SPATIAL MODELING OF ATLANTIC YELLOWFIN TUNA POPULATION DYNAMICS:  
A HABITAT BASED ADVECTION-DIFFUSION-REACTION APPROACH WITH  
APPLICATION TO THE LOCAL OVERFISHING STUDY.

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* abstract
This paper's aim is to present a spatial multigear population dynamics model forced by the environment for the Atlantic Ocean yellowfin tuna. The model allows the population's distribution to be simulated as a function of different environment variables and observed fishing effort. It is age structured to account for age-dependent population and catchability parameters. It is based on an advection-diffusion-reaction equation in which the advective term is proportional to the gradient of a habitat suitability index derived from temperature, salinity and tuna forage data. Functional relationships between movement parameters, catchability and environmental variables are based on non linear relationships estimated with generalized additive models (GAM) to characterize, on the one hand, the yellowfin's environmental preferences and, on the other hand, their catchability to different gears. Analytically formalized, GAM's relationships characterizing environmental preferences enable the habitat index to be calculated at each point in time and space. Also formulated analytically, the relationships characterizing catchability to different gears enable the calculation of predicted catches, which are compared to observed catches to estimate the model parameters.

In this paper, the local overfishing phenomenon of adult tunas in the Gulf of Guinea is addressed through different simulations. The importance of the local overfishing phenomenon in simulations is discussed.

* Introduction
Yellowfin tuna (Thunnus albacares) is a cosmopolitan species whose distribution mainly covers tropical and sub-tropical waters of the three oceans. In the Atlantic Ocean, three main fleets fish for this important pelagic resource. During recent years, total yellowfin catches in the Atlantic Ocean were around 150,000 MT and raised a 175,000 MT maximum in 1991 (Anon. 1997). Because tuna populations exhibit particular characteristics (e.g.: the importance of a « cryptic » fraction of the biomass in the population dynamics, massive movements and migrations linked with the environment, very heterogeneous fisheries spread on ocean scale distribution areas,...), spatial models are needed to realistically represent their dynamics (Sibert et al. 1998). Among the different exploited species in the Atlantic Ocean, yellowfin tuna is an interesting candidate to apply an advection-diffusion-reaction model forced by the environment. Indeed, yellowfin exhibits important movements at different scale, which make space occupation a central problem for management and conservation (Fonteneau et al. 1998, Maury 1998). Yellowfin movements seem to be directly linked to a highly variable environment (Fonteneau et Marcille 1988, Cayré et al. 1988, Mendelssohn and Roy 1988, Mendelssohn 1991, Marsac 1992): tunas continuously look for micronecotic aggregates for feeding and their distribution in the three dimensions is limited by their physiology to well defined moving environmental ranges.

1 The purse seine fleet (mainly French and Spanish vessels in the eastern Atlantic and Venezuelan vessels in the western side of the Ocean) catches all yellowfin sizes in surface waters, the boat-boat fleet which catches mainly young fishes associated with other tropical tunas (skipjack -Katsuwonus pelamis- and bigeye -Thunnus obesus-) in coastal waters and the longline fleet which catches older yellowfin and bigeye in open sea waters.
In this context, environmental characteristics are probably the major driving force for yellowfin population movements (Cayré 1990). Consequently, the ecological forcing of the environment on yellowfin distribution, movements and catchability must be explicitly incorporated in any realistic small-scale spatial modeling. GAM analysis of the relationships linking yellowfin density to the hydrological environment conducted by Maury (1996) helped to distinguish 4 main scales of variability in the Atlantic yellowfin population movements. At each scale there is a corresponding movement type, which can be associated to the variability of a given environmental factor (Maury et al. unpublished). Such scale-dependant relationships are used here to analytically formulate a heuristic age-dependent habitat model for yellowfin. This model is used to force an advection-diffusion-reaction equation, which represents the space-time population dynamics. Given this model, different ecological assumptions can be explored. In this paper, we particularly focus on yellowfin population local overfishing.

