



ISIS-Fish, a generic and spatially explicit simulation tool for evaluating the impact of management measures on fisheries dynamics[☆]

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Abstract

Assessing the impact of management scenarios on multi-species multi-fleet fisheries requires spatially and seasonally explicit simulation tools. No such tools are currently available in fisheries science. This paper presents a software that evaluates the impact of management measures on the dynamics of a complex fishery. The simulation model is generic in order to be used for different types of fisheries. Existing knowledge about each fishery is stored in a database included in the software, and may be easily modified. This includes the parameters describing each population and each fishing activity. Furthermore, the software allows for flexibility in several model assumptions. Both management measures and behaviour of fishermen in reaction to these measures may be interactively designed through a Script language. The simulation tool thus enables one to compare the respective impacts of conventional management measures like catch and effort controls, and measures more recently advocated like marine protected areas.

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1. Introduction

Many fish stocks seriously suffer from overexploitation and traditional management measures have failed to reduce the exploitation level to a sustainable level (Botsford et al., 1997). It is thus important to be able to quantify the impact of alternative management scenarios (for instance, marine protected area (MPA)). In this regard, assessing the impact of fishing activity and management scenarios requires evaluating

the mortality induced on exploited resources. However, most fisheries are complex systems due to the diversity of both exploited resources (multi-species) and fishing activities (multi-fleet) in so-called mixed fisheries, and to spatial and seasonal heterogeneities in the distributions of resources and fishing activities. In mixed fisheries, resources are exploited either simultaneously or sequentially by fishing units resorting to different types of fishing activity. It is thus difficult to evaluate the dynamics of both resources and exploitation, and subsequent fishing mortality for each population (Murawski and Stewart, 1996). The diversity of fishing activities and resulting catches arises from the variety of fishing grounds exploited, species targeted and gears used, but also from other factors like individual fishers' behaviour, economic or

[☆] Integration of Spatial Information for Simulation to evaluate the impact of management measures on FISHerries.

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environmental conditions. In addition, fishermen are aware of large-scale spatio-temporal distributions of resources and allocate fishing effort accordingly. At large scales, fluctuations of these spatial distributions are mainly due to concentrations of particular demographic stages in some areas at certain seasons in relation with specific events of the life cycle (reproduction, feeding ...), and corresponding migrations between these areas. In this context, considering the spatial and seasonal allocation of fishing effort among fishing grounds is essential to evaluate the dynamics of the fishery. In mixed fisheries, these aspects are all the more important since fishermen may switch not only fishing grounds, but also target species and fishing gears. Spatially-explicit models are deemed necessary to understand the dynamics of many biological systems, in particular ecosystems subject to human activities (Maxwell and Costanza, 1997). In the light of this overall complexity, the dynamics of the system, even if expressed through mathematical equations, may not be investigated analytically, and a simulation tool is indispensable to be able to evaluate the dynamics of a complex fishery. In fisheries science, there are currently no tools available for this purpose. The developed tools are based on either equilibrium models (without dynamic allocation of fishing effort) (Murawski, 1984; Pikitch, 1987; Mesnil and Shepherd, 1990; Walters et al., 1999), models that are not spatially-explicit (Laloe and Samba, 1991; Laurec et al., 1991; Sparre and William, 1993), or models that were developed for a particular fishery and cannot

be easily transposed to another context (Allen and McGlade, 1987; Walters et al., 1999; Holland, 2000).

In this paper, we first present a generic model of the dynamics of mixed fisheries that is spatially and seasonally explicit, and we describe the dynamics of populations, fishing activities and management. Then we present the software that was developed based on this model. It may be used to integrate existing knowledge on a given fishery. Management scenarios may be designed interactively, as well as the behaviour of fishermen in reaction to management measures. Simulations may then be run to assess the impact of management scenarios on the fishery. A mixed fishery example illustrates the use of the software.

2. Model description

The fishery model is designed to assess the performance of local and temporal management measures involving spatial and seasonal control variables for regulating exploitation, e.g. fishing effort and catches. The fishery model is based on three submodels (Fig. 1), namely a population dynamics model, a model for fishing activity and a model for management measures. Each submodel is spatially and seasonally explicit. The fishery takes place in a region defined by its contour and a regular grid. The spatial resolution of the grid in latitude and longitude is chosen with respect to the dynamics being described, and depending on the precision of available information.

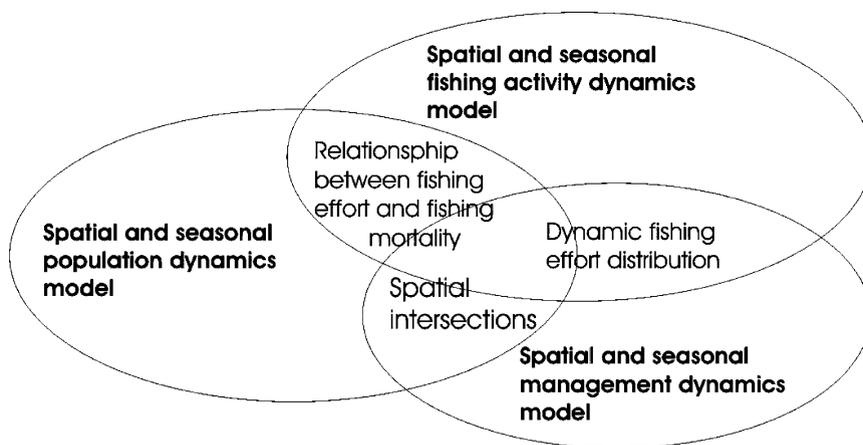


Fig. 1. A synoptic view of the spatial mixed fishery model decomposed into three submodels interacting through time and space. Submodels interact via spatial and temporal intersection.

Within the region, zones (i.e. sets of contiguous grid cells) are defined independently for each population, each fishing activity and each management measure. The model has a monthly time step. Seasons (i.e. sets of successive months) are also defined independently for each population, each fishing activity and each management measure. Within each zone and season, relevant variables such as fishing effort for a specific activity or abundance of a given population, are assumed to be homogeneous and uniformly distributed.

2.1. Population dynamics model

This model describes the dynamics of a non-limited number of populations. Biological interactions between populations, like competition and predation relationships, are not considered in the model for two reasons: (i) in commercial fisheries, they may be easily shadowed by fishing-related mortalities due to the high level of fishing pressure (Hilborn and Walters, 1992), and (ii) they are very difficult to quantify (Shepherd, 1998). Still, population dynamics are dependent upon each other because of non-selective fishing gears which catch several species at the same time. Population dynamics focuses on seasonal variations in spatial distribution in relation with large-scale migrations. These variations are tied to the life cycle of the species. Models based on patches and migrations between patches are appropriate to describe dynamics accounting for seasonal and spatial variations (Lebreton, 1996).

A spatially-explicit stage-structured model described the dynamics of each population (Table 1),

Table 1
Principal parameters for describing a population in the population dynamics model

Non-spatial biological parameters	Number of stages and stage width
	Natural mortality per stage
	Fecundity function
	Weight at stage
	Distribution of reproduction over months
	Distribution of recruitment over months
Spatial biological parameters	Growth function
	Population zones including reproduction and recruitment zones
	Coefficients of migration and emigration
	Number of immigrants
	Catchability coefficients

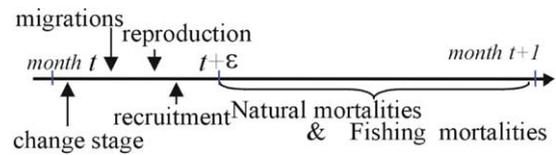


Fig. 2. The chronology of processes underlying the simulation model.

where stages correspond to either age, length, or any other demographic stages. For a given population, spatial distribution of abundance is fixed within each season. Migrations are assumed to take place at the beginning of a season. Reproduction and recruitment, i.e. the process by which young individuals become catchable by at least one gear in the fishery, also delineate specific zones and seasons. Unlike migrations, these processes may occur at each time step of the season, in order to be able to mimic reproduction and recruitment distributions observed in fish populations. At each time step, the chronology of the processes affecting a population is the following: changing stage, migration, reproduction, recruitment and, fishing and natural mortalities (Fig. 2). Processes are assumed to occur instantaneously at the beginning of the time step, except fishing and natural mortalities that take place during the whole time interval after instantaneous processes.

