Aquat. Living Resour. 12 (2) (1999) 77-88 / © Ifremer/Cnrs/Inra/Ird/Cemagref/Elsevier, Paris

SHADYS ('simulateur halieutique de dynamiques spatiales'), a GIS based numerical model of fisheries. Example application: the study of a marine protected area

Olivier Maury *, Didier Gascuel

École nationale supérieure agronomique de Rennes (ENSAR), Laboratoire halieutique, 65, route de St-Brieuc, 35042 Rennes cedex, France.

Received September 23, 1998; accepted January 21, 1999.

Abstract – This paper presents the simulator SHADYS ('simulateur halieutique de dynamiques spatiales'). SHADYS is a tool devoted to the representation of spatial processes involved in fisheries dynamics. It puts together three fundamental entities in an explicit spatio-temporal way: the environment, the fish populations under consideration and the fishing fleet. It is based on simple, realistic and well identified mechanisms (density-dependent habitat selection, advection and diffusion of a fish population, fishermen search strategy, etc.) implemented by interfacing numerical models with a GIS (geographic information system). As a virtual laboratory, SHADYS allows experiments to be performed in a theoretical world, such experiments being generally impossible to perform in reality. As an illustration, different scenarios of a marine refugia-based management have been explored using the SHADYS simulator. Different simulations are conducted to assess the short-term effects on yield of a marine protected area. It is shown that for diffusive or migratory species, the yield per recruit as a function of the protected surface can reach a maximum. Under this condition, the concept of 'space overfishing' is meaningful. Protected areas then behave like 'sources' and exploited areas like 'sinks'. For resident populations, the larger the protected area is, the lower the catches per recruit are. Regarding the spatial distribution of the fishing effort, it is shown that if it is spatially distributed in order to maximize catches, then fishing boats will slowly tend to be distributed all along the boundaries of the protected area. © Ifremer/Cnrs/Inra/Ird/Cemagref/Elsevier, Paris

Population dynamics / simulator / diffusion-advection / fishing effort distribution / overfishing / marine refuge / GIS

Résumé – SHADYS (simulateur halieutique de dynamiques spatiales), un simulateur numérique de pêcheries lié à un système d'informations géographiques (SIG). Application à l'étude d'une réserve marine. L'objectif de cet article est la présentation du simulateur SHADYS (simulateur halieutique de dynamiques spatiales). SHADYS est un outil voué à la représentation des processus spatiaux en jeu dans la dynamique des pêcheries. Il met en relation de manière spatio-temporellement explicite trois entités fondamentales : l'environnement, les populations représentées et la flottille de pêche. Il est fondé sur des mécanismes simples, réalistes et clairement identifiés (sélection densité-dépendantes de l'habitat, advection et diffusion d'une population de poissons, stratégies de recherche développées par les pêcheurs, etc.) mis en œuvre grâce au couplage de modèles numériques et d'un système d'informations géographiques (SIG). SHADYS est un laboratoire virtuel qui permet de réaliser sur un monde théorique des expériences généralement impossibles en réalité. En guise d'illustrations, différents scénarios de gestion sont testés à l'aide du simulateur pour évaluer les effets, à court terme, de la mise en place d'une réserve marine sur la production. On montre ainsi que, pour des espèces « diffusives » ou migratrices, la courbe de rendement par recrue en fonction de la surface protégée peut passer par un maximum. Dans ces conditions, on peut parler de « surexploitation de l'espace ». Les réserves marines se comportent alors comme des « sources » et les zones exploitées comme des « puits ». À l'inverse, pour des populations sédentaires, plus la taille de la réserve est importante, plus les captures par recrue sont faibles. En ce qui concerne la répartition spatiale de l'effort de pêche, on montre que s'il se répartit de manière à maximiser les captures, les navires de pêche vont progressivement se concentrer le long des frontières de la zone protégée. © Ifremer/Cnrs/Inra/Ird/Cemagref/Elsevier, Paris

Dynamique des populations / modèle de simulation / diffusion-advection / répartition de l'effort de pêche / surexploitation de l'espace / réserve marine / SIG

* Corresponding author, e-mail: maury@ird.fr

1. INTRODUCTION

A fishery is a complex system made up of dynamically interacting subsystems. Because each component (either environmental components, resource components or anthropic components) of the fishery system is heterogeneously distributed in space, spatial co-occurrence of the elements is a necessary condition for their interaction. Thus, space is a fundamental functional feature to be taken into account when modelling a complex system such as a fishery. By means of simple models, several authors have shown the importance of taking into account space at different scales in population dynamics [2, 10, 11, 14, 20, 33]. In fisheries science, numerous studies have brought to the fore the central role of space in fisheries dynamics [12, 21, 34, 35] and in stock assessment [9, 13], and the potential benefit one could gain from spatially managing fisheries by setting up temporary effort bans in a given area [27] or marine protected area [1].

In this perspective, the simulator SHADYS (simulateur halieutique de dynamiques spatiales) is devoted to the representation and the study of complex spatial fisheries behaviors at different spatio-temporal scales [23]. It enables, on one hand, the study of fish distribution in relation to their habitat and, on the other, the study of resource/fishermen spatial interactions. SHADYS is based on simple and well-known properties and mechanisms implemented in a fully spatially explicit manner by means of a GIS. The aim of this paper is to provide a general presentation of SHADYS.

The main assumptions of the SHADYS simulator, its architecture and spatially explicit implementation are first presented. Then, as an illustration, SHADYS is used through different simulations to characterize various potential consequences of a refugia-based management. Indeed, the design of protected areas (refuges, natural parks, etc.) is one of the most common tools in terrestrial populations management and it is becoming more and more important in marine environment applications. Two kinds of effects potentially result from the creation of protected areas: short-term changes in yield per recruit (Y/R), aggregate biomasses and reproductive biomasses and long-term effects like conservation of specific and genetic biodiversity, increasing population viability and habitat protection [7].

The simulations presented attempt to show as simply as possible the short-term effects of the setting-up of a protected area in terms of yield per recruit. Indirect consequences of marine refuges on fishing effort distributions are also investigated.

2. PRESENTATION OF THE SIMULATOR SHADYS

SHADYS is a spatialized fisheries simulator based on a GIS interface (savane software © Orstom 1995). The modelled ecosystem is made up of subsystems whose dynamics are coupled together. In this way, SHADYS puts together three fundamental entities in an explicit spatio-temporal way: the environment, the fish populations considered and the fishing fleet (*figure 1*).

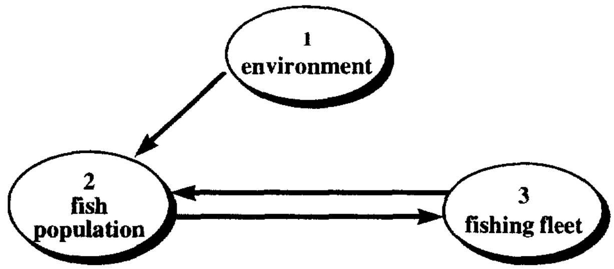

Figure 1. SHADYS framework is based on three fundamental entities: environment, population and fishing fleet.

