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Preferred feeding habitat of skipjack tuna in the eastern central Atlantic and western Indian Oceans: relations with carrying capacity and vulnerability to purse seine fishing

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Abstract

A single Ecological Niche model was developed for skipjack tuna (*Katsuwonus pelamis*) in the eastern central Atlantic Ocean (AO) and western Indian Ocean (IO) using an extensive set of precise spatial occurrence data from the European purse seine fleet during 1998-2014. Productive fronts of chlorophyll-a were used as proxy for food availability while mixed layer depth, sea surface temperature, oxygen concentration, salinity, current velocity and sea surface height anomaly were selected to define skipjack physical oceanographic preferences. The common environmental feeding niche identified for skipjack emphasized highly contrasted oceanographic regimes between oceans with seasonal occurrence of gyre-type productive features at mesoscale in the IO and large scale upwelling systems that seasonally shrink and swell in the AO. About 60% of free-school (FSC) sets and 46% of fishing aggregating device (FAD) sets were found within favourable feeding grounds for skipjack. About 34% of FAD sets in the AO were however found to occur at a distance further than 100 km from favourable feeding conditions, mostly in the poor environment of the Guinea Current, and 10% for the FAD sets observed in the IO, as compared to 8% for all FSC sets. The ecological role of the Guinea Current remains unclear as regards to feeding and spawning since this particularly poor environment is remote from upwelling-rich areas while skipjack is known to spawn nearby feeding grounds (income breeding strategy). The results also emphasized in the IO a higher exposure of schools to purse seiners in months where preferred feeding habitat is reduced which may result in a geographic concentration of skipjack populations at the habitat scale. Finally, the significant positive correlation observed between the annual size of favourable habitat for feeding, the annual nominal catch rates and the total catches of skipjack in the IO i) agrees with the near full exploitation of skipjack in the IO since the 2000s and in the recent years for the AO, and ii) suggests to interpret the size of favourable habitat for feeding as an indicator of carrying capacity of the environment to sustain populations of this fast-reproducing species.

Keywords: Habitat, skipjack tuna, FAD, free schools, feeding, Atlantic Ocean, Indian Ocean, ecological niche, environmental conditions, exploitation status.

Introduction

Among tuna and tuna-like species, albacore (*Thunnus alalunga*, ALB), bigeye (*Thunnus obesus*, BET), Atlantic bluefin (*Thunnus thynnus*, BFT), Pacific bluefin (*Thunnus orientalis*. PBF), skipjack (*Katsuwonus pelamis*, SKJ), southern bluefin (*Thunnus maccoyii*, SBF) and yellowfin (*Thunnus albacares*, YFT) are the most commercially important species. The mean annual catch of the major commercial tunas has been about 4.5 million t since 2003, from which skipjack accounts for the greatest proportion of world catch (58%), mostly for canning (FAO, 2014). Skipjack catches have been increasing over the last 60 years to reach the highest level at 2.9 million t in 2014, ranking it as the third most-fished species (FAO, 2014).

In the Indian Ocean, catches of skipjack increased slowly from the 1950s, reaching around 50,000 t at the end of the 1970s, mainly due to the activities of pole and liners and gillnetters. The catches increased rapidly with the arrival of the purse seiners in the early 1980s to reach their highest level at around 615,000 t in 2006. Since then, catches decreased and have been varying between 340,000 t in 2012 and 440,000 t, in 2008, with about 400,000 t of skipjack caught in 2015. Meanwhile, skipjack catches also increased over time in the Atlantic Ocean since the early 1950s and varied around 240,000 t in the recent years.

Skipjack is a cosmopolitan fast-swimming fish species inhabiting tropical and sub-tropical pelagic waters. Skipjack is an opportunistic feeder, mainly feeding on small fishes (e.g. cigarfish, flying fish), crustaceans and cephalopods (Grande, 2013). Skipjack is considered having the faster growth rate among tuna species reaching around 45 cm and 65 cm at one and two years of age, respectively (Murua et al., Submitted). Estimated maximum age is around 6-7 years, with a rapid growth rate in the first two years. Skipjack oocyte development is defined as asynchronous and therefore the oocyte recruitment is continuous during extended periods where spawning occurs in multiple batches (Grande et al., 2012; Schaefer, 2001). Skipjack female length at 50% maturity (i.e. length at 50% of population reaching maturity as a measure of first maturity) is around 40 cm and full maturation is reached at about 49 cm (Grande et al., 2014). Its spawning capacity is also large with, on average, around 1 million eggs per batch (Grande et al., 2014). Skipjack is considered an income breeding species (Grande et al., 2016), whereby the energy required for reproduction is mainly supplied directly from the food intake rather than from accumulated energy reserves (McBride et al., 2015). Income breeding allows for high investments in reproduction when the resources are available (Kjesbu et al., 2009). Skipjack tuna is therefore characterized by particularly large growth and reproductive potential.

Skipjack can perform long migrations and their spatial distribution includes tropical and sub-tropical regions of all oceans. Tagging programmes showed that skipjack can make large horizontal migrations up to an average of 1,280 and 1,066 nautical miles in the eastern Pacific and Indian Oceans, respectively (Fonteneau and Hallier, 2015). Vertical movements are however restricted compared to other tuna species to surface layers due to limited tolerance to low levels of dissolved oxygen and temperature (Graham and Dickson, 2004). The habitat of skipjack was associated with surface water temperature between 15ºC and 30ºC (Barkley et al., 1978) with a preferred range from 23ºC to 28ºC (Arrizabalaga et al., 2015).

In this paper, we linked the ecological traits of skipjack tuna to environmental variables through an Ecological Niche Model approach (ENM) and investigated their requirements with regards to feeding. We used a substantially larger dataset of presence data from EU Purse seiners compared to Druon et al. (2015) to identify a common environmental envelop which, in turn, is used to model the preferred feeding habitat of skipjack tuna in both the eastern central Atlantic and western Indian oceans. We then analysed for each area and fishing mode (free-swimming school *versus* FAD) the distances of fishing sets to the closest predicted habitat to appraise the relation of fishing activity with the preferred feeding habitat of skipjack. The seasonal and decadal habitat variability and spatial extent are furthermore discussed with respect to their possible impact on the overall catches and FAD fishing.

Methods

Description of the Ecological Niche Modelling

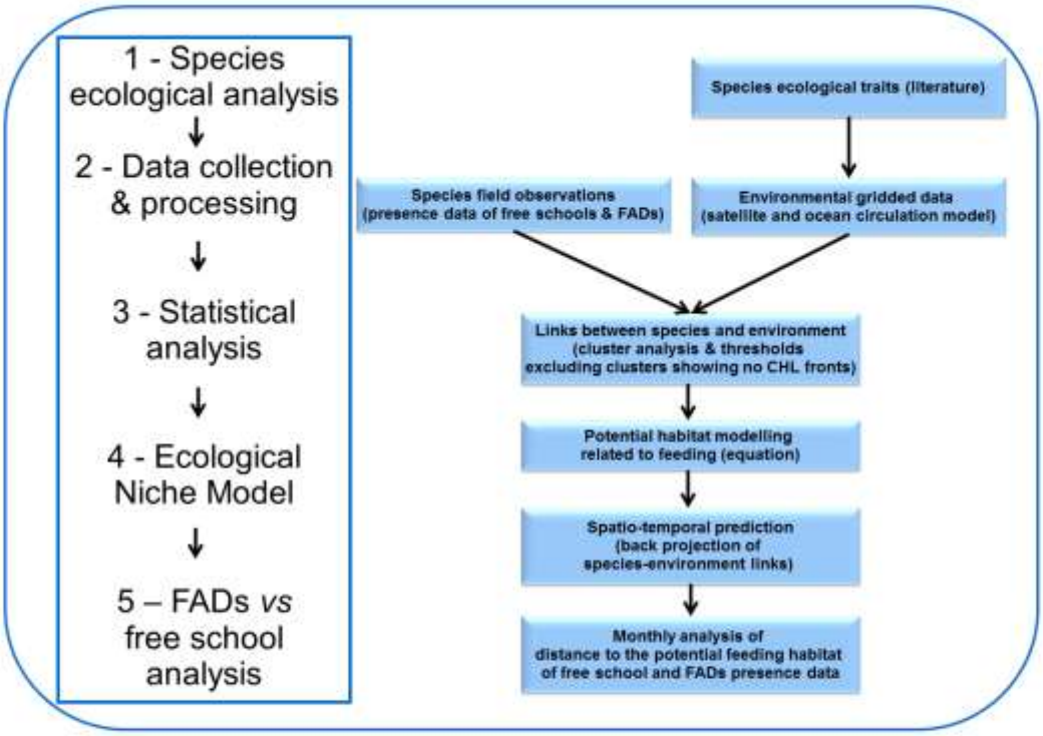


Figure 1 *Flowchart of the Ecological Niche Model (ENM) approach for tropical tunas.*

The methodological approach is the same than in Druon et al. (2015) except that: i) the larger dataset available (see below) allowed a common parameterization of the habitat model in the eastern central Atlantic and western Indian Oceans, ii) the daily habitat value is a linear function of the chlorophyll-a gradient value (see SI) instead of a discrete value (i.e. fixed values of 0, 0.3 and 1) and iii) the time-series was extended from 2003-2013 to 1998-2014 using both SeaWiFS and MODIS-Aqua-derived chlorophyll-a data with specific sensor calibrations.

Data

Skipjack tuna presence data

The presence data originate from logbooks of the European purse seine fleets operating in the Atlantic and Indian Oceans during 1997-2014 for Spanish and 1997-2015 for French data. A total of 155,064 non-redundant presence data of skipjack 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. The additional Spanish fleet data increased the coverage in the south of the eastern central Atlantic Ocean (8-18°S) and in the north of the western Indian Ocean (8-15°N). Skipjack tuna can be caught in free-swimming schools (FSC) and in schools associated with floating objects now predominated by artificial fish aggregating devices (FADs) deployed at sea by fishermen and monitored with GPS buoys.

