

OPTIMAL NUMBER OF SITES IN MULTI-SITE FISHERIES WITH FISH STOCK DEPENDENT MIGRATIONS

ALI MOUSSAOUI

Université Aboubekr Belkaid, Faculté Des Sciences,
Département de Mathématiques, 13000, Tlemcen, Algerie

PIERRE AUGER

IRD, UMI 209, UMMISCO, IRD France Nord, F-93143, Bondy, France
and
UPMC Univ Paris 06, UMI 209, UMMISCO, F-75005, Paris, France

CHRISTOPHE LETT

UMI IRD 209 UMMISCO, Centre de Recherche Halieutique Méditerranéenne
et Tropicale, Avenue Jean Monnet, BP 171, 34203 Sète Cedex, France

(Communicated by Erik Bollt)

ABSTRACT. We present a stock-effort dynamical model of a fishery subdivided into fishing zones. The stock corresponds to a fish population moving between these zones, on which they are harvested by fishing fleets. We consider a linear chain of identical fishing zones. Fish movements between the zones, as well as vessels displacements, are assumed to take place at a faster time scale than the variation of the stock and the change of the fleet size. The vessels movements between the fishing areas are assumed to be stock dependent, i.e. the larger the stock density is in a zone the more vessels tends to remain in it. We take advantage of these two time scales to derive a reduced model governing the dynamics of the total harvested stock and the total fishing effort. Under some assumption, we obtain either a stable equilibrium or a stable limit cycle which involves large cyclic variations of the total fish stock and fishing effort. We show that there exists an optimal number of fishing zones that maximizes the total catch at equilibrium. We discuss the results in relation to fish aggregating devices (FADs) fisheries.

1. Introduction. This manuscript deals with pelagic multi-site fisheries such as fisheries on fish aggregating devices (FADs) or on artificial habitats (AHs) (Kakimoto, 2004, Lan et al., 2006, Nelson, 2003). In this manuscript, we consider a 1D linear chain of FADs that would be located along the coast or along a reef around an island. It is assumed that fishes of the open sea can visit a FAD where they can stay for a short time (a few days) and then return to the open sea (Girard et

2000 *Mathematics Subject Classification.* 34K20, 34K26, 37N25, 92D25.

Key words and phrases. Population dynamics, stock-effort model, Time scales, aggregation of variables, stability.

Work partially supported by the Franco-Algerian Cooperation: Tassili no. 10MDU800.

al., 2004, Hilborn et al., 1989, Hilborn et al., 2006). We also take into account a local (artisanal) fishery that exclusively exploits the FADs (Fonteneau et al., 2000, Moreno et al., 2007, Pioch, 2008). Therefore, the fishing fleet is assumed to go from FAD to FAD where it captures fishes. This manuscript looks for existence of an optimal number of FADs of the multi-site fishery, i.e. a number of FADs that maximizes the total capture of the multi-site fishery. Indeed, if we consider a chain with a few FADs, an increase of the number of FADs would increase the total capture. Similarly, if there is a large number of FADs, the fishery would be over-exploited. Therefore, it makes sense to look for an intermediate number of FADs that would optimize the total capture. We already have shown that there exists such an optimal number of FADs for a multi-site fishery (Auger et al., 2010). However, this was shown in a simplified case where fishing boats move from a FAD to a neighboring one at constant rates. However, it is obvious that fishing boats are more likely to leave a FAD when fish density on this FAD is small and inversely. In other words, the dispersal rates of the fishing fleet might be fish density dependent rather than density independent as in Auger et al. (2010). The aim of this manuscript is to look for existence of a number of FADs that maximizes the total capture in the more realistic case of density dependent movement of fishing boats.

In this manuscript, we use two time scales, a fast one corresponding to fish and boat dispersal from FAD to FAD and a slow one for fish growth, capture and investment in the fishery. Taking advantage of these two time scales, we are able to use aggregation methods that allow us to reduce the dimension of the complete model and to derive a global model at the slow time scale governing the total fish density and the total fishing fleet (Auger et al., 2008a, 2008b). Taking into account density dependent dispersal can have very important consequences on the global dynamics of the system. For example, we refer to some earlier works in which we investigated the effects of prey density dependent dispersal of predators as well as predator density dependent dispersal of prey in a system of patches (Mchich et al., 2002, 2007, Dao Duc et al., 2008, El Abdllaoui et al., 2007). These works have shown that density dependent dispersal can have important consequences on the global dynamics of the predator-prey system.

Coming back to our fishery model, in the density independent case, we have shown in Auger et al. (2010) that two cases could occur, either the fishing fleet goes extinct, i.e. the fishing fleet goes extinct and the fish density tends to its global carrying capacity, or existence of a gas Fishery Equilibrium (FE) allowing the fishery to persist, i.e. the fish density as well as the fishing fleet asymptotically tend to equilibrium values, see (Auger et al., 2010). We shall show in this manuscript that assuming density dependent boat dispersal has important consequences on the global dynamics of the fishery. In particular, a stable limit cycle can also occur. However, we shall see that we can still prove the existence of an optimal number of fishing sites that maximizes the total capture of the multi-site fishery.

The manuscript is organized as follows. In the next section, we present a model that takes into account spatial effects by distinguishing L fishing areas connected by fast fish-density dependent movements of fishing vessels. To perform the analysis of this model, we build a reduced model, called aggregated model, which describes the dynamics of the total fish stock and the total fishing effort on the chain of sites. Studying this aggregated model, we show the existence of an optimal number of sites that maximizes the total fish catch at equilibrium.

