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Spatially explicit estimates of stock size, structure and biomass of North Atlantic albacore Tuna (*Thunnus alalunga*)

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Abstract

The development of the ecosystem approach and models for the management of ocean marine resources requires easy access to standard validated datasets of historical catch data for the main exploited species. They are used to measure the impact of biomass removal by fisheries and to evaluate the models skills, while the use of standard dataset facilitates models inter-comparison. Unlike standard stock assessment models, new state-of-the-art ecosystem models require geo-referenced fishing data with highest possible spatial resolution. This study presents an application to the north Atlantic albacore tuna stock with a careful definition and validation of a spatially explicit fishing dataset prepared from publically available sources (ICCAT) for its use in a spatial ecosystem and population dynamics model (SEAPODYM) to provide the first spatially explicit estimate of albacore density in the North Atlantic by life stage.

Density distributions are provided (http://doi.pangaea.de/10.1594/PANGAEA.831499) together with the fishing data used for these estimates http://doi.pangaea.de/10.1594/PANGAEA.830797, http://doi.pangaea.de/10.151594/PANGAEA.828168, http://doi.pangaea.de/10.1594/PANGAEA.828170, and http://doi.pangaea.de/10.1594/PANGAEA.828171 (see section Source Data References).

1 Introduction

Industrial fishing of albacore tuna (*Thunnus alalunga*) in the North Atlantic started after the Second World War. Since albacore is a highly-migratory species inhabiting both international waters and various Exclusive Economical Zones (EEZs), its management is conducted through international organizations, like the International Commission for the conservation of Atlantic Tunas (ICCAT: http://www.iccat.org) for the Atlantic Ocean. Stock assessment studies conducted by these management bodies have tried to reconstruct the past history of the stock, based on biological knowledge and the use of

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fishing data (catch, effort and size frequency of catch) to account for fishing mortality and to fit statistically the stock assessment models.

These standard stock assessment studies focused on temporal dynamics of the stock and the computation of fishing mortality. There is a lack of comprehensive understanding of the spatial structure and biomass dynamics of this species, as proposed in the objective of a large pluri-disciplinary research project like EURO-BASIN (http://www.euro-basin.eu) for the study on "climate and human forcing, ecosystem impact and consequences for living resources management in the North Atlantic." The model SEAPODYM (Spatial Ecosystem And Populations Dynamics Model) was used to fill this gap (Dragon et al., 2014).

SEAPODYM describes the spatial dynamics of both micronekton functional groups (Lehodey et al., 2010a) and detailed age structured population of their predators like tunas (Lehodey et al., 2008) with a system of advection–diffusion-reaction equations and environmental forcing (temperature, currents, primary production and dissolved oxygen concentration). SEAPODYM also predicts catch and size frequency of catch by fleet when fishing data (catch and effort) are available, and these data are fitted with a Maximum Likelihood Estimation procedure to achieve optimal parameterization of the model (Senina et al., 2008). In contrast with standard stock assessment models, these fishing data are spatially disaggregated, the highest possible resolution being the one used for the model grid. Different life stages are considered in the age-structured populations: larvae, juveniles and immature and mature adults. After the juvenile phase, fish become autonomous, i.e., they have their own movement (linked to their size and habitat) in addition to be transported by oceanic currents. Fish are considered immature until pre-defined age at first maturity and mature after this age, i.e., contributing to the spawning biomass, and with their displacements controlled by a seasonal switch between feeding and spawning habitat.

Here we present the results of this approach to estimate the stock size and population structure of albacore tuna and provide distributions of albacore density in the North Atlantic by life stage, together with the fishing data used for the estimate.

2 Data

The application of SEAPODYM to north Atlantic albacore was performed with oceanic variables (temperature currents, primary production, euphotic depth and dissolved oxygen concentration) provided at a resolution of $2^\circ \times$ month from the ocean circulation model NEMO (http://www.nemo-ocean.eu/) coupled to the biogeochemical model PISCES (Pelagic Interaction Scheme for Carbon and Ecosystem Studies; Aumont and Bopp, 2006) and forced by the atmospheric reanalysis NCEP-NCAR for the period 1960–2008 (https://climatedataguide.ucar.edu/climate-data/ncep-ncar-r1-overview). These models have been extensively validated elsewhere and demonstrated good skills to realistically simulate seasonal to interannual and decadal physical and biogeochemical ocean variability (Lengaigne et al., 2003; Gorgues et al., 2005; Bopp et al., 2005; Aumont and Bopp, 2006). However, this configuration did not resolve mesoscale features as well as coastal upwelling regions.

The fishing data (catch, fishing effort and size frequencies of catch) of Atlantic tunas by gear, region and flag declared to ICCAT is available on the web site of this fisheries management organization (http://www.iccat.es/en/accesingdb.htm). These raw data were checked and processed to prepare a fishing dataset by fishery for SEAPODYM albacore application. This dataset (ASCII) is provided together with estimated gridded albacore tuna density by life stage (NetCDF) on PANGAEA (see section Source Data References).

