Received: 9 October 2015
IOTC-2015-WPTT17-31

Preferred habitat of tropical tuna species in the Eastern Atlantic and Western Indian Oceans: a comparative analysis between FAD-associated and free-swimming schools

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Abstract

An ecological niche modelling (ENM) approach was developed to describe the suitable habitat of skipjack (SKJ) and juvenile yellowfin (YFT) tuna in the Tropical Atlantic and West Indian Oceans. The environmental envelop of the potential habitat in each ocean was defined using occurrence data independently of the fishing mode and derived from purse seine fishing sets of the French fleet during 1997-2014. Daily satellite-derived chlorophyll-a content (CHL) and fronts (CHL gradient) were used as a proxy for food availability while circulation model derived-sea surface temperature, salinity, height anomaly, current and oxygen as well as the mixed layer depth contributed to identify the physical suitable conditions of each species. Only the cluster that showed no CHL front was excluded for the parameterization in order to enhance the favourable feeding habitat. In a second step, the distances of both the free swimming schools (FSC) and schools associated with drifting Fishing Aggregating Devices (FADs) to the closest potential habitat were computed and compared. The results highlighted (i) high spatial seasonality of both the simulated feeding habitat and tuna populations in the Indian Ocean compared to the tropical Atlantic, (ii) major differences between both oceans regarding the distance of FAD catches to the potential habitat with median values above 200 km in the Atlantic and below 16 km in the Indian Ocean, while equivalent distances for FSC were observed for both species and areas (below 2 km and 43 km respectively) in agreement with stomach content analysis, (iii) an increased rate of FAD fishing operations in the decade from 2003 to 2013 (up to about 70% in the Atlantic and 96% in the Indian Ocean) occurring mostly in poor environments in the tropical Atlantic while frequently in relatively productive waters in the Indian Ocean (except east of 58°N) as well as an overall 300% increase of juvenile YFT presence in both ocean sets and (iv) a recent intensification of fishing effort from March to May in the Mozambique Channel in agreement with an increase of favourable habitat, while no effort of that fleet occurred in the open waters off the Gabon upwelling (from 1°N to 5°S and East of 17°W) from May to September where favourable habitat was enhanced by the model. In all cases the seasonal maximum number of fishing sets corresponded to the minimum extent of potential habitat, which commonly varied by 30% from year to year. Overall, this comparative analysis emphasizes the strong attraction of tropical tuna species to floating objects although feeding opportunities may vary considerably depending on hydrographic regimes and on the dynamics of productive habitats.

Keywords: Habitat, tropical tunas, yellowfin tuna, skipjack tuna, FAD, free schools, feeding, Tropical Atlantic, Indian Ocean, ecological niche, environmental conditions.

Highlights:

- An extensive set of presence data of SKJ and juvenile YFT tunas with accurate location and fishing mode was compiled in the tropical Atlantic and Indian oceans from 1997 to 2014.
- Daily potential tuna feeding habitats at large spatial scale are proposed using satellite-derived surface chlorophyll-a and circulation model-derived physical data.
- Daily chlorophyll-a fronts were mainly used as a proxy of food availability for tunas.
- Sea surface values of temperature, currents, height anomaly, salinity, oxygen and the mixed layer depth defined the abiotic envelop.
- Results suggest that drifting FAD-associated fishing may drive part of tropical tunas away from productive habitats in the eastern tropical Atlantic while low if any influence was found in the western Indian Ocean due to major differences in hydrographic regimes and dynamics of productive habitat.

Introduction

Over the last decade, fishing on tropical tuna schools associated with drifting fish aggregating devices (FADs) has contributed to about 40% of the annual global tuna catch estimated at about 4 million t (Dagorn et al., 2013b; Fonteneau et al., 2013). In the recent years, FAD-fishing has represented more than 60% of the global purse seine catch, i.e. about 1.7 million t y^{-1}. The rising of purse seine fishing on associated schools is mainly explained by the steadily increasing deployment of artificial FADs in combination with the technological improvements and decreasing costs of satellite-tracked buoys that are now equipped with echo-sounders to estimate biomass of associated fish (Lopez et al., 2014). Overall, FADs have substantially increased the productivity of purse seine fisheries and resulted in a major decrease in the mean weight of yellowfin (*Thunnus albacares*; YFT) and bigeye tuna (*Thunnus obesus*; BET) in the catch, as schools associated with drifting floating objects are mainly comprised of skipjack and juveniles of YFT and BET (Fonteneau et al., 2013).

Recently, the increasing use of FADs has raised concerns within the tuna Regional Fisheries Management Organisations (RFMOs) as their massive use can result in (i) excessive mortality on BET stocks that have been subject to overfishing, (ii) decrease in the expected yield-per-recruit of YFT and BET that are fished too small, (iii) increase in the overall levels of bycatch and associated discards at-sea, including ghost-fishing (Amandè et al., 2012, 2010; Filmalter et al., 2013), (iv) impacting fragile coral-reef ecosystems through beaching (Balderson and Martin, 2015; Maufroy et al., 2015), and (v) potential negative effects on the biology and ecology of tunas and pelagic species associated with FADs (Hallier and Gaertner, 2008; Jaquemet et al., 2011; Marsac et al., 2000). While the reporting and availability of data on FAD-fishing has improved in the recent years, the management of the FAD purse seine fishery has been mainly driven through the implementation of time-area closures so as to decrease the catch of juvenile BET (Davies et al., 2012). In the Indian Ocean, the IOTC has recently adopted a precautionary approach by setting a cap of 550 active buoys at-sea by purse seiner in order to limit the unmonitored increase in overall purse seine fishing effort through increasing FAD use (Chassot et al., 2014; Fonteneau and Chassot, 2014; Maufroy et al., 2014).

While the reasons of association of tropical tunas with drifting floating objects remain unclear (Castro et al., 2002; Fréon and Dagorn, 2000), the main factors explaining such behaviour must confer them an evolutionary advantage which seems to include at least social aspects (Robert et al., 2014). In particular, the associative behaviour of tropical tunas has been hypothesised to result in increased feeding capabilities as drifting floating objects may be used as indicators of biologically-rich waters (Hall, 1992). The massive deployment of artificial FADs over large areas covering the whole purse seine fishing grounds did modified the historical location of drifting floating objects susceptible to associate tunas (e.g. Torres-Irineo et al., 2014). This might in turn modify the environmental conditions encountered by tunas that could be less favourable for feeding (Marsac et al., 2000). However, no study has addressed yet the changes in habitat that tropical tunas may have experienced in relation with the expansion of FAD-fishing grounds.

In this paper, we link the ecological traits of skipjack and juvenile yellowfin to environmental variables through an Ecological Niche Model approach (ENM) and investigate their requirements with regards to feeding. We use a large dataset of presence data to identify the appropriate environmental envelop used to model the habitat of skipjack and juveniles of yellowfin tunas in the Western Tropical Atlantic and Eastern Indian oceans. We then analyse for each area and for each species the distance to the closest potential habitat of free-swimming schools separately from the FAD fishing sets. The seasonal and decadal habitat variability and spatial extent are discussed with respect to their potential impact on the effect of FAD fishing.

Materials and methods

Description of the Ecological Niche Modelling

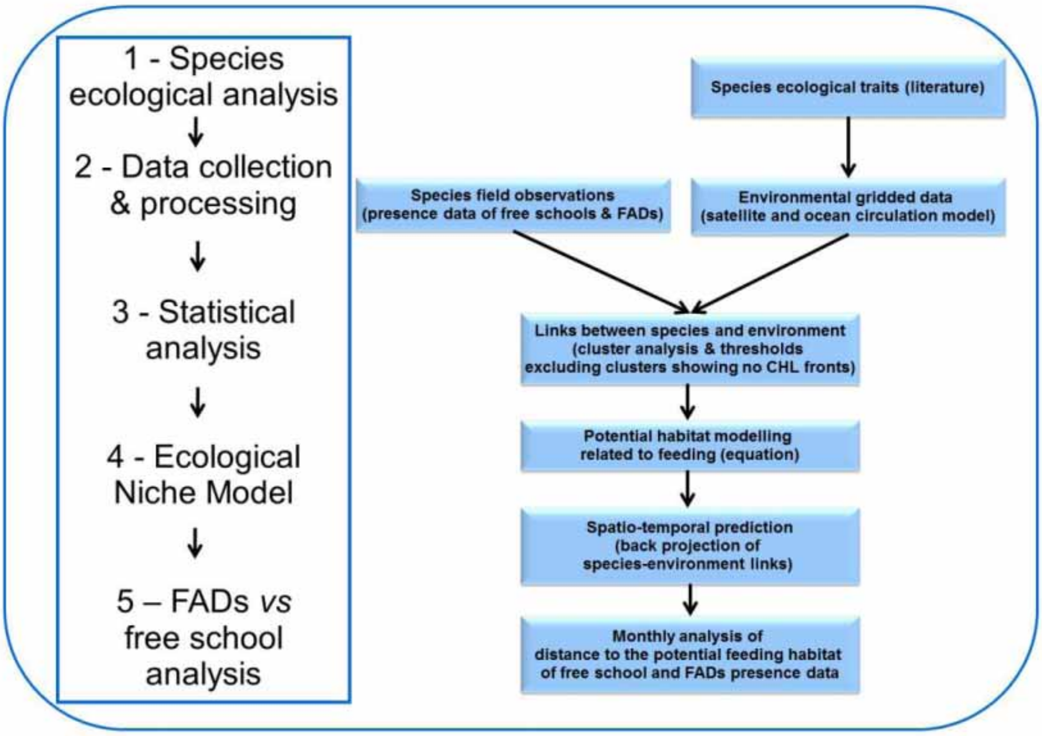


Figure 1 *Flowchart of the Ecological Niche Model (ENM) approach for tropical tunas.*

The methodological approach used in our ENM is essentially composed of five main steps (Figure 1): 1) identify the main behaviours and ecological traits of tropical tunas based on literature; 2) collect and process the presence data and environmental covariates by geographical area; 3) derive a cluster analysis to identify a suite of relevant thresholds of environmental variables related to tuna ecology that describe the preferred feeding habitat characteristics, 4) develop a habitat model to classify on a daily basis the degree to which each portion of the study area (i.e. model grid cell) is either suitable or unsuitable for habitat (environmental envelop) and finally 5) derive a comparative analysis by geographical area, species and fishing mode of the distance to the closest potential habitat.

