Spatial Modeling of Atlantic Yellowfin Tuna Population Dynamics: Application of a Habitat-Based Advection-Diffusion-Reaction Model to the Study of Local Overfishing

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Abstract

This paper presents a spatial multigear population dynamics model forced by the environment for Atlantic Ocean yellowfin tuna. The model simulates the population's distribution as a function of environmental variables and observed fishing effort. It is age-structured to account for age-dependent population processes and catchability. 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 nonlinear relationships estimated with generalized additive models (GAM) to characterize, on the one hand, yellowfin 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 problem of local overfishing of adult tuna in the Gulf of Guinea is addressed through different simulations and discussed.

Introduction

Yellowfin tuna (*Thunnus albacares*) is a cosmopolitan species whose distribution covers tropical and subtropical waters of the three oceans. In the Atlantic Ocean, three main fleets fish for this important pelagic resource. 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 bait-boat fleet catches mainly young fishes associated with other tropical tunas (skipjack, *Katsuwonus pelamis*; and bigeye, *Thunnus obesus*) in coastal waters; and the longline fleet catches older yellowfin and bigeye in open sea waters. During recent years, total yellowfin catches in the Atlantic Ocean were approximately 150,000 t and reached a 175,000 t maximum in 1991 (ICCAT 1997).

Because tuna populations exhibit particular characteristics (i.e., the presence of a cryptic fraction of the biomass in the population dynamics [Fonteneau and Soubrier 1996], massive movements and migrations linked to the environment [Cayré et al. 1988a,b], very heterogeneous fisheries spread over ocean scale distribution areas, etc.), spatial models are needed to realistically represent their dynamics (Sibert et al. 1999). Among exploited species in the Atlantic Ocean, yellowfin tuna is an interesting candidate for application of an advection-diffusion-reaction model forced by the environment. Indeed, yellowfin exhibits important movements at different scales, which make spatial distribution a central problem for management and conservation (Fonteneau 1998, Maury 1998).

Yellowfin movements seem to be directly linked to a highly variable environment (Mendelssohn and Roy 1986; Cayré et al. 1988a,b; Fonteneau and Marcille 1988; Mendelssohn 1991; Marsac 1992): tunas continuously look for micronectonic aggregates for feeding and their three-dimensional distribution is limited by physiology to well defined dynamic environmental ranges.

In this context, environmental characteristics are probably the major driving force for yellowfin population movements (Cayré 1990). Consequently, environmental forcing on yellowfin distribution, movements, and catchability must be explicitly incorporated in any realistic high resolution spatial model. GAM analysis of the relationships linking yellowfin density to the ocean environment distinguished four main scales of variability in the Atlantic yellowfin population movements (Maury 1998). At each scale there is a corresponding movement type, which is associated with the variability of a given environmental factor (Maury 1998, Maury et al. 2001). Such scale-dependent 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. Using this model, different ecological assumptions can be explored. In this paper, we particularly focus on local overfishing of yellowfin populations.

Spatial Modeling of the Population Dynamics of Yellowfin Tuna

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 et al. 1994) but their use in fishery science has grown only 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 the tuna population linked to environmental heterogeneity. To model this linkage, we transform the environmental multivariate heterogeneity into the variability of a single functional parameter, which characterizes the habitat suitability and depends on physiological stage of the fish. For this purpose, population functional responses to the environment need to be determined. In addition, it is necessary to estimate catchability and its variations with the ocean environment and the fishery configuration. Then, given modeled fish density, observed fishing effort, and modeled catchability, expected catches can be calculated and compared with observed catches to estimate the model parameters (Fig. 1).

Model Formulation

Advection-Diffusion-Reaction of the Population

An advection-diffusion-reaction equation is used to model yellowfin population dynamics, spatial distribution, and movements. In such a model, fish movement has two components: a random one, a diffusion term which characterizes "dispersive" movements; and a directed one, an 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):