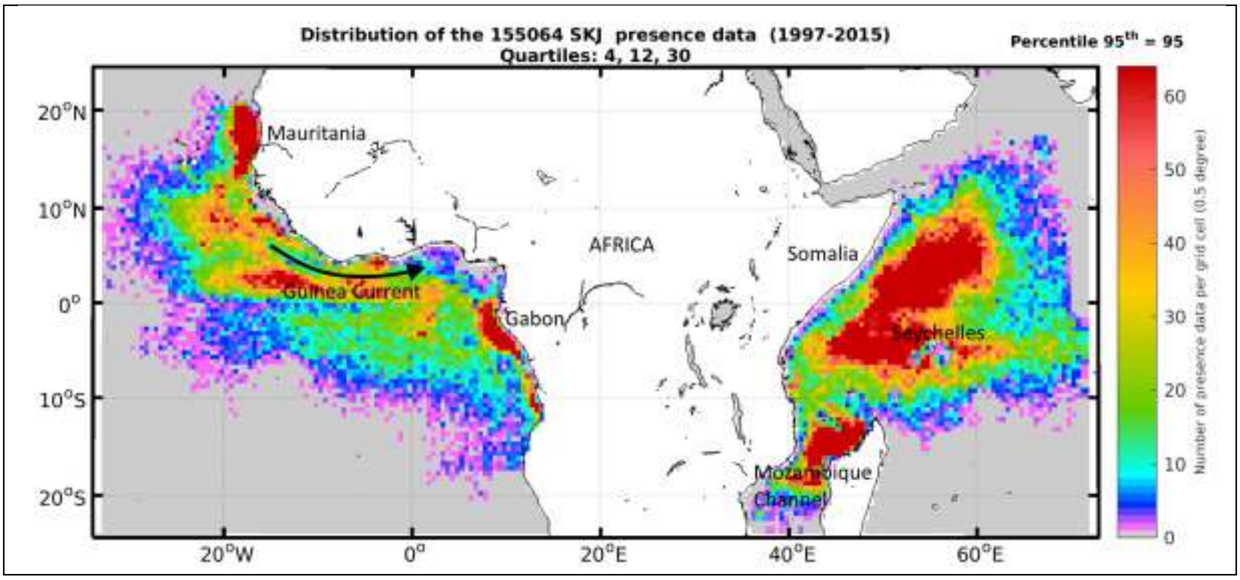


Figure 2 *Geographical distribution of skipjack presence data (for both free-swimming schools and FADs) collected from 1997 to 2014 by European purse seiners (in number of observations by 0.5 degree grid cells).*

Chlorophyll-a data

Surface chlorophyll-a concentrations and fronts were used at a daily time scale from SeaWiFS and MODIS-Aqua ocean colour sensors using the OCI algorithm (http://modis.gsfc.nasa.gov) from 1998 to 2010 and from 2003 to 2015, respectively. The SeaWiFS and MODIS-Aqua spatial resolutions of 1/12˚ and 1/24˚ respectively were used to identify meso-scale CHL fronts. The particularly low satellite coverage in the equatorial area of the eastern central Atlantic due to clouds did not allow however merging both sensors' habitat information without generating a substantial bias of habitat size in the multi-annual time series. Consequently for time consistency, we used separately SeaWiFS and MODIS-Aqua data for the Atlantic area to generate distinct time-series of habitat size (see below).

Physical data

Physical data (sea surface height anomaly - SSHa, Sea surface current intensity - SSC, sea surface temperature - SST, sea surface salinity - SSS, sea surface dissolved oxygen - O2) were extracted from the global ocean model of the EU-Copernicus Marine Environment Monitoring Service (http://marine.copernicus.eu/). 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 ocean 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 mixed layer depth (MLD) was defined as the maximum of the vertical density gradient which was derived from the temperature and salinity profiles. The surface oxygen content is the mean value of the upper 28 m.

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 1997-2014 for the physical variables of the ocean models and from 1998 to 2015 for the CHL data using both the FSC and FAD-associated presence data.

The link of each selected environmental variable with presence was analysed with a cluster analysis by ocean basin (Atlantic Ocean - AO and Indian Ocean - IO) combining both fishing modes (FSC and FAD). 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 considered separately the biological variables (CHL and CHL gradient) from the physical variables in the cluster analysis to optimize the number of points in each analysis since CHL data are much less frequent (due to clouds) than the physical variables (always defined). The environmental envelop was defined taking relatively extreme values of the variables from the extreme clusters, i.e. taking the minimum level (e.g. percentile 5th) of the lower cluster and the maximum level (e.g. percentile 95th) of the upper cluster to take into account potentially under-represented environments in the presence data. For the cluster analysis of the biological variables however, the cluster(s) that showed very low levels of CHL gradient, i.e. with no CHL front, was excluded. Therefore, only the clusters that at least medium levels of CHL gradient were selected to define suitable feeding habitats as a tracer of relevant CHL fronts. Preferred habitat hereafter defines the habitat related to feeding.

Less restrictive thresholds were selected for the biotic variables (15th, 20th and 85th percentile values) because tunas are hypothesized to be often in the vicinity of CHL fronts and not always at the fronts' location, while the more restrictive abiotic limitations (5th and 95th percentile values) were set to characterize the abiotic preferences. Overall, these thresholds were used as they represent relatively extreme environmental boundaries while rejecting the distribution tails of extreme clusters which likely correspond to very extreme and unusual environments or misclassified data in the clustering.

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 feeding habitat of skipjack tuna, using the areas of favourable biotic conditions (represented by CHL concentrations and CHL gradient) and abiotic preferences (range of SST, SSHa , SSC, MLD and SSS and a minimum threshold for O2). The favourable environmental envelop predicted the daily suitability of cells within the habitat for skipjack 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 expressed in frequency of occurrence.

Comparative analysis by fishing mode and area

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 1998 to 2014. We then compared the distribution of distances to the closest favourable habitat between the FSC and the FAD-associated presence data for each area. A more detailed monthly analysis of the distances to the closest habitat was also performed to investigate the seasonal links between the number of sets and size of preferred feeding habitat.

Skipjack tuna catch rates and comparison with habitat size

Mean annual catch rates (t d^{-1}) of skipjack were computed as the ratio between the annual catch of skipjack and the cumulated fishing effort expressed in fishing days. Temporal correlations between catch rates and favourable habitat size were investigated at basin scale with Spearman's rank correlation coefficients. Two estimates of habitat size were performed in the Atlantic area using independently SeaWiFS (1998-2010) and MODIS-Aqua sensors (2003-2014) in order to avoid coverage bias over time when using combined sensors due to the important cloud cover.

Results

Habitat modelling and parameterization

The cluster analysis described a wide range of trophic conditions in which skipjack feed, from oligotrophic in some regions of the western Indian Ocean and equatorial Atlantic to eutrophic in the upwelling areas of the tropical Atlantic. Table 1 presents the habitat parameterization by species and areas resulting from the cluster analysis while the slope of daily feeding habitat index was derived from the chlorophyll-a front preferences of skipjack tuna (see details in SI: Levels of productive habitat and model equations).

Table 1 Model parameters defining skipjack tuna preferred habitat in the eastern central Atlantic and western Indian Oceans

Skipjack	Minimum value	Intermediate value	Maximum value
CHL ($mg.m^{-3}$) * (MODIS / SeaWiFS)	0.13 / 0.11	N/A	5.27 / 4.20
gradCHL ($mg.m^{-3}.km^{-1}$) ** (MODIS / SeaWiFS)	0.00058 / 0.00078	0.0050 / 0.0055	N/A
SST (°C) ***	21.6	N/A	30.0
SSHa (m) ***	-0.20	N/A	0.67
SSC ($m.s^{-1}$) **	0.04	N/A	0.54
MLD (m) ***	6	N/A	158
O2 ($mmol.m^{-3}$) ***	196	N/A	N/A
SSS (psu) ***	30.3	N/A	36.2

* *15th and 85th percentile values derived from the cluster analysis with biological variables only.*
** *20th percentile value (minimum value) derived from the cluster analysis with physical variables only and slope of the cumulative distribution (intermediate value).*
*** *5th and 95th percentile values derived from the cluster analysis with physical variables only.*

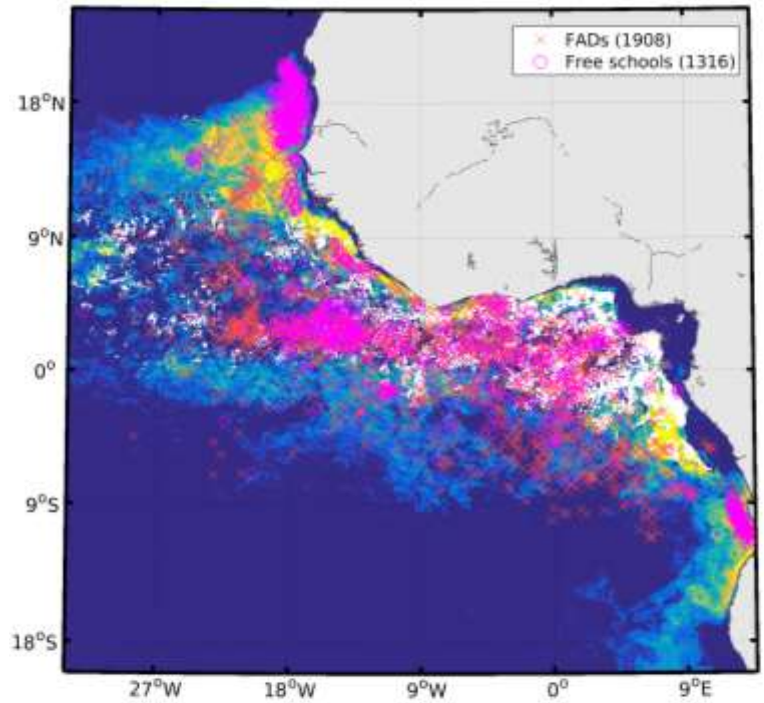
Outputs of the habitat model

Figure 3 presents the seasonal variability of preferred habitat for skipjack tuna (Atlantic: October-March and May-September - Indian: March-May and August-November) with the overlay of the EU purse seiner activity (FAD and FSC sets) in some selected years. In the AO, FSC sets were mostly located in upwelling areas off Mauritania and Gabon in the 2000s and 2010s (Figure 3 a-d), while a smaller fraction of FSC catches that occurred in the Guinea current from October to March in the