2.1. Environment modelling

From a statistical point of view, the distributions of environmental components are neither random nor uniform. On the contrary, we can observe discrete aggregative structures (patches) or continuous structures, such as gradients [18]. This is what Kolosa and Rollo [15] termed structural heterogeneity. SHADYS allows the heterogeneity of artificial environmental landscapes drawn from marine benthic biotopes to be varied.

The landscape structure is generic enough to be transposed to other types of ecosystems such as a pelagic one[1]. Both patchy and gradient distributions of environmental factors are combined in the SHADYS environment.

At each time step, a linear gradient moves from one side of the SHADYS space to the other with sinusoidal speed which mimics seasonal variability. It can be considered as a model of a seasonal variable such as temperature for instance. For convenience sake, we term it the thermic gradient. Patches are distributed in space. They can, for instance, represent rocky zones spread over a muddy bottom. The spatial structuration, distribution, diversity and fragmentation of patches can be varied by discrete amounts in the simulator. A self-referencing process, analogous to fractal surface development, is used to generate these heterogeneity levels and to vary them with a single parameter. Patch distribution is then randomly perturbed to avoid too great a symmetry (*figure 2*). If rocky zones (in black in

[1] Many different local enrichment phenomena cover high seawaters and constitute a real 'panther skin' [19]. In SHADYS, patches are spread into space. They can also be, for instance, considered as a representation of productive 'oasis' covering the oligotrophic pelagic environment.

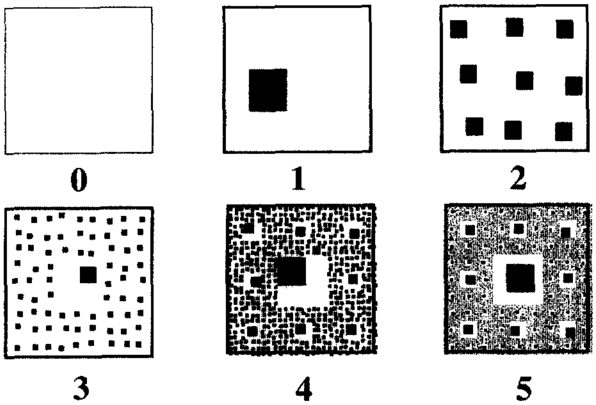

Figure 2. The six different levels of patch heterogeneity in SHADYS space.

figure 2) are considered, the landscape is totally non-connective. By contrast, if muddy zones (in white) are considered, the landscape is totally connective. Thus, the distribution of patches is either connective or not.

All the environmental variables (here, temperature and bottom characteristics) are distributed in time and space. Environmental heterogeneity is the complex combination of their spatio-temporal distribution. That is the measurable heterogeneity [15]. From the perspective of coupled systems, the heterogeneity of the environmental landscape constrains the spatio-temporal distribution of the population [3, 21]. Thus, it is important to know the response of the population to its environment. That response enables, at each point in space, what we call the 'biotic affinity' of the environment to be defined. This is estimated from the structural landscape and noted $ba_{x,y}$. It matches the functional heterogeneity, the local fitness as it is perceived by the fish which synthesize the local suitability of an habitat [8, 21, 31]. We can then transform the measurable heterogeneity of a multivariate environmental landscape into the variability of a single functional parameter, the biotic affinity:

$$ba_{x,y,t} = f(e1_{x,y,t}, e2_{x,y,t}, \ldots, en_{x,y,t}) \quad (1)$$

where $ba_{x,y,t}$ is the biotic affinity at point x, y and time t and $ei_{x,y,t}$ the environmental factor i at x,y,t.

As in the basin model of MacCall [21], the biotic affinity is represented as an altitude: the lower the altitude is, the stronger the biotic affinity is and the more favorable the place is. In SHADYS, the biotic affinity is the sum of a linear function of the discrete patchy factor and a non-linear function of the gradient factor [23]:

$$ba_{x,y,t} = \delta(T_{x,y,t} - Topt)^2 + \beta \cdot bc_{x,y,t} \quad (2)$$

where T is the local temperature, $Topt$ the optimal temperature, bc the biotic constant linked to the bottom characteristics and δ, β parameters.

The non-linear relationship used to relate biotic affinity to the temperature is based on the definition of an optimal temperature. It defines a range of temperatures where the biotic affinity is almost constant. The more fish depart from that 'optimal environmental window' [6], the more rapidly the biotic affinity decreases. Functionally, the transition between different patches is gradual. Muddy bottoms are separated from rocky zones by an ecotone where the biotic affinity exhibits intermediate values. Thus, in SHADYS, the biotic affinity is a continuous variable in space and time. By representing the biotic affinity as an altitude, SHADYS converts, for each period, temperature and bottom characteristic maps into a tri-dimensional numerical model of biotic affinity (NMBA) (*figure 3*). The NMBA then enables the biotic affinity of the population considered, in each area and time period, to be known. They provide a heuristic representation of the environmental landscape's functional heterogeneity related to the population considered. NMBA heterogeneity has two components: one is continuous and temporally variable (the thermic gradient) and the other is equally continuous but patchily distributed (the bottom characteristics).

The combination of these simple patchy and gradient structures enables the simulation of complex landscapes characterized by a very large diversity of biotic affinity and connectivity, fragmentation and structuration variables by discrete levels.

2.2. Fish population dynamics modelling

Recruitment is assumed to be distributed in proportion to the NMBA at time 0. The population modelling takes into account the age structure but a single cohort is considered after recruitment. An advection-diffusion-reaction model is used to represent the spatial dynamics of recruited stages. In such a model, movement has a random component (diffusion) and a directed one (advection). The model is based on a partial differential equation, continuous in time and space [4, 26, 34, 35]:

$$\frac{\partial N}{\partial t} = \frac{\partial\left(D \cdot \frac{\partial N}{\partial x}\right)}{\partial x} + \frac{\partial\left(D \cdot \frac{\partial N}{\partial y}\right)}{\partial y} - \frac{\partial(uN)}{\partial x} - \frac{\partial(vN)}{\partial y} - (M + F) \cdot N \quad (3)$$

where $N = N_{x,y,t}$ is the fish density at point (x,y) at time t, $D = D_{x,y,t}$ the diffusivity coefficient, $u = u_{x,y,t}$ and $v = v_{x,y,t}$ the advection coefficients, $M = M_{x,y,t}$ the local natural mortality rate and $F = F_{x,y,t}$ the local fishing mortality rate. The different processes considered to influence population dynamics locally are displacement and mortality (*figure 4*).

