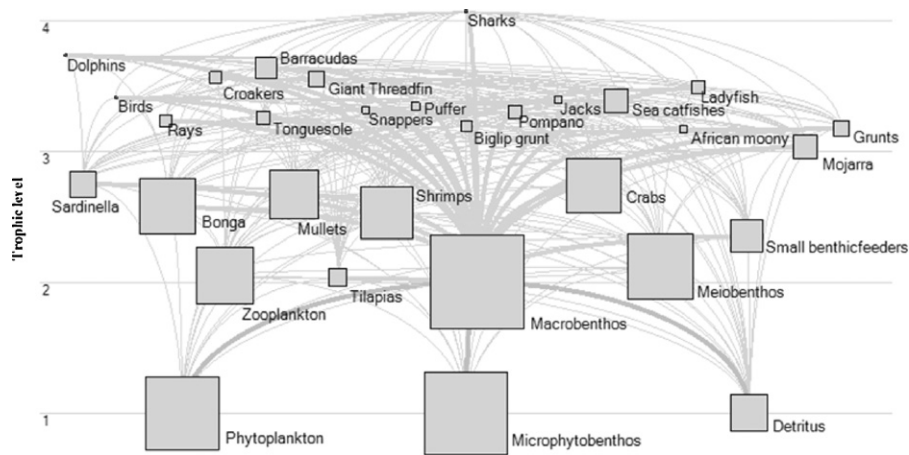


Fig. 4. Flow diagram of the balanced 2003 reference Ecopath model. The components of the ecosystem are structured along the vertical axis according to their trophic level (TL). Heavy colored lines indicate trophic links between predators and preys of the Macro-benthos, which has been identified as the main base of the trophic flows. The area of each rectangle is proportional to the biomass of each group.

Finally, these analyses were reversed considering the 2006–2008 model as a starting point and introducing a fishing mortality in order to simulate back the 2003 state.

2.6. Comparison between the MPA and a fished area

We constructed an Ecopath model of the Bolong de Sangako (see Section 2.1) for the 2008–2009 period (see Table A4). We calculated AI in the Sangako for the Ecopath groups defined in the Bamboung model, using data from 2008 to 2009 scientific surveys. We used simple means extrapolated to the whole Sangako surface from densities per seine surface and a catchability q (same principle as Eq. (2)). Indeed, the only two years of data prevented us to conduct a delta approach. Moreover the absence in the surveys of several species reduced the number of trophic groups to 26 (suppression of 5 groups). Biological parameters (M , Q/B) and diet were assumed the same as for the Bolong de Bamboung model. Based on expert knowledge and field observations (Ecotin, unpublished data), we assumed a global fishing mortality of 0.4 for the targeted groups.

The aim of this analysis was to compare the Bamboung with a high fished area and see if fishing can be considered as the main driver of the observed differences between these two areas. Trophic spectra of the Sangako and the different Bamboung models were compared using ET-Transpose. A final analysis was conducted using the ET-Diagnosis routine by applying to the 2003 Bamboung model a high fishing effort and comparing the results with the Sangako model.

3. Results

3.1. Estimation of yearly abundance indices (AI)

We found a year effect (with $p < 0.5$) for eighteen Ecopath fish groups on the nineteen groups of the Bamboung model. Only Rays had no year effect for both the probability of presence and the index of positive values. Their abundance was thus assumed constant. Conversely, the year effect was found highly significant ($p < 0.05$) for ten groups demonstrating biomass variations across the years. The season and sector factors had a significant effect on seventeen groups emphasizing the importance of the environmental variations in the population's distributions (see Table A5).

Focussing on the analysis of the yearly abundance indices (AI), different trends appeared for all the fish groups (Fig. 3a). Among the main groups, some showed clear increasing trends, as for instance the predator groups Croakers, Sea catfishes or Snappers. Other

like the prey group Mullet was decreasing. The Bonga exhibited year to year changes in abundance without any clear trend. However, during the 2006–2008 period, the total biomass seemed quite stable supporting the retaining of a mean value model. We decided to exclude 2009 as illegal fishing was reported. Probably resulting decrease trends were observed for predators (Barracudas, Grunts, Snappers, Puffers, Biglip grunt). This mean value model also enabled to smooth the year to year biomass variations linked to the sampling procedure and other effects as environmental ones. On the eight prey groups, six exhibited a decline in abundance between 2003 and the 2006–2008 period, one remained constant (Rays) and one increased (African moony) (Fig. 3b). On the eleven predator groups, ten showed an increase in biomass and one a small decrease (Barracudas).

The two sided Wilcoxon non parametric tests showed that the distributions of the bootstrapped 2003 and 2006–2008 AI differed by a location shift different from 0 with a highly significant probability (p -value < 0.05) for all the trophic groups except the Rays. This was logical as no year effect on the survey yields data has been found for this group. The differences observed between 2003 and the 2006–2008 period could so be considered as statistically significant.

3.2. Trophic network structure of the Bamboung in 2003

The Ecopath mass-balanced model provided estimates for all groups (biomass, mean TL, see Table 1), and a general scheme of the trophic network (Fig. 4). The calculated TLs varied between 1 and 4.07, with higher values for the Sharks, Dolphins, Croakers, Barracudas, and Giant Threadfin groups ($TL > 3.5$), the top predators. The importance of the flows decreased with increased TL, emphasizing the importance of the primary production and the secondary consumers. Benthic chains (from Macro- and Meio-benthos) appeared at the trophic base of the entire ecosystem whereas the planktonic chains appeared quite weak (Fig. 4).

The specific influence of the fishery on two predators and some of their preys was highlighted using MTI (Fig. 5). Sardinella and Mojarra underwent a negative predation impact from the Giant Threadfin itself strongly impacted by the fishery (a relative catch augmentation of 1 unit led to a relative decrease by half of the Giant Threadfin biomass). Consequently, even if the Sardinella and the Mojarra were fished, the augmentation of the fleet had a weak but positive impact on them. These trends were present in several cases indicating possible fishery closure effects: an important biomass

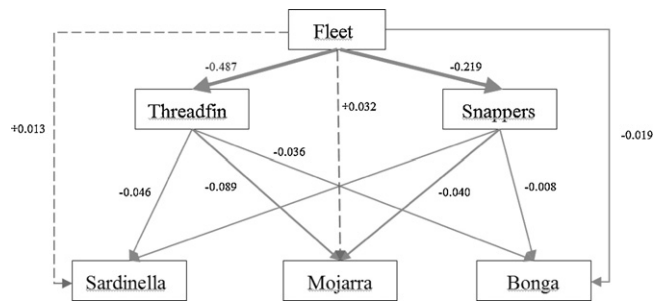


Fig. 5. Diagram of the mixed trophic impact (MTI) focussing on the influence of the fishery on two predators and three of their preys. The dashed lines correspond to positive effect and the full ones to negative effects. The widest lines correspond to strong effects (>0.1) (values are given next to them).

increase in predators and a possible decrease in their preys as the result of a top-down effect.

