

Habitat modeling for the blue shark (*Prionace glauca*) by sex and size classes in the Indian Ocean

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Abstract

This paper is a regional focus in the Indian Ocean (IO) of a global analysis of blue shark (*Prionace glauca*) habitat by size and sex classes (small juveniles, large juvenile males and females, adult males and females, Druon et al., in prep.). The habitat modeling, calibrated using fishing interaction data (i.e., fishery observer data) and electronic tracking data, uses two feeding proxies, i.e., the satellite-derived productivity fronts in mesotrophic areas and the mesopelagic micronekton in oligotrophic areas, and two abiotic variables, i.e., temperature and sea surface height anomaly. The temperature niche includes sea surface temperature (*SST*) and temperature 100 m below the mixed layer depth ($T_{mld+100}$) to ensure that both the horizontal and vertical extent of this thermoregulated species' habitat are covered. Here we show that the overall feeding niche displays highly diverse biotic and abiotic conditions although the blue shark population tends to progress from mesotrophic and relatively cold surface waters for the juvenile stages (North and South of IO) to more oligotrophic and warm surface waters for the adults (central IO). However, warm temperatures or low productivity limit the habitat of mostly the juveniles in the Central and/or North IO mainly in Apr-Jun and Jul-Sep. Large females tend to have more habitat overlap with small juveniles than large males, notably

driven by temperature preferences. Large females also display an intermediate range of *SST* avoidance resulting in an important lack of habitat overlap with large males mostly in Jan-Mar and Apr-Jun in the South IO around 30°S. In Oct-Dec however, fisheries observer data show a higher habitat overlap between large males and females in this intermediate *SST* range, which may correspond to mating. These results on blue shark habitat provide key elements useful to stock assessment models and potential leads for conservation and management measures of this near-threatened species.

Keywords

Blue shark | *Prionace glauca* | Ecological niche | Habitat | Chlorophyll-a gradient | Mesopelagic micronekton | Mesotrophic | Oligotrophic | Water temperature

1. Introduction

The blue shark (*Prionace glauca*) is a ubiquitous elasmobranch caught by major pelagic fisheries (e.g., longline, handline) in the IOTC area of competence (IOTC, 2017). Similar to other shark and bycatch species in the Indian Ocean, the stock assessment (SA) for the blue shark is conducted approximately every four years by scientific experts at the occasion of the annual Working Party on Ecosystem and Bycatch (WPEB). The last SA was done in 2017 and scientists concluded that the blue shark stock was neither overfished nor subject to overfishing (green status on Kobe plot), however, trajectories indicated that under the current catch levels the blue shark might become overfished and subject to overfishing in the future (IOTC, 2017). A new evaluation of the status of the blue shark stock in the Indian Ocean will be evaluated this year (2021).

Bycatch species, including blue shark, are generally “data-poor”, making SA relatively difficult and limited. In addition, the scientific knowledge on the biology and ecology (reproductive and growth parameters, seasonal distributions, etc.) of such species is generally poor and can sometimes be completely lacking while this knowledge is essential for SA models, especially for age-structured and spatially explicit models.

Only a few studies on the blue shark distribution patterns are available at the scale of the Indian Ocean basin based on data from fishery observers and scientific surveys (e.g., Mejuto and Garcia-Cortés 2005; Coelho et al. 2018). Coelho et al. (2018) describe a latitudinal gradient with larger blue sharks in the equatorial and tropical areas while small specimens occur in more temperate waters, where nursery areas would also be found (near South Africa and the southwest tip of Australia). Patterns related to potential mating and reproductive areas and seasons for the blue shark remain at this stage poorly known in the Indian Ocean. An alternate approach to the analysis of fishery interaction data would be the modeling of the habitat and ecological niche of blue shark, which has never been done for this species in the Indian Ocean.

In this paper, we present the habitat modeling of the blue shark by size and classes (small juveniles, large juvenile males and females, adult males and females) using two feeding proxies, i.e., the satellite-derived productivity fronts in mesotrophic areas and the mesopelagic micronekton in oligotrophic areas, and two abiotic variables, i.e., temperature and sea surface height anomaly. The temperature niche includes sea surface temperature (*SST*) and temperature 100 m below the mixed layer depth ($T_{mid+100}$) to ensure that both the horizontal and vertical extent of this thermo-regulated species' habitat are covered. The model was calibrated by size and sex classes using fishing interaction data (i.e., fishery observer data) and electronic tracking data. Results are discussed in light of the respective seasonal distributions of the different size and sex classes. Such results improve scientific knowledge on that species' ecology, allowing scientists to provide informed and useful advice for the conservation and management of this relatively common species in IOTC fisheries.

2. Methods

The global habitat analysis for the blue shark (Druon et al. in prep.) consisted in identifying the environmental niche for each size and sex class by comparing a large set of occurrence data (fishing interaction data and track data) with fields of biotic (chlorophyll-a fronts, mesopelagic micronekton) and abiotic (temperature at the surface and in the upper mesopelagic layers, sea surface height anomaly) variables. We particularly accounted for the ecological traits of the species and literature knowledge that highlighted some under-sampling of extreme environments in our presence dataset.

2.1. Blue shark occurrence data

We collected extensive blue shark presence data in the main oceans and seas for the global model calibration and validation, mostly from observer programs of the longline and purse seine fisheries and from electronic tagging programs. The collection of occurrence data has 589,450 observations in the global ocean, and the total number of observations available with appropriate information (small juveniles with size information, larger blue sharks with size and sex, and high-position quality for electronic tags) is of 265,595. The Indian Ocean dataset contains a total of 6,473 presence data including seven individual electronic tags tracks (PSAT tags). Only data (electronic tag data and fishery observer data) for which geographical precision was below 50 km were considered in the study (as longline sets can sometimes be over 100 km). These data were stratified by size and sex classes as the following (number of presence data in the global ocean and in the IO): (i) the small juveniles (hereafter SJ) with fork length (hereafter FL) below 125 cm (n = 60,904; 306 in the IO), (ii) the large juvenile females (hereafter LJF) with FL from 125 to 180 cm (n = 54,611; 291 in the IO), (iii) the large juvenile males (hereafter LJM) with FL from 125 to 190 cm (n = 90,792; 2,014 in the IO), (v) the adult females (hereafter AF) with FL above 180 cm (n = 29,773; 1,017 in the IO), and (vi) the adult males (hereafter AM) with FL above 190 cm (n = 29,515; 2,845 in the IO).

2.2. Environmental variables and ecological niche

The modeling of blue shark feeding habitat was guided by the main ecological traits of the species (see full details in Druon et al. in prep.). The methodology used to derive the habitat modeling, including model calibration and validation, was developed globally and applied in the IO for the purpose of this regional analysis. Blue shark is known to have an extended habitat from equatorial to temperate latitudes (Vandeperre et al. 2014; Maxwell et al. 2019) with contrasting environments in terms of productivity. Large predators, and blue shark in particular, were shown to be attracted by mesoscale features such as fronts or eddies (Scales et al. 2018; Braun et al. 2019) in relatively rich waters (mesotrophic), but also to evolve in relatively poor surface waters (oligotrophic) and to feed in the mesopelagic layer. We, therefore, retained specific feeding proxies (surface chlorophyll-a fronts and mesopelagic micronekton) for the habitat modeling to cover these contrasted productive environments. This species displays diving profiles that reveal a hunting tactic associated with an important behavioral thermoregulation (Campana et al. 2011; Braun et al. 2019). Water temperature while diving at various depths within the mesotrophic or

oligotrophic environments, as well as sea surface height anomaly in regards to the mesoscale activity, both clearly play a key role in the global distribution of blue sharks and were selected as highly discriminant variables in the habitat modeling.

