

**HORIZONTAL AND VERTICAL MOVEMENTS OF SWORDFISH TAGGED WITH
POP UP-SATELLITE TRANSMITTERS IN THE SOUTH-WEST INDIAN OCEAN,
OFF SOUTH AFRICA**

Wendy M. West¹, Sven E. Kerwath^{1,2}, Charlene da Silva¹, Christopher G. Wilke¹, Francis Marsac^{2,4}

Correspondence author: W. West, Department of Agriculture, Forestry and Fisheries, Private Bag X2,

Roggebaai 8012, South Africa. Email: WendyW@daff.gov.za. Telephone number: +27 21 402 3120.

Fax number +2721402 3043

¹ Department of Agriculture, Forestry and Fisheries, South Africa

² Zoology Department, University of Cape Town, South Africa

³ IRD, UMR EME (IRD/IFREMER/UM2), France

⁴ Department of Oceanography University of Cape Town, South Africa

Abstract

Eleven longline-caught swordfishes were tagged with pop-up satellite (PSAT) tags off the coast of South Africa. Although post-release mortality rates were high, four fishes (36%) yielded datasets longer than two months. Fish condition on visual assessment or duration hooked on the longline was a poor indicator of release success. All four swordfish undertook periodical diel diving behaviour, but one fish dived mainly at night. Basking behaviour was not observed as all fishes stayed below 8 m of water depth. Bathymetry and moon phase did not seem to influence diving depth, but dives seemed to be restricted by a temperature ceiling of ca. 8°C. Maximum and minimum water temperature encountered by the fish generally matched those found in other studies around the world. Diving patterns did not change with average swimming speed, but longer presence in shallow waters during faster swimming was observed in one fish. All swordfishes remained within the region but one fish crossed the 20 deg longitude boundary twice indicating that there might be a link to the Southern Atlantic stock. Swordfish horizontal movement showed no clear link with bathymetry or chlorophyll-a, but two fishes seemed to trace the edge of meso-scale eddies.

Keywords: Broadbill swordfish *Xiphias gladius*, South Africa, Horizontal movement, Vertical movement, PSAT tags, South West Indian Ocean

Introduction

The broadbill swordfish *Xiphias gladius* (Xiphidae), a large pelagic predator of temperate, subtropical and tropical waters of all oceans is a commercially important target of longline and driftnet fisheries around the world with annual global catch of up to 100 000 mt. Physiological adaptations allow Swordfish to tolerate a wide range of temperatures (Nakamura 1985). As a result, this species can spend more time in cooler waters, generally above the thermocline (Collette 1995) and occupies a broader latitudinal range than most other billfishes (Palko et al. 1981, Abascal et al. 2009). Unlike tuna, swordfish do not shoal, but occur more widely dispersed although densities are higher along ocean fronts and other oceanographic features, where current and temperature gradients trap planktonic organisms and baitfishes (Potier et al. 2012).

Globally swordfishes are thought to occur within several different stocks, but stock-structure determination based on genetic analyses is not straight-forward (Rosel and Block 1996), especially for species where genetic variation is low (Reeb et al. 2000). Conventional and electronic tagging of swordfish shows that individuals are capable of extensive movements of thousands of kilometres (Brown, 1995, Garcia et al. 2003, Sperling et al. 2005). Regular migrations of adult swordfish between temperate and tropical areas within ocean basins have been recorded in the Atlantic and Pacific oceans (ICCAT 2011, Reeb et al. 2000), but localized sub-populations associated with oceanographic features such as seamounts and fronts are thought to exist (Sedberry 2001). Juveniles seem to be more common in tropical areas (Nishikawa et al. 1985).