2. The complete model. Let $n_s(t)$ be the fish density of the free stock (unattached to FADs) at time t . Let $n_i(t)$ be the fish density and $E_i(t)$ the fishing effort on FAD i at time t , $i \in [1, L]$. Let k_i be the fish carrying capacity for FAD i and k_s of the free stock. We assume that the coastal area has a global fish carrying capacity $K = k_s + \sum_{i=1}^L k_i$, which is constant. We assume that fish movements and boat displacements occur at a fast time scale τ , whereas fish growth and the dynamics of the fishery occur at a slow time scale $t = \epsilon\tau$, $\epsilon \ll 1$ being a small dimensionless parameter. Boats are supposed to move only to the left and right neighboring patches. The following system describes the time evolution of the fishery:

$$\begin{cases} \frac{dn_s}{d\tau} = \sum_{i=1}^L m_{si}n_i - \sum_{i=1}^L m_{is}n_s + \epsilon r_s n_s \left(1 - \frac{n_s}{k_s}\right) \\ \frac{dn_i}{d\tau} = m_{is}n_s - m_{si}n_i + \epsilon \left(r_1 n_i \left(1 - \frac{n_i}{k_i}\right) - qn_i E_i\right) \\ \frac{dE_i}{d\tau} = \beta_{i,i-1}(n_{i-1})E_{i-1} + \beta_{i,i+1}(n_{i+1})E_{i+1} - (\beta_{i-1,i}(n_i) + \beta_{i+1,i}(n_i))E_i + \epsilon(-c + pqn_i)E_i \end{cases} \quad (1)$$

where $i \in [1, L]$, we assume that the fish migration rate m_{ij} depend on the carrying capacity. If the carrying capacity of a patch i is high, fish are more likely to stay on this patch. If the carrying capacity is small, fish are rapidly leaving the patch. According to these assumptions, we choose $m_{ij} = \frac{m_0}{k_j}$. We assume that the movement rates for the fishing vessels, $\beta(n_i)$ depend on the fish stock in the particular patch:

$$\beta(n_i) = \frac{1}{\beta n_i + \beta_0} \quad (2)$$

When n_i increases, then $\beta(n_i)$ decreases. We can explain these rates of migration by the fact that the aim of the fleets owners is to increase their revenues. So, the fishing vessels try to operate in the most abundant patch. Consequently, the tendency of each fleet to leave a patch must increase when the stock is locally small. We also assume that boats leaving a patch distributes in equal proportion to go in the right and left directions, when the stock is very small, then the rate of migration should be the same in both directions. The fish population is assumed to follow a logistic growth with an intrinsic growth rate r_1 on FAD i , $i \in [1, L]$, and r_s on free zone. Like we said before we assume that the overall carrying capacity is a constant K and that:

$$\begin{cases} k_s & = \alpha K \\ \sum_{i=1}^L k_i & = (1 - \alpha)K. \end{cases} \quad (3)$$

Where $0 < \alpha < 1$ is the proportion of the total carrying capacity that is unattached to the FADs.

3. The aggregated model. From the complete (1), we apply aggregation methods (Auger et al.,1998) to obtain a reduced system: a two dimensional system of ordinary differential equations governing the total fish stock and the total fishing effort at the slow time scale. The sufficient conditions for a system to be perfectly as well as approximately aggregated have been investigated in the frame of general population models by Iwasa et al. (1987), Iwasa et al. (1989) and Levin and Pacala. (1997). Some aggregation methods permit to reduce a system with a large number of variables involving different time scales into an aggregated system with a few

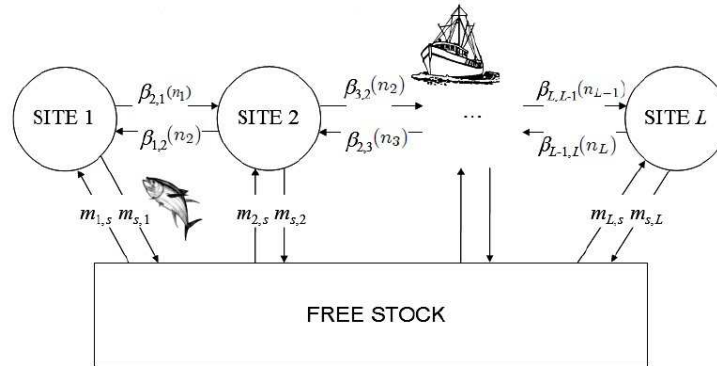


FIGURE 1. Schematic representation of the multi-site fishery model. Fishes move between every site and the free stock, while boats move between sites.

global variables. The method is based on perturbation technics and on the application of an adequate version of the Center Manifold Theorem. For instance, we can find several statements of the center manifold theorem in various contexts (ordinary differential equations, partial differential equations, delay differential equations, difference equations). Carr (1981), Hirsch (1970), and Sakamoto (1990) give a detailed description of the theorem with many applications. The center manifold theorem states some conditions under which there exists a regular manifold containing the non trivial part of the dynamics. This kind of manifolds is associated to non hyperbolic singularities and is local ones. In 1971, Fenichel (Fenichel, 1971) stated a theorem which provides conditions under which an invariant manifold persists to small enough perturbations, in the case of vector fields, the center Manifold Theorem given by Fenichel allows us to approximate by a Taylor expansion with respect to the small parameter ε the restriction of the complete model to this invariant manifold. The first order expansion gives the aggregated model. If this model is structurally stable, then the complete model is topologically equivalent to the reduced model and we can have a good idea of the behavior of the complete model by using the aggregated model. Our reduction method is based on this approach, see Poggiale (1994), Auger and Roussarie (1994), Auger and Poggiale (1996), Michalski et al. (1997). The aggregation of the complete model consists in supposing that the fast dynamics has attained a stable equilibrium and in substituting this fast equilibrium into the equations of the complete model. The first step to achieve aggregation is to neglect the small terms of the order of ε in Eq.(1) and to look for the existence of stable equilibria for its fast part.