Animals are counted at the beginning of the time step. For a given population, abundance at time t is denoted:

$$N(t) = (N(t, 1), \dots, N(t, s), \dots, N(t, s_{\max})), \quad (1)$$

where $N(t, s)$ is the row vector $(N(t, s, 1), \dots, N(t, s, z), \dots, N(t, s, z_n))$, for each stage s and zone z of the population, and s_{\max} and z_n being respectively the number of stages and the number of zones of the population. The notation for $N(t)$ as a row vector follows from Lebreton (1996). Population dynamics can be written in a matrix form.

Each process affecting population dynamics is thus modelled through a matrix. Let us denote *season* the season of the population corresponding to t . $Cs(\text{season})$ describes change of stage for the season. Let cs_{ij} be the proportion of stage j growing to stage i at this season. Note that cs_{ij} is zero for $i < j$, $\sum_{j=1}^{s_{\max}} cs_{ij} = 1$ and $cs_{s_{\max}, s_{\max}} = 1$. Therefore, $Cs(\text{season})$ is a lower block triangular matrix where

each block is a square matrix of dimension z_n . The i th diagonal block is equal to $Cs(\text{season}, i, i) = \text{Diag}(cs_{ss}, \dots, cs_{ss})$, and the i th \times j th upper block is $Cs(\text{season}, i, j) = \text{Diag}(cs_{ij}, \dots, cs_{ij})$.

Concerning migration processes, $\mathbf{Mig}(\text{season})$ is the matrix of migration and emigration for the season. It is a block diagonal matrix $\mathbf{Mig}(\text{season}) = \text{Diag}(\mathbf{Mig}(\text{season}, s), s = 1, s_{\max})$ where $\mathbf{Mig}(\text{season}, s)$ is the matrix of element $mig(\text{season}, s)_{ij}$, the migration rate from zone i to zone j at this season. Note that $mig(\text{season}, s)_{ii}$, the proportion of fish staying in the zone i , is equal to $1 - \sum_{i \neq j} mig(\text{season}, s)_{ij} - e(\text{season}, s)_i$, where $e(\text{season}, s)_i$ is the proportion of fish emigrating from the zone i to outside the region.

Possible immigration is modelled through $N^{\text{immig}}(\text{season})$, the number of fish immigrating in the region at the season, $N^{\text{immig}}(\text{season})$ is structured like $N(t)$ per stage and per zone (see Eq. (1)).

Regarding reproduction and recruitment, $\mathbf{R}(t)$ represents the number of fish recruited at t . $\mathbf{R}(t)$ structured like $N(t)$ (Eq. (1)), and is obtained from recruitment and reproduction equations detailed in Appendix A.

Survival rates are framed into the diagonal block matrix $\mathbf{Sr}(t)$:

$$\mathbf{Sr}(t) = \text{Diag}(Sr(t, 1), \dots, Sr(t, s), \dots, Sr(t, s_{\max})),$$

where $\mathbf{Sr}(t, s)$ is a diagonal matrix of element $sr(t, s, z) = \exp(-F(t, s, z) - M(s))$ the survival rate between t and $t + 1$ for stage s in zone z . This rate is based on the exponential decay model widely used in fisheries science. Here, $F(t, s, z)$ and $M(s)$ are expressed in per month, and respectively denote the instantaneous fishing mortality rate of stage s in zone z between t and $t + 1$ (see detailed calculations in Appendix B), and the instantaneous natural mortality coefficient (in per month) of stage s . Natural mortality is assumed to be constant over zones and over months. Fishing mortality is computed from fishing effort as described below.

Under these notations and given the chronology of processes (Fig. 2), the dynamics of the population at any time step t writes:

$$N(t + \varepsilon) = R(t) + \mathbf{Mig}(\text{season})Cs(\text{season})N(t) + N^{\text{immig}}(\text{season}) \quad (2)$$

$$N(t+I) = \mathbf{Sr}(t)N(t + \varepsilon) \quad (3)$$

where ε is by convention an infinitely small time interval. Eq. (2) may be simplified depending on whether t corresponds to the recruitment season and/or to the beginning of a season of migration, and/or to stage change.

2.2. Exploitation submodel

Exploitation of fish resources is quantified by fishing effort, which is a function of fishing gears used and the amount of time spent fishing. In our model, fishing units, i.e. fishing vessels and corresponding crew, are not individually identified, but arranged in fleets according to fishing trip duration. Each fleet is thus characterized by a maximum monthly fishing effort per fishing unit (Table 2). Fleets serve to account for the spatial range of exploitation through the duration of fishing trips. Fishing units are assumed to be identical and fishers are assumed to work at full effort capacity all year long.

Fishing effort is allocated between several fishing activities. Each fishing activity exhibits seasonal patterns and is modelled at several time scales. At the scale of the fishing operation (e.g. a tow for a trawler), fishing activity is described by *métiers* (Biseau and

Table 2
Principal parameters of the fishing activity dynamics model including several fleets

Structural entities of the model	Parameters of the entity
Fleet	Number of fishing units Number of fishing trips per month Duration of fishing trip
Gear	Value of the controllable parameter (numerical or categorical) Selectivity function for each species Standardisation factor
Métier	Gear used (unique) Seasons Zones Target species and corresponding target factors
Strategy	Set of métiers used Proportion of fishing units per fleet Monthly distribution of fishing units among the métiers used

Gondeau, 1988) defined by a fishing gear, target species, and seasons during which the métier is practised in specific zones (métier zones) (Table 2). The time taken to travel to a given métier zone decreases the time available for fishing. A target factor associated to each species quantifies the strength with which the species is sought for by the métier. Each fishing gear is characterized by a parameter (either numerical or categorical) that can be controlled through management measures (e.g. mesh size for a net, or hook type for a longline). The probability of catching a fish of a given species with the gear depends on this parameter through a selectivity model (see e.g. Wileman et al., 1996). The gear is also characterized by a standardization factor used to get comparable effort units among gears. This factor is particularly relevant for mixed fisheries, since fishing effort must be consistent among gears to compute fishing mortalities (see below).

At the scale of the year, fishing activity is described through *strategies* corresponding to sets of fishing units that resort to the same sequence of métiers during the year (Laloe and Samba, 1991). Each strategy thus comprises a number of fishing units from each fleet. Each strategy is characterized by the list of métiers practised and the monthly allocation of fishing effort between these métiers. In each strategy and each fleet, a proportion of fishing units may change fleets in order to allow for possible adaptation of fishing units to management measures.

2.3. Management submodel

The main purpose of the simulation model is to quantitatively assess the relative performances of a range of management measures applicable to a mixed fishery. We aim at comparing the impact of conventional management measures including catch limitation (total allowable catch (TAC)), effort limitation (total allowable effort (TAE)) and gear restrictions, to measures like MPAs. Because our model is spatially explicit with a monthly time step, we may consider management measures that apply either during some months or throughout the year, and are either global (at the scale of the region) or local (within a particular zone). In this way, a large variety of MPA designs may be evaluated.

Each management measure is defined by several parameters (Table 3): the zone (management zone),

Table 3

Principal parameters for describing a management measure in the management dynamics model

Structural entities of the model	Parameters for the specification of the entity
Measure	Management zone Management season (months) Period of application (years) Control condition required for application
Fishers' reaction	Decision rules

the months (management season) and the years of application. Each measure results in one or several constraints on exploitation, that leads fishing units to modify fishing effort in some respect. These changes are termed “fishers’ reaction to management measures” in the following. Constraints become effective under certain conditions to be specified. For instance, in the case of a species under TAC management, the control condition is that total catch since the beginning of the year exceeds the TAC value. In the case of a temporary MPA, the condition is that the current month belongs to the management season of the MPA. An example of fishers’ reaction to the implementation of a MPA is that fishers usually fishing in the management zone change fishing zones and even fishing activities. Fishers’ reaction to a measure depends on their usual fishing activity determined by the strategy and the métier practised during the management season. Accounting for these reactions the impact of a management measure on both resources and fishing activities can be assessed in a more realistic way.

The model considers any management measure which can be structured as defined above, and to combine them into management scenarii. Likewise, any fishers’ reaction may be implemented in the model (see Section 3). When a management measure becomes effective, it impacts any métier whose fishing zone intersects the management zone. Fishermen practising one of these métiers react as specified in the decision rule. This may affect fishing activity in several ways:

1. by modifying a characteristic of the impacted métier, for instance the value of the controllable parameter of the gear, the target factors, or the métier zone;

2. by changing métiers; the effort allocated to the impacted métier is then reported to one or several other métiers, either in the same strategy or in other strategies;
3. by reducing the number of fishing units per fleet and/or strategy; this is the case when the management measure aims at controlling the number of fishing units (license management).

The three submodels, viz. population, exploitation and management, are coupled through the relationship between fishing mortality and fishing effort (Fig. 1).