* 1. Spatial Modeling of the Yellowfin Tuna Population Dynamics
The model developed here includes three coupled components: environment, population and fishing effort. The population dynamics component is modeled with an advection-diffusion-reaction model. Such models have a long history in ecology (Skellam 1951, Okubo 1980, Holmes 1994) but their use in fishery science has grown recently (MacCall 1990, Bertignac et al. 1998, Sibert et al. 1999). To be realistic in our case, they must reflect the heterogeneous distribution and movement of tuna population linked to the environment heterogeneity. To model that linkage, we transform the environmental multivariate heterogeneity into the variability of a single functional parameter characterizing the habitat suitability and depending on fish's physiological stages. For that purpose, population functional responses to the environment need to be determined. On the other hand, it is necessary to estimate catchability and its variations with the hydrological environment and the fishery configuration. Then, given modeled fish density, observed fishing effort and modeled catchability, theoretical catches can be calculated and compared with observed catches to estimate the model parameters (Fig. 1).

** 1.1. Model Formulation
*** 1.1.1. Advection-Diffusion-Reaction of the Population
An advection-diffusion-reaction equation is used to model the yellowfin population dynamics, spatial distribution and movements. In such a probabilistic model, fish movement has two components: a random one, the diffusion term which characterizes « dispersive » movements, and a directed one, the advection term which describes movement directed along the habitat suitability gradient. Both components are included in a partial differential equation (PDE) continuous in time and space (Okubo 1980, Bertignac et al. 1998, Sibert et al. 1999). The equation used in the present work includes a density-dependent diffusion term to model possible density-dependent habitat suitability (DDHS) (MacCall 1990, Maury 1998, Maury and Gascuel 1999):
\[
\frac{\partial N}{\partial t} = \left( \frac{\partial}{\partial \kappa} \left( D + k \cdot \gamma \cdot N^r \right) \right) \frac{\partial N}{\partial \kappa} + \left( \frac{\partial}{\partial y} \left( D + k \cdot \gamma \cdot N^r \right) \right) \frac{\partial N}{\partial y} + \left( \frac{\partial b}{\partial \kappa} - N \right) \frac{\partial b}{\partial \kappa} + \left( \frac{\partial b}{\partial y} - N \right) \frac{\partial b}{\partial y} - Z \cdot N
\]

(1)

With \( N = N_{x,y,t} \) representing the considered cohort density at point \((x, y)\) at time and age \(t\), \( D = D_{x,y,t} \) the diffusivity coefficient, \( k \) and \( \gamma \) are constants characterizing the shape of the density-dependence habitat selection relationship (the more the fish density increases, the more the habitat suitability decreases). \( ba = ba_{x,y,t} \) is the local habitat suitability (biotic affinity) and \( Z = Z_{x,y,t} \) the local mortality rate including the natural and the local fishing mortality rate.

For simplicity, we do not allow the diffusion \( D \) and the natural mortality coefficient \( M \) to vary with the habitat suitability. On the other hand, the advection term is proportional to the habitat suitability (ab) spatial gradient. Then, the modeled fish move with respect to the local "favorability" gradient and swim towards a better environmental suitability. Numerical solving of equation (1) is done with an "alternating-direction implicit method" (Press et al. 1994) on a \( 1^\circ \times 1^\circ \) square from 30° south to 50° north. A daily time step and closed reflective boundaries are used (Neumann conditions: \( \frac{\partial N}{\partial \kappa} = 0 \) at boundaries) to model an impassable frontier such as a shore.

*** 1.1.2. Functional Responses to the Environment and Calculation of the Biotic Affinity, \( ba \)

Habitat suitability depends on various biotic and abiotic factors. At the same time, functional responses linking the biotic affinity \( ba \) to measured environmental factors are likely to be non-linear functions (dome shapes functions, thresholds, etc...). Maury (1998) and Maury et al. (unpublished) conducted a multivariate GAM\(^2\) analysis of the relationships linking yellowfin density to the environment. Amongst numerous factors, they found that the sea surface temperature (SST), the salinity (sal) and a tuna forage index (secondary production index SPI-6 calculated by transporting the satellite derived primary production with marine currents -Maury 1998-) explain the major part of the Atlantic yellowfin tuna distribution variability at four different spatio-temporal scales from a local scale \( (1^\circ \times 1^\circ \times 15 \text{ days}) \) to the scale of the whole distribution area\(^3\).

In the present work, the parametric formulation of functional relationships linking the habitat suitability to the environment is derived from GAM relationships obtained by Maury (1998) as is their interpretation. Four relationships are retained to characterize the environmental forcing. Each of them vary with the age of the fish:

- A threshold relationship for salinity which combines two different linear relationships (a constraint for low salinity levels and a limitation for high levels) (cf. Fig. 2).
- A gaussian relationship between the log of the biotic affinity and the temperature (cf. Fig. 2).
- A linear relationship between the log of the biotic affinity and the tuna forage indices SPI-6.