2.1 Catch and effort

North Atlantic tuna is exploited all year round by longline fisheries, mainly from Japan, Chinese Taipei, and Korea, targeting subadult and adult albacore, and surface fisheries (Spain, France, Ireland and Portugal) targeting mainly immature and sub-adult fish in the Bay of Biscay and adjacent waters of the northeast Atlantic (Celtic Sea) in summer and autumn. All together these fisheries represented 98 % of the total catch declared to ICCAT between 1960 and 2008 (Fig. 1). Caribbean Countries (Venezuela, Panama,

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Cuba, Trinidad and Tobago, Belize, Dominican Republica, Grenada, Barbados, Santa Lucia and UK Bermuda), contributed to the remaining catch (1.9 %), mostly by longlining. Longline fishing effort decreased in the 1970s and 1980s due to a shift towards targeting on tropical tuna for the sashimi market, as illustrated by the decline of the albacore/bigeye price ratio from ∼ 1/1 in the 1960s to ∼ 1/3 in the 2000s (Fonteneau, 2008). Total reported landings for the North Atlantic generally began to decline after the 1960ies, due to a reduction of fishing effort by the traditional surface (troll and baitboat) fisheries, and since 1986 in the case of longline (ICCAT, 2010). New surface fisheries (driftnet and mid-water pair pelagic trawl) developed in the 1990s.

ICCAT also maintains a database with monthly tuna catch and effort provided with geographical coordinates at monthly spatial resolution of 1° or 5° squares. These data were extracted to be used for the optimization of the model SEAPODYM. Given the broad spatial resolution available for Spanish fleets, additional files at higher resolution were provided by AZTI Tecnalia. Spatialized catch effort data exist in the ICCAT database for the most important fisheries, but there is a lack of information in the early years, and for less important fisheries (ICCAT, 2013). The spatialized catch effort data available in the database can represent a fraction or the entire total catch for a given fleet. Over the period 1960–2007, spatially-disaggregated data represented in average ∼ 25 % of the total catch with low percentage in the 1960s (2.8–24.8 %) but higher values in the following decades, in the range of 10.8–46.9 % (Table 1; Fig. 1). While the dataset was sufficient to optimize the habitats and movements and population dynamics parameters (Dragon et al., 2014), the fishing mortality in the simulation was consequently underestimated, though there are potential compensatory mechanisms at play in the optimization that can account partly for the total fishing effect as expressed in the data even if all the catch is not included (see discussion).

A careful data screening led to the exclusion of a few obvious wrong data (e.g., with geographical coordinates on land). Fishery records for the Spanish-Canary had only few (110) records with both catch and effort together and thus was not included. Fisheries were defined first based on the fishing gear and the fishing Country. Fishing effort

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on albacore decreased drastically in the early 1970s in the longline Asian fleets due to the introduction of monofilament longline fishing gear allowing change in the target species, with bigeye tuna becoming increasingly fished in relation with the development of the sashimi market. Based on catch series the change seems to have occurred earlier in the Japanese (after 1972) than in the Korean (after 1979) and Taiwanese (after 1986) longline fishery. For this latter, the change also was associated to a spatial shift of fishing grounds. Therefore, a strong pattern existed in the distribution of catch (Fig. 2) showing well developed longline fisheries in the whole north Atlantic basin in the first part of the historical fishing period (before 1986) but declining in the more recent period (after 1986). The fishing ground of the surface fisheries in the North-east Atlantic showed a tendency to retract and concentrate in the Gulf of Biscay. To keep the most possible homogeneous definition of fisheries in relation to their fishing gear catchability the Asian longline fisheries have been subdivided into two periods (Table 2). In total and excluding the Canary Islands fishery, thirteen fisheries were defined for the period 1956–2010 (Table 2), with fishing gears longline, troll, mid-water trawl and bait fishing. The temporal resolution was monthly and the spatial resolution either 1 or 5° square.

As indicated above, the level of coverage for spatially-disaggregated fishing data was much lower than the total catch, though it was highly variable from one fishery to another. The Fig. 3 compares these two datasets for the 6 main fisheries (> 98 % of total catch declared to ICCAT). Japanese and Taiwanese longline fleets appear complete while other longline fleets (Korea; USA) were partially covered (Fig. 3). Indeed, it is very likely that complete coverage of spatially geo-referenced catch and effort were due to extrapolation from geo-referenced catch and effort samples while for the other fleets this extrapolation was not produced. Though the size of actual samples would be useful information it may be difficult to recover it for all the historical fishing period. For surface gears, the coverage from spatialized catch and effort is 7.3 % of total catch available for the Spanish fleets and 23 % for the French ones. Part of these gaps, especially for the Spanish fleets, came from the lack of resolution in the model that might not include coastal data. The catch in Canary Islands in one single cell was also not

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included due to the lack of effort data. Finally the southern boundary of the North stock for ICCAT was 5° N while it was the equator for the SEAPODYM domain. This explains the higher catch level of Chinese Taipei longline fishery used in SEAPODYM after 1987 compared to ICCAT total catch series.