Step 1 - Specifying the tropical tuna habitat

This first step of ENM consists of identifying the relevant ecological traits of skipjack and juvenile yellowfin tunas that link presence to their environment. Tuna species are opportunistic feeders with a high mobility. Tropical tunas species were reported to aggregate at the vicinity of thermal fronts while other tuna species such as albacore (*Thunnus alalunga*) and Atlantic bluefin (*Thunnus thynnus*) have been shown to be attracted by chlorophyll-a frontal features (Druon et al., 2011; Polovina et al., 2001; Royer et al., 2004). We hypothesized here that tropical tunas are also attracted by chlorophyll-a fronts as they represent a major feature of primary production that stands long enough to sustain zooplankton production and upper trophic levels. The horizontal gradient of chlorophyll-a (hereafter gradCHL) was thus used as a proxy for food availability. A specific range of chlorophyll-a concentration is also associated with that proxy. Skipjack and juvenile yellowfin tunas are known to have a limited tolerance to temperature, their presence being restricted to warm surface waters (e.g. Arrizabalaga et al., 2015). Therefore, a specific range of sea surface temperatures (SST) was introduced. Sea surface height anomaly (hereafter SSHa) was tested as a variable potentially impacting the distribution of feeding habitat of both species. SSHa is indeed mainly influenced by seasonal changes in temperature and geostrophic currents that create eddies and gyres, i.e. divergent and convergent areas, potentially responsible for enhanced primary productivity and prey aggregation (e.g. Bakun, 2013; Polovina et al., 2006). Arrizabalaga et al. (2015) and Teo and Block (2010) notably found that the tropical tunas grow in warmer and less productive environments with near null or positive SSHa compared to temperate tuna species (with negative SSHa levels). Physical variables used in the habitat model to better characterize the specific oceanic features that attract these species in the two oceans were: sea surface currents (SSC), mixed layer depth (MLD), sea surface oxygen (O2) and salinity (SSS).

Step 2 - Data

The second step of our framework focuses on the collection and suitable preparation of input data for the model.

Tuna presence data

The presence data originate from catch data collected by the French purse seine fleets operating in the Atlantic and Indian Oceans during 1997-2014. A total of 46,662 and 14,238 non-redundant presence data of skipjack and juvenile yellowfin tuna (i.e. reported as <10 kg) with accurate location were collected in the studied areas. Redundancy filtering ensured that observations on the same day were separated by more than 2.3 km, i.e. about half of the model cell.

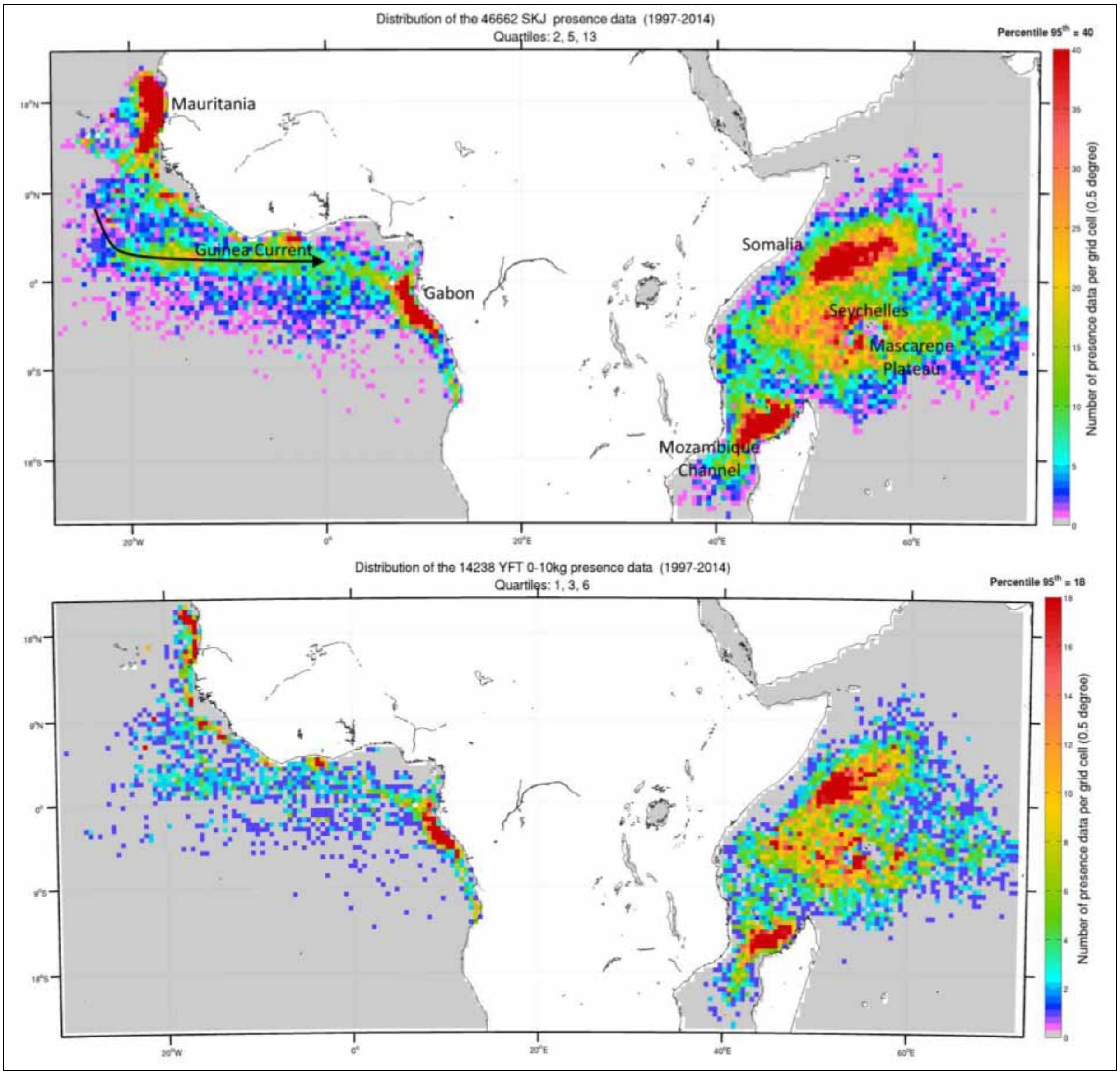


Figure 2 *Geographical distribution of skipjack (upper) and juvenile yellowfin tuna (lower) presence data (for both free-swimming schools and FADs) collected from 1997 to 2014 (in number of observations by 0.5 degree grid cells).*

Chlorophyll

Surface chlorophyll-a concentrations and fronts were used at a daily time scale from the MODIS-Aqua ocean colour sensor (http://modis.gsfc.nasa.gov) for the period from mid-2002 to 2014. The MODIS spatial resolution of 1/24˚ was used to identify meso-scale CHL fronts and to define the reference grid of the habitat model. Daily CHL data were pre-processed using iterations of a median filter in order to recover missing data at the edge of valid data. The median filter and Gaussian smoothing procedure (see Druon et al., 2012 for details) allowed for the recovery of ca. 8% of the CHL data. The relative gain in coverage was however much higher after the gradient calculation of CHL (+38%) and the habitat computation (+57%). Front enhancement of daily CHL data was calculated with an edge-detection algorithm which was shown to perform better than the histogram methods in detecting horizontal gradients given clear viewing conditions (Ullman and Cornillon, 2000). Note that the daily time scale was required here to allow the identification of CHL fronts which would be blurred or would disappear if using time-integrated data. We therefore only used the daily data for computing CHL fronts and the habitats. We extracted a 3-day mean CHL value however for the statistical analysis in order to substantially increase the number of presence data and analysis robustness. The 24 hour variability of CHL level was thus assumed to be low.

Physical data

Physical data (SSHa, SSC, SST, SSS, O2, MLD) were extracted from ocean model of the MyOcean Consortium (http://www.myocean.eu), a core marine service within the European Global Monitoring for Environment and Security (GMES) Program whose objective is to develop an integrated capacity for ocean monitoring and forecasting. Monthly mean data were extracted from the global model (Glorys2V3) at 1/4˚ horizontal resolution and 75 unevenly spaced vertical levels. The model includes a variational data assimilation scheme for temperature and salinity vertical profiles and satellite sea level anomaly (Oddo et al., 2009). Original physical data were interpolated on the MODIS-Aqua grid, i.e. at the resolution of 1/24˚. The monthly data were linearly interpolated to daily values. Such monthly to daily interpolation is believed to produce suitable estimates of the seasonal changes that define tuna habitat. SST and SSS were taken from the upper model layer (ca. 3 m) while SSC was taken as the mean of the upper layers of the MyOcean models (ca. 13.5 m) in order to capture the transport of the mixed layer. The current intensity was included in the habitat model as a directionless quantity. The MLD was defined as the maximum of the vertical density gradient. The surface oxygen content is the mean value of the upper 28 m.

