

Implementation of artificial habitats: Inside or outside the marine protected areas? Insights from a mathematical approach



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ABSTRACT

At the world scale, many exploited species are currently threatened or undermined by human activities, particularly fishing. Given this situation, establishing artificial habitats (AHs) and marine protected areas (MPAs) is seen as a way of both conserving biodiversity and managing fishing activities. AHs have two main effects: (1) they attract fish from the surrounding areas and concentrate them in the AH, and (2) they increase the capacity of the environment, as a result of the installation of new individuals or, in some cases, of new species. MPAs decrease fish accessibility by constraining the spatial distribution of the fishing effort. We have developed a system of ordinary differential equations (ODEs) that can be used to describe the evolution of fish density, fishing effort, and landings depending on whether AHs are deployed in a MPA or in a fishing area. The analytical study of the ODE system is simplified by means of assuming that processes occur on different time scales. Fish reproduction and landings were assumed to occur at a “slow” time scale, whereas, fish displacement was assumed to occur at a “fast” time scale. For both scenarios of AHs implementation (in an MPA or in a fishing area), we show the existence of different equilibria according to hypotheses based on a purely attractive or purely productive effect of the AH. In all cases, the deployment of AHs in the fishing area leads to an equilibrium with lower fish biomass and lower fish landings than when AHs are deployed within the MPA. This suggests that AHs should not be fished in order to maximize long term fish productivity and fish landings in the surrounding areas. In addition, we attempt to establish a correspondence between our theoretical results and the management plan for artisanal fisheries on the Senegalese coast, which includes the implementation of both AHs and MPAs. This suggests that there is not enough coordination between the non-governmental organizations deploying the AHs and the institutions managing MPAs. Indeed, AHs are usually either immersed in an MPA or subject to local fishing ban, but in fact regulation is inadequate. In this context, the deployment of AHs as part of fisheries management would be premature and could have potentially adverse effects on the resource.

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1. Introduction

Coastal fish resources usually benefit artisanal fisheries, which is a major guarantee for the local food supply and local economy. In West Africa, climatic changes and economic collapse have both

reduced agriculture outcomes and increased unemployment, which have been offset by an increase in the number of people engaged in artisanal fishing. Furthermore, the lack of governance had led to increases in the granting of fishing licenses to the foreign industrial fishing fleet and in illegal fishing (Gagern and van den Bergh, 2013; Pala, 2013; Pauly et al., 2013). As a result, the coastal ecosystem of Senegal is facing serious stress due to falling fish abundance combined with an increasing demand at the local, regional, and world levels (Pauly et al., 2005; Thiao et al., 2012).

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This means that additional management efforts are required in order to prevent the collapse of the fisheries, which would threaten food security in West Africa.

Marine protected areas (MPAs) are now often a recommended tool for conservation and fishery management (e.g., Halpern, 2003). Indeed, fish biomass has been observed to increase in several effective MPAs and have benefited adjacent fisheries as a result of spill-over (Russ et al., 2004; McClanahan et al., 2006; Brochier et al., 2013), although there is still some controversy about whether these results can be extrapolated more generally or not (Agardy et al., 2011; Westhead et al., 2012; Kerwath et al., 2013). A number of studies have demonstrated the importance of MPA design for their effectiveness and their impact on adjacent fishery yields (e.g., Kaplan and Botsford, 2005). Theoretical models have also shown that the fishery catches in a given area can be expected to be maximized when part of this area is closed to fishing (Bensenane et al., 2013). Artificial habitats (AHs), also known as artificial reefs, have been extensively used for (1) the compensatory restoration of damage to natural resources (e.g., Bohnsack and Sutherland, 1985; Powers et al., 2003), (2) as an effective method of increasing fishery productivity (Kerwath et al., 2013), (3) providing additional recreational and commercial fishing opportunities for hard-substrate dependent fisheries, and (4) enhancing the foraging base of fish (Ditton et al., 2002; Stephens and Pondella, 2002). However, there is still some controversy among the scientific community about whether AHs function by producing more fish or simply by attracting existing fish into the AH (Bohnsack 1989; Grossman et al., 1997; Bortone, 1998; Powers et al., 2003; Osenberg, 2002; Claudet and Pelletier, 2004; Brickhill et al., 2005). It should be stressed that AHs establishment must be viewed as part of a concerted methodology using an eco-systemic and socio-systemic approach to sustainable fisheries enhancement (Pioch et al., 2011).

MPAs and AHs are spatial management tools that managers are keen to use to locally compensate for the increasing ecosystem stress and to ensure the sustainability of fisheries in addition to other measures such as seasonal fishery closure (also known as “biological rest”). Thus, the question arises of how MPAs and AHs must be combined for an efficient management. There is no straightforward answer since (1) installing AHs in MPAs could

offset MPA spill-over as a result of AHs “fish attractive effect” and subsequently reduce fishery yields by over-protecting the fish, whereas, (2) the deployment of AHs within fishing areas could enhance fish catchability, which may in turn also reduce fishery yields as a result of over-exploitation.

Particularly in Africa, it is often difficult to carry out field surveys especially when using sophisticated methods (e.g., Brehmer et al., 2003). Thus, we propose to shed a mathematical light on the question of how MPAs and AHs must be combined by studying the impacts of the antagonistic effects described above in the context of a simple model of fish population dynamics and associated fishery yields. The model used is generic enough to answer this general question. It relies on scientific knowledge translated into mathematical language in a set of ordinary differential equations describing the evolution of the fish population and the fishing effort. This approach enabled us to test the sensitivity of the results for a set of hypotheses concerning the attraction or production effect of the AHs.