\(^2\) General Additive Models (GAM) are non parametric statistical methods which allow to determine non linear relationships between variables (Hastie and Tibshirani 1990).

\(^3\) Les données océanographiques utilisées dans la présente étude (SST, salinité de surface, profondeur de l'isotherme 20°C ainsi que l'indice de production secondaire -IPS- calculé par déplacement selon les courants marins de données de chlorophylle satellitaire -Maury 1998-) sont issues de simulations du modèle OPAT.1 (Dahulacque et al. 1995) développé au LODYC (Laboratoire d'Océanographie Dynamique et de Climatologie, Paris VI) dans le cadre du projet OPERA (Morillère 1989, Morillère et al. 1989).
Figure 2.: GAM relationships between the log of the biotic affinity and the salinity (first line) and the SST (second line) for young yellowfin (age 1) on the left column and for adult fishes (age 5+) on the middle column (redrawn from Maury et al. -unpublished-). On the right, modeled relationships (arbitrary units): for salinity (first line), the limiting relationship corresponds to adult fishes (grey curve) and the relationship for juveniles is the sum of the limiting relationship and the constraining relationship (black curve). Concerning SST (second line), an age-dependent gaussian relationship is retained (on the right).

The generalized additive modelling is an additive formulation of the considered relationships. The biotic affinity definition requires a transformation to a multiplicative model which is more in accordance with the ecological niche theory seen as an hyper-volume with n environmental dimensions (Hutchinson, 1957):

\[
\log(-ab_{reg} + 1) = \left( \frac{\alpha_{reg}}{\alpha_{reg}} \frac{e^{\gamma_{reg} \cdot salinity - \kappa \cdot salinity + \lambda_{reg} \cdot IPS}}{2 \cdot ab_{reg}} \right) - \gamma_{reg} \cdot salinity - \kappa \cdot salinity + \lambda_{reg} \cdot IPS
\]

\[
\gamma_{reg} = 0 \text{ if age > 3}
\]

\[
\kappa = 0 \text{ if salinity < 0.036kg.kg}^{-1}
\]

(2)

With $\alpha_{reg}$, $\beta_{reg}$, $\gamma_{reg}$, $\kappa$, $\lambda_{reg}$ parameters. Five of the six parameters used to model the biotic affinity are age-dependent.

*** 1.1.3. Fish Diffusion

The diffusivity coefficient $D$ varies with the mean distance crossed by a fish during a time step. This distance varies with the swimming speed of the fish, which varies with their size (Sharp et Dizon 1976). In the model, a power law with an exponent $\theta$ characterizes the potential non-linearity of this relationship (Aleyev 1977):

\[
D = \delta \cdot t^\theta
\]

(3)

The Gascuel et al. (1992) two stances growth model is used to convert age into size in order to calculate diffusion as a function of fish’s age (Fig. 3).
Figure 3.: yellowfin diffusivity modelization as a function of their age for different $\theta$ parameters (arbitrary units).

*** 1.1.4. Natural Mortality

The yellowfin natural mortality rate used for stock assessment by the ICCAT\(^4\) scientific committee is arbitrarily fixed at 0.8 year\(^{-1}\) for age 0 to 1 fish and at 0.6 year\(^{-1}\) for older fish. The use of two mortality levels allows for the fact that juveniles mortality is likely to be higher than adults mortality. In the present work, a natural mortality curve depending on age is used. The use of a second order polynomial function characterize a high mortality level for young fish, a minimal mortality level for adults and a slight senescence for oldest fish (Fig. 4).

Figure 4.: monthly natural mortality rate as a function of yellowfin age (days). Continuous line, the ICCAT natural mortality coefficient used by ICCAT. Dashed line, the natural mortality used in the present work.

*** 1.1.5. Recruitment

Our advection-diffusion-reaction model only deals with the recruited stages. It does not explicitly represent the recruitment process, which gives the initial state to each cohort dynamics. The recruitment spatial distribution is obtained with a simple algorithm. For each of the seven cohorts modeled, the recruitment levels are calculated with a monthly VPA. Then, recruitment in the model is uniformly distributed in the tropical areas where salinity on the first of January is lower than an arbitrarily fixed threshold equal to 0.03 kg/kg\(^3\). Those low salinity regions, thought to be nursery zones, are mainly located from the Guinea Gulf to Guinea shores and in front of the Amazon mouth (Fig. 5).