Step 3 - Environmental analysis

The third step of our ENM involved exploring the variability of the environmental variables to identify relevant threshold values that separate favourable from unfavourable habitat. This analysis was made for the period 1997-2013 for the physical variables of MyOcean and from 2003 to 2014 for the CHL data of the MODIS-Aqua sensor using both the FSC and FAD-associated presence data.

The link of each selected environmental variable with presence was analysed with a cluster analysis following the procedures reported in Berthold et al., 2010 and Hartigan, 1975. The analysis was derived by studied ocean (AO and IO) and by species (skipjack and juvenile yellowfin). Selected variables were the 3-day mean CHL (log transformed), the 3-day mean horizontal gradient of CHL (gradCHL, log transformed), SST, SSS, MLD, O2, SSC, SSHa and month. We tested from 2 to 5 clusters and retained the combination (4 or 5 clusters) that allowed the clearest and simplest interpretation of the tuna seasonal behaviour in each area and species. The selection of relevant thresholds for the habitat model was driven by the cluster analysis using both FSC and FAD-associated schools presence data to set the boundary values of the suitable habitat by species and area. The environmental envelop was defined as described below excluding the cluster(s) that show very low levels of CHL gradient, i.e. with no CHL front. Therefore, only the clusters that show medium or high levels of CHL gradient were selected in the habitat modelling as a tracer of small and large CHL fronts respectively.

Suitable feeding habitats for each species were defined using common boundary limits for the biological proxies (CHL and CHL fronts) across areas stating that large and small scale CHL fronts have the same level of productivity independently of their location. The boundary limits for the physical variables were instead specific of the considered ocean since the eastern tropical Atlantic is mostly characterized by large upwellings with low seasonality and most of the primary productivity that occurs in the eastern Indian Ocean is related to meso-scale features (e.g. gyres) with a relatively high seasonality due to monsoon regimes (Schott et al., 2009). Consequently, the 15th percentile value of CHL in the Indian Ocean (IO) – with a lower minimum value – and the 85th percentile value in the Atlantic Ocean (AO) – with a higher maximum value – were selected as boundary limits in both areas for each species. The 20th percentile value of the IO – with a lower minimum value – was chosen as a minimum threshold for defining the smallest CHL fronts in both areas for each species. Less restrictive thresholds were selected for the abiotic variables (5th and 95th percentile values) because tunas are hypothesized to be often in the vicinity of CHL fronts and not always at the fronts' location, while the abiotic limitations were set to characterize the preferred hydrography which is different in the two oceans. Overall, these thresholds were used as they represent relatively extreme environmental boundaries while rejecting the potentially misclassified distribution tails of clusters. In order to circumvent the extremely low CHL coverage (< 2%) in the Guinea current and off Gabon due to cloud coverage and the overestimation of unfavourable physical environments over the preferred biotic conditions, the model parameterization in the Atlantic Ocean includes the overall physical environment enhanced by presence data. Another cluster analysis for the physical variables only (excluding CHL and gradCHL) was computed for the Atlantic Ocean and the 5th and 95th percentile values of extreme clusters were selected to define the abiotic envelop.

Step 4 - Formulation of the Ecological Niche Model

Once the environmental variables were selected and the threshold values were set, the next step consisted of defining the specific ecological niche of tuna species, using the areas of favourable biotic conditions (represented by CHL concentrations and CHL gradient) and abiotic preferences (SST, SSHa , SSC, MLD, O2 and SSS). The favourable environmental envelops predicted the daily suitability of cells within the habitat for tuna feeding on a scale of 0 to 1 (see SI for more details). The areas meeting the daily biotic and abiotic requirements of the habitat model were then integrated over time to yield seasonal suitability maps of the relative frequency of occurrence.

Step 5 – Comparative analysis by fishing mode, area and species

The model performance and the fishing mode analysis were estimated by computing the distance between the respective presence data sets and the closest favourable habitat (3-day composite) for the period from 2003 to 2013. We then compared the distribution of distances to the closest favourable habitat between the FSC and the FAD-associated presence data for each area and species. A more detailed monthly analysis of the distances to the closest habitat was also performed to investigate potential seasonal variability that links catches with potential habitat.

Results

Habitat modelling and parameterization

The cluster analysis described a wide range of trophic conditions in which skipjack and juvenile yellowfin feed, from oligotrophic in some areas of the Western Indian Ocean to eutrophic in the upwellings of the Atlantic. Table 1 presents the habitat parameterization by species and areas resulting from the cluster analysis (see Materials and methods section). We noticed that the under-representation of the cluster off Gabon, which is a particularly cloudy area, did not properly represent the minimum values for SSS and MLD. We therefore selected for these variables the 5th percentile value of the related cluster from an analysis that only included physical variables (see * in Table 1).

The intermediate thresholds for CHL and gradCHL defining the levels of productive habitat were chosen using the cluster analysis and the differences between the oligo- and eutrophic environments. These intermediate values that differentiate the small from the large fronts are the same than used for the Atlantic bluefin tuna (Druon et al., Submitted).

Table 1 Model parameters defining skipjack and yellowfin tuna habitats in the tropical Atlantic and western Indian oceans.

Skipjack Tuna	Minimum value Tropical Atlantic	Minimum value Western Indian	Intermediate value All areas	Maximum value Tropical Atlantic	Maximum value Western Indian
CHL (mg.m^{-3})	0.12 for all areas		0.25 for all areas	5.14 for all areas	
gradCHL (mg.m^{-3}.km^{-1})	0.00026 for all areas		0.0030 for all areas	N/A	
SST (°C)	20.8*	25.4	N/A	29.4	29.9
SSHa (m)	-0.208*	0.188	N/A	0.070	0.677
SSC (m.s^{-1})	0.04*	0.08	N/A	0.59	0.60
MLD (m)	6*	28	N/A	73	154
O2 (mmol.m^{-3})	189*	196	N/A	228	209
SSS (psu)	29.8*	34.4	N/A	36.2	35.7
Juvenile yellowfin tuna					
CHL (mg.m^{-3})	0.11 for all areas		0.25 for all areas	2.39 for all areas	
gradCHL (mg.m^{-3}.km^{-1})	0.00029 for all areas		0.0030 for all areas	N/A	
SST (°C)	22.2*	25.54	N/A	29.5	30.0
SSHa (m)	-0.178*	0.191	N/A	0.089	0.688
SSC (m.s^{-1})	0.04*	0.07	N/A	0.55	0.56
MLD (m)	5*	27	N/A	74	160
O2 (mmol.m^{-3})	191*	196	N/A	230	207
SSS (psu)	28.8*	34.4	N/A	36.1	35.7

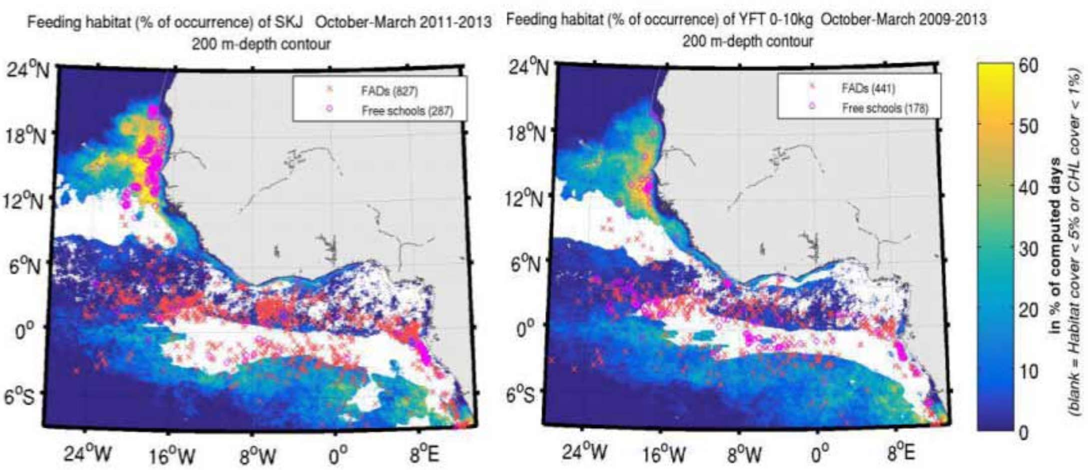
**Area with partially very low CHL data availability due cloud coverage, thus the 5th or 95th percentile value of the cluster analysis with physical variables only was used instead.*

Outputs of the habitat model

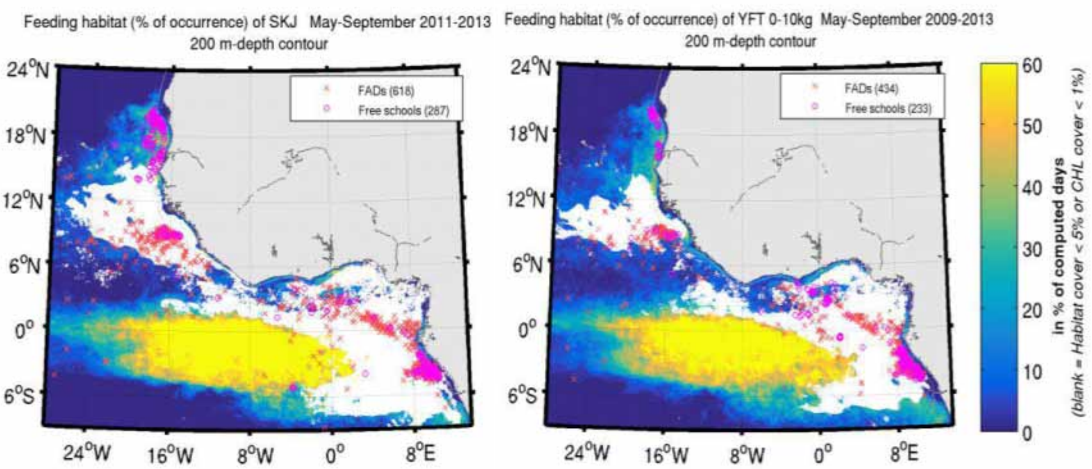
We present in this section the spatio-temporal distribution of modelled habitats and evaluation. Figure 3 presents the seasonal variability of preferred habitat for SKJ and juvenile YFT with the overlay of catches (FAD and FSC) in recent years (for the periods 2012-2013 and 2011-2013 respectively). The months from October to March and May to September in the AO are shown as these periods represent high and low number of sets and low and high size of preferred habitat respectively. The months from March to May and from August to November are shown in the IO since both periods correspond to high levels of catch operations and enhance the maximum latitudinal extents of preferred habitat (South and North respectively). FSC are mostly located in upwelling areas in the AO while FAD fishing mostly occur in the Guinea current during the less productive period from October to March (Figure 3 a) noting that FADs represent 89% of catch operations of small tunas (91% for SKJ in weight for 2012-2013). In the IO instead, preferred habitat and catches show a strong North-South seasonality with FSC and FADs most of the time in the vicinity of preferred habitat noting that FAD fishing represents 96% of catch operations for small tunas (94% for SKJ in weight for 2012-2013).