$$\frac{\partial N}{\partial t} = \frac{\partial\left((D + k\gamma N^{\gamma})\frac{\partial N}{\partial x}\right)}{\partial x} + \frac{\partial\left((D + k\gamma N^{\gamma})\frac{\partial N}{\partial y}\right)}{\partial y} + \frac{\partial\left(\frac{\partial b}{\partial x}N\right)}{\partial x} + \frac{\partial\left(\frac{\partial b}{\partial y}N\right)}{\partial y} - ZN \quad (1)$$
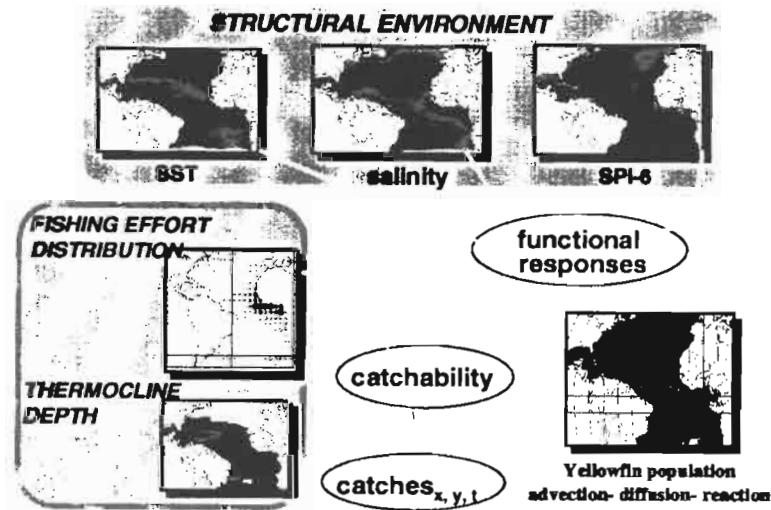
Figure 1.   Schematic diagram of the model. Population movements are forced by the sea surface temperature (SST), the water salinity, and a forage index (SPI-6). The catchability is calculated locally as a function of local fishing effort density and thermocline depth (see text).

With $N = N_{x,y,t}$ representing the cohort density at point (x, y) at time and age t and $D = D_{x,y,t}$ the diffusivity coefficient; k and g are constants characterizing the shape of the density-dependence habitat selection relationship (the more the fish density increases, the more the habitat suitability decreases); $b = b_{x,y,t}$ 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 (b) spatial gradient. Therefore, the modeled fish population moves with respect to the local "suitability" gradient, and swims toward better environmental suitability. Equation 1 is solved numerically using an "alternating-direction implicit method" (Press et al. 1994) on a $1° \times 1°$ square from 30° south to 50° north. A daily time step and closed reflective boundaries are used (Neumann conditions: $\dfrac{\partial N}{\partial x} = 0$ at boundaries) to model an impassable frontier such as a shore.

Functional Responses to the Environment and Calculation of the Biotic Affinity, b

Habitat suitability depends on various biotic and abiotic factors. At the same time, functional responses linking the biotic affinity b to measured environmental factors are likely to be nonlinear functions (dome-shaped
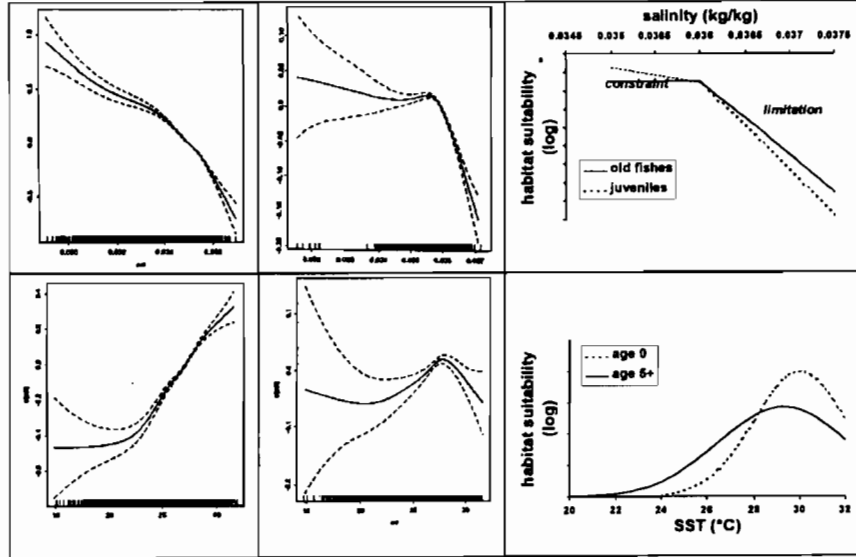
Figure 2. Observed GAM relationships between the log of the biotic affinity and the salinity (first row) and the SST (second row) for young yellowfin (age 1) on the left and for adult fishes (age 5+) in the middle (redrawn from Maury et al. 2001). On the right, the modeled relationships (arbitrary units): for salinity (first row), an age-dependant threshold relationship is used and for SST (second row), an age-dependent gaussian relationship is retained.

