An ecosystem driven model for spatial dynamics and stock assessment of North Atlantic Albacore tuna

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Abstract

An application of the Spatial Ecosystem And Population Dynamics Model SEAPODYM is developed for the North Atlantic albacore tuna population (*Thunnus alalunga*). We investigate the spatio-temporal dynamics of this species distinguishing the influences of environment and international fishing. Incorporating historical data (1960-2008), a maximum likelihood approach allows the estimation of biological parameters (thermal and oxygen tolerance) and stock spatial distribution varying over time. Juvenile albacore tunas are predicted in warm surface waters whereas adults inhabit cooler and deeper waters. Positive correlations between juveniles and tropical large-scale climate indices highlight the importance of environmental drivers when estimating stock recruitment biology and spatio-temporal distribution. A methodology is proposed to use SEAPODYM outputs to estimate stock abundance and maximum sustainable yield (MSY). MSY is computed taking into account the spatial dynamics of the species, the environmental variability and is based on a mechanistic modelling of larval recruitment. MSY estimates converge towards an asymptotic value (15,997 mt) of the same magnitude than standard stock assessment estimates conducted for the international tuna commission. In agreement with all assessment studies, the stock status is estimated from overfished in the 1990’s to recovered in the 2000’s. Our results show that the stock recovery results both from fishing actions, including total allowable catches established in the 2000’s, and from the beginning of a North Atlantic Oscillation warm phase, leading to more favourable recruitment conditions. Following a parsimonious ecosystemic approach, SEAPODYM offers a faithful and spatially dynamic modelling framework that now includes direct tools for spatialized management advice and for distinction between environmental and fishing effects.

Résumé

Une application du modèle spatial d’écosystème et de dynamique de population SEAPODYM est développée. Nous avons analysé la dynamique spatio-temporelle des thons germon dans l'Atlantique Nord (*Thunnus alalunga*) en distinguant les effets de l'environnement et d'une pêcherie internationale. À partir des données historiques (1960-2008), une méthode de maximum de vraisemblance permet l'estimation des paramètres biologiques (tolérance thermique et à l’oxygène) et de la distribution spatio-temporelle du stock. Le modèle prédit que les juvéniles de thon germon résident dans des eaux chaudes en surface alors que les adultes sont dans des eaux plus froides et plus profondes. Des corrélations positives entre juvéniles et des indices climatiques tropicaux à grande échelle soulignent l’importance des facteurs environnementaux pour l’estimation de la biologie du recrutement des stocks et de leur distribution spatio-temporelle. Une méthode est
proposée pour utiliser les sorties du modèle SEAPODYM et estimer une production moyenne maximale durable (MSY). Le MSY est calculé en prenant en compte la dynamique spatiale de l'espèce et la variabilité environnementale, et est basé sur une modélisation des mécanismes du recrutement larvaire. Les estimations du MSY convergent vers une valeur asymptotique (15,997 mt) du même ordre de grandeur que la valeur estimée par les modèles standards utilisés par la Commission thonière internationale. En accord avec toutes les études d’estimation de stock, le statut du stock est estimé avoir évolué de surpêché dans les années 1990 à sain dans les années 2000. Nos résultats montrent que le rétablissement du stock s’explique à la fois par les activités de pêche, incluant des quotas de captures établis dans les années 2000, et par le début d'une phase chaude de la NAO, à l’origine de conditions plus favorables dans les eaux de l’Atlantique Nord. Suivant une approche écosystémique parcimonieuse, SEAPODYM propose un cadre de modélisation fidèle et spatialement dynamique qui désormais inclut des outils directement utilisables pour des conseils spatialisés de gestion et pour la distinction des effets environnementaux de ceux de la pêche.

Key Words
Ecosystem modelling, *Thunnus alalunga*, SEAPODYM, management reference points, fishing impact, decadal variability

Mots clés
Modélisation d'écosystème, *Thunnus alalunga*, SEAPODYM, points de référence pour la gestion, impact des pêches, variabilité décennale
INTRODUCTION

Regional Fisheries Management Organizations are increasingly encouraged to address both exploitation and environmental variability issues (Hofmann and Powell 1998). These new concerns require the development of ecosystemic modelling tools. For pelagic ecosystems with “highly-migratory” species like tunas, ecosystem models need to describe population spatio-temporal dynamics and their dependency on environmental forcing. Since ecosystem models are also designed for fisheries management, they should provide reliable quantitative estimates of stock size, spawning biomass and other key population characteristics. They should hence take into account the distribution of fishing activities over past and recent times. This would discriminate between impacts due to fishing and environmental changes. Combining long-term fishing data and environmental forcing in an ecosystem model allows thus to understand the processes affecting large and regional scales for the spatial distributions, habitat use and migratory behavior of marine species.

Historical series of spatially disaggregated fishing data are compiled by international commissions in charge of high seas fisheries management, e.g., the International Commission for the Conservation of Atlantic Tunas (ICCAT) for the Atlantic Ocean. In fishery management, various reference points are currently in use depending on the quality and quantity of fishing data available (Gabriel and Mace 1999). Most of them are related to maximum sustainable yield (MSY), such as spawning biomass at MSY (SB\textsubscript{MSY}) and fishing mortality at MSY (F\textsubscript{MSY}). Fisheries datasets are thus critical to accurately estimate MSY (Hilborn 2007), to account for fishing impact and to provide the first test of validity for the ecosystem models. Current stock assessments and MSY estimations are conducted at an aggregate stock-level spatial resolution. But, there is increasing demand for modelling tools allowing testing spatial management measures in response to heterogeneous fisheries distributions and local stock depletion. In the most elaborated ecosystemic approaches, fishing data are georeferenced and are directly used to optimize the model parameters through statistical methods.

This is the case of the Spatial Ecosystem And POpulation DYnamics Model (SEAPODYM) (Bertignac et al. 1998; Lehodey et al., 2003; 2008). The model includes a spatially explicit description of age-structured population dynamics from larvae to adult in an Eulerian framework. It also includes a forage model predicting the local density of prey population (Lehodey et al. 2010a, 2014). The dynamics of both forage and predator species are driven by local environmental forcing (temperature, currents, primary production, euphotic depth, and dissolved oxygen concentration) predicted by coupled physical–biogeochemical models. The model parameters, controlling
movement and habitat characteristics, are estimated with a maximum likelihood estimation approach that minimizes the differences between the observed and predicted fishery values from multiple fisheries (Senina et al. 2008). The model has been used to simulate both historical and future spatial distributions of tropical tuna populations (Lehodey et al. 2010b; 2013a) in the Pacific Ocean. It was also used for evaluating spatial conservation measures established by the Western Central Pacific Fisheries Commission to limit the fishing mortality of bigeye tuna (Sibert et al. 2012).

As for other tuna species, the fishing pressure on Albacore has increased over the last three decades in the World Ocean. Previous studies have identified 6 separate stocks in the North and South Pacific, the Indian Ocean, the Mediterranean Sea and the North and South Atlantic (Chow and Ushimama 1995; Miyake et al. 2004). Current status of albacore stocks range from moderately exploited in the South Pacific Ocean to recovered in the North Atlantic Ocean (ICCAT 2013).