The main favourable habitats appear in the AO in the upwelling off Mauritania while the upwelling off Gabon is largely masked near the coast by high cloud coverage (> 98%), i.e. low CHL coverage (Figure 3 a and b). The two upwellings show opposite periods of maximum and minimum activity, the maximum off Mauritania being from March to October while it is from May to September off Gabon. A large fraction of the Guinea current area is also masked by clouds, especially in summer, but autumn and winter reveal a low productivity period (low frequency of favourable habitat). The area south of the Guinea current (from 1°N to 5°S and East of 17°W) is highlighted as favourable habitat by the model from May to September while, from our dataset, no fishing effort occurred. In the IO (Figure 3 c and d), favourable habitats appear along the Somalian coastal area and in the Mozambique Channel from March to May while, from August to November, most of the preferred habitat occurs off Somalia and Seychelles areas, mostly North of 10°S and West of 58°E and the Mascarene plateau North of 10°S.

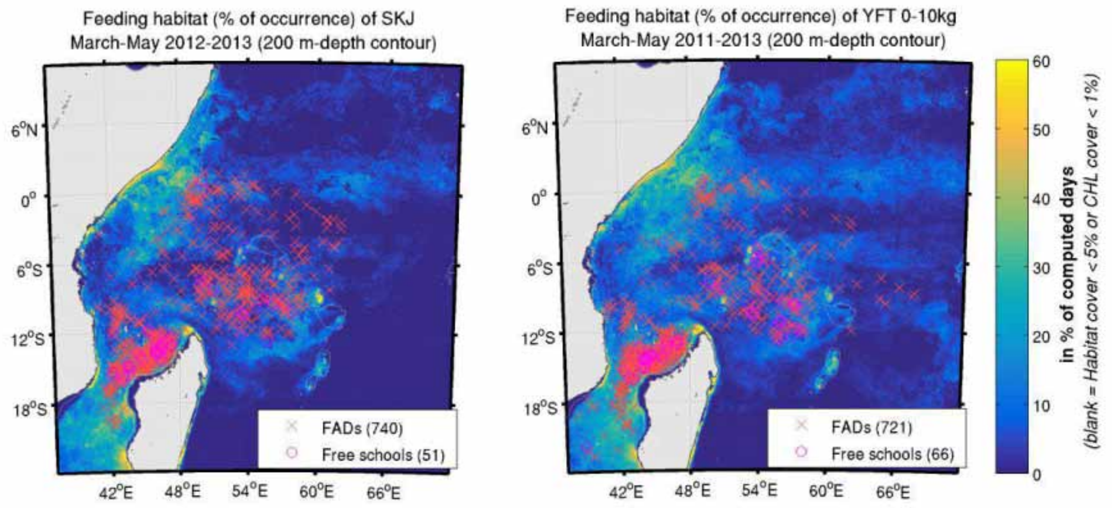
a) Atlantic: skipjack (left, 2011-2013) and juvenile yellowfin (right, 2009-2013) potential habitat from October to March



b) Atlantic: skipjack (left, 2011-2013) and juvenile yellowfin (right, 2009-2013) potential habitat from May to September



c) Indian: skipjack (left, 2012-2013) and juvenile yellowfin (right, 2011-2013) potential habitat from March to May



d) Indian: skipjack (left, 2012-2013) and juvenile yellowfin (right, 2011-2013) potential habitat from August to November

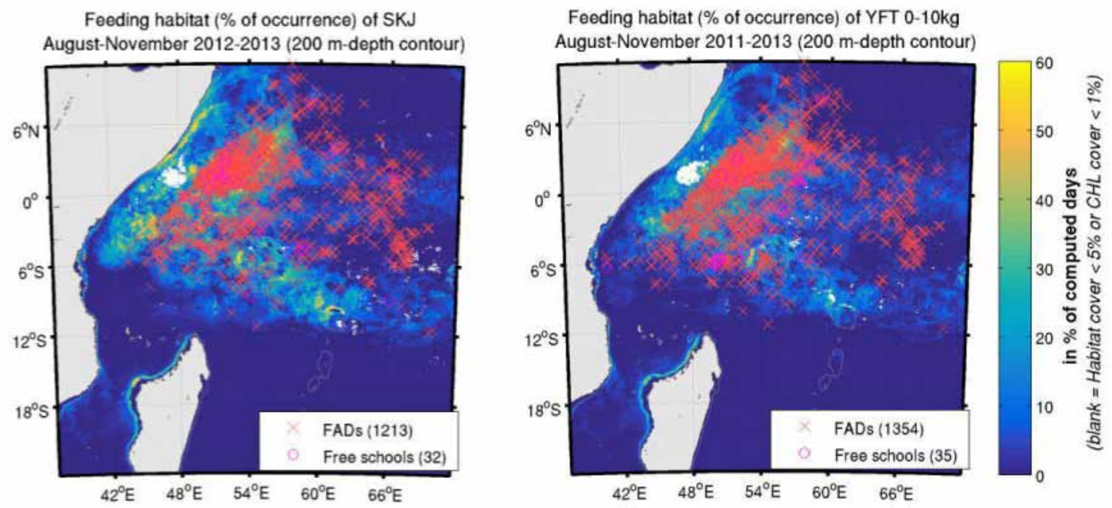
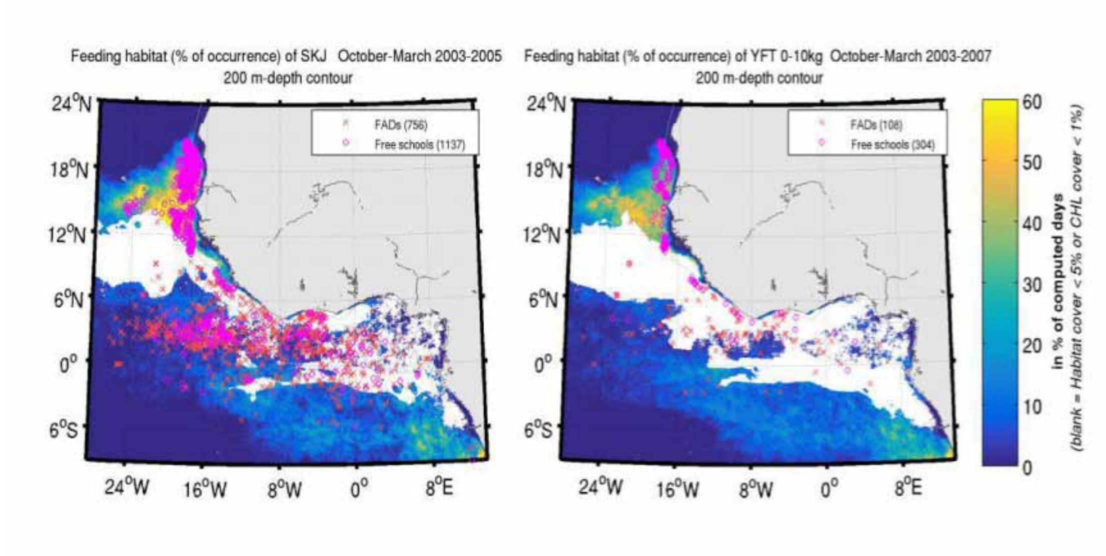


