Hierarchical interpretation of nonlinear relationships linking yellowfin tuna (Thunnus albacares) distribution to the environment in the Atlantic Ocean

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Abstract: Using generalized additive models, we show evidence for nonlinear relationships between various hydrological factors and age-structured catch per unit effort of Atlantic yellowfin tuna (Thunnus albacares) for two fishing fleets. Catchability effects are distinguished from tuna environmental preference effects in the catch per unit effort variability. With respect to catchability, an important nonlinear effect of local fishing effort is highlighted for each fleet. It is interpreted as resulting from a local overfishing phenomenon of adult yellowfin tuna and from vessel fishing tactics (cooperation/spying). The environmental preferences obtained facilitate the interpretation of the hierarchical spatial distribution and age-dependent movements of the yellowfin population. We show that, on a large spatiotemporal scale (the whole ocean), low salinity is a good predictor of yellowfin habitat. Juveniles are mainly distributed in low-salinity waters (<0.035 kg·kg⁻¹) when adults extend their range to waters of 0.036 kg·kg⁻¹. On a mesoscale, adult population annual reproductive transatlantic displacements are probably driven by temperature and salinity gradients to warm and low-salinity locations that are favorable for juveniles. North–south seasonal movements of the population are clearly related to warmwater seasonal oscillations. On a small scale, ocean thermic stability and gradients of sea surface temperature are important physical factors determining yellowfin concentration.

Résumé : On met en évidence, à l’aide de modèles additifs généralisés, les relations non linéaires existant entre différents facteurs hydrologiques et les captures par unité d’effort en thons albacore (Thunnus albacares) de deux flottilles de pêche dans l’Atlantique. L’analyse est structurée en âges. On identifie les effets qui relèvent de la capturabilité et ceux qui relèvent des préférences environnementales des thons. En ce qui concerne la capturabilité, un effet non linéaire important de l’effort de pêche local sur les rendements est mis en évidence pour chacune des flottilles. Il est interprété comme résultant, d’une part d’un phénomène de surexploitation locale des albacores adultes et, d’autre part, des tactiques de pêche des navires (coopération/espionnage). Les préférences environnementales des thons obtenues permettent d’interpréter hiérarchiquement la répartition spatiale et les mouvements de la population d’albacores selon l’âge des animaux. On montre qu’à grande échelle spatio-temporelle (tout l’océan), les faibles salinités sont un bon marqueur de l’habitat des albacores. Les juvéniles sont répartis principalement dans les eaux peu salées (<0,035 kg·kg⁻¹) alors que les adultes étendent leur aire de répartition jusqu’à des eaux de 0,036 kg·kg⁻¹. Aux méso-échelles, les déplacements reproductifs transatlantiques annuels semblent dirigés le long des gradients de température et de salinité vers les eaux chaudes et dessalées favorables aux juvéniles. Les mouvements saisonniers nord–sud de la population sont clairement liés aux oscillations saisonnières des eaux chaudes. À échelle fine, la stabilité thermique de l’océan et l’existence de gradients thermiques de surface sont des facteurs physiques importants de la concentration des albacores.

Introduction

Numerous studies have related fish spatial distribution to environmental factors (Cushing 1982; MacCall 1990; Mann 1993). In the case of highly migratory pelagic species such as tunas, fish distribution is directly linked to the environment. Environmental factors are known to be responsible for fish movements, at least on a large spatial scale (Mendelssohn and Roy 1986; Marsac 1992; Lehodey et al. 1997). Therefore, improving knowledge about environmental factors influencing tuna population dynamics is an objective key issue for management and conservation of tuna stocks.
Yellowfin tuna (Thunnus albacares) is a cosmopolitan species mainly distributed in the tropical and subtropical oceanic waters of the three oceans. In the Atlantic Ocean, tagging and catch at size data analyses have shown that yellowfin tuna move massively at different scales in the whole tropical Atlantic Ocean (Bard 1994; Fonteneau 1994). Environmental conditions are probably the main causes driving migration phenomena and massive population movements (Cayré et al. 1988; Cayré 1990). Nevertheless, no clear functional relationship has been determined between yellowfin local abundance, migration patterns, and environment variables.

In this study, we focus on the relationships between the local abundance of yellowfin tuna and different hydrological factors such as salinity, temperature, gradients of sea surface temperature (SST), wind, thermocline depth, currents, and various indices of hydrological stability. For this purpose, generalized additive models (GAMs) are used to link catch per unit effort (CPUE) data for two different fleets (both purse seiners and longliners) to three-dimensional hydrological data from an ocean global circulation model. GAMs are used to characterize the nonlinear relationships. Including in the analysis the effects of auxiliary variables influencing catchability enables us to interpret CPUE data as local abundance indices. Environmental data are then considered both in synchrony with abundance data and with a temporal delay.