In mesotrophic areas, the daily detection of productive oceanic features (chlorophyll-a fronts) from ocean color satellite sensors (currently MODIS-Aqua) is a good generic proxy for food availability to fish populations (Druon et al. 2021). Being active long enough (from weeks to months) to allow the development of mesozooplankton populations (Druon et al. 2019), productivity fronts were shown to attract epi- and mesopelagic fish and top predators (Briscoe et al. 2017; Druon et al. 2017; 2016; Olson et al. 1994; Panigada et al. 2017; Polovina et al. 2001). After a first development phase of productivity fronts (3-4 weeks; Druon et al. 2019), the substantial levels of mesozooplankton biomass reached in the resilient chlorophyll-a fronts may represent concomitant feeding hotspots for the small pelagic fish, with the active aggregation of highly mobile predators (e.g., bluefin tuna in Druon et al. 2016; fin whale in Panigada et al. 2017). Daily chlorophyll-a (CHL , $\text{mg}\cdot\text{m}^{-3}$) data were gathered from the MODIS-Aqua ocean color sensor (2002–2018; $1/24^\circ$ resolution) using the Ocean Color Index (OCI) algorithm (Hu, Lee and Franz 2012) and extracted from the NASA portal (<https://oceancolor.gsfc.nasa.gov/13/>) with the archive reprocessing of January 2018. Small and large chlorophyll-a fronts were derived from and refer to variable levels of chlorophyll-a gradient values. The lower chlorophyll-a gradient level, the lower productivity front resilience and potential feeding opportunity for predators, and vice-versa. The histogram distribution of these gradient values was used in log-form to derive a dependent linear function, which is the main component of the daily feeding habitat in the mesotrophic environment ($CHL > CHL_{min}$). In the oligotrophic environment instead ($CHL < CHL_{min}$), the estimate of mesopelagic micronekton (*'micronekton upper mesopelagic & micronekton migrant upper mesopelagic'*, in wet weight $\text{g}\cdot\text{m}^{-2}$) extracted from the EU-Copernicus Marine Environment Monitoring Service model (<https://marine.copernicus.eu/access-data>) was used. As for feeding proxies for the habitat model, we therefore used the mesopelagic micronekton in oligotrophic areas ($CHL < CHL_{min}$) and productivity fronts in mesotrophic areas ($CHL > CHL_{min}$), CHL_{min} being a relatively low chlorophyll-a threshold. The value of CHL_{min} for each blue shark class was identified using a cluster analysis with the global dataset.

The discriminant abiotic variables for the habitat model (based on a cluster analysis, see Druon et al. in prep.) were the sea surface temperature (SST), the sea surface height anomaly (SSH_a), and the temperature 100 m below the mixed layer depth ($T_{mid+100}$). Water temperature is strongly

influencing blue shark distribution due to thermoregulation needs (Campana et al. 2011; Braun et al. 2019). *SSHa* is mainly influenced by seasonal changes in temperature and the geostrophic currents that characterize eddies and gyres, which are known to shape the vertical and horizontal distribution of the full pelagic food web (Polovina et al. 2001; Tew Kai and Marsac 2010; Godø et al. 2012). *SSHa* was overall shown to impact blue shark habitat (Selles et al., 2014; Vandeperre et al. 2014). A simple range of favorable conditions for each abiotic variable is used to, as a result, exclude the unsuitable abiotic habitats, while the biotic variables were used as feeding proxies, thus perceived as attracting factors. Finally, the temperature at 100 m below the mixed layer depth ($T_{mld+100}$) showed to be a relevant variable for identifying the upper depth of the mesopelagic layer, from which micronekton was extracted (about 138 ± 32 m). This upper depth of the mesopelagic layer corresponds to a high time spent during the night by large blue sharks, while deeper dives during the day coexist with shallower dives in response to thermoregulation needs (Campana et al. 2011; Braun et al. 2019). Consequently, $T_{mld+100}$ was considered to represent an averaged-dive temperature. We selected the same minimum temperature value for $T_{mld+100}$ than for *SST* since the minimum levels of *SST* and $T_{mld+100}$ were considered as surface and mean-dive extreme temperature tolerance for each size and sex class. The fields of temperature, mixed layer depth, and sea surface height anomalies were extracted from the EU-Copernicus Marine Environment Monitoring Service global model (<https://marine.copernicus.eu/access-data>).

All biotic and abiotic variables were integrated (mean value) over a 25 km radius centered on each presence data for the identification of the environmental envelope. This radius was selected to account for the geolocation precision of most of the presence data (about < 50 km).

The envelope modeling has two main components depending on the level of surface chlorophyll-a level: the oligotrophic ($CHL < CHL_{min}$) and mesotrophic ($CHL_{min} < CHL < CHL_{max}$) feeding habitats that use mesopelagic micronekton and productivity fronts (chlorophyll-a horizontal gradients), respectively (Figure 1). Both components were associated with the abiotic variables, i.e., temperature and *SSHa*, where a value of 1 was set for favorable levels and a value of 0 otherwise, therefore excluding unfavorable levels from the habitat. As described above, a minimum temperature value in the upper mesopelagic layer ($T_{mld+100}$) was used to exclude too cold waters for diving blue sharks in oligotrophic environments (mesopelagic micronekton feeding proxy), while a suitable range of *SST* was used to exclude unsuitable low and high levels from the habitat in mesotrophic waters (chlorophyll-a front feeding proxy). Where an avoidance by a specific class

of a range of sea surface temperature was detected (large blue shark females, LJF and AF), the associated daily feeding habitat in this intermediate SST range was set to 0.

