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Habitat and movements of the swordfish *Xiphias gladius* in the southern Indian Ocean oligotrophic gyre and beyond: preliminary results of swordfish tagging experiments in Reunion Island

by

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ABSTRACT

Habitat and migratory movements of swordfish in the Indian Ocean are still poorly known despite decades of research. Past tagging efforts were limited in time and space both due to a low survival rate of tagged swordfish and high cost of electronic tags. The limited number of swordfish tagged with conventional tags has provided a broad idea on the scale of horizontal displacements and tagging experiments using Pop-Up Satellite Archival Tags (PSATs) off South Africa have shown apparent site fidelity of swordfish in that area. Yet, the overall knowledge of the vertical habitat, dispersion rates and migratory patterns at the scale of the western Indian Ocean are still poorly known. Here we present results of swordfish tagging experiments using PSATs in the southwestern Indian Ocean that were carried out in the framework of EU-funded project PESCARUN where a total of 7 PSATs were deployed on swordfish between September 2021 and December 2022. We also used data from two swordfish tagged with PSATs in November 2012 and in December 2015 in the framework of the SWIOFP and PELICAN projects, respectively. All tagging operations took place within southwestern Indian Ocean oligotrophic gyre (in proximity with Reunion Island). To date, a total of 8 PSATs surfaced and reported data. During relatively short deployment periods (100 days max at liberty) swordfish performed large-scale movements throughout the western Indian Ocean reaching the Mozambique Channel in the west and equatorial waters in the north. Some individuals, however, showed ‘homing’ movements around Reunion Island circling back to the tagging place. All tagged individuals showed a similar vertical habitat occupation pattern: upper mixed layer/thermocline during the night and deeper hence colder mesopelagic layers around 500-900 m during daytime. Swordfish spent most of daytime (~80%) below 200 m depth suggesting that mesopelagic environment is its principal habitat in the western Indian Ocean. Diving behaviour along the northward migratory tracks showed habitat compression towards equatorial waters apparently rather driven by temperature limitations than dissolved O_2 concentrations. Our results provide the first insights on the high rates of swordfish individuals’ dispersion at ocean-scale level.

Introduction

Swordfish (*Xiphias gladius*) is an important commercial target species in the Indian Ocean for many local fishing fleets (France: Reunion and Mayotte Islands, Seychelles, Indonesia, Sri Lanka, India) and distant-water fleets (Spain, Portugal, and Taiwan) (IOTC, 2022). Despite knowing there is a single stock of swordfish in the Indian Ocean area (Muths *et al.*, 2015), population connectivity, migratory behaviour and mixing level over the area are still poorly known for this species.

Conventional "spaghetti" tagging programs in the western equatorial Indian Ocean (ABF, 2010) and the eastern Indian Ocean (Stanley, 2006) suggest active migratory behaviour associated with long-distance movements for *X. gladius*. However, inherited limitations of conventional tagging do not permit to evaluate potential migratory patterns, swordfish behaviour and habitat in the region. Most of Indian Ocean electronic tagging experiments either fails (Poisson, Taquet, 2001) or demonstrated relatively limited displacements associated with highly productive zone of the southwestern Indian Ocean and Mozambique Channel (West et al., 2012). These experiments collected very limited data on habitat and vertical behaviour either due to early mortality of fish or poor performance of electronic tags.

In the framework of EU-funded project PESCARUN a total of 7 PSATs were deployed on swordfish between September 2021 and December 2022 withing exclusive economic zone (EEZ) of the Reunion Island, France. Three of them allowed to collect data on long swordfish tracking (from 77 to 101 day). We also used data from two swordfish tagged with PSATs in November 2012 and in December 2015 in the framework of the SWIOFP and PELICAN projects, respectively (Romanov et al., 2016).

2. Material and Methods

2.1. Tags

A MiniPAT electronic tag developed by Wildlife Computers Inc.[1] was used for tagging experiments. It was programmed to record depth, temperature and light for a 100-days period (Table 1). Tags used in previous project were programmed

[1] https://wildlifecomputers.com/ Wildlife Computers 8310 154th Avenue NE, Redmond, WA 98052, USA

for 90 days (PELICAN) and for 180 days (SWIOFP). Time series for depth (5-min interval for 100 days deployments) was programmed to be always transmitted by satellite, as well as light levels recorded during twilight periods (used for geolocation) and profiles of depth and temperature (PDT; 4-hour interval) (Wildlife Computers, 2016).

Tags were rigged with a Domeier (umbrella-type) plastic anchor (Domeier et al., 2005) provided by Wildlife Computers Inc. that attached with a stainless-steel tether. All tags considered here were equipped with onboard tag emergency release mechanism (TERM) that release tag on approaching to crushing depth ~2000 m (Wildlife Computers, 2016). The tag was also pre-programed to release from fish in case of 3 days inactivity, i.e. quasi-constant depth range (+/- 2.5m) assuming such inactivity corresponds to mortality of tagged fish: dead fish either fell to the sea bottom shallower than tag crushing depth or float at the surface. The inactivity clause also triggers data transmission process in case of fish mortality or tag premature detachment.

2.2. Swordfish tagging

Swordfish was caught either using a Florida-style swordfish buoy gear (SBG) or during dedicated fishing with drifting pelagic longline (Romanov et al., 2013, 2022). To increase chance to catch swordfish in good condition and therefore probability of its survival a specific fishing technique with short longline gear (306 hooks deployed on average, range of 200-340) was used. Very short drifting (period between end of setting and start of hauling, average 3.0 hours, range 2.2-3.3) and soaking time (average 7.0 hours, range 4.7-7.7) was also applied. Branch lines of 26 m length were equipped with circle hooks (16/0 and 18/0 size) in order to reduce potential hooking injury.

During SBG fishing a total of 2 swordfish were caught, both meet tagging requirements. During horizontal longline fishing a total of 12 swordfish were caught but only 5 individuals were tagged. The tag was anchored under the first dorsal fin. The hook was removed from one fish caught with buoys, for the rest the monofilament leader of the fishing gear was cut at maximum proximity to the hook at time of fish release.