Albacore tuna is a long-lived (> 13 years) species that matures at ~4.5 years and has a fast growing juvenile phase (Arena et al. 1980; Santiago and Arrizabalaga 2005). They have high fecundity rates (Arena et al. 1980) and exhibit year-round spawning in tropical waters. In subtropical waters though, seasonal peaks are observed during springs and summers (Ueyanagi 1971; Bard 1981; Collette and Nauen 1983). For the last 50 years, albacore tuna has been heavily exploited in the entire North Atlantic by various fishing gears. But despite the long history of albacore fisheries and general knowledge of its life-history, the population's underlying spatial dynamics and habitat utilization remain poorly understood.

We use SEAPODYM with the ICCAT historical multinational fishery dataset in order to develop the understanding of the past and present dynamics of the North Atlantic albacore tuna population. Here, we aim at i) identifying processes affecting large and regional scales spatial distributions, habitat use and migratory behavior of this commercially valuable and ecologically important species, ii) discriminating between the impact of fishing and the influence of climate variability on the Albacore population ecology and iii) using for the first time SEAPODYM spatialized outputs to get albacore stock assessment and MSY estimates by taking into account the spatial dynamics of the species, the environmental variability and a mechanistic modelling of larval recruitment.

METHODS: MODELLING APPROACH AND FORCING DATASETS
**SEAPODYM description**

Briefly, SEAPODYM predicts catch distribution by fleet when georeferenced fishing data are available. Data used are georeferenced catch, fishing effort, catch per unit of effort (CPUE) and the size frequencies of catch. These data are predicted by the model using the observed fishing effort, a catchability coefficient and a selectivity function. All parameters (see Table A1 in Appendix) are estimated during the optimization process based on a Maximum Likelihood Estimation (MLE) approach (Senina et al. 2008). The successive phases of the optimization experiment allow estimating parameters defining the fisheries catchability and selectivity, and also key parameters controlling mortality, spawning, recruitment, feeding habitats and movement rates (see details in Senina et al. 2008; Lehodey et al. 2010b). Catch and CPUE are computed at the time step of the simulation, i.e. one month in the present case, and length frequencies are aggregated quarterly for comparison with observations. The model is driven by local environmental forcing on a 2° grid (see details below). The albacore tuna dynamics is spatially explicit and age-structured from larvae to adult (see details below). SEAPODYM predictions, i.e. monthly density maps of larvae, juveniles, young and adult fish, have the same resolution than the environmental forcing. The cost function, for the MLE approach, minimizes the differences between predicted and observed CPUE and size frequencies from each fishery (see the approach and recent applications in Senina et al. 2008; Lehodey et al. 2010b; Lehodey et al. 2013a). Details of the present case are given in the Appendix. Temperature and ocean current data are also used in the model to predict the dynamics and distribution of forage biomass (Lehodey et al. 2010a). Forage is used as potential prey for young and adult albacore tunas and as the predators of their larvae. However, the parameters of the forage model were calibrated and described in a separate study (Lehodey et al. 2010a).

**Oceanic forcing variables**

Due to the lack of historical synoptic datasets for oceanic physical variables before the 1980s, and before 1998 for the ocean color (i.e., SeaWiFS, Peach 1997), ocean reanalyses with satellite derived primary production are not available to simulate albacore tuna dynamics with SEAPODYM before 1998. As an alternative, hindcast simulations with coupled ocean physical-biogeochemical models can be used. These simulations are forced by atmospheric data for which a few reanalyses are available (e.g., NCEP, Kalnay et al. 1996; ERA40, Uppala et al. 2005).

In this project, model domain covers the entire North Atlantic ocean (1°S: 68°N; 260°E: 375°E) and we used a 2° x month physical configuration from 1960 to 2008. This configuration uses physical
and biological forcing from a hindcast simulation with the coupled NEMO-PISCES model (Aumont and Bopp 2006; Madec 2008). This model is on an ORCA2 grid and forced by the atmospheric reanalysis NCEP-NCAR. This reanalysis provides a nearly 50-year record of global analyses of atmospheric fields based on the recovery of satellite, and in situ data (http://www.cgd.ucar.edu/cas/guide/Data/ncep-ncar_reanalysis.html, Kalnay et al. 1996). The ocean hindcast simulates reasonable seasonal, interannual and decadal variability at basin-scale and at a coarse resolution of 2° x month. Finally, climate impact on the whole reanalysis period is also assessed by correlating albacore abundance time series to climate indices (North Atlantic Oscillation NAO, Barnston and Livezey 1987; Tropical Northern Atlantic Index, Enfield et al. 1999 and Atlantic Meridional Mode, Chiang and Vimont 2004). Correlation coefficients between each of the time series were calculated and their significance (probability of type-1 error = 0.05) tested with a parametric bootstrap (Dragon et al. 2010).

Biological model configuration

a) Fishing data

Georeferenced fishing data for North Atlantic albacore tuna were extracted from ICCAT database (http://www.iccat.es/en/accesingdb.htm) for the period 1956-2010. Depending on the year, spatial locations were available for 20% to 50% of ICCAT recorded landings (Figure 3 in Lehodey et al. 2014). Additional files at higher resolution of the Spanish fleets were provided by AZTI (http://www.azti.es). In the North Atlantic, landings declined from 50,000 mt in the 1960’s to 20,000mt in the 2000’s (Lehodey et al. 2014). Fisheries were defined first based on the fishing gear, the fishing ground and the fishing country. Longline fisheries, mainly from Japan, Taiwan, and Korea, target all year round immature and adult albacore tunas. Surface fisheries (i.e. bait-boats, trollers and pelagic trawlers) are mainly from Ireland, France, Portugal and Spain. They target immature and sub-adult fish in the Bay of Biscay and adjacent waters of the northeast Atlantic in summer and autumn. In the longline Asian fleets, fishing catches on albacore tuna decreased drastically after 1972 (Japan), 1979 (Korea) and 1986 (Taiwan, ICCAT 2013). The fishing effort of the Asian fleets kept growing though, but shifting to different targets such as bigeye and yellowfin tunas (resp. Thunnus obesus and Thunnus albacares). In order to keep homogeneous the definition of fisheries in relation to their fishing gear catchability, each Asian fishery has been subdivided into two periods. In total, thirteen fisheries were defined for the period 1956-2010 (Table 1), with fishing gears longline, troll, gillnet, mid-water trawl, purse-seine and bait-fishing. The model temporal resolution is monthly and data were aggregated to this resolution when necessary. Georeferenced fishing data were aggregated at the spatial resolution of the environmental grid, i.e.
Length frequencies of catch for North Atlantic Albacore, indicators of the age-population structure, were also available from ICCAT database. They were extracted according to the definition of fisheries above for the period 1956-2010 with a quarterly temporal resolution and spatial resolutions from 1°x 1° to 10°x 20°. Given that very few albacore reach a size above 130 cm (Le Gall 1974; ICCAT 2013), this value was set as a maximum threshold and samples with length frequency data above this value were removed to avoid including wrong data due to species misidentification (for details see Lehodey et al., 2014).