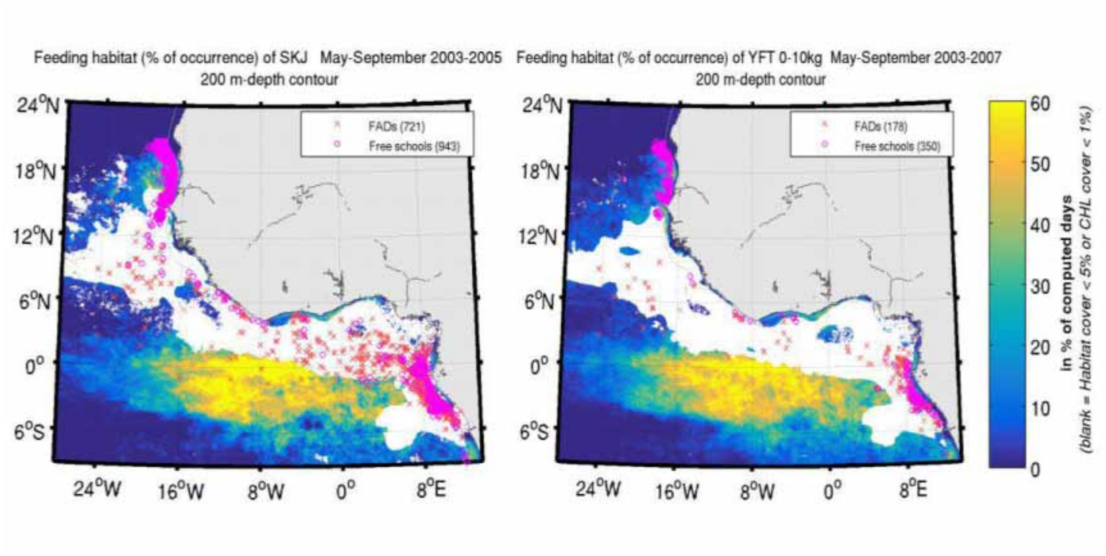
Figure 3 ***Seasonal habitat and catch operations at the end of the 2003-2013 decade:*** *October to March (a), May to September (b) in the Atlantic, March to May (c) and August to November (d) in the Indian Ocean potential habitats for skipjack (left panels) and juvenile yellowfin tuna (right panels). The FAD-associated presence data (red crosses) and free-swimming schools (pink circles) are overlaid with the respective number of presence data. The year range represented on the maps was chosen to plot a substantial number of presence data (SKJ Atlantic: 2011-2013, YFT Atlantic: 2009-2013, SKJ Indian: 2012-2013, YFT Indian: 2011-2013). The preferred habitat is expressed in frequency of occurrence and blank areas correspond to habitat coverage below 5%.*

Figure 4 presents the same as Figure 3 but at the beginning of the 2003-2013 period (within 2003 to 2007), thus highlighting the spatial and seasonal differences of habitat and fishing effort during that decade. Between the start and the end of the considered decade, a severe reduction of fishing operations on free-schools occurred in the AO mostly in upwelling areas with a relative share with FAD-fishing from 58% down to 28% for SKJ and from 70% down to 32% for the juvenile YFT.

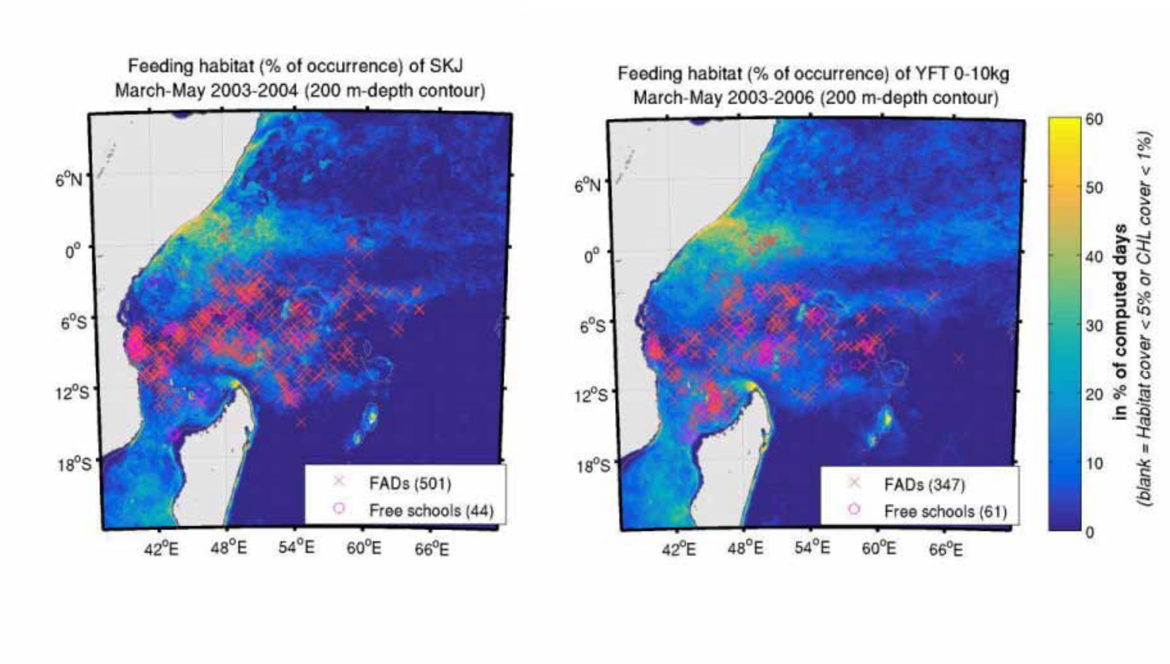
a) Atlantic: skipjack (left, 2003-2005) and juvenile yellowfin (right, 2003-2007) potential habitat from October to March



b) Atlantic: skipjack (left, 2003-2005) and juvenile yellowfin (right, 2003-2007) potential habitat from May to September



c) Indian: skipjack (left, 2003-2004) and young yellowfin (right, 2003-2006) potential habitat from March to May



d) Indian: skipjack (left, 2003-2004) and young yellowfin (right, 2003-2006) potential habitat from August to November

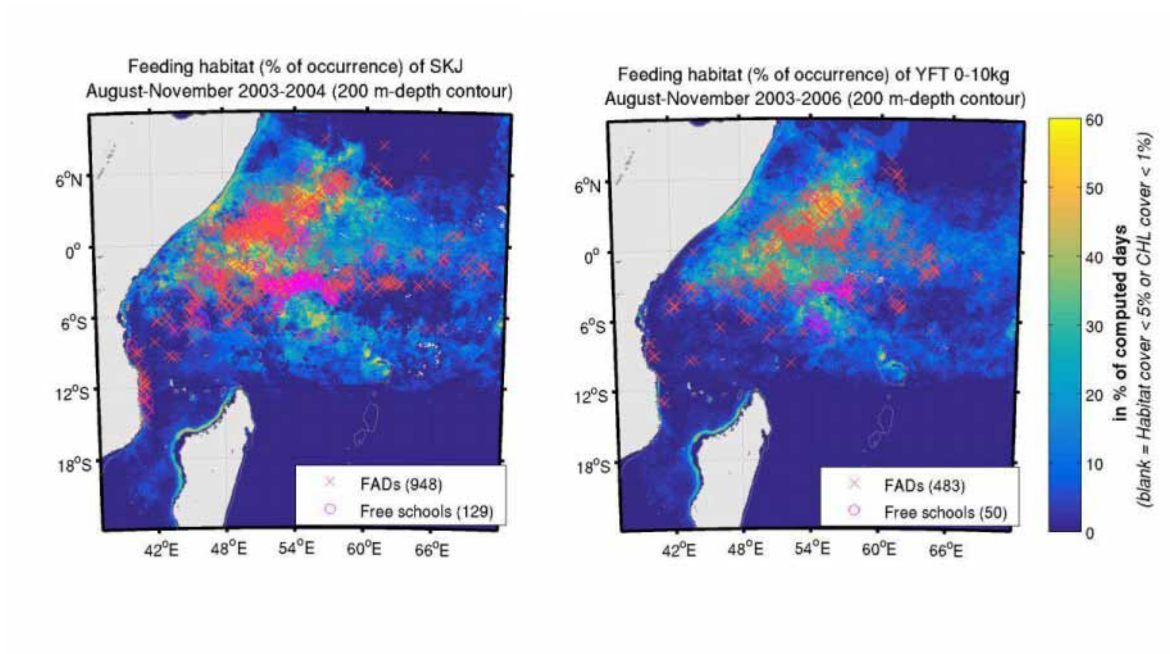


Figure 4 ***Same than Figure 3 but at the start of the 2003-2013 decade, i.e. 2003-2005 for skipjack and 2003-2007 for young yellowfin tuna (a,b) in the tropical Atlantic and 2003-2004 for skipjack and 2003-2006 for young yellowfin tuna (c,d) in the Indian Ocean.***

The FAD-associated number of fishing operations in the AO instead was stable for SKJ while it increased by 306% for juvenile YFT mostly in the poor environment of the Guinea current. In the IO, the rate of FAD-related fishing operations was already high in the years 2003-2006 but it still slightly increased with values from 89% to 96% for SKJ and from 88% to 96% for the juvenile YFT. However, the FAD-associated number of fishing operations in the IO substantially increased for SKJ (+35%) and drastically increased for juvenile YFT (+343%) with a new fishing effort in the Mozambique Channel from March to May in response to habitat change (Figure 3 c and Figure 4 c) and a substantially higher presence of FADs in a poorer environment east of 58°N in the period from August to November (Figure 3 d and Figure 4 d). While no major trend of favourable habitat was detected in the northern latitudes of both AO and OI between the start and end of the studied decade, a substantial increased frequency of favourable feeding conditions (up to about twice the frequency) occurred in some areas in the southern latitudes. These areas are the open waters off the Gabon upwelling (from 1°N to 5°S and East of 17°W) from May to September in the AO and the Mozambique Channel in the IO from March to May in the IO