2.2 Size frequency of catch

Length frequencies of catch for North Atlantic Albacore 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 varying from $1^\circ \times 1^\circ$ to $10^\circ \times 20^\circ$ (Fig. 4). The resolution used to measure the fish also varied with size-bins of 1, 2 or 5 cm (Fork Length). The screening of data allowed detecting inconsistencies with a relatively large number of samples larger than 150 cm while all studies on the growth of albacore suggest that fish rarely grow up over 130 cm. Given that SEAPODYM uses a single average size-at-age value by cohort and does not yet allow including growth variability around this value, a threshold value of 130 cm has been arbitrarily fixed and all length frequency data above this value removed from the original data set. In addition, since the presence of fish larger than 130 cm in a given sample may indicate a problem of species identification by the observer, a precautionary approach was followed with a data filter to remove the whole sample (i.e., all size data collected from the same boat, date and area). The number of remaining samples was well distributed over the entire fishing ground and increased in the second half of the fishing period (Fig. 4).

3 North Atlantic Albacore population dynamics

3.1 Life cycle and population age-structure

As other tuna species, albacore are multiple or batch spawners releasing millions eggs of small size (~ 1 mm). A few days after spawning, hatching larvae start to feed on

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microzooplankton and the growth is fast in warm waters (above 24 °C). A review of scientific literature on albacore growth studies indicated very close weight-at-size relationships whatever the oceanic region (Fig. 5a). The size–weight relationship selected is the allometric relationship $W = aL^b$ with W the weight (kg), L the fork length (cm) and a and b the two coefficients (respectively 6.959×10^{-06} and 3.2351) estimated by Hoyle and Davies (2009).

There are more discrepancies between size-at-age estimates. In addition, due to the lack of samples in the range 0–40 cm, none of the growth studies can correctly represent the growth of albacore during the early life stage, i.e., roughly the 1st year of life. The integrated growth study from Santiago and Arrizabalaga (2005) was first used to parameterize the age structure, but produced inconsistencies between the value of $L_\infty = 122$ cm FL and the length frequency samples. Despite the threshold value set to 130 cm (cf. above), there were still a very large proportion of fish larger than L_∞. An intermediate solution was selected with L_∞ set to 137 cm FL while a linear growth was assumed during the first year of life (Fig. 5b).

There is still some uncertainty on sexual maturity, with the first maturity estimated to occur at size between 75 and 85 cm FL (Lam Hoai, 1970; Hayashi et al., 1972) with 50 % of fish mature at 90 cm at age 5 years (Bard, 1981). The first age at maturity was set to 4.5 years (84 cm). Thus the structure of the population was defined with 157 cohorts, a 1 month cohort for the larval life stage, two monthly cohorts for the juvenile stage, 51 monthly cohorts for young immatures (3 months to 4.5 years), 102 monthly cohorts for adults and a last "+ cohort" accumulating older fish after age 13 years).

3.2 Estimates of abundance distributions

The model simulates the distributions of cohorts in number of individuals, but outputs are aggregated by life stage (Fig. 6). Larvae and juvenile densities are in number of individuals while for young and adult stages they are converted to g m^{-2} using age-size and size–weight relationships (Fig. 5). The North Atlantic albacore population was predicted to extend between the equator and 60° N in agreement with catch data dis-

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tribution. The main spawning ground was predicted within the subtropical and tropical warm waters. Though there is continuous spawning activity all year round in the tropical waters, there was a peak of activity in the second quarter in the Sargasso Sea, coinciding with the seasonal displacement of a large portion of the adult mature fish contracting from its maximal northern extension at the end of summer-autumn towards subtropical region in winter (Fig. 6). Young immature fish distributed along a southwest-northeast axis north from the main spawning ground and reaching the Gulf of Biscay and adjacent waters where they were exploited by surface fisheries. These features agree well with the knowledge on this species as described in the literature (Le Gall, 1974; Nishikawa et al., 1985; Arrizabalaga et al., 2004; Goni and Arrizabalaga, 2005; ICCAT, 2010).

The total biomass was estimated to have fluctuated between 900 and 600 thousand metric tonnes over the historical fishing period 1960–2008 (Fig. 7). After a decreasing trend from the early industrial fishing period until the late 1970s the biomass was estimated to stabilize then increase from the 1990s due to the release of fishing pressure by the longline fisheries and more favorable recruitment conditions.

4 Validation

The catch, CPUE and size frequencies of catch are predicted by the model using the observed fishing effort, a catchability coefficient and a selectivity function estimated during the optimization process using a maximum likelihood estimation (MLE) approach (Senina et al., 2008). The cost functions for the maximum likelihood estimation approach minimize the difference between predicted and observed CPUE and size frequencies from each fishery. Details of the optimization experiment in its evaluation are provided in Dragon et al. (2014). Other recent applications of this approach to tuna species can be found in Senina et al. (2008), Lehodey et al. (2010b, 2013) and Sibert et al. (2012).