b) Population structure

The structure of the population was defined with 157 monthly cohorts, the last one being a “plus cohort” accumulating older fish. The age at first maturity was set to 4.5 years, i.e. 54 months (Santiago and Arrizabalaga, 2005). In addition to this age structure, the model takes into account the 4 different life-stages: larvae (0 to 1 month), juveniles (1 to 3 months), young immature fish (3 to 54 months) and mature adult fish (over 54 months) by describing the dynamics of each stage with different equations (Lehodey et al, 2008). The growth of albacore tuna is simulated with one length and one weight coefficient by cohort obtained from independent studies (Bard 1981; Gonzales-Garces and Farina-Perez 1983 among others). According to Santiago and Arrizabalaga (2005), age at first maturity was set to 54 months that approximately corresponds to fish of 84 cm in fork-length (Lehodey et al. 2014). At each time step (one month), survival relationships describe ageing processes while advection-diffusion-reaction equations describe migrations, recruitment and mortality. For each time step, the local mortality rates of each cohort is defined as the sum of a natural mortality (calculated from senescence and predation components that are locally variable depending on environment/habitat conditions) and a fishing mortality (decomposed spatially by fishery, time step and fish age, Lehodey et al. 2008).

After juvenile stage, fish are considered autonomous: they have their own movement (linked to their size and habitat) in addition to be transported by oceanic currents. Furthermore, adult mature fish contribute to the spawning biomass and their displacements are controlled by a seasonal switch between feeding and spawning habitats. This seasonal switch is activated by a day-length function. Hence, it is effective outside the equatorial region where day length variations are marked enough
to allow the shift to be detectable above a threshold value that is estimated (Lehodey et al. 2008).

Estimation of fishery indicators and state of stock

The MSY is assumed to be reached when the curve of catches in function of effort reaches its maximum (Gaertner et al. 2001). To estimate MSY with SEAPODYM, we ran simulations with the optimal parameterization achieved and with a scaling factor of fishing effort. The scaling factor increases from 0 (no fishing effort) to 12 times the mean fishing effort of the last five years (2004-2008). A 5-year average of fishing effort allowed integrating medium term fishing activity and attenuating the influence of potential outlier records. Since in addition to fishing mortality, the population dynamics in SEAPODYM includes the impact of environmental variability (e.g., on natural mortality and larval recruitment), we explored how MSY did change for different time periods. We used four simulation lengths: 20 years (30 replicates starting from January 1960 to January 1989), 30 years (20 replicates starting from 1960 to 1979), 40 years (10 replicates starting from 1960 to 1969) and finally the whole NEMO-PISCES time period (1 replicate of 49 years starting in January 1960). The four lengths of simulation allowed to test (i) if MSY estimations vary according to the simulation lengths, (ii) if the catch curves and MSY estimations converge towards a common value and (iii) if different environmental conditions impact MSY estimation. The mean and standard deviation of MSY estimates were calculated in each group of simulation, except the last one that has only one replicate. Fishing mortality was approximated as:

$$F \approx 1 - \frac{SB}{SB_0}$$

with $SB$ the average spawning biomass of the 49-year simulation over the last 5 years of the dataset (2004-2008) and $SB_0$ the virgin spawning biomass over the same 5 years, calculated from a simulation with no fishing effort.

RESULTS

Spatio-temporal fit to catch data

The North Atlantic albacore catch distribution extends between the equator and 55°N. Longline fisheries cover the entire tropical region and extend North West to the temperate region. French
mid-water trawl and French and Spanish troll fisheries extend offshore from the Gulf of Biscay to 30° W. For catch and CPUE data of each fishery, the fit quality was good based on three indices: Root Mean Square Error (RMSE), standard deviation and Pearson correlation (Appendix Figure A1). The overall spatial fit between predicted and observed catch and CPUE (Appendix Figure A2) is especially good in the core habitat of the species (R-squared goodness of fit >60%), where maximum catch occurred over time. The fit is degraded on the borders of the catch distribution, in relation with low level of catch and a lack of resolution near the coast, especially the Gulf of Biscay.

Considering the temporal fit, the catchability coefficients of Japanese, Korean and tropical Taiwanese longline fleets were found to slightly decrease over time since the 1980s, or even earlier for Japanese fleet. Thus, a linear negative trend in catchability was added for these fisheries to allow a better fit (Table 2). A positive trend was detected for the Taiwanese subtropical longline fishery only. The correlation coefficients between observed and predicted catch time series are globally high (almost all fisheries with r > 0.8) and range between [0.52; 0.95] for catch time series (see Supplementary Material S1). The best fit (r = 0.95 for catch and r = 0.92 for CPUE) is obtained for the Taiwanese longline fishery (L4) that presents a high selectivity leading to the capture of large fish only (see Supplementary Material S1). Overall, Asian longline fleets present high total catch compared to the US longline (L3) fishery that has the highest selectivity. The model also predicts too small amount of large fish (>70 cm) in the Spanish bait-boat fishery (B13). This pattern can be due to a lack of size data for this fishery during the optimization period. The strong seasonality of CPUE is very well predicted for Spanish troll (T12) and bait fishing (B13) fleets. But, the predicted range of variability is too small compared to observations, leading to a discrepancy between predicted and observed catch.

Finally, hindcast and forecast simulations (see Supplementary Material S2) show that the model can predict correctly fishing catch and CPUE outside the time window used for the optimization (1981-2000). The validation fit to both catch and CPUE is high (r > 0.75) for all fisheries that have reported catch and effort during periods not included in the optimization.

Parameters estimation

a) Natural mortality and recruitment

In SEAPODYM, the mortality mechanism depends on five parameters (Table A1). All estimates of
standard deviation were inferior to 0.01 for mortality and recruitment parameters (Table A1). Two parameters were significantly correlated ($\rho = -0.9984$): the slope coefficient and the minimal value of senescence mortality. Figure 1a presents the average mortality-at-age coefficients that are estimated using the cohort density as weights of the mean. The mortality is estimated to decrease rapidly in the early life stage from above 0.06 mo$^{-1}$ in average in the first year of life to a minimum of 0.02-0.04 mo$^{-1}$ (0.24-0.48 yr$^{-1}$) between 3 and 10 years, then slowly increasing for older cohorts (Fig. 1a). For larvae, average monthly natural mortality rates computed from model outputs are estimated higher than the theoretical average rates that do not include local effects (Fig. 1a). This difference can be explained by the drifting phase of larvae that prevent them from escaping unfavorable habitats, contrarily to fish in older life-stages.

**b) Spawning and feeding habitats**

The favorability of spawning and feeding habitats and the function controlling the seasonal switch between them depend on twelve parameters (Table A1). Figure 1b presents the spawning habitat favorability index that depends on the density of larvae predator and temperature in epipelagic layers. Since adult fish can migrate to favorable spawning grounds following temperature gradients leading to their optimal spawning temperature, Figure 1b was calculated over the entire study area. Spawning favorability is maximal (> 0.9) for Sea Surface Temperature (SST) at 25.77°C (std. err.: 1.74°C) and predator density under 0.05 g/m². The resulting distribution of larvae ranged between SST 22°-30°C. The seasonal timing of spawning migration was estimated to peak at Julian date 81 (22 March), i.e., the spring equinox, and to impact adult fish located north of 9.5°N. Below this latitude, albacore tuna movements continue to be fully driven by the feeding habitat index.