functions, thresholds, etc.). Maury et al. 2001 conducted a multivariate GAM analysis of the relationships linking yellowfin density to the environment. Generalized additive models (GAM) are nonparametric statistical methods which allow one to determine nonlinear relationships between variables (Hastie and Tibshirani 1990). Among numerous factors, they found that the sea surface temperature (*SST*), the salinity (*salt*), and a tuna forage index (secondary production index *SPI-6*, calculated by transporting the satellite-derived primary production with ocean currents [Maury 1998]) explain the major part of the Atlantic yellowfin tuna distribution variability at four different spatiotemporal scales, from a local scale ($1° \times 1° \times 15$ days) to the scale of the whole distribution area. All the oceanographic data used (SST, salinity, thermocline depth, oceanographic currents used to derive *SPI* from satellite-derived primary production) are simulated data from the OGCM OPA7.1 (Delecluse et al. 1993).

In the present work, the parametric formulation of relationships linking the habitat suitability to the environment is derived from GAM relationships obtained by Maury (1998). Four relationships are used to characterize environmental forcing. Each varies with the age of the fish:

- A threshold relationship for salinity which combines two different linear relationships (a constraint for low salinity and a limitation for high levels) (Fig. 2).

- A gaussian relationship between the log of the habitat suitability and the temperature (Fig. 2).

- A linear relationship between the log of the biotic affinity and the tuna forage indices *SPI-6*.

The generalized additive models we used to assess the shape of the relationships between yellowfin abundance and environmental factors are additive representations of the relationships between environmental factors and habitat suitability. The definition of biotic affinity suggests a transformation to a multiplicative model, which is more in accordance with the ecological niche theory where a niche is viewed as a hyper-volume with n environmental dimensions:

$$
\begin{cases}
\log(-b_{age} + 1) = \left[\dfrac{\alpha_{age}}{\sigma_{age}} e^{\left(\frac{sst - \beta_{age}}{2\sigma_{age}} \right)^2} \right] - \gamma_{age} salt - \kappa\, salt + \lambda_{age} SPI_6 \\[12pt]
\gamma_{age} = 0 \ \text{if } age > 3 \\[6pt]
\kappa = 0 \quad \text{if } salt < 0.036 \mathrm{kg\,kg}^{-1}
\end{cases}
$$

$$
\Leftrightarrow
\begin{cases}
b_{age} = -\dfrac{e^{\left[\frac{\alpha_{age}}{\sigma_{age}} e^{\left(\frac{sst - \beta_{age}}{2\sigma_{age}} \right)^2} \right]} e^{\lambda_{age} SPI_6}}{e^{\gamma_{age}\, salt} e^{\kappa\, salt}} + 1 \\[18pt]
\gamma_{age} = 0 \ \text{if } age > 3 \\[6pt]
\kappa = 0 \quad \text{if } salt < 0.036 \mathrm{kg\,kg}^{-1}
\end{cases}
\tag{2}
$$

Five of the six parameters used to model the biotic affinity are age-dependent (α_{age}, β_{age}, σ_{age}, γ_{age}, λ_{age}) while κ is the same for all ages.

Fish Diffusion

The diffusivity coefficient D is related to the mean distance that a fish moves during a time step. This distance varies with the swimming speed of the fish, which depends on their size (Sharp and Dizon 1978). In the model, a power law with an exponent θ characterizes the potential nonlinearity of this relationship (Aleyev 1977):

$$D = \delta l^{\theta} \tag{3}$$

The two stanzas growth model of Gascuel et al. (1992) is used to convert age into size to calculate diffusion as a function of age (Fig. 3).

Natural Mortality

The yellowfin natural mortality rate used for stock assessment by the ICCAT (International Commission for the Conservation of Atlantic Tunas) 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 rates accounts for the fact that juvenile mortality is likely to be higher than adult mortality. In the present study, an age-dependent natural mortality curve is used. The use of a second order polynomial function characterizes a high mortality rate for young fish, a lower mortality rate for adults, and slight increase for the oldest fish due to senescence (Fig. 4).