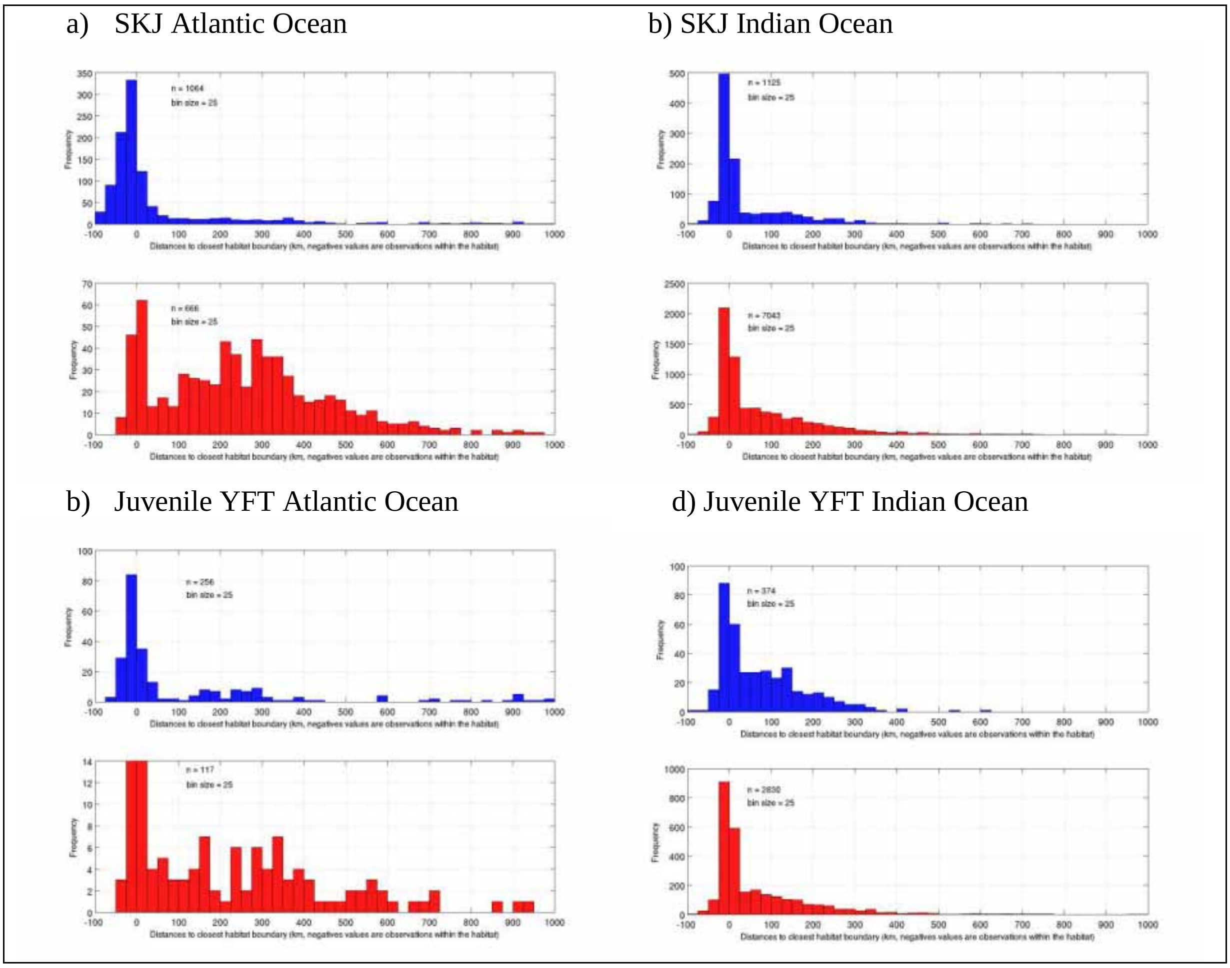
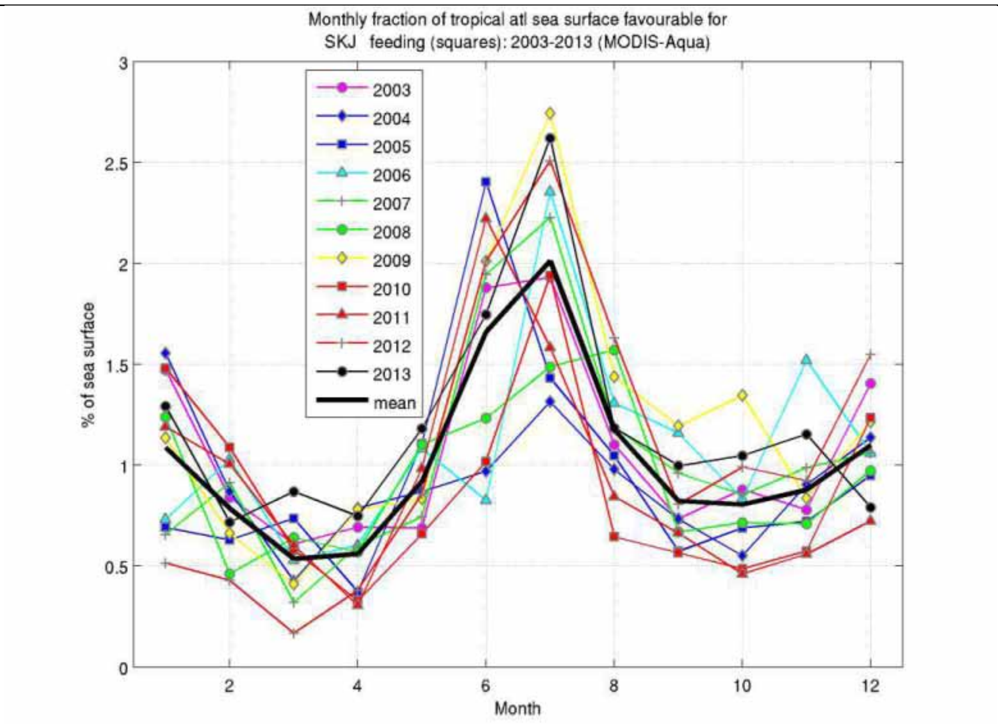
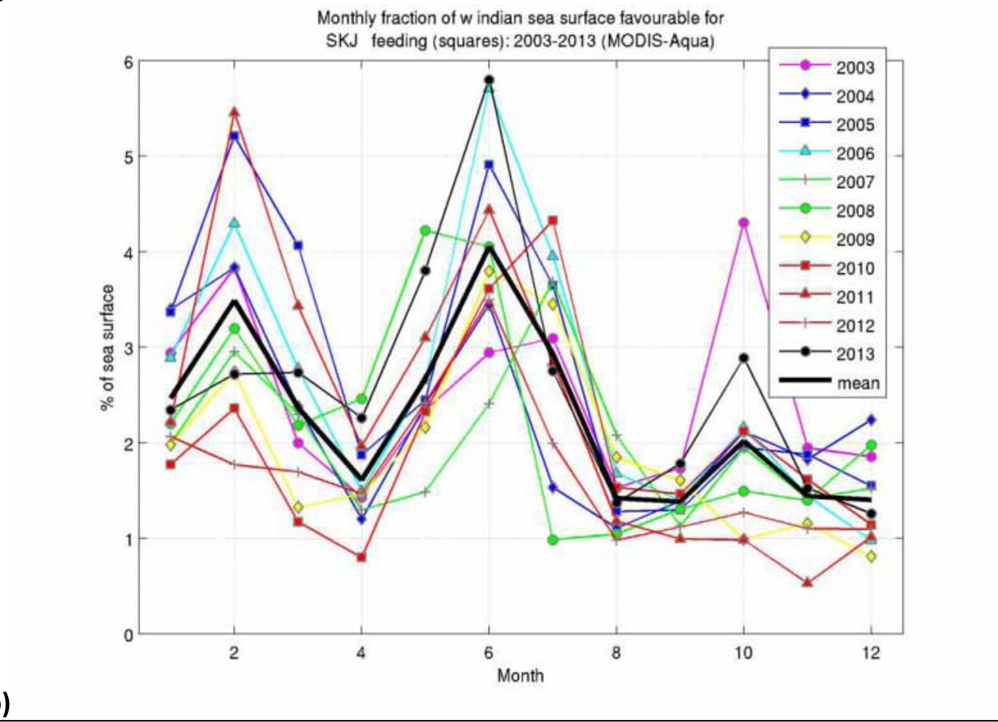


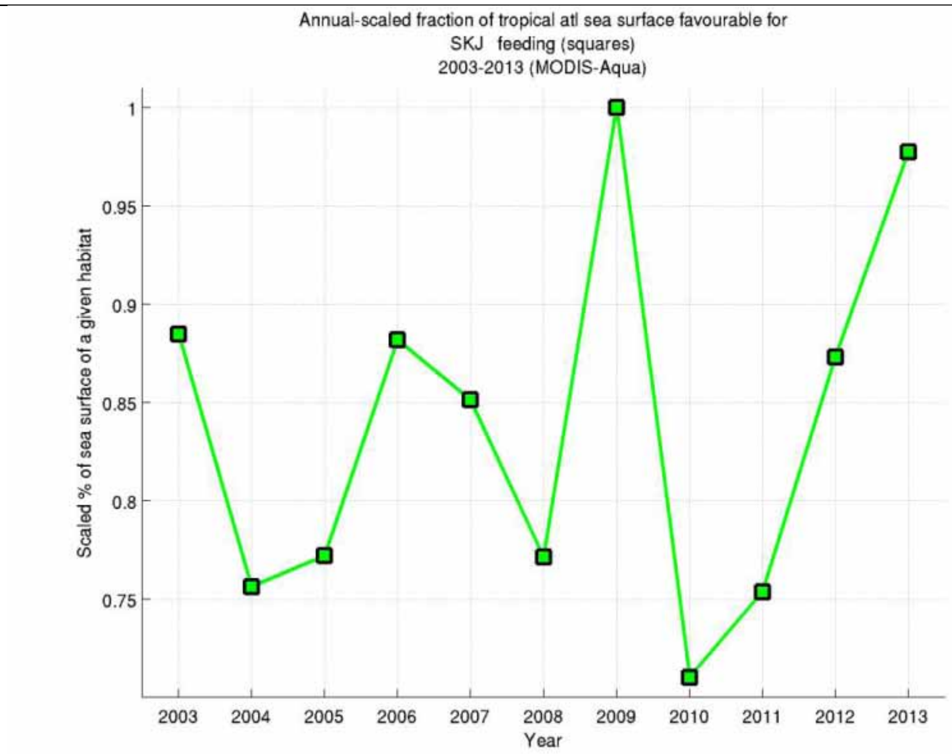
Figure 5 ***Distance histogram to closest preferred habitat of presence data associated with free-swimming schools (upper panel in blue) and FADs (lower panels in red) for skipjack (a, b) and juvenile yellowfin (c, d) in the eastern Atlantic (a, b) and eastern Indian oceans (b, d) from 2003 to 2013. Negative values correspond to presence data inside the preferred habitat.***