\(^4\) International Commission for the Conservation of Atlantic Tunas
Figure 5.: the model's nursery zones where the recruitment calculated by VPA is distributed (see text). Case of the first of January 1980.

The obtained population is considered to be pre-recruited. Then, to get a « close to equilibrium » state, it is re-distributed without mortality during five time steps by using equation (1) with environmental conditions corresponding to the first of January of the considered year and age 0 functional responses to the environment. The obtained distribution of age 0 fish is used to initialize simulations.

*** 1.1.5. Purse-Seiners Catchability Parameterization

The GAM analysis of commercial CPUE's conducted by Maury (1998) and Maury et al. (unpublished) provides a model of catchability to purse-seiners for the period 1980-1991. In the model, the catchability is related to the local fishing effort and to the depth of the thermocline (approximated by the 20°C isotherm depth). To characterize the increase of local catchability when local fishing effort increases and the raise of a plateau (Maury 1998, Maury et al. unpublished), we use a simple non-linear function (Fig. 6). The increasing part of the curve corresponds to the increase of purse seiner's catchability when the fishing effort increases (cooperation and spying between vessels). The decreasing part of the curve observed for adult fishes is interpreted as a local overfishing phenomenon (Maury and Gascuel unpublished) and then, it is not included in the model catchability (τ ≥ 1 in equation 4).

Figure 6.: GAM relationships between the log of the 1980-1991 mean catchability and the fishing effort for young yellowfin (age 1) on the left column and for adult fishes (age 5+) on the middle column (redrawn from Maury et al. unpublished). On the right, parametric model retained to represent such relationships between yellowfin catchability to purse seiners and fishing effort.

The thermocline depth effect on catchability is considered to be linear (the deeper the thermocline is, the lower the catchability is) and it varies with yellowfin age. Then, the catchability model is expressed as follows:

\[ \ln(q + 1) = \frac{\mu_{age} \cdot f}{(1 + \omega \cdot f)^\tau} - \rho_{age} \cdot Z \cdot 20 \quad \Leftrightarrow \quad q_{age} = \frac{\mu_{age} \cdot f}{\rho_{age} \cdot Z \cdot 20} - 1 \]  

(4)

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5 The fishing data used in the present study comes from the ICCAT (International Commission for the Conservation of Atlantic Tuna) data base which centralizes statistical data for all tuna fisheries in the whole Atlantic ocean, in the present study were only used catches by age and effort for the FIS (France, Ivory Coast and Senegal) purse seiners during the period 1980-1993.
Where $\mu_{age}$ are the parameters characterizing the increase of catchability with effort; $\alpha$, a parameter characterizing the saturation of such effect; $\tau$, a shape parameter (Fig. 5) and $\rho_{age}$, the weight of the "thermocline effect" on catchability.

**2.1. Parameters Estimation and Model Validation**

***2.1.1. Model Tuning and Fitting to FIS Purse Seiners CPUEs***

Considering 8 age classes for yellowfin (from age 0 to 5+), the whole model (functional responses + population dynamics + catchability) has 47 parameters ($\sigma_{age}$, $\beta_{age}$, $\sigma_{age}$, $\gamma_{age}$, $\lambda_{age}$, $D$, $\theta$, $\tau$, $\mu_{age}$, $\omega$, $\rho_{age}$) whose effects are more or less independent. Even with the high number of CPUE observations available for the present study (35725 observations at 1 degree/15 days resolution), the identification of such a non linear numerical model is a very complex task which requires immense computing time. Thus, as a first step, we chose to tune "by hand" the model parameters and only to estimate numerically, at each step, the catchability parameters $\mu_{age}$ 0 and 1 and $\mu_{age}$ 2, 3, 4 and 5+. The fit of these six parameters provides statistical criteria characterizing the fit of model to observed data.

Assuming a lognormal distribution for CPUEs, a simple least square fit on $\ln(CPUE+t)$ is used to fit catchability parameters and to guide the other parameters tuning. Then, assuming that the observed $\ln(CPUE_x+t)$ ($k=1...n$ observations) are a realization of the random vector $[\ln(CPUE_x+t)]_n$, the regression statistical model is written as follows:

$$\ln(CPUE_{i,j,t}+1) = f(x_{k,t}, \theta) + \varepsilon_{i,j,t} \quad k = 1...n$$

$f$ being a deterministic function of the variables $x$ and the parameters $\theta$ and $\varepsilon_{k,t}$ are the errors which are assumed to be independent for each observation.