The subsystems interact such that the environmental functional heterogeneity constrains spatial and temporal variations in the directed movement parameters:

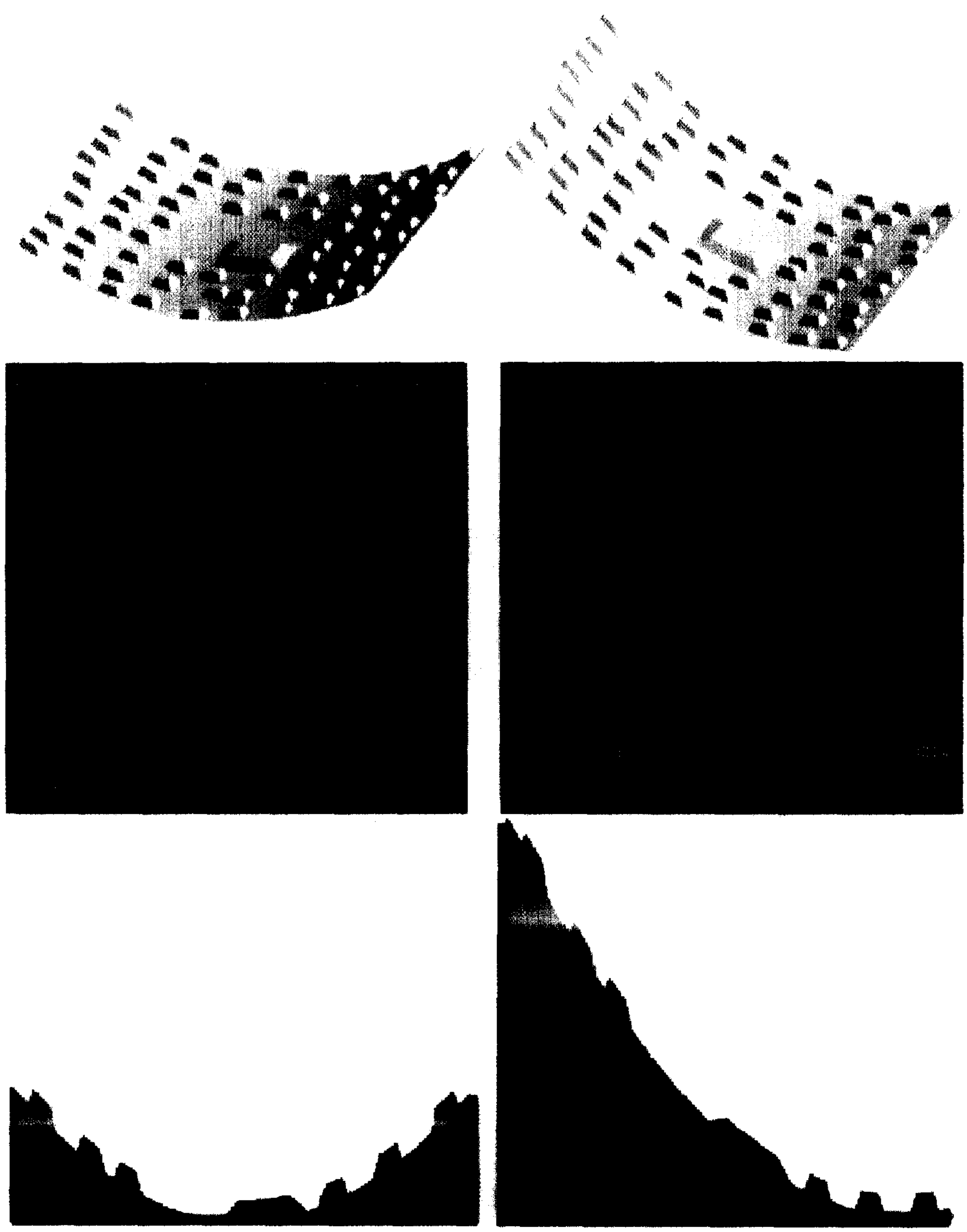

Figure 3. The 'numerical model of biotic affinity' (NMBA) combines patch and gradient heterogeneity in a functional perspective. It is represented by a topography. The higher the altitude is, the more unfavorable the environment is. On the left, the NMBA from January 1; on the right, the NMBA from April 1. On the top, three dimensional views; in the middle, maps of biotic affinity (from black for high biotic affinity to red for low biotic affinity); on the bottom, cross sections along the red lines.

$$u_{x,y,t} = -\frac{\partial(vp_{x,y,t})}{\partial x} \quad \text{and} \quad v_{x,y,t} = -\frac{\partial(vp_{x,y,t})}{\partial y} \qquad (4)$$

where $vp_{x,y,t}$ is the vital potential at point (x,y) and time t, which is defined as being equal to the biotic affinity $ba_{x,y,t}$ corrected by a density-dependent effect with a generalized 'constant slope' equation [21]:

$$\begin{aligned} vp_{x,y,t} &= ba_{x,y,t} \cdot \left(1 - \left(\frac{N_{x,y,t}}{K_{x,y,t}}\right)^{\gamma}\right) \\ &= ba_{x,y,t} - K_t \cdot N^{\gamma}_{x,y,t} \end{aligned} \qquad (5)$$

where γ is a constant characterizing the shape of the density-dependence relationship and $K_{x,y,t}$ the local

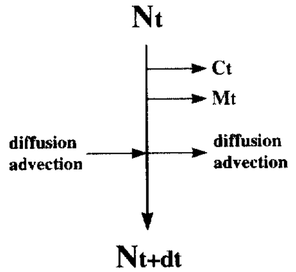

Figure 4. Schematization of the different process considered locally to model fish density (N) from time t to time $t+dt$. C represents catches and M the natural mortality coefficient.

carrying capacity (proportional to $\sqrt[\gamma]{ba_{x,y,t}}$) and k a spatial constant.

Reorganizing equations (3), (4) and (5), it is interesting to note that the density-dependent part of the advection term in equation (3) acts, in fact, like a spatially varying diffusion term (equation (6)).

$$\frac{\partial N}{\partial t} = \frac{\partial\left((D + k \cdot \gamma \cdot N^{\gamma}) \cdot \frac{\partial N}{\partial x}\right)}{\partial x} + \frac{\partial\left((D + k \cdot \gamma \cdot N^{\gamma}) \cdot \frac{\partial N}{\partial y}\right)}{\partial y} + \frac{\partial\left(\frac{\partial ab}{\partial x} \cdot N\right)}{\partial x} + \frac{\partial\left(\frac{\partial ab}{\partial y} \cdot N\right)}{\partial y} - Z \cdot N \qquad (6)$$

A numerical solution of equation (6) is obtained using an 'alternating-direction' implicit method [28] on a 10 000-cell (100 × 100) square grid with six time periods a month (for more details about the numerical approximation, see *appendix*). All the forcing parameters are potentially spatially variable. Closed reflective boundaries are used (Neumann conditions: $\frac{\partial N}{\partial x} = \frac{\partial N}{\partial y} = 0$ at the boundaries) to model an impassable frontier such as a shore for instance.