We conclude the present study with an attempt to transpose the theoretical results obtained to a concrete case study of fishery management in Senegal. The question is of major relevance as artisanal fisheries make up an important part of the national economy. Artisanal fisheries operate from ports located throughout the Senegalese shore and account for up to 80% of the national total fish catch (FAO, 2003). In the context of international support and in response to the decrease in fish biomass and collapse of demersal fish species (Thiao et al., 2012), a growing number of MPAs are currently being implemented in Senegal. These co-exist, but do not always coincide with AHs deployment programs (Fig. 1). Knowing that in the coming years local authorities will be encouraged to deploy AHs according to the Senegalese National strategic plan for MPAs (*Comm. Pers.* Ministère de l'Environnement et du Développement Durable du Sénégal, 2014), it is required to investigate the potential interactions between AHs and MPAs.

2. Method

Mathematical approaches have long been used to solve fishery problems to explore the general behavior of the ecosystem–fisheries interacting system. Such methods have focused on the

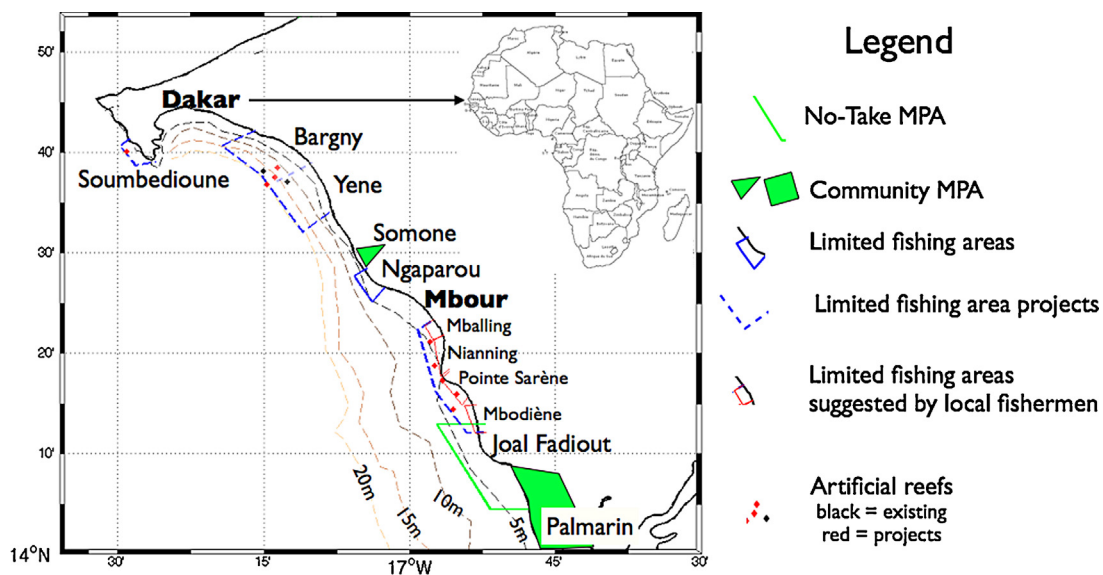


Fig. 1. Synthesis of existing and planned marine protected areas (MPAs) and artificial reefs along a part of the south coast of Senegal. No-take MPAs, created by Presidential decree, and community MPAs are managed by the DAMCP (Direction des Aires Marine Communautaires Protégées/Senegalese ministry of the environment), while ‘limited fishing areas’ (called ZPP) are managed by the DPM (Direction des Pêches Maritimes/Senegalese ministry of fisheries and marine economy) and artificial reefs were deployed by international NGOs and local fishermen.

search for possible equilibria and the “attractors” involved in the system (e.g., Bensenane et al., 2013). Slow and fast processes can be segregated in the differential equations, which allowed us to build a reduced model by applying variable aggregation methods (Iwasa et al., 1987, 1989; Auger et al., 2008). Fish movements are usually classified as fast processes, while population growth and fishing are classified as slow processes.

Let us consider a coastal area where fisheries are managed by (1) the implementation of a no-take marine protected area (MPA) and (2) the deployment of a volume of AHs either in the MPA or in the fishing area. Let ‘V’ be the total water volume of the coastal area which is divided into two parts, a MPA with volume αV and a fishing area of volume $(1 - \alpha)V$, α being the ratio of the protected part. In order to simplify the problem and to focus on the interaction between MPAs and AHs, we make the hypothesis of a uniform environment with a constant depth, ‘k’ being the carrying capacity per unit volume of water. The total carrying capacity ‘K’ of the zone without AHs is then $K = kV$. Volume is the common size measurement for AHs rather than surface because their height is variable. In the MPA, (respectively, in the fishing area), a volume $V_1 \leq \alpha V$ (respectively, a volume $V_2 \leq (1 - \alpha)V$), can be covered by AHs. We also define the proportion of the volume of AHs in the MPA (respectively, in the fishing area) as $V_1/\alpha V$ (respectively, $V_2/(1 - \alpha)V$). Artificial reefs blocks size range from 1 to 60 m³. Reef complex can reach up to 10⁶ m³ distributed on areas up to 50 km² (Bohnsack and Sutherland, 1985).

The model considers the fish community as a whole; this can be seen as a pool of species sharing the same logistic growth with a growth rate, r , and the same movement behavior. The fish population is assumed to be isolated from other populations, i.e., there are no migrations out of the domain considered. The fishery associated with this fish community is defined by the cost per unit effort, c , the market price, p , and the fish catchability, q , although the latter can also be seen as a property of the fish. Such a system was studied by Bensenane et al. (2013) by means of a set of three ordinary differential equations describing the time evolution of the fish populations in the MPA and in the fishing area, and of the fishing effort. In this study, we modified this model in order to take into account the effects of introducing AHs into the environment as suggested in the literature (i.e., introducing fish production and attraction phenomena). On the basis of the literature, we formulate the

In an extended literature study, Bohnsack and Sutherland (1985) reported experimental cases showing very diverse increase of biomass on artificial reefs, ranging from null to 35 times greater biomass than on open bottom areas.