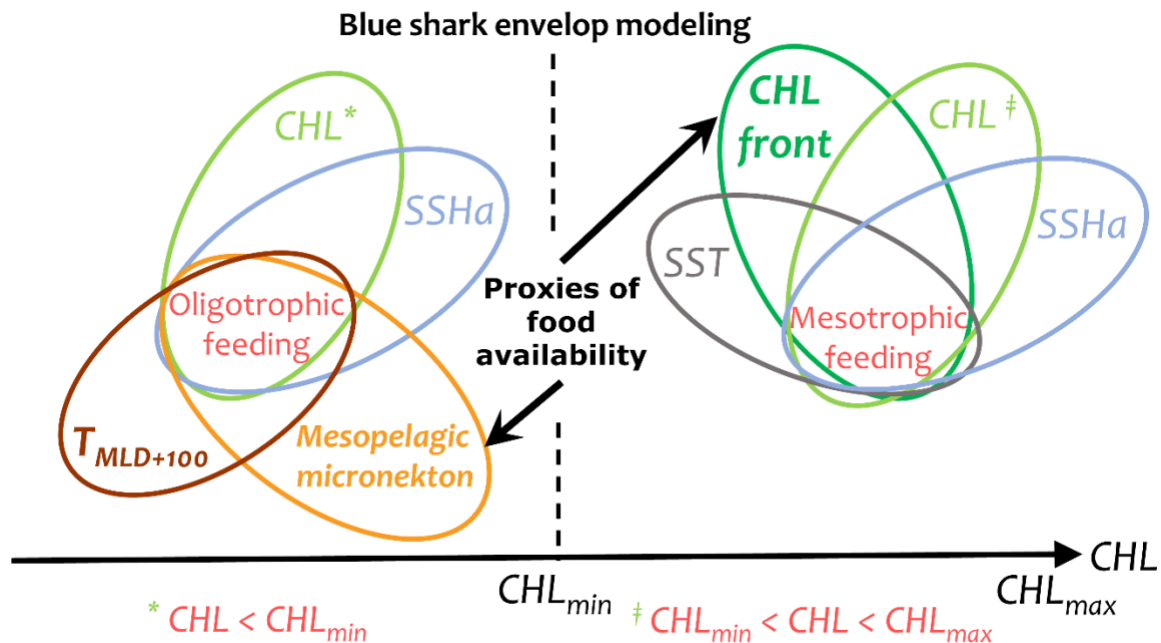


Figure 1. Scheme of the blue shark envelope modeling linking the environmental variables and the ecotrophic types of feeding in oligotrophic ($CHL < CHL_{min}$) and mesotrophic ($CHL_{min} < CHL < CHL_{max}$) environments with mesopelagic micronekton and productivity fronts (chlorophyll-a horizontal gradients) as feeding proxies, respectively. The abiotic variables (SST, $T_{mld+100}$ and SSHa) were used to exclude unsuitable environments. CHL: surface chlorophyll-a content; SST: sea surface temperature; $T_{mld+100}$: Temperature 100 m below the mixed layer depth; SSHa: sea surface height anomaly.

The habitat model for both feeding proxies has two parameters besides the distinct CHL range on which they apply ($CHL < CHL_{min}$ for mesopelagic micronekton and $CHL_{min} < CHL < CHL_{max}$ for productivity fronts): a minimum and intermediate value of the mesopelagic micronekton ($MMnekton$) and horizontal gradient of chlorophyll-a ($gradCHL$). These minimum and intermediate threshold values for each feeding proxy define the slope of daily habitat quality for feeding in the oligotrophic and mesotrophic environments (see Druon et al., in prep. for details). Overall, the daily feeding habitat function for both feeding proxies ($MMnekton$ and $gradCHL$), which is based on the distribution of these proxies at the location of presence data (at low and

high *CHL* levels, respectively), quantitatively reflect the level of feeding opportunities. However, no direct correspondence between these oligo- and mesotrophic feeding proxies could be made. Nevertheless, even if the blue shark of all classes are present in highly variable environments, this species globally appears to modify its feeding strategy in its lifespan from relatively cold and rich environments (i.e., mesotrophic areas simulated by productivity fronts) to warmer and poorer surface waters (i.e., oligotrophic areas simulated by mesopelagic micronekton) so that the energy intake by food always compensates the energy spent for thermoregulation, movements and growth.

Overall, we thus defined a daily feeding habitat index that represents increasing levels of predicted food availability within each feeding proxy depending on the *CHL* level, from small to large productivity fronts or from low to high abundance levels of mesopelagic micronekton. The value of the daily productive habitat index from 0 to 1 was then weighted by the various abiotic limitations (by 0 or 1 if out- or inside the favorable range, respectively). The time composites are expressed in frequency of suitable habitat occurrence (%) computed as a mean of 0-to-1 daily values quantitatively associated with the respective feeding proxy. The multi-annual seasonal time composites were computed from the monthly means in order to set an equal weight between months, therefore compensating from the seasonal lower habitat coverage. This is particularly the case during Jan-Mar in the North IO due to the higher cloud coverage associated with the monsoon that impedes the satellite chlorophyll-a estimate. We presently focused the model validation in the Indian Ocean using literature and presence data. Thorough quantitative model performance is performed in the publication presenting the global model (Druon et al. in prep.).

3. Results

The results presented in this paper are a focus on the Indian Ocean of the global blue shark habitat modeling work that is fully detailed in Druon et al. (in prep.) and for which we briefly summarize here the results regarding the main seasonal habitat differences among the considered size and sex classes. The distribution of blue shark presence over both feeding proxies and *CHL* levels shows that adults are mostly located in oligotrophic environments with higher *SST* levels, while small juveniles display a higher preference for mesotrophic environments with lower *SST* levels, while large juveniles have a balanced presence in both ecotrophic environmental types. Blue shark populations, therefore, tend to move from a mesotrophic to an oligotrophic

environment throughout their lifespan, which generally are in higher and lower latitudes, respectively. All stages are nevertheless present in both environments revealing the particularly large distribution and environmental tolerance of the blue shark. A major peculiarity of the environmental-presence data relationship regards the avoidance of large juvenile and adult females in an intermediate range of *SST*. The results of the global model highlight that large females are three to four-fold less present than large males in the range of 21.7-24°C and 22.1-23.4°C for LJF and AF, respectively (5% presence for LJF compared to 17% for LJM, and 4% presence for AF compared to 13% for AM). The impact of this apparent avoidance by large females is presented in the mean seasonal habitat maps (Figures 3-6) showing the isotherms of the avoided range for the respective size classes.

The favorable feeding conditions for the blue shark (by size and sex classes) were extrapolated in the environmental space for the period 2003-2018 in the Indian Ocean. The mean seasonal distribution of feeding habitat for the five blue shark classes (2003-2018, in frequency of suitable habitat occurrence, %, Figures 2-6) highlights the main habitat similarities and differences among classes. Presence data are represented as pink dots for observer data and colored line transects for the electronic tagging data. The chlorophyll-a isocontours of CHL_{min} outline on each map the distribution of feeding habitat arising from the mesopelagic micronekton (oligotrophic) and productivity front (mesotrophic) proxies ($CHL < CHL_{min}$ and $CHL_{min} < CHL < CHL_{max}$, respectively). The generally higher levels of feeding habitat in the oligotrophic environments reflect the more stable (although relatively lower) estimated levels of mesopelagic micronekton biomass compared to the presence of productivity fronts in mesotrophic areas.