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Longline fisheries covered the entire tropical region and extend north-west to the temperate region, while French midwater trawl and French and Spanish troll fisheries extended offshore from the Gulf of Biscay to 30° W. The predicted catch fitted very well observed catch over the historical fishing period used for the simulation both spatially and temporally (Fig. 8). The fit was degraded only on the borders of the catch distribution, in relation with low level of catch and also likely the closed equatorial boundary. The best fit (correlation between monthly time series of prediction and observation $r = 0.95$ for catch and $r = 0.93$ for CPUE) was obtained for the subtropical Taiwanese longline fishery (L4) that presented a high selectivity leading to the capture of large fish only. The worst fits were for fisheries L3 ($r = 0.53$ and 0.66) and B13 ($r = 0.72$ and 0.43). However, despite relatively low correlation values of CPUE for Spanish bait boats (B13) and troll fisheries (T12: $r = 0.52$), the seasonality was very well predicted. The low correlation values were due to too small range of predicted variability compared to observation. More detailed analysis on the fit to data is provided in Dragon et al. (2014).

5 Discussion

The development of ecosystem approach and models for the management of ocean marine resources requires multi-disciplinary collaborations and an easy access by researchers to standard validated datasets of historical catch data for the main exploited species. These data are essential both to include the impact of biomass removal by fisheries in the ecosystem models and to serve as the primary source for their evaluation. However, researchers involved in these developments have not necessarily the background in fisheries sciences and the detailed knowledge on the history of the fisheries that is required to understand and use these data correctly. Here, we provide an example of a careful definition and validation of a fishing dataset for the north Atlantic albacore for its use in a spatial ecosystem and population dynamics model.

While ecosystem models should take advantage of the progress in the 3-D simulations of the physics and chemistry of the ocean (e.g., http://www.myocean.eu/), the

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standard stock assessment studies often rely on temporal trends of fishing indicators over one or a few large geographical boxes, leading in some cases to a lack of data collection and sampling effort to build complete spatially explicit fishing datasets. In this study, the best spatially explicit distribution of catch, effort and size frequency of catch data was prepared from publically available sources for north Atlantic albacore. However, despite that ICCAT developed a substantial effort to collect data of all tuna fisheries in the Atlantic Ocean, this geo-referenced dataset covers only partially the total catch for this tuna stock. Though the level of coverage increased in the more recent decades it always remained below 50 % of the total declared catch. Now that ecosystem and spatially explicit models of population dynamics are developed, a priority should be given in the coming years to the rescue of existing datasets to increase this level of coverage as far as possible. Thereafter, a second geo-referenced dataset should be built with all the necessary expertise and precautions to raise the spatialized catch data to the level of total catch. These products would therefore become useful standard datasets for the research community allowing comparative studies and providing the best possible account of total fishing mortality over the entire historical fishing period. For the present and future years, the increase to 100 % coverage of fisheries with geo-referenced data is essential and should be easily achieved with the development of Vessel Monitoring Systems and Electronic Catch Reporting.

On the modeling side, the spatial resolution needs to be increased to include the coastal domain where substantial amount of albacore tuna are caught. This is particularly true for the Bay of Biscay where a large surface fishery by French and Spanish fleets occur. The grid (ORCA2) used in this study gave a very crude representation of this area and consequently excluded a lot of fishing data occurring in the shelf coast outside of the model domain. In addition, the coarse resolution used was inaccurate to simulate the oceanography in this particular area. Nevertheless, at basin-scale, the first application of the model SEAPODYM to the north albacore tuna stock with this spatialized fishing data set provided realistic population dynamics under the influence of both environmental variability and fishing pressure, based on a robust statistical approach

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and a validation of model outputs (see also Dragon et al., 2014). As noted above the fishing mortality was likely underestimated in the simulation though it was not possible to estimate how the lack of direct fishing mortality was expressed through the optimization process due to non-linear mechanisms and compensatory mechanisms. Size frequency of catch, catch and CPUE observed at a given time and place is the result of past complex dynamics including all biomass removal by the fisheries. Therefore, even if these observations are partial they provide hidden information on the state of the stock in the optimization approach that can modify the estimates of various parameters, especially regarding natural mortality and recruitment, as well as in the selectivity functions of fishing gears.

This first spatially explicit estimate of the stock size, structure and biomass of North Atlantic albacore was provided together with fishing data to assist in the development of basin scale ecosystem assessments. Regular updates should be provided when better environmental forcings and more complete geo-referenced fishing datasets become available. In particular, a careful method of extrapolation from georeferenced catch, effort and size frequency of catch by fishery needs to be developed to produce a spatially-explicit dataset of total fishing effort and catch. Similar efforts should be conducted for other major exploited species of the North Atlantic basin (both large and small pelagic species).

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Table 1. Total annual catch 1960–2008 (metric tonnes) used in SEAPODYM north Atlantic albacore simulation compared with total annual catch by all fisheries declared in ICCAT database. Difference in metric tonnes and corresponding percentage of coverage.