Recruitment

Our advection-diffusion-reaction model only deals with the recruited life history stages. It does not explicitly represent the recruitment process, which provides the initial state to the dynamics of each cohort. The spatial distribution of recruitment is obtained with a simple algorithm. For each of the seven cohorts modeled, the recruitment levels are calculated by a monthly VPA. 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^{-1}. Those low salinity regions, thought to be nursery areas, are mainly located from the Gulf of Guinea to Guinea shores and seaward of the Amazon River mouth (Fig. 5).

The population obtained is considered to be prerecruited. To get a "close to equilibrium" state, the prerecruits are redistributed without mortality for five time steps by using equation 1 with environmental conditions corresponding to the first of January of the year being modeled and age-0 functional relationships to environmental conditions. The resulting distribution of age 0 fish is used to initialize simulations.

Parameterization of Purse-Seiner Catchability

The GAM analysis of commercial CPUE conducted by Maury et al. 2001 provides a model of catchability to purse-seiners for the period 1980-1991. The fishing data used in the present study comes from the ICCAT database
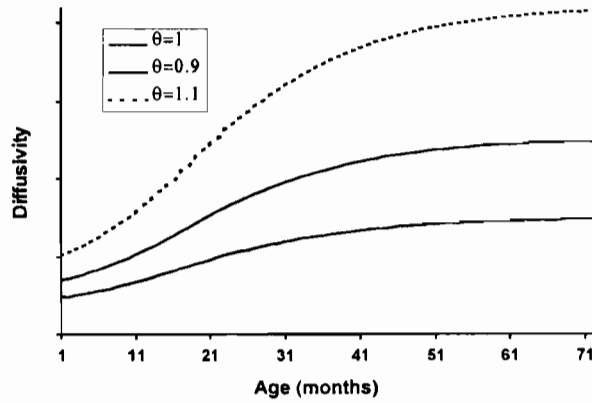
Figure 3.   Yellowfin diffusivity modeled as a function of their age for different q parameters (arbitrary units).
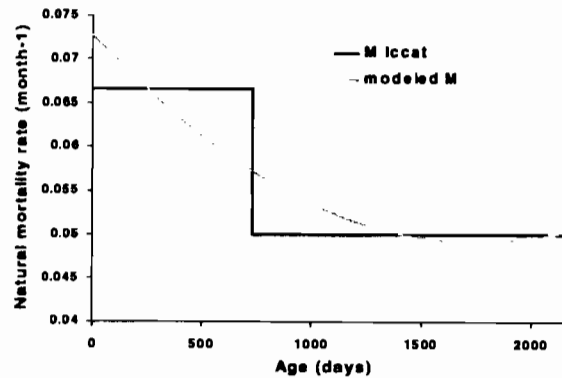

Figure 4.   Monthly natural mortality rate as a function of yellowfin age (days). Black line, the natural mortality coefficient used by ICCAT. Grey line, the natural mortality used in the present work.
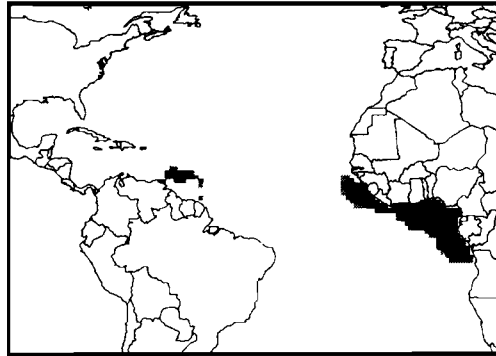
Figure 5.   Model nursery zones where recruitment calculated by VPA is distributed (see text). Case of 1 January 1980.
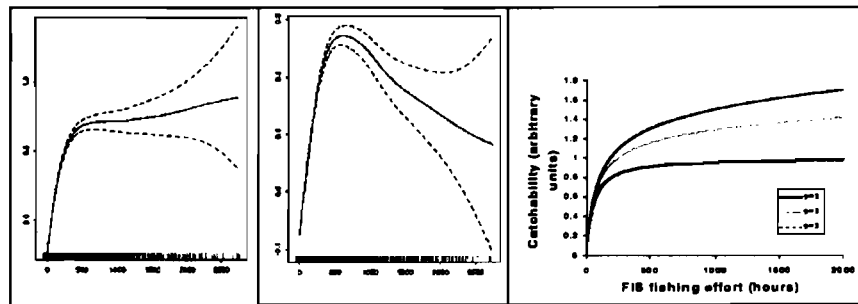