2.3. Horizontal movements

Light-based geolocation data were processed using GPE3 application available at Wildlife Computer portal (https://my.wildlifecomputers.com/). Model used sea surface temperature (SST) NOAA High Resolution SST data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Web site at http://www.esrl.noaa.gov/psd/ and bottom topography with 1 degree step (ETOPO1 Bedrock) (Amante, Eakins, 2009.). Model provides maximum likelihood geolocations and maximum likelihood track with 50%, 95% and 99% likelihood areas. Model was set to use abovementioned bathymetry and SST as constrains with various settings of max fish swimming speeds from 1.0 to 5.0 m s^{-1} with 0.5 m s^{-1} increments. Most 'realistic' movement pattern (based on subjective criteria) was obtained at 3.0-3.5 m s^{-1} swimming speed.

2.4. Vertical behaviour and habitat

For habitat use analysis we developed day vs. night distributions of time-at-depth inferred from 5-min resolution time series. Dawn/dusk observations were excluded from day and night periods which correspond to 08:00-17:00 local time and 20:00-05:00 respectively.

Temperature time series (that is not transmitted) was reconstructed by interpolation using PDT data (Profile of Depth and Temperature provided for 4-hour intervals) and depth time series (5-min interval). PDT was also used to show the vertical thermal structure of the water column and to calculate the isothermal layer depth (ILD = thermocline) (Kara et al., 2000).

3. Results

3.1. Tag retention and performance

A total of seven swordfish were tagged with miniPATs during project PESCARUN in 2021-2022. Two tags have popped up by the pre-programmed date. A total of 3 mortalities were observed: one (PTT 203180) after 2 trays of tracking (a handling error, release with long trailing gear), one immediate (PTT 203178) (attacked by a predator, apparently by a bluntnose sixgill shark *Hexanchus griseus* at about 03h57 local time at the depth between 136 and 350 m), and one mortality for an unclear reason after 67 days of tracking (PTT 203184). One tag detached prematurely for unknown reason almost immediately after tagging. One tag never reported data.

Together with previous projects PELICAN (CITEB) – 1 SWO (69 days) and SWOPAT (IRD) – 1 SWO (88 days) we have analysed 5 long-term tracking of swordfish from 2012 to 2022 (Figure 2).

3.2. Horizontal movements

All tracks demonstrate high migratory activity of swordfish tagged off Reunion Island. Migratory movements span over three diverse habitats: Indian Ocean Subtropical Gyre Province (ISSG), East African Coastal Province (EAFR), and Indian Monsoon Gyre Province (MONS) (Longhurst, 2007).

All tagged individuals (apart from specimens subjected to immediate post-release mortality) undertake rather consistent (up to 2 months) unidirectional fast migratory movement away from tagging point except one individual (PTT 203184) that performed circular movement around Reunion Island with short excursion to Madagascar waters (Figure 2). The swordfish covered a total distance of 8531 nmi, for an overall average distance of 1706 (±526) nmi. Mean daily displacement was 19.34 (±5.75) nmi, giving an average speed of 0.81 (±0.24) nmi. It should be taken into consideration that these calculations do not take into account regular numerous vertical movements of the fish between the surface and ocean depths of 700-800 m, which will considerably increase the overall distance travelled by swordfish. The longest horizontal distance travelled by a single individual was 2348 nmi, achieved by swordfish 153475. The total distance travelled is not proportional to the number of days of data recording but rather depends on average hourly travel speeds.

Our data suggest two modes of swordfish migratory behaviour: 1) Fast unidirectional migratory movements with rare abrupt changes of movement direction (tags 120650 and 153475 whole track, tags 203179 and 203185 first month after tagging) and 2) slow 'residential' displacement within limited area associated with frequent changes in direction of displacements (tags 203179 and 203185 last two months after tagging) or return movement within limited area (tag 203184) (Figure 3).

3.3. Vertical behavior and habitat

Overall pattern of swordfish vertical distribution shows that this species is typical mesopelagic species occupying mesopelagic habitat below 200 m during the day and moving to epi-pelagic zone at night (Figure 4, 5).

Mean depth profiles (Fig. 5) demonstrate that the swordfish was much more active during the day, moving between deep layers 400-800 to the surface quickly passing through intermediate depths 10-400 m. During sunset (mostly between 17:00 and 19:00 swordfish moves to the upper mixed layer (0-150 m) where it stays all night long. At night vertical migration range of swordfish is much narrower and matches the mixed layer and upper part of the thermocline.

Comparison of vertical habitat data collected for each tagged swordfish individually suggests two patterns of daytime vertical habitat utilization: uniform and split daytime vertical habitat occupation pattern (Fig 6). Uniform pattern was observed for specimens that stay around reunion island or moved in westward. It should be noted that in the waters around Reunion Island and ISSG in general swordfish occupies deep water layers deeper than 500 m, mostly between 600 and 800 m depth. ISSG waters is characterized by high heat content, deep propagation of warm waters, oligotrophic conditions and high oxygen concentrations (Jayne, Marotzke, 2002; Gouretski, Koltermann, 2004, Longhurst, 2007).

In contrast all specimens that moved northward demonstrate split habitat occupation that was associated with northward displacements (Fig 6). Our data demonstrate that outside ISSG swordfish spent less time in deep waters (deeper 500 m) but also do not cross ambient temperature lower than 9°C, commonly visited in the waters around Reunion Island and ISSG overall (Fig. 7). Such behavioral pattern suggest that temperature is not a limiting factor for swordfish migration into deep layers.

Climatic environmental data shows a prominent gradient in temperature and dissolved oxygen distribution along section from ISSG (Reunion Island) waters toward equatorial waters (Gouretski, Koltermann, 2004) (Fig. 8). Our analysis demonstrates that changes in swordfish maximal depth distribution are well correlated with depth of oxyline 4.0-4.5 ml/l (Fig. 9). Therefore, SWO depth distribution affected by apparent habitat compression at relatively high oxygen concentration 4.0-4.25 ml/l

4. Discussion

Our results are in concordance with earlier observations from other ocean on swordfish migratory nature. Fast south-north return movements of swordfish were recorded in several PSAT tagging experiments in Atlantic and Pacific

(Abascal et al., 2009, 2015; Neilson et al., 2009; Evans et al., 2014). However, 'residential' behaviour was rarely observed for this species in other oceans. The average daily migratory speed 19.34 nmi day^{-1} estimated here is lower than speed of swordfish horizontal displacement observed by Abascal et al. (2009, 2015): 28.8 and 53.9 nmi day^{-1}, Dewar et al (2011) 31.8 nmi day^{-1}, and Sepulveda et al (2010) 77.8 nmi day^{-1}. Apparently, such differences are related with periods of 'residential' behaviour observed in our study: displacement speed during residential phase was 9.9-12.2 nmi/day compare much slower than during migratory phase ~ 25 nmi/day. Active and fast movements of swordfish means that status of local stocks and success of local fisheries are highly depends on emigration-immigration balance and probably on oceanographic and local productivity processes that apparently drive swordfish movements and residence time.