3.3. Analysis of the MPA effect in the Bolong of BAMBONG

Biomass trophic spectra (BTS) built from the two reference Ecopath models in 2003 and 2006–2008 highlighted the main differences before and after the closure of the fishery. An increase by a factor 2.5 in the predator biomass (mean of $3.2 < TL < 4.2$) and a decrease by a factor 1.7 in the prey biomass (mean of $2.4 < TL < 2.9$) were observed (Fig. 6). As a result, the total biomass remained more or less the same (Table 2).

The trophic spectrum simulating the removal of the fishery in 2003 showed patterns quite different to those observed in 2006–2008. The simulated increase at the high TLs (3.2–4.2) was lower than observed in the actual data. The fishing mortality withdrawal was not sufficient to explain all the observed increase in predators' biomass. An important gap remained between the simulation and the observation also for intermediate TLs (2.4–2.9). The simulation was really close to the situation in 2003 with a very slight increase in biomass, whereas the biomass decreased more than twice in the observed data (Fig. 6). It showed that the release of the fishing pressure seemed to be more or less compensated by the increase in predators' abundance due to the fishing closure. This indicated that changes in the fishing mortalities due to the closure of the fishery were not the only driver of the biomass variations between the two periods. Abundances observed in 2006–2008 could also result from behavioural effects and/or environmental changes not linked to the MPA. These aspects are considered below in the discussion section.

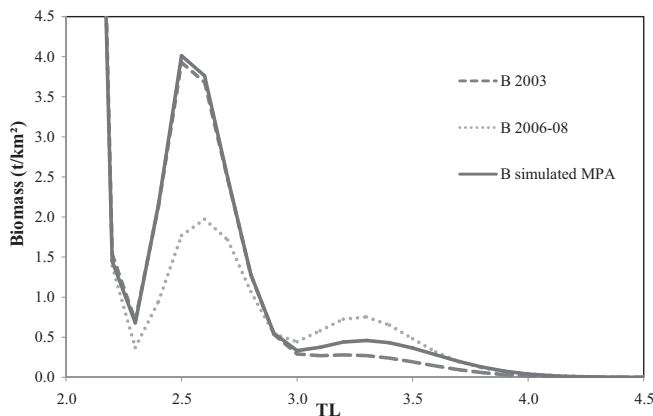


Fig. 6. Biomass trophic spectra (BTS) of the 2003 and 2006–2008 reference Ecopath models, and of the simulated MPA starting from the 2003 reference situation (2003 represented using a dashed line, 2006–2008 a pointed line and the simulation a full one).

Table 2

Summary statistics and network flow indices of the two reference models for the years 2003 and 2006–2008.

| Parameter | 2003 | 2006–2008 |
|--|-------|-----------|
| Sum of all consumption | 2030 | 1818 |
| Sum of all exports | 1151 | 1207 |
| Sum of all respiratory flows | 1260 | 1114 |
| Sum of all flows into detritus | 1697 | 1728 |
| Total system throughput (TST) | 6138 | 5867 |
| Sum of all production | 2773 | 2659 |
| Calculated total net primary production | 2411 | 2321 |
| Total primary production/total respiration | 1.914 | 2.083 |
| Net system production | 1151 | 1207 |
| Total primary production/total biomass | 18.29 | 18.22 |
| Total biomass/total throughput | 0.021 | 0.022 |
| Total biomass (excluding detritus) | 131.8 | 127.4 |
| Connectance Index | 0.337 | 0.337 |
| System Omnivory Index | 0.146 | 0.154 |
| Mean trophic level | 1.77 | 1.77 |
| Mean trophic level of fishes | 2.73 | 3.13 |
| Predatory cycling index | 1.40 | 1.48 |
| Finn's cycling index | 3.54 | 3.66 |
| Finn's mean path length | 2.5 | 2.5 |
| Ascendency | 25.5 | 27.2 |
| Overhead | 74.5 | 72.8 |

3.4. Sensitivity testing

The different fishing hypotheses showed a very weak impact on the 2003 Ecopath models BTS with a maximum difference of 5% ($TL = 2.4$, increase for $F = 0.4$) explained by the estimated biomasses. The different P/B calculation hypotheses showed also a very weak impact on the 2006–2008 models BTS with differences only for the intermediate trophic levels explained by the biomasses estimated in the reference 2006–2008 model (P/B EcoTroph, H_03) (Fig. 7a).

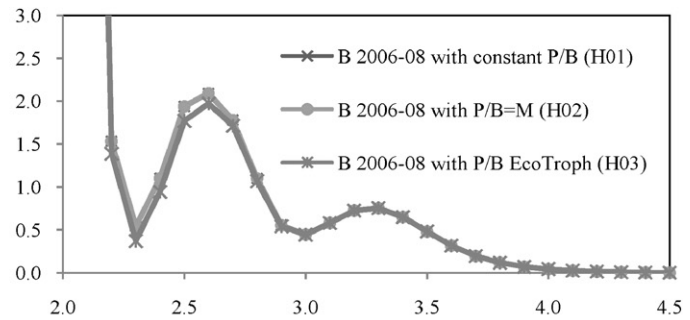
Considering the two AI calculations, the results obtained by comparison between the 2003 and 2006–2008 models for the second choice (only highly significant year effects retained) were not similar quantitatively: a 1.4 fold increase (2.5 in the reference model; see Section 3.3) in the predator biomass and a 1.7 fold decrease in the prey biomass (same in the reference model) (Fig. 7b). The second model thus reflected more precautionary conclusions indicating weaker effects of the fisheries closure on the high TLs. It has to be considered as the minimum demonstrated changes.

The BTS simulating the implementation of an MPA in 2003 showed that patterns induced by the fishing closure were quite similar whatever the AI estimation method was. In both cases, the simulated biomass remained almost stable for the intermediate TLs whereas the observed ones decreased. But the simulation was changed for the high TLs. The second AI estimation choice showed that the ET simulation explained more than the observed 1.4 fold increase in biomass. This is explained by the weaker biomass increase between 2003 and 2006–2008 (more precautionary model), the higher level of predator biomass in 2003, and so a stronger impact of the simulated fishery closure.