Finally, the relationships obtained and their analyses lead us to propose a spatiotemporal hierarchical framework of the processes linking yellowfin tuna to their environment at different scales (small scale (~50 km), mesoscale (~500 km), and macroscale (~5000 km)). From this perspective, observed movement patterns at different scales can clearly be related to the environment.

Materials and methods

Two types of data are used in the present study: fisheries data from the International Commission for the Conservation of Atlantic Tunas (ICCAT) database and hydrological data from the numerical oceanographic model OPA7.1 (Delecluse et al. 1993).

ICCAT catch and effort data

In this study, we use commercial CPUE data from both French, Ivoirian, and Senegalese (FIS) purse seiners for the period 1980–1991 and Japanese longliners for 1980–1993. These two fleets were chosen because their combined catches incorporate the total distribution and size range for this species.

FIS purse seiners target mainly yellowfin, bigeye (Thunnus obesus), and skipjack tuna (Katsuwonus pelamis) on a wide geographical range but only in the eastern tropical Atlantic. During the period 1980–1991, they kept a relatively stable fishing pattern covering almost the whole yellowfin size spectrum from 30 cm (age 0) to 180 cm (age 5+) (Anonymous 1997). For this fleet, CPUE data are calculated at age (0 to 5+). We use the age decomposition method developed by Gascuel (1994) to age the catch at size data. The method is based on the length at age curve estimated by Gascuel et al. (1992) and assumes a normal distribution of size at age with standard error proportional to mean size increment for each considered cohort. Size to age conversions are computed on a monthly basis for the six spatial zones homogeneous in fish sizes routinely used by ICCAT. FIS purse-seiner CPUE at age are expressed for the six age groups as number of fish per 1000 hooks. Their spatial resolution is 1 × 1° and their temporal resolution is 15 days. They are used here to characterize yellowfin behavior as a function of their age on a small scale (~50 km) and a macroscale (~500 km).

Japanese longliners fish the entire Atlantic Ocean, totally covering and probably extending beyond the whole yellowfin distribution range. They fish in deep waters (100–150 m for traditional longlines during the 1980s and down to 300 m for deep longlines during the 1990s) and target mainly adult bigeye and bluefin tuna. Adult yellowfin tuna constituted important by-catches for this fleet during the period under study (Anonymous 1997). Their fishing pattern remained stable during the period 1980–1993, but because they only fish for adult yellowfin between 110 and 170 cm (ages 4 and 5+), we did not age the catches. Japanese longliner CPUE data (CPUEzone, time = catches in weightzone, time /effortzone, time) are expressed as tonnes per 1000 hooks. Their spatial resolution is 5 × 5° and their temporal resolution is 30 days. They are used here to characterize adult yellowfin behavior on a macroscale (~500 km) and a macroscale (~5000 km).

Hydrological data from model OPA7.1

The French Institute of Meteorology (Meteo-France) provided the hydrological data used. These data come from the hydrodynamic model OPA7.1 (Delecluse et al. 1993) developed and validated by the Laboratoire d’Océanographie Dynamique et de Climatologie laboratory (Paris VI). The model is forced by observed winds and assimilates oceanographic data collected routinely, such as temperature profiles and currents, which keep results very close to in situ observations. Simulated data cover the whole tropical Atlantic Ocean from 20°N to 20°S. The model does not work well for coastal zones. The coastal boundaries used in the present analysis correspond to the continental shelf limit and ignore more coastal zones. The spatial resolution is a 0.5 × 0.5° horizontal square grid along 10 depth levels and the temporal resolution is 5 days for the period 1980–1995.

The parameters available for the present study are the temperature of the water column in degrees Celsius (at 5 m assimilated to SST and 15, 25, 36, 51, 70, 90, 110, 130, and 150 m), the depth of the 20°C isotherm in metres (Z20), which is usually used to approximate the thermocline depth in the tropical Atlantic Ocean (although arbitrary, this definition gives a measure of thermocline depth consistent with observations), the salinity of the surface water at 5 m depth (kilograms per kilogram), the zonal and meridional components u and v (metres per second) of the water currents at 5 and 51 m depth, and the zonal (x) and meridional (y) components of the pseudo wind stress (newtons per square metre per second), which can be seen as the energy transmitted to the water by the wind.

For a more synthetic description of the hydrological conditions, different parameters were calculated. The water convergence index in cell (x, y), which is based on surface currents, is

\[\text{conv} = (u_{x,-1} - u_{x,+1}) + (v_{y,-1} - v_{y,+1})\]

The current shear index between 5 and 51 m deep, which measures the shear effect exerted on the purse-seine gear, is

\[\text{CI} = \sqrt{(u_5 - u_{51})^2 + (v_5 - v_{51})^2}\]
The pseudo wind stress module (newtons per square metre per second) is

\[ |\text{wind}| = \sqrt{x^2 + y^2} \]

The thermocline gradient is \( gZ20 = \frac{T_2 - T_1}{Z_2 - Z_1} \), where \( Z_1 \) and \( Z_2 \) are the first available depths, respectively, just below and just above the depth of the thermocline (\( Z20 \)) and \( T_1 \) and \( T_2 \) are the corresponding temperatures. The more negative \( gZ20 \), the stronger the thermocline.