Oligotrophic feeding mostly occurs for all classes in the Central Indian Ocean, while mesotrophic feeding generally arises in the outskirts of the basin. However, both ecotrophic types display a seasonal contraction, mostly on the northern boundary, and the mesotrophic habitat shows a maximum extent from October to March. The blue shark habitat in the Indian Ocean is generally widely spread from about 45°S to 25°N. This habitat is limited by temperature in the south and shows major unsuitable areas for feeding due to very high *SST* levels in the north of the IO (see in Figure 2 the *SST* isocontour of 28.7°C enhancing the mean upper *SST* limitation between all classes, 28.7°C ±0.38) or due to low productive areas in the latitudes from 15°S to 25°S. These unsuitable habitats have a larger extent for the males compared to females in the IO. The other main difference between size and sex classes arises from the avoidance of females in the intermediate range of *SST* levels. The *SST* avoidance isocontours of females shown on the same size-class males' maps (Figures 3-6) show a major lack of habitat overlap between males and

females mostly from January to June. Additionally, the maximum difference between classes of lowest preferred temperature (*SST_{min}*) is between the adult males (14.8°C) and the small juvenile (12.3°C), and large juvenile females (11.6°C). This implies a substantial lack of habitat overlap between these classes in the southern IO (Figures 2, 3 and 6, the 14.8°C isocontours are shown in Figure 2). Historic observer data (Coelho et al. 2018) agree with both the intermediate SST avoided by females and minimum SST levels defined in the global analysis in Jan-Mar and Oct-Dec in the South IO, respectively (Figures 7-8, see discussion for interpretation).

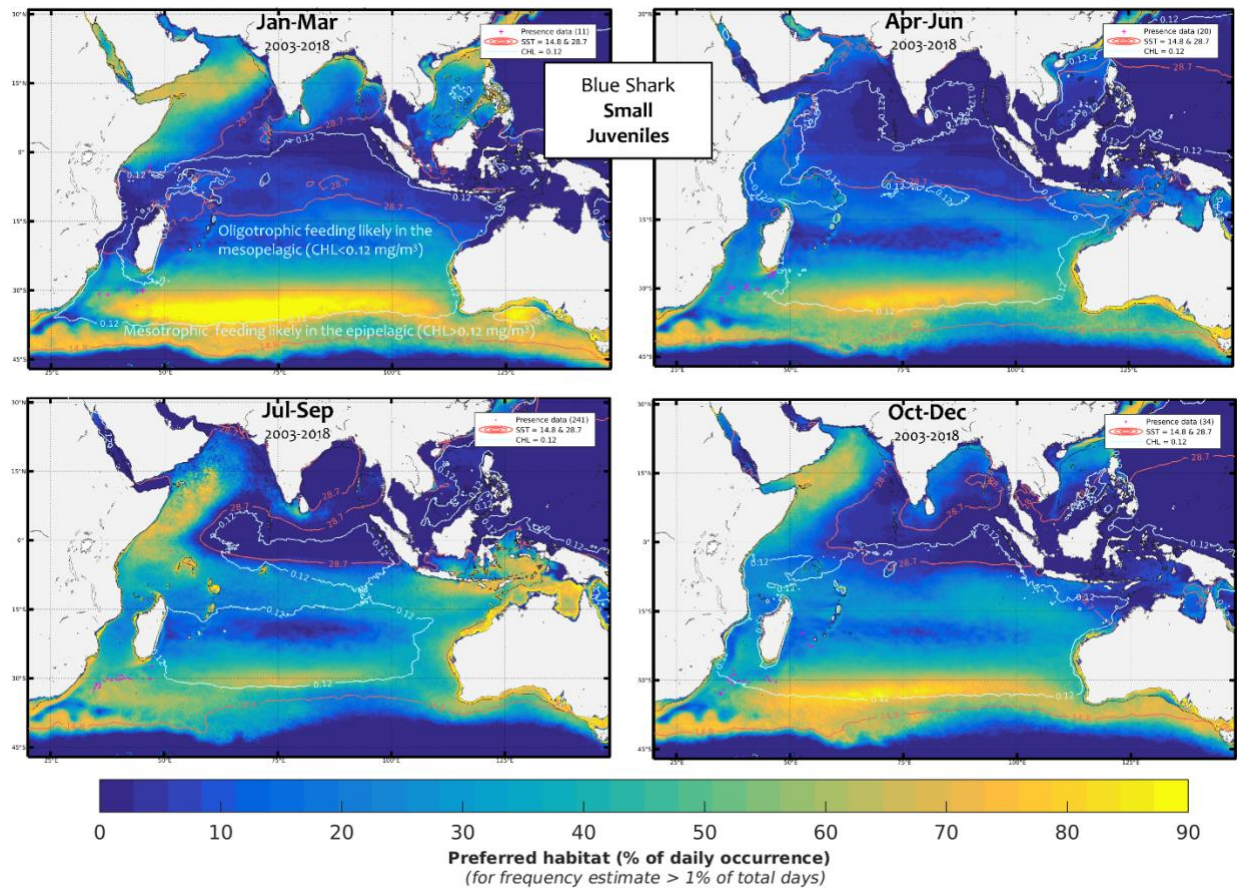


Figure 2. Mean seasonal distribution of blue shark feeding habitat for the small juveniles (SJ, <125 cm FL, 2003-2018, in frequency of suitable habitat occurrence, %) in the Indian Ocean. The chlorophyll-a isocontour of $0.12 \text{ mg}\cdot\text{m}^{-3}$ (CHL_{\min}) separates the mean area of oligotrophic feeding (below this value using mesopelagic micronekton as feeding proxy) and mesotrophic feeding (above this value using productivity fronts). Presence data are represented as pink dots for observer data and colored line transects for electronic tagging data (start and end of months are shown by a black star). The SST isocontour of 28.7°C is shown to enhance the mean upper SST limitation between all classes ($28.7^{\circ}\text{C} \pm 0.38$). The habitat limitation in the $15\text{-}25^{\circ}\text{S}$ area is instead due to low productivity (mesopelagic micronekton). The SST isocontour of 14.8°C outlines the lower SST tolerance of adult males, highlighting one of the most important habitat differences with small juveniles (SST_{\min} of 12.3°C).