The attraction effect was simulated by an “attraction function”, β , which is an additive migration rate toward the AHs (Eq. (1)).

$$\beta(V_1) = \left(\frac{\beta_0 V_{AH}}{1 + \sigma V_{AH}} \right) \tag{1}$$

where V_{AH} is the volume of AHs deployed, and β_0 and σ are parameters describing the shape of the curve. This function is strictly positive and monotone, increasing with V_{AH} and displaying a plateau. σ describe the steepness of the attraction increase, from linear ($\sigma = 0$) to an increasingly rapid reach of the plateau β_0/σ , which is the maximum attraction rate when V_{AH} becomes very large, for $\sigma > 0$. In the absence of attracting effect ($\beta_0 = 0$), our model consider an ideal free distribution (IFD) of the fish, i.e., an optimal distribution of the fish according to the distribution of carrying capacity. The attraction function (Eq. (1)) describes the part of fish movement that does not correspond to the IFD, but represents the perturbation induced by fish displacement due to the purely attractive effect of the AHs (Fig. 2). It makes sense to consider that the attraction increase reach a plateau for large AHs volume; indeed Bohnsack and Sutherland (1985) reports radius of attraction of several hundred meters around the AHs location, regardless to the AHs volume but more related to the shape of the AHs. The value of β_0/σ must be compared to the value of the parameter “a”, which describes the fish mobility for space occupation (Table 1). If $\beta_0/\sigma \ll a$, the attraction effect might be negligible by comparison with the fish movement that tends to the ideal free distribution (IFD). On the contrary, if $\beta_0/\sigma \gg a$, the attraction effect might dominate the fish movement that tends to the IFD. Model I:

The situation where the AHs are deployed in the MPA then corresponds to the following system, with n_1 and n_2 , respectively being the fish population density in the MPA and in the fishing area, a the fish mobility parameter, E the fishing effort and $\varepsilon \ll 1$ is a small dimensionless parameter. We consider $K = V k$, V being the total volume of the area considered and k the average carrying capacity per unit of volume in this area. We assume that the depth of the area considered is constant and that the nature of the bottom is homogeneous, so that k is the same for any part of the area

$$\begin{cases} \frac{dn_1}{d\tau} = \left(\frac{a}{(1 - \alpha)K} + \beta(V_1) \right) n_2 - \left(\frac{a}{\alpha K + V_1 \delta K} \right) n_1 + \varepsilon \left(r n_1 \left(1 - \frac{n_1}{\alpha K + V_1 \delta K} \right) \right) \\ \frac{dn_2}{d\tau} = \left(\frac{a}{\alpha K + V_1 \delta K} \right) n_1 - \left(\frac{a}{(1 - \alpha)K} + \beta(V_1) \right) n_2 + \varepsilon \left(r n_2 \left(1 - \frac{n_2}{\alpha K + V_1 \delta K} \right) - q n_2 E \right) \\ \frac{dE}{d\tau} = \varepsilon (p q n_2 - c E) \end{cases} \tag{2}$$

hypothesis that AHs can (1) add an additional carrying capacity per unit of volume, δk , to the area where they are deployed, accounting for the production effect, and (2) modify the fish ideal free distribution (IFD) between the fishing area and the

considered. τ is the fast time (Eq. (2)).

Model II:

Similarly, the following system describes the situation where AHs are deployed in the fishing area (Eq. (3)):

$$\begin{cases} \frac{dn_1}{d\tau} = \left(\frac{a}{(1 - \alpha)K + V_2 \delta K} \right) n_2 - \left(\frac{a}{\alpha K} + \beta(V_2) \right) n_1 + \varepsilon \left(r n_1 \left(1 - \frac{n_1}{\alpha K} \right) \right) \\ \frac{dn_2}{d\tau} = \left(\frac{a}{\alpha K} + \beta(V_2) \right) n_1 - \left(\frac{a}{(1 - \alpha)K + V_2 \delta K} \right) n_2 + \varepsilon \left(r n_2 \left(1 - \frac{n_2}{(1 - \alpha)K + V_2 \delta K} \right) - q n_2 E \right) \\ \frac{dE}{d\tau} = \varepsilon (p q n_2 - c E) \end{cases} \tag{3}$$

MPA, as a result of the attraction effect. Thus, the total carrying capacity of the MPA is given by $\alpha V k + V_1 \delta k$. Similarly, the carrying capacity of the fishing area is given by $(1 - \alpha) k V + V_2 \delta k$.

Models I and II are called complete models as they take into account processes going on at different time scales. They are composed with two parts, a fast one and a slow one. The fast part

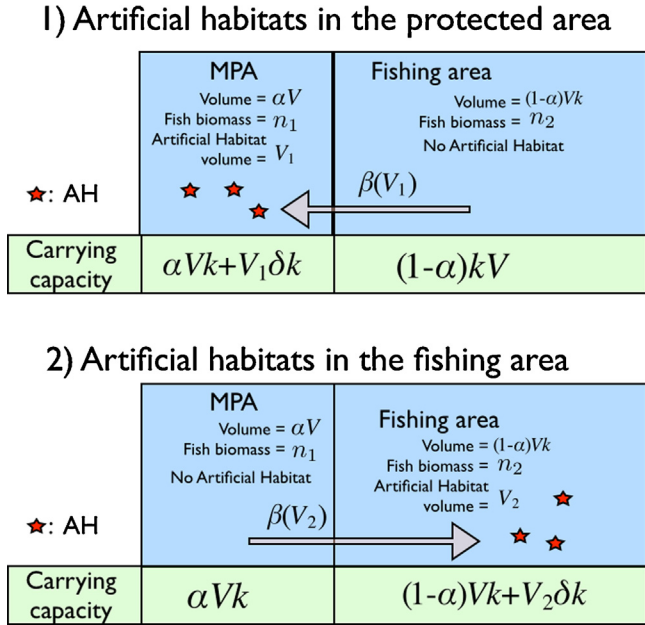


Fig. 2. Illustration of the two situations considered in this study: (1) artificial habitats (AHs) implementation plan in the fishing area or (2) in the marine protected area.

relates to fish migration between the MPA and the fishing area while the fish growth, landings and fishing effort (investment in fishing means) vary at the slow time $t = \varepsilon \tau$. Slow terms of the complete models are those multiplied by ε and correspond to fish growth, fishing mortality and fishing effort. For slow–fast models, we refer to the early work of Tikhonov (1952). However, in the present work, we apply aggregation methods of variables based on a Fenichel version of the center manifold theorem, described in Auger et al., 2008; (see also Poggiale et al., 2008). Here we use the so called “quick derivation method”. A first step of this method is to look for the existence of asymptotically stable equilibria of the fast part of the complete model. In a second step, we replace fast variables in terms of the fast equilibria into the complete model. This allows to derive a reduced model also called the aggregated model governing slow variables at a slow time scale. By setting $\varepsilon = 0$ we neglect small perturbation terms in the complete models and we get the fast system corresponding only to fish migration

between the MPA and the fishing area. There is an extra equation for the derivative of the fishing effort with respect to the fast time, which is equal to zero, meaning that E is constant at the fast time. Because migration is conservative, $n = n_1 + n_2$ is also constant at the fast time.