The SST spatial gradient in cell \((x, y)\) is

\[
\text{PSST} = \frac{\partial \text{SST}}{\partial x} + \frac{\partial \text{SST}}{\partial y} = \frac{\text{SST}_{t+1} - \text{SST}_{t-1}}{2\Delta x} + \frac{\text{SST}_{y+1} - \text{SST}_{y-1}}{2\Delta y}
\]

The SST spatial gradient is calculated with \( \Delta x = \Delta y = 0.5^\circ \) and is expressed as degrees Celsius per 1000 km.

Different authors have suggested that past hydrological events are as important as present conditions in explaining tuna distribution (Mendelssohn and Roy 1986; Stretta 1989). Two lags (15 and 30 days) are considered to take into account the local hydrological evolution (cooling or warming) at a given moment. Then, two synthetic water mass warming indices are calculated: \( \delta \text{SST15} = \text{SST}_1 - \text{SST}_{t-15} \) and \( \delta \text{SST30} = \text{SST}_1 - \text{SST}_{t-30} \).

**Use of GAMs**

GAMs are nonparametric generalizations of multiple linear regression techniques (Hastie and Tibshirani 1990; Swartzman et al. 1992). GAM fitting methods are based on empirical transformations by local smoothing techniques. The general formulation of a GAM is given by

\[
S(Y)_j = \sum T_i(X_i(j)) + \varepsilon(j)
\]

where \( Y_j \) is the response variable for observation \( j \), \( X_i \) are the covariates, \( S \) is the linked function, \( T \) are unknown functions that are nonparametrically estimated using scatterplot smoothers, and \( \varepsilon \) is a random variable in any distribution of the exponential family.

This recent statistical method is beginning to be commonly used in fishery science (e.g., Mendelssohn and Cury 1987; Curry and Roy 1989; Maravelias 1999). The advantage of GAMs is that they enable multivariate analysis with no a priori assumptions of linearity. In our application, we assume a normal distribution for the log of CPUE + 1. In this case, there is no transformation \( S \) (Hastie and Tibshirani 1990; Swartzman et al. 1994) and the expected value of the variable \( Y \) is expressed as a sum of smooth functions of the covariates.

We use a logarithmic transformation of the CPUE to normalize the asymmetrical CPUE frequency distribution and because of the a priori multiplicative nature of the processes under study. The general form of the models fitted is

\[
\ln(\text{CPUE} + 1) = \sum T_i(X_i) + \sum T_j(X_j) + \varepsilon, \quad \varepsilon \sim N(0, \sigma^2)
\]

where \( X_i \) are the covariates involved in catchability and \( X_j \) are the covariates involved in fish density. We use a cubic spline smoother for functions \( T \) and the S-Plus software package (©AT&T Bell Laboratories) to fit the models.

Different models are tested to highlight the role of environmental variables on yellowfin density. In each model, all the significant covariates supposed to be involved in catchability are systematically added, associated with the particular environmental variable considered. Because of the important seasonality of the fishery, spatiotemporal effects were systematically included. When they modify the relationship under consideration, significant interaction effects with other environmental variables are added by fitting a spline to the product of the covariates. Following Swartzman et al. (1992), a pseudo \( R^2 \) coefficient defined as the fraction of the total deviance explained by the model is systematically computed for each model tested. Although different from the classic \( R^2 \), this definition gives a good measure of the explanatory importance of the model. A deviance analysis is then performed to check the significance of each considered factor with an approximate \( F \) test computed for each covariate (Hastie and Tibshirani 1990; Venables and Ripley 1994) and to quantify its variability as a fraction of the total variability explained by the model (inertia).

The FIS purse-seine CPUE analysis is done at a resolution of 1° × 1° × 15 days. OPA7.1 environmental data are aggregated at this scale by using a surface weighted mean. The data file obtained contains 35 725 CPUE observations. The model fitted has the following general form:

\[
\ln(\text{CPUE} + 1) = s(\text{year}) + s(15 \text{ days} \times \text{ICCAT zone}) + s(\text{effort}) + s(\text{wind}) + s(\text{CL}) + s(\text{thermocline depth}) + s(\text{thermocline strength}) + s(\text{environmental variable}) + s(\text{interaction effects with other variables})
\]

where \( A \) is the sum of all the transformations supposed to be involved in FIS purse-seine catchability. The year effect is supposed to take into account biomass fluctuations and possible fishing power tendency, as has already been observed for Atlantic yellowfin tuna fisheries (Gascuel et al. 1993). The term \( 15 \text{ days} \times \text{ICCAT zone} \) measures a mean spatioseasonal effect in the period considered by fitting a spline to the product of time by the categorical variable zone. It gives equal weight to each zone and 15-day period whatever the fishing fleet distribution. For each effect considered, a general analysis on the whole data set and an analysis by age are done based on the six annual age groups usually used by the ICCAT scientific committee (ages 0 to 5+).