Figure 6.   GAM relationships between the log of the 1980-1991 mean catchability and the fishing effort for young yellowfin (age 1) in the left panel and for adult fishes (age 5+) in the middle panel (redrawn from Maury et al. 2001). In the right, the parametric model used to represent the relationship between yellowfin catchability to purse-seiners and fishing effort.

which centralizes statistical data for all tuna fisheries in the whole Atlantic Ocean. In the present study, only catches by age and effort for the FIS (France, Ivory Coast, and Senegal) purse-seiners during the period 1980-1993 were used. 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 in catchability when local fishing effort increases and the approach to an asymptote (Maury 1998, Maury et al. 2001), we use a simple nonlinear 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 over-fishing (Maury and Gascuel 2001) and is not included in the model catchability ($\tau \geq 1$ in equation 4).

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

$$\ln(q+1) = \frac{\mu_{age}f}{(1+\omega f)^{\tau}} - \rho_{age}\,Z20 \Leftrightarrow q_{age} = \frac{e^{\frac{\mu_{age}f}{(1+\omega f)^{\tau}}}}{e^{\rho_{age}\,Z20}} - 1 \tag{4}$$

Where q is the catchability; f is the fishing effort; $Z20$ is the thermocline depth; μ_{age} is the parameter characterizing the increase of catchability with effort; ω, a parameter characterizing the saturation of such effect; τ, a shape parameter (Fig. 6) and ρ_{age}, the weight of the linear thermocline effect on catchability.

Parameter Estimation and Model Validation

Model Tuning and Fitting to FIS (France, Ivory Coast, and Senegal) Purse-Seiner CPUEs

When the six modeled age classes for yellowfin (from age 0 to 5+) are taken into account, the whole model (functional responses + population dynamics + catchability) has 47 parameters (α_{age}, β_{age}, σ_{age}, γ_{age}, κ, λ_{age}, D, θ, τ, μ_{age}, ω, ρ_{age}) (Table 1). Even with the high number of CPUE observations available for this study (35,725 observations at 1 degree per 15 days resolution), the identification of such a nonlinear numerical model is a difficult task. Thus, as a first step, we chose to tune the model parameters "by hand" and to estimate only the catchability parameters $\mu_{age\,0\,and\,1}$ and $\mu_{age\,2,\,3,\,4\,and\,5+}$ numerically at each step. The fit of these six parameters provides statistical criteria characterizing the fit of the model to observed data.

Assuming a lognormal distribution for CPUE, a simple least square fit to $\ln(CPUE+1)$ is used to estimate catchability parameters and to guide tuning of the other parameters. Assuming that the observed $\ln(CPUE_{k}+1)$

Table 1.   Parameter values estimated by calibrating the model.

Preferences		Catchability		Diffusion	
α_{0-1-2}	2.0	μ_{0-1}	10.0^{-6}	δ	$72 \text{ nm}^2 \text{ days}^{-1} \text{ cm}^{-1}$
α_{3-4-5+}	5.2	$\mu_{2-3-4-5+}$	3.10^{-6}	θ	1.05
β_{0-1-2}	30°C	$\omega_{0-1-2-3-4-5+}$	0.02		
β_{3-4-5+}	29.7°C	$\tau_{0-1-2-3-4-5+}$	1.0		
σ_{0-1-2}	2.0	$\rho_{0-1-2-3-4-5+}$	0.1		
σ_3	2.6				
σ_{4-5+}	2.8				
γ_0	6.0				
γ_1	4.0				
γ_2	0.5				
γ_{3-4-5+}	0				
κ	50.0				
$\lambda_{0-1-2-3-4-5+}$	0.1				

($k = 1...n$ observations) are a realization of the random vector $[\ln(CPUE+1)]_k$, the statistical model is written as follows:

$$\left[\ln(CPUE_{i,j,t} + 1)\right]_k = f\left(\mathbf{x}_{\underset{k}{i,j,t}}, \theta\right) + \varepsilon_{\underset{k}{i,j,t}} \quad k = 1...n$$

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

Since the observed $\ln(CPUE+1)$ series is highly heteroscedastic (its variance is linked with the $\ln(CPUE+1)$'s value), we use a weighted least square criterion (SCE) which gives to each observation an importance proportional to the inverse of the fortnightly variance σ_{qz}^2:

$$SCE = \sum_{i=1}^{n} \frac{\left[\ln(CPUE_i + 1) - \ln(C\hat{P}UE_i + 1)\right]^2}{\sigma_{qz}^2}$$

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

$e_k = \dfrac{f(x_k, \hat{\theta}) - \left[\ln(CPUE_k + 1)\right]_{obs.}}{\hat{\sigma}\sigma_{qz}}$ should behave as independent random vari-

ables $N(0,1)$. Assuming independent errors, the focus is now on the normality of residuals and their homoscedasticity. A simple graphical examination of the residuals (Fig. 7) shows that, apart from diagonal structures characterizing positive distributions, residuals form a horizontal band centered around zero.