2.1. Fast equilibrium

The first step consists in setting $\varepsilon = 0$ in the complete model I. This model is the fast model I for fish (Eq. (4)):

$$\begin{cases} \frac{dn_1}{d\tau} = \left(\frac{a}{(1-\alpha)K} + \beta(V_1) \right) n_2 - \left(\frac{a}{\alpha K + V_1 \delta K} \right) n_1 \\ \frac{dn_2}{d\tau} = \left(\frac{a}{\alpha K + V_1 \delta K} \right) n_1 - \left(\frac{a}{(1-\alpha)K} + \beta(V_1) \right) n_2 \\ \frac{dE}{d\tau} = 0 \end{cases} \quad (4)$$

The fast model is conservative of the total fish density, $n(t) = n_1(t) + n_2(t)$, and of the fishing effort both remain constant. Similarly fast model II reads as follows (Eq. (5)):

$$\begin{cases} \frac{dn_1}{d\tau} = \left(\frac{a}{(1-\alpha)K + V_2 \delta K} \right) n_2 - \left(\frac{a}{\alpha K} + \beta(V_2) \right) n_1 \\ \frac{dn_2}{d\tau} = \left(\frac{a}{\alpha K} + \beta(V_2) \right) n_1 - \left(\frac{a}{(1-\alpha)K + V_2 \delta K} \right) n_2 \\ \frac{dE}{d\tau} = 0 \end{cases} \quad (5)$$

We shall now take advantage of the difference between the time scales in order to reduce the dimension of the complete models. It is usual in slow–fast models, as a first step of reduction or aggregation, to look for the existence of a stable equilibrium of fast models (4) and (5). This fast equilibrium is obtained by writing the second fast variable n_2 as $n_2 = n - n_1$ i.e., in terms of the “constant” n and of the first fast variable. Then, we substitute this expression of n_2 into the first equation of the fast model which is set equal to zero at equilibrium. A straightforward calculation leads to the fast equilibrium (Eq. (6)).

$$\begin{cases} n_1^* = v_1^* n \\ n_2^* = v_2^* n \end{cases} \quad (6)$$

v_1^* and v_2^* represent the asymptotic distribution of individuals respectively in zone 1 and 2 due to fish migration, in absence of any other process. For model I they are given by the following expressions (Eq. (7)):

Table 1

List of parameter values in the differential equation models describing the changes in fishing effort, fish population growth, and movement according to the volume of artificial habitats (AHs) deployed in the marine protected area ‘MPA’ or in the fishing area. We considered a homogeneous environment of 10×10 km with an average depth of 10 m, roughly corresponding to the marine area front of Yenne coast (Fig. 1).

Parameter	Value used	Description
V	100	Volume of water in the area considered (10^7 m^{-3})
k	1	Fish carrying capacity per unit volume of water (tons. 10^7 m^{-3})
K	Vk	Total fish carrying capacity in the area considered
r	0.5	Fish growth rate
a	2	Fish mobility
α	0.2	Ratio of the area considered which is protected (MPA)
c	1	Fishing cost per unit effort
p	1	Fish price
q	1	Fish catchability
V_1, V_2	0–20 (αV)	Volume of artificial habitats (AHs) deployed in the MPA (V_1) or in the fishing area (V_2)
β_0	0; 0.3	AH attraction parameter 1
σ	0.1	AH attraction parameter 2
δk	0; 5	Fish carrying capacity per unit volume of AH (tons. 10^7 m^{-3})

$$\begin{cases} v_1^* = \frac{\frac{a}{(1-\alpha)K} + \beta(V_1)}{\frac{a}{(1-\alpha)K} + \beta(V_1) + \frac{a}{\alpha K + V_1 \delta K}} \\ v_2^* = \frac{\frac{a}{\alpha K + V_1 \delta K}}{\frac{a}{(1-\alpha)K} + \beta(V_1) + \frac{a}{\alpha K + V_1 \delta K}} \end{cases} \quad (7)$$

For model II, we get (Eq. (8)):

$$\begin{cases} v_1^* = \frac{\frac{a}{(1-\alpha)K + V_2 \delta K}}{\frac{a}{(1-\alpha)K + V_2 \delta K} + \beta(V_2) + \frac{a}{\alpha K}} \\ v_2^* = \frac{\beta(V_2) + \frac{a}{\alpha K}}{\frac{a}{(1-\alpha)K + V_2 \delta K} + \beta(V_2) + \frac{a}{\alpha K}} \end{cases} \quad (8)$$

It can be easily shown that the fast equilibrium for fish is globally asymptotically stable in the positive quadrant for any values of the slow varying variables n and E that are “constant” at the fast time scale.