The Japanese longliners CPUE analysis is done at a resolution of 5° × 5° × 30 days. OPA7.1 environmental data are aggregated at this scale. The data file obtained contains 5035 CPUE observations. The model fitted has the following general form:

\[
\ln(\text{CPUE} + 1) = s(\text{year}) + s(\text{latitude} \times \text{longitude} \times \text{month}) + s(\text{effort}) + s(\text{thermocline depth}) + s(\text{environmental variable}) + s(\text{interaction effects with other variables})
\]

where \( B \) is the sum of all the transformations supposed to be involved in Japanese longliner catchability.

The spatiotemporal effect is considered by fitting a three-dimensional spline to the surface defined by the three covariates latitude, longitude, and month. Including the parameters considered to be involved in local catchability in the GAMs allows us to interpret the local CPUE as a local abundance index.
Results

Parameters involved in fishing power and catchability

Effort

For the FIS purse seiners, as for the Japanese longliners, fishing effort is consistently highly significant and explains the highest part of CPUE variability for all models considered (93% for purse seiners and 48% for longliners (Table 1)). The general relationship between ln(CPUE + 1) and fishing effort is nonlinear for both fleets. For purse seiners, the curve increases rapidly for effort values below a threshold level of around 500 fishing hours. Then, either it slowly increases for ages 0, 1, 2, and 3 or it decreases for ages 4 and 5+ (Fig. 1). For longliners, the curve continuously decreases with a negative exponential shape (Fig. 2).

Thermocline

For FIS purse seiners, the thermocline depth has a clear monotonous negative effect on CPUE during the period considered (Fig. 3). CPUE is higher than the average when the thermocline is less than 50 m deep, and it is lower beyond that point. This effect is constant with age but has a much more important statistical explanatory power for older fishes (ages 3, 4, and 5+) than for young fishes (ages 1 and 2) (Table 1). Removing the interaction effect between SST and thermocline depth enables the thermocline effect to be isolated. Indeed, thermocline depth and SST are not independent variables but are positively correlated. The thermocline gradient (gZ20) is less important in terms of the explained variance of the model (Table 1). Nevertheless, its effect is quite clear (Fig. 3). The stronger the thermocline gradient (the more the gZ20 index is negative), the higher the purse-seine CPUE.

For Japanese longliners, which are fishing deeper than purse seiners, thermocline depth has a monotonous positive effect (Fig. 2) and explains an important part of the variance of the model (17.4%, cf. Table 2).

Other effects

The wind effect on FIS purse-seine CPUE is consistently highly significant but explains very little of CPUE variability (Table 1). The pseudo wind stress seems to have no negative effects on purse-seiner CPUE until 1000 N·m⁻²·s⁻¹. Beyond this threshold value, the wind has a negative effect on FIS vessel efficiency and catches are lower.

The current shear effect on purse-seine CPUE is significant in most models considered but explains little of the model variance. The curve exhibits a decreasing tendency beyond a threshold level of around 0.4 m·s⁻¹.

Table 1. Statistical characteristics of models based on FIS purse-seiner data.