In the Indian Ocean, swordfish is caught primarily (95%) by longline gear. Catches are thought to be sustainable at present, as catch rates are below and the biomass is just above the levels that would produce Maximum Sustainable Yield (MSY) (IOTC-SC14 2011). Swordfish effort is spatially and temporally disaggregated, but areas north of the Seychelles and in the Mozambique Channel around southern Madagascar produces the highest catch rates. The latter region was identified as a management unit of particular concern, because it seems to be more depleted than other regions in the Indian Ocean, and may have limited mixing with other regions (IOTC-SC14 2011). However, knowledge of biology and spatio-temporal distribution and movement of swordfishes in the western Indian Ocean is limited as it is mainly deduced from information on catch distribution from and analyses of biological samples (genetics, stable isotopes and gonad maturation) collected by observer programmes. These studies suggest that, as in other oceans, spawning occurs in tropical waters and spawning grounds are thought to be located east of La Reunion Island (Poisson 2006). Spawning takes place in the austral summer and swordfish larvae have been found in the seas east of Madagascar and in the northern Mozambique channel. To date there is no information on swordfish horizontal and vertical movements from this region as this species is difficult to tag in traditional mass tagging programmes, not at least because they are more widely dispersed than other large pelagic such as tuna and suffer from high mortality rates when taken aboard (Abascal et al. 2009), which results in very low tag return rates (Beckett, 1974). Pop-up Archival Satellite Tags (PSAT) provide an opportunity to study horizontal movements of individual animals over extended time periods as well as temperature and depth preferences (Block et al. 1999), but studies of swordfish in other oceans have so far provided mixed results. Problems associated with PSAT tagging of swordfish are due to

exhaustion and stress induced mortality of captured fish (Moyes et al. 2006, Skomal 2007), possible altered behaviour of tagged individuals, premature pop-up of tags, failure to transmit the information, low retrieval rates (Sepulveda et al. 2010), as well as difficulties related to recreate accurate positioning due to the diel vertical migration of swordfish into the deep scattering layer.

In this contribution we report on the first successful deployment of PSAT's on swordfish in the South Western Indian Ocean region. This study forms part of a larger initiative, the South West Indian Ocean Fisheries Programme (SWIOFP), component IV, which comprises of studies intended to aid the assessment and sustainable utilisation of the pelagic fishes in the region. The study presented here was aimed at (1) developing a protocol to maximise the success rate of tagging swordfishes caught by longline (2) to gain preliminary information on the horizontal and associated vertical movement of swordfish and (3) to put this information in context with current knowledge on the species movements and compare it to results from studies in other oceans.

Materials and Methods

Fishing operations

Swordfish were caught during a research cruise aboard the *RV Ellen Khuzwayo* in October/November 2011 operating along the East Coast of South Africa between Durban and Richards Bay adjacent to the southern Mozambique Channel and between 100 - 380 nautical

miles off the coast. During the return trip to the vessel's home port of Cape Town a final set was made on the western Agulhas Banks off the South Coast of South Africa. Fishing was undertaken with a drifting pelagic longline similar to American commercial operations and set from a Lindgren Pitman spool off the stern of the vessel.

A maximum of 360 hooks was deployed per set with five hooks to a basket and branch lines of 18 metres in length. Each branch line was fitted with a hook timer and eighteen Temperature Depth Recorders (TDRs) were equally spaced along the length of the main line to allow for the determination of the time and depth at which the highest strike rates for swordfish occurred. The first set, deployed at 21h30 and retrieved at 06h00 the next morning, indicated that catches occurred between midnight and 02h00. Based on this information, subsequent sets, made with 360 hooks were straddling this period, with a soak time of five hours. Hauling rate was directly dependant on the catch rate and the weather conditions, but most sets were completely retrieved around 08h00. After several sets had been completed it was evident that best catches of swordfish were made when the main line attained a depth of 30 m to 40 m and the vessel's speed during deployment and the spacing of the branch lines was adjusted accordingly to maintain this main line depth with a resultant depth of baits between 40 m and 50 m. The exposure time that a fish had been on the hook was also recorded to retrospectively link the condition of the fish at time of assessment for possible tag and release.

Capture

During retrieval of the longline the branch line of any potential catch was immediately disconnected from the main line and connected to a rope (fighting line) that was used to pull the catch close to a well-lit doorway in the gunwale amidships. Once the swordfish was close to the vessel, tension on the fighting line was released to assess the fishes' swimming behaviour. Only lively fish with a strong fighting response, hooked in the mouth and bigger than 1.5 m LJFL (Lower Jaw Fork Length, equivalent to a mass greater 50kg) were deemed suitable for tagging. Swordfish that had everted their stomachs, were bleeding from the gills or exhibited buoyancy (swim bladder) problems by turning onto their side or back and floating were not considered.