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.

Model Validation and Consistency of the Outputs

The nonlinear features of our model make parameter estimation a complex task. Indeed, different parameter sets may give very close values to the objective function. Thus, even with many observations, simple tuning is problematic and results have to be evaluated for their ecological plausibility. 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, etc.) are very different from the purse seine fishery data used to fit the model. The global consistency of the model outputs is analyzed by comparing the predicted monthly distribution of adult (age 5+) yellowfin (Fig. 8C) with the mean spatial distribution of longliner catches calculated by averaging the monthly longliners catches over the period 1956-1993 (Fig. 8A). Because longliners mainly catch fish aged 4-5 years and older, such a comparison is only applicable to characterize 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 of 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 the adult yellowfin population (age 4-5+). Results concerning young fishes (age 0-1) seem consistent also with scientific knowledge concerning spatial distribution and movements of juvenile yellowfin (Bard and Hervé 1994). The distribution of 2-3 year-old yellowfin is more questionable and requires further investigation concerning the parameterization of seasonal catchability (for details, see Maury 1998).

Simulations Analysis: Local Overfishing of Yellowfin

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 2001). In general, local overfishing is well documented for tuna fisheries (Fonteneau and Soubrier 1996, Fonteneau

Figure 7.   Reduced residuals versus estimated values of the response variable .

et al. 1997). Concerning the Atlantic yellowfin tuna, a spatial VPA analysis indicated that very high local mortality rates could be exerted on reproductively active adult fish in the eastern Atlantic ocean ($F = 0.8$ per quarter during the first quarter of the year) (Maury 1998). Such high mortality rates are likely to induce important local depletions of adult fish. The comparison of two simulations of the spatial distribution of age 5+ fish clearly demonstrates the effect of local overfishing. The first simulation accounts for the observed FIS purse-seiner catches (Fig. 8B). The second simulates a virgin population without fishing pressure (Fig. 8C). For age 0-3 fish, fish density is very high compared to the realized catches and the effects of local overfishing do not appear in simulations. For older fish, important local biomass depletions appear in the simulated population when observed FIS purse-seiner catches are taken into account (Fig. 8B). At different periods during the year, one can observe a "wound" and "healing" pattern as producted with theoretical simulations by Maury and Gascuel 2001. The pattern is less clear for age 4 fish than for age 5+ fish. The highest depletions of fish occur in February, March, and April, off the Gulf of Guinea. In May, the adult population "heals" before it experiences significant "wounds" again after July in the Gulf of Guinea. At that time, fish are sufficiently concentrated off Senegal to remain 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. 8A).