<table>
<thead>
<tr>
<th>Parameter considered</th>
<th>Model formulation</th>
<th>F test (p(F))</th>
<th>Pseudo $R^2$</th>
<th>Parameter inertia (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Effort</td>
<td>ln(CPUE + 1) = A</td>
<td>0.0000</td>
<td>0.25</td>
<td>93.0</td>
</tr>
<tr>
<td>Z20 general</td>
<td>ln(CPUE + 1) = A + s(SST):s(Z20)</td>
<td>0.0000</td>
<td>0.26</td>
<td>2.0</td>
</tr>
<tr>
<td>Z20 age 0</td>
<td>ln(CPUE + 1) = A + s(SST):s(Z20)</td>
<td>0.0000</td>
<td>0.17</td>
<td>4.9</td>
</tr>
<tr>
<td>Z20 age 1</td>
<td>ln(CPUE + 1) = A + s(SST):s(Z20)</td>
<td>0.0000</td>
<td>0.15</td>
<td>0.3</td>
</tr>
<tr>
<td>Z20 age 2</td>
<td>ln(CPUE + 1) = A + s(SST):s(Z20)</td>
<td>0.0000</td>
<td>0.19</td>
<td>0.1</td>
</tr>
<tr>
<td>Z20 age 3</td>
<td>ln(CPUE + 1) = A + s(SST):s(Z20)</td>
<td>2 × 10⁻⁵</td>
<td>0.20</td>
<td>2.5</td>
</tr>
<tr>
<td>Z20 age 4</td>
<td>ln(CPUE + 1) = A + s(SST):s(Z20)</td>
<td>0.0000</td>
<td>0.20</td>
<td>2.7</td>
</tr>
<tr>
<td>Z20 age 5+</td>
<td>ln(CPUE + 1) = A + s(SST):s(Z20)</td>
<td>0.0000</td>
<td>0.19</td>
<td>1.2</td>
</tr>
<tr>
<td>gZ20 general</td>
<td>ln(CPUE + 1) = A + s(SST):s(Z20)</td>
<td>0.0280</td>
<td>0.25</td>
<td>0.3</td>
</tr>
<tr>
<td>Wind</td>
<td>ln(CPUE + 1) = A + s(wind):s(SST)</td>
<td>0.0089</td>
<td>0.25</td>
<td>0.005</td>
</tr>
<tr>
<td>CI</td>
<td>ln(CPUE + 1) = A</td>
<td>2.7 × 10⁻⁸</td>
<td>0.25</td>
<td>0.06</td>
</tr>
<tr>
<td>Salinity g⁰</td>
<td>ln(CPUE + 1) = A + s(salinity)</td>
<td>0.0000</td>
<td>0.26</td>
<td>6.8</td>
</tr>
<tr>
<td>Salinity age 0</td>
<td>ln(CPUE + 1) = A + s(salinity)</td>
<td>0.0000</td>
<td>0.19</td>
<td>3.6</td>
</tr>
<tr>
<td>Salinity age 1</td>
<td>ln(CPUE + 1) = A + s(salinity)</td>
<td>0.0000</td>
<td>0.18</td>
<td>17.4</td>
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<tr>
<td>Salinity age 2</td>
<td>ln(CPUE + 1) = A + s(salinity)</td>
<td>0.0000</td>
<td>0.16</td>
<td>21.2</td>
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<td>Salinity age 3</td>
<td>ln(CPUE + 1) = A + s(salinity)</td>
<td>0.0000</td>
<td>0.19</td>
<td>3.7</td>
</tr>
<tr>
<td>Salinity age 4</td>
<td>ln(CPUE + 1) = A + s(salinity)</td>
<td>0.0000</td>
<td>0.20</td>
<td>0.0</td>
</tr>
<tr>
<td>Salinity age 5+</td>
<td>ln(CPUE + 1) = A + s(salinity)</td>
<td>0.0004</td>
<td>0.19</td>
<td>0.1</td>
</tr>
<tr>
<td>SST g⁰</td>
<td>ln(CPUE + 1) = A + s(SST) + s(SST):s(Z20)</td>
<td>0.0002</td>
<td>0.26</td>
<td>2.9</td>
</tr>
<tr>
<td>SST age 0</td>
<td>ln(CPUE + 1) = A + s(SST) + s(SST):s(Z20)</td>
<td>0.0000</td>
<td>0.19</td>
<td>0.5</td>
</tr>
<tr>
<td>SST age 1</td>
<td>ln(CPUE + 1) = A + s(SST) + s(SST):s(Z20)</td>
<td>0.0000</td>
<td>0.17</td>
<td>4.1</td>
</tr>
<tr>
<td>SST age 2</td>
<td>ln(CPUE + 1) = A + s(SST) + s(SST):s(Z20)</td>
<td>0.0000</td>
<td>0.15</td>
<td>2.5</td>
</tr>
<tr>
<td>SST age 3</td>
<td>ln(CPUE + 1) = A + s(SST) + s(SST):s(Z20)</td>
<td>0.0000</td>
<td>0.19</td>
<td>1.1</td>
</tr>
<tr>
<td>SST age 4</td>
<td>ln(CPUE + 1) = A + s(SST) + s(SST):s(Z20)</td>
<td>0.0000</td>
<td>0.20</td>
<td>1.3</td>
</tr>
<tr>
<td>SST age 5+</td>
<td>ln(CPUE + 1) = A + s(SST) + s(SST):s(Z20)</td>
<td>1.3 × 10⁻⁵</td>
<td>0.19</td>
<td>1.0</td>
</tr>
<tr>
<td>Convergence</td>
<td>ln(CPUE + 1) = A + s(SST) + s(convergence) + s(convergence):s(SST)</td>
<td>0.0400</td>
<td>0.26</td>
<td>0.06</td>
</tr>
<tr>
<td>PSST</td>
<td>ln(CPUE + 1) = A + s(Psst) + s(SST):s(Psst)</td>
<td>0.0000</td>
<td>0.26</td>
<td>2.0</td>
</tr>
<tr>
<td>dSST15</td>
<td>ln(CPUE + 1) = A + s(dSST15) + s(SST):s(dSST15)</td>
<td>0.0000</td>
<td>0.26</td>
<td>0.6</td>
</tr>
<tr>
<td>dSST30</td>
<td>ln(CPUE + 1) = A + s(dSST30) + s(SST):s(dSST30)</td>
<td>0.0000</td>
<td>0.26</td>
<td>0.4</td>
</tr>
</tbody>
</table>
Parameters involved in yellowfin tuna distribution