Tagging procedure

Swordfish chosen for tagging were lead alongside the vessel to the gunwale doorway and the MK 10 PSAT (Wildlife Computers) tag placed on the fish by means of a pole (Evans et al. 2012) to which the tag was temporarily affixed with elastic bands. The high (2.8m) freeboard of the vessel at the gunwale doorway necessitated the use of an extended (6m) carbon-fibre jab-pole. The tag was fitted with a custom made stainless steel Floy-type anchor (Evans et al. 2012) attached by a stainless steel leader with a swivel midway between tag and anchor. The anchor was inserted into the dorsal musculature of the fish in a position just below the dorsal fin. Once tagged a second jab-pole fitted with a biopsy corer was used to collect a muscle biopsy from the fish. The area below the dorsal fin was targeted for the muscle sample. A muscle sample was considered to be of secondary importance and consideration was always

given to minimizing the potential impacts on the fish after the placement of the tag, if the fish struggled against the restraining fighting line after tagging it was immediately release by cutting the line and allowed to swim free. An additional biopsy was collected when possible. Time of release and deployment positions of tagged swordfish were recorded using the vessel's onboard GPS system and the immediate post-release behaviour of the swordfish after tagging was noted. All released fishes were monitored as long as they remained visible from the vessel.

Tag setup

Tags were set to pop to the surface and transmit summarised depth, temperature and light sensor data after 90 and 180 days (Table 1) and to summarize depth and temperature data at intervals ranging from 25m to >900m and 2.5°C to >32.5°C, respectively. Tags were also programmed to corrode the pin in case of premature detachment detected when a tag recorded a constant depth for more than 24 hours. A mechanical release device (RD1800, Wildlife Computers) was used to cut the tether when animal reached a depth exceeding 1800 m.

Movements in depth and course

Vertical movement

Time intervals were set at 4 measurements (180 day tags) recording data at 1h00, 7h00, 13h00 and 19h00 or 6 measurements (90 day tags) recording data at 2h00, 6h00, 10h00, 14h00, 18h00 and 22h00. The tags recorded the depth (m) and temperature (°C) in bins. Data

were provided by Argos and processed using the Wildlife Computer software (Wildlife Computers, Redmond, WA, USA) which produced text (.txt) files that could be manipulated in Microsoft Excel.

Horizontal movement

Light sensor data was processed using the Wildlife Computer software. The most plausible track of the animal was determined with a non-state based random walk model using forward sampling as described by Tremblay et al. (2009). After a range of plausible maximum speeds, based on literature, was tested, 4km/h was selected as input for the final model.

Data analysis

The periodicity of the dives was determined by spectral analyses in Statsoft Statistica V10. The graphs and tables were generated in Microsoft Excel 2010, Golden Surfer 11, Statsoft Statistica V10 and Sigmaplot 2010. Statistical tests (Kendall rank correlation tests) were run in the statistical programming environment 'R' i386 2.15.1.

Results

General

Out of 59 caught swordfishes 11 swordfish were successfully released with PSAT tags (Table1). Three swordfish that had been tagged were exhibiting unnatural behaviour on

release, indicated by limited buoyancy control, and were immediately gaffed and landed. The tags were recovered and reset for subsequent deployment. One swordfish that swam strongly downwards on release was seen floating to the surface minutes later just at the edge of visibility, approximately 25m from the vessel. No attempt could be made to retrieve this fish due to restricted manoeuvring ability of the vessel which was still connected to the mainline and further exacerbated by rough sea conditions. Satellite communication was received from this tag several hours later confirming that the fish had died and remained floating. Out of the 11 successful releases, only two popped up close to the programmed release date. A further two tags were remained attached to the fishes for at least two months, completing the dataset (n=4) that was used for further analyses. The remainder of the tags started transmitting after less than a week, indicating that the fish had floated at the same depth for prolonged periods or had sunk to the bottom, triggering the release of the tag at the set maximum depth of 1800 m (Figure 1). Duration after being hooked, behaviour, or fish size did not seem to have an effect on release success. Two of the four fish with meaningful datasets were not considered to be in 'good' condition on release and the tag on fish 57671 was placed too low on the fishes flank but this did not preclude the fish from resuming natural behaviour as reflected by the vertical movement patterns over a considerable time period (Figure 2).