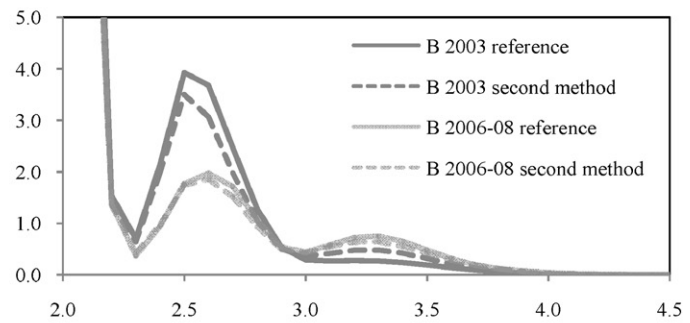
The sensitivity testing based upon the fishing mortality F hypotheses formulated in 2003 in the reference model showed that the closest simulation for the high TLs was obtained with a total closure of the fishery ($mF = 0$) for all the fishing hypotheses (Fig. 7c). The simulation was not qualitatively modified: the simulated fishery closure explained partially the biomass increase for the high TLs and not the decrease for the intermediate ones. However, the simulation for the predators was sensitive to this parameter. The high F hypothesis seemed to better fit to the 2006–2008 model but was not realistic. This emphasized the importance of the fishery withdrawal as a driver of the biomass variations. But we could not reject the impact of other effects.

The sensitivity testing on the top-down parameter α confirmed the existence of other effects inducing the biomass changes

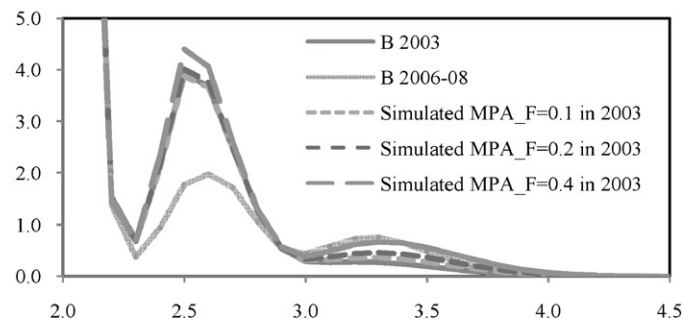
(a) Model sensitivity to the P/B hypotheses in 2006-08



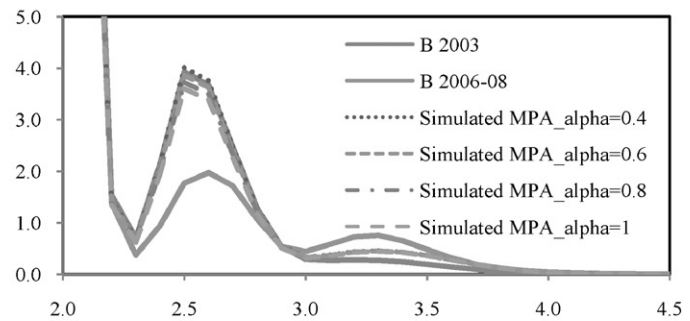
(b) Model sensitivity to the abundance indices calculation method



(c) Simulation sensitivity to the fishing hypotheses in 2003



(d) Simulation sensitivity to the Top-Down parameter α



(e) Reverse analysis

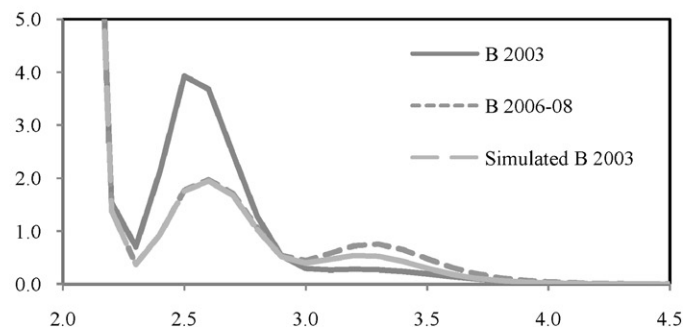


Fig. 7. Biomass trophic spectra (BTS) constituting the sensitivity testing. Each parameter is taken separately. Abscises of the graphs are the trophic level and the y-axis the biomass (in tons per km²).

(Fig. 7d). The different BTS obtained by increasing the value of the α parameter, and so the importance of the top-down effect in the trophic flows (Gascuel et al., 2009), showed that the simulation was only slightly improved for the intermediate TLs. Even with $\alpha = 1$, the simulated decrease for the intermediate TLs was really not sufficient to explain the observed one.

This analysis showed that the simulation model was sensitive to two parameters, the fishing hypothesis in 2003 and the AI estimation. The various calculations of P/B and α had a weak influence on the results. The final conclusion was not changed by these sensitivity tests, the observed variations in biomass for the intermediate and high TLs were not totally explained by the closure of the fishery.

The reverse analysis, starting from the different 2006–2008 models and applying a fishing mortality of 0.2, indicated the same conclusion (Fig. 7e). The reference simulation showed a biomass decrease for the high TLs but not important enough to reach the 2003 observed situation; and a stationary situation for the intermediate TLs not reflecting the observed biomass increase. This confirmed that the biomass decrease of the predators, starting from the high values observed in 2006–2008, could not explain the biomass increase of the preys.