Since the observed $\ln(CPUE_x+t)$ series is highly heteroscedastic (its variance is linked with the $\ln(CPUE_x+t)$'s value), we use a weighted least square which gives an equal importance to all the observations:

$$SCE = \sum_{i=1}^{n} \left( \frac{\ln(U+i) - \ln(\hat{U}+1)}{\sigma_{rt}^2} \right)^2$$

The least square estimator corresponds with the maximum likelihood of $\theta$ if measurement errors are independent and normally distributed (Bard 1974). If the model is correct, weighted reduced residuals

$$c_t = \frac{f(x_t, \hat{\theta}) - \ln(PUE_t+1)}{\hat{\sigma}.\sigma_{rt}}$$

must behave as an independent random variables series $N(0, 1)$.

Assuming independent errors, the focus is now on residuals normality and homoscedasticity. A simple graphical examination of the residuals plot (Fig. 7) shows that, apart diagonal structures characterizing positive distributions, residuals form a horizontal band centered around zero.

![Figure 7: reduced residuals versus estimated values of the response variable $f(x_{i,j,t}+\hat{\theta})$.](image-url)
However, normality of residuals is clearly not observed and their distribution is very asymmetric. Consequently, the simple minimum least square criteria we used is not consistent with the maximum likelihood estimator of the model given the data.

**Table 1:** Parameters values estimated by calibrating the model.

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<th>Parameters</th>
<th>Prefences</th>
<th>Catchability</th>
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<td>$\gamma_{4,5}$</td>
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<td>$\lambda_{0,1,2,3,4,5}$</td>
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</tr>
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</table>

*** 2.1.2. Model Validation, Consistency of the Outputs

The non-linear features of our model make estimation of its parameters a very complex task. Indeed, different parameter sets may give very close values of a simple least square statistical criterion. Thus, even with many observations, the simple tuning of such an overparameterized non-linear model is problematic and results are limited by their ecological interpretability. On the other hand, it is important to use independent information to validate the model. For this, data from the longline fishery were used for validation. The longline fishery characteristics (selectivity, spatial distribution, catchability trends, ...) are very different from the purse seine fishery whose data were used to fit the model. The global consistency of the model outputs is analyzed by comparing the predicted adults (age 5+) yellowfin distribution by month with the mean spatial distribution of longliner catches calculated by averaging the longliners catches by month on the period 1966-1993 (Fig. 8). Because longliners mainly fish for age 4-5+ fishes, such a comparison is only interesting in characterizing the model's ability to represent the spatial distribution and movements of the adult population.

Even with such a rough validation method (we compare mean catch distribution with the model predictions which concern the fish population spatial distribution for a given year), the model results seem to be very consistent and represent fairly well the large scale spatial distribution and movements of adult yellowfin population (age 4-5+). Results concerning young fishes (age 0-1) seem to be consistent as well with scientific knowledge concerning spatial distribution and movements of juvenile yellowfin (Bard and Hervé 1994). The 2-3 year old yellowfin is more questionable and requires further investigation concerning the parameterization of seasonal catchability (for details, see Maury 1998).

* 3. Simulations Analysis: the Yellowfin Local Overfishing

Strong local fishing pressure is likely to induce a significant local decrease of both resource biomass and fishing yields. That is what we call « local overfishing » (Maury and Gascuel unpublished). From a general point of view, local overfishing phenomena are well known for tuna fisheries (Fonteneau and Soubrier 1996, Fonteneau et al. 1997). Concerning the Atlantic yellowfin tuna, a spatial vpa analysis indicated that very high local mortality rates could be exerted on the adult reproductive fishes in the eastern Atlantic ocean (F=0.8 quarter⁻¹ during the first quarter of the year) (Maury 1998). Such very high mortality levels are likely to induce important local depletions of adult fish. The comparison of two simulations of the spatial distribution of age 5+ fishes clearly emphasizes the local overfishing hypothesis. The first simulation accounts for the observed FIS purse seine catches. The second simulates the population without any fishing pressure, as it could have been in a virgin state (Fig. 8). For age 0-1-2-3 fish, fish density is very high for catches and the local overfishing phenomenon does not appear in simulations.
Taking into account the observed FIS purse seiners catches in the simulations, important local biomass depletions appear in the simulated population (Fig. 8). At different periods during the year, one can observe a « wound » and « healing » phenomenon as analyzed with theoretical simulations by Maury and Gascuel (unpublished) (it is less clear for age 4 fishes than for age 5+ fishes). The highest fish depletions occur in February, March and April, off the Guinea Gulf. In May, the adult population « heals » before it experiences significant « wounds » again after July in the Guinea Gulf. At that time, fish are sufficiently concentrated off Senegal as to stay numerous despite the significant catches. From July to the end of the year, there are almost no 5+ fish in the Gulf of Guinea. Such depletion of old fish in the Gulf of Guinea could explain the low longline catches observed in the area from August to November (Fig. 8).