Thus, fish move in relation to the local gradient of vital potential and swim towards a more suitable environment. Like a liquid, they 'flow' into canyons to the bottom of NMBA's valleys and the only information they perceive from the environment is the local gradient of vital potential. Fish distribution must be seen as dynamically constrained by the environment. In SHADYS, the seasonally moving 'biotic affinity landscape' leads the fish population to move from one side of the space to the other (*figure 5*). In this case, the population is always 'late' compared to the environment. It is perpetually swimming after the inaccessible moving optimal environment, encountering local holes or bumps during its displacements. Those heterogeneous 'obstacles' create particular structures such as over or under-concentrations and plumes [23]. The NMBA shown in *figure 5* is connective (the population moves into a connective matrix). In a non-connective matrix, holes would have replaced bumps and would trap fish locally.

Each simulation concerns a single cohort from recruitment to death. Individual growth is modelled with a Von Bertalanffy growth curve and an allometric weight/length relationship is used to compute yield and biomass.

2.3. Fishing fleet modelling

A fishing fleet composed of n vessels is simulated. Fishing gear selectivity is assumed to be the same for all boats and is modelled with a sigmoid length-dependent relationship:

$$s = \frac{l^{\beta}}{l_c^{\beta} + l^{\beta}} \qquad (7)$$

where s is the selectivity, β a constant, l_c the 'half catch' length (which corresponds to $s = 1/2$) and l the fish length.

For each time period, each boat is fishing in a cell chosen in a given fishing zone which does not necessarily cover the whole space. A coefficient α is used to characterize the vessel's fishing strategy. In each time period, each fisherman is assumed to assess randomly a fraction α of the total number of spatial cells and to apply the vessel's fishing effort in the most abundant cell he is aware of [9]. α varies from 0 to 1. If $\alpha = 0$, fishing effort is attributed randomly; if $\alpha = 1$, the abundance of fish in all cells is assumed to be perfectly known by the fishermen and the fishing effort is exerted in the cell with the highest abundance. SHADYS allows the simulation of cooperation between fishermen or spying. In this case of cooperation or spying, the search capacity of one vessel is used by all the others. Each vessel can be individually endowed with a low detection capacity of high fish concentrations, which enables it to be hardly more effective than if it fished randomly. However if several vessels fish in the same area, their effort is allocated to the most abundant cell encountered by all the vessels located in the fishing zone considered. Under such conditions, the more numerous the vessels in a zone, the greater is their capacity to locate fish concentrations. The increase in fishing effort has then a positive impact on the local fishing power [17] of each vessel.

3. APPLICATION: THE SIMULATION OF A MARINE PROTECTED AREA

As an illustration of SHADYS capabilities, different simulations are conducted to characterize the potential effects of a marine refuge. To allow easy displacement of the population, they are based on a mid-heterogene-

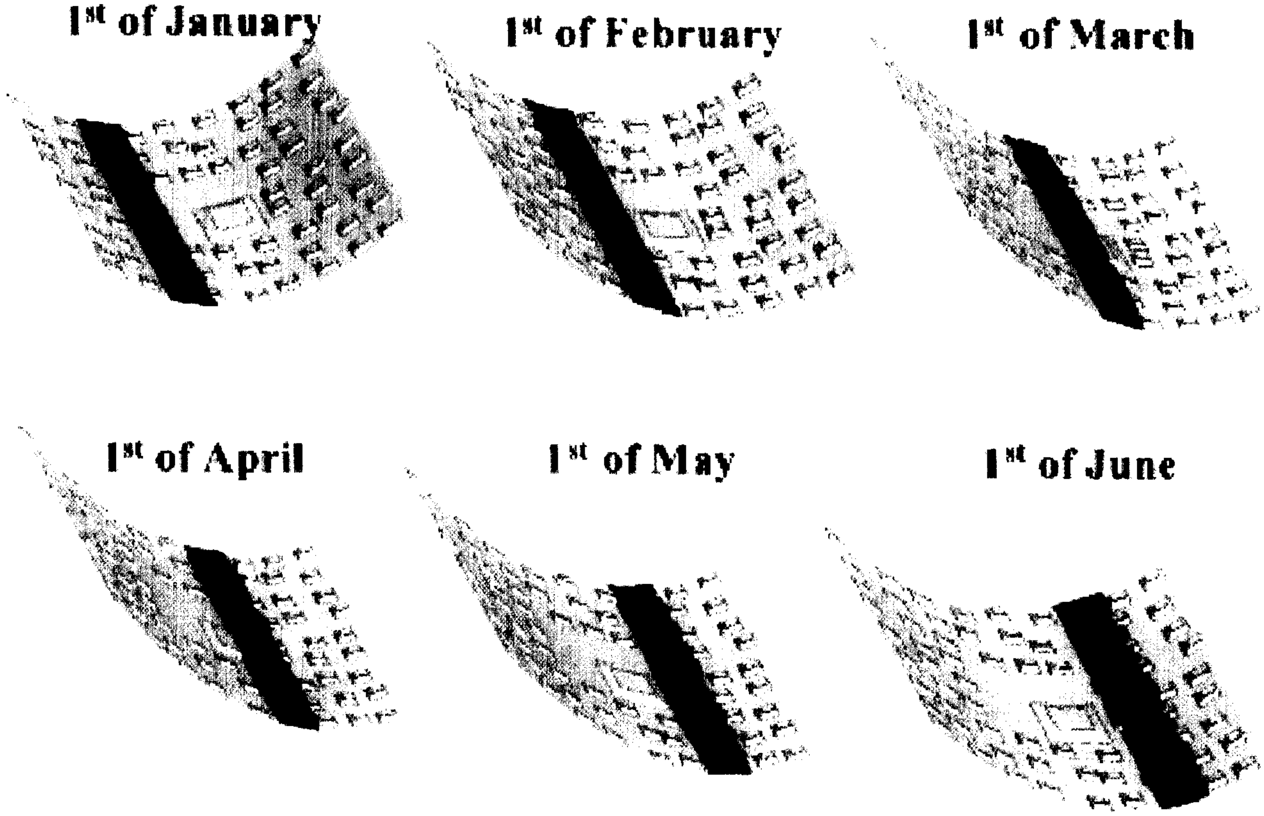

Figure 5. As a liquid, fish population (in color) flows toward the valley of the theoretical dynamical NMBA (in grey) and follows the most suitable environmental places which are moving continuously according to a seasonal oscillation.

ity level (3) (see *figure 2*) and a connective landscape. Fishing pressure corresponds to a 1 000-vessel fleet, randomly distributed in space ($\alpha = 0$), and the fishing mortality level is sufficiently high to induce a marked growth overfishing situation. A marine refuge is simulated at the centre of the SHADYS space. Its location is assumed to result from external constraints (protection of other species for instance). Four characteristic types of population are distinguished:

– a resident one which experiences no seasonal movement ($\delta = 0$ in equation (2)) and a very low diffusion value ($D \approx 0$ in equation (3));

– a weakly diffusive one which experiences no seasonal movement ($\delta = 0$ in equation (2)) and a medium diffusion value (low D in equation (3));

– a highly diffusive one which experiences no seasonal movement ($\delta = 0$ in equation (2)) and a high diffusion value (high D in equation (3));

– a 'migratory' one which experiences a seasonal movement ($\delta >> 0$ in equation (2)) and a small diffusion value (low D in equation (3)).