2.2. The aggregated models

The next step is to make an approximation that fast variables are at equilibrium, the fast equilibrium. In other words, it is assumed that fast variables are constant at the slow time. It consists in the substitution of the fast equilibrium (n_1^*, n_2^*) into the equations of the complete model and addition of fish equations leading to a reduced model, called the “aggregated model”, which reads as follows for model I (Eq. (9)):

$$\begin{cases} \frac{dn}{dt} = rn \left(1 - \left(\frac{v_1^{*2}}{\alpha K + V_1 \delta K} + \frac{v_2^{*2}}{(1-\alpha)K} \right) n \right) - qv_2^* n E \\ \frac{dE}{dt} = pqv_2^* n E - cE \end{cases} \quad (9)$$

Mathematical aggregation of variables is a method based on the Fenichel center manifold theorem and we refer to Auger et al. (2008). In the present case, the reduced model is obtained by a spatial aggregation of fish biomass. For spatial aggregation of variables, we also refer to the review Auger et al. (2012a,b). Here we use a slow time t such as $t = \varepsilon \tau$.

For model II, we get (Eq. (10)):

$$\begin{cases} \frac{dn}{dt} = rn \left(1 - \left(\frac{v_1^{*2}}{\alpha K} + \frac{v_2^{*2}}{(1-\alpha)K + V_2 \delta K} \right) n \right) - qv_2^* n E \\ \frac{dE}{dt} = pqv_2^* n E - cE \end{cases} \quad (10)$$

The quick derivation method is valid when the aggregated model is structurally stable; this is the case of aggregated models (9) and (10). Also, the small parameter ε must be small enough. When parameters of the complete model are of the order of 1, numerical simulations performed for previous examples have shown that epsilon should be at least smaller than 10^{-1} , see simulations in Poggiale et al. (2008). Under this condition, trajectories starting at the same initial condition of the complete and aggregated models remain very close one to the other. As another illustration in fishery modeling, we refer to an example with three time scales where we compared trajectories of complete and aggregated models for different values of small parameters, Hieu et al., 2014.

2.3. Analysis of the aggregated models

Both aggregated models can be rewritten as follow (Eq. (11)):

$$\begin{cases} \frac{dn}{dt} = rn \left(1 - \frac{n}{\bar{K}} \right) - qV_2^* n E \\ \frac{dE}{dt} = pqV_2^* n E - cE \end{cases} \quad (11)$$

where the global carrying capacity is given by the following expressions (Eq. (12)):

$$\frac{1}{\bar{K}} = \frac{v_1^{*2}}{\alpha K + V_1 \delta K} + \frac{v_2^{*2}}{(1-\alpha)K} \quad (12)$$

for model I and for model II by (Eq. (13)):

$$\frac{1}{\bar{K}} = \frac{v_1^{*2}}{\alpha K} + \frac{v_2^{*2}}{(1-\alpha)K + V_2 \delta K} \quad (13)$$

Both aggregated models are of the same form as the classical Lotka–Volterra predator–prey models with prey logistic growth. Consequently, we know that there exist only three equilibria: $(0,0)$, $(\bar{K}, 0)$ and (n^*, E^*) where

$$n^* = \frac{c}{pqV_2^*}$$

and

$$E^* = \frac{r}{qv_2^*} \left(1 - \frac{c}{pqv_2^* \bar{K}} \right)$$

Regarding stability analysis, we know that:

- When $c > pqv_2^* \bar{K}$, $E^* < 0$ and the equilibrium $(\bar{K}, 0)$ is globally asymptotically stable in the positive quadrant.
- When $c < pqv_2^* \bar{K}$, $E^* > 0$ and the equilibrium (n^*, E^*) is globally asymptotically stable in the positive quadrant while $(\bar{K}, 0)$ is a saddle.

Solving the differential equations makes it possible to plot the analytical solutions corresponding to the stable (“sustainable”) equilibrium between fishing and population growth. Indeed, after an oscillating phase the solutions of the model tend toward constant values of the fishing effort and fish population biomass. Once the system is stabilized, the variables n and E are almost constant, close to the equilibrium of the aggregated models, and we save and keep them in a table for different set of parameters values. Parameters were adjusted so that such a positive equilibrium (n^*, E^*) does exist and is globally asymptotically stable (Table 1). The reserve (MPA) was set to 20% of the total area.

3. Results and discussion

3.1. The mathematical model

The sustainable equilibria were compared on the basis of (1) the volume of AHs deployed in the MPA or in the fishing area, (2) the attractive effect of the AHs on fish distribution and (3) the productive effect of the AHs on the fish carrying capacity. We discuss the impacts on fish population and fish landings according to a set of contrasted situations by considering firstly the case when AHs are deployed in the MPA, and secondly the case when AHs are located in the fishing area. Having a “pure” attractive effect in these models is possible by setting $\delta k = 0$ (δk = the increase of carrying capacity of the AH), but it is not possible to have a pure productive effect because increased local

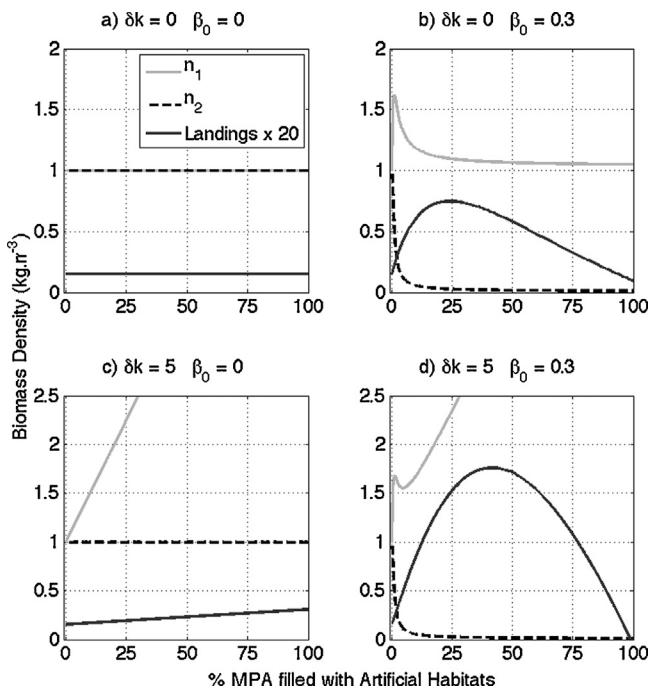


Fig. 3. Fish biomass density in the marine protected area ‘MPA’ (n_1) and in the fishing area (n_2) and fish landings per unit volume of the fishing area at equilibrium, according to the percentage of the MPA filled with artificial habitats (AHs) when considering a null (a and c; $\beta_0=0$) or non nul (b and d; $\beta_0=0.3$) attractive effect and considering a null (a and b; $\delta k=0$) or non nul (c and d; $\delta k=5$) productive effect of the AHs (n_1 and n_2 are superposed in Fig. 3a).

carrying capacity inevitably cause change of the ideal free distribution. We assume that from an ecological point of view this is meaningful and was not a problem for the question addressed.