**Salinity**

Sea surface salinity has an important explanatory power on FIS purse-seine CPUEs and explains 6.8% of the general model inertia (Table 1). The general relationship between FIS CPUE and surface salinity is characterized by a regularly decreasing curve (Fig. 4). Most catches are made for salinity levels ranging between 0.033 and 0.036 kg·kg⁻¹, but the highest CPUE values occur in low-salinity waters (<0.035 kg·kg⁻¹). For young fishes, the inertia of the model explained by salinity is very high, especially for ages 1 and 2. It decreases at age 3 and is very low for ages 4 and 5 (Table 1; Fig. 5). The relationship with salinity has the same decreasing shape for 0, 1, and 2-year-old fishes. At these ages, CPUEs are higher than the average for salinity lower than 0.035 kg·kg⁻¹ and lower for higher salinity values. For older fishes (ages 4 and 5+), low salinity levels below 0.0355 kg·kg⁻¹ have no effects on CPUEs. Salinity values higher than 0.036 kg·kg⁻¹ seem to have slight negative effects on age-4 and age-5+ CPUEs.

The relationship between longline CPUEs (adult fishes)
and surface salinity is highly significant. Like the relationship for adult fishes with purse-seiner CPUEs, there is no effect of low salinity levels until 0.036 kg·kg⁻¹. For values higher than this threshold, salinity seems to be limiting and CPUEs decrease suddenly (Fig. 2).

**Temperature**

In the general model, SST has an important explanatory power on FIS purse-seine CPUE and explains 2.9% of the model inertia. Most yellowfin catches occur in water temperatures ranging from 25 to 30°C. The general relationship between FIS CPUEs and SST exhibits a constant increase for SST between 22 and 30°C (Fig. 6). In all the models by age, SST is highly significant and explains between 0.5 and 4.1% of the model inertia (Table 1). The inertia of the model explained by SST is high for young fishes, especially for ages 1, decreases at age 2, and is low for ages 3, 4, and 5+ (Table 1; Fig. 5). For young fishes (ages 0, 1, and 2), the relationship between FIS CPUEs and SST exhibits a monotonic increasing shape. Older fishes (ages 4 and 5+) tolerate colder waters. The curve characterizing their relationship with SST is dome shaped with a maximum around 27–28°C (Fig. 6).

For Japanese longliners, most catches occur for surface temperatures between 24 and 28°C. Surface temperature effect on CPUE has a low statistical significance for longliners (Table 2). The relationship with temperature at 150 m depth ($T_{150}$) is statistically more significant (Table 2). Most catches occur in the range between $T_{150} = 12$ and 17°C, and the curve exhibits a linear increase (Fig. 2).

**SST gradient**

Taking all ages together, the spatial thermic gradient has an important negative effect on fish density. PSST account for 1.13% of the model inertia. Most of the catches are associated with values of PSST between 0 and 25°C·1000 km⁻¹, but higher CPUEs are observed in low-gradient zones for PSST values lower than 10°C·1000 km⁻¹ (Fig. 7). Other parameters are significant: the CPUE – convergence index relationship is slightly increasing with a mean positive effect on FIS CPUE for convergence and a mean negative effect for divergence.

Once the interaction effects with SST have been removed (Table 1), the relationship between FIS CPUE and surface temperature evolution ($\Delta S$T15 and $\Delta S$T30) is clear and significant. Surface cooling induces higher CPUEs whereas surface warming induces lower CPUEs. The effect is the same whether a 15- or a 30-day time lag is considered.

**Discussion**

As for any statistical analysis, results from GAM analysis are sensitive to many factors and must be considered with caution. Moreover, the environmental data that we use come from an oceanographic numerical model. Even though accurate and well tested, environmental data from the OPA model remain approximations of reality. Thus, the interpretation and consistency of our results with ecological theory remain an important feature to be taken into account.

**Use of yellowfin tuna CPUE data as local abundance indices**

CPUE is the most often used abundance index in fisheries science. Nevertheless, its use is critical and sets a certain number of problems due to the nonlinearity of the CPUE–abundance relationship. This nonlinearity is generally attributed to the spatial heterogeneity of the resource and to the searching tactics of the fishers (Clark and Mangel 1979; Hilborn and Walters 1992; Gillis et al. 1993). In the case of tuna fisheries, the use of CPUE as local abundance indices is affected by specific phenomena, which are responsible for a
nonlinearity and a high variability of the local CPUE–effort relationship.

For these reasons, the covariates known to be involved in catchability were systematically added in each model studied. Among those variables, fishing effort was found to have the strongest effect on CPUE for both fleets considered. Maury and Gascuel (2001) have studied with theoretical simulations the nonlinearity of the local CPUE–effort relationship. They have shown that such a nonlinear relationship can be interpreted in terms of vessels’ spatial distribution strategies and of cooperation tactics for the increasing part of the curve and of local fish depletion for the decreasing part.