Vertical behaviour of swordfish observed here also corresponds to generic pattern of *X. gladius* circadian movement pattern in tropical zone: night aggregation close to ocean surface, within the upper mixed layer and daytime occupation of mesopelagic habitat. Regular swordfish excursions to the ocean surface during the day are also known (Takahashi et al., 2003; Abascal et al., 2009; Evans et al., 2014) however reasons of such behavior are not well understood yet. One of the potential reasons is heating of fish body in warm surface waters after excursions to cold mesopelagic layers. However, this migratory pattern (daytime short movement to the surface) does not occurs every day making this explanation questionable. Another potential reason of surface daytime excursion that swordfish exploring surface waters for food resources. In particular higher percentage of daytime surface excursions in equatorial waters may reflect higher local productivity of the area and presence of abundant epipelagic prey (Potier et al., 2007, 2009; Romanov et al., 2009) while in the oligotrophic waters of ISSG, where epipelagic prey resources are poor (Romanov, Zamorov, 2007; Romanov et al., 2008), swordfish apparently rely on migrating prey from deep sound scattering layers.

Swordfish demonstrate differences in depth occupation in relation to local oceanographic conditions: preferred temperature range of 9-12°C was the same irrespectively of the area. Also, deep propagation of warm waters in the ISSG allows swordfish to explore deeper layers. In the same time, apparent habitat compression at relatively high oxygen concentration 4.0-4.25 ml/l due to shallowing of oxygen-depleted layer in the equatorial waters may also play important role limiting swordfish presence in deep layers (Abecassis et al., 2012).

Further swordfish electronic tagging in combination with environmental sampling are needed in order to obtain more information on vertical behaviour, migratory routes, residence time and mixing level between various areas of the Indian Ocean.

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Table 1 Summary of tagging information for swordfish

PTT	Serial number	Species	LJFL (cm) estimated	Programmed period (days)	Anchor	Tagging			Pop-up			Fish fate	Days at liberty: first transmission / surfacing	Distance travelled / distance per day (nmi)
						Date	Lat	Long	Date: first transmission / surfacing	Lat (first transmission)	Lon (first transmission)			
120650	11P0500	SWO	170	180		15.11.2012	24°06’S	50°11’E	09.02.2013	-31°08’S	40°38’E	Mortality	86 / 86	2138 / 24.3
153475	15P0292	SWO	230	90	Domeier	17.12.2015	21°10’S	55°05’E	27.02.2016 / 24.02.2016	01°30'S	60°37'E	Survival	72 / 69	2348 / 26.1
203178	20P0700	SWO	100	100	Domeier	18.01.2022	20°49’S	55°33’S	05.04.2022	20°49’E	55°33’E	Mortality, shark predation	0	N/A
203179	20P0701	SWO	160	100	Domeier	28.07.2022	23°24’S	54°58’E	06.11.2022	14°35’S	57°11’E	Survival	101 / 101	1220 / 12.1
203180	20P0752	SWO	120	100	Domeier	17.09.2021	20°52’S	55°13’S	18.09.2021	20°52’S	55°13’E	Mortality, fish handling error	2	28 / 14
203181	20P0787	SWO	120	100	Domeier	27.07.2022	23°15’S	54°22’E	Non reported					
203183	20P0789	SWO	120	100	Domeier	30.07.2022	23°13’S	55°21’E	07.08.2022	18°31’S	55°56’E	Premature, attachment failure	8	N/A
203184	20P0790	SWO	160	100	Domeier	03.08.2022	21°44’S	54°53’E	09.10.2022	22°14’S	55°08’E	Mortality	67 / 67	1187 / 17.7
203185	20P0792	SWO	120	100	Domeier	31.07.2022	23°14’S	55°30’E	08.11.2022	-13.3822	47°51’E	Survival	100 / 100	1639 / 16.4