Monthly fraction of tropical atl sea surface favourable for
SKJ feeding (squares): 2003-2013 (MODIS-Aqua)
% of sea surface
Month
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
mean

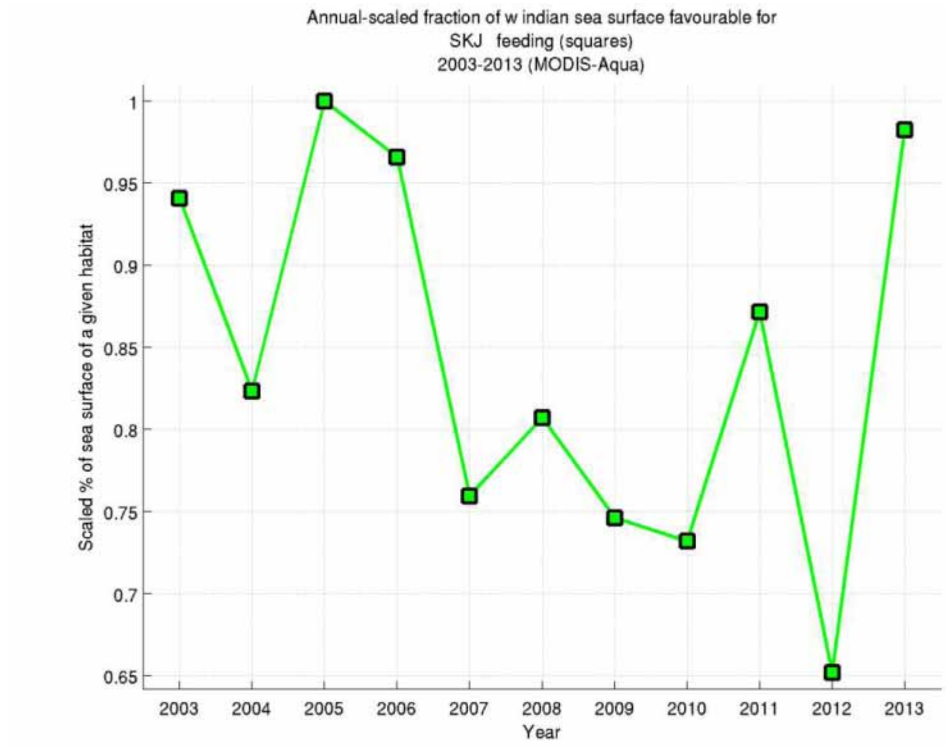
a)


Monthly fraction of w indian sea surface favourable for
SKJ feeding (squares): 2003-2013 (MODIS-Aqua)
% of sea surface
Month
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
mean

b)



c)



d)

Figure 6 Monthly (a, b) and normalized annual (c, d) variability of ocean surface potentially favourable to skipjack tuna habitat from 2003 to 2013 in the (a, c) eastern tropical Atlantic and (b, d) the Indian oceans.

The distribution of distances to closest favourable habitat for SKJ and juvenile YFT are the same in both oceans (Figure 5), with a large fraction of free-schools closer than 100 km of the preferred habitat (82% and 66% in the AO and 81% and 66% in the IO respectively) as well as FAD-associated presence data in the IO (71% and 74% respectively), while less than about 30% of FAD sets in the AO are closer than 100 km of the favourable habitat (24% and 37% for SKJ and juvenile YFT respectively, lower panels of Figure 5 a and b). For both species, the 50th percentile distance from presence data to the closest favourable habitat was in the range from about 0 to 40 km depending on species and fishing mode except for the FAD-associated schools in the tropical Atlantic that show values above 200 km (see Supplementary Information Table SI- 1). Distances to preferred habitat for free-schools were therefore low with no substantial difference with FAD sets in the Indian Ocean and similar distances were obtained for free-schools in the Atlantic Ocean. The results show however that most FAD sets in the tropical Atlantic were highly distant from preferred habitat as defined by the model.

The inter-annual variability of habitat size for both species is similar and only SKJ habitat size is shown in both oceans (Figure 6 a and b). The maximum extent of favourable habitat in the AO (Figure 6 a) occurs from May to August with a high year-to-year seasonal variability (ranging from -65% of the mean in 2004 and +30% in 2009) while the minimum size of favourable habitat was shown to occur from September to April with a lower inter-annual variability (±30% of the mean size). The situation in the IO is slightly more complex due to the spatial shift of habitat with two peaks in February and June. The minimum habitat extent occurred at transition periods with an absolute minimum in August-September and a secondary minimum in April. As for the AO, the maximum year-to-year seasonal variability appeared at maximum extent of habitat. The maximum number of fishing operations (not shown) occurred at minimum extent of habitat, i.e. from October to March in the AO and in March-April and August-September in the IO.

The overall inter-annual variability of skipjack favourable habitat showed no clear trend in both oceans (Figure 6 c and d) although a higher variability of habitat size seemed to after 2009.

Discussion

Modelling methods

We used a cluster analysis to select the relevant environmental envelop of a species' favourable habitat including both free-swimming schools and FAD-associated presence data but excluding the one or two cluster(s) showing very low values of CHL gradient. This methodology hypothesizes that i) the preferred habitat targeted is related to feeding (CHL front in the vicinity), which is consistent with the ecology of juvenile yellowfin tunas, and that ii) skipjack tunas are opportunistic spawners with an indistinct spawning habitat since most of schools in the OI are in the vicinity of favourable feeding habitat independently of the fishing mode. On the other hand, the relative low occurrence of natural floating objects in some areas may explain the higher distances of SKJ and juvenile YFT to their preferred habitat in the Atlantic Ocean. If FADs are used outside the natural zones of high occurrence of floating objects (e.g. Guinea current, Maufroy et al., n.d.), our results suggest that SKJ and juvenile YFT could be extracted from their natural and productive habitat. This is in agreement with observer data (Maufroy et al., n.d.) which show a higher ratio FADs over natural floating objects in the AO, suggesting a higher change of effective habitat than in the IO.

A limitation of the approach is the cloud coverage that may hamper the detection of favourable habitat if the coverage of CHL data is very low (below 1%). This occurred in the area near shore of the

Gabon upwelling and part of the Guinea current where the largely missing CHL data impedes the detection of favourable habitat. We therefore selected for the OA the largest physical conditions derived by the presence data independently of the presence or not of CHL fronts. The areas where CHL coverage was below 1% or habitat coverage below 5% were shown as undetermined (blank). While the near shore upwelling off Gabon remained undetermined habitat, CHL coverage in part of the Guinea current was sufficient to highlight the poor habitat during the high fishing season (October to March).

Potential feeding habitat and influence of FADs

The two oceans show highly contrasted situations in terms of spatial seasonality of favourable feeding habitat and type of productive systems. The IO is marked by a high monsoon-derived spatial seasonality and primary productivity is dominated by meso-scale features with mostly small CHL fronts. The AO instead shows a lower seasonality and higher differences in habitat productivity with the two main upwelling systems off Mauritania and off Gabon (large and small CHL fronts) and the particularly low productive current of Guinea in winter. The recently more productive waters in the Mozambique Channel from August to November agrees with the increased number of fishing sets in that area at the end of the 2003-2013 decade. The important spatial seasonality of favourable feeding habitat in the OI appears to act as a driver of fleet mobility that may limit the drift of FADs in poor environments. The recent increase of FAD use in that area seems however to be responsible for the drift of a higher number of sets in poor environments east of 58°N. The waters off Somalia in late summer were instead left with no effort in the second half of the decade due to piracy threat. While most free school fishing appears to occur in the upwelling areas in the AO, the strong and constant eastward Guinea current was revealed to represent an area of high FAD-associated fishing in a low productive environment. This result agrees with studies on stomach contents (see review in Dagorn et al., 2013) where, in the AO, tuna associated with floating objects have more empty stomachs, are in poorer condition and grow slower than fish caught in free-swimming schools (Hallier and Gaertner, 2008). By contrast in the IO, no difference in the diet of tuna between drifting floating objects and free-swimming schools was found in a rich-food area, but skipjack and small yellowfin tuna associated with drifting FADs in a poor-food area have more empty stomachs than in rich-food area (Jaquemet et al., 2011). The results would support the hypothesis of FADs acting as an ecological trap in the AO although the role of FADs may have other implications than feeding (spawning, protection, etc.) that cannot be reflected by the current approach.

The link between the high number of sets and minimum habitat size suggests that tuna populations concentrate in these periods with a higher vulnerability to fishing. Because FADs favour the schooling of tunas, periods of habitat shrinkage may lead to habitat change from favourable to unfavourable and would explain, together with the active drifting, their potential adverse influence for feeding such as in the AO in winter. On the opposite, the use of FADs in areas where the favourable habitat for feeding expands may not show such adverse influence. These results are in line with Wang et al. (2014) that showed the alteration by FADs of the environmentally-based migration of skipjack tunas in the Western and Central Pacific Ocean. In their study, no migratory change was observed with the onset of El Niño Southern Oscillation events for FAD sets while free-schools showed migratory adaptation. They suggest that FADs appear to offer skipjack and alternative strategy to large-scale movement. Our results suggest that the positive or adverse influence of this strategy on tuna feeding is related to the occurrence and dynamics of favourable habitats. An analysis that would evaluate the occurrence of natural floating objects in favourable feeding habitats would help in understanding the potential benefit of tuna attraction with FADs as regard to feeding.