Vertical movement

The spectral analysis periodograms (Figure 4) indicated dominant or peak frequency at 0.25 for tags with 4 measurements per 24 hours (#57663 and #57673) and at 0.17 for tags with 6 measurements per 24 hours for (#57664 and #57671), suggesting diel cycles for all fishes. Three of the four fish, swordfish #57663 displaying this behaviour most clearly, followed a regular, distinct diel cycle; diving deep (500m – 800m) during daylight hours from 6h00 to

13h00, ascending to the surface from 13h00 to 18h00, remaining in the surface layers (0 – 400m) at night from 19h00 to 2h00 until they dive back down to deeper water at dawn (2h00 to 6h00) (Figure 3). Swordfish #57671 exhibited the opposite diving pattern, as it remained in shallow water during the day (10h00 to 18h00) to 22h00 and dived deep later in the night (22h00 to 2h00) (Figure 3).

The bathymetry at the swordfish's location in time was plotted alongside the swimming depth and temperature recordings on the tag (Figure 2). The bathymetry did not seem to influence the maximum diving depths made by the swordfish. The maximum temperatures encountered by the four swordfishes were between 25°C and 26.7°C, the minimum temperatures 3°C to 9.2°C. The maximum diving depths were 748 m, 668 m, 1092 m, and 812 m for #57663, #57664, #57671 and #57673, respectively. It was seldom that the maximum depth bin >900m was reached and there is some visual evidence that suggests that diving depth was restricted by the temperature at depth (Figure 2). There was no evidence of basking behaviour (the minimum depth was >8m), though the swordfish spent 2/3 to 3/4 of their time shallow (0-400m), independently of the water depth (Table 2). The median diving depths two days before and after full- and new moon, summarised in box-and-whisker plots for three of the four swordfish with the most data (Figure 5), showed no evidence for deeper dives around full moon.

It was hypothesised that the diving pattern changes with swimming speed in terms of the percentage of animal presence in shallow and deep water and the frequency of dives (Table 2). In three of the swordfish (#57663, #57664 and #57673) there was no correlation between the swimming speed and the percentage time spent at shallow or deep depths (Kendall rank

correlation, $\tau = -0.107$, $\tau = 0.316$, $\tau = 0.109$ and $p > 0.05$ for #57663, #57664 and #57673, respectively). Swordfish #57671 indicated that a significantly less amount of time was spent diving deep as the swimming speed increased (Kendall rank correlation, $\tau = -0.486$, $p < 0.05$) For the four swordfish there was no correlation between the swimming speed and the number dives each week (Kendall rank correlation, $\tau = 0.0166$, $\tau = 0.444$, $\tau = -0.191$, $\tau = -0.189$ and $p > 0.05$ for swordfish #57663, #57664, #57671 and #57673, respectively).

Horizontal movement

All of the tagged swordfish remained in the general area (South West Indian Ocean region). Fish #57671, which was tagged in the Atlantic west of 20° longitude, the border of the IOTC region, straddled this artificial boundary twice during large, circular movement into the South West Indian Ocean (Figure 6). The three swordfish tagged in the Mozambique channel also displayed a circular movement pattern, all swimming back towards the tagging location (Figure 6).

It was hypothesised that swordfish would swim faster over areas of greater depth. The movement tracks in Figure 6 are made up of circles of location estimates (the most likely position being chosen through the Tremblay et al. 2009 model) over time. The spacing between location circles is indicative of swimming speed; i.e. location circles that are close together indicate slower movement. In a preliminary analyses we found, however, no correlation between average weekly horizontal swimming speed and the average bathymetry

for the four swordfish (Kendall rank correlation, $\tau = 0.333$, $\tau = -0.318$, $\tau = 0.158$, $\tau = 0.259$ and $p > 0.05$ for swordfish #57663, #57664, #57671 and #57673, respectively).

The weekly sea surface temperature (SST) plots indicate a potential link in movement patterns to mesoscale eddies in swordfish #57664 (Figure 7 i) and #57671 (Figure 7 l).

Plotting the tracks over weekly chlorophyll-a surface plots revealed no patterns so these plots weren't included in the results here.