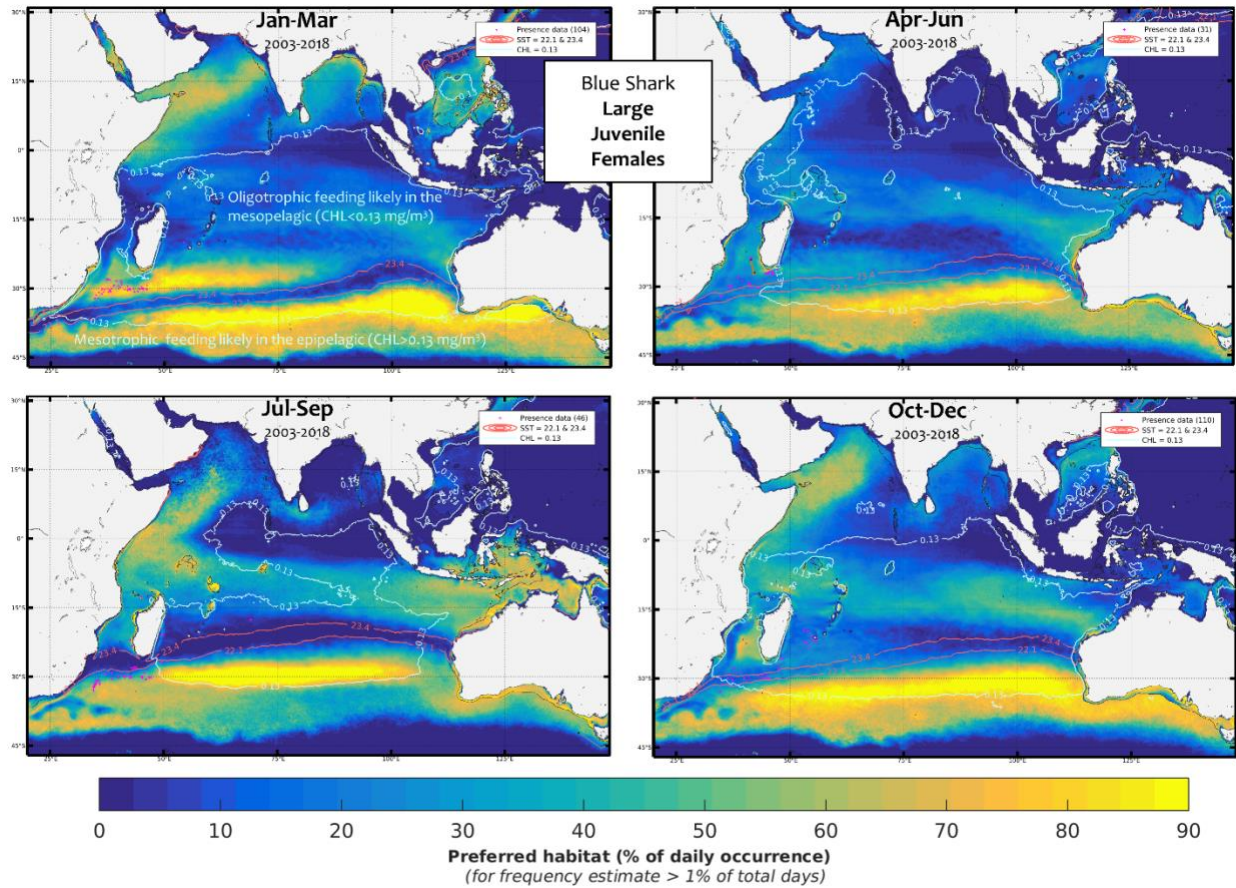


Figure 3. Mean seasonal distribution of blue shark feeding habitat for the large juvenile females (LJF, 125-180 cm FL, 2003-2018, in frequency of suitable habitat occurrence, %) in the Indian Ocean. The chlorophyll-a isocontour of $0.13 \text{ mg}\cdot\text{m}^{-3}$ (CHL_{\min}) separates the mean area of oligotrophic feeding (below this value using mesopelagic micronekton as feeding proxy) and mesotrophic feeding (above this value using productivity fronts). Presence data are represented as pink dots for observer data and colored line transects for electronic tagging data (start and end of months are shown by a black star). The SST isocontours of large juvenile females avoidance (21.7°C and 24°C) allow evaluating the potential lack of habitat overlap with large juvenile males.

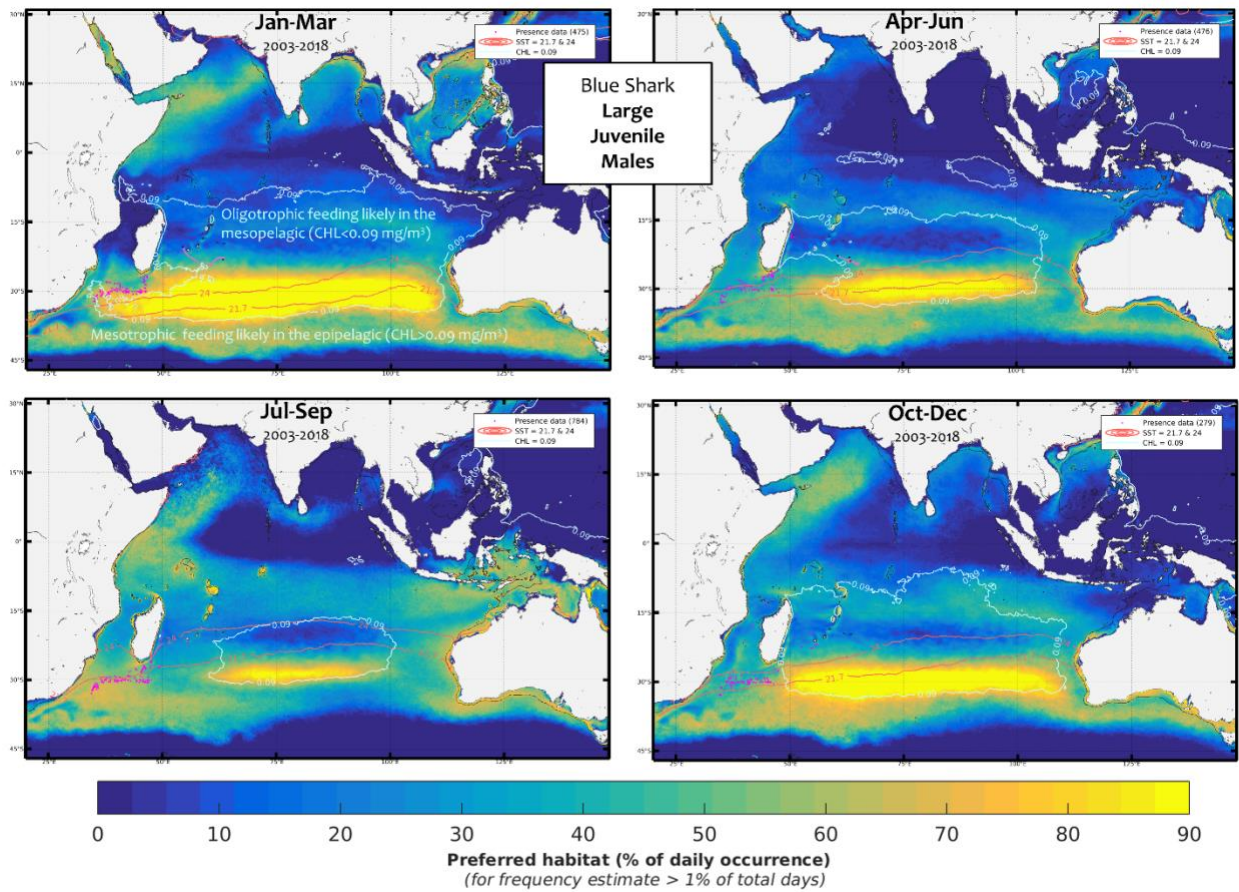


Figure 4. Mean seasonal distribution of blue shark feeding habitat for the large juvenile males (LJM, 125-190 cm FL, 2003-2018, in frequency of suitable habitat occurrence, %) in the Indian Ocean. The chlorophyll-a isocontour of $0.09 \text{ mg}\cdot\text{m}^{-3}$ (CHL_{\min}) separates the mean area of oligotrophic feeding (below this value using mesopelagic micronekton as feeding proxy) and mesotrophic feeding (above this value using productivity fronts). Presence data are represented as pink dots for observer data and colored line transects for electronic tagging data (start and end of months are shown by a black star). The SST isocontours of large juvenile females avoidance (21.7°C and 24°C) allow evaluating the potential lack of habitat overlap with large juvenile males.