Year	Catch in SEAPODYM	Total ICCAT	Difference	%	Year	Catch in SEAPODYM	Total ICCAT	Difference	%
1960	1588	52 869	51 281	3.00	1985	15 190	40 826	25 636	37.21
1961	1203	42 730	41 527	2.82	1986	20 553	47 554	27 001	43.22
1962	5950	58 787	52 836	10.12	1987	9429	38 115	28 686	24.74
1963	10 463	60 340	49 877	17.34	1988	5489	33 059	27 570	16.60
1964	16 024	64 634	48 610	24.79	1989	3475	32 071	28 595	10.84
1965	10 626	60 658	50 032	17.52	1990	5652	36 881	31 229	15.33
1966	5930	47 363	41 433	12.52	1991	7964	27 931	19 968	28.51
1967	10 105	59 142	49 037	17.09	1992	6638	30 851	24 213	21.52
1968	10 475	45 220	34 746	23.16	1993	8928	38 135	29 207	23.41
1969	6916	46 730	39 814	14.80	1994	10 172	35 163	24 992	28.93
1970	11 945	45 895	33 950	26.03	1995	7550	38 377	30 828	19.67
1971	12 090	56 821	44 731	21.28	1996	5646	28 803	23 156	19.60
1972	8803	48 781	39 978	18.05	1997	5158	29 023	23 865	17.77
1973	12 678	45 700	33 022	27.74	1998	9789	25 746	15 957	38.02
1974	13 512	49 606	36 094	27.24	1999	10 686	34 551	23 865	30.93
1975	11 870	41 888	30 018	28.34	2000	7894	33 124	25 230	23.83
1976	23 211	57 235	34 024	40.55	2001	12 321	26 253	13 932	46.93
1977	20 027	54 031	34 004	37.07	2002	7820	22 741	14 922	34.39
1978	17 994	50 121	32 127	35.90	2003	9788	25 567	15 778	38.29
1979	15 362	51 372	36 010	29.90	2004	9494	25 960	16 466	36.57
1980	7777	38 691	30 914	20.10	2005	12 136	35 318	23 182	34.36
1981	9641	34 531	24 890	27.92	2006	7268	36 989	29 721	19.65
1982	14 124	42 673	28 549	33.10	2007	3365	21 991	18 626	15.30
1983	15 471	51 490	36 020	30.05	2008[a]	1302	20 483	19 181	6.36
1984	17 572	41 800	24 228	42.04					

[a] Incomplete data for this year.

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Table 2. Revised definition of fisheries for the North Atlantic albacore (E = effort; C = catch) to be used for SEAPODYM application. LL = longline; TROL = Trolling; MWTD = mid-water trawling; BB = bait-boat pole-and-line; Tro = tropical; subTro = subtropical; mt = metric tonnes.

Fishery code	Country	Gear	Time Period	Catch unit (Effort unit)$^{-1}$	Nb of CE data	Resolution (deg)
L1	Japan	LL	1956–1972	Nb (nb. hooks)$^{-1}$	5481	5
L2	Japan	LL	1973–2010	Nb (nb. hooks)$^{-1}$	15 734	5
L3	USA	LL	1987–2010	Nb (nb. hooks)$^{-1}$	69 200	1
L4	Taiwan-subTro	LL	1967–1986	Nb (nb. hooks)$^{-1}$	2527	5
L5	Taiwan-Tro	LL	1967–1986	Nb (nb. hooks)$^{-1}$	935	5
L6	Taiwan-SubTro	LL	1987–2007[a]	mt (nb. hooks)$^{-1}$	343	5
L7	Taiwan-Tro	LL	1987–2007[a]	mt (nb. hooks)$^{-1}$	514	5
L8	Korea	LL	1966–1979	kg (nb. hooks)$^{-1}$	1928	1
L9	Korea	LL	1980–2010	kg (nb. hooks)$^{-1}$	4495	5
T10	France	TROL	1967–2009	Nb (nb. Sets)$^{-1}$	6289	1
T11	France	MWTD	1989–2007[a]	kg (nb. Sets)$^{-1}$	605	1
B12	Spain	TROL	1987–2005[a]	Nb (nb. Sets)$^{-1}$	2856	1
B13	Spain	BB	1987–2005[a]	Nb (nb. Sets)$^{-1}$	1644	1
B14	Spain-Canary[b]	BB	1975–2010	kg (day at sea)$^{-1}$	110	1

[a] Catch and effort data from recent years not yet available from the ICCAT database.
[b] Not used.

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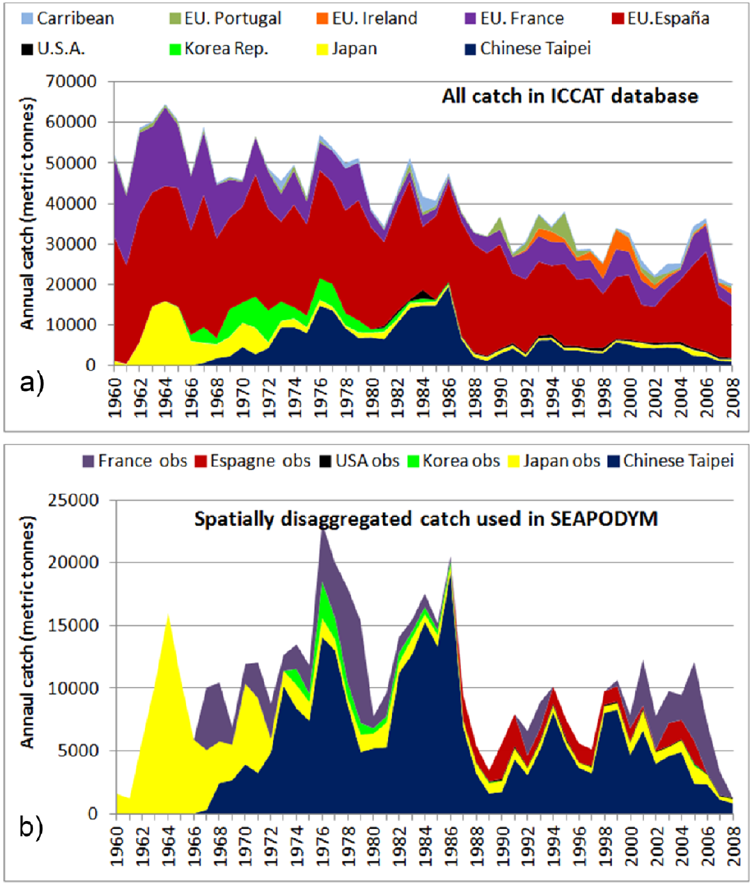