Discussion

General

This work reports on the first successful deployment of PSAT tags on swordfish in the South Western Indian Ocean region. PSAT tagging studies of swordfishes have been carried out in other areas where this species is common, including the North Atlantic (Dewar and Polovina 2005, Neilson et al. 2009) and the Northeast, northwest and Southwest Pacific (Takahashi et al. 2003, Sepulveda et al. 2010, Evans et al. 2012). In our study, only 4 out of 11 (36%) tagged swordfish yielded data over more than two months, as most tags were released shortly after deployment, due to the death of the fish. A high post release mortality rate has been described from similar studies for harpooned and longline caught swordfishes (Neilson et al. 2009, Abascal et al. 2009). Harpooning basking swordfishes with a tagging pole might be preferable; as it reduces stress and lactate build up common to animals that remain hooked for prolonged periods of time, and might therefore reduce post release mortality. However, in

the current study we did not find any evidence of a relationship between the length of time an animal was hooked on the longline before retrieval and release success. Moreover, the visual assessment of tagged swordfishes was misleading as animals that seemed to be in good condition died shortly after release and animals that appeared sluggish yielded satisfactory results. Swordfish typically remained close to the surface for some time before sinking to the bottom, triggering the tags' release mechanism (Figure 1). A more detailed analysis of capture and tagging effects is necessary to improve the success rate of future swordfish tagging studies.

Vertical movement

The prevalent vertical movement pattern found here, alternating between deep dives (500-800 m) during the day and residing in shallow waters during the night, has been found in most studies (Abascal et al. 2009, Sepulveda et al. 2010, Sedberry and Loefer 2001). Sepulveda et al. (2010) described three different behavioural patterns for swordfish vertical movement and our results are consistent with behaviour I (diel vertical migration) and behaviour III (prolonged surface oriented activity), mainly exhibited by fish #57671, which spent extended periods in shallow waters without diving deep, based on the data provided by the tag. However, we found no evidence of basking behaviour as reported from elsewhere (Sepulveda 2010, Takahashi 2003) and fish #57671 seemed to exhibit the reverse pattern of behaviour I with deeper dives during the night. The differences in behaviour exhibited by fish 57671 might be ascribed to the fact that it resided in a different area, the Agulhas region, than the other three fishes, which largely remained in the Southern Mozambique Channel.

Boyce et al. (2008) summarised 18 studies on the temperature ranges of swordfish from 1950 to 2006 in the Indian, Atlantic and Pacific Oceans. The minimum and maximum temperatures were 3°C and 30°C, respectively, and the mean minimum and maximum temperatures were 8.89°C and 27.86°C, respectively. These ranges are in line with our study of minimum and maximum temperatures of 3°C and 26.7°C, respectively. This wide temperature range is probably due to physiological adaptations that give swordfish a tolerance for colder temperatures and extreme temperature changes (Boyce et al, 2008). Apart from temperature, the depth to which swordfish dive might be influenced by environmental factors such as salinity, oxygen content, turbidity, wind and current (Laurs et al. 1984; Podesta et al. 1993; Bigelow et al. 1999, 2006; Damalas et al. 2007; Tserpes et al. 2008) as well as general bathymetry, which could limit maximum diving depth (Sepulveda et al. 2010). In our study, the swordfishes remained over areas much deeper than their maximum diving depth and no relationship between bathymetry and diving depth was evident. However, dives seemed to be restricted in depth by the presence of water temperatures below 8°C, which is in line with findings from elsewhere (Carey and Robison 1981, Sepulveda et al. 2010). Despite their wide temperature tolerance range (Takahashi et al. 2003, Abascal et al. 2009, Sepulveda et al. 2010) swordfish are thought to having to spend extended periods of time in shallow water following deep dives in colder water (Beckett, 1972) and low oxygen concentrations at depth (Carey and Robison 1981, Abascal et al. 2009) due to physiological requirements. Similarly, the four swordfish studied here spent the majority of their time in depths <400m, although not basking at the surface. The presence of

prey also influences the depths to which swordfish dive to and the amount of time spent feeding at those depths (Abascal et al. 2009).

It has been previously documented that surface fluorescence influences the movement of prey, affecting the maximum dive depths of swordfish around those times, diving deeper in the presence of more light around full moon (Carey and Robison, 1981, Abascal et al. 2009, Draganik and Cholyst 1988). In our preliminary analyses a range of $n=9$ to $n=40$ (Figure 5) diving depth data points was a combination of day and night dive depths and had not been restricted to diving depths during daylight hours due to the reverse diving behaviour of swordfish #57671. The inconsistent relationship between diving depths and moon phase could be due to the limited data available per animal, the reverse diving pattern seen in #57671. The high frequency of cloud cover could also be a reason why no clear trends were found, but further analyses of the data are necessary.