3.1. Fast equilibria. The fast model is obtained by neglecting the slow dynamics, leading to equations (4):

$$\begin{cases} m_{si}n_i - m_{is}n_s & = 0 \\ \beta_{21}(n_1)E_1 - \beta_{12}(n_2)E_2 & = 0 \\ \beta_{L-1,L}(n_L)E_L - \beta_{L,L-1}(n_{L-1})E_{L-1} & = 0 \end{cases} \quad (4)$$

and for $i = 2, \dots, L - 1$

$$\beta_{i,i-1}(n_{i-1})E_{i-1} + \beta_{i,i+1}(n_{i+1})E_{i+1} - (\beta_{i-1,i}(n_i) + \beta_{i+1,i}(n_i))E_i = 0. \quad (5)$$

The fast model is conservative. At the fast time, the total fish density $n(t) = n_s + \sum_{i=1}^L n_i$ remains constant and the total fishing effort $E(t) = \sum_{i=1}^L E_i(t)$ remains constant.

A simple calculation leads to the following result:

$$\begin{cases} n_s^* = v_s^* n \\ n_i^* = v_i^* n \\ E_i^* = \mu_i^*(n) E \end{cases} \quad (6)$$

where for $i = 1, \dots, L$

$$\begin{cases} v_s^* = \frac{k_s}{K} \\ v_i^* = \frac{k_i}{K} \\ \mu_i^*(n) = \frac{\beta v_i^* n + \beta_0}{\beta(1-\alpha)n + L\beta_0} \end{cases} \quad (7)$$

The constants v_i^* represent the fast equilibrium proportions of the stock on each patch i , $i = 1, \dots, L$, whereas $\mu_i^*(n)$ admit the same interpretation for the fishing effort. As we see there is a fast equilibrium for each pair of values of the global variables n and E .

Coming back to the complete model (1), we substitute the fast equilibria and add the fish stock and the fishing effort equations. The state variables are replaced in terms of the fast equilibria as follows:

$$\begin{cases} n_i^* = v_i^* n \\ E_i^* = \mu_i^*(n) E \end{cases} \quad (8)$$

After some algebra, one obtains the following system of two equations governing the total fish stock and fishing effort variables at the slow time scales, that we call the aggregated model:

$$\begin{cases} \frac{dn}{dt} = rn(1 - \frac{n}{K}) - q(n)nE \\ \frac{dE}{dt} = (-c + pq(n)n) E \end{cases} \quad (9)$$

where

$$\begin{cases} r = \alpha r_s + (1 - \alpha) r_1 \\ q(n) = q \sum_{i=1}^L v_i^* \mu_i^*(n) = q \frac{\tau_1 n + (1 - \alpha)\beta_0}{\beta(1 - \alpha)n + L\beta_0} \end{cases} \quad (10)$$

and $\tau_1 = \beta \sum_{i=1}^L v_i^{*2}$

The dynamics of equation (9) is a good approximation of the real dynamics of the global variables in the complete equation (1) if equation (9) is structurally stable, which is the case, and ϵ is small enough, which is assumed.

3.2. Asymptotic behavior. The $\dot{E} = 0$ nullclines are two straight lines: $E = 0$ and $n = n^*$. where n^* is given by

$$n^* = \frac{(-pq(1 - \alpha)\beta_0 + c\beta(1 - \alpha)) + \sqrt{\Delta^*}}{2pq\tau_1} > 0 \quad (11)$$

where:

$$\Delta^* = (pq(1 - \alpha)\beta_0 - c\beta(1 - \alpha))^2 + 4Lc\beta_0pq\tau_1 > 0.$$

The $\dot{n} = 0$ nullclines are $n = 0$ and $r\left(1 - \frac{n}{K}\right) - q(n)E = 0$. The latter could be explicitly expressed as:

$$E = \frac{r}{q} \left(1 - \frac{n}{K}\right) \frac{(\beta(1 - \alpha)n + L\beta_0)}{\tau_1 n + (1 - \alpha)\beta_0} \quad (12)$$

The system (9) has 3 equilibrium $(0, 0)$, $(K, 0)$ and $(n^*, \frac{r}{q(n^*)}(1 - \frac{n^*}{K}))$. This last equilibrium belongs to the positive quadrant provided that $n^* < K$.

When $L\tau_1 < \beta(1 - \alpha)^2$, the nontrivial $\dot{n} = 0$ nullcline Eq. (12) has a maximum value in the positive quadrant, \bar{E} , and we denote \bar{n} the corresponding fish stock value. In the Appendix, the stability properties of these equilibrium points are shown. The origin $(0, 0)$ is always a saddle point. According to parameters values, we obtain the next five cases:

- If $L\tau_1 > \beta(1 - \alpha)^2$ and $n^* > K$ then (n^*, E^*) does not belong to the positive quadrant and $(K, 0)$ is a stable node.