Fig. 1. Annual catch of North Atlantic albacore tuna by flag. **(a)** All aggregated catch declared to ICCAT; **(b)** available geo-referenced catch data used with SEAPODYM.

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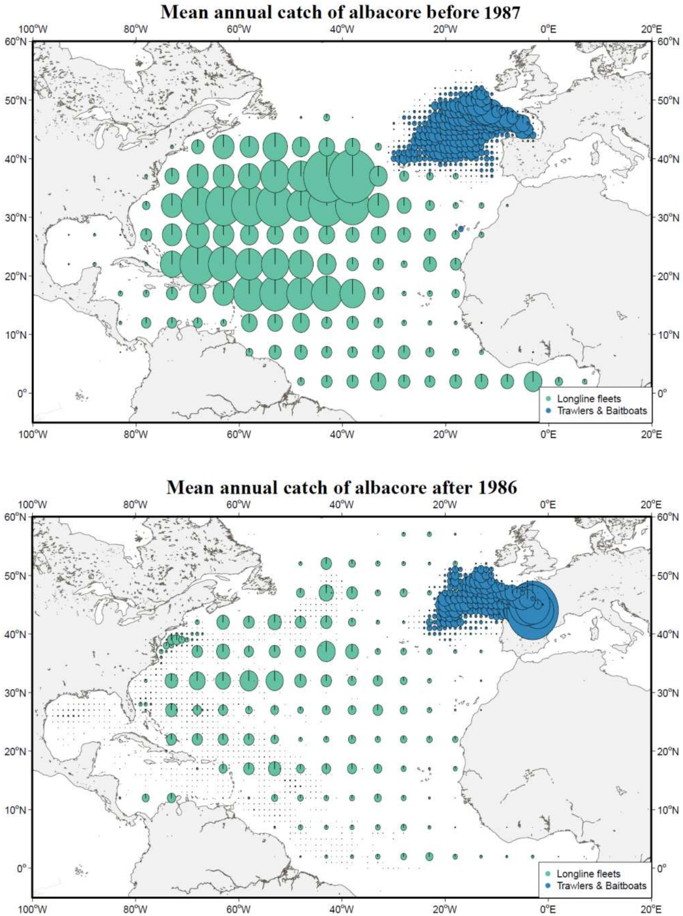

Fig. 2. Spatial distribution of mean annual catch of north Atlantic albacore by longline (green) and surface (blue) fishing gears before (1960–1986) and after (1987–2008) 1 January 1987. The circles are proportional to the catch with the same scale for both panels.

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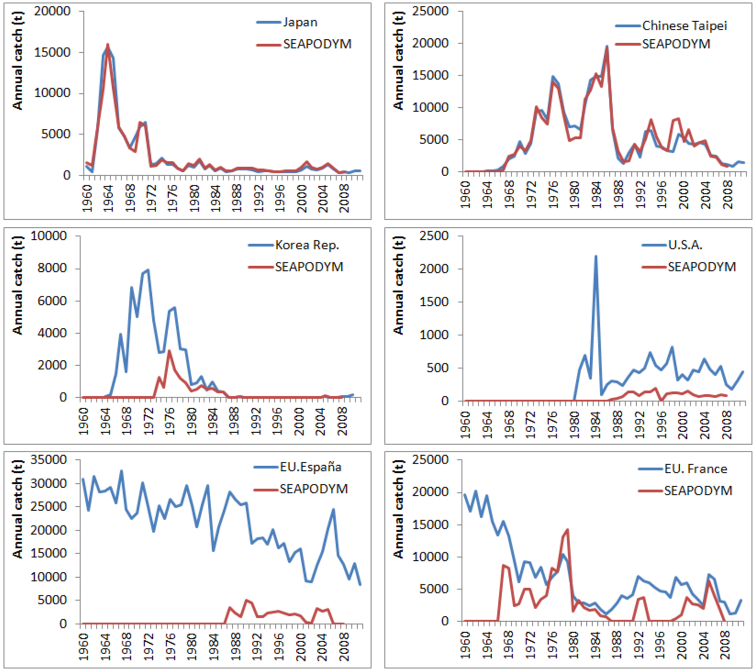

Fig. 3. Time series of annual catch data with geographical coordinates used in the simulation with SEAPODYM and total annual catch declared to ICCAT for the main north Atlantic albacore tuna fisheries over the historical fishing period. When data were declared in number of fish a conversion factor has been used, i.e.: 16 kg fish^{-1} for Japanese, Chinese-Taipei and US longline, 8 kg fish^{-1} for French and Spanish surface fisheries.