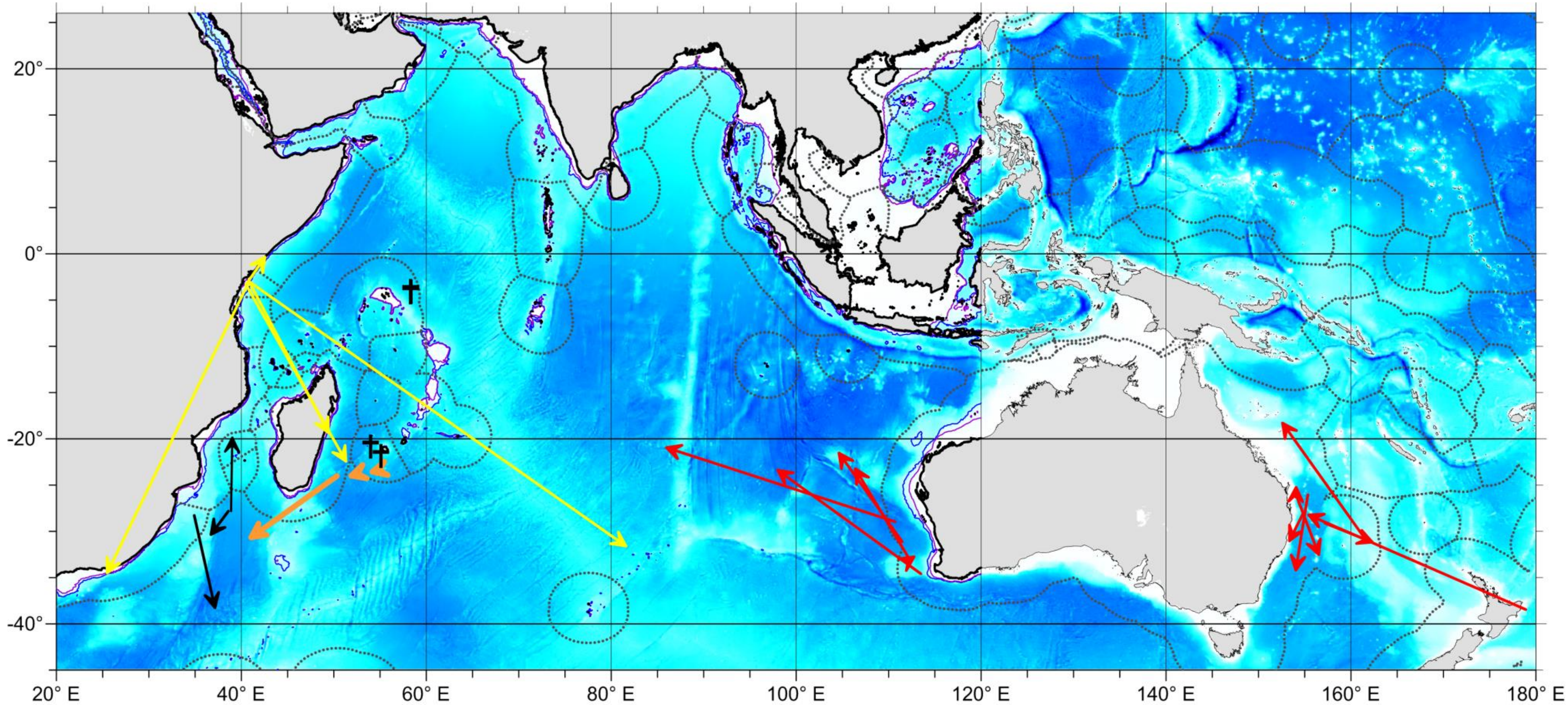

Figure 1. Past swordfish tagging experiments in the Indian Ocean and adjacent areas of the Pacific. Conventional tagging: red arrows are from Stanley (2006), yellow arrow are from ABF (2010). PSAT tagging (direct direct distance travelled): black crosses (100% SWO mortality) are from Poisson, Taquet (2001), black arrows are West et al. (2012), and orange arrows are IRD SWIOFP Project tags (Marsac, 2013 pers. comm.).

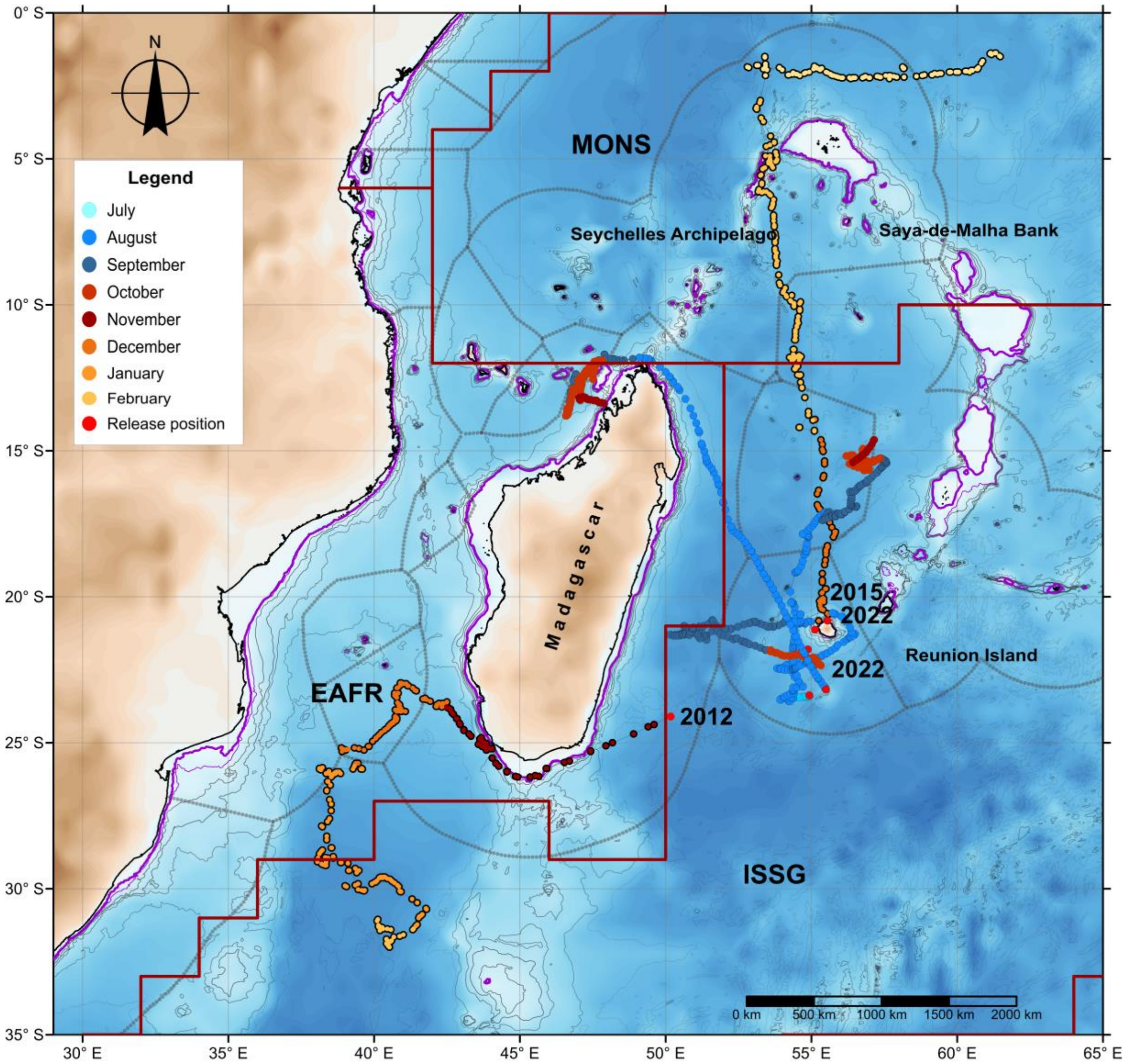

Figure 2. Most likelihood tracks of swordfish tagged around Reunion Island. Burgundy line shows limits of the biogeochemical provinces of Longhurst: Indian Ocean Subtropical Gyre Province (ISSG), East African Coastal Province (EAFR), and Indian Monsoon Gyre Province (MONS) (Longhurst, 2007). Approximate position of the 200-mile Exclusive Economic Zones (EEZs) of coastal states (grey dotted line), the 200 m isobath (purple line) and bathymetry from 1000 to 5000 m (in 1000 m steps, light lines) are shown. Coastline and bathymetry data are from GEBCO (GEBCO, 2010), EEZs are from VLIZ (2014).