Figure 1c presents the feeding habitat index that combines sensitivity to temperature and dissolved oxygen, as a proxy for prey accessibility in surface, sub-surface and deep layers. For the oxygen functional relationship, estimates of both the threshold value (4.14 mL.L$^{-1}$) and the slope (0.00001) indicate a high sensitivity of albacore to oxygen levels in its habitat. The optimal temperature in the water column inhabited by the fish is estimated to range between 19°C from age 1yr to 10°C for the oldest/largest fish (Fig. 1c).

**c) Movement**

Fish movements depend on two parameters controlling diffusion and directed movements (advection). As for mortality above, advection and diffusion coefficients were weighted by the
cohort density (see Supplementary Material S3) to provide a more meaningful metric of movement coefficients by age (size). The mean maximum diffusion rate reaches 2000 nmi² month⁻¹. The mean maximum sustainable speed ($V_{\text{max}}$ in body length per second, BL.s⁻¹) remains below 0.15 BL.s⁻¹, with a theoretical maximum value estimated to its lower boundary value ($V_{\text{max}} = 0.95$ BL.s⁻¹). The speed decreases with age (size) together with the habitat gradient, due to increasing accessibility to forage biomass of deeper layers.

**Biomass estimates and population dynamics**

**a) Stock estimates and fishing impact**

Figure 2 presents the changes over time in the unfished biomass of different albacore tuna life-stages. The number of albacore recruits aged of 6 months is estimated around 8,000,000 (Fig. 2a, grey line). The young immature biomass ranges between 400,000 and 500,000 metric tones (mt) (Fig. 2b, grey line). North Atlantic albacore spawning (adult) biomass is estimated to ~250,000 mt (Fig. 2c, grey line) and the total biomass ranges between 600,000 and 800,000 mt after 1975 (Fig. 2d, grey line).

Figure 2 also presents virgin biomass estimates (i.e., in absence of fishing, black lines): between 800,000 and 1,200,000 mt for the total biomass (Fig. 2d); between 300,000 and 500,000 mt for the adult biomass (Fig. 2c); between 6,000,000 and 14,000,000 for the recruits number (Fig. 2a) and between 500,000 and 800,000 mt for the biomass of immature fish (Fig. 2b). Globally, the simulation with no fishing mortality shows that the fishing impact has been relatively stable (around 35%) since the 1990s for both young immature and adult fish, the maximum impact (40%) occurring in the Gulf of Biscay and adjacent waters between the coast of Spain and Ireland. Note however that fishing impact is underestimated due to the incomplete coverage of georeferenced fishing data (Lehodey et al. 2014).

**b) Variations in spatial dynamics of albacore at different life stages**

Regarding the spatial dynamics, Fig. 3 illustrates the distribution for winter season (January-February-March) of larvae (a), young (b) and adult fish (c). The distributions of other seasons are illustrated in Supplementary Material S4. In average, spawning grounds and larvae are predicted to concentrate in the warm waters of the subtropical western Atlantic with a peak in June-July. The biomass of spawners (adult fish) is predicted to increase in this area by over 50% between December and May (Fig. 3). Nevertheless, the model predicts spawning all year round. Spawning is also predicted along the eastern Coast of USA in the Gulf Stream region but at a much lower
intensity (~1,000 recruited larvae km\(^{-2}\)) and during the first quarter mainly (peaking in March). In comparison to the spawning ground, distribution of young immature fish (30-80 cm) is shifted northward along a southwest-northeast axis reaching the south-west of Ireland and the Gulf of Biscay where they are caught by French and Spanish troll and mid-water trawler fleets. Predicted adult fish seasonal distribution shows a latitudinal migration pattern with maximum extension to the north during 3rd and 4th quarter of the year, i.e. summer to fall, and a southward movement to subtropical region in the 1st and 2nd quarter (winter to spring).

c) Decadal changes in albacore population

Model simulations without fishing are presented in Figure 2 to distinguish climate and fishing effects on albacore tunas. The no-fishing model predicts a multi-decadal variability leading to a decreasing trend from the 1960s, reaching a minimum in the 1980s and increasing since then (Figure 2). The effect of fishing strongly accentuates the decreasing trend. This trend can also be detected spatially on Figure 4 and coincides with the peak of activity by longline fisheries targeting albacore and the traditional surface fisheries in the gulf of Biscay and adjacent waters. In the 1990s, there was a drastic reduction of effort by the longline fisheries targeting albacore while new surface fishing gears (driftnet and pair pelagic/mid-water trawlers) appeared in European waters (see Supplementary Material S1). The driftnet fishery was banned in 2002. More favorable recruitment conditions are predicted to occur for the last decade (Fig. 2 and 4), leading to increasing trend of the stock biomass but more slowly than what is predicted in the simulation without fishing.

Regarding broad climate variability, larvae abundance is correlated positively with two tropical climate indices: the Tropical Northern Atlantic Index (\(\rho = 0.40\)) and the Atlantic Meridional Mode (\(\rho = 0.38\)). And the total biomass (cumulated young and adult abundances) is correlated to the NAO index with a 9-month lag (\(\rho = -0.15\)).

Estimation of fishery indicators and status of stock

The average catch for years 2004 to 2008 is of 601,430 mature and immature fish, i.e. ~15,036 mt. Catch curve replicates have shapes similar to asymmetric Gaussian distribution functions (Appendix Figure A3). A decrease and convergence in MSY estimates is observed while simulation lengths increase from 20 to 40 years (mean+/− sd: 20-year = 162.43+/− 23.83; 30-year = 121.66+/− 17.56; 40-year = 103.32+/− 11.24). Globally, the longer the simulation the smaller the MSY estimate and the closer it is to the 49-year simulation MSY estimate (106.39%, i.e. ~15,997 mt).
The Kobe phase plot (Fig. 5) is built with MSY equal to 106% of the 2004-2008 mean recorded catches. On the x-axis, the annual spawning biomasses of the 49-year simulation are divided by the estimated MSY spawning biomass (197,742 mt). On the y-axis, the annual fishing mortalities of the 49-year simulation (ranging from 0.02 to 0.47) are divided by the MSY fishing mortality (0.5244). Based on this estimation, the status of the north Atlantic albacore stock since the beginning of the industrial fishery in 1960 (Fig. 5) remained in the green "no Risk" panel except between 1987-1998 when it was overfished (SB < SBMSY). There are however, several sources of uncertainty that are discussed below.
DISCUSSION

In this study, we optimized a SEAPODYM parameterization for albacore tuna in the North Atlantic Ocean. We reconstructed the spatial population dynamics over its 50-year fishing history with a 2° x month NEMO-PISCES bio-physical forcing. We obtained a reasonable spatio-temporal fit between predicted and observed catch and biologically plausible parameterization, hence providing confidence in the model outputs of this commercially valuable and ecologically important species. In addition, our study highlights the seasonal and decadal spatial changes in albacore dynamics and provides for the first time with a spatially-explicit model like SEAPODYM, the key management indicators based on MSY.