- If $L\tau_1 > \beta(1 - \alpha)^2$ and $n^* < K$ then (n^*, E^*) belong to the positive quadrant and is globally asymptotically stable while $(K, 0)$ is a saddle.

- If $L\tau_1 < \beta(1 - \alpha)^2$ and $n^* > K$ then (n^*, E^*) does not belong to the positive quadrant and $(K, 0)$ is a stable node.

- If $L\tau_1 < \beta(1 - \alpha)^2$ and $\bar{n} < n^* < K$ then (n^*, E^*) belong to the positive quadrant and is globally asymptotically stable while $(K, 0)$ is a saddle.

- If $L\tau_1 < \beta(1 - \alpha)^2$ and $n^* < \bar{n} < K$ then (n^*, E^*) belong to the positive quadrant and is unstable. $(K, 0)$ is a saddle, In this case, there exists a limit cycle. see Fig. 7.

The catch per unit of time at equilibrium reads:

$$Y^* = q(n^*)n^*E^* = rn^* \left(1 - \frac{n^*}{K}\right) \quad (13)$$

It can be shown that Y^* has a maximum equal to $\frac{rK}{4}$ for $n^* = \frac{K}{2}$ and for the following number of sites L_{opt} such that:

$$L_{opt} = \frac{pq(1 - \alpha)K}{2c} + \frac{\beta}{2\beta_0} \left(\frac{pq}{2c} \sum_{i=1}^{L_{opt}} k_i^2 - (1 - \alpha)K \right) \quad (14)$$

The first term of the previous expression is similar to the optimal number of FADs that was obtained by Auger et al. (2010) in which we assumed that boats move from a FAD to the neighboring one at a constant rate, i.e. with a density independent dispersal of fishing boats. We can rewrite this expression as follows :

$$L_{opt}^{DD} = L_{opt}^{DI} + F \quad (15)$$

where L_{opt}^{DD} is the optimal number of FADs found in the density dependent migration case and L_{opt}^{DI} in the density independent case. Therefore, the following extra terms:

$$F = \frac{\beta}{2\beta_0} \left(\frac{pq}{2c} \sum_{i=1}^{L_{opt}} k_i^2 - (1 - \alpha)K \right) \quad (16)$$

quantify the effect of the density dependent dispersal of the fishing fleet.

$L_{opt}^{DD} < L_{opt}^{DI}$ if and only if

$$\sum_{i=1}^{L_{opt}^{DD}} k_i^2 < \frac{2c}{pq} \sum_{i=1}^{L_{opt}^{DD}} k_i$$

Therefore, if the previous relation holds, the number of optimal FADs in the density dependent case is less than in the density independent case and inversely. This occurs when the cost of the fishery is large enough or when the price of the unit of biomass is small enough.

case 1: If all sites are identical i.e. we have:

$$k_i = \frac{(1 - \alpha)K}{L}$$

we obtain

$$L_{opt}^{DD} = L_{opt}^{DI} = \frac{pq(1 - \alpha)K}{2c}. \quad (17)$$

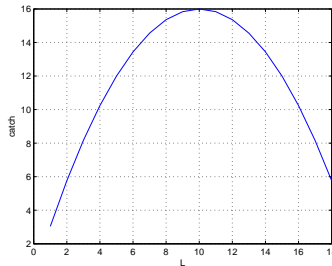


FIGURE 2. Case of identical patches: catch as a function of the number of sites showing a maximum for a value given by expression (17). $K = 100, rs = 0.55, r1 = 0.7, q = 1, c = 3, p = 1, \alpha = 0.4, \beta = 0.4, \beta_0 = 0.4$.

Figure 2 shows that the total capture shows a maximum for a numerical value L_{opt} which corresponds to the expression (17).

Case 2 : Different types of sites

We still consider a multisite fishery with L patches. Those L patches are assumed to be categorized into N groups. each group i is divided into N_i identical patches. $\sum_{i=1}^N K_i = (1 - \alpha)K$, $k_i = \frac{K_i}{N_i}$, and $\sum_{i=1}^N N_i = L$, where K_i is the carrying capacity of the group i ,

L_{opt} is given by expression (14). However, in general, it is not possible to calculate L_{opt} from expression (14) because L_{opt} also appears in the sum of the right hand side of equation (14). Therefore, we are now proposing a procedure that allows to calculate L_{opt} . For this, we assume that the multi-site fishery is composed of different groups of sites, such that a group has N_i sites and each site of each group $i = (1, N)$ has the same and given carrying capacity k_i . The procedure consists in fixing the number of sites in $N - 1$ groups and then after some calculation we can get the following expression which allows us to calculate explicitly the value of L_{opt}

(14).

$$\begin{aligned}
L_{opt} &= \frac{pq(1-\alpha)K}{2c} + \frac{\beta}{2\beta_0} \left(\frac{pq}{2c} \sum_{i=1}^N N_i \left(\frac{K_i}{N_i} \right)^2 - (1-\alpha)K \right) \\
&= \frac{pq(1-\alpha)K}{2c} + \frac{\beta}{2\beta_0} \left(\frac{pq}{2c} \sum_{i=1}^N \frac{K_i^2}{N_i} - (1-\alpha)K \right) \\
&= \frac{pq(1-\alpha)K}{2c} + \frac{\beta}{2\beta_0} \left(\frac{pq}{2c} \left(\sum_{i=1}^{N-1} \frac{K_i^2}{N_i} + \frac{K_N^2}{L_{opt} - \sum_{i=1}^{N-1} N_i} \right) - (1-\alpha)K \right)
\end{aligned} \tag{18}$$

then

$$L_{opt} = \frac{(a+c) + \sqrt{(a-c)^2 + 4b}}{2} \tag{19}$$

where

$$\begin{aligned}
a &= \frac{pq(1-\alpha)K}{2c} + \frac{\beta}{2\beta_0} \left(\frac{pq}{2c} \sum_{i=1}^{N-1} \frac{K_i^2}{N_i} - (1-\alpha)K \right) \\
b &= \frac{\beta pq}{4\beta_0 c} K_N^2 \\
c &= \sum_{i=1}^{N-1} N_i
\end{aligned}$$

Figure 3 shows an example where we consider two groups of patches. The carrying capacity of the first group is fixed $K_1 = 30$ with $N_1 = 4$.