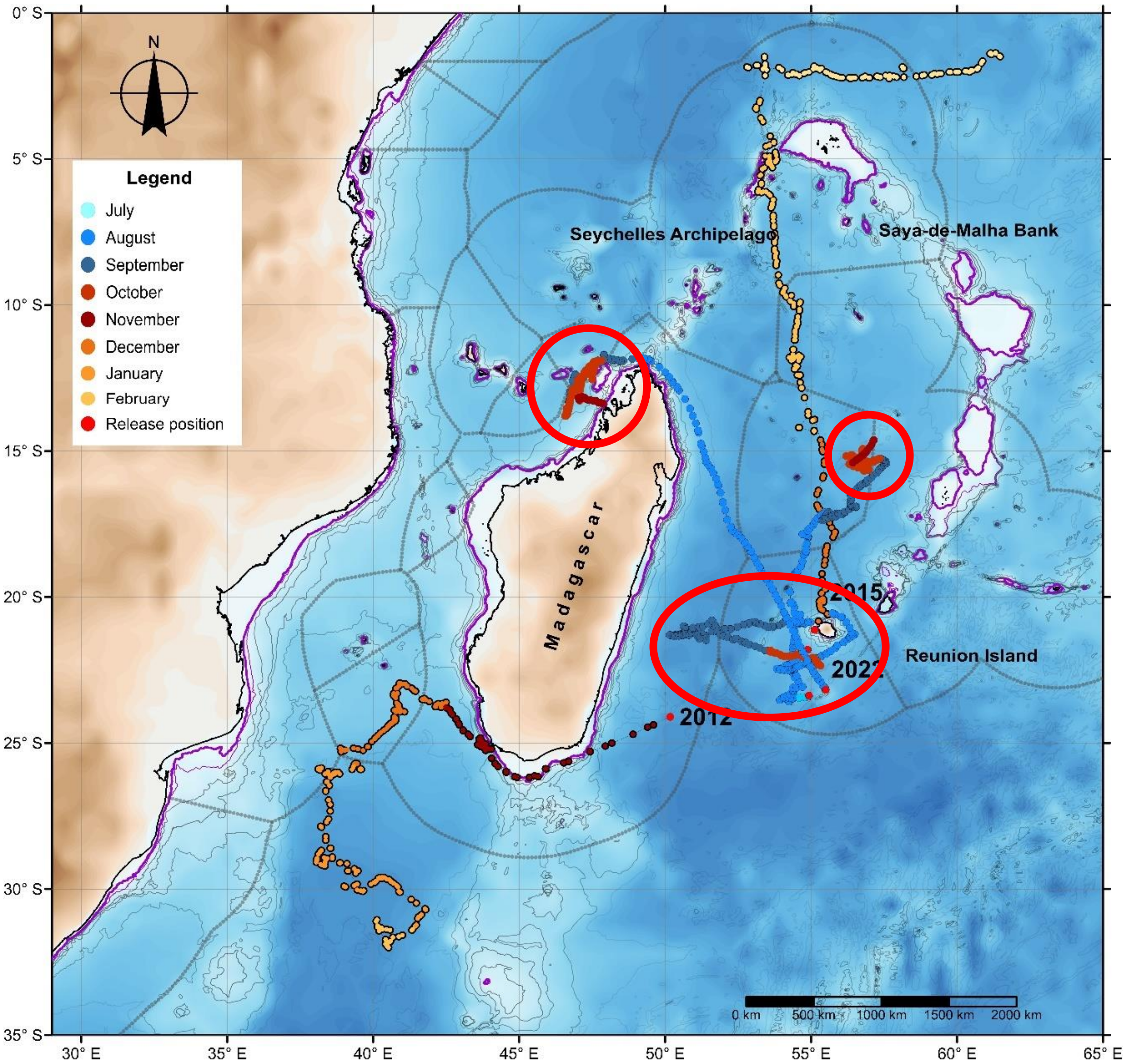

Figure 3. Most likelihood tracks of swordfish tagged around Reunion Island shown areas of presumed ‘residential’ behaviour (red circles). Approximate position of the 200-mile Exclusive Economic Zones (EEZs) of coastal states (grey dotted line), the 200 m isobath (purple line) and bathymetry from 1000 to 5000 m (in 1000 m steps, light lines) are shown. Coastline and bathymetry data are from GEBCO (GEBCO, 2010), EEZs are from VLIZ (2014).

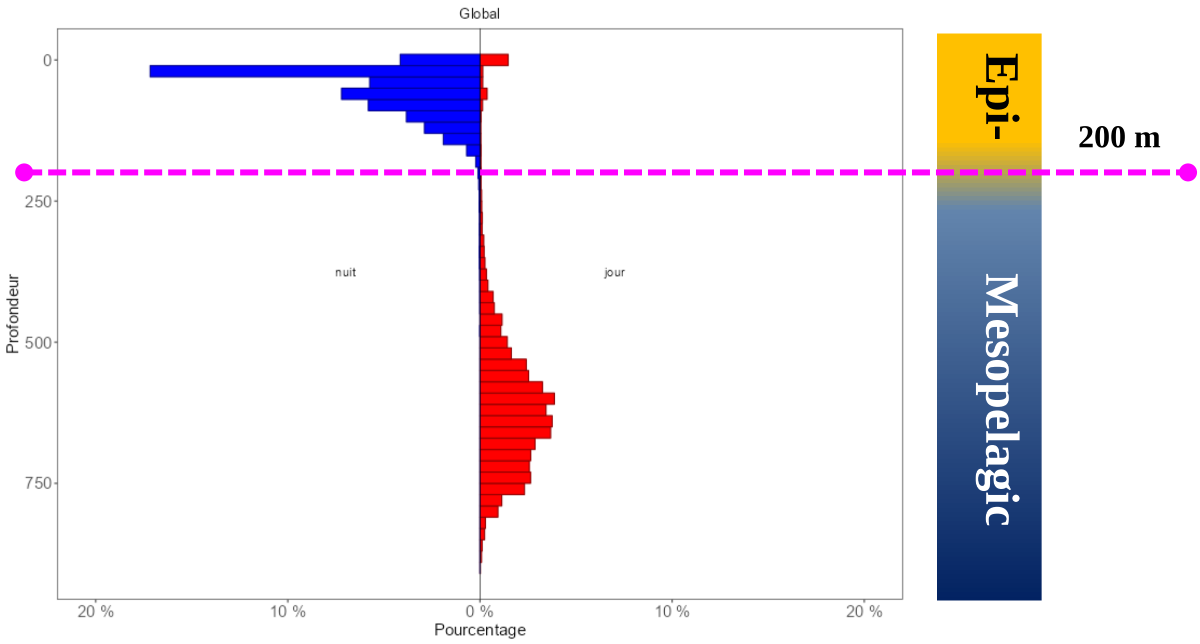

Figure 4. Summary of vertical distribution of swordfish during this study (time at depth, %).