From this perspective, low purse-seine CPUE levels observed for low effort levels could be a consequence of the fishers’ experience: the fishers do not explore the zones they know to be scarce in tuna. When purse-seiner effort increases (i.e., the number of searching hours), their catchability rises dramatically because vessels’ local fishing power increases due to cooperation (or spying) in locating tuna schools. However, catchability levels off when the total number of hours searched by the whole fleet of vessels is sufficient to locate with a high degree of certainty the greatest concentrations of tuna in the area considered. This threshold is close to 500 h of search per 1 × 1° square during 15 days. For young fishes, which are quite numerous in the environment, local exploitation rates remain relatively low despite the increase of effort and CPUE keeps rising with respect to effort. For older fishes, which are less numerous, the increase in local exploitation rates can be sufficient to lead to local overfishing. Where this occurs, local CPUEs decrease, while local effort keeps on increasing. In the same way, longliners are likely to deplete their fishing zone locally when they are numerous and their yields fall when their local effort increases.

The results that we obtained confirm and emphasize the effects of environmental factors (thermocline depth and strength, wind strength, and currents) on catchability. The negative effect of thermocline depth on purse-seine catchability was also observed in the Pacific Ocean by Inada et al. (1997). It seems to be mainly due to the fact that the thermocline acts as a barrier for yellowfin tuna, especially for young ones that cannot swim in cold waters. When the
thermocline is deep or weak, tuna easily escape from the purse-seine nets whereas when it is shallow and strongly marked, tuna are trapped and they cannot escape from the seine (Sharp and Dizon 1978; Evans et al. 1981; Fonteneau 1996). The decrease of catchability for the deeper thermocline seems to be stronger when thermocline depth exceeds 60–70 m, which corresponds approximately to the depth of closing for the seine nets used by FIS purse seiners during the period considered. Such a phenomenon is probably different at present because FIS vessels use much deeper seine nets. Winds have a negative effect for high values. During the period considered, it had been noticed that purse-seine operations were risky when winds exceeded force 4 on the Beaufort scale (Marsac 1992). It is important to take into account the negative impact of shear indices on FIS purse-seine CPUEs. Nevertheless, current shear seems to limit fishing activity for values higher than 0.4 m·s⁻¹, which only occur along the equator where countercurrents (mainly the Lomonossov undercurrent) flow to the east, while major surface fluxes are westward. In this zone, purse-seine operations are known to be very risky.

Environmental constraints at different scales

Pelagic fishes live in a variable spatially heterogeneous environment. Because their displacements have an obvious nonrandom component (Sibert and Fournier 1994; Sibert et al. 1996, 1999), their distribution and movements must be constrained by functional relationships (preferendii and constraints) with the environment (Cayré 1990; MacCall 1990; Begon et al. 1996). Such relationships can be local in the case of home range or resource-directed movements or nonlocal in the case of real migrations emancipated from local constraints (Dingle 1996). Our GAM analysis helps to characterize the main relationships between yellowfin tuna distribution, movements, and migrations patterns and the environment at different scales.

At the scale of the whole Atlantic Ocean, water salinity seems to be closely related to the maximal distribution range of the population. Indeed, looking at salinity maps, it is quite clear that zones where the salinity level is lower than 0.036 kg·kg⁻¹ correspond to the distribution area of adults, whereas zones where salinity level is lower than 0.035 kg·kg⁻¹ correspond to the distribution area of juveniles (Fig. 8). Donguy et al. (1978) noted a clear relationship between
skipjack catches and salinity in the western Pacific Ocean. Nevertheless, water salinity is generally not considered to be a determinant of yellowfin distribution (Blackburn 1965; Sund et al. 1981; Stretta 1989). By contrast, our results suggest that salinity could be an important marker of the yellowfin distribution range in the Atlantic Ocean. Two reasons could be advocated. For young tuna (ages 0, 1, and 2), salinity could be a marker of favorable trophic areas. Indeed, low salinity levels in the Gulf of Guinea are due to fluvial waters supplies. Such freshwater runoffs contain very high

Fig. 8. Comparison between SST maps (top panels) and surface salinity maps (middle panels) in 1991 and mean distribution of the adult yellowfin tuna population estimated by averaging and interpolating all longline catches from 1956 to 1993 (bottom panels).

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Fig. 9. Hierarchical organization in space and time of the envi-
ronmental forcing on the yellowfin tuna population in the tropi-
cal Atlantic Ocean. Scale 4 corresponds to the maximal
distribution range, scale 3 corresponds to the east–west annual
displacements, scale 2 corresponds to the north–south seasonal
movement of the population, and scale 1 corresponds to the local
concentration dynamics; more local scales concern the dynamics
of schools and individuals.