3.5. Analyses of the Ecopath indices

We used the ecosystem indices estimated by Ecopath to compare the 2003 and the 2006–2008 models (Table 2). The calculated total system throughput (TST) was the imprint in both models of a highly productive tropical coastal ecosystem compared to other models of this type from the literature like the small Chiku tropical lagoon (TST = 158 t km⁻² year⁻¹, Taiwan [Lin et al., 1999]), the Laguna de Rocha (451 t km⁻² year⁻¹, Uruguay [Milessi et al., 2010]), the Golfo Dulce, a tropical Pacific fjord (1404 t km⁻² year⁻¹, Costa Rica, [Wolff et al., 1996]). The values were in the range of the one found for another highly productive African tropical coastal ecosystem, the Ebrié lagoon (6240 t km⁻² year⁻¹, Ivory Coast [Villanueva et al., 2006]). The slight decrease of the total biomass due to the important decline of the preys explained the difference observed between 2003 and 2006–2008 TST. The mean trophic level of the ecosystem remained constant after the fishing closure, but the mean trophic level of the fishes increased by 0.4 due to a higher proportion of predators. The System Omnivory Index (SOI) also slightly increased reflecting a more complex trophic structure. The Connectance Index (CI) remained constant. According to Christensen et al. (2005), a system primary production/respiration ratio near 1 indicates an ecosystem approaching maturity (Odum, 1969). Comparing the values obtained in each model, the ecosystem was less mature in 2006–2008 than in 2003. The FCI calculated were outside the range of values defined for coastal ecosystems (4.0 and 15.0% [Heymans and Baird, 2000]) but the increase between 2003 and 2006–2008, as the increase of the predatory cycling index, suggested a trend towards a more mature ecosystem. The high value of the overhead showed an important theoretical possibility to create new relations between the trophic groups and also to support perturbations. The decrease of its value between 2003 and 2006–2008 could be explained by a not yet stabilized state for the ecosystem.

3.6. Comparison Bamboung/Sangako

In the Sangako, the number of groups was less important with the absence of the top predators Sharks, Dolphins, Threadfins and Croakers (see Table A4). The mean trophic level is slightly lower by 0.01 in comparison to the Bamboung model in 2003. The comparison between the two ecosystems BTS showed that we had a low biomass level in the fished area in comparison with the Bamboung even in 2003, a year before the closure of the fishery (Fig. 8).

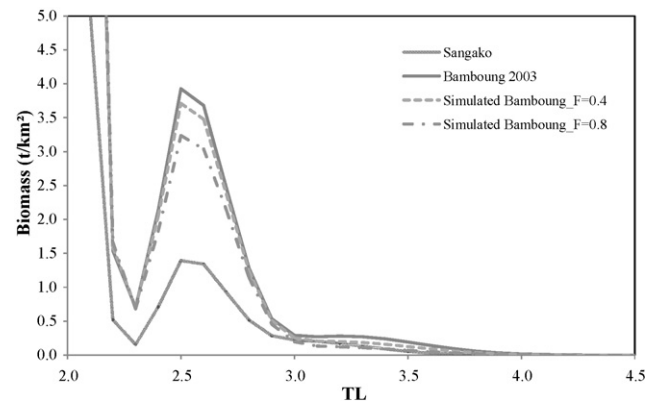


Fig. 8. Biomass trophic spectra (BTS) of the 2003 Bamboung reference model, the reference Sangako model, and of the simulated increase in fishery starting from the 2003 reference situation.

Simulations using the ET-Diagnosis procedure showed that these differences between ecosystems may not be due only to a direct fishing effect. Applying different mF to the 2003 Bamboung reference model, simulations based on fishing mortalities of $F = 0.4$ (Sangako reference F hypothesis) and $F = 0.8$ (very high fishing effort) showed that low biomass such as the ones observed in the Sangako could not be simulated (Fig. 8). There was always a remaining gap for the intermediate TLs and also for the high ones. We established the same conclusions considering the reverse simulation analysis considering a closure of the fishery in the Sangako. The simulated MPA had still very low biomass levels practically equal to the ones observed initially. Abundances observed in the Sangako and the Bamboung could result from behavioural effects and/or environmental changes not linked to the MPA. These aspects are discussed below.

4. Discussion

4.1. Trophic functioning of the Bolong de Bamboung MPA ecosystem

This modelling approach provided some useful insights into the trophic structure and functioning of the Bolong de Bamboung MPA. As in any Ecopath model, the results and their uncertainty strongly depend on the input data. We only had one year of data for the pre-MPA period. It was a shame but such a dataset with before and after data is rare. We had to make a strong hypothesis: 2003 had to be taken as the representative state of the Bamboung before the implementation of the MPA. This is a source of uncertainty counterbalanced by the high validity of the AI calculated using 12 sampling stations on a small area. We also developed a bootstrap method to compare the AI obtained in 2003 and 2006–2008. This method strengthened our results by showing significant differences between the two periods and a robust AI estimation. The model we developed so constitutes a good snapshot of the state and changes of the ecosystem. The biomass information was collected on the field following a strict survey plan between 2003 and 2009. Moreover, the development of another Ecopath model (Villanueva, 2004), based also on field study and for the entire Sine-Saloum, gave us the possibility when data were not available for the small Bamboung area to use parameters calculated for the same global ecosystem (K and L_{inf} used in the natural mortality M calculation, the diet matrix and the definition of some groups). However the lack of biomass information for some groups, mostly invertebrates, constrained us to use conventionally estimate EE and so let the model estimate the biomasses. Considering the role of the benthic compartment as a main flow source in this estuarine ecosystem (Diouf, 1996), this is a source of uncertainty that need to be

examined in the future by field studies to improve the quality of the model. Thus the biomass estimated by the model and representing at the present time the needs of the predators could be corrected and give some new insights into the trophic functioning. The fact that benthic chains (from macro- and meio-benthos) appeared at the trophic base of the entire ecosystem whereas the planktonic chains appeared quite weak was not surprising. The MPA is indeed located in a mangrove area with rich, turbid waters and mud substrate. Allochthonous matter and detritus based recycling are, as in other estuaries, a main flow source for the ecosystem (Lobry et al., 2008; Nicolas, 2010).

The model was built as a closed ecosystem without any migrations inside or outside for any species. Migrations (trophic as well as ontogenic migrations) are known to take place in the estuary (Albaret, 1999) and it would be interesting to evaluate the movements of the fishes at all phases and so to improve the model, especially as the fish composition contains marine and estuarine species spending part of their life history outside the Bamboung. In fact, only a small part of the ichthyofauna can be considered as permanent residents in this study (Albaret and Simier, 2005). Furthermore, the fish home range size has implications for marine reserve function. It can also be affected directly by the reserve through relocation (Kramer and Chapman, 1999).

One of the interests of this study was to estimate the impact of the fishery in 2003 and its closure in 2004. As no data were available to estimate yield for each Ecopath groups in 2003, we had to consider a constant fishing mortality of 0.2. This value constituted a good compromise, representing about one fifth of the total mean yield per km² for the entire Sine-Saloum (Ecotin, unpublished data). This was especially consistent with the fact that the Bolong de Bamboung was known as a not much exploited area before the implementation of the MPA (Tito de Moraes, unpublished data). However, the real situation was surely different with a more or less important fishing pressure on the different targeted groups. This could be one of the explanations of the difference observed between the MPA simulation and the Ecopath model of the observed situation in 2006–2008 considering that the strength of the fishery on a species influences the speed of its reaction after the closure (Chateau and Wantiez, 2005). Nevertheless these simulations allowed us to bring to light a MPA effect that we will discuss hereafter.