Conclusion

The ENM approach applied to skipjack and juvenile yellowfin tunas revealed a strong link between their presence and the occurrence of small and large CHL fronts. The important North-South seasonality of the detected habitats and related CHL fronts in the OI agrees with the spatial distribution of fishing sets. Recent niche of productive environments appeared to be exploited by the fishing fleet in the Mozambique Channel while the extensive use of FADs in the OI recently tended to increase the number of fishing operations in a poorer equatorial environment east of 58°N. The different hydrographic regime in the AO, with low spatial seasonality and winter shrinkage of habitat in the high linear current of Guinea, appeared to be responsible of a significant eastward drift of FADs towards poor environments. The apparent difference of FAD influence on tuna feeding between the AO and the IO enhances the strong and equivocal role of tuna aggregation under floating objects.

Acknowledgement

The authors particularly thank the NASA Ocean Biology (OB.DAAC), Greenbelt, MD, USA, and the Myocean Consortium for the quality and availability of the ocean colour and ocean modelling products respectively. The authors are especially grateful to ORTHONGEL and all past and current personnel involved in the data collection and management of purse seine fisheries data that were funded by the European Union through the Data Collection Framework (Reg 199/2008 and 665/2008). We particularly thank the staff of the 'Observatoire Thonier' of the Research Unit MARBEC (IRD/Ifremer/UM/CNRS).

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Supplementary Information

Presence data by fishing mode and area

The presence data for skipjack and juvenile yellowfin tunas are relatively well distributed by month following catchability and by fishing mode in the Atlantic while the number of FAD-fishing represents 87% of fishing operations in the western Indian Ocean (Figure SI- 1).

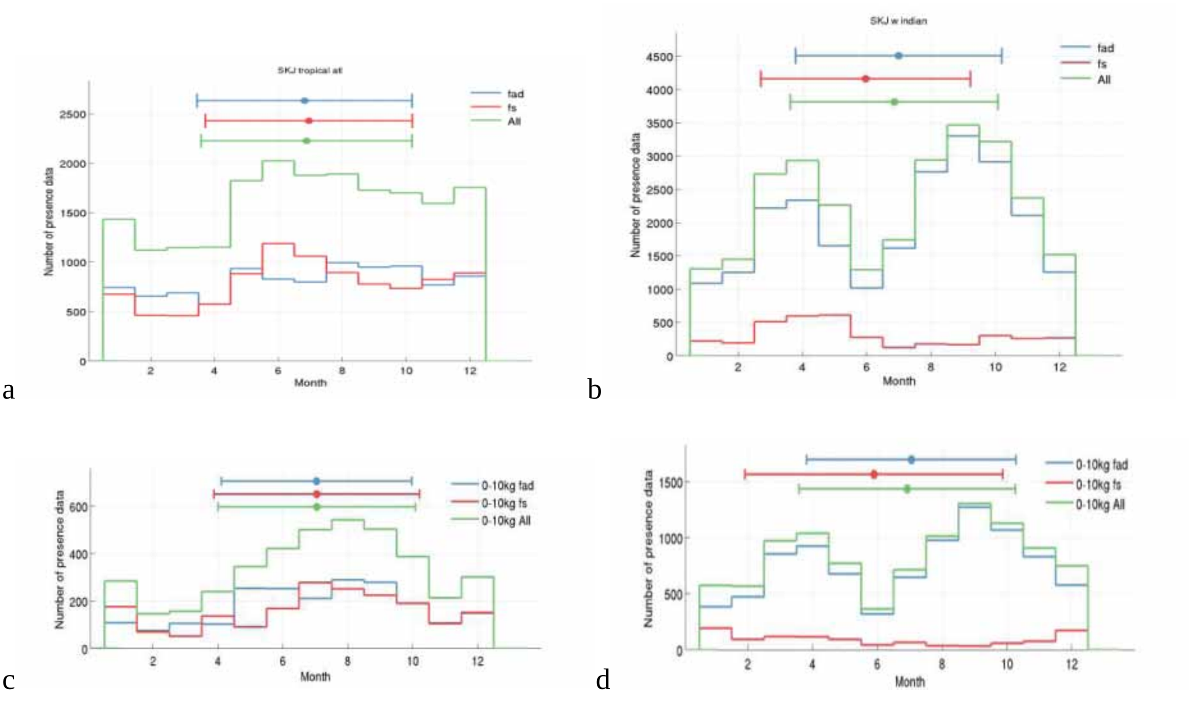

Figure SI- 1 ***Monthly distribution of a-b) skipjack and c-d) juvenile yellowfin tuna presence data by fishing mode (fs and fad) collected in the a-c) tropical Atlantic and b-d) Indian oceans from 1997 to 2014 (mean and standard deviation are shown).***

Levels of productive habitat and model equations

In order to reflect feeding opportunities within the mesotrophic (e.g. Indian Ocean) to eutrophic (e.g. upwelling in the tropical Atlantic) environments in which tunas feed, we added an intermediate level of productivity, so that we now consider three types of feeding habitat: highly, moderately and poorly productive; a similar approach was recently followed to model hake nurseries (Druon et al., 2014).The highly productive habitat was represented by the larger frontal systems which, by their size and persistence, contain productive water masses with potentially well-developed food webs. The moderately productive habitat refers to smaller – less productive – frontal systems which may still represent regional forage hot spots. We defined three threshold values for CHL and two for gradCHL that delimit the highly and moderately productive from the unfavourable feeding habitat (Figure SI- 2). The daily values of the highly and moderately productive feeding habitat were set to 1 and 0.3 respectively. The value of 0.3 was chosen as an ad-hoc value for the moderately productive habitat as it represented a substantially less favourable feeding habitat (about 3-fold) than the highly productive conditions (of value 1) and was markedly above 0. The value of the productive habitat was then weighted by the abiotic limitations.

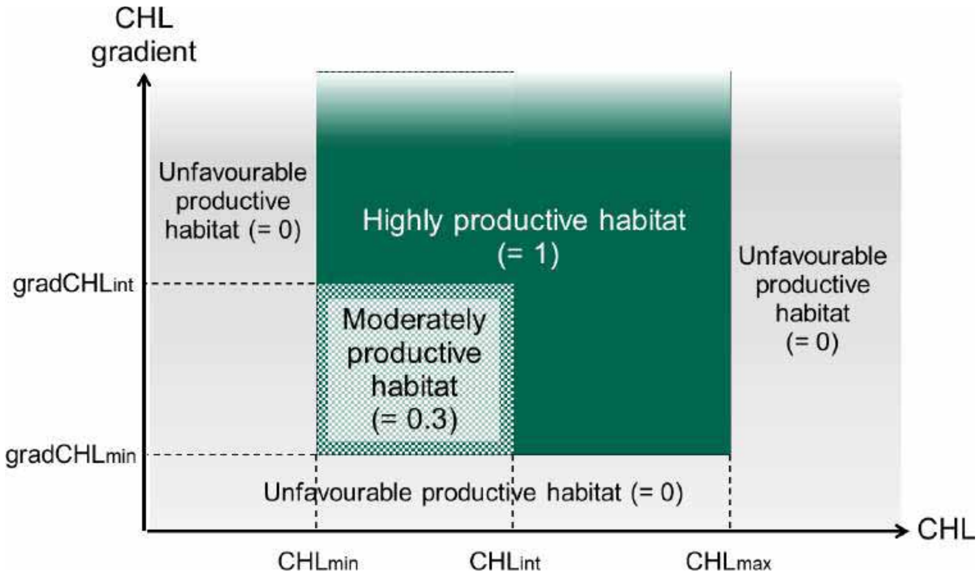

Figure SI- 2 ***Definition of the three productive habitats (unfavourable, moderate and high of value 0, 0.3 and 1 respectively in the model) based on levels of surface chlorophyll content (CHL) and horizontal chlorophyll gradient (gradCHL), thus referring to small and large productive fronts.***

The feeding and spawning habitats are thus defined by the model grid cells that daily satisfy the suitable environmental conditions following the equations:

$$Feeding\ Habitat_{Day,Cell} = Productive\ Habitat_{0/0.3/1} * AbioticFactor_{range_{0/1}}$$

$$Feeding\ Habitat_{Day,Cell} = CHL_{min/int/max_{0/0.3/1}} * gradCHL_{min/int_{0/1}} * SST_{range_{0/1}} * SSHa_{max_{0/1}} * MLD_{0/1} * O2_{range_{0/1}} * SSS_{range_{0/1}} * SSC_{range_{0/1}}$$

Each habitat cell was attributed a daily value of 0 or 0.3 or 1 and the integration in time resulted in a habitat expressed in frequency of occurrence.

Model evaluation

Table SI- 1. 50^{th} percentile distance between presence data (skipjack and juvenile yellowfin) and closest 3-day preferred habitat (km) and fraction of presence data further than 100 km of preferred habitat (%) by area and fishing mode. Negative values of 50^{th} percentile distance correspond to the distance between presence data inside the habitat and the habitat boundary.

D_{50th}: 50^{th} percentile distance to 3-day preferred habitat (km) ***$F_{>100km}$: Fraction of presence data further than 100 km of 3-day preferred habitat (%)***		**Tropical Atlantic**			**Indian Ocean**		
		n	D_{50th} (km)	***$F_{>100km}$ (%)***	*n*	D_{50th} (km)	***$F_{>100km}$ (%)***
Skipjack tuna	Free-swimming schools	*1064*	-9	***18***	*1125*	-1	***20***
	Fishing Aggregating Devices	*666*	245	***76***	*7043*	16	***30***
Juvenile yellowfin tuna	Free-swimming schools	*256*	2	***34***	*374*	43	***34***
	Fishing Aggregating Devices	*117*	200	**63**	*2830*	6	***26***