Then for each stock and fleet parameterization, various surface values of the protected zone are simulated.

For a resident stock (*figure 6a, b*), reducing the fraction of the stock available to the vessels by protecting an area induces a decrease in yield per recruit. This statement must nevertheless be qualified. Indeed, increasing the protected surface does not increase linearly the protected fraction of the stock. For instance in *figure 6b*, Y/R sometimes increases slightly when the protected surface increases. This is mainly due to the spatial heterogeneity of the population. At that portion of the curve (65 % of the total surface), the increase in the area of the refuge covers an uninhabited zone. Consequently, the stock is not less available but the effort is concentrated on the non-protected area and production rises.

For a diffusive stock (*figure 6c–f*), the consequences a marine refuge will have on yield per recruit depend on the diffusivity level of the stock considered. Nevertheless, in most cases, the yield per recruit of an overfished diffusive stock sharply increases before falling to zero when the protected surface increases to 100 %. In this case, the effect of a protected area is a decrease

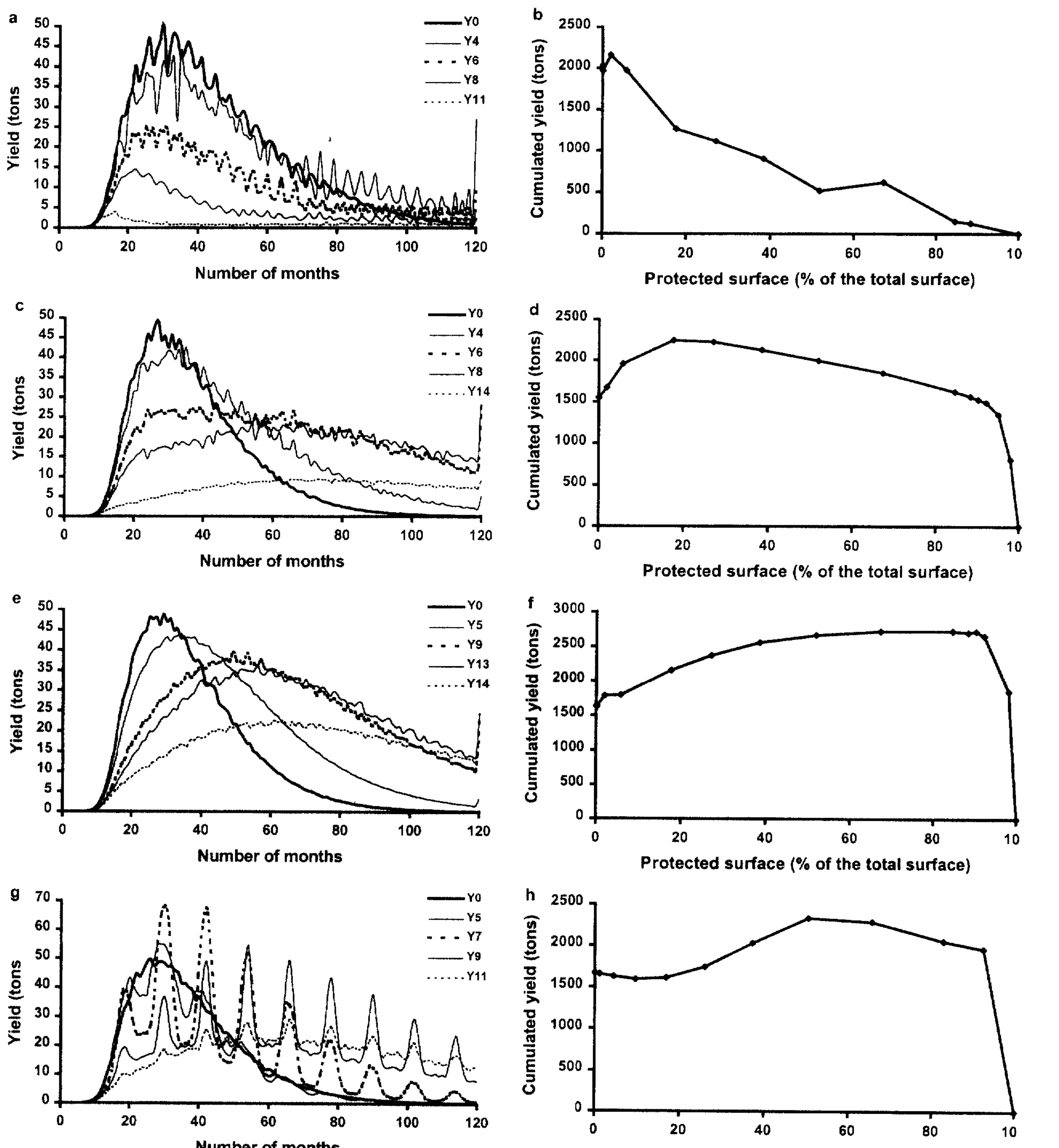

Figure 6. On the left, a single cohort yield curve as a function of time (i.e. age) for different surface values of the protected zone (Y_0, no protected zone: Y_5 to Y_{14}, increasing surface of the protected zone). On the right, yield cumulated on the whole cohort life versus the protected surface. (a, b), A resident species: (c, d), a medium diffusive species: (e, f), a highly diffusive species: (g, h), a 'migratory' species.

in the effective effort for constant nominal effort. Thus, by reducing the overall catchability, the effect of the marine refuge on yield per recruit is a shift in maximal production to older ages: the more protected the fish are, the later (older and bigger) they will be caught.

For a migratory species, seasonally moving from one side of SHADYS space to the other (*figure 5*), the curve of yield per recruit against protected surface reaches a maximum as with diffusive species. The main difference between them is the temporal variability in the production induced by the refuge (*figure 6g, h*); the population is alternately inside and outside the protected zone. The solution for stabilizing production could be a moving refuge following stock movements, or a large refuge protecting the population wherever it is.

To study the influence of a marine refuge on the fishing effort distribution, another simulation was conducted where the fishing fleet was assumed to have a search strategy aimed at locating the highest fish density zones ($\alpha = 0.005$). At the beginning of the simulation (*figure 7*), the population is little exploited and heterogeneously covers the whole area according to NMBA's constraints. At the end of the simulation, the highly exploited population is concentrated in the protected zone.

Because the fish population is diffusive and fishermen have a 'deterministic' strategy (search for the highest fish density), the fishing effort distribution inevitably evolves towards a distribution along the refuge boundaries where highest fish densities are found (*figure 7*). In the refuge, spatial fish density follows a Gaussian distribution (apart from the landscape structure, that is the consequence of isotropic diffusion with open frontier, – Dirichlet conditions) and behaves like a source while the fishing ground behaves like a sink.