2.4. Relationship between fishing effort and fishing mortality

For each population exploited in the fishery (denoted *pop*), fishing mortality per stage and per zone is computed at each time step of a simulation. Catch is then derived using conventional equations (see below). Since we assume that both fish abundance of a given stage and fishing effort of a given métier are uniformly distributed over their respective population and métier zones, the contribution of fishing effort to fishing mortality is directly tied to the intersection

between the population zone and the métier zone. In addition, fishing mortality depends on additional parameters like catchability (the probability that a fish present in the zone at that season be caught by a standardized unit of effort (Seber, 1982)), selectivity, target factor and standardization factor.

Using notations in Table 4, the fishing mortality of stage *s* in the population zone z_{pop} at time *t* is a weighted sum of the standardised effort per métier $SE(\text{met}, t)$:

$$F(t, s, z_{pop}) = q(s, z_{pop}) \times \sum_{m \in \text{ListMetAff}(t, z_{pop})} Sel(s, gear(\text{met})) SE(t, \text{met})$$

where

$$SE(\text{met}, t) = \text{Tarf}(t, \text{met}) \text{Std}(gear(\text{met})) \text{Nop}(\text{met}) E(t, \text{met}, \text{str})$$

and

$$E(t, \text{met}) = \sum_{fl \in \text{ListFl}} \sum_{str \in \text{ListStr}(\text{met})} P(\text{str}, \text{met}, t) \times \text{Inter}(z_{\text{met}}(t), z_{pop}) (T(fl) - Tt(t, \text{met})) \text{Nfu}(fl, \text{str})$$

Table 4

Some notations to write the relationship between effort and fishing mortality

Notation	Definition
<i>pop</i>	A population exploited by the fishery
<i>met</i>	A métier of the fishery
<i>str</i>	A strategy of the fishery
z_{pop}	A population zone of the fishery
z_{met}	A métier zone of the fishery
$z_{\text{met}}(t)$	Union of métier zones of métier <i>met</i> at <i>t</i>
$\text{ListMetAff}(t, z_{pop})$	List of métiers fishing population <i>pop</i> in z_{pop}
$\text{ListStr}(\text{met})$	List of strategies using métier <i>met</i>
ListFl	List of fleets of the fishery
$q(s, z_{pop})$	Catchability of stage <i>s</i> of population <i>pop</i> in z_{pop}
$Se(t, \text{met})$	Standardised effort of métier <i>met</i> at <i>t</i>
$E(t, \text{met}, \text{str})$	Nominal effort of métier <i>met</i> in strategy <i>str</i> at time <i>t</i>
$\text{Tarf}(t, \text{met})$	Target factor of métier <i>met</i> on population <i>pop</i> at time <i>t</i>
$\text{Std}(gear(\text{met}))$	Standardization factor of the gear used by métier <i>met</i>
$\text{Nop}(\text{met})$	Number of fishing operations per trip for métier <i>met</i>
$P(\text{str}, \text{met}, t)$	Proportion of effort (in number of fishing units) allocated to métier <i>met</i> in strategy <i>str</i> at time <i>t</i>
$T(fl)$	Maximum monthly time at sea per fishing unit of fleet <i>fl</i>
$Tt(t, \text{met})$	Travel time to reach $z_{\text{met}}(t)$
$\text{Nfu}(fl, \text{str})$	Number of fishing units of fleet <i>fl</i> in strategy <i>str</i>
$Sel(s, gear(\text{met}))$	Gear selectivity of met for stage <i>s</i> of the population considered
$\text{Inter}(z1, z2)$	Intersection between zones <i>z1</i> and <i>z2</i> (a list of cells of the grid)

Catch rates between t and $t+1$ are derived from the instantaneous fishing mortality at time t using the Baranov catch equation (Baranov, 1918) widely used in fisheries science:

$$cr(t, s, z_{pop}) = \frac{F(t, s, z_{pop})}{F(t, s, z_{pop}) + (M(s)/12)} \times (1 - \exp[-(F(t, s, z_{pop}) + M(s))]) \quad (4)$$

Given the chronology of processes (Fig. 2) catch between t and $t+1$ are calculated from the abundance at $t+\varepsilon$ ($N(t+\varepsilon)$ in Eq. (2)) and at $t+1$ ($N(t+1)$ in Eq. (3)):

$$c(t, s, z) = cr(t, s, z)(N(t+\varepsilon, s, z) - N(t+1, s, z)) \quad (5)$$

The vector $C(t)$ resulting from Eq. (5) is structured like $N(t)$ (Eq. (1)). The matrix form for computation of catch rates from fishing effort is detailed in Appendix B.

3. Software architecture

A number of specifications were imposed regarding the software. The simulation tool should be easy to use by both expert users, like modellers, and others, i.e. applied fisheries biologists and fisheries managers. The former will use it as a heuristic tool to gain some insight into the dynamics of mixed fisheries and evaluate the impact of alternative management scenarii. For the latter, it will be applied to various fisheries in order to generate discussions with fishers about possible management measures, and to show them the interest of data quality in the assessment. The tool will then be useful to help decision-making through simulation gaming.

Consequently, the software must enable one to carry out a large number of simulations with different parameters and assumptions for populations, fishing activities and management measures. This flexibility is also made necessary to be able to modify the description of the dynamics as further knowledge and information about fisheries become available. Indeed, the knowledge of mixed fisheries is constantly evolving, due to new information and new research. They

also change because of technological and economic evolutions. Flexibility is brought through an editor/interpreter of equations that facilitates changes in model equations. The simulation tool is thus generic and applicable to many fisheries. Mathematical equations as well as algorithms, i.e. decision rules, and stochasticity may be entered and/or modified through the interpreter. Changes in equations are possible for the growth model, the length–weight relationship, the relationship between female fecundity and individual length, the stock–recruitment relationship, the selectivity model and the reaction of fishermen to management measures.

Given the models presented above, a substantial amount of information is required to properly describe a mixed fishery. In addition, even in well-known fisheries, there always remain uncertainties about dynamics (say populations, exploitation, management and fishers' reaction) so that alternative hypotheses have to be considered. Investigating a single management scenario thus requires several simulations. To avoid repetitive inputs for successive simulations, the simulation tool is coupled with a database containing fisheries-related information and simulation results. The database is permanent, modifiable and updateable. It is then easy to add new entities to the fishery, like populations, métiers or management measures.

The simulation tool is used either from input files containing the data and the parameters of the simulation, or through dialog boxes. An arbitrary number of populations, fishing activities, and management measures may be considered. The simulations may be run either in batch mode or interactively, and simulation results may be saved in the database. To have a quick overview of the impact of the management scenario on the dynamics, a window presenting an abstract of the results is opened at the end of the simulation. To get more details, simulation outputs may be viewed on a map of the region or as time series plots. Several graphics may be visualized at the same time, and the user may choose a range of variables to map or plot, e.g. catch or effort per métier. Main simulation parameters are recalled in a control panel.

Progressive (simple dialog boxes with an access to advanced ones) and user-friendly interfaces are developed to facilitate the use of the software by non-experts. An illustration of the interfaces is given in Fig. 3.