4.2. Using trophic model as a tool to evaluate MPA effect

EcoTroph showed that the differences observed between the 2003 and the 2006–2008 Ecopath models were partly explained by the closure of the fishery. It indicated a direct MPA effect but also other effects intervening. We observed a rather constant total biomass but an increase of 150% of the predator biomass ($3.2 < TL < 4.2$) and a decrease of 40% of the prey biomass ($2.4 < TL < 2.9$) based on the reference model. These trends were consistent with the previous works made on the Bamboung fish population where an increase in the percentage of big fishes and a decrease of the microphages has been documented (Albaret and Simier, 2005). However, the ET-Diagnosis simulation routine reproduced only partly the observations. The huge increase observed in predators' abundance, higher than the simulated one, suggested the entrance of new predators into the reserve, due to either a refuge effect from outside fisheries (e.g. Afonso et al., 2008; Eggleston and Parsons, 2008), or to a foraging arena effect, predators benefiting from unexploited preys within the MPA and adapting their movement relative to the location of resources (Ollason et al., 2006). Such a behavioural effect would represent approximately half of the observed increase in abundance, the other half being due to the removal of the fishing mortalities.

The observed decrease of the prey was also badly explained by the closure of the fishery. That was not surprising considering the recruitment fluctuations of the pelagic fishes constituting this box. The recruitment of the underlying species (especially the Bonga [*Ethmalosa fimbriata*], see Fig. 3a) is highly variable. The fishes spent a part of their life time in the sea and migrate towards the estuary for spawning. Reproduction occurs inside the estuaries but could also occur at sea (Charles-Dominique and Albaret, 2003). What's more this species is fished outside the MPA, in the sea and the Sine-Saloum (Deme et al., 2001). A direct MPA effect is logically not the only responsible for the observed biomass variations. Behavioural effects may perhaps also occur, preys taking off an MPA where predators' abundance is increasing (see Hammond et al., 2007). Moreover the top-down control could have been much more important than what we thought, explaining a part of the observed decrease for the prey groups. In our simulation, the biomass of these preys slightly increased (except assuming a low fishing effort in 2003 or a high top-down effect) showing that the closure of the fishery had a stronger impact than the increase in predation. This indicated one more time that the observed decrease of the preys resulted from other effects, especially an environmental one.

The sensitivity testing made on the AI calculation allowed us to validate a minimal MPA effect on the high TL with an increase of 40% of their biomass. In this case, the best ET simulation is obtained considering a remaining catch with a $F = 0.04$ and this implies poaching inside the MPA. It is known that poaching affects marine reserves by reducing the benefits inside and outside the MPA boundary (Sethi and Hilborn, 2008). However, the gap between the observed situation and the simulation at the intermediate TLs remained the same emphasizing the role of other effects in these changes and the influence of the fishery input data. This sensitivity testing showed that the reference method could overestimate the MPA effect. But even by retaining only the highly significant variations (second method), the observed changes are qualitatively the same: a constant total biomass, a biomass increase in predators and a decrease in preys. What's more, the differences in mean AI have been showed significant by a bootstrap method.

Meta-analyses made on several MPAs showed that they have positive effects on the biomass with an increase of around 450% (Lester et al., 2009). In our case we observed no global increase but a rather constant total biomass. This situation has already been documented, for example in Australia, where more big fishes were observed in the reserve and more small in the fished area but with no difference of total biomass (Edgar and Stuart-Smith, 2009). This reflects a change in the fish composition with the return of the predators and the decrease of the prey but with no influence on the total biomass. The global MPA effect we demonstrated is still a limited effect regarding the calculation made on the density, biomass and diversity in the MPAs literature (Gell and Roberts, 2003; Lester et al., 2009). This limited effect could be possibly due to several reasons:

- An already low fishing effort in 2003 explaining the limited reaction (see Chateau and Wantiez, 2005). In fact, the MPA has been implemented in cooperation with the local fishermen in an already low fished area.
- Poaching: a remaining F in 2006–2008 also validated by expert advice as illegal fishing has been observed in the MPA directed towards the catch of predator species. By catching a part of the increasing predator biomass, this practice could limit the observed MPA effect and reduce the expected benefits (Sethi and Hilborn, 2008).
- A partial compensation by an environmental effect, especially on the small pelagic fishes (climate effect on the recruitment [Oliveira and Stratoudakis, 2008; Zeeberg et al., 2008]). The variable recruitment could explain the very low biomass observed for

the 2006–2008 period and so explaining part of the simulation bias.

- A still short period of simulation. In fact, we considered a five years period but MPA effect could be longer to reveal, as for example the changes on the species richness described by (Dufour et al., 2007). The ecosystem is not yet mature (as shown by Ecopath network indices) and it could be necessary to follow the incoming developments to improve the MPA effect diagnostic. What's more, recent works suggest that indirect effects on taxa that occur through cascading trophic interactions take longer to develop than direct effects on targeted species (Babcock et al., 2010).

Then, the differences observed between the Bamboung and the Sangako were already very important in 2003, the fishing pressure not explaining all the process as we saw with the ET simulation. This could indicate two coupled effects on the fish behaviour that are not included in EcoTroph. In fact, it has been showed that the flight distance, i.e. distance at which an organism begins to flee an approaching threat, of fishes targeted by fishers differed between a MPA and a fished area (Feary et al., 2011) and so a possible flee effect. The same process can take place in the Sangako, a small area fished since a long time and where the fishes could have so fled. This could explain the very low biomass level in the Sangako and consequently the rather high one for the Bamboung. The effect could be the opposite for the Bamboung where the fishing was already low in 2003. We saw that the observed biomass increase for the predators does not result only from a local production and the reason could be a behavioural refuge effect inside this area. This effect could have been already partly effective in 2003, as explained by the already low fishing pressure and prey availability, and afterwards strengthened by the implementation of the MPA. These effects are obviously hypothetical but could have played a role in the fish assemblage and the biomass variations observed in the two areas. These considerations open a discussion on the behavioural effects of a MPA, an aspect not much studied but obviously contributing to the MPA-induced changes in fish communities (Shumway, 1999). Furthermore the prey biomass in the Sangako was only slightly lower than that of the Bamboung in 2006–2008, and this low level was not explained by a high fishing effort. These considerations indicate one more time a possible environmental effect explaining an important part of the low prey biomass observed.