Characterizing the habitat of albacore tunas

The model predicts variations in spatial distribution for the different albacore life stages. In agreement with previous studies (Goni and Arrizabalaga 2005), juvenile albacore tunas are predicted in warm surface waters whereas adults inhabit cooler and deeper waters. Juveniles are also predicted to spend winter time in subtropical area, as mentioned in ICCAT (2013). Positive correlations between larvae abundance and three tropical climate indices also suggest that warmer subsurface waters benefit directly to albacore recruitment. Increased larvae density occurs during positive phases of the Atlantic Meridional Mode (AMM). These are characterized by an anomalous SST gradient across the mean latitude of the Atlantic Intertropical Convergence Zone (ITCZ) coupled to a northward anomalous shift of the ITCZ (Chiang and Vimont 2004). Increased larvae density also occurs when the Tropical Northern Atlantic Index displays positive values. This index is characterized by warmer average of monthly sea surface temperatures in the ITCZ (Enfield et al. 1999). Tropical physical processes such as the deepening and oxygenation of mixed water layer are likely to impact positively larvae abundance. These climate indices are known to modulate sea surface temperatures in the subtropical North Atlantic, such as positive anomalies of sea surface temperature during AMM warm phases increase albacore spawning habitat extension. Positive correlations between albacore recruitment and tropical large-scale environmental indices are in accordance with results from previous studies (Goni and Arrizabalaga 2005; Sagarminaga and Arrizabalaga, 2010; Dufour et al. 2010 among others). The impact of climate indices and regime shifts on youngs and adults is lagged for NAO, which is coherent with a propagation in the older age-classes of weaker or stronger larval recruitment associated to environmental driven variability.
In the North Atlantic, the model predicts spawning grounds in subtropical western waters where spawning activity was effectively observed, especially offshore Venezuela in the Sargassum Sea (Le Gall 1974; Nishikawa et al. 1985) and in the Gulf of Mexico (Richards 1984). Furthermore, the model predicts spawning during the spring-summer months (Apr-Sep), with a peak around July in agreement with the current knowledge of the species biology (ICCAT 2013; SCRS 2013). However, some larvae were also found in winter, suggesting a residual spawning activity in winter season in tropical waters as proposed by Richards (1984).

In their juvenile stage, albacore tunas inhabit the epipelagic layer of sub-tropical regions or temperate waters in summer. When they grow bigger, they are captured on longline gear in the upper mesopelagic layer (Allen et al. 2006) at depths of 150–250 m, where water temperatures are 18–25°C (Domokos et al. 2007; Arrizabalaga et al. 2014), i.e. in the range of temperatures estimated by the model. The species is also known to be sensitive to low concentration in dissolved oxygen (O₂). According to Graham et al. (1989), the albacore tunas have low tolerance to oxygen concentrations below 3.7 mL.L⁻¹. Our estimated value (4.14 mL.L⁻¹) agrees well with this result. It is also consistent with Arrizabalaga et al (2014) who reported few observations below this value, and estimated preference for values above 6.4 mg/L (0.20mmol/L).

Regarding subpopulation structure, density maps of young and adult fish did not display strong spatial discontinuity in spawning grounds and feeding habitats. This result agrees with previous result showing no evidence of sub-populations of albacore within the North Atlantic basin, based on blood groups and tag-recapture analyses (Arrizabalaga et al. 2004). Introducing mesoscale activity with higher grid resolution could perhaps modify this conclusion and would need to be explored to test the hypothesis of a sub-population in the North-Eastern Atlantic (Fonteneau 2010). The link with the albacore Mediterranean stock (ICCAT, 2013) needs also to be investigated.

Stock assessment goodness of fit

For an ocean basin approximately two times the north Atlantic basin, the biomass of South Pacific albacore with the standard stock assessment model MULTIFAN-CL was estimated above one million metric tonnes with a spawning biomass around 500,000 mt (Hoyle et al. 2012). Similarly the north Pacific albacore spawning biomass was estimated just under 500,000 mt (ISC 2011). Proportionally to the size of the north Atlantic basin, these estimates are fully coherent with the
estimate of the present study, i.e., above 600,000 mt for the total biomass and 250,000 mt for the spawning biomass.

Stock assessment studies for the North Atlantic albacore were conducted by ICCAT with Virtual Population Analysis approach (VPA, Shepherd and Pope 2002) and more recently the stock assessment model MULTIFAN-CL (ICCAT 2013; SCRS 2013). The VPA study provided the lowest estimates of spawning biomass in the range of 10 000-20 000 mt for the recent years (ICCAT 2013). A first MULTIFAN-CL study estimated the total biomass to decrease from 200,000 mt in the 1960s to ~110,000 mt in the last decade, with the adult spawning biomass similarly decreasing from a range of 75 000-125 000 to 20,000-60,000 mt (ICCAT 2013). The estimate was revised in the latest stock assessment study with higher spawning biomass between 100,000 and 200,000 mt (SCRS 2013). This latest result is more consistent with the SEAPODYM estimate. It should be also noted that all stock assessment studies (either with SEAPODYM, VPA or MULTIFAN CL) agree on the recovery phase of the North Atlantic spawning biomass since the end of the 1990's.

Although albacore tuna has been fished for long, there are few quantitative estimates of stock size and size- or age-specific biological parameters. Many of the biological parameters included in stock assessment models for albacore tunas are currently derived from studies of other stocks or tuna species (ICCAT 2013). The natural mortality rate is usually assumed to be constant for all age classes in ICCAT stock assessment studies. Recent albacore stock assessment studies assumed a natural mortality rate of 0.3 yr\(^{-1}\) (0.025 mo\(^{-1}\), ICCAT 2013), somewhat lower than the coefficient used (0.4 yr\(^{-1}\) or 0.033 mo\(^{-1}\)) for the most recent stock assessment in the south Pacific (Hoyle et al. 2012). In SEAPODYM, mortality coefficients vary with age, time and space. Due to the representation of fish movements in the model, fish can escape unfavourable habitats (with higher mortality rates) and concentrate in good habitats (with lower mortality rates), thus resulting in lower effective mortality rates than predicted from. The SEAPODYM estimate is thus within or just above the upper range of average natural mortality coefficients used in stock assessments studies (between 0.2 and 0.5 per year). However, during the spawning period, the mechanism is inversed since adults are not in their preferred habitat. It is also higher for young cohorts (1 to 6 yr) than in the estimate for the south Pacific albacore with the same model (Senina pers. comm.). Sensitivity to the parameters defining the population structure (size-age and age at maturity) would need to be investigated further.

Finally, regarding fishing time series, seasonality was globally well predicted. But, a discrepancy between predicted and observed catch was obtained for some fisheries, for which there is a lack of details either on the target species or the fishing strategy. We expect to improve future stock
assessment estimates by (i) enhancing the definition of fisheries, (ii) increasing the accessibility to reliable and high-resolution geo-referenced catches and length frequencies data and (iii) including in SEAPODYM the fishing mortality by subtracting the monthly or annual amounts of non geo-referenced catch to the estimated albacore stock.