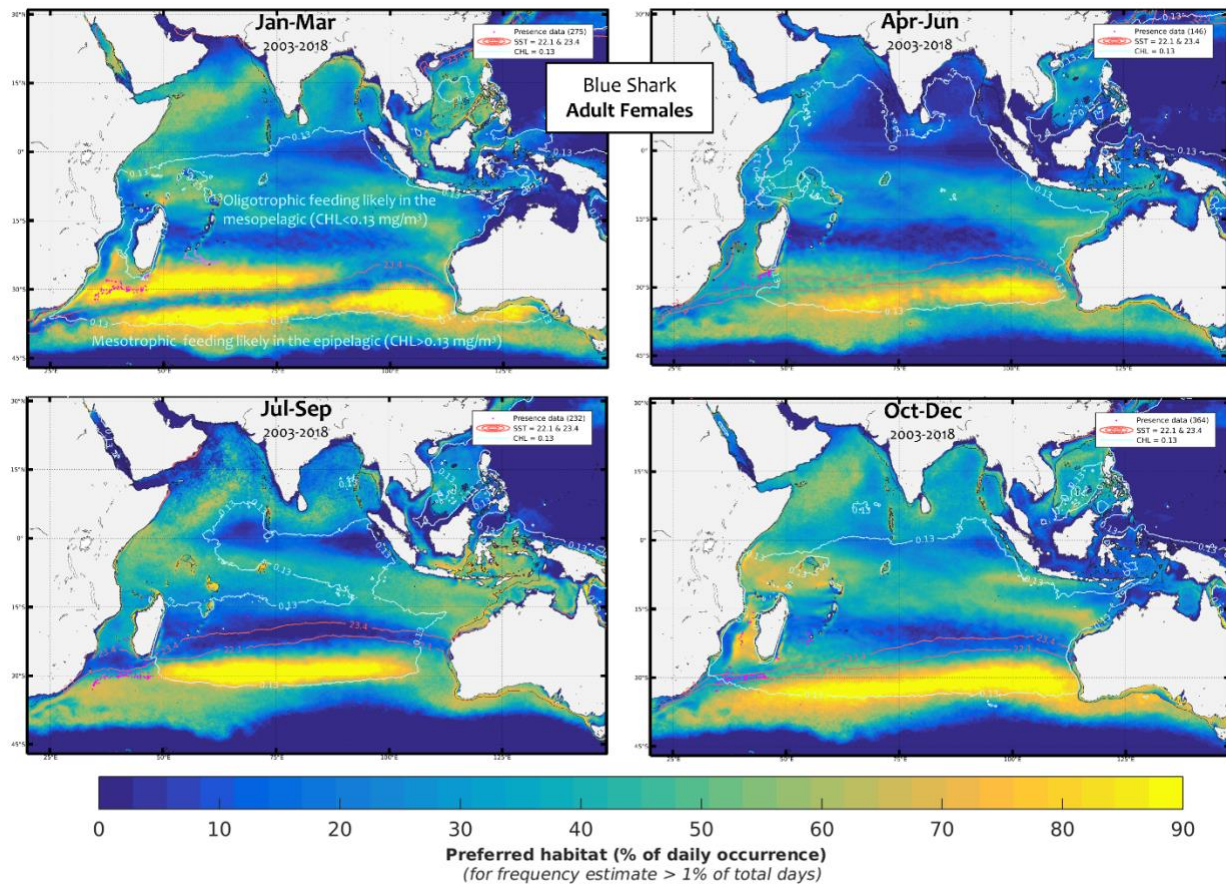


Figure 5. Mean seasonal distribution of blue shark feeding habitat for the adult females (AF, >180 cm FL, 2003-2018, in frequency of suitable habitat occurrence, %) in the Indian Ocean. The chlorophyll-a isocontour of $0.13 \text{ mg}\cdot\text{m}^{-3}$ (CHL_{\min}) separates the mean area of oligotrophic feeding (below this value using mesopelagic micronekton as feeding proxy) and mesotrophic feeding (above this value using productivity fronts). Presence data are represented as pink dots for observer data and colored line transects for electronic tagging data (start and end of months are shown by a black star). The SST isocontours of adult females avoidance (22.1°C and 23.4°C) allow evaluating the potential lack of habitat overlap with adult males.