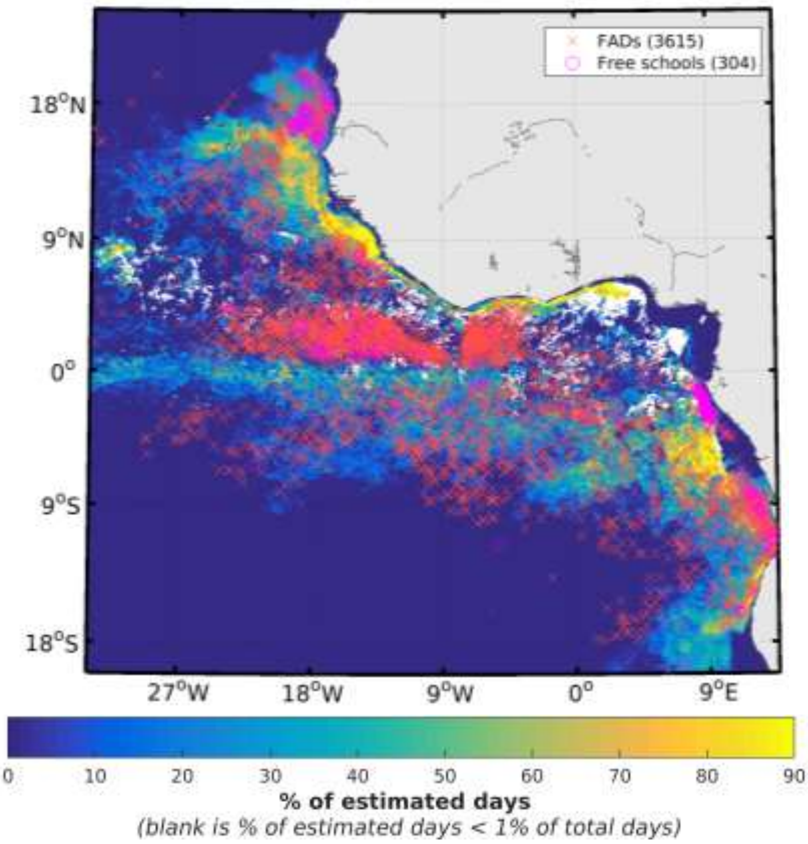
2000s was mostly replaced by FAD fishing in the 2010s (Figure 3 a-b). FAD fishing mostly occurred in the Guinea current during the less productive season from October to March (Figure 3 a-b) and, to a lesser degree, off the upwelling areas (Figure 3 a-d). FAD fishing however severely increased after 2008 from October to March. The period from May to September showed in comparison substantially lower number of sets at a time of maximum extent of favourable habitat with an increased proportion of FAD sets from the 2000ss to the 2010s. Note the important negative anomaly of habitat south of the equator during summer 2004 (Figure 3 c) due to exceptionally high levels of salinity, i.e. above 36 PSU.

In the IO between 2002 and 2012, the number of FSC sets with skipjack substantially decreased and the fraction of FAD sets was always above 90%. Both habitat and fishing grounds in the IO were highly seasonal with an extended habitat from August to November in the northern area, especially off Somalia, and a restricted habitat size from March to May with fishing operations mostly located in the Mozambique Channel. The size of preferred feeding habitat presented however a substantial decreasing trend over that decade with a higher proportion of FADs in relatively unfavourable habitat.

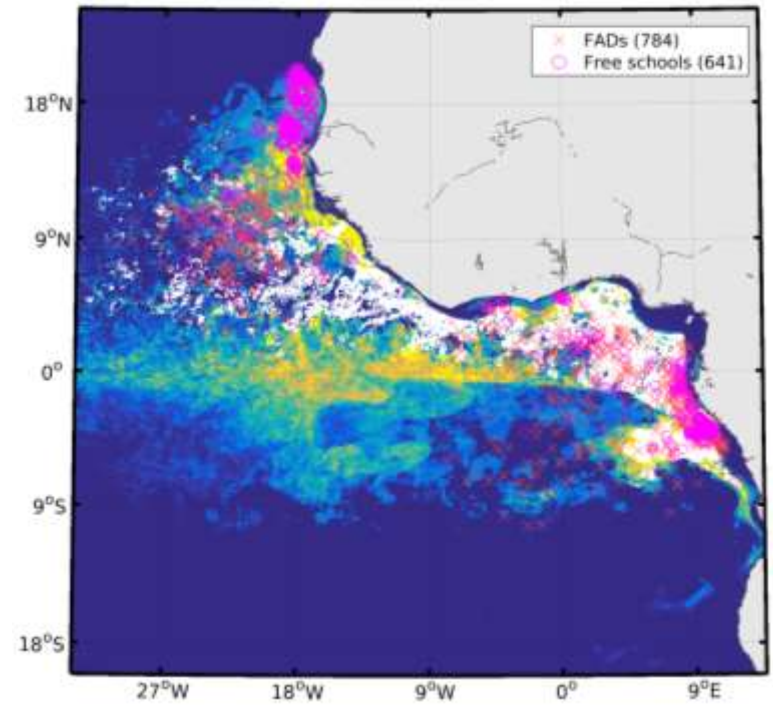
a) Atlantic: skipjack preferred feeding habitat from October to March 2003-2004



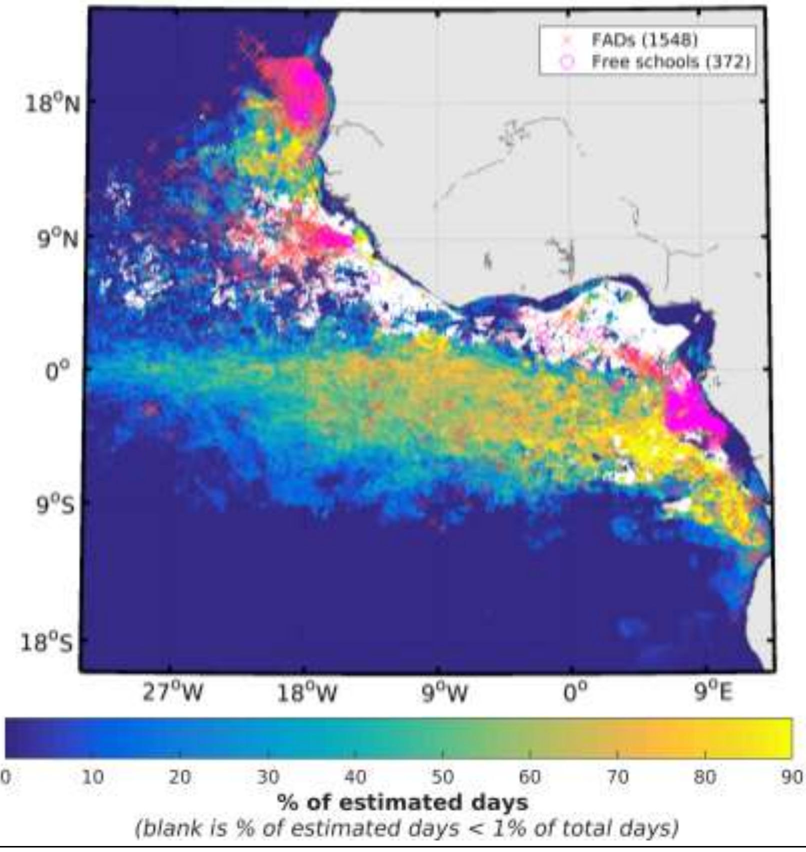
b) Atlantic: skipjack preferred feeding habitat from October to March 2012-2013



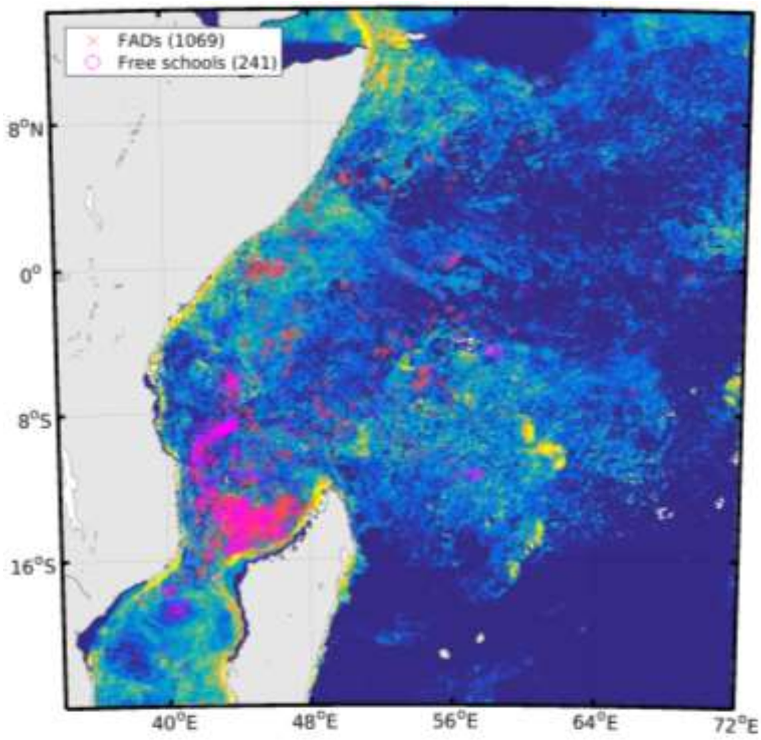
c) Atlantic: skipjack preferred feeding habitat from May to September 2004