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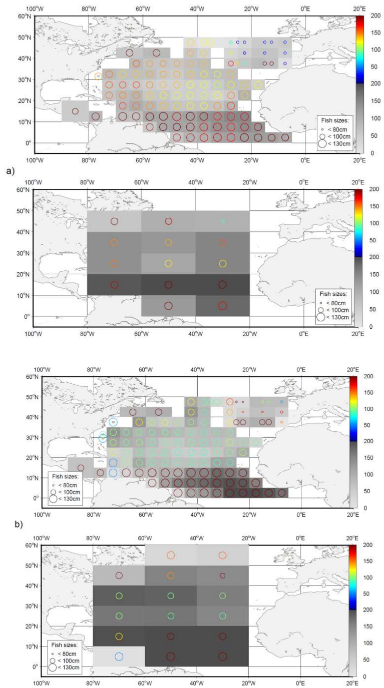

Fig. 4. Length frequency data before **(a)** and after **(b)** 1 January 1987. The data samples are aggregated at different spatial resolutions illustrated by rectangles with grey shading proportional to the number of samples (black and white colorbar from 0 to 200 samples). In the centre of each region, a circle gives the predicted mean size of fish (the larger the circle, the longer the fish) and the variance associated to this mean (colorbar). Data are presented for high (top) and medium (bottom) resolution. The low resolution data (three geographical boxes: 90° W–10° E; 30° N–6° N, 80° W–0°; 60° N–30° N and 60° W–20° E; 6° N–30° S) is not shown.

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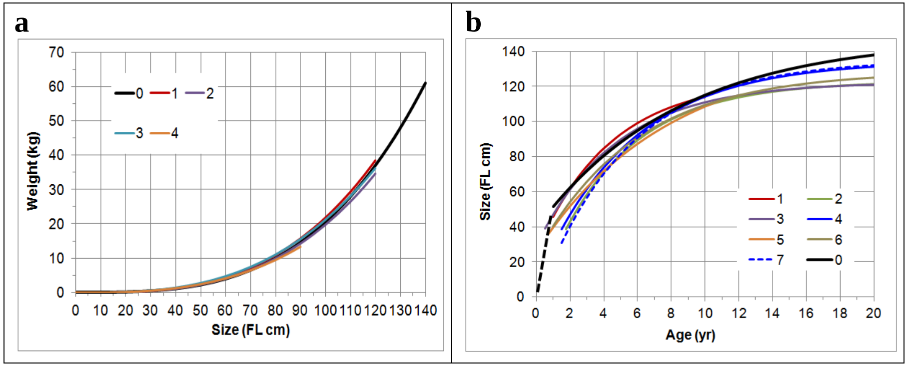

Fig. 5. Weight at length **(a)** and size at age **(b)** relationships used in SEAPODYM simulation (black curve) compared to other functions proposed in the literature. References for weight-at-size: 0: this study (Hoyle and Davies, 2009, for South Pacific albacore), 1: Santiago (1993) for North Atlantic albacore, 2: Penney (1994) for South Atlantic albacore, 3: Chen et al. (2010) for North Pacific albacore, 4: Megalofonou (1990) for Mediterranean albacore. References for size-at-age: 0: this study (adapted from MULTIFAN estimate in Santiago and Arrizabalaga, 2005), 1: Bard (1981), 2: ICCAT (1996), 3: Santiago and Arrizabalaga (2005), 4: Bard (1973), 5: Gonzales-Garces (1983), 6: Fernandez (1992), 7: Yang (1970).

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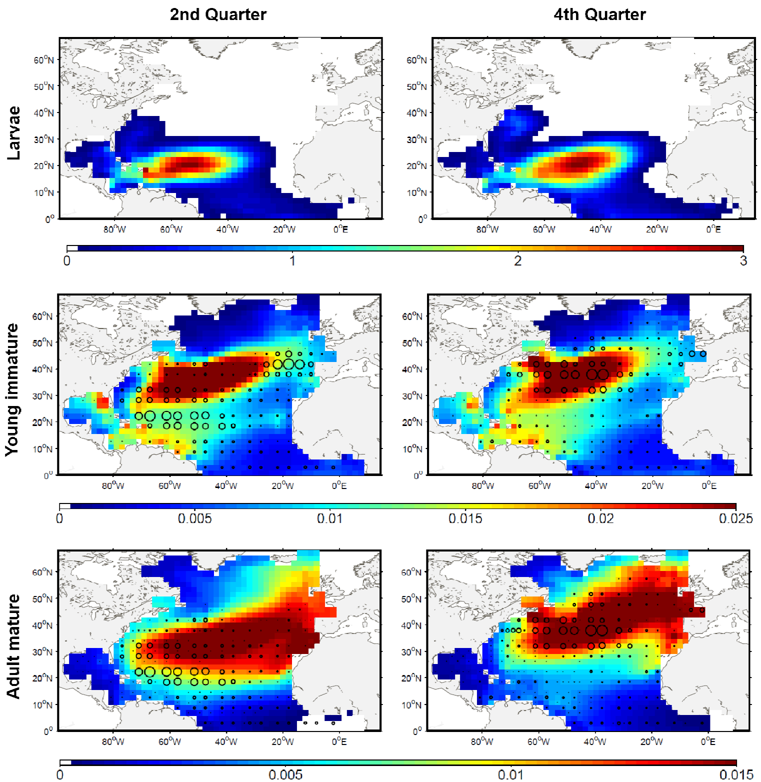