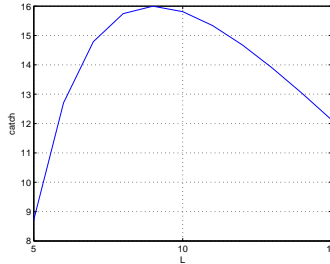


FIGURE 3. Vessels movements among L patches categorized into 2 groups. Catch as a function of the number of sites showing a maximum for a value given by expression:(19), $r_s = 0.55$, $r_1 = 0.7$, $\alpha = 0.3$, $K = 100$, $q = 1$, $c = 3.89$, $p = 1$, $\beta = 0.4$, $\beta_0 = 0.2$, $K_1 = 30$, $K_2 = 40$, $N_1 = 4$.

Figure 3 shows that the total capture shows a maximum for a numerical value $L_{opt} = 9$.

Figures 4 and 5 show the same as figure 3 but in the case of three and four groups respectively.

Figure 4 shows that the total capture shows a maximum for a numerical value $L_{opt} = 12$.

Figure 5 shows that the total capture shows a maximum for a numerical value $L_{opt} = 15$. It can be checked that the numerical values of L_{opt} corresponding to

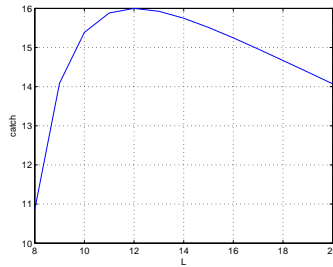


FIGURE 4. Vessels movements among L patches categorized into 3 groups. Catch as a function of the number of sites showing a maximum for a value given by expression (19). $r_s = 0.55, r_1 = 0.7, \alpha = 0.3, K = 100, q = 1, c = 2.706, p = 1, \beta = 0.4, \beta_0 = 0.2, K_1 = 20, K_2 = 22, K_3 = 28, N_1 = 4, N_2 = 3$.

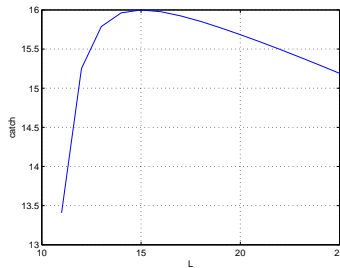


FIGURE 5. Vessels movements among L patches categorized into 4 groups. Catch as function as the number of patches.

the maximum observed respectively for the three previous curves, figures 3, 4 and 5 correspond to the values given by expression (19).

4. Discussion. Following Auger et al. (2010), we have developed our model as a synthetic representation of fisheries that use artificial structures (e.g., fish aggregating devices -FADs-, Dempster and Taquet., 2004) to attract fish (like some natural structures do, e.g., logs, seamounts). A number of authors reported that fish abundance around FADs depend on different factors including FAD type (Rountree et al., 1989, D'Anna et al., 1999) and FAD size (Rountree, 1989, Nelson, 2003). We used this information in our model to group the different fishing sites (i.e., FADs), assuming that FADs in each group were homogeneous (same type and size, and therefore same carrying capacity k_i) but that FADs between groups were different. This allowed us proving the existence of an optimal number of FADs that maximizes catch in the context of fish-density dependent movement of boats, and complementing the result established by Auger et al. (2010) in the simpler case of constant movement rates.

This work also shows that under some conditions on parameters, a stable limit cycle can occur. This result is similar to the one that was obtained in the case of a system of two patches with fish density dependent movement of boats, Mchich et al. (2002). In the present work, we could thus generalize this previous result to a

system of $N(N > 2)$ patches. the existence of a limit cycle has direct important consequences for the viability of the fishery. Indeed, for some time periods both the fish density and the fishing effort can be very close to zero (Figs 7 and 8). This could drive the fish population to extinction as well as provoke drastic decreases in the fishery activity. Therefore, such as in Mchich et al. (2002), one might try to control the system to avoid the occurrence of such a limit cycle in order to maintain the system at some desirable stable equilibrium.

We saw that, under some conditions on the model parameters (16), the optimal number of fishing sites in the present model was lower than in the model proposed by Auger et al. (2010). This situation is favored when the fishery operates under difficult conditions, i.e., high cost per unit of fishing effort c , low price per unit of fish p , or low fish catchability q . In these conditions, a shift in the fishery strategy, from boats moving constantly from site to site as in Auger et al. (2010), to a movement of boats that depends on fish density like here, would lead to the same catch per unit of time but on a reduced number of fishing sites, hence to larger benefits.

Of course, the use of aggregation methods allowed us to simplify the mathematical analysis of the complete model, a set of $2L + 1$ equations, into a simple two dimensional aggregated model. This simplification was possible because we assumed that there were two time scales, a fast one for movements of fish and boats between patches, and a slow one corresponding to the fish population growth and to the fishery dynamics.