4. DISCUSSION

4.1. Why a simulator?

As a scientific method, simulation aims to explore the consequences of assumptions concerning the functioning of reality and being formalized in a model. It is, precisely, their formulation in a model (their transformation into objects) which allows us to investigate such assumptions. The formal coherence of the model is, indeed, used to deduce non-trivial consequences from its underlying hypotheses. In this way, simulation is a form of virtual experimentation which is the natural extension of modelling. It allows the study of systems that are too complex to be analyzed differently.

Thus, simulation is not directly informative about reality, but about our knowledge of reality. For this reason, simulation is a theoretical axiomatic process

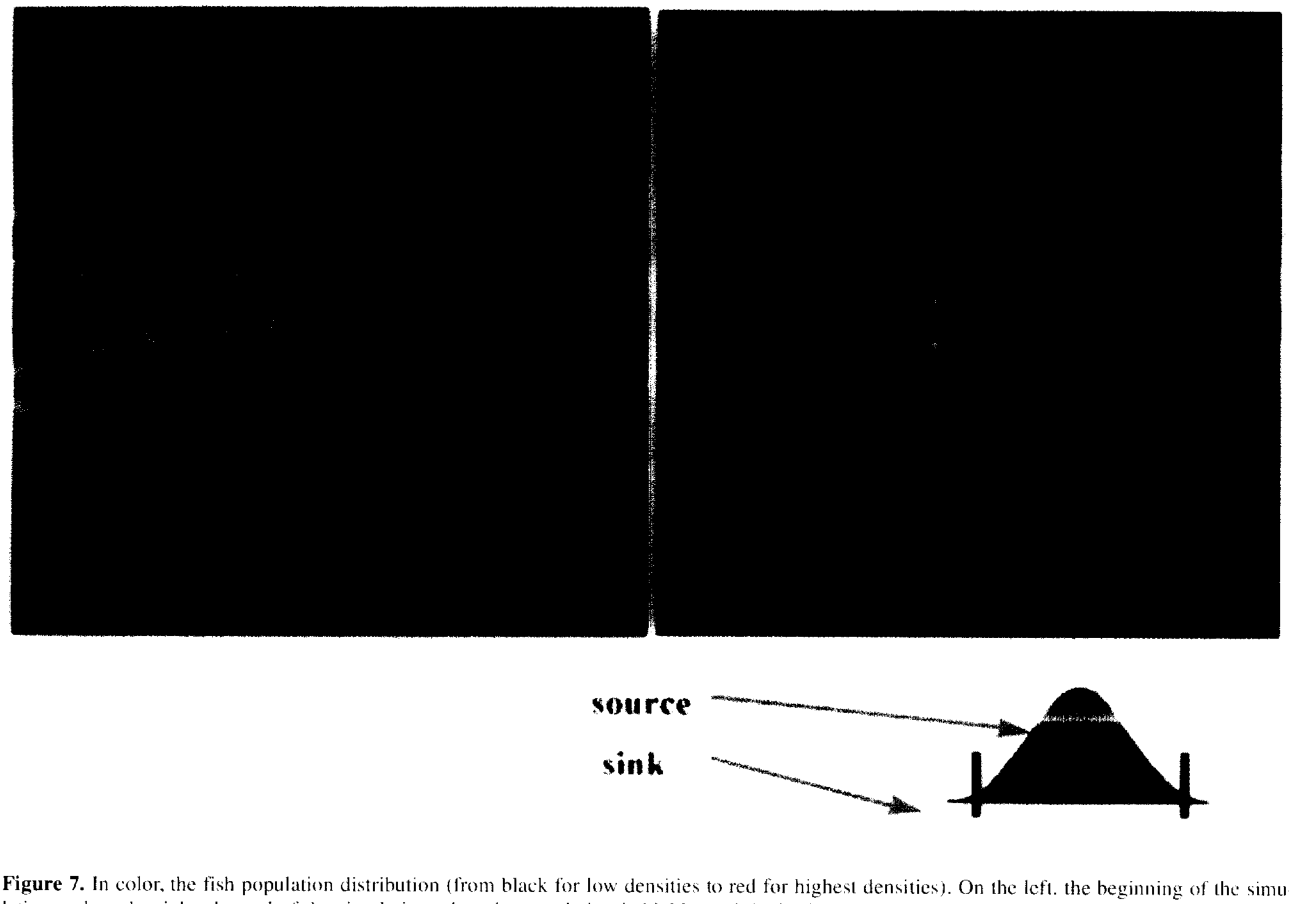

Figure 7. In color, the fish population distribution (from black for low densities to red for highest densities). On the left, the beginning of the simulation and on the right, the end of the simulation when the population is highly exploited. Fishermen are represented in black on the left and in red on the right. On the bottom, cross section of the marine refugia along the vertical axis at the end of the simulation.

which enables the exploration of different possible realities by inferring them from a set of assumptions (axioms) on the functioning of reality. Simulation is a 'thought experimentation' which uses, on the one hand, powerful representation and calculation tools to extend the imagination, and, on the other hand, the coherence of a formal system to coordinate images and elaborate concepts. By creating a simulator, we create an object reality which can be manipulated such as to observe its functioning, decompose it and try to understand it better.

From this perspective, SHADYS is a simulator designed to study the complexity of spatial phenomena in marine population dynamics and their consequences in stock assessment and management [23]. Indeed, one of the main problems of fisheries science is the unobservability of its object of interest. Thus, experimentation is often impossible in practice. However, as Larkin [16] wrote, "fisheries science itself will not advance much unless management becomes experimental". For such an experimental purpose, SHADYS as a virtual laboratory enables the exploration of management scenarios, to test theoretical hypotheses, such as 'local overfishing' for instance (unpubl. data), and their consequences on assessment [22, 25] or to simulate realistic data to validate spatial assessment methods [24].

One of the most important features of SHADYS is its ability to represent simultaneously the dynamics of the environment, the dynamics of the resource and the dynamics of the fishing activity using a clear and visual formal representation. The synthetic representation of this complex interaction is based on generic representations of each interacting system. The two component (patch and gradient) representation of environment heterogeneity allow a wide range of possible environments to be modelled; the density-dependent advection-diffusion equation used is a flexible population model; and the stochastic process used to distribute fishing effort is a simple and efficient means of simulating fishing tactics.

In this way, the generic design of the simulator and the flexibility of its GIS-based architecture provide a clear and visual representation of a wide range of fishery configurations and a possible adaptation to real fisheries. In this latter case, the NMBA has to be related to real environmental parameters with observed relationships [23]. Such an application of SHADYS to real fisheries is currently being developed on tuna fisheries by the authors.