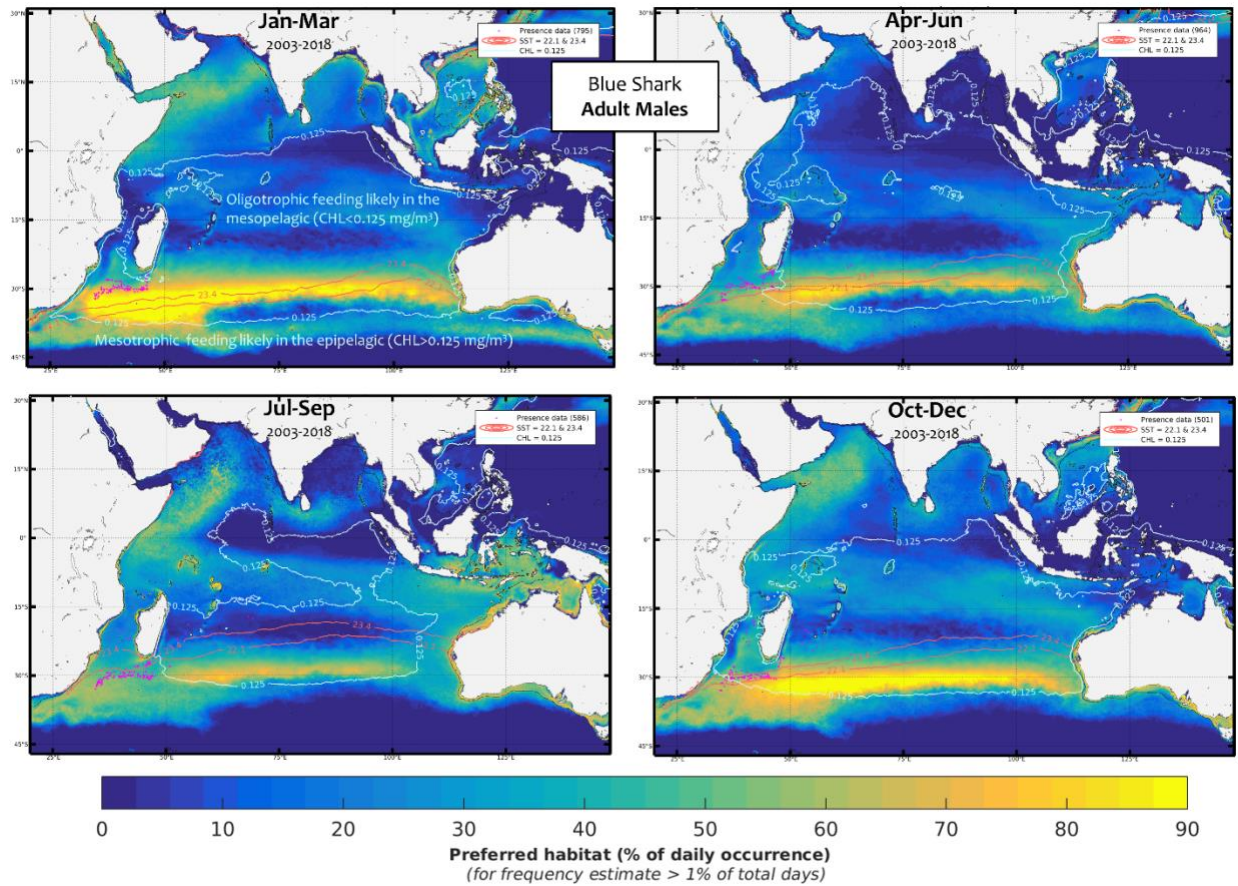


Figure 6. Mean seasonal distribution of blue shark feeding habitat for the adult males (AM, >190 cm FL, 2003-2018, in frequency of suitable habitat occurrence, %) in the Indian Ocean. The chlorophyll-a isocontour of $0.125 \text{ mg}\cdot\text{m}^{-3}$ (CHL_{\min}) separates the mean area of oligotrophic feeding (below this value using mesopelagic micronekton as feeding proxy) and mesotrophic feeding (above this value using productivity fronts). Presence data are represented as pink dots for observer data and colored line transects for electronic tagging data (start and end of months are shown by a black star). The SST isocontours of adult females avoidance (22.1°C and 23.4°C) allow evaluating the potential lack of habitat overlap with adult males.

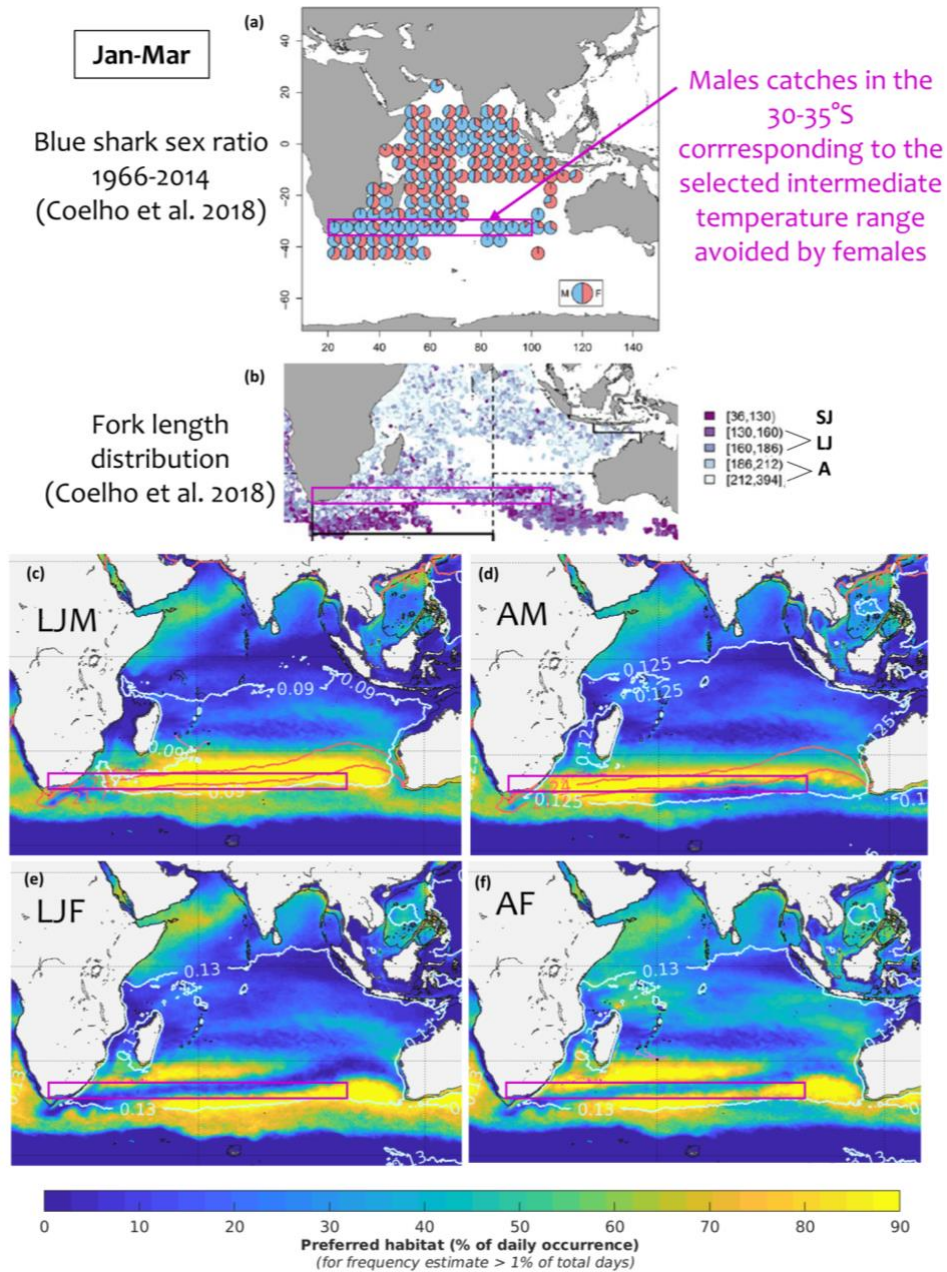


Figure 7. Comparison of the blue shark (a) sex ratio and (b) fork length distributions in Jan-Mar in the Indian Ocean on a 5° grid (observer data, 1966-2014, Coelho et al. 2018) with the corresponding feeding habitats of (c) large juvenile males (LJM), (d) adult males (AM), (e) large juvenile females (LJF) and (f) adult females (AF) (2003-2018). The purple box (30-35°S; 20-100°E) shows the presence of large males and the absence of large females in agreement with the habitat results using the intermediate SST levels avoided by females (SST isocontours as red lines).