It could also be interesting to consider that intra-specific competition might be smaller in the area where AHs are deployed. This would lead to add extra negative quadratic terms in the two first equations governing n_1 and n_2 according to the concept of emerging carrying capacities (Sieber et al., 2014). We intend to consider that matter in a next contribution. In the present work, it makes sense to consider that the fish growth is governed by a logistic equation where intra-specific competition is taken into account in the quadratic Verhulst term depending on the carrying capacity. It is also reasonable to consider that the main factor that determines fish spatial distribution is the amount of resource available locally in each area. Therefore, in this work, we make the assumption that migration terms follow the IFD at equilibrium.

Model I (Eq. (2)) describes the effect of the deployment of AHs inside the MPA. At equilibrium, in the absence of any attractive or productive effect of AHs, the fish densities in the MPA and in the fishing area are the same (Fig. 3a). Considering the case of AHs with pure attractive effect (without production), model I predicts a strong decrease of fish density in the fishing area together with a strong increase of fish density inside the MPA for very little percentage of the MPA covered with AHs (3%, Fig. 3b). For larger percentage of the MPA covered with AHs the fish population both inside and outside the MPA decrease. Fish landings are maximal when volume of AHs reach ~25% of the MPA (Fig. 3b). This increase of the landings is due to a boosted effect of the MPA that enhance fish reproduction while the subsequent decrease must be due to the fact that fish population is too far from the IFD due to artificial attraction in the MPA and then do not benefit the carrying capacity of the fishing area. When considering a production effect without

any purely attractive component of the AHs (Fig. 3c), the fish population inside the MPA increased linearly along with the increase of AHs volume. When the MPA is entirely filled with AHs, the total carrying capacity reach 6 kg m^{-3} (carrying capacity of the AHs plus the initial carrying capacity of the environment, with $\delta k=5 \text{ kg m}^{-3}$ and $k=1 \text{ kg m}^{-3}$, Table 1). The fish density in the fishing area remained constant, and the landings linearly increased along with the increase of AHs volume (Fig. 3c). In the case of AHs having both productive and purely attractive components, the fish population inside the MPA increased along with the AHs volume (until 6 kg m^{-3} , as for Fig. 3c) while the fish population in the fishing area constantly decrease. The landings display a maximum when volume of AHs is ~40% of the MPA (Fig. 3d). In this case, the landings may exceed the biomass density in the fishing area, which was possible because of the different time scales of these variables. Indeed, the fish biomass density was in fast time, for example ~1 day, while the landings were in slow time, and consequently integrated over ~1 month (at least one order of magnitude between fast and slow time). To summarise, when considering AHs with an attractive effect, we found that there was a particular volume of AHs deployed in the MPA which maximized fish landings (Fig. 3b and d). Although not shown in the figures, increasing the value of the attractive effect β_0 results in a lower value of the optimal value of AHs. Also, the value of the fish landed with the optimal volume of AHs was higher when AHs have a production effect, since each AH increased the capacity of the environment by δk .

The second model (Eq. (3)) describes the effect of the deployment of AHs in the fishing area. At equilibrium, considering the case of AHs with pure attractive effect without production, model II predicts a decrease of the fish population inside the MPA and a decrease of the landings along with the increasing volume of AHs, while the fish population in the fishing area would slightly increase (Fig. 4b). A similar dynamic was found in the case of AHs

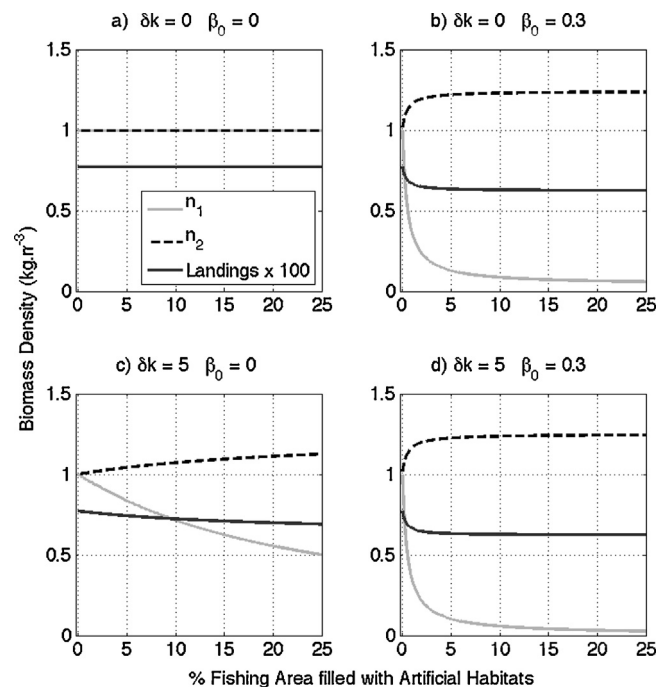


Fig. 4. Fish biomass density in the marine protected area ‘MPA’ (n_1) and in the fishing area (n_2) and fish landings per unit volume of the fishing area at equilibrium, according to the percentage of the fishing area filled with artificial habitats (AHs) when considering a null (a and c; $\beta_0=0$) or non nul (b and d; $\beta_0=0.3$) attractive effect and considering a null (a and b; $\delta k=0$) or non nul (c and d; $\delta k=5$) productive effect of the AHs (n_1 and n_2 are superposed in Fig. 4a).