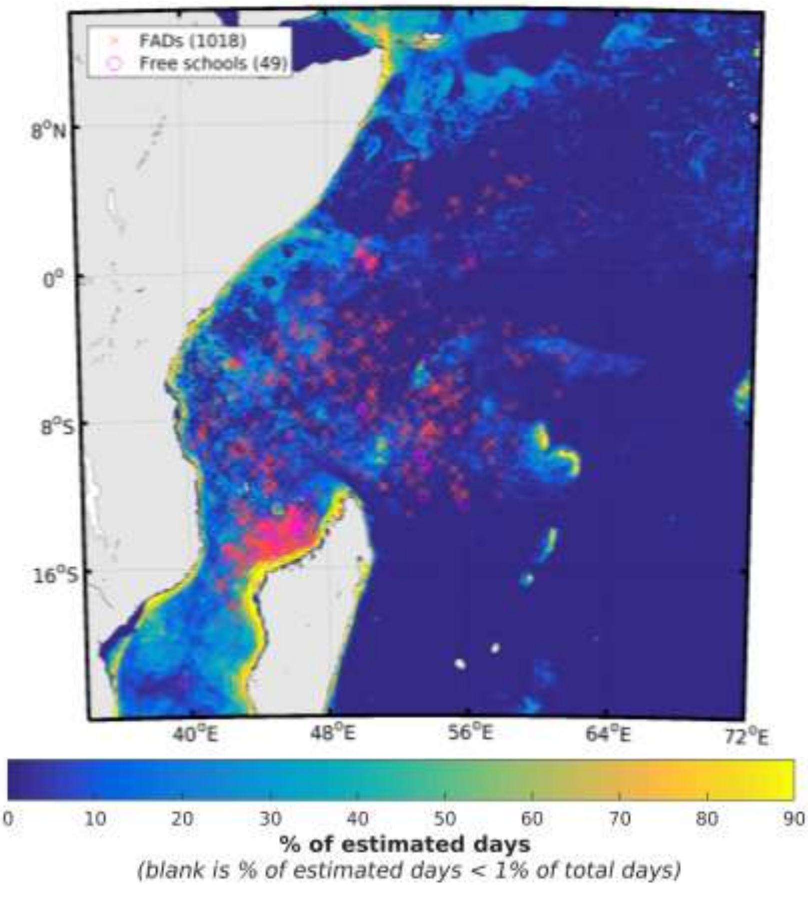
d) Atlantic: skipjack preferred feeding habitat from May to September 2013



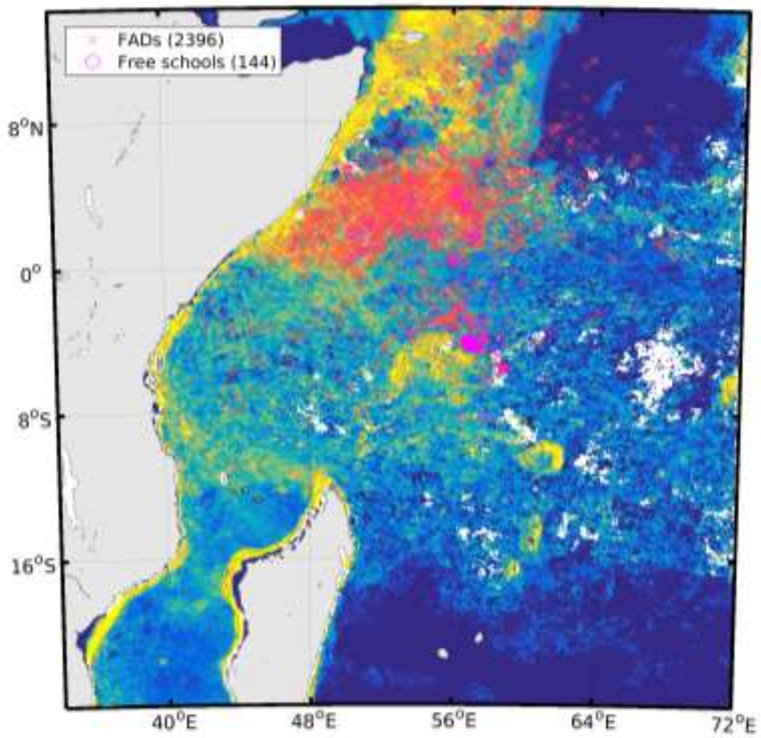
e) Indian: skipjack preferred feeding habitat from March to May 2002



f) Indian: skipjack preferred feeding habitat from March to May 2012



g) Indian: skipjack preferred feeding habitat from August to November 2002



h) Indian: skipjack preferred feeding habitat from August to November 2012

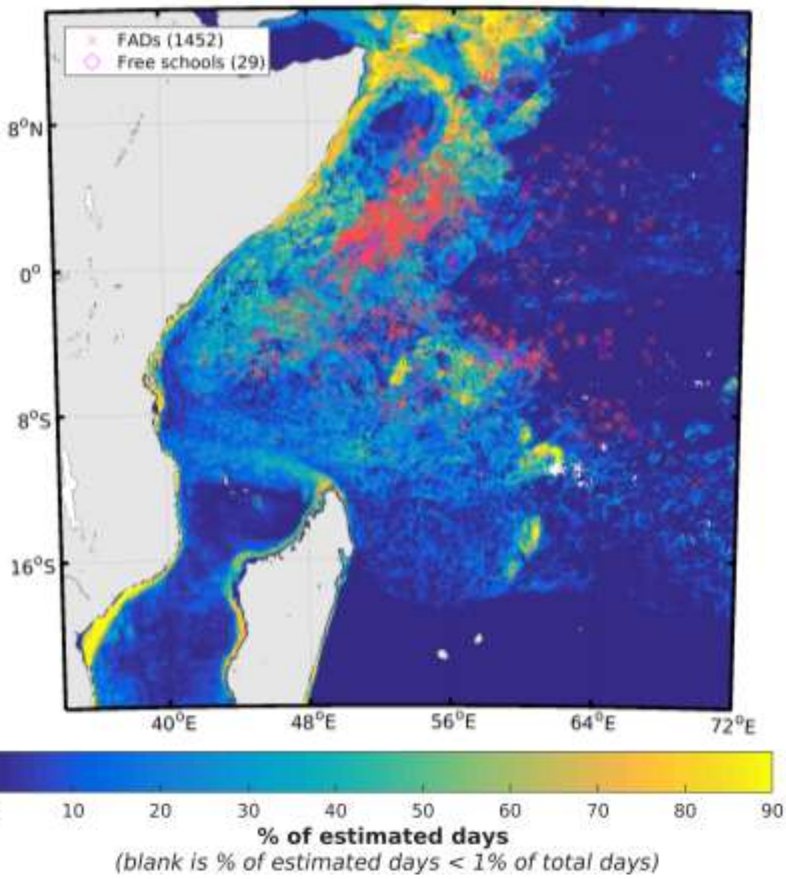


Figure 3 ***Seasonal habitat and catch operations of skipjack tunas in the eastern central Atlantic from October to March 2003-2004 (a), 2013-2014 (b), from May to September 2004 (c), 2014 (d) and in the western Indian Ocean from March to May 2002 (e), 2012 (f) and from August to November 2002 (g), 2012 (h). The FAD-associated presence data (red crosses) and free-swimming schools (pink circles) are overlaid with the respective number of presence data. The month range and years presented were chosen to show the main seasonal fishing and extreme values of habitat size. The preferred habitat is expressed in frequency of occurrence and blank areas correspond to habitat coverage below 1%.***

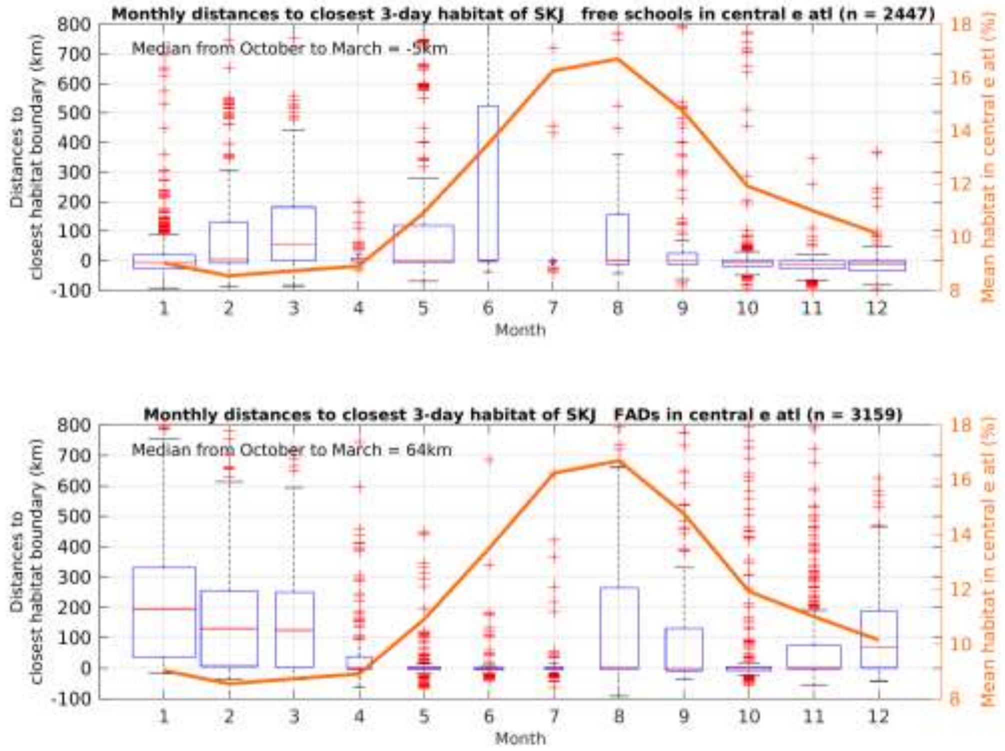
Figure 4 details the monthly distribution of closest distances to favourable feeding habitat of presence data by area and by fishing mode (FSC/FAD). In the AO 61% of free-swimming school sets were within the preferred habitat and, on the other hand, 16% were beyond 100 km of preferred habitat (n = 2,447) while for FAD sets 34% were within the preferred habitat and 34% were beyond 100 km of preferred habitat (n = 3,159). Most FSC sets in the AO were, especially in recent years, done in upwelling areas within short distance to preferred feeding habitat and in months for which the habitat size was restricted (October to March and May, Figure 4a upper graph). High distance of FAD sets to closest feeding habitat was instead observed in particular from January to March at (Figure 4a lower graph). These maximum distance values mostly corresponded to FADs in the Guinea current (Figure 3 a-b). The size of habitat varied from about 9% of the studied area in winter up to about 17% in summer.