Fig. 6. Seasonal average (1991–2000) distributions of north Atlantic albacore in the 2nd (left) and 4th (right) quarter for recruited larvae (Nb. km^{-2}), young immature fish ($g\,m^{-2}$) and adult mature fish ($g\,m^{-2}$). Circles are proportional to observed catch. Fisheries selecting small size fish (< 85 cm, T10 to B13) are superimposed on young fish distributions and those selecting large size fish (> 85 cm, L1 to L9) on adult fish distributions.

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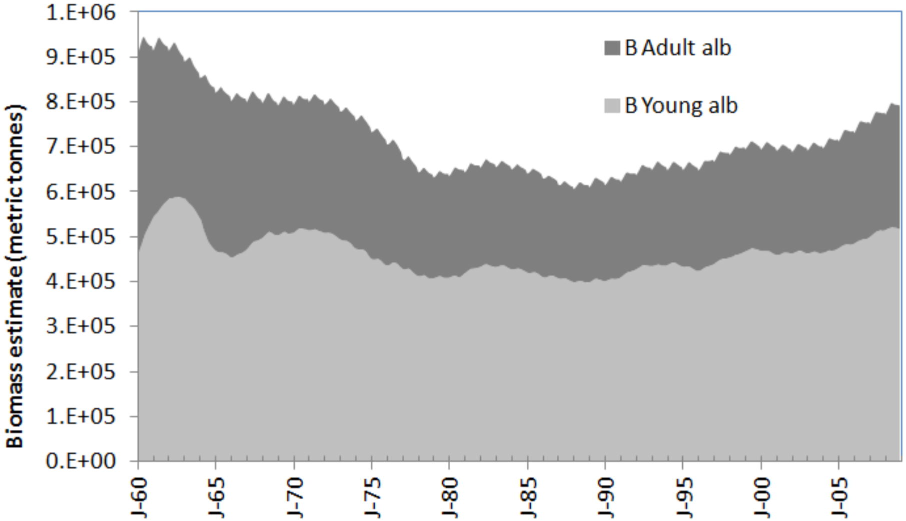

Fig. 7. Total biomass estimate for young immature (light grey) and adult mature (dark grey) of the north Atlantic albacore stock.

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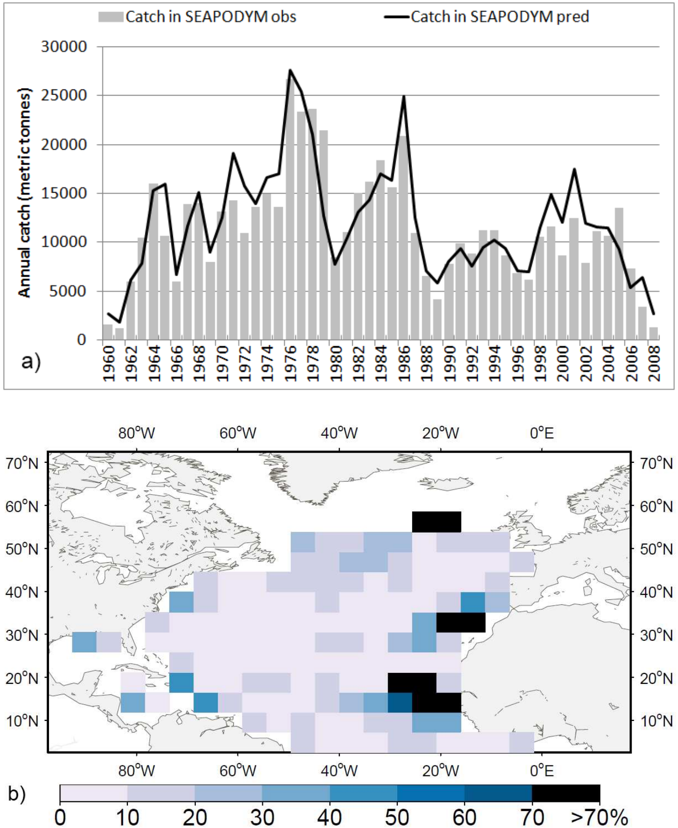

Fig. 8. Fit to catch data. **(a)** Total annual predicted and observed catch used in SEAPODYM simulation. **(b)** Relative error in predicted total catch aggregated in 5° × 5° over 1960–2008.

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