with productive effect without any purely attractive effect, but with a much softer decrease of the fish population in the MPA (Fig. 4c). In the case of AHs having both productive and purely attractive components, the dynamic remains similar but with more accentuated reduction of the fish population in the MPA (Fig. 4d). The decrease tended toward a lower limit that was more rapidly reached when the AHs had an attractive effect (Fig. 4b and d). The fact that the fish population and the fish landings decreased along with the increasing volume of AHs can be counter-intuitive when considering AHs had no attractive effects, but only a productive effect (Fig. 4c). This can easily be understood as an extension of the result of Bensenane et al. (2013) showing that reducing the size of the MPA also reduces fish landings at equilibrium. Indeed, under the present hypothesis, adding productive AHs in the fishing area increases its carrying capacity, which is similar to reducing the ratio of the carrying capacity that fall in the MPA, given that the environment was initially considered to have a uniform carrying capacity. Thus, increasing the ratio of the total carrying capacity within the fishing area displaces the system from the initial optimum MPA design. Similarly, local destruction of natural habitat in the fishing area (e.g., bottom trawling or dynamite fishing) would also displace the system from the optimal MPA design by increasing the ratio of total carrying capacity that fall in the MPA. This would not be the case for e.g., chemical pollutions which are not local and may also affect the MPA mainly depending on the hydrodynamics.

The present models do not include a major feature of the AHs, i.e., changes in fish catchability. On the one hand, it has been reported that certain types of large AHs can act as a local protection that reduces fish catchability by preventing bottom trawling, since the AH could break the trawl (Polovina and Sakai, 1989; Guillen et al., 1994). Such local protection may compensate for the negative effect of deploying AHs in the fishing area. Nevertheless, in the Senegal case study, all AHs are deployed at less than six nautical miles from the coast where trawl activities are forbidden. On the

other hand, a number of other types of fishing gear may still be used over AHs deployed in fishing areas and in this case fish catchability is increased by the attractive effect of the AHs (Polovina, 1991). Furthermore, it was often observed that broken nets were wrapped around the AH and killed the fish, acting as ghost fishing (Kaiser et al., 1996). This may worsen the negative impacts of deploying AHs in the fishing area predicted by the model.

Fish species display very different moving behaviors, which may induce a variety of response to the attractive effect of AHs. However, models I and II predicted no effect of the mobility parameter when considering a null attractive effect ($\beta_0=0$), whatever the productive effect of the AHs (δk). In the case of a purely attractive effect of AHs, both models predict an effect of the mobility parameter “ a ” (see Eqs. (2) and (3)). In the case of deploying AHs in MPAs, model I predicts a maximum increase of the landings for species with the mobility parameter value of 1 ($a=1$, Fig. 5a). For species with a shorter home range ($a < 1$), there was a limited or null benefit for fisheries when AHs are in the MPA. Benthic species, such as octopuses, or exploited sessile species may fall into this category. However, even if these species are sedentary as adults, they undergo wide spatial dispersion during their pelagic larval stage, a “slow” process that may occur on the same time scale as population growth. Larval dispersal was not taken into account in our model. Taking the larval dispersal into account would generate a slow spill-over for these species toward the fishing area, which might compensate for the weak (null) landings predicted by the model at equilibrium.

Since the attraction migration function used in the model was not calibrated to field data, it is not possible to define exactly which fish species correspond to this “moderate moving behavior”. However, a number of observations suggest that demersal fish species, such as stingrays, certain groupers, and other predators on the lookout, may fall into this category in Senegal (Brochier et al., 2013). For more mobile species ($a > 1$), the benefits (increased landings) of deploying AHs in the MPA progressively decline as the moving capacity increases (Fig. 5a). Model I predicted the highest fish population in the MPA for more mobile species ($a \sim 20$ in Fig. 5a). The fish population in the MPA decreases for higher mobility. On the other hand, the more mobile they are, the higher the fish biomass density was predicted in the fishing area. For extremely mobile species, the density in both areas was predicted to converge to the same value ($a > 100$, not shown).

When deploying the AHs in the fishing area, model II predicts that the fish species with the more mobility capabilities would have the higher biomass density, both in the MPA and in the fishing area. The highly mobile species may also dominate the landings (Fig. 5b).

The attractive power of AHs also depends on the environment where it is deployed. If AHs are deployed in sandy or rocky environment, the attractive effect will be different according to the fish community composition. Indeed, the AHs attractive effect will be stronger on sandy environment (Bohnsack, 1989). This effect is independent of the purely attractive component used in the model (Eq. (1)), but rather depends on the increase in carrying capacity, δk , provided by each AH. If the value of δk is very small compared to the total carrying capacity, K , the fish distribution resulting from ideal free distribution (IFD) will not be affected. In contrast, if the value of δk is not negligible compared to K , deploying AHs with significant carrying capacities might modify the fish IFD to a significant degree.

Finally, a number of possible side effects of the AHs were not included in this mathematical approach. These include pollution, disruption of the migratory routes, increased epidemic risks, or changes in fish assemblages as a result of promoting one species/

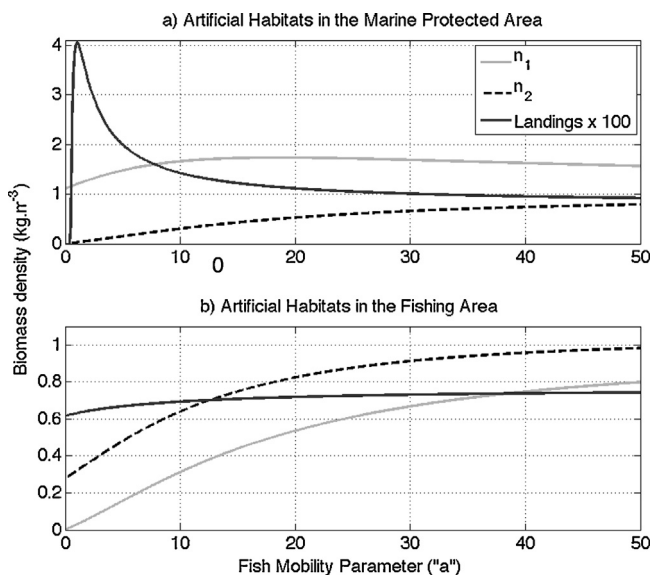


Fig. 5. Fish biomass density in the marine protected area ‘MPA’ (n_1) and in the fishing area (n_2) and fish landings per unit volume of the fishing area at equilibrium, according to the moving capacity of the fish species (parameter a reported in Eqs. (2) and (3)), for a volume of artificial habitats ‘AHs’ of 2% the total water volume in the area considered; a) when AHs are deployed in the MPA (=10% of the MPA); b) when AH are deployed in the fishing area (=2.5% of the fishing area). The attractive parameter (β_0) was set constant (0.3); there was no effect of the mobility parameter when considering a null attractive effect, whatever the productive effect of the AHs (δk).