In practice, it has been shown on numerical examples that as soon as $\epsilon = 10^{-1}$ or 10^{-2} the approximation made for "aggregating" the complete model into a reduced one is relevant, and the trajectories obtained with the aggregated model remain close to those obtained with the complete model (Poggiale and Auger, 2004). Therefore, if we think about a fish stock that grows annually and about boats and fish that change patches every week or so, then the method could be applied and the aggregated model used to make predictions about the complete system, as we did here. One could also consider the complete model without different time scales, i.e., $\epsilon = 1$, and in this case perform a numerical analysis. One could fix any parameter except the number of patches L and look for the existence and the stability of a unique positive equilibrium of the model. For each number of patches L , one could then calculate the total catch at equilibrium and look if there exists also an optimal number of patches.

A new case is interesting and new with respect to our previous study Auger et al., (2010) in which no limit cycle occurred. In the present model, the limit cycle is the result of the stock dependence of the vessels migration rates. It is assumed that vessels leave rapidly the fishing zone with decreasing fish stock density because the catch income becomes too low. As a consequence, although the fish stock decreases a lot, it cannot go to extinction because, since the fishing fleets also decrease drastically, the fish stock can recover. Then, the fishery revenue increases and new vessels participate to the fishery, so starting a new cycle. Belvèze (1984) has reported that the total sardine catch in the southern Moroccan sea has shown important fluctuations during the period of 1940 /1983. Mchich et al., (2002) have suggested that these fluctuations need not necessarily lead to extinction but could stabilize in a periodic variation merging periods of low and high fishery activity. This cyclic process of overexploiting periods followed by periods of recovering of the fishery activity should be a direct consequence of the efficiency of the fishery vessels. The model also suggests that the total process would be a long term process.

The reason is that two types of processes are involved in the dynamics, fast ones associated with decisions of vessels to rapidly increase their captures and slow ones related to the demography of the fish population and the variations of the investment in the fleets.

Appendix. Stability analysis

The Jacobian matrix $J(n, E)$ reads:

$$J(n, E) = \begin{bmatrix} r - \frac{2rn}{K} - q(n)E - q'(n)nE & -q(n)n \\ pE(q'(n)n + q(n)) & -c + pq(n)n \end{bmatrix}$$

(a) At the point $(0, 0)$, the Jacobian matrix:

$$J(0, 0) = \begin{bmatrix} r & 0 \\ 0 & -c \end{bmatrix}$$

has two real eigenvalues with opposite signs and thus $(0, 0)$ is a saddle point.

(b) At the point $(K, 0)$, the Jacobian matrix:

$$J(K, 0) = \begin{bmatrix} -r & -q(K)K \\ 0 & -c + pq(K)K \end{bmatrix}$$

has two real eigenvalues, one is negative $\lambda_1 = -r$ and $\lambda_2 = pq(K)K - c$. Two cases appear:

- if $n^* < K$, then $\lambda_2 > 0$ and $(K, 0)$ is a saddle point.
- if $n^* > K$, then $\lambda_2 < 0$ and $(K, 0)$ is a stable node.

(c) At the point $\left(n^*, \frac{r}{q(n^*)} \left(1 - \frac{n^*}{K}\right)\right)$, the Jacobian matrix $J(n^*, E^*)$ becomes:

$$J(n^*, E^*) = \begin{bmatrix} -\frac{rn^*}{K} - q'(n^*)n^*E^* & -q(n^*)n^* \\ pE^*(q'(n^*)n^* + q(n^*)) & 0 \end{bmatrix}$$

where

$$\det J(n^*, E^*) = \frac{pq(n^*)n^*E^*}{(\beta(1-\alpha)n^* + L\beta_0)^2} \times (\tau_1\beta(1-\alpha)(n^*)^2 + 2L\tau_1\beta_0n^* + L\beta_0^2) > 0.$$

On the other hand, we have:

$$\text{tr}J(n^*, E^*) = \frac{-rn^*}{K} - \frac{q\beta_0(L\tau_1 - \beta(1-\alpha)^2)n^*E^*}{(\beta(1-\alpha)n^* + L\beta_0)^2}$$

It is straightforward to see that $\text{tr}J(n^*, E^*) < 0$ whenever $L\tau_1 > \beta(1-\alpha)^2$. what yields the asymptotic stability of (n^*, E^*) .

When $L\tau_1 < \beta(1-\alpha)^2$, two different cases happen:

- $n^* > \bar{n}$, then $\text{tr}J(n^*, E^*) < 0$, and thus (n^*, E^*) is asymptotically stable.
- $n^* < \bar{n}$, then $\text{tr}J(n^*, E^*) > 0$, and thus (n^*, E^*) is unstable. In this case, there exists a limit cycle.

This can be proved by showing that the trace can be rewritten as

$$\begin{aligned} & \text{tr}J(n^*, E^*) \\ &= -rn^* \frac{\tau_1\beta(1-\alpha)(n^*)^2 + 2\beta_0\beta(1-\alpha)^2n^* + \beta_0(L\beta_0(1-\alpha) + LK\tau_1 - K\beta(1-\alpha)^2)}{K(\beta(1-\alpha)n^* + L\beta_0)(\tau_1n^* + (1-\alpha)\beta_0)} \end{aligned}$$

and then that its sign changes when n^* is smaller or larger than \bar{n} .