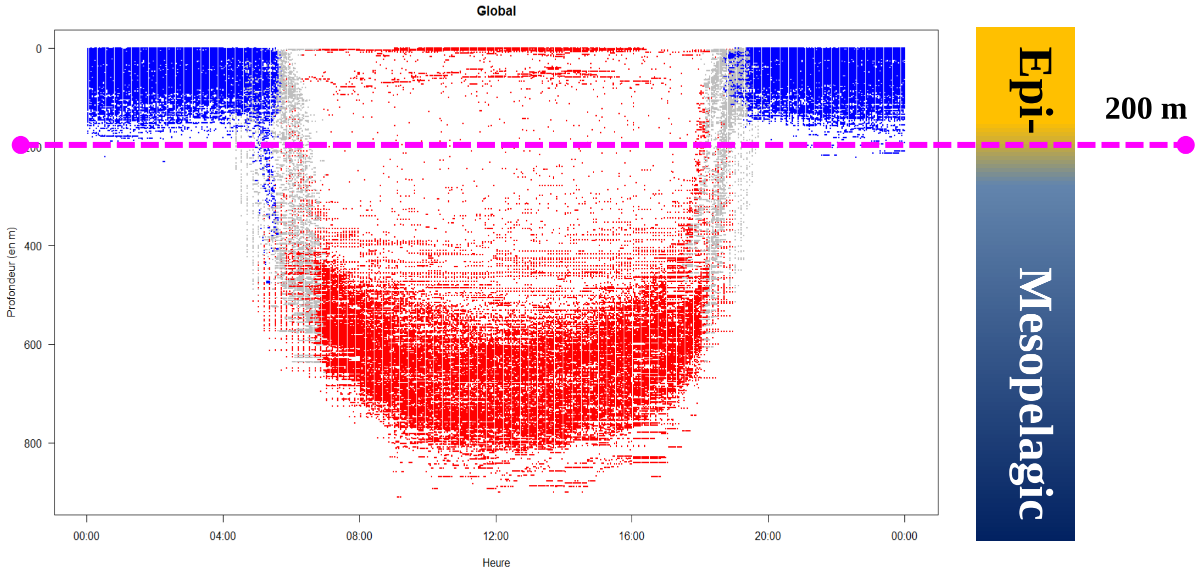

Figure 5. Cumulative summary of vertical distribution of swordfish during over 24 hours.

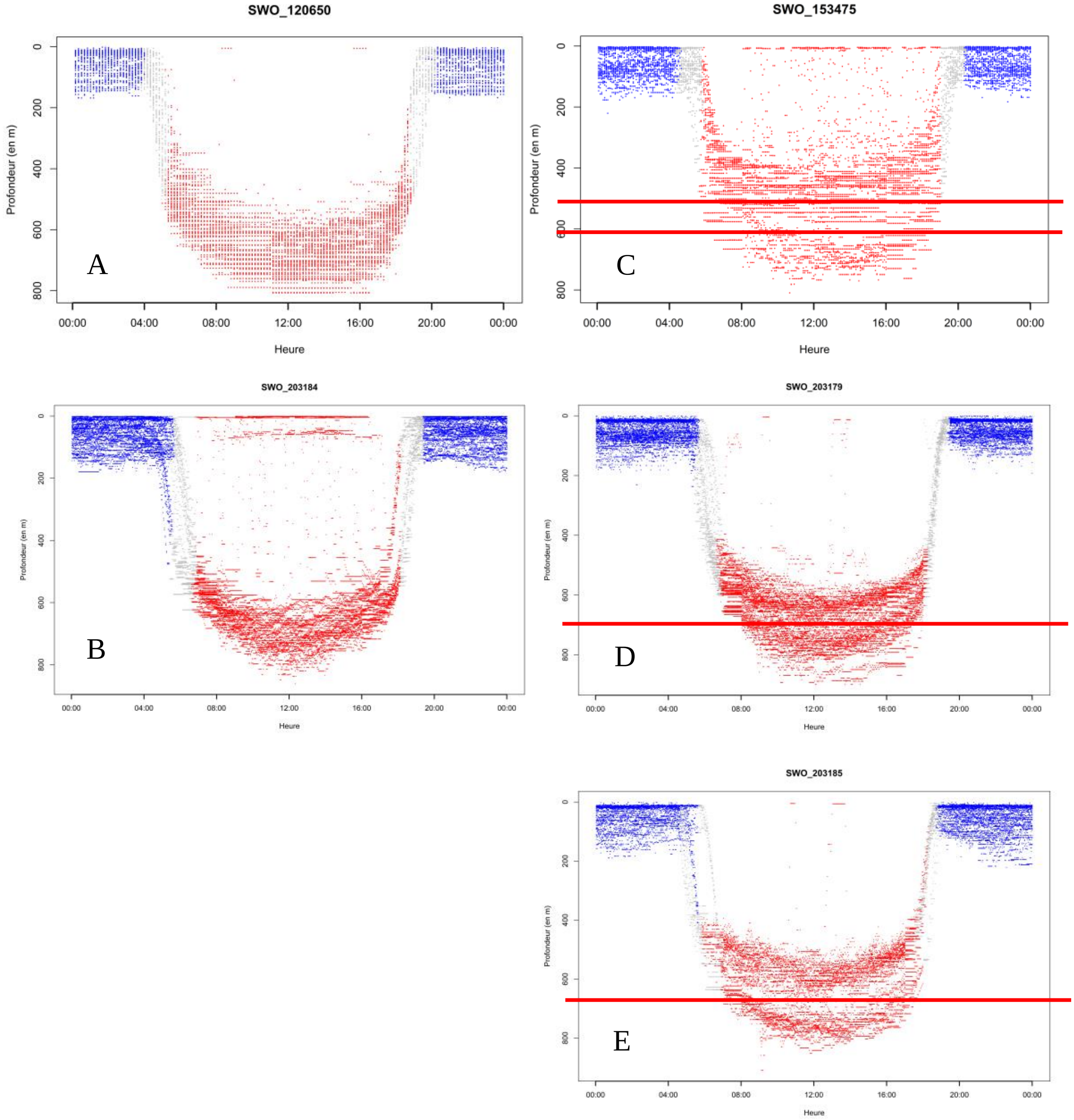

Figure 6. Comparison of the swordfish vertical distribution over 24 h showing uniform (A, B; tags 120650 and 203184) and split vertical habitat occupation pattern (C, D, E; tags 153475, 203179 and 203185). Red lines indicate approximate depth of habitat split.