In the IO instead, there was much less distance difference between fishing modes with 56% of FSC sets within the preferred habitat and 4% beyond 100 km of preferred habitat (n = 4,255) and 47% of FAD sets within the preferred habitat and 10% beyond 100 km of preferred habitat (n = 26,143) (see Table SI- 1). An inverse relationship between the number of sets (width of boxes in the boxplot) and habitat size was marked in the IO with most FSC sets done from March to May and most FAD sets done from March to May and October-November that corresponded to periods of minimum habitat size (about 5-10% of the studied area against 15 to 25% for the maximum size, Figure 4b).

Figure 5 shows time-series from 1998 to 2015 of annual habitat size and catch rate of skipjack tuna scaled to maximum values in the eastern central Atlantic and western Indian oceans. Habitat size in the AO showed substantial year-to-year variability but no overall habitat trend was observed while catch rates tripled and total catches doubled over the same period. FAD fraction of catches (in weight) of the EU fleet in the AO increased from 50-75% prior 2005 to 88-93% after 2006.

In the western Indian Ocean, after an increasing trend of both the habitat size and catch rates from 1998 to 2003-2004 (+38 to +56% respectively), substantial decreasing trends were observed from 2003-2004 onwards (-42 to -57% respectively). The similar observed trends in the IO led to a correlation coefficient of 0.8 between habitat size and catch rates. Total catches showed wide year-to-year amplitude until 2007 and marked lower levels since then. FAD fraction of catches (in weight) of the EU fleet showed from 2009 onwards an overall increasing trend from about 85% to about 95% of total purse seine catches.

a) Atlantic Ocean



b) Indian Ocean

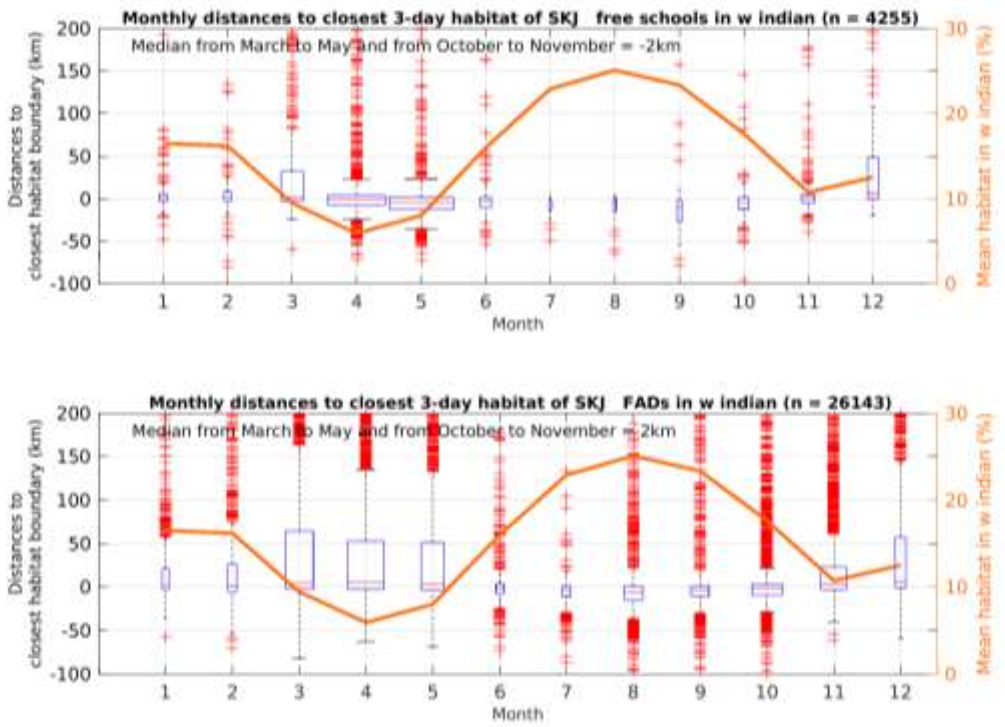
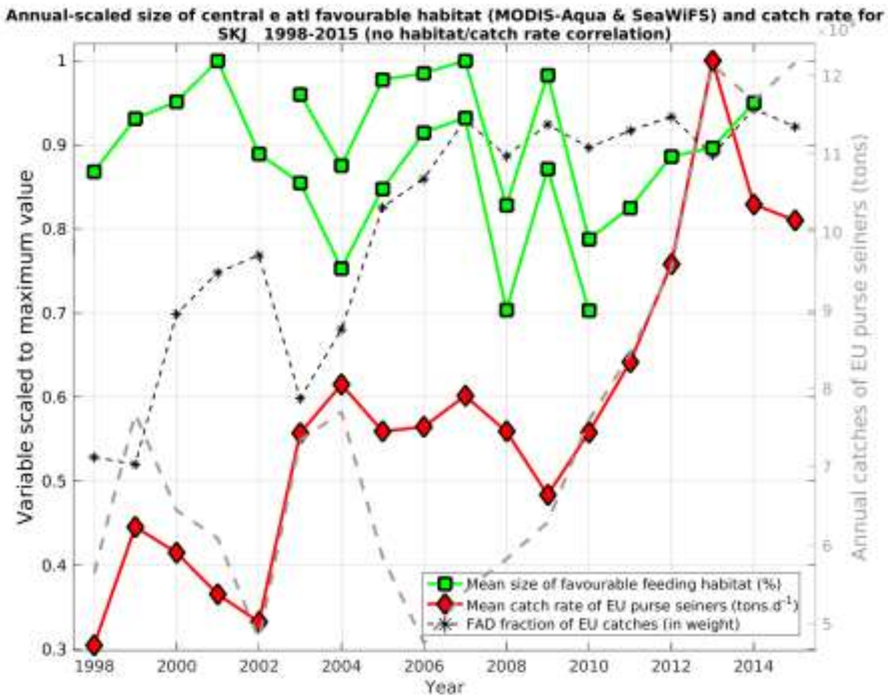
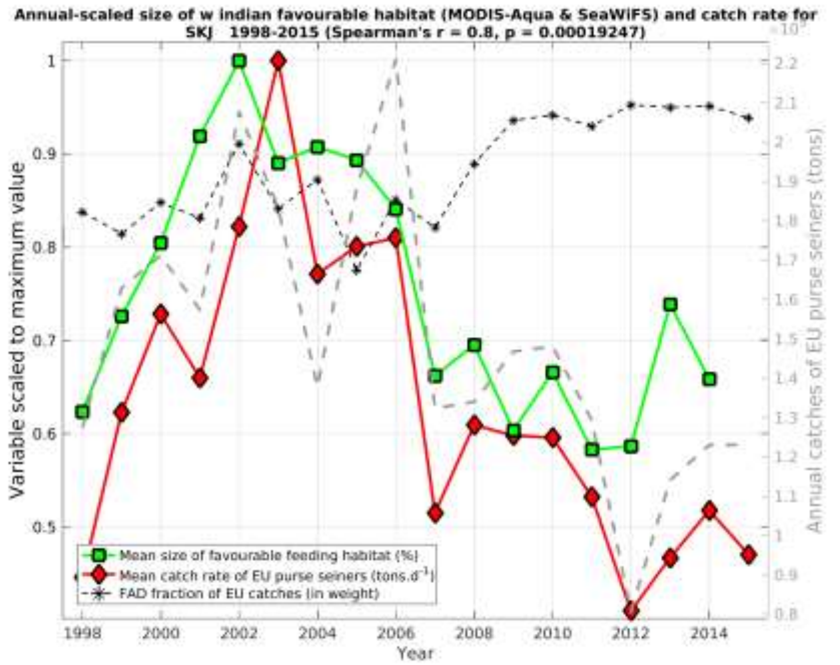


Figure 4 ***Monthly boxplots of distances to closest preferred habitat of presence data associated with free-swimming schools (upper panels) and FADs (lower panels) for skipjack (a) in the eastern central Atlantic and (b) in the western Indian oceans from 1998 to 2014. Negative values correspond to presence data inside the preferred habitat. The width of boxes is proportional to the number of monthly sets while the box length corresponds to the interquartile range (median value in red, whiskers cover 99.3% of data if normally distributed, red crosses are outliers). Monthly habitat size is overlaid (right axis).***



a)



b)

Figure 5 Skipjack annual habitat size (green squares) and catch rate (red diamonds, EU and associated purse seiners) scaled to maximum values and total catches (dashed grey line, EU and associated purse seiners, tons, right axis) in the (a) eastern central Atlantic and (b) western Indian oceans. The proportion of FAD catches in weight (EU purse seiners, black stars) is also overlaid. Two independent time-series of annual habitat size were derived in the Atlantic area, using SeaWiFS (1998-2010) and MODIS-Aqua (2003-2014) sensors respectively, in order to avoid biased estimates when combined (in relation to high cloud cover, see Methods for details).