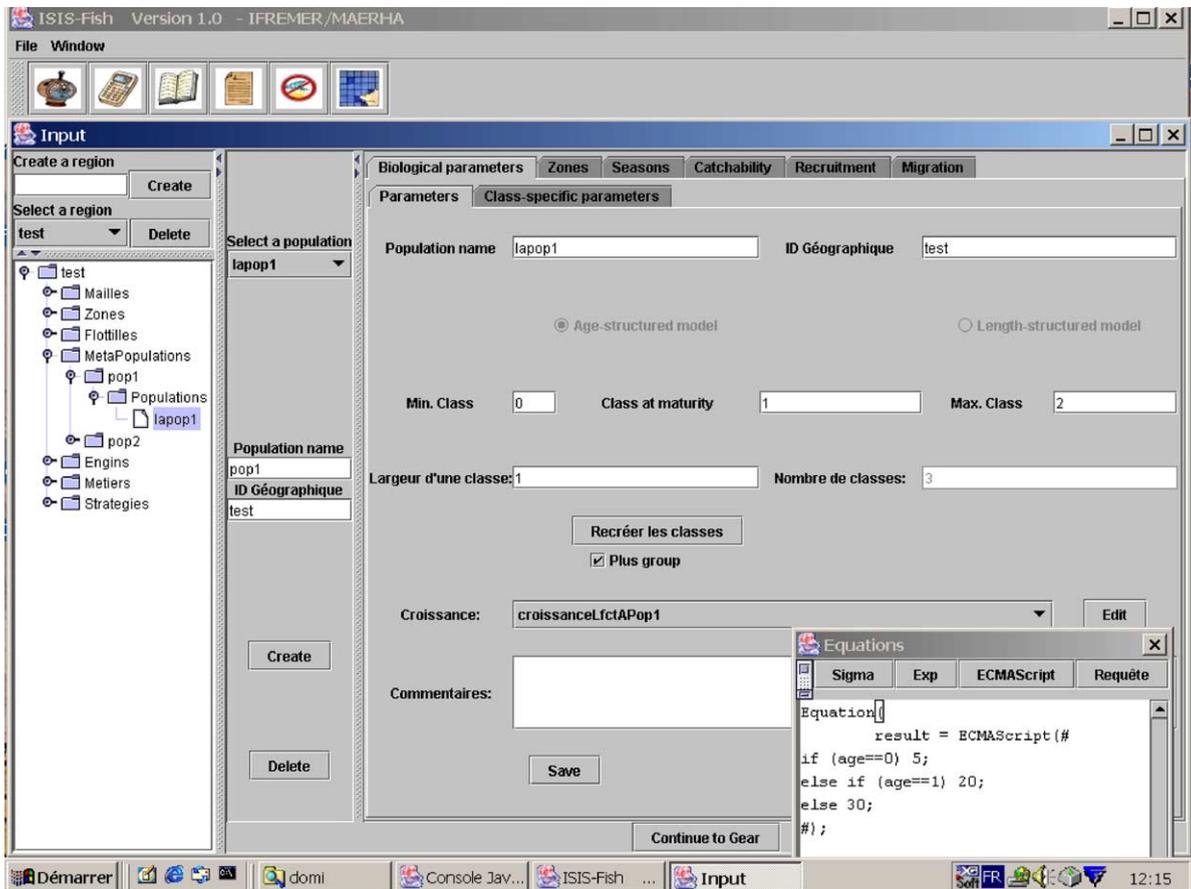


Fig. 3. An extract of the ISIS-Fish interfaces: the interface to input biological parameters of a population. On the left top, a band is drawn with the 6 icons to open the 6 types of interfaces (Launcher, Results, Inputs, ECMASCRIP Editor, Management Rules, Graphical Tool to control the inputs). Below the Input interface is opened. On the left, the structure of the database concerning the fishery under-interest is presented through a tree, on which we can clic to access to any object of the fishery. On the right, the interface to enter parameters of population 1 is opened on the biological parameters onglet. The other shifts to enter zones, seasons, catchability, recruitment and migration parameters are accessible by the dark onglet. The growth curve is edited inside the equation editor.

Because the software is aimed at being used by many users located in different sites, it is desirable that: (i) its latest version may be quickly accessed; (ii) no additional software is needed to run it, and (iii) it may run on any computer platform. The solution found to meet these constraints is to store the software in the site where it is developed and to allow a remote access via Internet and Intranet. To avoid any saturation of the server, the software can be launched either locally (i.e. on the user computer) or on the server using a Web interface. The software was developed under the constraint of minimal cost, and so that it may be used with any exploitation system. It was

coded in JAVA (Flanagan, 1997) and ECMASCRIP (McFarlane, 2003), with an architecture based on Enterprise Java Beans (EJB, Sun Microsystems). Object-oriented programming provides an intuitively natural to approach ecosystem modelling (Silvert, 1993) and is particularly adapted for complex biological systems (Congleton et al., 1997). On the server, a relational database was chosen rather than an object database for cost reasons. Another advantage in using JAVA lies in the availability of numerous standardized libraries, in particular regarding graphical user interfaces. ECMASCRIP is an interpreted language close to Javascript, that was chosen for the

parts of the code that can be changed interactively (see above in this section). This way, the simulation tool may evolve as underlying dynamics are modified and new processes are considered. Graphical components were entirely coded by developers to reduce costs. Model computations could have been deported to an external software, but this would have made the tool platform-dependent; they were thus internalised. To avoid directly coding EJBs, which would be very tedious and error-prone, a code generator using XML (<http://java.sun.com/xml/docs.html>) descriptions of the Beans and corresponding template files was developed. This program automatically generates all the Beans with an expansion factor of 70.

The present version of the software was validated with the example presented in the next section. On the present server (a PC with a Pentium III 1 GHz processor, 512 Mo RAM, and 2 ultra 160 SCSI hard drives of 20Go) running a 10 years simulation for a fishery example, when two management measures are considered takes on average 5 min.

The software was developed by a computer engineer in a small company (<http://www.cogitec.com>). It took almost 3 years, to precise specifications of the user needs in terms of underlying model and software facilities (Pelletier et al., 2001), and to develop a first version of the software. A computer engineer designed the software architecture adapted to our requirements and the software was validated through theoretical examples of mixed fisheries.

4. Application

A simple theoretical example of a mixed fishery was input in the database to illustrate the structure of the model and show the outputs of the software. This example was also used to validate the computer code. The fishery is characterized by a square region of 25 cells with a spatial resolution of 1° in latitude and longitude. Two age-structured populations and four population zones are defined (Fig. 4, left). In this example, the populations have the same zones but differ according to their seasonal dynamics (Table 5) and biological parameters (Table 6).

Population 1 may only be caught from age 1, contrary to population 2 whose young-of-the-year are accessible to fishing, resulting in bycatch that are of no commercial values and are discarded. Reproduction and recruitment for each population are described in Table 7. Fishing activity is characterised by three métiers distributed between two strategies (Table 8). Métier 1 and métier 2 use gear 1 which catches population 1 from age 1 with selectivity per age group equal to (0, 1, 1) and population 2 from age 0 with a selectivity per age group equal to (0.5, 1, 1, 1). Métier 3 uses gear 2 which catches population 1 and 2 from age 2 with selectivity per age group respectively equal to (0, 0, 1) and (0, 0, 1, 1). The standardisation factor is 5 for gear 1 and 3 for gear 2. For each métier zone (Fig. 4, right), a travel time to reach the zone is defined: 2 for zm1; 1 for zm2; 2 for zm3; 1 for zm4 and 0 for zm5.

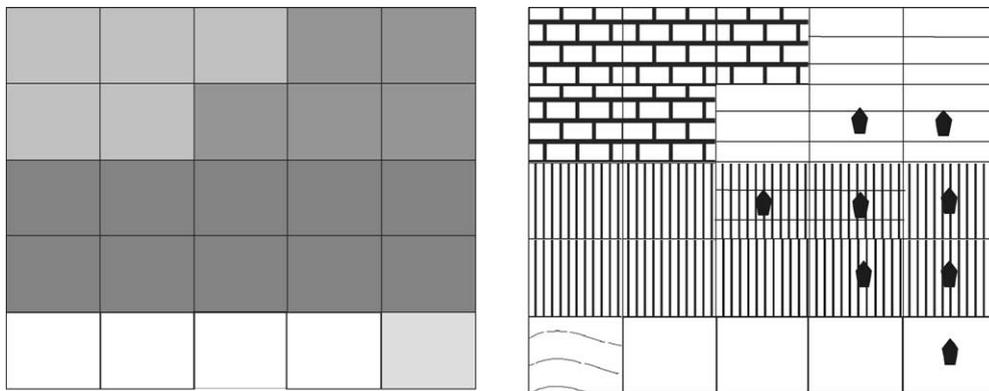


Fig. 4. Population and métier zones of the mixed fishery example: population zones in the region (left, in grey, from left to right and top to down zp1, zp2, zp3, zp4) and métiers zones in the region (right, from left to right and top to down zm4, zm3, zm5, zm1, zm2).

Table 9
Seasonal distribution of the métiers and target species

Métier	Season	Fishing zones	Species	Target factor	Primary species
Métier 1	January–December	zm1, zm2	Population 1	4	Yes
Métier 1	January–December	zm1, zm2	Population 2	1	No
Métier 2	January–April	zm1	Population 1	2	Yes
Métier 2	January–April	zm1	Population 2	2	Yes
Métier 2	May–December	zm3	Population 1	2	Yes
Métier 2	May–December	zm3	Population 2	1	No
Métier 3	January–April	zm4	Population 1	1	No
Métier 3	January–April	zm4	Population 2	4	Yes
Métier 3	May–December	zm4, zm5, zm2	Population 1	1	No
Métier 3	May–December	zm4, zm5, zm2	Population 2	4	Yes

Note that primary species indicates whether a species is an important target species for the métier.