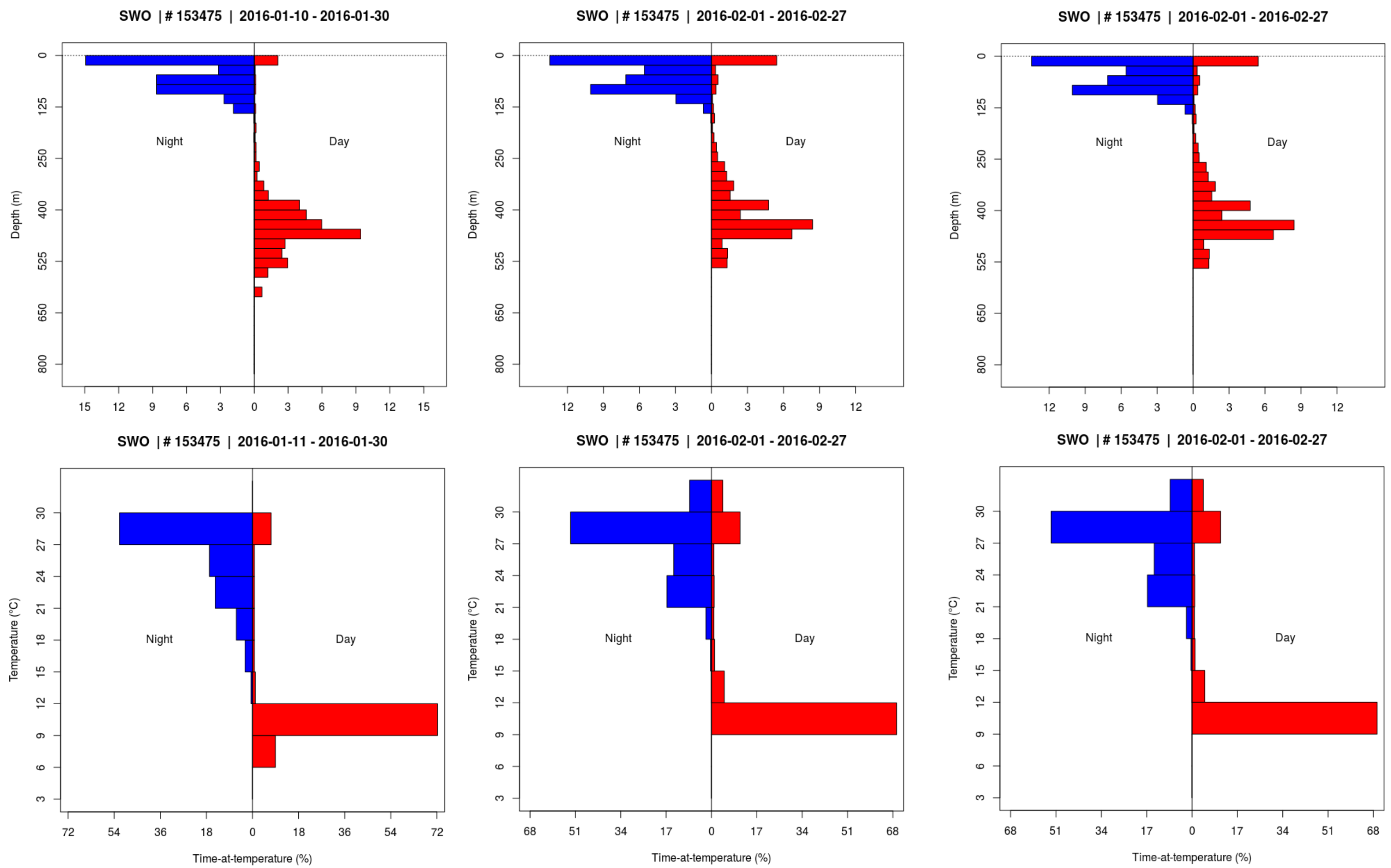

Figure 7. Summary of swordfish #153475 vertical distribution (upper panel) and temperature niche occupation (lower panel) during northward migration from Indian Ocean Subtropical Gyre province (left), within transitional zone between ISSG and Monsoon Province (center) and within Equatorial Countercurrent (Monsoon Province) (right).