Improving reference points estimation

Every two or three years, ICCAT publishes reports presenting stock assessment and MSY estimates of North Atlantic albacore population to assist in the management of this species. Based on the recent issues (ICCAT 2013; SCRS 2013), the average total catch from 2004 to 2008 is 28,148 mt with an average MSY of 30,200 mt and 80% confidence bounds of 26,800 mt to 34,100 mt, depending on the relative importance of the surface and longline fisheries catch levels. In recent years, ICCAT reports indicated that the population of North Atlantic albacore tuna has been overfished but it is not undergoing overfishing (ICCAT 2013; SCRS 2013). Since 2007 however, it has been observed that total catches were below the recommended total allowable catches (TAC) of 28 000 mt, as defined from ICCAT's MSY estimate (ICCAT 2013).

MSY was estimated from SEAPODYM outputs with catches and biomasses averaged over the last five years. The MSY estimates converged towards an asymptotic value (15,997 mt) which is smaller, but of the same magnitude (10^3 mt), than the ICCAT value (30,200 mt in ICCAT 2013 and 31,680 mt in SCRS 2013). One critical issue in the present MSY estimate is certainly the partial knowledge of catches that may result in the underestimation of fishing mortality. As a first guess, it could be expected that increasing the amount of effort and catch would proportionally increase the biomass estimate (and thus MSY). But this is not straightforward, especially since length frequency data also used in the optimization integrate the signal due to all fishing mortality. Therefore, there may be compensatory mechanisms at play during the parameter optimization, especially regarding mortality estimates. It seems necessary then to revise this study in the future. The parameter optimization framework of this model should allow quantifying the propagation of the error (uncertainty and bias) on catches. However, this question is very wide and may point out very different and challenging mathematical problems: we need first to be able to quantify the error distribution of MSY with respect to a given error distribution (e.g. Gaussian distribution) on some SEAPODYM model inputs or parameters of interest (see error propagation method, Saltelli et al. 2004, Evans et al. 2014). A second step consists in determining this error distribution of model...
inputs. This is usually done qualitatively by taking into account literature and expert knowledge. But the theoretical framework of parameter estimation procedure should give us a consistent way to estimate the errors quantitatively with respect to the error on observations (catches).

In the meantime, uncertainty and bias should be reduced on fishing and biological data (Sinclair 1993; Maunder 2002). All the reports of stock assessment models highlight the lack and/or low resolution of data that induce substantial error on current stock status due to the wide range of reference point estimations (SCRS 2013). Previous studies also showed that small changes in parameter estimates could substantially affect the values of reference points (see a review in Maunder and Aires-da-Silva 2011). Consequently, variations in parameters estimations or stock assessment methodologies may have large implications for the whole stock assessment. Nevertheless, similar tendencies can be observed on the Kobe plot produced from SEAPODYM estimate (Figure 9) and from ICCAT (2013; Figure 6). Starting in the 1960's in the “no-risk” panel, the North Atlantic albacore population was considered overfished after 1986 and slowly recovered in the 2000's. The change in stock status likely results both from fishing actions and climate variability. As presented by Santiago and Arrizabalaga, 2005, the important fishing activity in the 1990’s coincides with a positive peak in the NAO index inducing colder conditions, less favourable to larvae survival, and then juvenile recruitment and young and adult growth. On the contrary, TAC were established in the 2000’s at the beginning of the current NAO warm phase, leading to the recovery of the North Atlantic albacore stock.

**Future studies**

This first optimization experiment for the north Atlantic albacore stock using SEAPODYM provides results in agreement with the literature on ranges, trends, and distributions (seasonal, age-class and spatial) of this species. Globally, fishing activities impact increasingly the albacore population and accentuate the decreasing trend observed since the 1960s. Significant correlations with climate indices also highlight the impact of climate variability on albacore abundance at the ocean basin and multidecadal scales. The first estimates of reference points were also obtained from SEAPODYM outputs, with MSY accounting for both population dynamics characteristics and environmental variability with a direct link between them through the mechanisms of larvae recruitment and natural mortality. The MSY estimate from SEAPODYM outputs is smaller than the total catches since 2007, that are below the recommended TAC defined from ICCAT's MSY estimate.
Following a parsimonious ecosystemic modelling approach, SEAPODYM offers a robust and spatially dynamic modelling framework that now includes direct tools for management advice (Sibert and Hampton 2003) and for the distinction between environmental and fishing effects. Given the long life span of albacore, it becomes crucial to introduce reasonable forecast of the stock under combined influences of fishing, decadal variability and climate change. Combining environmental and fishing effects to a mechanistic framework, SEAPODYM is well adapted to reconstruct the past history of fish population dynamics, but also their potential future projections under climate change scenarios as those proposed by IPCC (Solomon et al. 2007). Environmental and climate change variability, along with confidence indices, can be easily included from statistical perturbations on IPCC physical forcing over the next two or three decades. Uncertainties on key model parameters need also to be included. The next important step for management advice, subsequent management decisions and the sustainable exploitation of marine species would thus rely on forecasts of MSY estimates and of their uncertainty envelop.

Acknowledgements

Conceived and designed the experiments: ACD IS HA PL. Performed the experiments: ACD IS. Analyzed the data: ACD IS PL. Contributed reagents/materials/analysis tools: BC AC OT HA. Wrote the manuscript: ACD IS OT PL HA. We are grateful to ICCAT for the access to its public fishing database and particularly to Carlos Palma for his helpful advices on these data. The authors wish to thank Alain Fonteneau for his suggestions and helpful comments on a first version of the manuscript. The work was also improved by discussions with three anonymous reviewers. This work was supported by the European-funded EURO-BASIN project (www.euro-basin.eu) and the Space Oceanography Division of CLS, France.

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APPENDIX

Parameter optimization experiment

In the optimization experiment, model parameters are estimated by fitting model predictions of catch, catch per unit effort, and size frequency of catch to observations. In SEAPODYM, all error distributions are assumed to be normal. Size selectivity by fishery can have 3 functional forms: logistic and sigmoid functions with two degrees of freedom (slope and threshold) and asymmetric Gaussian with three degrees of freedom (slope, threshold and right asymptote). All initial parameter values were derived from similar experiments conducted for the south Pacific Albacore (hereinafter SPA, see Table 7.2 in Lehodey et al. 2013b). Given the long life span of albacore (>13 years), the changes in Asian longline gears in the 1980s and the greater lack of geo-referenced fishing data after year 2000 (Lehodey et al. 2014), we chose an optimization period going from January 1981 to December 2000. Since the initial conditions for the age-space model solutions are highly uncertain, we started the simulations in 1971, i.e. 10 years before starting the optimization in order to allow rebuilding of the spatial solutions and the new recruitment stipulated by estimated parameters before fitting the data.