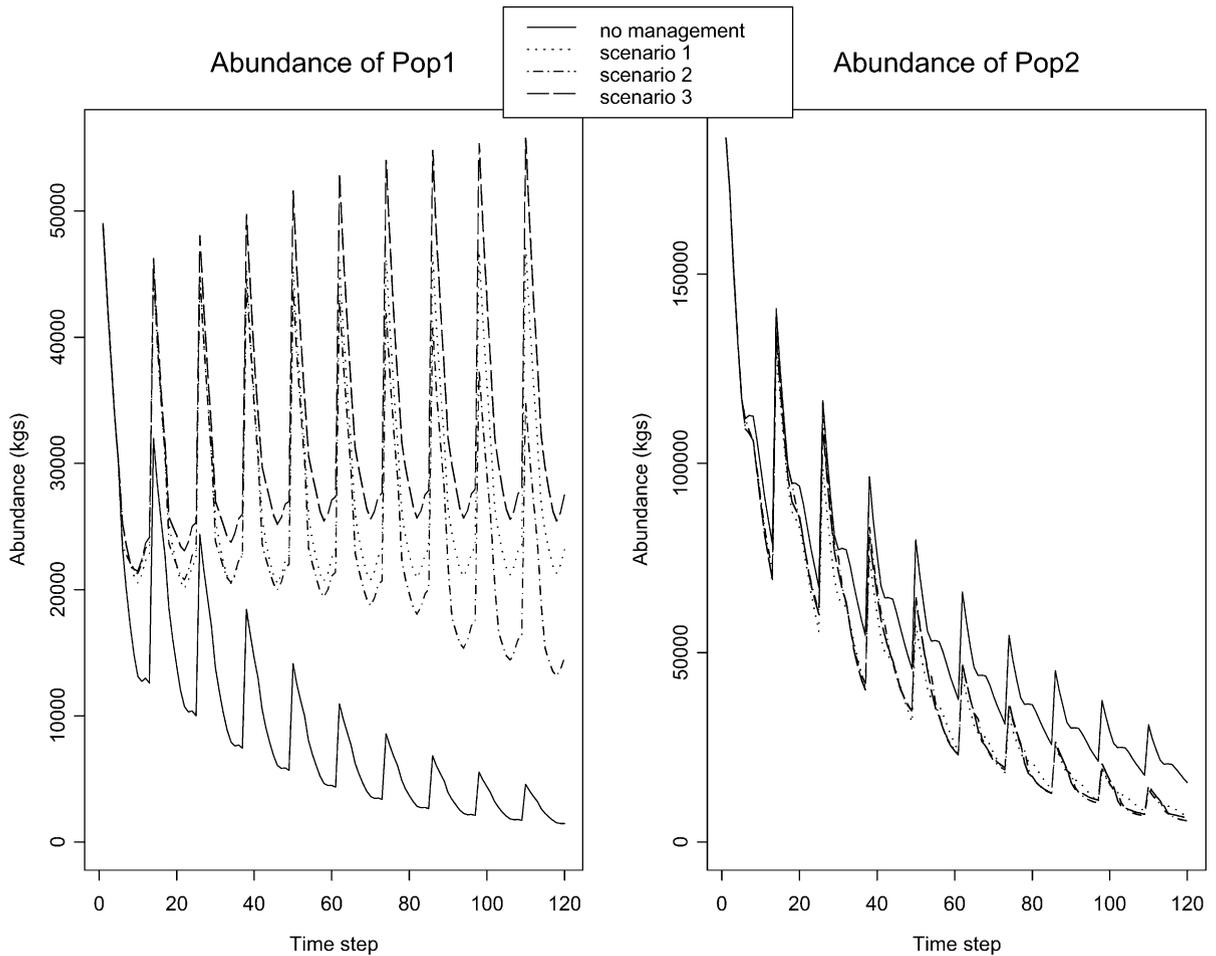


Fig. 5. Simulation results for the mixed fishery example; comparison of the impacts of different management scenarii on the abundances of the two populations.

The seasonal distributions of the three métiers as well as the target species per métier and season are specified in Table 9. Fishing units are grouped into two fleets characterised by trip duration of 5 and 14 days, respectively, and a number of trips per months equal to 4 and 2, respectively.

For this fishery, two types of management measures are considered. The first one is a MPA defined by a management season and a management zone. Note that the management zone and the management season need not correspond to a métier zone or a population, but in the example, they do for the sake of simplicity. For the same reason, we consider here that all fishing activities are forbidden in the MPA during the season

of application. During this period, all the métiers with a métier zone intersecting the management zone are affected by the measure. In this example, a simple fishers' reaction is defined as follows: if the métier zone is not totally included in the MPA, the effort of the métier is reallocated to the part of the métier zone not included in the management zone, and otherwise, the effort of the métier is cancelled (as if it could not be reallocated to another métier).

The second management measure is a TAC, a more traditional measure. It is defined by a species, a maximum catch per year, and the years of application. As soon as the TAC is reached, landings of this species are forbidden. The TAC impacts all the métiers that

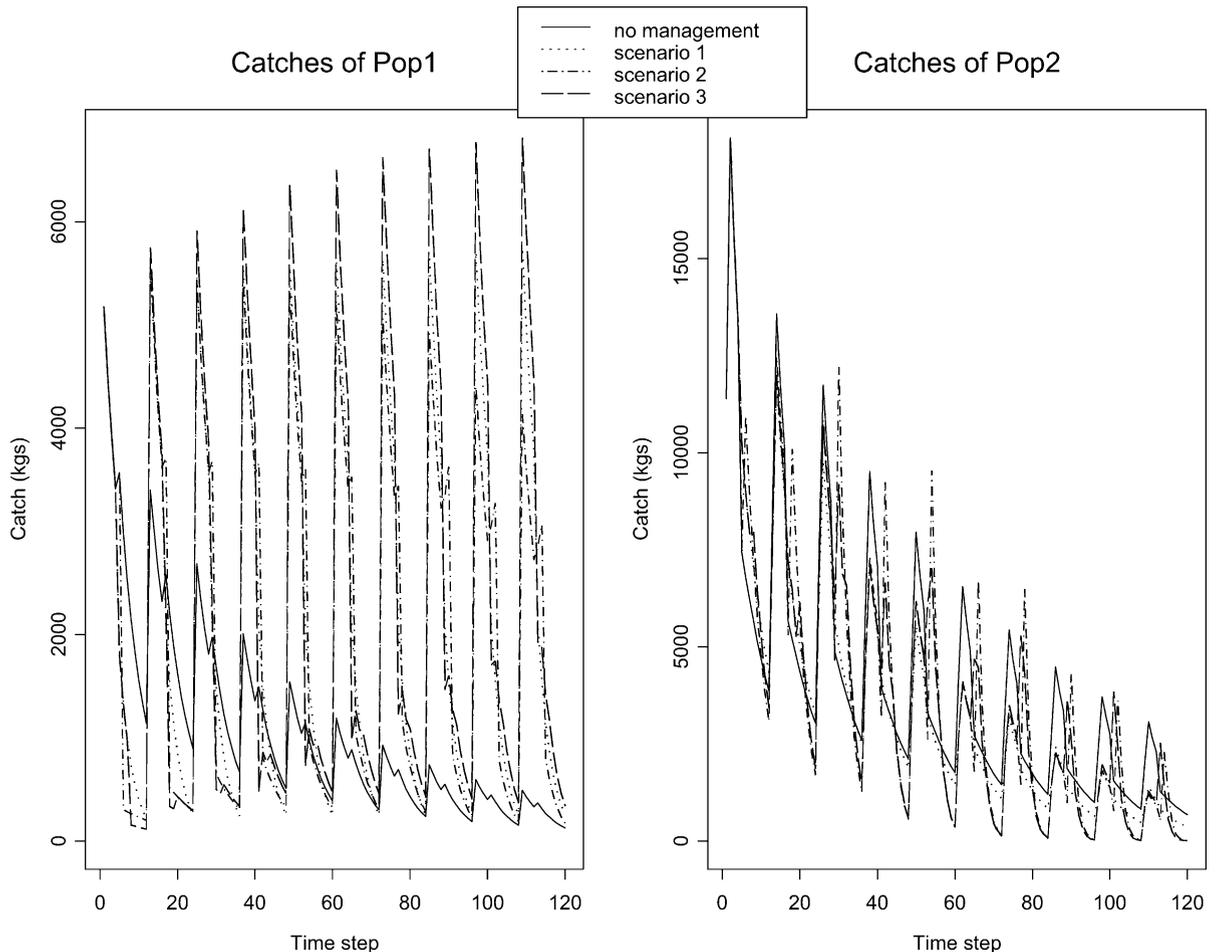


Fig. 6. Simulation results for the mixed fishery example; comparison of the impacts of different management scenarii on the catches of the two populations.