family or functional group. In order to provide the best prediction of the effect of AHs on the different fish species in Senegal, it would be necessary to design specific experiments to observe fish home ranges and their sensibility to AHs attraction. This could be done in the field using individual tagging systems (e.g., Bijoux et al., 2013).

It appears from the mathematical model used here that AHs must be deployed inside an MPA in order to have a positive impact on fish landings at equilibrium. This is in line with field observations (Simon et al., 2011) and other bio-economics models (Boncœur, 2008). The mathematical equilibrium described here may not correspond to a given time, but rather to an average state of the fishery reached a few years after introducing the MPA management plan. The time needed to reach this average state mainly depends on the age at maturation, the fecundity, and the longevity of the species present in the ecosystem (Brochier et al., 2013).

3.2. Implications for MPA and AH management in Senegal

We can apply our results to the case of the use of MPAs and AHs in Senegal. The status of MPAs in Senegal ranges from no-take MPAs (established by a presidential decree), to restricted fishing areas and yearly alternate fishing/no-take areas, for those created by the local fishery community (Fig. 1). In most cases, AHs have been deployed or are planned to be deployed inside the newly established MPAs and our model predicts that they might have some beneficial effects for the fisheries at equilibrium.

In regulated areas, fishing over the AHs is forbidden. To the best of our knowledge, there are two kinds of AH structures deployed in Senegalese waters. First, a mix between concrete structures and natural stones (“gabion”). Generally the height of these structures do not exceed 75 cm and are deployed in less than 20 m depth waters by fishers collectivity, state institutions, international collaborator (Japan), and NGOs. Second, more than 150 out-of-service buses and boats which were sunk by the Senegalese recreational fishing league (FSPS¹) between 1994 and 2008.² The first category of AHs were immersed within protected areas or surrounded by a fishing restriction radius as recommended by the Centre de Recherche Océanographique de Dakar-Thiaroye ‘CRODT’ (Watanuki and Gonzales, 2006), while the second category of AHs were immersed in fishing areas.

The attractive power of AHs deployed along the south Senegalese coast might be further enhanced because most of the sea bottom is sandy and hard substrates are limiting environmental factors for certain high commercial value demersal fish species, such as the thiof (*Epinephelus aenus*). Thus, our results suggest that there is a threshold volume of AHs deployed inside MPAs that should not be exceeded in order to remain in the part of the curve where adding further AHs within the MPA still benefits the fisheries at equilibrium (Fig. 3b and d). Further studies may be relevant in order to estimate more accurately the value of this threshold for each MPA. Furthermore, the local change in the benthic community may lead to the colonization of the area by new species and *via* trophic cascades have unpredictable effects on the fish community.

However, the two biggest AHs in Senegal (>100 m³) have been deployed in fishing areas with no MPA nearby (Yenne and Bargny villages; Watanuki and Gonzales, 2006; Terashima et al., 2007). At both locations, fishing was forbidden within a 500 m radius

during the first two years and biological monitoring showed an increase of fish biomass in the area (Terashima et al., 2007; Watanuki and Gonzales, 2006). At the end of the NGOs monitoring, the fishery control stopped and there was a struggle among the fishermen to fish over the AHs (Thiam et al., 2012). In line with our model results, the fisheries in this area have first experienced an increase of landings after the AHs were deployed and during the time when there was no fishing activity on the AHs (2004–2006). Once the management has stopped (after 2006), our theoretical model predicts that fish landing should have drop below the initial state (prior the AHs deployment in 2004), once the system is stabilized. Local investigations are currently being conducted by a Senegalese institution, the CRODT, to confirm or not this negative effect.

To date more than eight organizations are involved in creating and managing MPAs or in deploying AHs in Senegal. These includes state institutions (e.g., DAMCP, DPM, CRODT, DPSP)¹, fishery organizations (e.g. FSPS, CLPAs)¹, and at least three NGOs and associations. As a result, until now it is not clear which institutions have authority for AHs deployment and MPAs management. There is a need for close interaction between management and initiatives of MPAs and AHs in order to ensure long-term control and sound monitoring of these. Indeed, the level of illegal fishing over AHs will determine the effectiveness of AHs deployment for the whole fishery community. If the fishing rate near the AHs is too high, these would be converted into a negative investment, which actually reduces the overall fish landings of the Senegalese fishermen. Furthermore, AHs must be regularly inspected to report on their state (e.g., structure silting, phantom net). The present paper confirms previous warnings on the use of AHs in the context of weak governance that cannot guarantee that fishery management measures will be applied. AHs can be an interesting investment in the context of fishery management, but only if the management plan ensures long-term monitoring of the MPA where AHs are deployed, including their maintenance and continuous monitoring programs.

Acknowledgements

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¹ DAMCP=Direction des Aires Marines Communautaires Protégées; DPM= Direction des Pêches Maritimes; DPSP=Direction de la Protection et de la Surveillance des Pêches; FSPS =Fédération Sénégalaise de Pêche Sportive; CLPA= Comité Local de Pêche Artisanale.

² Opening allocation of Mr. Abdou G. Diouf, president of the FSPS, at the international symposium on artificial reef management held in Dakar, 11–14 November 2008.

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