Discussion

Modelling methods

Compared to Druon et al. (2015), the substantial increased number of presence data (+230%) allowed identification of comprehensive ecological niche of skipjack tuna and a common parameterization between the eastern central Atlantic and western Indian Oceans. The larger latitudinal extent of the presence data as well as the increased number of years taken into account (+6 years, 1998-2014) also contributed to a more robust habitat modelling as a wider range of environmental conditions were analysed. The linear function that links the daily habitat value with the size of chlorophyll-a fronts in the present study (see Figure SI- 2) allowed to consider a more realistic feeding capacity of productive fronts of different size compared to the discrete function of Druon et al. (2015) which identified only two size classes of fronts (small and large). Larger productive fronts are more resilient than features of smaller size and thus more able to maintain well-developed food webs where skipjack can feed for growth and reproduction.

We used two distinct cluster analyses for the biotic and abiotic variables in order to identify the model parameterization as the number of available chlorophyll-related data was much lower (2.5-fold in the IO and 8-fold in the AO) than the physical variables which were always available. The use of a cluster analysis that combined biotic and abiotic covariates would have allowed taking much less physical variability into account. The clustering method ensured to consider under represented habitats in the dataset. The model parameterization avoided to consider the cluster in the biotic analysis that showed absence of chlorophyll-a fronts so that the resulting habitat relates to the feeding behaviour.

Variability of preferred feeding habitat

The common feeding niche identified for skipjack emphasized highly contrasted oceanographic regimes with seasonal occurrence of gyre-type mesoscale productive features in the IO and large scale upwelling systems that seasonally shrink and swell in the AO after the influence of trade wind systems. The ranges of environmental covariates selected for the habitat model agree with field observations and literature although the latter often refers to near lethal levels rather than preferences. The identified range of preferred SST by the cluster analysis of 21.6-30.0°C using ocean modelling data particularly agrees with the extreme range of SST measured at sea by French purse seiners at the location of skipjack tuna sets of 21.5-30.0°C (2.5th percentile in the AO – n = 45247 and 97.5th percentile in the IO – n = 46030 respectively) (IRD, unpublished data). The minimum content of surface dissolved oxygen found by Barkley et al. (1978) for long-term survival of skipjack tuna of 3-3.5 ml.l^{-1} (134-156 mmol.m^{-3}) and as a preference for the world oceans of ca. 3.8 ml.l^{-1} (170 mmol.m^{-3}) found by Arrizabalaga et al. (2015) is consistent with the minimum preferred value of 4.4 ml.l^{-1} (196 mmol.m^{-3}) presently estimated. The preferred range of mixed layer depth from 6 to 158 m agrees with the distribution found by Arrizabalaga et al. (2015) (Supplementary Information) with an upper limit that appears to be near the extreme observed level. The distribution of surface salinity compiled by the same authors for the world oceans (ca. 33.0-37.2 psu) is relatively different from the present study for the lower boundary (30.3-36.2 psu) notably due to the large number of sets in the Gabon upwelling where salinity levels are particularly low. The larger range of SSHa distribution (ca. from -0.4 to 0.8) identified by Arrizabalaga et al. (2015) for skipjack in the world oceans compare to our findings (from -0.20 to 0.67 m) is coherent since our area of interest is more restricted.

Overall, less than 12% of all sets with suitable habitat coverage (n = 36004) were further than 100 km of preferred feeding habitat and a quarter of these remote sets were from FAD fishing in the Guinea Current. The latitudinal migration of skipjack tuna in the IO matched the peaks of productivity predicted by the habitat model off Somalia in summer-autumn and in the Mozambique Channel area in spring. In the AO instead, the match of catches and habitat occurred in the upwelling areas but not in the Guinea Current especially at the peak number of fishing sets from October to March. The Guinea Current in this period is characterized by the absence of productive fronts, high SST, high SSHa and low O2 levels which represent highly contrasted conditions compared to the upwelling areas. As skipjack appear, to some degree, to migrate between the productive and relatively cool upwelling areas and the poorer and warmer equatorial waters (see apparent movements by conventional tagging in Bard, 1986; ICCAT, 2014), and even if this species is known to spawn opportunistically year-round, we question whether the Guinea Current may represent a privileged area for reproduction as these environmental conditions favour larvae survival (thermal stability and lower presence of predators). We noticed in particular that the SST range of most sets in the Guinea Current (5-95^{th} percentile values of 25.2-29.4°C) had little overlap with the SST of sets in the upwelling areas (Mauritanian values are 21.6-25.9°C and Gabon values are 22.6-27.7°C) so that productivity hot-spots for adult feeding may represent a poor environment for larvae survival in the AO in terms of temperature requirements. Larvae of skipjack were found from 24.1 to 28.5°C in the Atlantic except one larva at 22.6°C in the South Atlantic (Kikawa and Nishikawa, 1980) while increased abundances were found in the Pacific for an increasing temperature from 23 to 29°C (Forsbergh, 1989). While the Mauritanian upwelling remained excluded from the optimal SST range for skipjack larvae (from 24.1 to 28.5°C) from January to March, the SST in the Guinea Current was at the upper boundary of larvae preferred levels (from 28.5 to 29.5°C, see figure Figure SI- 4). Furthermore, the lack of lipid storage in skipjack muscle and liver that was observed in the Indian Ocean (Grande et al., 2016; Grande, 2013) severely limits however the effective use of remote feeding grounds for reproduction. Similar environment than in the Guinea Current (no productive fronts, high SST, high SSHa and low O2 levels) was observed as the poorest cluster of presence data in the IO mostly in the Mozambique Channel (mostly from March to May) and, in a sparser manner, in the rest of the studied area (from October to December). These poor environments particularly correspond to the observed distribution of high lipid contents in gonads (highest levels in FSC from April to May in the Mozambique Channel and elevated levels in FAD sets in the Seychelles and Somalia surrounding waters (Grande, 2013). Further analysis is thus required to clarify the ecological role of the Guinea Current for skipjack tuna populations.

The overall model results on the potentials of skipjack for feeding agrees with studies on stomach contents (see review in Dagorn et al., 2013) where, in the AO, tuna associated with floating objects (mostly in the Guinea Current) have more empty stomachs, are in poorer condition and grow slower than fish caught in free-swimming schools (mostly in upwelling areas) (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 tuna associated with drifting FADs in a poor-food area have more empty stomachs than in rich-food area (Jaquemet et al., 2011).

Preferred feeding habitat, skipjack stock and purse seine fishing

The number of fishing sets (independently of catches) was found to be inversely proportional to habitat size on a monthly basis (see Figure 4b, note the width of boxes is proportional to the number of monthly sets), so that habitat shrinkage appears to increase school vulnerability to purse seiner fishing. In other words, fishers appear to seasonally have a greater ability to locate schools (independently of their size) when the feeding habitat is reduced. This is particularly the case in the IO where an important spatial shift of favourable habitat and populations was observed and a large majority of both FSC and FAD sets were at reasonable close distance to favourable habitat (92% and 83% of sets are closer to 50 km respectively). This relation of seasonal vulnerability to fishing is somehow less clear in the AO. If most sets occurred when the size of preferred feeding habitat is lowest from October to March, a substantial number of FAD sets occurred at the maximum size of feeding habitat in August and September. Furthermore, 40% of FAD sets were further than 50 km (mostly in the Guinea Current from January to March) against 21% for FSC sets. The unclear ecological role of the Guinea Current for skipjack as well as the relatively lower available environmental information in that area due to clouds prevents from further interpreting this result on seasonal vulnerability of schools to fishing in the AO.

The significantly positive correlation in the IO of the annual size of feeding habitat with the annual catch rates ($r = 0.8$, $p < 0.001$) and total catches ($r = 0.70$, $p < 0.001$) of purse seiners from 1998 to 2014 is particularly intriguing, and especially the decreasing trend after 2006 (*Figure 5* b). In terms of stock status, the latest Kobe plot available for the IO shows continuous increasing exploitation of skipjack populations from the 1950s to the end of the1990s. There has been since 2000 a sustained fishing pressure, however the latest assessment concluded that skipjack was not overfished and not subject to overfishing in the Indian Ocean. While a decreasing size of preferred feeding habitat appeared to increase the vulnerability of schools to fishing, it also led, at the multi-annual scale, to a decrease of catch rates and total catches after 2006 (*Figure 5* b). If the decrease of total catches could be explained by the reduction of effort since 2008-2010 due to piracy, the decrease of catch rates cannot: it should have been maintained as independent of effort or even increased by a higher fishing efficiency, notably due to an increased use of FADs with more efficient equipment and to the reduction of habitat size in the same period (higher vulnerability to seiners). The decrease of catch rates together with total catches after 2006 suggests the population may have decreased. The significant correlation between annual catch rates and habitat size in a context of an important and sustained fishing pressure in the IO suggests that skipjack population responds rapidly to a change in their environment. Skipjack tunas grow fast and mature early. In the Indian Ocean, 50% of the females would be mature at around 40 cm (Grande et al., 2014; Stéquert and Ramcharrun, 1996). Despite difficulties associated with absolute age estimates and some large inter-individual variability in growth, mark-recapture data suggest a fast growth in the first months of life that would result in skipjack being mature at around 6 months old (Eveson et al., 2015). The overall size of preferred feeding habitat may therefore be interpreted as an indicator of the carrying capacity of the environment to sustain the growth of a skipjack population.

There is no such correlation with the multi-annual habitat size in the AO as the catch rate and total catches substantially increased in the recent years (by ca. 30% and 50% respectively) while the habitat size did not show any overall trend. This is notably due to the importance of fishing agreements in the Atlantic Ocean where access to some coastal fishing grounds to the European purse seine fleet have been variable over time. For instance, recent access to Mauritanian EEZ resulted in a major increase in catch rates of skipjack (de Molina et al., 2014). The latest scientific advice in the AO after the recent increase of catch levels was: "although it is unlikely that the eastern skipjack stock is overexploited, current catches could be at, or even above, the maximum sustainable yield.[…] The Committee recommends that the catch and effort levels do not exceed the level of catch in recent years" (ICCAT, 2015). The recent increase of catch levels in the AO tends to show that the stock could have been underexploited (notably in relation to closure areas) so that no specific correlation with habitat size can be expected.