**SPACE**

- homing to low salinity and warm waters
- water temperature movements
- SST gradients, tuna forage

**TIME**

- convergence, fronts... schools
- individuals

nutrient levels, which are generally favorable for young fish
nutrition (Bakun 1996). Thus, young tuna forage develop-
ment is probably related to fluvial enrichment (Caverivière et al. 1976). The other possible explanation is linked to the
metabolic cost of osmotic regulation, which could prevent
young yellowfin from reaching high salinity levels.

At a large scale (5000 km), the adult yellowfin population
moves massively across the Atlantic Ocean. During the
fourth and first quarters, fish converge from their entire dis-
tribution area towards the main spawning ground in the Gulf
of Guinea (Capisano and Fonteneau 1991; Bard 1994;
Fonteneau 1994). After breeding, adults disperse in the
whole Atlantic Ocean to feed in the distribution area charac-
terized by salinity, whereas juveniles stay in the lower-
salinity waters of the Gulf of Guinea. In this way, east–west
adult reproductive displacements take place inside the maxi-
imum distribution range related to salinity and are probably
directly related to warmwater seasonal oscillations (Fig. 8).

At a medium scale (1000 km), the fish population moves
seasonally along a north–south axis along the African coast
for the juveniles and in the open ocean for adults (Bard 1994; Fouche 1994) (Fig. 8). Such seasonal migrations
should be related to the annual cycle of the meridional oscil-
lation of warm waters. Our results show that adults stay
preferentially in zones where surface waters are in the range
of 26–29°C and where deeper waters (150 m depth) are
warmer than 15°C. Juveniles, whose temperature regulatory
system is not yet effective (Cayré 1990), stay in surface wa-
ters in areas where SST is higher than 27°C. Preadults (ages
2 and 3) also follow warm waters around 27°C but seem to
be more tolerant of temperature variations. Warmwater pref-
ferences are well known for tunas. They allow tunas to warm
their body after a deep dive in cold waters (Sharp and Dizon

At a local level (100 km), tunas seem to be influenced by
both local hydrological and biological features, which may
concentrate them. Among the various factors, which may act
at this scale on yellowfin concentration, tuna prey distribu-
tion must be fundamental. However, the high variability of
the spatial distribution of the various small pelagic fish and
cephalopods targeted by tunas (Cayré et al. 1988; Roger
1990) is not directly linked to local enrichment processes
such as upwelling, dome, or divergence (Fonteneau and
Marcille 1988). Indeed, a time lag is necessary to relate pri-
mary production to the concentration of tuna forage. Without
considering displacements by oceanic currents, Garcia and
Cota (1996a, 1996b) have found a correlation between phyto-
plankton production and yellowfin CPUE with a time
delay of between 3 and 5 months in the Gulf of Mexico. By
using a secondary production index estimated by advection–
diffusion of primary production data following marine cur-
rents, Lehodey et al. (1998) and Maury (1998) suggested
that a 3- to 7-months time lag could separate phytoplankton
peaks from the tuna prey’s highest concentration.

Independently of biological factors, our results also sug-
gest physical causes of local fish concentration such as the
spatial stability of water masses. Because yellowfin follow
the temperature gradient to reach warm waters, they do not
stay within the high horizontal gradient $x$ (PSST). When wa-
ter temperature exhibits rapid changes, fishes are pushed by
the unfavorable cooling side of the area. Associated with
secondary production patches and local effects of seamounts
or islands (Fonteneau 1991, 1996), they could be responsible for local (100 km) yellowfin concentrations. More local scales (100 m to 10 km), particularly concerning individuals and schools dynamics, are only considered through catchability in the present study. Nevertheless, they are probably at the center of important variability in fish abundance. Factors probably involved at these very local levels are the presence of floating objects and the existence of small-scale hydrological events such as local fronts or convergences. Such hydrological features may control tuna forage concentration as convergence does, for instance, by concentrating floating objects (Bakun 1996). Such a behavior, well known by the fishers that follow convergence lines to locate tuna schools, is probably too local to be detected accurately by our 1 \times 1° \times 15 \text{ days} analysis.

Because environmental constraints and forcing have various spatiotemporal frequencies, the population level may also be considered as hierarchically organized in space and time. In the case of the Atlantic yellowfin tuna population distribution, different hierarchically organized scales can be distinguished (Fonteneau 1996). At each of these levels of variability, we can associate an environmental factor, as pointed out by our results (Fig. 9). Finally, the complex dynamics of the yellowfin tuna distribution and movements emerge from the interaction of these different processes occurring at different scales.

Beyond the help that it can bring to fishers, the knowledge of the nonlinear environmental processes and their hierarchical organization is of critical importance for fisheries science and fisheries management faced with environmental variability at different scales. One of the main recommendations emerging from the Rio conference on sustainable development was to learn to think from the local to the global scale and vice versa. By articulating global and local scales, a hierarchical understanding of ecosystems is a means of going in this direction.

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