Only the FIS purse-seiner 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-seiner fleet with a catch level of the same order of magnitude as FIS), local overfishing of old fish would have been much more significant, perhaps too significant to be considered plausible. Consequently, four alternative hypotheses must be studied in future work:
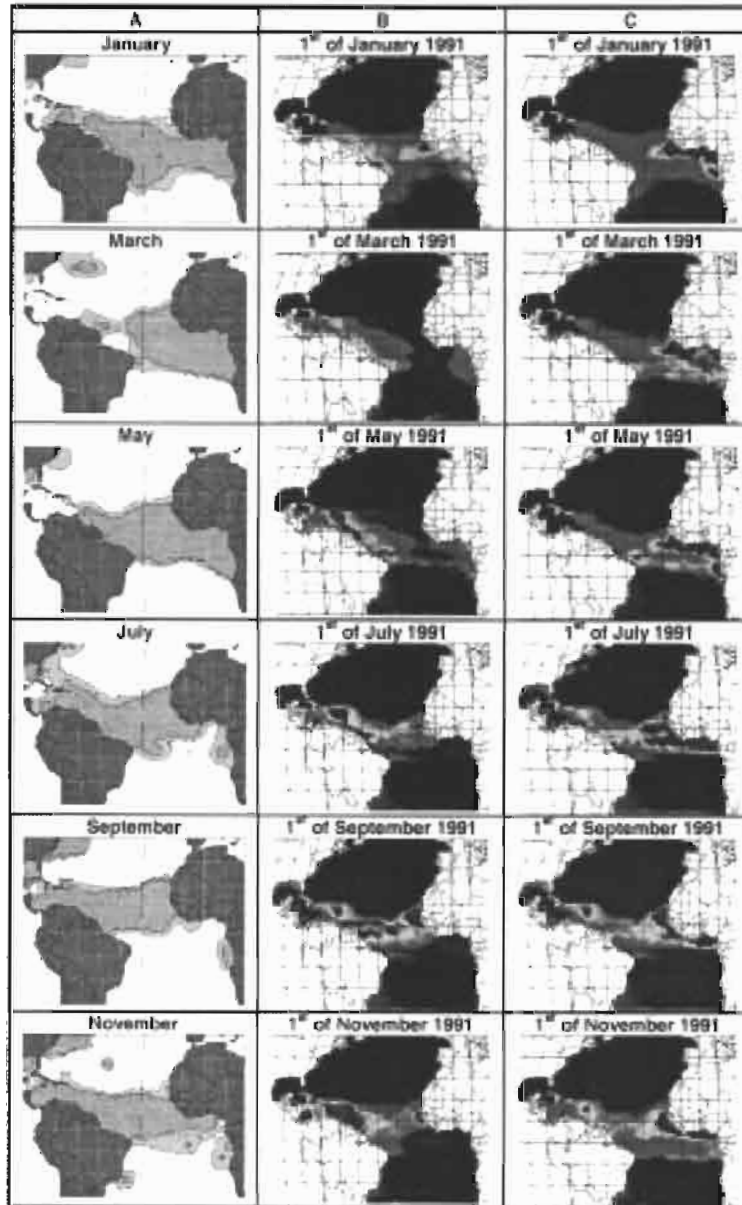
Figure 8.   On the left (A), spatial distribution of cumulative longliner catches over the 1956-1993 period. Middle (B) and right (C) columns, simulations of age 5+ yellowfin distribution in 1991. Two simulations are compared: one taking into account observed FIS purse-seiner catches (in the middle, B) and another without (on the right, C).

- Local overfishing 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 an insufficiently strong "healing" of old fish.

- The total number of fish derived from VPA recruitment is not sufficient to explain the high local catches. If this is the case, VPA may underestimate total fish abundance, for instance, by ignoring a potentially important cryptic biomass.

At this point, we are unable to distinguish which of these possibilities is most likely. Nevertheless, **our work suggests a potential for strong seasonal local overfishing of old yellowfin, even if the "wound" and "healing" phenomenon is exaggerated by our advection-diffusion simulation**. Such strong local overfishing may have significant impacts on the utility of CPUE as an abundance index (Maury and Gascuel 2001). Moreover, an important reduction in local biomass could have a long-term impact on the yellowfin population genetic structure. For example, strong local fishing pressure on the main reproductive grounds could select artificially for fish reproducing in marginal areas such as Cabo Verde (Santa Rita Vieira 1991).

To address this question, 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 population dynamics and the dynamics of fishing fleets. 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, local overfishing of yellowfin 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 have been performed which study the homing of adults to the Gulf of Guinea reproductive grounds and analyze the impact of the 1983-1984 environmental anomaly on fish spatial distribution and catches (Maury 1998).

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 analyses which take into account the antagonistic features of environmental influences on tuna distribution are needed. GAM models would be very useful for such nonlinear analysis. Different improvements of the model are currently under way:

- Integration of a diffusivity coefficient varying with environment favorability (Mullen 1989, Bertignac et al. 1998).

- Further study of the salinity effect into the model; it 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 of all parameters (including recruitment) with a likelihood approach should be attempted. Such a parameter estimation procedure could simultaneously incorporate data from both fishery and tagging.

Acknowledgments

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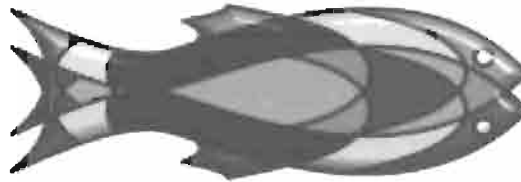
Spatial Processes and Management of Marine Populations

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