4.2. The source-sink behavior of marine refuges

The simulations of marine reserves presented here are extremely simplistic. Indeed, it is clear that in reality marine refuges are never located randomly. On the contrary, real refuge location and size must be chosen according to habitat quality. Nevertheless, despite their weak realism, the simulations presented here enable better understanding of the process at stake. From this perspective, it is shown that for diffusive or migratory species, the concept of 'space overfishing' is meaningful because the yield per recruit of an overfished stock plotted against the area protected can reach a maximum before decreasing. Thus, there is a non-null optimal domain of the protected area for a given fishing pattern, a given effort and a given location of the refuge. This is a non-trivial result. Indeed, it means that, contrary to current views, the introduction of a marine refuge can, in some cases of growth overfishing, induce a substantial increase in yield per recruit. Different works lead to similar conclusions [1, 5]. In these conditions, protected areas behave like 'sources' and exploited areas like 'sinks' [29, 30]. For resident populations, on the other hand, the larger the protected area is, the lower the catches per recruit are.

Because each population will have a specific response to a given protected zone, it is necessary to use a multispecific approach. In such a multispecific spatial management, a balance has to be found between the potential gain in yield for diffusive species and the loss in yield for resident species when a marine refuge is created.

With regards to fishing vessel distribution, it is shown that if fishing effort is spatially distributed in order to maximize catches, then fishing boats will tend to be slowly distributed along the boundaries of the protected area. Such phenomena has been clearly observed for the North Sea protected zones by Rijnsdorp et al. [32]. As noted by these authors, it could have important consequences in terms of local impacts on the ecosystem, especially on endemic species which are not present in the refuge but only in intensively fished zones. Thus, the marine refuge could lead to local overfishing situations and possible local extinction along its frontier. Another important consequence of such a fishing effort concentration could be a dramatic increase in technical interactions between vessels, which is a possible source of conflicts.

5. CONCLUSION

The use of a simulator like SHADYS enables a clear formal representation of complex phenomena which are difficult to observe in reality. Based on simple, realistic and well identified mechanisms, SHADYS enables the exploration of the potential consequences of hypotheses made on how fisheries function. As a virtual laboratory, it allows experiments in a theoretical world, such experiments being generally impossible to perform in reality.

The goal of the simulation of refuge presented was simply to illustrate SHADYS capabilities and not to provide an exhaustive study on marine refuges behavior. Nevertheless, some generical conclusions can be inferred in terms of spatial management. Indeed, they highlight the importance of the way space is occupied by a given species, on the potential effects of a marine refuge on yield per recruit. Three main types of species are distinguished: the resident ones, for which protecting an area necessarily causes a decrease of yield per recruit, the diffusive and the migratory ones for which the protection of space can enable an increase in yield per recruit but could well lead to a concentration of fishermen along the frontier of the protected zone. For these last two types, the notion of space overexploitation has a meaning. The protection of an area could be a way to limit interactions between human activities (including fishing) and ecosystems but our results raise interesting management questions: how to reconcile different species behaviors? How to locate protected areas (which will not be identical for all species)? Where and how large should they be (is it better to protect only one large area or several smaller ones)? How to limit the concentration of fishing effort along the refuge frontiers? Trying to answer these different questions requires developing and using spatial assessment and modelling methods which are not yet familiar. In considering real habitat functional heterogeneity and fish life cycles, adapting and fitting advection-diffusion-reaction models such as SHADYS for real cases could be a way in this direction. Nevertheless, such a monospecific approach is clearly insufficient in considering the long-term consequences of a marine refugia on biodiversity and viability. Considering all that ecosystem complexity still requires further increase in our knowledge of ecosystem functioning and improvement of our technical modelling capabilities.

Aknowledgements

The authors are grateful to Yunne-Jai Shin, Manuel Plantegenest and the anonymous referees for their relevant remarks on an earlier version of the manuscript and to Gregory Valatin for reading the English.

REFERENCES

[1] Attwood C.G., Bennett B.A., Modelling the effect of marine reserves on the recreational shore-fishery of the south-western cape, South Africa, S. Afr. J. Mar. Sci. 16 (1995) 227–240.

[2] Bascompte J., Solé R.V., Local and ensemble dynamics of linked populations: reply to Ruxton, J. Anim. Ecol. 63 (1994) 1003.

[3] Begon M., Harper J.L., Townsend C.R., Ecology, 3rd ed., Blackwell Science Ltd, 1996, 1068 p.

[4] Bertignac M., Lehodey P., Hampton J., A spatial population dynamics simulation model of tropical tunas using a habitat index based on environmental parameters, Fish. Oceanogr. 7 (1998) 326–334.

[5] Clark C.W., Marine reserves and the precautionary management of fisheries, Ecol. Appl. 6 (1996) 369–370.

[6] Cury P., Roy C., Optimal environmental window and pelagic fish recruitment success in upwelling areas, Can. J. Fish. Aquat. Sci. 46 (1989) 670–680.

[7] Dugan J.E., Davis G.E., Applications of marine refugia to coastal fisheries management, Can. J. Fish. Aquat. Sci. 50 (1992) 2029–2042.

[8] Fretwell S., Lucas H., On the territorial behavior and other factors influencing habitat distribution in birds, Acta Biotheor. 19 (1970) 16–36.

[9] Gauthiez F., Structuration spatiale des populations de poissons marins démersaux. Caractérisation, conséquences biométriques et halieutiques, thèse dr., Univ. C.-Bernard, Lyon, 1997, 158 p. + annexes.

[10] Hastings A., Spatial heterogeneity and ecological models, Ecology 71 (1990) 426–428.

[11] Hastings A., Complex interactions between dispersal and dynamics: lessons from coupled logistic equations, Ecology 74 (1993) 1362–1372.

[12] Hilborn R., Walters C.J., A general model for simulation of stock and fleet dynamics in spatially heterogeneous fisheries, Can. J. Fish. Aquat. Sci. 44 (1987) 1366–1369.

[13] Hilborn R., Walters C.J., Quantitative fisheries stock assessment. Choice, dynamics and uncertainty, Chapman and Hall, New York, 1992, 570 p.

[14] Kareiva P., Population dynamics in spatially complex environments: Theory and data, Phil. Trans. R. Soc. Lond. B 330 (1990) 175–190.

[15] Kolosa J., Rollo C.D., Introduction: the heterogeneity of heterogeneity: a glossary. Ecological heterogeneity, in: Kolosa J., Pickett S.T.A. (Eds.), Ecological Studies No. 86, Springer Verlag, Berlin, 1989.

[16] Larkin P.A., Fisheries management - an essay for ecologists, Ann. Rev. Ecol. Syst. 9 (1978) 57–73.

[17] Laurec A., Analyse et estimation des puissances de pêche, ICES J. Mar. Sci. 37 (1977) 173–185.

[18] Legendre P., Fortin M.-J., Spatial pattern and ecological analysis, Vegetatio 80 (1989) 107–138.

[19] Lemasson, Thons et environnement, Paris du 12 au 15 septembre 1988, Orstom. Coll. Colloques et Séminaires, Paris, 1989, 84 p.

[20] Levin S., Population models and community structure in heterogeneous environments, Biomathematics, vol. 17, Mathematical Ecology, Springer-Verlag, 1986.

[21] MacCall A.D., Dynamic geography of marine fish populations, Books in Recruitment Fishery Oceanography, University of Washington Press, 1990 153 p.