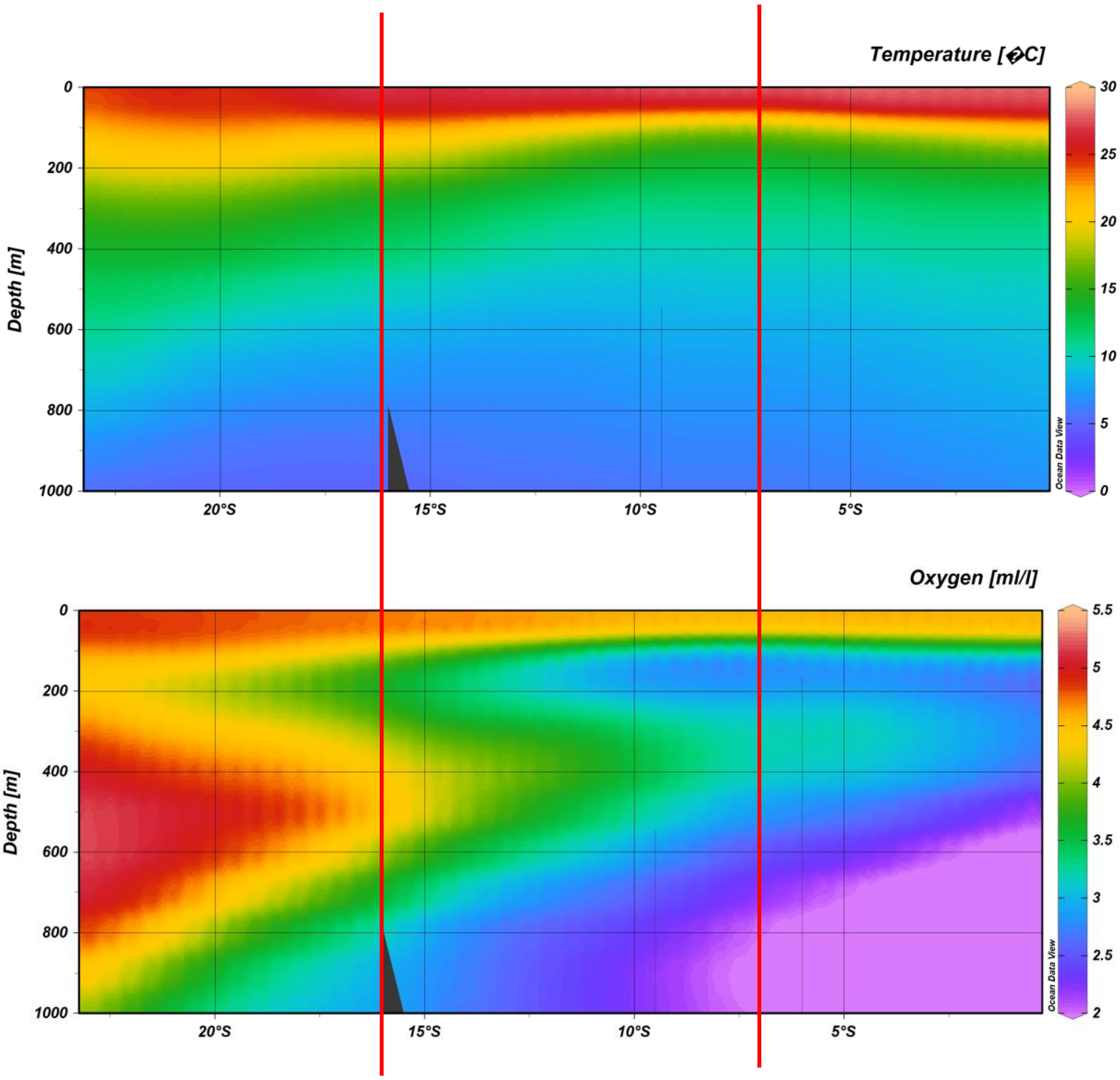

Figure 8. Température (°C) moyenne climatique et concertation en oxygène (ml/l) le long de la latitude 50°E, source des données Gouretski et Koltermann (2004). Red vertical lines show approximate areas of Ocean Subtropical Gyre province (left), transitional zone between ISSG and Monsoon Province, and Equatorial Countercurrent (Monsoon Province).

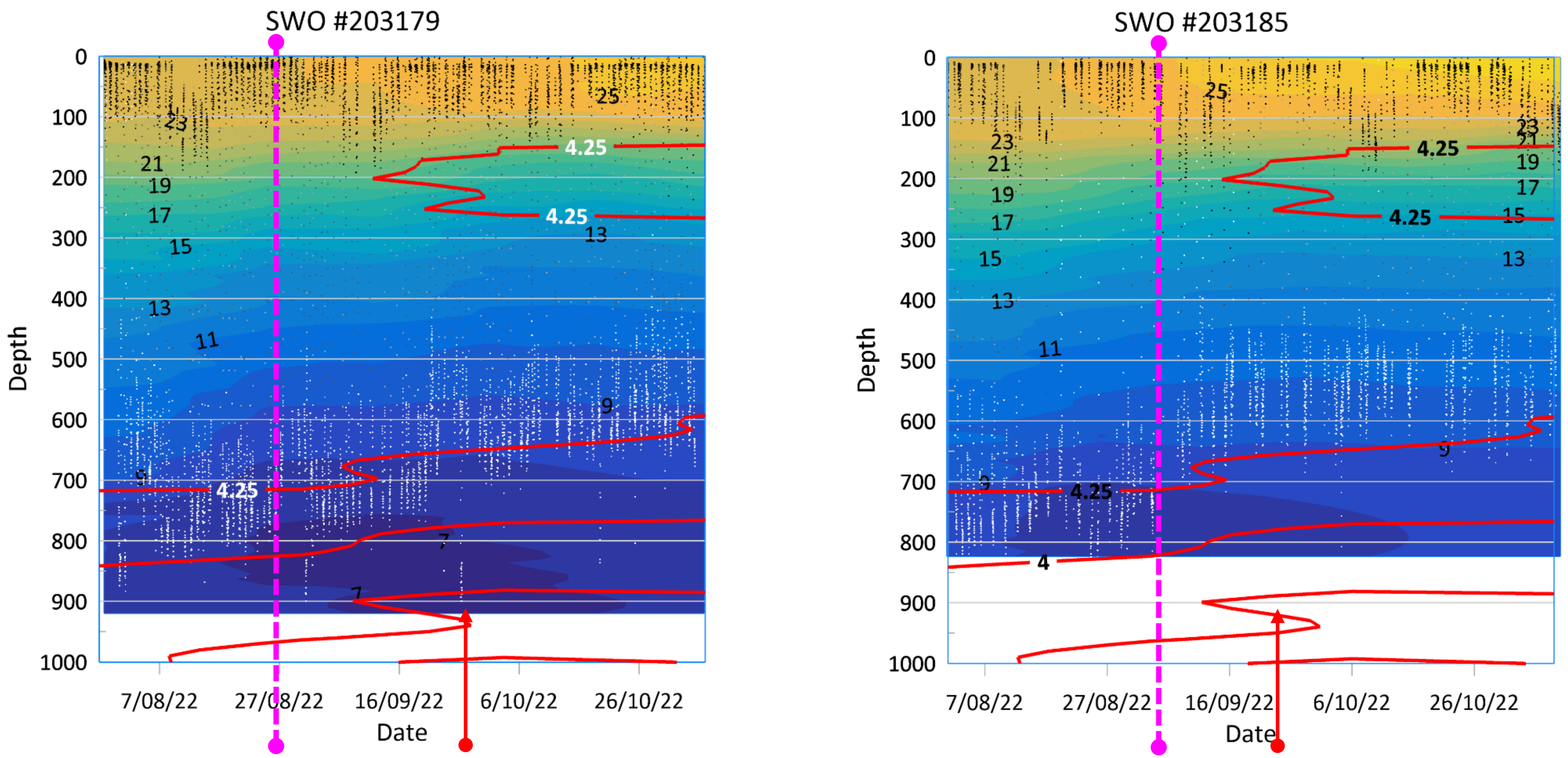

Figure 9. Superposition of climatic mean temperature (°C) (background) and oxygen concertation (ml/l) (red lines) along of latitude 50°E, (source Gouretski et Koltermann (2004)) and vertical distribution of northward-migrating swordfish (tags 203179 and 203185). Rose vertical lines show approximate limit of behaviour modification, while red arrows show start of ‘residential’ behaviour.