Fig. 6 shows a suitable Poincaré-Bendixson box where $L_{opt} = 3$, see Arrowsmith and Place (1992). A trajectory starting from an initial point A (which should be chosen with $n > K$ and $E > \bar{E}$) is turning around the unstable positive nontrivial equilibrium (n^*, E^*) and enters into the box at a point B. Any trajectory reaching the segment AB at a point M is entering into the box because the two components of its velocity are oriented towards the interior of the box. Any trajectory that enters the box cannot tend to the unique interior equilibrium (n^*, E^*) which is unstable. Consequently, by use of the Poincaré-Bendixson theorem, this proves the existence of a limit cycle within the domain delimited by this box. In this case, the total fishing effort as well as the total fish stock are, in the long term, varying periodically. Fig. 8 shows the time variations of the total fish stock and of the total fishing effort with respect to time. This case is interesting and new with respect to our previous study, (Auger et al., 2010) in which no limit cycle occurred. In the present model, the limit cycle is the result of the stock dependence of the vessels migration rates. It is assumed that vessels leave rapidly the fishing zone with decreasing fish stock density because the catch income becomes too low; As a consequence, although the fish stock decreases a lot, it cannot go to extinction because, since the fishing fleets also decrease drastically, the fish stock can recover. Then, the fishery revenue increases and new vessels participate to the fishery, so starting a new cycle.

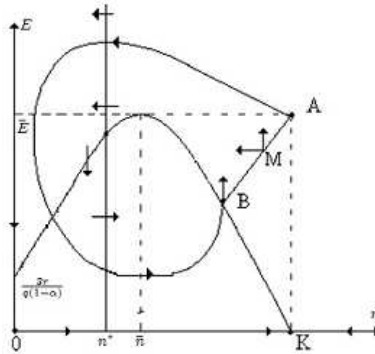


FIGURE 6. Poincaré-Bendixson box. Any trajectory entering the box is trapped in this box, in which the unique equilibrium is unstable.

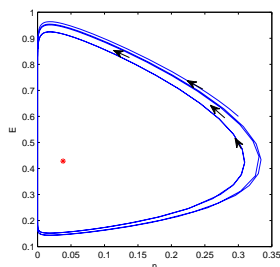


FIGURE 7. Phase portrait in the case of stable limit cycle. Parameters have been chosen as $L = 3, r = 0.1, K = 100, \alpha = 0.3, k_1 = 22, k_2 = 20, k_3 = 28, \beta = 0.05, \beta_0 = 0.4, p = 0.7, c = 0.008, q = 1$.

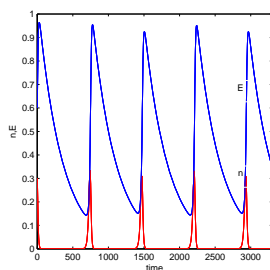


FIGURE 8. Time variations of the total fish stock and fishing fleet in the case of the stable limit cycle (same parameters as in Fig. 7).

REFERENCES

- [1] D. K. Arrowsmith and C. M. Place, “Dynamical Systems,” in “Differential Equations, Maps and Chaotic Behaviour,” Chapman and Hall, London, 1992.
- [2] P. Auger, C. Lett, A. Moussaoui and S. Pioch, *Optimal number of sites in artificial pelagic multi-site fisheries*, Canadian Journal of Fisheries and Aquatic Sciences, **67** (2010), 296–303.
- [3] P. Auger and J.-C. Poggiale, *Emergence of population growth models: Fast migration and slow growth*, J. Theor. Biol., **182** (1996), 99–108.
- [4] P. Auger and J.-C. Poggiale, *Aggregation and emergence in systems of ordinary differential equations*, Math. Comput. Model., **27** (1998), 1–21.
- [5] P. Auger and R. Roussarie, *Complex ecological models with simple dynamics: From individuals to population*, Acta Biotheor., **42** (1994), 111–136.
- [6] P. Auger, R. Bravo de la Parra, J.-C. Poggiale, E. Sánchez and T. Nguyen-Huu, *Aggregation of variables and applications to population dynamics*, in “Structured Population Models in Biology and Epidemiology,” Lecture Notes in Mathematics, **1936**, Springer, Berlin, 209–263, C. M. Clark, “Mathematical Bioeconomics: The Optimal Management of Renewable Resources,” 2nd ed., A. Wiley-Interscience, 2008.
- [7] P. Auger, R. Bravo de la Parra, J.-C. Poggiale, E. Sánchez and L. Sanz, *Aggregation methods in dynamical systems variables and applications in population and community dynamics*, Physics of Life Reviews, **5** (2008), 79–105.
- [8] H. Belvéze, “Biologie et Dynamique des Populations de Sardine (*Sardina Pilchardus Walbaum*) Peuplant les Cotes Atlantiques Marocaines et Propositions pour un Aménagement des Pêcheries,” Ph.D thesis, Bretagne Occidentale University, 1984.
- [9] J. Carr, “Applications of Centre Manifold Theory,” Applied Mathematical Sciences, **35**, Springer-Verlag, New York-Berlin, 1981.