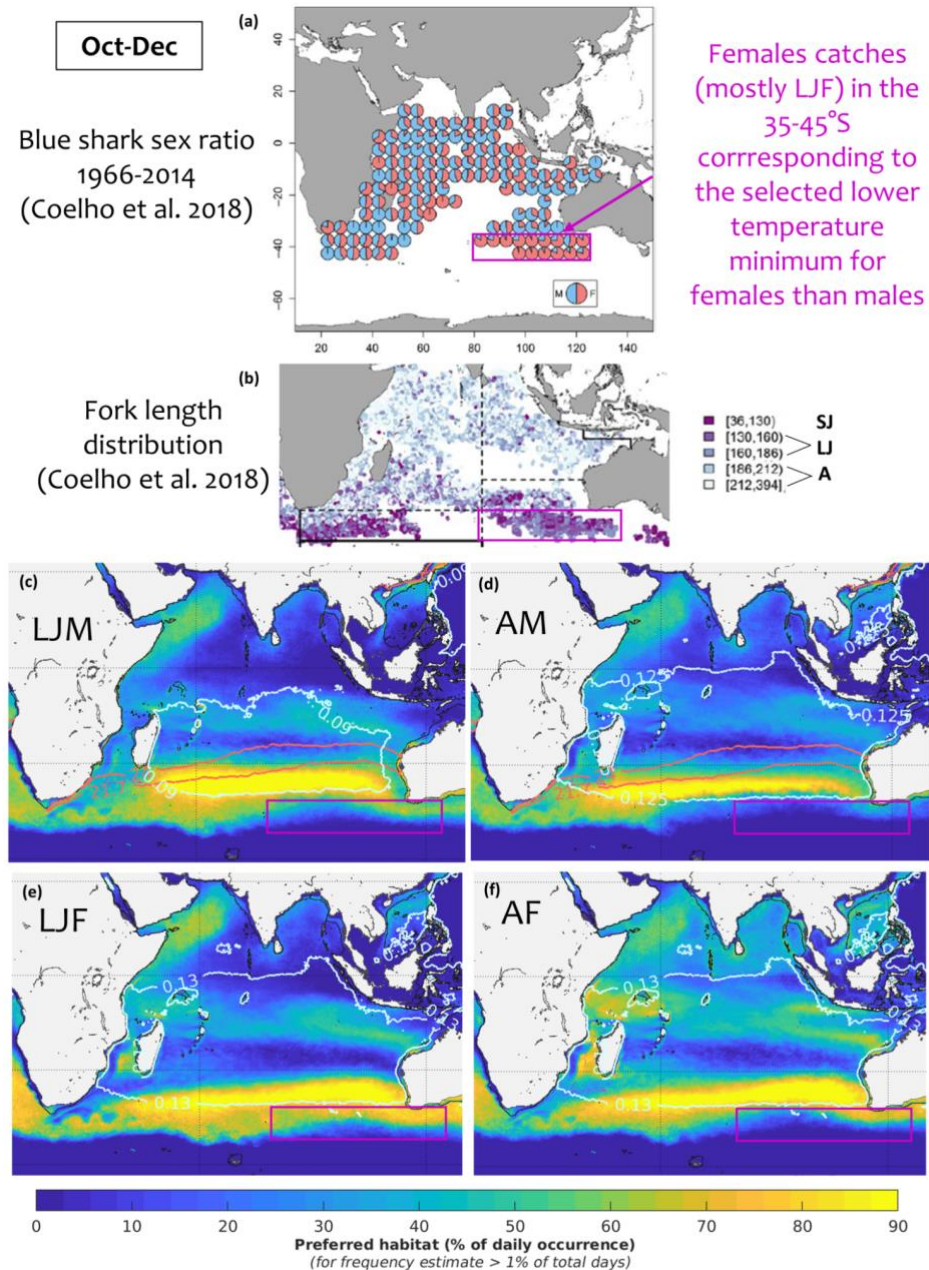


Figure 8. Comparison of the blue shark (a) sex ratio and (b) fork length distributions in Oct-Dec in the Indian Ocean on a 5° grid (observer data, 1966-2014, Coelho et al. 2018) with the corresponding feeding habitats of (c) large juvenile males (LJM), (d) adult males (AM), (e) large juvenile females (LJF) and (f) adult females (AF) (2003-2018). The purple box (35-45°S; 80-125°E) shows the predominance of large juvenile females in agreement with the habitat results notably using different lower SST limits as set in the global analysis (SST_{min} of 13.1°C for LJM, 14.8°C for AM, 11.6°C for LJF, 13.3°C for AF; SST_{min} for Small Juveniles is of 12.3°C - distribution is not shown).

4. Discussion

4.1. Model limitations

The limitations related to the feeding proxies (productivity fronts and mesopelagic micronekton) are mostly i) the habitat coverage that is limited by the unavailability of remote sensing products such as the *CHL* in high latitudes in winter due to the high presence of clouds, ii) the use of predicted mesopelagic micronekton produced by a three-dimensional model, which has its own limitations although the deeper the estimation the less temporal variability is expected, and iii) the complex interpretation of habitat suitability level between both feeding proxies. Regarding this latter limitation, the 0 to 1 daily feeding habitat value for the oligotrophic conditions (mesopelagic micronekton, $CHL < CHL_{min}$) cannot be compared in terms of feeding capacity to the habitat value estimated from the mesotrophic conditions (*CHL* gradient, $CHL_{min} < CHL < CHL_{max}$).

4.2. Tendency of ecological niche change throughout life stages

The decoupling of the feeding habitat for the different life stages is justified by the gradual change of blue shark feeding and thermoregulation strategy during its lifespan from frequent feeding in relatively cold mesotrophic water (likely near the surface) for small juveniles to less frequent feeding in relatively warm surface waters (feeding likely in the mesopelagic layer) for adults. As a result, oligotrophic daily habitat values more frequently reach the maximum value of 1, even if the feeding capacity is lower than in mesotrophic environments. Adult blue sharks are adapted to feeding in a less productive niche nonetheless ensuring their overall energetic needs for thermoregulation, movements and growth.

4.3. Ecological areas of interest

The current modeling approach focuses on the feeding proxies and on abiotic conditions and, therefore, the favorable environmental conditions associated with reproduction are not necessarily accounted for. Although reproduction (mating and giving birth to free-swimming pups) is seasonal and limited in time, it may generate substantial migration for encountering mature males or providing a favorable feeding environment to pups. Regarding this latter phase of giving birth, which likely corresponds to nurseries areas and to similar environments than the feeding habitat of small juveniles, these habitats are taken into account in the modeling carried

out in this work. Nursery areas seem to be located off the South African coast and southwest tip of Australia. Large females generally display an intermediate range of SST avoidance resulting in an important lack of habitat overlap with large males mostly from January to June in the South IO around 25-35°S. In Oct-Dec however, fishery observer data in the southwest basin (about 28-34°S, 35-47°E) show a higher habitat overlap between large males and females in this intermediate SST range, which may correspond to the mating period. However, it is worth noting that the habitat modeling relies on mostly feeding proxies and that mating may be spatially disconnected from active feeding.

The observer and electronic tagging data used in this study generally agree well with the predicted habitat for feeding, but also with the larger observer data in the last decades showing the exclusive presence of males in the catches between 30°S and 35°S in Jan-Mar (Figure 7; Coelho et al. 2018). During Oct-Dec, a lack of habitat overlap between large males and females is also matching the catch data in the south-west IO (35-45°S and 80-125°E; Figure 8; Coelho et al. 2018) where females are almost exclusively present. Although Coelho et al. (2018) catch data show the absence of females South-West of Madagascar in Oct-Dec, agreeing with the intermediate SST range avoided by large females (Figure 8), it is to be noted a substantial mismatch with our observer data that display both males and females in that area and period. Different spatial distribution of fishing effort between both these observer data might explain this mismatch between both observer datasets.

4.4. Concluding remarks

The results of the habitat modeling for the blue shark are useful to stock assessment modelers that need to understand the seasonal and spatial patterns of the blue shark population by sex and size classes in the Indian Ocean. Also, such results would be useful to expert scientists for proposing potential management measures for the conservation of this species such as retention bans in critical areas, or time-area management measures, or else. A possible option would also be to consider recommendations on which size and sex class(es) would be a priority for conservation to best sustain the population. This would help in analyzing what spatio-temporal protection measures could most efficiently protect the population and less affect the fisheries.

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