We endeavour to study the effect of the MPA inside but not outside the boundary. This is one of the aspects that also need to be developed considering the already proved benefits documented in the literature. The spill-over effect is characterized by a biomass or abundance gradient beginning at the MPA boundary and declining as a function of increasing distance (Millar and Willis, 1999; McClanahan and Mangi, 2000; Russ et al., 2003). It would be interesting to quantify this effect to see the benefits of the MPA for the local fishermen, especially as this effect has been showed quite weak in some studies (Valls et al., in press; Harmelin-Vivien et al., 2008). Another effect is the larval dispersion (Murawski et al., 2000; Botsford et al., 2006; Moffitt et al., 2009) that occurs in some species doing their reproduction in the estuary and so possibly in the MPA. No data are available but it would have been interesting to quantify the changes in the larvae abundance through the years and the implementation of the MPA. In fact, there is a remaining question, we proved a direct MPA effect considering the biomass increase of big fish, but could this effect be indirect and so concerns the reproduction and the larvae abundance.

Acknowledgements

We are grateful to the Senegalese team of the IRD that supports and helps this research: Oumar Sadio, Jean Raffray, François Sanse, Gaspard Bertrand and all the others. We also want to thank the researchers of the CRODT for their help in the construction of

the model and the supply of data, and the team of the *Pôle halieutique* of Agrocampus Ouest including the Fisheries science research team of the Agrocampus Ouest/INRA UMR "Ecologie et Santé des Ecosystèmes". Special thanks go to Sylvie Guénette, Lucile Mesnil-drey, Etienne Rivot, Olivier Le Pape and Laurène Jolly for their help at different levels of this study. This contribution was supported by an ANR project entitled AMPHORE and we want to thank the team of this project for their helpful comments. Lastly, we would like to thank the anonymous referees whose comments have greatly improved the quality of this work.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2012.01.019.

References

- Afonso, P., Fontes, J., Holland, K.N., Santos, R.S., 2008. Social status determines behaviour and habitat usage in a temperate parrotfish: implications for marine reserve design RID B-3960-2008. *Marine Ecology Progress Series* 359, 215–227.
- Albaret, J.-J. Les peuplements des estuaires et des lagunes, in: C. Lévêque, D. Paugy (Ed.), *Les Poissons Des Eaux Continentales Africaines: Diversité, Écologie, Utilisation Par L'homme*, Paris, 1999, pp. 355–379.
- Albaret, J.-J., 2003. Caractérisation de l'état de référence des peuplements de poissons d'une aire protégée en zone de mangrove: le bolon de Bamboung (Sine Saloum, Sénégal). Rapport de convention Narou Heuleuk/AFD/IRD, Dakar.
- Albaret, J.-J., Simier, M., 2005. Suivi biologique des peuplements de poissons d'une aire protégée en zone de mangrove: le bolon de Bamboung (Sine Saloum, Sénégal). Rapport final (Rapport de convention Narou Heuleuk/AFD/IRD), Dakar.
- Allen, K.R., 1971. Relation between production and biomass. *Journal of the Fisheries Research Board of Canada* 28, 1573–1581.
- Babcock, R.C., Shears, N.T., Alcala, A.C., Barrett, N.S., Edgar, G.J., Lafferty, K.D., McClanahan, T.R., Russ, G.R., 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proceedings of the National Academy of Sciences* 107, 18256–18261.
- Baran, E., 2000. Biodiversity of estuarine fish faunas in West Africa. *Naga, The ICLARM Quarterly* 23, 4–9.
- Bauer, D.F., 1972. Constructing confidence sets using rank statistics. *Journal of the American Statistical Association* 67, 687–690.
- Botsford, L.W., Micheli, F., Parma, A.M., 2006. Biological and ecological considerations in the design implementation and success of MPAs. In: *FAO Expert Workshop on Marine Protected Areas and Fisheries Management: Review of Issues and Considerations*, pp. 109–148.
- Charles-Dominique, E., Albaret, J.-J., 2003. African shads, with emphasis on the West African shad *Ethmalosa fimbriata*. *American Fisheries Society Symposium* 35, 27–48.
- Chateau, O., Wantiez, L., 2005. Comparison of coral reef fish communities between two fished and one protected reefs in New Caledonia South Lagoon Marine Park. *Cybiurn* 29, 159–174.
- Christensen, V., Walters, C.J., 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* 172, 109–139.
- Christensen, V., Walters, C.J., Pauly, D., 2005. *Ecopath With Ecosim: A User's Guide*. Fisheries Centre, University of British Columbia, Vancouver, BC, Canada.
- M. Colléter, Analyse de l'impact d'une Aire Marine Protégée (AMP) sur le fonctionnement trophique d'un écosystème: Modélisation Ecopath/EcoTroph de la réserve du bolong de Bamboung, Sénégal (Mémoire de fin d'études, Spécialisation halieutique d'Agrocampus Ouest), 2010.
- Constanza, R., D'Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., Van de Belt, M., 1997. The value of the world's ecosystem services and natural capital. *Nature* 387, 253–260.
- Deme, M., Diadhiou, H.D., Thiam, D., 2001. Effort de pêche, captures spécifiques et valeurs économiques des débarquements de la pêche continentale dans le fleuve Sénégal et au Sine Saloum. UICN, ISRA, Dakar.
- P.S. Diouf, Les peuplements de poissons des milieux estuariens de l'Afrique de l'Ouest: l'exemple de l'estuaire hyperhalin du Sine-Saloum, Thèse de Doctorat, 1996.
- Dufour, F., Guidetti, P., Francour, P., 2007. Comparaison des inventaires de poissons dans les aires marines protégées de Méditerranée: influence de la surface et de l'ancienneté. *Cybiurn* 31, 19–31.
- Edgar, G.J., Stuart-Smith, R.D., 2009. Ecological effects of marine protected areas on rocky reef communities—a continental-scale analysis. *Marine Ecology Progress Series* 388, 51–62.
- Efron, B., Tibshirani, R.J., 1993. An introduction to the bootstrap. In: *Monographs on Statistics and Applied Probability*. Chapman & Hall/CRC, Boca Raton, London, New York, Washington, D.C.
- Eggleston, D.B., Parsons, D.M., 2008. Disturbance-induced spill-in of Caribbean spiny lobster to marine reserves. *Marine Ecology Progress Series* 371, 213–220.
- Feary, D.A., Cinner, J.E., Graham, N.A.J., Januchowski-Hartley, F.A., 2011. Effects of customary marine closures on fish behavior, spear-fishing