Acknowledgement

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Supplementary Information

Presence data by fishing mode and area

The presence data for skipjack tuna were relatively well distributed by month and by fishing mode in the Atlantic while the number of FAD-fishing sets represented 87% of all fishing sets in the western Indian Ocean (Figure SI- 1). The ratio of FAD sets increased over time and in particular since 2011 in both areas.

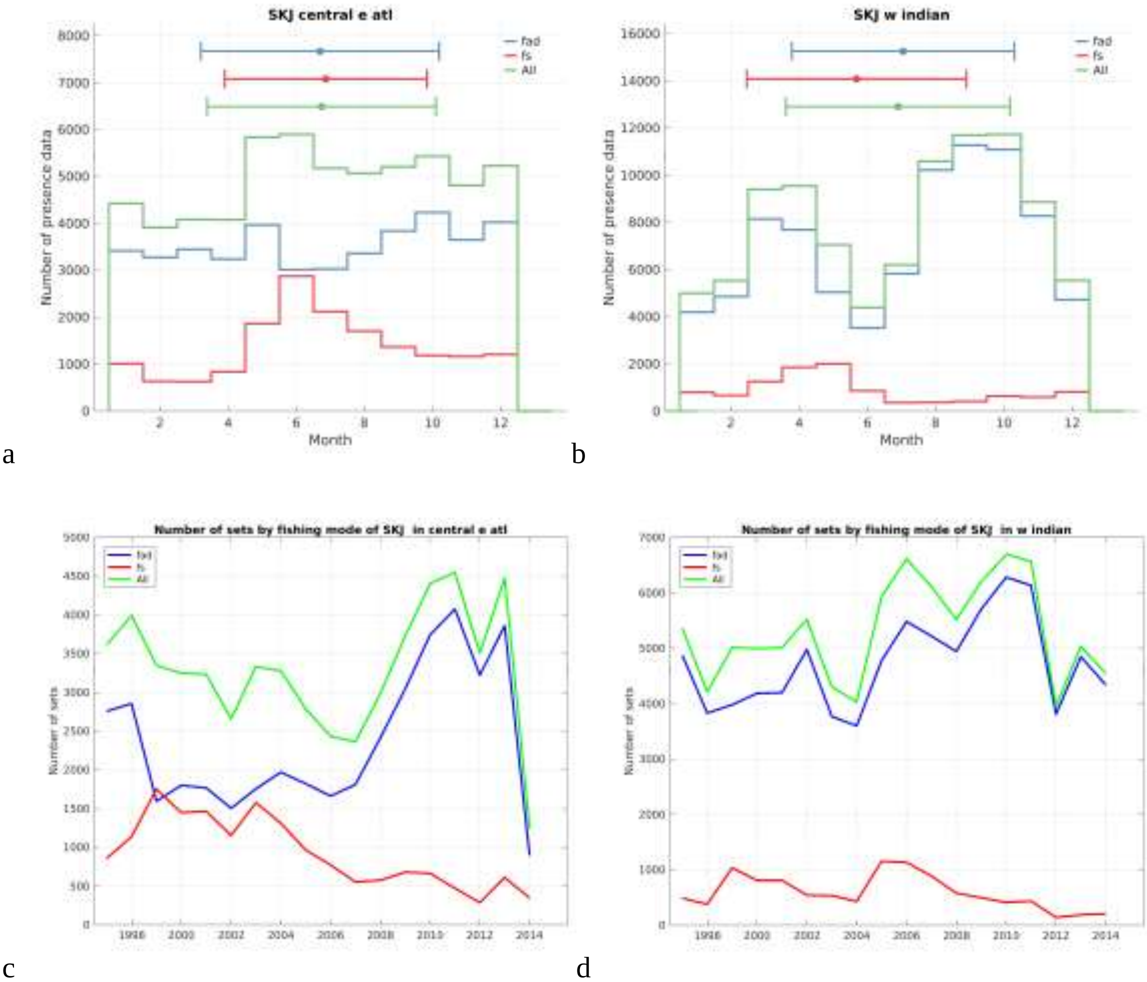
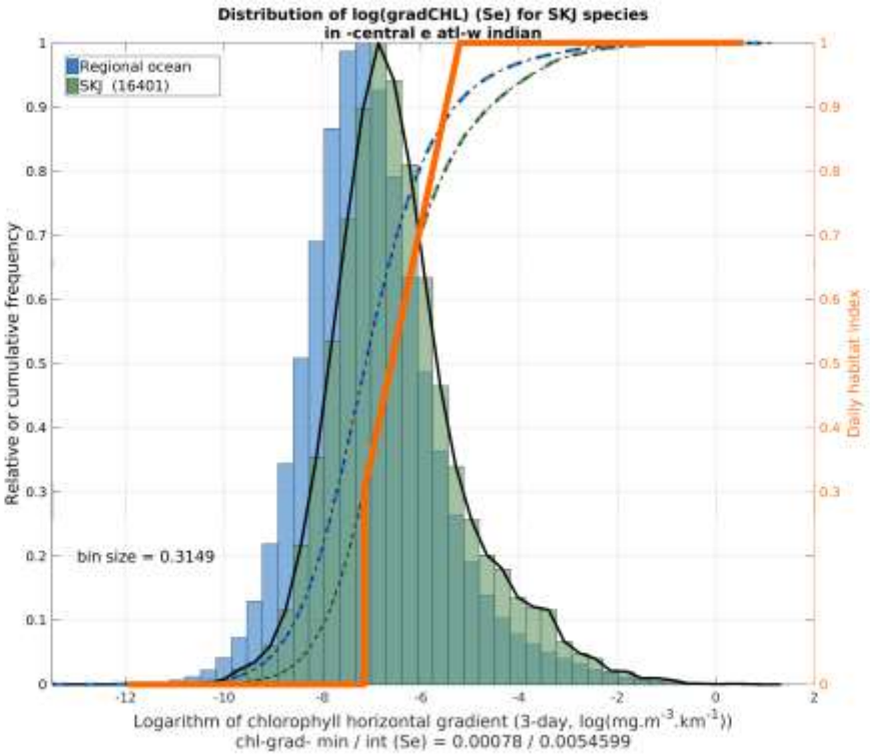
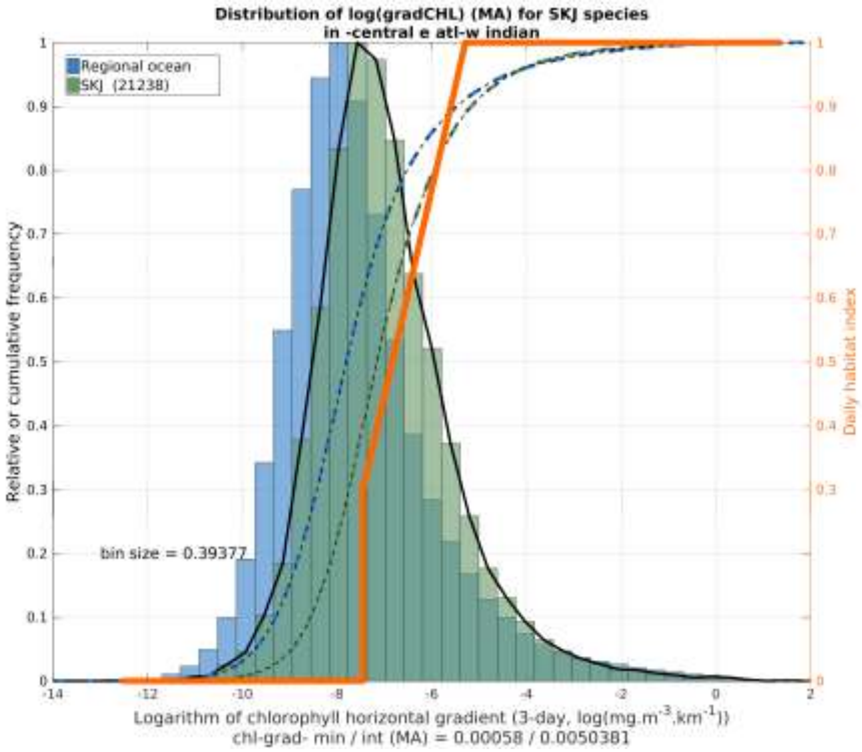


Figure SI- 1 ***Monthly (a-b) and annual (c-d) distribution of skipjack tuna presence data by fishing mode (FSC and FAD) collected in the (a-c) eastern central Atlantic and (b-d) western Indian Oceans (French data from 1998 to 2014 and Spanish data from 1998 to 2013 from purse seiners, mean and standard deviation are shown). Note that no Spanish data were available in 2014 in the Atlantic area.***

Levels of productive habitat and model equations



a) SeaWiFS



b) MODIS-Aqua

Figure SI- 2 *Definition of the daily favourable feeding habitat of skipjack tuna (from 0 to 1, orange line segments) based on levels of horizontal chlorophyll gradient (gradCHL, cumulative frequency and distribution - green dashed line and histogram), thus referring to small and large productive fronts detected using a) SeaWiFS sensor and b) MODIS-Aqua sensor. The cumulative frequency and distribution of gradCHL for both oceans (blue dashed line and histogram) are indicated for comparison with the preferred niche of skipjack tuna. The minimum and maximum levels of gradCHL that define the (0,1) values of the daily habitat index were set using the cluster analysis while the slope between these two points was defined by the maximum slope of the cumulative distribution of skipjack tuna (green dashed line).*

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 defined a daily habitat index that represent an increasing level of potential food availability from the medium-size CHL fronts to the large CHL fronts (on the opposite to Druon et al., 2015 that used three discrete levels). The highly productive habitats were indeed 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. While the minimum and maximum values of gradCHL, that define the (0,1) daily habitat index, were identified using the cluster analysis, the slope of daily habitat relating these two points (orange line segments, Figure SI- 2) was defined by the maximum slope of the cumulative frequency of skipjack tuna CHL gradient in logarithm from both oceans (green dashed line, Figure SI- 2). The discontinuity of the daily habitat index between 0 and 0.3 (no favourable habitat in that range) reflects the occurrence of the smallest CHL fronts that likely do not have the resilience to sustain a well-developed food web.