[22] Maury O., Coopération des navires, surexploitation locale et non linéarité de la relation PUE/effort locale dans les pêcheries thonières à la senne. Simulations sur SHADYS (Simulateur HAlieutique de DYnamiques Spatiales), Rec. doc. scient. ICCAT, SCRS/97/83, 1997, 6 p.

[23] Maury O., Modélisation spatiale en halieutique. Approche par simulateur sous SIG. Application à la modélisation hiérarchique de la population de thons albacore (*Thunnus albacares*) de l'Atlantique tropical, thèse dr. ENSAR, Rennes, 1998, 350 p.
[24] Maury O., Gascuel D., Pelletier D., Estimating fish numbers, fishing mortality and migration rates between different spatial zones: the spatial VPA methodology, ICES Annual Science Conference, 25 Sept.–3 Oct. 1997, Baltimore, Maryland USA, Assessment Methods ICES CM DD:09, 1997, 7 p.
[25] Maury O., Millischer L., Gascuel D., Fonteneau A., Le GAM, un outil d'estimation des biomasses locales. Application au thon albacore (*Thunnus albacares*) de l'Atlantique, in: Biométrie et halieutique, Société Française de Biométrie, 1998.
[26] Okubo A., Diffusion and Ecological Problems: Mathematical Models, Biomathematics vol. 10, Springer-Verlag, 1980, 254 p.
[27] Pelletier D., Magal P., Dynamics of a migratory population under different fishing effort allocation schemes in time and space, Can. J. Fish. Aquat. Sci. 53 (1996) 1186–1199.
[28] Press W.H., Teukolsky S.A., Vetterling W.T., Flannery B.P., Numerical recipes in C. The Art of Scientific Computing, 2nd ed., Cambridge University Press, 1994, 994 p.
[29] Pulliam H.R., Sources, sinks, and population regulation, Am. Nat. 132 (1988) 652–661.
[30] Pulliam H.R., Danielson B.J., Sources, sinks, and habitat selection: a landscape perspective on population dynamics, Am. Nat. 137 (1991) S50–S66.
[31] Rosenzweig M.L., Some theoretical aspects of habitat selection, in: Cody M.L. (Ed.), Habitat Selection in Birds, Academic Press, Orlando, 1985, pp. 517–540.
[32] Rijnsdorp A.D., Buys A.M., Storbeck F., Visser E., Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms, ICES J. Mar. Sci. 55 (1998) 403–419.
[33] Ruxton G.D., Local and ensemble dynamics of linked populations, J. Anim. Ecol. 63 (1994) 1002.
[34] Sibert J.R., Fournier D.A., Evaluation of advection-diffusion equations for estimation of movement patterns from tag recapture data, in: Shomura R.S., Majkowski J., Langi S. (Eds.), Proc. 1st FAO Expert Consultation on Interactions of Pacific Ocean Tuna Fisheries, FAO Fish. Tech. Pap. 336/1, 1994, 326 p.
[35] Sibert J., Hampton J., Fournier J., Skipjack movement and fisheries interaction in the western Pacific, in: Shomura R.S., Majkowski J., Harman R.F. (Eds.), Status of Interaction of Pacific Tuna Fisheries in 1995, Proc. 2nd FAO Expert Consultation on Interactions of Pacific Ocean Tuna Fisheries, FAO Fish. Tech. Pap. 365, 1996, pp. 402–424.

APPENDIX: NUMERICAL INTEGRATION

The following equation (equation (6)) is used to model fish population dynamics in SHADYS:

$$\frac{\partial N}{\partial t} = \frac{\partial\left((D + k\cdot\gamma\cdot N^{\gamma})\cdot\frac{\partial N}{\partial x}\right)}{\partial x} + \frac{\partial\left((D + k\cdot\gamma\cdot N^{\gamma})\cdot\frac{\partial N}{\partial y}\right)}{\partial y} + \frac{\partial(uN)}{\partial x} + \frac{\partial(vN)}{\partial y} - Z\cdot N$$

where $N = N_{x,y,t}$ is the fish density at point (x,y) at time t, $D = D_{x,y,t}$ the diffusivity coefficient, $u = u_{x,y,t}$ and $v = v_{x,y,t}$ the advection coefficients, $Z = Z_{x,y,t}$ the total mortality rate.

A second order spatially-centered finite differencing numerical scheme is used to approximate that equation. By setting $A_x = \frac{\partial\left((D + k\cdot\gamma\cdot N^{\gamma})\cdot\frac{\partial N}{\partial x}\right)}{\partial x}$, and $B_x = \frac{\partial(u\cdot N)}{\partial x}$, we can write at time t in the x dimension:

$$\begin{aligned} A_{x,t} &= \frac{\partial(D + k\cdot\gamma\cdot N^{\gamma})_{x,t}}{\partial x}\cdot\frac{\partial N_{x,t}}{\partial x} + (D + k\cdot\gamma\cdot N^{\gamma})_{x,t}\cdot\frac{\partial^2 N_{x,t}}{\partial x^2} \\ &\approx \frac{(D + k\cdot\gamma\cdot N^{\gamma})_{x+1,t} - (D + k\cdot\gamma\cdot N^{\gamma})_{x-1,t}}{2\cdot\Delta x}\cdot\frac{N_{x+1,t} - N_{x-1,t}}{2\cdot\Delta x} + (D + k\cdot\gamma\cdot N^{\gamma})_{x,t}\cdot\frac{N_{x+1,t} - 2N_{x,t} + N_{x-1,t}}{\Delta x^2} \\ &\approx [k\cdot\gamma\cdot(N^{\gamma}_{x+1,t} - N^{\gamma}_{x-1,t})\cdot(N_{x+1,t} - N_{x-1,t}) + 4\cdot(D + k\cdot\gamma\cdot N^{\gamma}_{x,t})\cdot(N_{x+1,t} - 2\cdot N_{x,t} + N_{x-1,t})]\cdot\frac{1}{4\cdot\Delta x^2} \end{aligned}$$

and

$$B_{x,t} = \frac{\partial u_{x,t}}{\partial x} \cdot N_{x,t} + u_{x,t} \cdot \frac{\partial N_{x,t}}{\partial x}$$

$$\approx \left(\frac{u_{x+1,t} - u_{x-1,t}}{2 \cdot \Delta x}\right) \cdot N_{x,t} + u_{x,t} \cdot \left(\frac{N_{x+1,t} - N_{x-1,t}}{2 \cdot \Delta x}\right) \qquad 1 < x < n$$

the A and B differentials are written in the same manner in y.

Such finite difference approximations could easily be used in an explicit numerical scheme. Nevertheless, although it is more difficult to handle, a fully implicit numerical scheme was preferred. Indeed, because SHADYS must enable a large range of movement parameters to be used, the numerical scheme must be stable even in the case of extreme parameters. In practice, we used the well-known two-dimensional alternating direction implicit scheme (ADI) which is a particular case of time splitting [28]. For a complete technical presentation of the numerical method used, see Maury [23].