- success, and underwater visual surveys. *Conservation Biology* 25, 341–349.
- Finn, J.T., 1976. Measures of ecosystem structure and function derived from analysis of flows. *Journal of Theoretical Biology* 56, 363–380.
- Froese, R., Binohlan, C., 2000. Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. *Journal of Fish Biology* 56, 758–773.
- Froese, R., Pauly, D., 2010. A Global Information System on Fishes, Fishbase., <http://www.fishbase.org>.
- Gasche, L., Gascuel, D., Shannon, L., Shin, Y.-J., 2012. Global assessment of the fishing impacts on the Southern Benguela ecosystem using an EcoTroph modelling approach. *Journal of Marine Systems* 90, 1–12.
- Gascuel, D., 2005. The trophic-level based model: a theoretical approach of fishing effects on marine ecosystems. *Ecological Modelling* 189, 315–332.
- Gascuel, D., Guénette, S., Pauly, D., 2011. The trophic-level-based ecosystem modelling approach: theoretical overview and practical uses. *ICES Journal of Marine Science* 68, 1403–1416.
- Gascuel, D., Hénichart, L.-M., 2011. Etude sur l'état de l'art du rôle des AMP dans la gestion des pêches, Rapport technique, "Volet Bio-écologie" (Rapport société BRL Ingénierie). Agence Française de Développement (AFD) et Commission Sous Régionale des Pêches (CSR/P), Nîmes.
- Gascuel, D., Pauly, D., 2009. EcoTroph: modelling marine ecosystem functioning and impact of fishing. *Ecological Modelling* 220, 2885–2898.
- Gascuel, D., Tremblay-Boyer, L., Pauly, D., 2009. EcoTroph (ET): A Trophic Level Based Software for Assessing the Impacts of Fishing on Aquatic Ecosystems. Fisheries Centre Research Reports 17.
- Gell, F.R., Roberts, C.M., 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in Ecology & Evolution* 18, 448–455.
- Gislason, H., Pope, J.G., Rice, J.C., Daan, N., 2008. Coexistence in North Sea fish communities: implications for growth and natural mortality. *ICES Journal of Marine Science* 65, 514–530.
- Guillard, J., 1998. Daily migration cycles of fish populations in a tropical estuary (Sine-Saloum, Senegal) using a horizontal-directed split-beam transducer and multibeam sonar. *Fisheries Research* 35, 23–31.
- Halpern, B.S., Warner, R.R., 2002. Marine reserves have rapid and lasting effects. *Ecology Letters* 5, 361–366.
- Hammond, J.I., Luttbeg, B., Sih, A., 2007. Predator and prey space use: dragonflies and tadpoles in an interactive game. *Ecology* 88, 1525–1535.
- Harmelin-Vivien, M., Le Diréach, L., Bayle-Sempere, J., Charbonnel, E., García-Charton, J.A., Ody, D., Pérez-Ruzafa, A., Reñones, O., Sánchez-Jerez, P., Valle, C., 2008. Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: evidence of fish spillover? *Biological Conservation* 141, 1829–1839.
- Heymans, J.J., Baird, D., 2000. Network analysis of the northern Benguela ecosystem by means of NETWORK and ECOPATH. *Ecological Modelling* 131, 97–119.
- Kavanagh, P., Newlands, N., Christensen, V., Pauly, D., 2004. Automated parameter optimization for Ecopath ecosystem models. *Ecological Modelling* 172, 141–149.
- Kramer, D., Chapman, M., 1999. Implications of fish home range size and relocation for marine reserve function. *Environmental Biology of Fishes* 55, 65–79.
- Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenko, J., Ruttenberg, B.I., Gaines, S.D., Airamé, S., Warner, R.R., 2009. Biological effects within no-take marine reserves: a global synthesis. *Marine Ecology Progress Series* 384, 33–46.
- Lin, H.-J., Shao, K.-T., Kuo, S.-R., Hsieh, H.-L., Wong, S.-L., Chen, I.-M., Lo, W.-T., Hung, J.-J., 1999. A trophic model of a sandy barrier lagoon at Chiku in Southwestern Taiwan. *Estuarine, Coastal and Shelf Science* 48, 575–588.
- Lobry, J., David, V., Pasquaud, S., Lepage, M., Sautour, B., Rochard, E., 2008. Diversity and stability of an estuarine trophic network. *Marine Ecology Progress Series* 358, 13–25.
- Longhurst, A., 1957. The food of the demersal fish of a West African estuary. *The Journal of Animal Ecology* 26, 369–387.
- McClanahan, T.R., Mangi, S., 2000. Spillover of exploitable fishes from a Marine Park and its effect on the adjacent fishery. *Ecological Applications* 10, 1792–1805.
- Milessi, A.C., Danilo, C., Laura, R.-G., Daniel, C., Javier, S., Rodríguez-Gallego, L., 2010. Trophic mass-balance model of a subtropical coastal lagoon, including a comparison with a stable isotope analysis of the food-web. *Ecological Modelling* 221, 2859–2869.
- Millar, R.B., Willis, T.J., 1999. Estimating the relative density of snapper in and around a marine reserve using a log-linear mixed-effects model. *Australian & New Zealand Journal of Statistics* 41, 383–394.
- Moffitt, E.A., Botsford, L.W., Kaplan, D.M., O'Farrell, M.R., 2009. Marine reserve networks for species that move within a home range. *Ecological Applications* 19, 1835–1847.
- Monaco, M.E., Ulanowicz, R.E., 1997. Comparative ecosystem trophic structure of three U.S. mid-Atlantic estuaries. *Marine Ecology Progress Series* 161, 239–254.
- Mosquera, I., Côté, I.M., Jennings, S., Reynolds, J.D., 2000. Conservation benefits of marine reserves for fish populations. *Animal Conservation* 3, 321–332.
- MSFD EU, Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy, 2008.
- Murawski, S.A., Brown, R., Lai, H.L., Rago, P.J., Hendrickson, L., 2000. Large-scale closed areas as a fishery-management tool in temperate marine systems: The Georges Bank experience. *Bulletin of Marine Science* 66, 775–798.
- Murawski, S.A., Wigley, S.E., Fogarty, M.J., Rago, P.J., Mountain, D.G., 2005. Effort distribution and catch patterns adjacent to temperate MPAs. *ICES Journal of Marine Science* 62, 1150–1167.