The optimization experiment was run in several successive phases to allow the proper estimation of all model parameters (listed in Table A1). Each phase ended once the cost function had reached a minimum (Equation 1, details in Senina et al. 2008). Despite a high amount of data used in the optimization approach (121,634 effort-catch events and 7,459 size-frequency samples), some parameters remain difficult to estimate. For instance, juvenile (age 2 and 3 months) mortality presents a lack of observability and can be highly correlated with antagonistic (e.g. recruitment) and related mechanisms (e.g. the age-classes mortality). Prior to the optimization experiment, sensitivity analyses to fishing data were thus conducted to determine the release order of the parameters (the most sensitive ones in the first phase etc.). Table A1 presents the parameters estimated along the optimization process, their initial values and the phase at which they were respectively released. Once released, a parameter is not fixed in the following phases. This progressive release of parameters along the optimization phases allows a large exploration of possible parameter values in accordance with the complex relationships between all model variables. In the final phase of the optimization, the most sensitive parameters are released for fine adjustment. The Hessian matrix is finally calculated in the vicinity of the cost function minimum. The covariance matrix, the estimates of standard deviation and the correlation table are finally deduced from the Hessian matrix. I
Equation 1:

The contribution to the negative log-likelihood function from (i) the discrepancy between observed and predicted CPUE and from (ii) the discrepancy between observed and predicted proportions of catch at size \((Q_{itf})\) in the sample data is given by the following formulation:

\[
\theta^L = \sum_t \sum_f CPUE_{tf}^{pred} - \sum_t \sum_f CPUE_{tf}^{obs} \log(CPUE_{tf}^{pred} + 10^{10}) \\
+ \sum_t \sum_f \log \left( \Gamma(CPUE_{tf}^{obs} + 1) \right) \\
+ 0.5 \sum_i \sum_t \sum_f \log \left[ 2\pi \left( \varepsilon_{itf} + \frac{1}{I} \right) \right] \\
+ I \sum_t \sum_f \log(\tau_{tf}) - \sum_i \sum_t \sum_f \log \left[ \exp \left( \frac{-(Q_{itf}^{obs} - Q_{itf}^{pred})^2}{2(\varepsilon_{itf} + \frac{1}{I})\tau_{tf}^2} \right) + 0.001 \right]
\]

Where

\[
\varepsilon_{itf} = Q_{itf}^{obs}(1 - Q_{itf}^{obs})
\]

\[
\tau_{tf} = \frac{p_L}{\min(1000, S_{tf})}
\]

And

\(S_{tf}\) is the size of the size-frequency sample taken from fishery \(f\) in time period \(t\)

\(I\) is the number of size intervals in the samples, and

\(P_L\) is a multiplier set by fish flags (default = 10)

The validation of the optimal parameterization and the model predictive skills was performed for the periods before (1960-1970) and after (2001-2008) the optimization time-window, i.e. using the full NEMO-PISCES forcing time series. To run the hindcast simulation from 1960 on, we assumed that (i) the 1960 albacore density spatial distribution was not different from the one in 1971 and (ii) the albacore abundance was higher in 1960, when the fisheries had just started their activities, than in 1971. The initial conditions of 1971 were thus rescaled with a constant factor (1.1) that was then adjusted so that the hindcast simulation starting in 1960 gives the same level of stock estimated in the 1970s with the optimal parameterization. We thus obtained a fully calibrated and parameterized 49-year long simulation over the whole historical fishing period (1960-2008).
Finally, three indices were combined to validate the model outputs and the quality of the optimal parameterization over the whole study period. The Root-Mean-Square-Error (RMSE) was used to evaluate the model goodness of fit, i.e. the measure of the differences between values predicted by the model and the values actually observed. The Pearson correlation coefficient was calculated to estimate the covariation between data, model outputs and all linear transformations of them. The standard deviation was calculated to check if the model predictions have the same variability/dispersion as observations.
FIGURE CAPTIONS

FIGURE 1:

a) Natural mortality rates (month⁻¹) estimated from SEAPODYM optimization experiment. The black thick curve corresponds to the theoretical average mortality curve with allowed range of variability delineated by thin black curves. Blue dots indicate the mean mortality rates weighted by the cohort density with blue segments giving +/- one standard error. The 157 cohorts of the population structure are represented.

b) Spawning index in relation to sea temperature in the epipelagic layers (°C) and predator density (predators of Albacore larvae, in g.m⁻²). The higher the spawning index, the more favorable the spawning habitat is. In the case of Atlantic albacore tunas, the optimal spawning habitat corresponds to predator densities under 0.04 g.m⁻² and water temperatures between 25 and 26.5°C.

c) Optimized function for temperature habitats in function of fish age (in month). One can see the age-dependency of thermal tolerance for Albacore tunas. Like many other poikilotherm species, older albacore tunas have a smaller thermal optimum (about 25°C for first cohorts and about 10°C for the oldest cohorts).

FIGURE 2:

Using the coarse resolution (2° x month) model configuration, SEAPODYM biomass estimates (light grey) for the north Atlantic albacore tuna stock of larvae (a), young immature (b), mature adults (c) and total population (d). The biomass estimates without fishing are shown in black.

FIGURE 3:

Winter average (1991-2000) distributions of north Atlantic albacore at different life-stages. a) larvae (Nb. km⁻²), b) immature youngs (t/km²) with total catch proportional to circle size of fisheries L1, L2, L4, L5, T10, T11, T12, B13 superimposed on young fish distributions, c) mature adults (t/km²) with total catch proportional to circle size of fisheries L1-9 and B13 on adult fish distributions.

FIGURE 4:

Mean distributions of north Atlantic albacore larvae (Nb. km⁻²), young immature and adult mature fish densities (metric t km⁻²) by decade.

FIGURE 5:

Kobe plot with fishing mortality in function of spawning biomass (relative to a MSY of 106% of 2004-2008 average catch). The Kobe plot is divided into 4 panels: red corresponds to the “overfished and overfishing phase” with spawning biomass inferior to MSY spawning biomass (SB MSY) and fishing mortality superior to MSY fishing mortality (FMSY). The green panel is the "no risk" area where fishing mortality is below FMSY and the spawning biomass is above SBMSY. The two yellow panels (overfishing and overfished) characterize intermediate situations. In black circles, the annual trajectory of the albacore fishery in the North Atlantic is represented along time.
Figure 3

(a) Larvae

(b) Young Immatures fish

(c) Adult Mature fish
Table 1: Revised definition of fisheries (E= effort; C= catch). Various fishing gears were used since the beginning of the albacore fishery: longline (LL), troll (T), mid-water trawl (MWTD) and bait-fishing (BB). For the Taiwanese fisheries, the abbreviations "subTro" and "Tro" stand for subtropical and tropical fishing areas.