The value of the productive habitat was then weighted by the abiotic limitations (by 0 or 1). The feeding habitat was thus defined by the model grid cells that daily satisfy the suitable environmental conditions following the equations:

$$Feeding\ Habitat_{Day,Cell} = Productive\ Habitat_{0\ to\ 1} * Abiotic\ Factor_{range_{0/1}}$$

With:

$$Productive\ Habitat_{0\ to\ 1} = CHL_{min/max_{0/1}} * gradCHL_{min/int/max_{0\ to\ 1}}$$

$$\begin{aligned} Abiotic\ Factor_{range_{0/1}} &= SST_{min/max_{0/1}} * SSHa_{min/max_{0/1}} * MLD_{min/max_{0/1}} * O2_{min_{0/1}} \\ &* SSS_{min/max_{0/1}} * SSC_{min/max_{0/1}} \end{aligned}$$

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

Model evaluation

Table SI- 1. Fraction of presence data within preferred habitat and further than 100 km of preferred habitat (%) by area and fishing mode.

$F_{<0km}$: Fraction of presence data within 3-day preferred habitat (%) ***$F_{>100km}$: Fraction of presence data further than 100 km of 3-day preferred habitat (%)***		**Central Atlantic** *n*	***$F_{<0km}$*** (in habitat)	***$F_{>100km}$*** (away from habitat)	**Indian Ocean** *n*	***$F_{<0km}$*** (in habitat)	***$F_{>100km}$*** (away from habitat)
skipjack tuna	Free-swimming schools	*2447*	**61%**	**16%**	*4255*	**57%**	**4%**
	Fishing Aggregating Devices	*3159*	**<u>34%</u>**	**<u>34%</u>**	*26143*	**47%**	**10%**

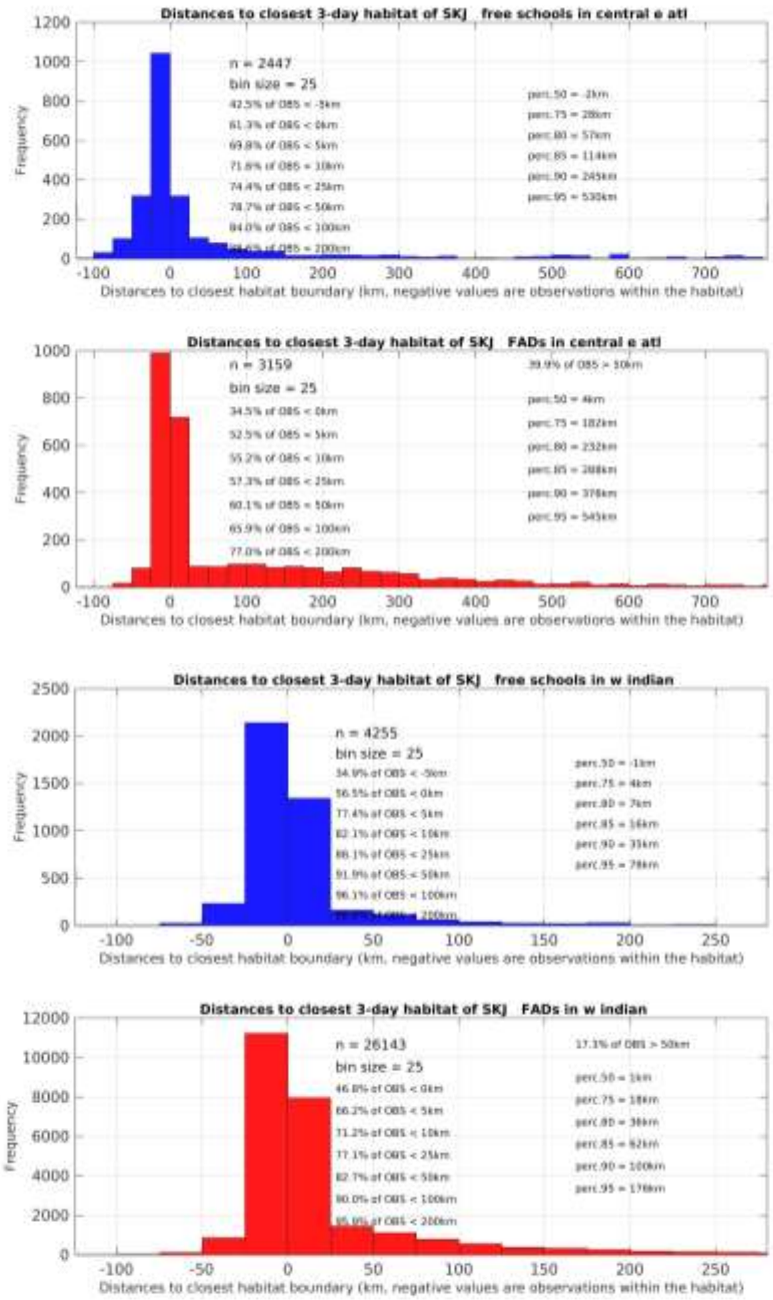


Figure SI- 3 Detailed histograms and statistics of distances of presence data (FSC – upper blue graph, FAD – lower red graph) to closest favourable feeding habitat boundary for a) eastern central Atlantic and b) western Indian Oceans. Negative values of distances correspond to presence data within the favourable habitat.

SST and skipjack larvae preferences

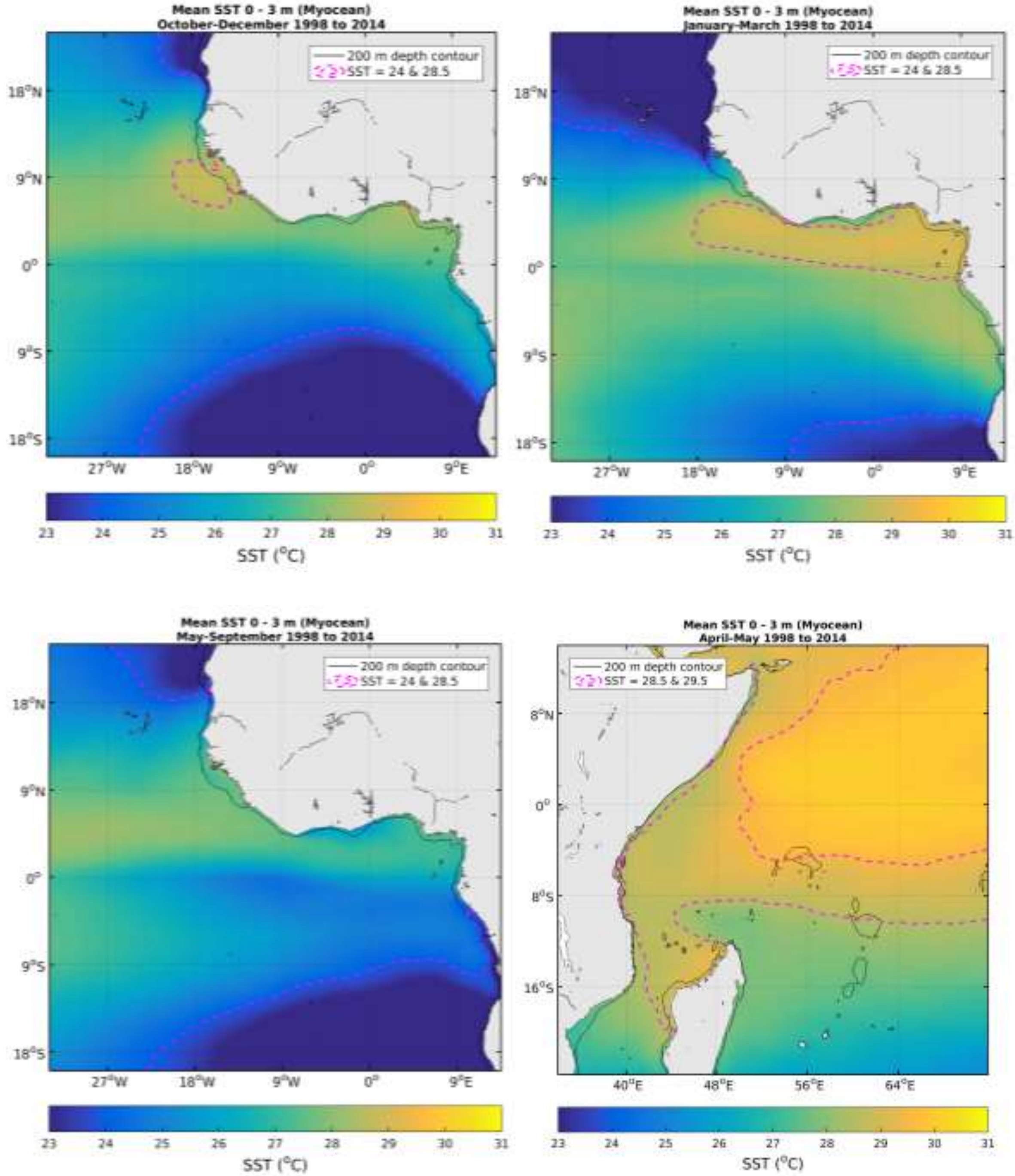


Figure SI- 4 Mean SST from 1998 to 2014 in the eastern cental Atlantic for October-December, January-March and May-September and in the western Indian Ocean for April-May. Lower (24°C) and upper range (28.5-29.5°C) of preferred SST levels for skipjack larvae are shown where relevant. SST levels in the Guinea Current from January to March are mostly in the range from 28.5 to 29.5°C. See Discussion for details.