- Nicolas, D., Des poissons sous influence? Une analyse à large échelle des relations entre les gradients abiotiques et l'ichtyofaune des estuaires tidaux européens, Thèse pour l'obtention du grade de docteur en écologie aquatique, 2010.
- Odum, E.P., 1969. The strategy of ecosystem development. *Science* 164, 262–270.
- Oliveira, P.B., Stratoudakis, Y., 2008. Satellite-derived conditions and advection patterns off Iberia and NW Africa: potential implications to sardine recruitment dynamics and population structuring. *Remote Sensing of Environment* 112, 3376–3387.
- Ollason, J.G., Yearsley, J.M., Liu, K., Ren, N., 2006. Modelling the behaviour of individuals and groups of animals foraging in heterogeneous environments. In: Boyd, I.L., Wanless, S., Camphuysen, C.J. (Eds.), *Top Predators in Marine Ecosystems: Their Role in Monitoring and Management*. *Conservation Biology* 12, 294–309.
- Pagès, J., Citeau, J., 1990. Rainfall and salinity of a Sahelian estuary between 1927 and 1987. *Journal of Hydrology* 113, 325–341.
- Palomares, M.L.D., Pauly, D., 1998. Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. *Marine & Freshwater Research* 49, 447–453.
- Panfili, J., Thior, D., Ecoutin, J.-M., Ndiaye, P., Albaret, J.-J., 2006. Influence of salinity on the size at maturity for fish species reproducing in contrasting West African estuaries. *Journal of Fish Biology* 69, 95–113.
- Le Pape, O., Chauvet, F., Mahévas, S., Lazure, P., Guérault, D., Désaunay, Y., 2003. Quantitative description of habitat suitability for the juvenile common sole (*Solea solea* L.) in the Bay of Biscay (France) and the contribution of different habitats to the adult population. *Journal of Sea Research* 50, 139–149.
- Pauly, D., 2002. Mass-Balance Trophic Models of West African Marine Ecosystems. SIAP, document technique (SIAP/EP/DT/03).
- Rababison-Andriamirado, G.A., Caveriviere, A., 1989. Les régimes alimentaires des prédateurs potentiels de la crevette *Penaeus notialis* au Sénégal. Place trophique des crevettes. Documents scientifiques CRODT 113.
- Russ, G.R., Alcalá, A.C., Maypa, A.P., 2003. Spillover from marine reserves: the case of *Naso vlamingii* at Apo Island, the Philippines. *Marine Ecology Progress Series* 264, 15–20.
- Sene, N., 1997. Contribution à l'étude qualitative du régime alimentaire de quelques poissons dans l'estuaire du Sine-Saloum. Documents scientifiques CRODT 142, Sénégal.
- Sethi, S.A., Hilborn, R., 2008. Interactions between poaching and management policy affect marine reserves as conservation tools. *Biological Conservation* 141, 506–516.
- Shumway, C., 1999. A neglected science: applying behavior to aquatic conservation. *Environmental Biology of Fishes* 55, 183–201.
- M. Simier, J.-M. Ecoutin, E. Ndiaye, Pechexp 2003: base de données RAP, Volet pêches expérimentales, Notice descriptive, IRD, 2003.
- Stefansson, G., 1996. Analysis of groundfish survey abundance data: combining the GLM and delta approaches. *ICES Journal of Marine Science* 53, 577–588.
- Sylla, M., Diop, M.S., 2006. Détermination des otolithes dans les fèces et les pelotes de régurgitation d'oiseaux piscivores au niveau de leurs principaux sites de reproduction au Sénégal, de la Gambie et de la Mauritanie.
- M. Thiaw, Les prédateurs ichtyophages de grande taille des milieux estuariens et lagunaires d'Afrique de l'Ouest: distribution, abondance, traits de vie, Mémoire de DEA, 2005.
- Tréca, B., 1996. Participation de l'ORSTOM au dénombrement international des oiseaux d'eau dans le delta du Sénégal.
- Ulanowicz, R.E., 1986. Growth and Development. *Ecosystem Phenomenology*. Berlin, Springer-Verlag.
- Ulanowicz, R.E., Puccia, C.J., 1990. Mixed trophic impacts in ecosystems. *Coenoses* 5, 7–16.
- Underwood, A.J., 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. *Journal of Experimental Marine Biology and Ecology* 161, 145–178.
- Valls, A., Gascuel, D., Guénette, S., Francour, P., Modeling trophic interactions to assess the potential effects of a marine protected area: a case study in the NW Mediterranean Sea, *Marine Ecology Progress Series*, in press.
- Vignot, C., 2007. Relations trophiques au sein des communautés de poissons d'un estuaire inverse d'Afrique de l'Ouest, le Sine Saloum au Sénégal (Mémoire de Master 2 Sciences de l'Univers, Environnement, Ecologie). Université Pierre et Marie Curie, Paris.
- Villanueva, M.C., Biodiversité et relations trophiques dans quelques milieux estuariens et lagunaires de l'Afrique de l'Ouest: adaptations aux pressions environnementales, Thèse de Doctorat, 2004.
- Villanueva, M.C., Lalèye, P., Albaret, J.-J., Laë, R., de Morais, L.T., Moreau, J., 2006. Comparative analysis of trophic structure and interactions of two tropical lagoons. *Ecological Modelling* 197, 461–477.
- White, J.W., Botsford, L.W., Moffitt, E.A., Fischer, D.T., 2010. Decision analysis for designing marine protected areas for multiple species with uncertain fishery status. *Ecological Applications* 20, 1523–1541.
- Wilcoxon, F., 1945. Individual comparisons by ranking methods. *Biometrics Bulletin* 1, 80–83.
- Wolff, M., Hartmann, H.J., Koch, V., 1996. A pilot trophic model for Golfo Dulce, a fjord-like tropical embayment, Costa Rica. *Revista de Biología Tropical* 44 (Suppl. 3), 215–231.
- WSSD, Plan de mise en oeuvre du Sommet Mondial pour le Développement Durable, paragraphe 32.c, Johannesburg, 2002.
- Zeeberg, J., Corten, A., Tjoe-Awie, P., Coca, J., Hamady, B., 2008. Climate modulates the effects of *Sardinella aurita* fisheries off Northwest Africa. *Fisheries Research* 89, 65–75.