Only the FIS purse seiners catches (more than 40% of the total yellowfin catches) are included in the simulations presented here. If all the other fishing fleets are taken into account (and particularly the Spanish purse seiners fleet whose catch level has the same order of magnitude as FIS), local overfishing of old fish would have been much more significant, perhaps too to keep realistic?

Consequently, four alternative hypotheses must be studied in future work:

- The overfishing phenomenon of old fish is actually extremely strong;
- Our model does not sufficiently concentrate the population of old fish in the Guinea Gulf to explain the very high catches which are observed;
- The yellowfin population « viscosity » is too high in the model and is responsible for a « healing » period of old fishes which is too low;
- The total number of fish derived from vpa recruitment is not sufficient to explain the high local catches. If this is the case, VPA could underestimate total fish abundance, for instance, by ignoring a potentially important cryptic biomass;

At this point, we can not distinguish which of these possibilities is most likely. Nevertheless, there is probably a strong seasonal local overfishing for old yellowfin, even if the « wound » and « healing » phenomenon is exaggerated by our diffusion-advection simulation. Such strong local overfishing may have significant impacts on the relevance of CPUEs as abundance indices (Maury and Gascuel unpublished). Moreover, an important local biomass exhaustion could have a long-term impact on the yellowfin population genetic structure. For example, a strong local fishing pressure on the main reproductive grounds could select artificially for fish reproducing in marginal areas such as Cabo Verde.

To address this question, an improvement of our ecological knowledge concerning yellowfin tunas is needed. By allowing theoretical ecological assumptions to be studied, our model could help make advances in this direction.

Conclusions

The advection-diffusion-reaction model of the Atlantic yellowfin tuna gives satisfactory results. Fish population distribution and movements seem to be well characterized, at least at the large scale for ages 0-1 and ages 4-5+. The model is devoted to spatialized assessment, in particular to a better understanding of the interaction between fishery dynamics and fishing fleet’s. In addition, since it is spatially explicit, our modeling study allows the exploration of ecological hypotheses concerning yellowfin movements and behavior given the environment. In this paper, yellowfin local overfishing is addressed...
through different simulations. It appears that the phenomenon is extremely marked in the model for old fish in the eastern Atlantic.

Other simulations (Maury 1998) have been performed which study the homing of adults to the Guinea Gulf's reproductive grounds and analyze the impact of the 1993-1984 environmental anomaly on fish spatial distribution and catches. The model presented here is still preliminary. Nevertheless, some conclusions can already be drawn. Despite many limitations, commercial fisheries data are often the only means of accurately estimating tuna distribution on a large scale. For this reason, it is necessary to identify technical and environmental factors involved in local catchability. From this perspective, the Atlantic Ocean has the advantage of being a small basin exploited by rather homogeneous fleets distributed over wide areas covering various biotopes. Nonlinear analysis which take into account the antagonistic features of environmental influences on tuna distribution is needed. GAM models would be very useful to make such a non-linear analysis.

Different improvements of the model are currently underway:
- Integration of a diffusivity coefficient varying with environment favorability (Mullen 1989, Bertignac et al. 1998).
- Further study of the salinity effect into the model which seems to be too strong in some regions and too weak in others.
- The secondary production index used here (SPI-6 index) is a mean index which is currently being improved by developing a new "tuna forage" modeling effort in collaboration with scientists from the LODYC (Laboratoire d'Océanographie Dynamique et de Climatologie, Paris VI). This model is based on a coupled bio-geochemical model as described by Lehodey et al. (1998). The model must consider catches from all fishing fleets in the Atlantic Ocean and not only from FIS purse seiners.

Finally, the model tuning presented here is extremely rough. A rigorous estimation off all parameters (including recruitment) with a likelihood approach should be done. Such a parameter estimation could incorporate simultaneously information from fishery data and from tagging data.

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