- [10] D. K. Dao, P. Auger and H. T. Nguyen, *Predator density dependent prey dispersal in a patchy environment with a refuge for the prey*, South African Journal of Science, **104** (2008), 180–184.
- [11] T. Dempster and M. Taquet, *Fish aggregation device (FAD) research: Gaps in current knowledge and future directions for ecological studies*, Reviews in Fish Biology and Fisheries, **14** (2004), 21–42.
- [12] A. El Abdllaoui, P. Auger, R. Bravo de la Parra, B. Kooi and R. Mchich, *Effects of density-dependent migrations on stability of a two-patch predator-prey model*, Mathematical Biosciences, **210** (2007), 335–354.
- [13] N. Fenichel, *Persistence and smoothness of invariant manifolds for flows*, Indiana University Mathematical Journal, **21** (1971/1972), 193–226.
- [14] A. Fonteneau, J. Ariz, D. Gaertner, T. Nordstrom and P. Pallares, *Observed changes in the species composition of tuna schools in the Gulf of Guinea between 1981 and 1999, in relation with the Fish Aggregating Device fishery*, Aquatic Living Resources, **13** (2000), 253–257.
- [15] C. Girard, S. Benhamou and S. L. Dagorn, *FAD: Fish Aggregating Device or Fish Attracting Device? A new analysis of yellowfin tuna movements around floating objects*, Animal Behaviour, **67** (2004), 319–326.
- [16] R. Hilborn and P. Medley, *Tuna purse-seine fishing with Fish-Aggregating Devices (FAD)–Models of tuna FAD interactions*, Canadian Journal of Fisheries and Aquatic Sciences, **46** (1989), 28–32.
- [17] R. Hilborn, F. Micheli and G. A. De Leo, *Integrating marine protected areas with catch regulation*, Canadian Journal of Fisheries and Aquatic Sciences, **63** (2006), 642–649.
- [18] M. W. Hirsch, C. C. Pugh and M. Shub, *Invariant manifolds*, Bull. Am. Math. Soc., **76** (1970), 1015–1019.
- [19] Y. Iwasa, V. Andraesen and S. A. Levin, *Aggregation in model ecosystems I. Perfect aggregation*, Ecological Modelling, **37** (1987), 287–302.
- [20] Y. Iwasa, S. A. Levin and V. Andraesen, *Aggregation in model ecosystems. II. Approximate aggregation*, IMA Journal of Mathematics Applied in Medicine and Biology, **6** (1989), 1–23.
- [21] H. Kakimoto, *Artificial fishing reef studies and effects*, Japanese Institute of Technology on Fishing Ports, Grounds and Communities (JIFIC), in Japanese, **II** (2004), 150–178.
- [22] C. H. Lan and C. Y. Hsui, *The deployment of artificial reef ecosystem: Modelling, simulation and application*, Simulation Modelling Practice and Theory, **14** (2006), 673–675.
- [23] R. Mchich, P. Auger and J.-C. Poggiale, *Effect of predator density dependent dispersal of prey on stability of a predator-prey system*, Mathematical Biosciences, **206** (2007), 343–356.
- [24] R. Mchich, P. Auger, R. Bravo de la Parra and N. Raïssi, *Dynamics of a fishery on two fishing zones with fish stock dependent migrations: Aggregation and control*, Ecol. Model., **158** (2002), 51–62.
- [25] J. Michalski, J.-C. Poggiale, R. Arditi and P. Auger, *Macroscopic dynamic effects of migrations in patchy predator-prey systems*, J. Theor. Biol., **185** (1997), 459–474.
- [26] G. Moreno, L. Dagorn, G. Sancho and D. Itano, *Fish behaviour from fishers' knowledge: The case study of tropical tuna around Drifting Fish Aggregating Devices (DFADs)*, Canadian Journal of Fisheries and Aquatic Sciences, **64** (2007), 1517–1528.
- [27] A. Moussaoui, *Effect of a toxicant on the dynamics of a spatial fishery*, African Diaspora Journal of Mathematics, **10** (2010), 122–134.
- [28] P. A. Nelson, *Marine fish assemblages associated with Fish Aggregating Devices (FADs): Effects of fish removal, FAD size, fouling communities, and prior recruits*, Fishery Bulletin, **101** (2003), 835–850.
- [29] S. Levin and S. Pacala, *Theories of simplification and scaling of spatially distributed processes*, in “Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions” (eds. D. Tilman and P. Kareiva), Princeton University Press, Princeton, (1997), 204–232.
- [30] S. Pioch, “Les ‘Habitats Artificiels’: Élément de Stratégie pour une Gestion Intégrée des Zones Côtières? Essai de Méthodologie d’Aménagement en 325 Récifs Artificiels Adapté à la Pêche Artisanale Côtière,” Ph.D. thesis, Paul Valéry University, Montpellier, Tokyo University of Marine Science and Technology, Tokyo, in French, 2008.
- [31] J.-C. Poggiale, “Applications des Variétés Invariantes a la Modélisation de l’Hétérogénéité en Dynamique des Populations,” Ph.D. thesis, Bourgogne University, Dijon, in French, 1994.
- [32] J.-C. Poggiale and P. Auger, *Impact of spatial heterogeneity on a predator-prey system dynamics*, Comptes Rendus Biologies, **327** (2004), 1058–1063.

- [33] R. A. Rountree, *Association of fishes with fish aggregating devices: Effects of structure size on fish abundance*, Bulletin of Marine Science, **44** (1989), 960–972.
- [34] K. Sakamoto, *Invariant manifolds in singular perturbations problems for ordinary differential equations*, Proc. Roy. Soc. Ed. Sect. A, **116** (1990), 45–78.

Received July 18, 2010; Accepted March 08, 2011.

E-mail address: ali.moussaoui@ird.fr

E-mail address: pierre.auger@ird.fr

E-mail address: christophe.lett@ird.fr