Table 10
Fishermen reactions to management measures

Management objectives	Management measures	Consequences on the métiers
(1) Protection of recruitment of population 2 and protection of juveniles of population 1	Close zp2 from May to December	<ul style="list-style-type: none"> • <i>Métier 1 et métier 2</i>: reduction of métier zone • <i>Métier 3</i>: none
(2) Reduction of global fishing mortality on population 1	TAC = 30,000 fishes on population 1	<ul style="list-style-type: none"> • <i>Métier 1 and métier 2</i>: are transferred to métier 3 • <i>Métier 3</i>: discards
(3) (1) and (2)	Close zp2 from May to december and TAC = 30,000 fishes on population 1	If TAC is reached before May <ul style="list-style-type: none"> • <i>Métier 1 and métier 2</i>: are transferred to métier 3 • <i>Métier 3</i>: discards else <ul style="list-style-type: none"> • <i>Métier 1 et métier 2</i>: reduction of métier zone until TAC is not reached and then transferred to métier 3 • <i>Métier 3</i>: nothing until TAC is not reached and then discards

may catch the species. In this example, fishers' reaction to the TAC is the following: for each métier, if the species is not a primary species (Table 9), then effort allocation is unchanged and catches of this species are discarded. Otherwise, the effort of the

métier is reallocated to other métiers, preferentially to métiers using the same gear and in the same strategy. If there are no other métiers practised when the TAC is effective, the effort of impacted métiers is simply cancelled.

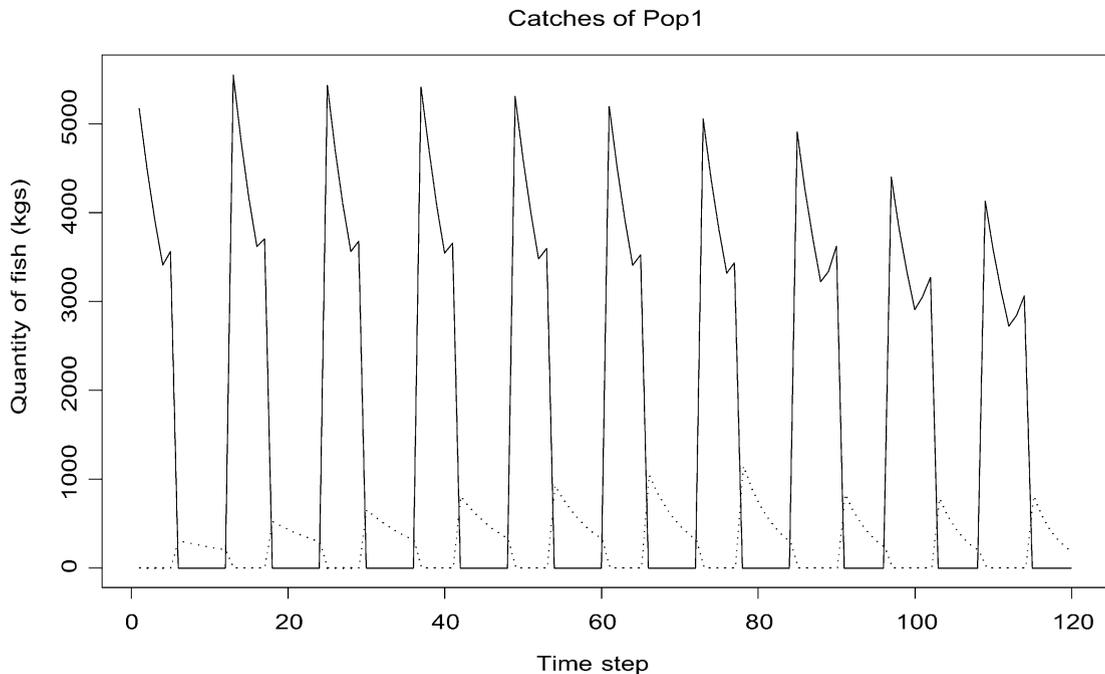


Fig. 7. Discards of population 1 induced by scenario 2 (landings in plain line and discards in dotted line).

The dynamics of this fishery was simulated over 10 years with the following initial numbers per age group and per zone for population 1 and population 2:

$$N(\text{pop1}, 0) = (0, 0, 0, 0, 0, 50000, 0, 0, 0, 30000)$$

$$N(\text{pop2}, 0) = (0, 0, 0, 0, 0, 50000, 0, 0, 0, 40000, 0, 0, 0, 20000, 0)$$

With the above chosen parameters and in the absence of management measure, both populations are overexploited with decreasing trends in abundance (Fig. 5) and in catch (Fig. 6). The dynamics of the fishery is obviously not sustainable and better catches could probably be achieved by adapting fishing effort to resource dynamics. We assessed the impact of three management scenarios on abundances and catches of both populations (Table 10). Each scenario aims at protecting different stages of the populations. The three management scenarios considered lead to increase abundance for population 1 (Fig. 5, left), but do not improve the situation of population 2 (Fig. 5, right). A MPA protecting the juveniles of population 1 (scenario 1 on Fig. 5, left) is more efficient than the TAC (scenario 2 on Fig. 5, left) at restoring a sustainable exploitation level for population 1. The same MPA should also protect the recruited stages of population 2, but the transfer of effort due to fishers' reactions results in a negative effect on population 2 (scenario 1 in Fig. 5, right).

In terms of yield, catches of population 1 increase under all scenarios, whereas catches of population 2 remain very low (Fig. 6). Note that catches include illegal catches, i.e. catches of a species for which the TAC is exhausted. These catches cannot be landed and are discarded at sea. In scenario 2, discards of population 1 represent a non-negligible part of catches (Fig. 7). This illustrates a common problem with TAC management when there are métiers incidentally catching populations for which the TAC is reached. It highlights the importance of having a multi-species approach to assess the impact of management measures.

5. Discussion perspectives

We propose a simulation tool to quantify the impact of a range of management measures (including conventional management measures and MPA), upon

the dynamics of a mixed fishery. To accommodate the complexity of such a system, the model is decomposed into three submodels coupled in space and time. The results from Section 4 illustrate the difficulty of designing management scenarios that lead to sustainable exploitation when several populations are taken into account. What may be beneficial for one population, may be harmful to the other. In any case, only models that accommodate multiple species and multiple fishing activities in a spatially- and seasonally-explicit framework, are able to depict the complex implications of management scenarios in a mixed fishery. Using our simulation tool, a variety of management scenarios can be contemplated under a range of underlying assumptions and parameter values for population dynamics and fishing activity.

We would like to compare our model with existing models developed for similar objectives, first in fisheries science and second in applied ecology. In particular, we discuss innovative modelling aspects brought by ISIS-Fish.

Up to now, among the few models developed to describe the dynamics of mixed fisheries, even fewer allow to test a variety of management measures including MPAs. Sparre and William (1993) proposed BEAM4, a bioeconomic model initially designed for sequential shrimp fisheries. Given an initial fixed allocation of fishing effort among fleets, the model computes projections "at equilibrium," i.e. all parameters being constant. In BEAM4, effort-based management measures may be assessed by modifying fleet size, fleet selectivity or spatial allocation of fishing effort. But the model is not spatially explicit, thus strongly limiting the MPA designs that can be tested. Walters and Bonfil (1999) presented a multi-species spatial stock assessment model for the groundfish fishery of British Columbia to compare management measures like global TACs, global effort limitation, and permanent closures of fishing grounds. The population dynamics is made spatial in that subpopulations in distinct fishing grounds mix with one another as a function of species dispersal rates and distances between grounds. There are no oriented large-scale migrations, nor seasonality in the model, which prevents from exploring seasonal management measures. Fishing activity is not structured in this model which considers a global fishing effort allocated between fishing grounds. Therefore, consequences of management

measures on exploitation features cannot be assessed. Holland (2000) coupled an age-structured model with dispersion and large-scale migrations for the main demersal species exploited in Georges Bank with an empirical model of exploitation dynamics describing the spatio-temporal distribution of fishing effort. This model is mainly aimed at testing MPA. Besides it is not generic and not intended to be applied to other fisheries.

With respect to spatial aspects of fisheries dynamics, previous models assume that fishing grounds match population zones exactly, which are thus common to all populations. Our model is innovative in fisheries science in the way spatial aspects are taken into account. This brings substantial flexibility in modelling and enables one to handle a variety of hypotheses about spatial dynamics of population, exploitation and management.