<table>
<thead>
<tr>
<th>Fishery code</th>
<th>Country</th>
<th>Gear</th>
<th>Time Period</th>
<th>Catch unit / Effort unit</th>
<th>Nb of EC data</th>
<th>Resolution (degree)</th>
</tr>
</thead>
<tbody>
<tr>
<td>L1</td>
<td>Japan</td>
<td>LL</td>
<td>1956-1972</td>
<td>Nb / nb. hooks</td>
<td>5481</td>
<td>5</td>
</tr>
<tr>
<td>L2</td>
<td>Japan</td>
<td>LL</td>
<td>1973-2010</td>
<td>Nb / nb. hooks</td>
<td>15734</td>
<td>5</td>
</tr>
<tr>
<td>L3</td>
<td>USA</td>
<td>LL</td>
<td>1987-2010</td>
<td>Nb / nb. hooks</td>
<td>69200</td>
<td>1</td>
</tr>
<tr>
<td>L4</td>
<td>Taiwan-subTro</td>
<td>LL</td>
<td>1967-1986</td>
<td>Nb / nb. hooks</td>
<td>2527</td>
<td>5</td>
</tr>
<tr>
<td>L5</td>
<td>Taiwan-Tro</td>
<td>LL</td>
<td>1967-1986</td>
<td>Nb / nb. hooks</td>
<td>935</td>
<td>5</td>
</tr>
<tr>
<td>L6</td>
<td>Taiwan-SubTro</td>
<td>LL</td>
<td>1987-2007</td>
<td>mt / nb. hooks</td>
<td>343</td>
<td>5</td>
</tr>
<tr>
<td>L7</td>
<td>Taiwan-Tro</td>
<td>LL</td>
<td>1987-2007</td>
<td>mt / nb. hooks</td>
<td>514</td>
<td>5</td>
</tr>
<tr>
<td>L8</td>
<td>Korea</td>
<td>LL</td>
<td>1966-1979</td>
<td>mt / nb. hooks</td>
<td>1928</td>
<td>1</td>
</tr>
<tr>
<td>L9</td>
<td>Korea</td>
<td>LL</td>
<td>1980-2010</td>
<td>mt / nb. hooks</td>
<td>4495</td>
<td>5</td>
</tr>
<tr>
<td>T10</td>
<td>France</td>
<td>T</td>
<td>1967-2009</td>
<td>Nb / nb. sets</td>
<td>6289</td>
<td>1</td>
</tr>
<tr>
<td>T11</td>
<td>France</td>
<td>MWTD</td>
<td>1989-2007</td>
<td>mt / Nb.Sets</td>
<td>605</td>
<td>1</td>
</tr>
<tr>
<td>B12</td>
<td>Spain</td>
<td>T</td>
<td>1987-1995</td>
<td>Nb/Nb.Set</td>
<td>2856</td>
<td>1</td>
</tr>
<tr>
<td>B13</td>
<td>Spain</td>
<td>BB</td>
<td>1987-2005</td>
<td>Nb/Nb.Set</td>
<td>1644</td>
<td>1</td>
</tr>
</tbody>
</table>
Table 2:
Estimates of catchability by fishery and annual increase (%) since 1971.

<table>
<thead>
<tr>
<th>Fishery</th>
<th>q</th>
<th>slope</th>
<th>Annual % change since 1998</th>
</tr>
</thead>
<tbody>
<tr>
<td>L1 Japan LL bef. 1972</td>
<td>5.00E-5</td>
<td>-0.003</td>
<td>-3.6%</td>
</tr>
<tr>
<td>L2 Japan LL aft. 1971</td>
<td>5.77E-5</td>
<td>-0.002</td>
<td>-2.4%</td>
</tr>
<tr>
<td>L3 USA LL</td>
<td>5.00E-5</td>
<td>0.000</td>
<td>0.0%</td>
</tr>
<tr>
<td>L4 Taiwan subtrop. LL bef. 1987</td>
<td>12.65E-5</td>
<td>0.000</td>
<td>0.0%</td>
</tr>
<tr>
<td>L5 Taiwan trop. LL bef. 1987</td>
<td>99.30E-5</td>
<td>0.0015</td>
<td>1.8%</td>
</tr>
<tr>
<td>L6 Taiwan subtrop. LL aft. 1986</td>
<td>7.97E-5</td>
<td>0.0015</td>
<td>1.8%</td>
</tr>
<tr>
<td>L7 Taiwan trop. LL aft. 1986</td>
<td>36.75E-5</td>
<td>-0.001</td>
<td>-1.2%</td>
</tr>
<tr>
<td>L8 Korea LL FB bef. 1980</td>
<td>0.01</td>
<td>0.001</td>
<td>1.2%</td>
</tr>
<tr>
<td>L9 Korea LL FB aft. 1979</td>
<td>0.2095</td>
<td>-0.0005</td>
<td>-0.6%</td>
</tr>
<tr>
<td>T10 French troll</td>
<td>34.58E-5</td>
<td>0.000</td>
<td>0.0%</td>
</tr>
<tr>
<td>T11 French MWDT</td>
<td>0.02869</td>
<td>0.000</td>
<td>0.0%</td>
</tr>
<tr>
<td>T12 Spain Troll</td>
<td>14.61E-5</td>
<td>0.000</td>
<td>0.0%</td>
</tr>
<tr>
<td>B13 Spain BB</td>
<td>40.99E-5</td>
<td>0.000</td>
<td>0.0%</td>
</tr>
</tbody>
</table>
FIGURE APPENDIX

FIGURE A1:
Three indices are presented in a Taylor Diagram to evaluate the goodness of fit to catch data by fishery. In SEAPODYM, all error distributions are assumed to be normal. The standard deviation is presented on the x- and y-axes. Fisheries close to 1 (as the blue dot representing fishery L2) have model predictions with the same variability/dispersion as observations. The Pearson correlation coefficient is presented on a radial grid from 0 to 1. Fisheries close to 1 (as the purple dot representing fishery B13) have good covariation between data and model outputs. Finally, the normalized Error is presented on concentric circles which centre is on the value 1 of the x-axis (green point). Fisheries close to the centre have small differences between values predicted by the model and the values actually observed, i.e. they have high goodness-of-fit.

FIGURE A2:
Map of R-squared goodness of fit metrics representing the spatial fit between observed and predicted catch over the period used for optimization (white squares indicate negative correlation between observations and predictions), overlaid with the total catch in each cell (black circles proportional to catch).

FIGURE A3:
Predicted catch (in % of average catch from 2004 to 2008) in function of fishing effort (in % of the average fishing effort from 2004 to 2008).

a) with 20-year long simulation starting from 1960 (dark grey line) to 1989 (light grey line),
b) with 30-year long simulations starting from 1960 to 1979,
c) with 40-year long simulations starting from 1960 to 1969 and
d) with one 49-year long simulation starting in 1960.
For panels a, b and c, red full line indicate the simulation mean and dashed lines indicate the mean +/- standard deviation.
Appendix Figure A2
pred C L5 vs. obs C L5
$r=0.66$

pred CPUE L5 vs. obs CPUE L5
$r=0.76$

pred C L6 vs. obs C L6
$r=0.87$

pred CPUE L6 vs. obs CPUE L6
$r=0.72$
pred C T11 alb vs. obs C T11
$r = 0.81$

pred CPUE T11 alb vs. obs CPUE T11
$r = 0.59$

pred C T12 alb vs. obs C T12
$r = 0.72$

pred CPUE T12 alb vs. obs CPUE T12
$r = 0.59$
Supplementary Material Figure S4

a) Larvae

Maps showing the distribution of larvae in different seasons:
- **JFM**: April/May/June
- **AMJ**: July/August/September
- **JAS**: October/November/December
- **OND**: January/February/March

The maps display the concentration of larvae across different geographical regions, with a color scale ranging from 0 to 3 indicating the intensity of larval presence.
b) Young Immatures fish
c) Adult Mature fish