First, each model entity, say populations, métiers, and management measures, has his own zones and seasons, and the model may deal with a non-limited number of entities. To our knowledge, none of the existing spatially-explicit fisheries models aimed at quantifying the impact of management measures, whether multispecies models (Sparre and William, 1993; Pet et al., 1996; Walters et al., 1999) or single species models (Polacheck, 1990; Holland and Brazee, 1996; Pet et al., 1996; Maury and Gascuel, 1999; Sanchirico and Wilen, 2001; Apostolaki et al., 2002 and many other papers), allows for such flexibility. Only, individual-based models, e.g. (Gross et al., 1992; Tyler and Rose, 1994; Grimm, 1999) may achieve a larger flexibility (see below).

Second, independent zones for each population and for each activity are more appropriate for mixed fisheries since (i) populations do not have the same spatial and seasonal distributions, and (ii) the spatial allocation of fishing effort for a given métier may not be tied to a single target species: it may depend on other species and other factors as well.

Third, the spatial resolution of our model is not fixed, but may be chosen according to the amount of information available to describe the fishery. In ecological modelling, most existing spatial models are based on a regular grid in which patches are composed of one or several cells, making overlapping among dynamic patches difficult to deal with (Wu and Levin, 1997). These authors propose a patch-based

spatial modelling approach to address this question. Our model is similar to that of Wu and Levin (1997) in that dynamics relies on spatial co-occurrences of model entities. But, ISIS-Fish is not a patch-based model and is mostly aimed at analysing the dynamics of real fisheries for operational management purposes.

The second progress inherent to our model pertains to multi-specific aspects. Few management-oriented spatially-explicit fisheries models deal with multi-species issues (Sparre and William, 1992; Wu and Levin, 1997; Walters et al., 1999). However, accounting for multiple species is indispensable to quantify the impact of technical interactions in mixed fisheries (Laurec et al., 1991). To the exception of BEAM4 (Sparre and William, 1992), models previously quoted consider age-structured populations with the same growth and reproduction function and population-specific parameters. In our model, several populations may be considered for a given species, and populations have specific spatio-temporal dynamics, growth and reproduction functions. As the models cited above, our model does not consider biological interactions between populations that are difficult to quantify (Shepherd, 1998). ISIS-Fish rather focuses on technical interactions that bear more consequences for fisheries dynamics (Hilborn and Walters, 1992).

The third innovation in our model deals with management measures. First, unlike existing models, ISIS-Fish allows for free specification of management zones, which makes it possible to test any MPA design, i.e. areas with partial or total restrictions to fishing, that may or may not match fishing grounds. Besides, several management measures may be applied simultaneously to the fishery. A combination of several management measures is indeed more realistic, and is likely to be more efficient at regulating exploitation in mixed fisheries.

Second, fishers' reactions to management measures, recognised as essential to realistic perceptions of management impact (Sanchirico and Wilen, 2001) are explicitly modelled. This behaviour is rarely considered in existing models, which in addition deal only with reactions to MPA. Modelled behaviours are either simplistic (Horwood et al., 1998; Apostolaki et al., 2002 among others) or case-specific (Holland, 2000). The way fishers' reaction is coded in ISIS-Fish makes it possible to model any kind of reaction for

any management measure, including dynamic reactions depending on model variables.

Beyond the question of mathematical modelling, developing simulation tools raises the question of selecting the appropriate framework for implementation of model equations. We identified a number of desirable properties for ISIS-Fish (Pelletier et al., 2001): (i) the model should be generic and flexible; (ii) the software should comprise a database for easy integration and update of knowledge; (iii) the number of populations, fishing activities and management measures should not be a limitation; (iv) the software should be free for users and accessible via Internet by several users at the same time.

Consequently, we chose to develop ISIS-Fish from an object-oriented approach allowing a natural description of a complex system such as a mixed fishery (Silvert, 1993; Congleton et al., 1997). Regarding point (i), ISIS-Fish is generic in that it may be applied to various fisheries, ranging from simple cases to complex examples. In Section 2, the model has been presented from the standpoint of maximum complexity. In the previous section, the simulation tool was applied to a quite simple mixed fishery example with only two exploited population and three métiers. It can also be used for simpler examples such as a single-species fishery with only one fishing activity and simple spatio-temporal variations. Besides, ISIS-Fish is flexible because parts of the model may be changed without recompiling the code. This is made possible by the object language, and the editor/interpreter of equations. Analysing the sensitivity of complex systems to different parameters requires flexibility in the model to quantify alternative hypotheses. Regarding population dynamics, non-flexible assumptions of this model pertain to the chronology of processes, the survival and catch equations, and to the fact that migrations are oriented and defined by coefficients. Still, the model enables to consider a large number of hypotheses regarding population dynamics, which is helpful because several components of the dynamics may be poorly known, particularly those linked to spatial and seasonal aspects, and to reproduction and recruitment. Regarding exploitation, the structure of fishing activity in métiers and strategies is not flexible either. But refinements of the model are currently under development. It seems important to add an economic submodel, e.g. exploitation costs and seasonal

variations in species prices, since these strongly influence selection of fishing activity. It is also desirable that fishing effort may depend upon variables like previous catches and individual efficiency (Biseau et al., 1999). The largest flexibility is attained in the management model, the impact of almost any management measure and any assumption about fishers' reactions can be quantified. For all these reasons, ISIS-Fish is largely generic and flexible compared to existing simulation tools in fisheries science.

Another important aspect of the tool (point (ii)) deals with integration of knowledge. Depending on the level of complexity of the model considered for a given fishery, the information needed to run the simulations may vary, and this software may be viewed as a tool to embrace all information and knowledge available for the fishery of interest. Application to a given fishery requires literature review and data analysis to estimate model parameters. Simulation results should help to highlight domains in which further data collection is necessary to evaluate fishery's dynamics. Applications to real fisheries are currently under development, in particular an application to the Celtic Sea demersal trawl fishery. The database included in the software enables one to store several fisheries.

In ecological modelling, several simulation models have been developed with software such as STELLA (Voinov, 1999; Costanza, 2001). In fisheries science, STELLA has mostly been used for single species models (Jessup, 1998; Wilson et al., 1998; Dew, 2001). Given constraints (iii) and (iv), we selected the software architecture presented in Section 3 rather than developing the simulation tool using a modelling package like STELLA (Costanza, 2001).

The specifications set on the software are rather innovative in fisheries science, and this type of simulation tool may also be considered for investigating other ecosystems subject to human activities. Often, simulation tools are developed for a given ecosystem and may not be adapted to other ones, or alternatively, the description of the ecosystem may not be changed without rewriting parts of the code. This software may thus be of interest not only to fisheries scientists, but also to other domains of ecology and environmental sciences. The aim of such a tool is to be widely used, so that it can evolve to better accommodate further user needs.

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Appendix A. Computation of reproduction and recruitment outcomes

Reproduction begins at the first month of the reproduction season, $trepro_{beg}$. Until the last month of this season, $trepro_{end}$, births occur according to a maternity function f_{ma} (function of the number of matures) and fluctuate with the proportion of matures available to reproduction in each reproduction zone $zrepro$. The number of births at t in $zrepro$ is $B(t, zrepro) = f_{ma}(Prepro(t, zrepro)Nmat(t, zrepro))$, where $Prepro(t, zrepro)$ and $Nmat(t, zrepro)$ are respectively the proportion of matures available for reproduction, and the number of matures in $zrepro$ at t . At each time step until the end of the recruitment season, newborns suffer natural mortality.

$B(t, zrepro)$ are framed into a matrix Mb of dimension $(trepro_{beg} - trepro_{end} + 1) \times zrp_n$ where $(trepro_{beg} - trepro_{end} + 1)$ is the number of reproduction months and zrp_n is the number of reproduction zones.

Recruitment starts at $trecreat_{beg} = trepro_{beg} + \Delta$, Δ being the smallest age (in months) at which a young fish may be recruited. Each batch of births in a given month recruits during δ months, so that making recruitment extends until $trecreat_{end} = trepro_{end} + \Delta + \delta$. Recruitment takes place in several recruitment zones and each zones is linked to specific reproduction zones (see Table 7 for illustration). Let us denote:

- **Precru** is the vector of length δ and $Precru_i$ is the proportion of the batch recruited at the i th month of its own recruitment. For a given batch of birth $B(t, zrepro)$ born in $zrepro$, $Precru_i B(t, zrepro)$ of them recruit at $t + \Delta + i - 1$.
- **Pztorz** is the matrix of dimension $zrp_n \times zrcn$ ($zrcn$ denoting the number of recruitment zones), such that $Pztorz(zrepro, zrecru)$ is equal to 1 if matrix births in $zrepro$ can recruit in $zrecru$ and 0 otherwise.

- $Mr = Mb Pztorz$ is the matrix of dimension $(trepro_{beg} - trepro_{end} + 1) \times zrcn$; $Mr(t, zrecru)$ is the number of births occurred at t that will be recruited in $zrecru$.

Finally, the number of recruits in $zrecru$ at t is

$$Nr(t, zrecru) = \frac{1}{zrcn} \sum_{i=1}^{\delta} Precru(i) Mr(t - \Delta - i - trepro_{beg} + 1, zrecru) \times \exp\left(-\frac{M(1)}{12}(\Delta + i - 1)\right)$$

In order to be used in Eq. (2), recruitment is framed into a vector $R(t)$ of the same structured as $N(t)$ in Eq. (1) where

$$R(t, 1, z) = \begin{cases} 0, & \text{if } z \text{ is not in a} \\ & \text{recruitment zone} \\ Nr(t, zrecru)/zpn & \text{if } z \text{ is not in } zrecru \end{cases}$$

where zpn is the number of population zones in the recruitment zone $zrecru$ and $R(t, i, z) = 0$ if $i \geq 2$.

Appendix B. Computation of survival rates and catch rates

We describe here the algebra corresponding to the computation of survival rates and catch rates at any time step t . Computations are expressed under matrix form. Survival and catch rates at time t are calculated from the instantaneous fishing mortality induced on each stage of each population in its zones of presence. Fishing mortality is itself computed from fishing effort.

Step 1: Calculate effort per métier, strategy and fleet

Additional notations to those in Table 4 are as follows:

- ListMet:** the set of métiers practised at t of length $nbmet$
- TT(t):** the vector of elements $TT(t, met)$ for each métier met in **ListMet**
- Nop:** the vector of elements $Nop(met)$ for each métier met in **ListMet**
- Std:** the vector of elements $Std(gear(met))$ for each métier met in **ListMet**

V1: a unity vector (each element is equal to 1) of appropriate length
P(str, t): the matrix of element $P(str, met, t)$ for each métier met in $ListMet$, and of dimensions the number of strategies and $nbmet$

Fishing effort is first standardized per fishing unit:

$$B = Nop \cdot Std$$

where \cdot stands for Hadamard product, i.e. $\forall i, B_i = Nop_i Std_i$; the result is a vector of dimension the length of $ListMet$.

For each fleet, we compute

$$A2(fl) = T(fl) * V1 - TT(t)$$

where $*$ is the term to term product, i.e. $A2(fl)_i = T(fl)V1_i - TT(t)_i = T(fl) - TT(t)_i$ (the result being a vector of dimension the length of $ListMet$), and

$$A3(fl) = B \cdot A2$$

(the result being a vector of dimension the length of $ListMet$)

For each strategy, we compute

$$A4(fl, str) = P(str, t) \cdot A3$$

(the result being a vector of dimension the length of $ListMet$), and

$$A5(fl, str) = Nfu(fl, str) * A4(fl, str)$$

(the result being a vector of dimension the length of $ListMet$).

End of loop over strategies

End of loop over fleets

At this stage, effort per métier for each fleet in each strategy is stored in a three-dimension matrix $EfMetStrFl$ in order to be able to compute effort per métier either per fleet or per strategy.

Effort per métier is written:

$$A6 = \sum_{fl} \sum_{str} A5(fl, str)$$

(the result being a vector of dimension the length of $ListMet$).

Step 2: Calculate effort per métier zone

Additional notations are as follows:

NbCells(z): the number of cells of zone z

$$PZ(t, met) =$$

$$NbCells(z_{met}(t))$$

InvNbCellsPZ(t): the vector of element $1/PZ(t, met)$ for all the métiers of $ListMet$

ListMetZone(t): the set of métier zones visited at t

IndMetZone(t): the matrix of dimension the number of métiers in $ListMet$ and the number of zones in $ListMetZone$ such that $IndMetZone(t, met, z) = 1$ if met is practised in z at t , and 0 otherwise

NbCellsMetZone: the vector of $NbCells(z)$ for all the zone z in $ListMetZone$

For each métier, we assume that effort is uniformly distributed over the métier zones of the métier at time t . Effort per cell (unity of space) is thus computed from the total number of cells of the métier zones of the métier at t .

$$A7 = InvNbCellsPZ(t) \cdot A6$$

Effort per cell is then allocated to métier zones:

$$A8 = A7 \cdot IndMetZone(t)$$

where \cdot denotes the following product between a vector and a matrix, say $\forall i, j, A8_{ij} = A7_i IndMetZone(t)_{ij}$. Standardized effort per métier and métier zone is stored in a two-dimension matrix equal to the product $NbCellsMetZone \cdot A8$.

Step 3: Fishing mortalities

For each population, matrix **A8** is used to compute fishing mortality per stage and per population zone. For this purpose, selectivity, target factors, catchability, and the intersection between population zones and métier zones must be taken into account.

For each population denoted pop additional notations are as follows:

Tarf(t):	the vector of element $Tarf(t, met)$ for all métiers in $ListMet$
$ListPopZone(pop)$:	the set of population zones of pop
$ListPopStage(pop)$:	the set of stages of pop
IntMetZonePopZone(t):	the matrix of dimension the number of zone in $ListMetZone$ times the number of zones in $ListPopZone$ such that $IntMetZonePopZone(t, z_{met}, z_{pop}) = Nbcells(z_{met} \cap z_{pop})$
$Sel(t) = (Sel(t, s, gear(met)))_{s \in ListPopStage(pop), met \in ListMet(t)}$:	the matrix of element $Sel(t, s, gear(met))$. The dimension of this matrix is the number of stages in $ListPopStage$ times the number of métiers in $ListMet$
Cat:	the matrix of element $q(s, z_{pop})$. The dimension of this matrix is the number of stages in $ListPopStage$ times the number of zones in $ListPopZone$

Taking into account the target factor, we compute:

$$A9 = Tarf(t) \cdot A8$$

where \cdot is the vector-matrix product, where the result is a matrix of dimensions the length of $ListMet \times$ the length of $ListMetZone$.

We then compute effort per population zone from effort per métier zone by the matrix product:

$$A10 = A9 InterMetZonePopZone(t)$$

the result being a matrix of dimensions the length of $ListMet(t)$ times the length of $ListZonePop(pop)$.

Taking into account selectivity, we compute:

$$A11 = Sel(t) \wp A10$$

where \wp denotes a particular operator between two matrices, i.e. $A11_{ijk} = Sel(t)_{ij} A10_{jk}$; the result is a three-dimension matrix of dimension the length of $ListPopStage(pop)$ times the length of $ListMet(t)$ times the length of $ListPopZone(pop)$.

Taking catchability into account, we compute:

$$A12 = A11 \diamond Cat$$

where \diamond points out a particular operator resulting in a three-dimension matrix, such that $A12_{ijk} = A11_{ijk} \diamond Cat_{ik}$; **A12** is thus a matrix of dimension the length of $ListPopStage(pop)$ times the length of $ListMet(t)$ times the length of $ListPopZone(pop)$.

Fishing mortality per stage and per population zone is obtained by summing **A12** over the second dimension:

$$FM_{ij} = \sum_l A12_{ilj}$$

FM being a matrix of dimension the length of $ListPopStage(pop)$ times the length of $ListPopZone(pop)$.

FM corresponds to the fishing mortality endured by population pop at time t and will be denoted

$$FM(t)$$

$$= (F(t, s, z_{pop}))_{s \in ListPopStage(pop), z_{pop} \in ListPopZone(pop)}$$

For each stage of pop and each zone of pop , corresponding catch rates (Eq. (4)) are stored in a partitioned diagonal matrix as for survival rates:

$$Cr(t) = Diag(Cr(t, I), \dots, Cr(t, s), \dots, Cr(t, smax))$$

where block $Cr(t, s)$ is a diagonal matrix of dimension the number of population zones of pop :

$$Cr(t, s) = Diag(cr(t, s, I), \dots, cr(t, s, zn))$$

Step 4: Catches per métier

Catch calculated in Eq. (5) are framed into a matrix **C(t)** of element $c(t, s, z_{pop})$ and dimension the number of stages in $ListPopStage$ times the number of zone in $ListPopZone$. Catch per métier may then computed as follows:

$$A12 \frac{C(t, pop)}{FM}$$

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