Our preliminary analyses of a relationship between swimming speed and diving pattern, indicated by the number of dives and the percentage of time spent in shallow and deep water, respectively, showed no clear trends. Only one fish spent significantly more time in shallow waters when travelling faster. Travelling in shallow water might be favourable because of lower water density, higher temperatures that might be physiologically favourable, or advantageous surface currents, but more analyses are needed to confirm this hypothesis.

Horizontal movement

The azimuthal direction of travel (Hoolihan 2005) displayed by these four animals has been observed in other studies of large pelagic predators such as Atlantic sailfish (Jolley and Irby 1979), striped marlin (Holts and Bedford 1990; Brill et al. 1993), blue marlin (Yuen et al. 1972, Holland et al. 1990) and black marlin (Pepperell and Davis 1999). This movement pattern and direction of travel may be due to the swordfish being at liberty to the currents speed and direction (Brill et al. 1999) though this was not measured in this study, or the existence of a bounded home range in this area, as suggested for swordfish populations in other oceans (Evans et al. 2012).

Currently, the Regional Fisheries Management Organisations IOTC and ICCAT are responsible for management swordfish caught in the fishing grounds off South Africa, using the 20°E longitude line to separate management responsibilities. The boundaries and connectivity of many pelagic species is poorly understood, and it is important to study their horizontal movement patterns as they are highly dispersed and capable of large-scale migrations (Evans et al. 2012). Swordfish #57671 is an example of an animal that straddled the artificial management boundary as it was tagged in the Atlantic Ocean; swam into the Indian Ocean and returned into the Atlantic Ocean. Similar patterns have been found for other large pelagic predators off South Africa (da Silva et al. 2011) and further studies are required on the extent of the connectivity between large pelagic predator stocks across the boundary of these two oceans.

Although there was no statistically significant correlation between the average horizontal swimming speed and depth in the preliminary analysis carried out here, a more detailed analysis of the available data is required. Swordfish are known to spend more time around bathymetric features such as sea mounts and along the shelf edge, as these areas are usually associated with oceanographic conditions that increase productivity and therefore attract bait organisms.

We found some visual evidence that the horizontal movement patterns along the tracks of #57664 and #57671 (Figure 7) could be related to meso-scale oceanographic features such as eddies. Schools of pelagic fish, including tunas and billfish, are known to aggregate along the edge of such features. The role meso-scale eddies play in affecting the distribution of micronekton (fishes, crustaceans and squid), prey for pelagic predators, is unclear. In a study by Potier et al. (2012) swordfish displayed a clearer association with mesoscale structures in the Mozambique Channel than tunas, with a clear preference for divergences, which is consistent with the occurrence of its main prey, the flying squids (Ommastrephidae). Similar conclusions have been drawn from earlier studies by Seki et al. (2002), Sabarros et al. (2009), Mitchum and Polovina (2001), Tew-Kai and Marsac (2010).

Conclusion

Our preliminary analyses of data of the first PSAT tagged swordfish off South Africa revealed vertical movement patterns that are mostly consistent with studies elsewhere in the world, although there were some differences, namely the complete absence of basking behaviour, the inconsistent relationship of diving pattern with moon phase and the reverse diving pattern displayed by one of the animals. Swordfish dives seemed to be restricted by a

temperature ceiling at depth and a significantly higher percentage of time was spent in shallow > 400m waters. The fact that all animals remained within the region over the study period suggests the presence of a local stock in the South West Indian Ocean which might be related to the areas of high productivity. The movement of one animal between the Atlantic and Indian Ocean suggests that the 20° longitude management boundary might not be appropriate in terms of stock delineation, but a more in depth analysis, including fisheries patterns and size frequencies of South African caught swordfishes is needed. More in-depth analyses with more tagged animals is required to understand the vertical and horizontal movement of swordfish in the region, as this information will assist in improving assessment and management of the fisheries targeting these animals.

Acknowledgements

This work was partly funded by the SWIOFP programme, the IRD and the South African Department of Agriculture, Forestry and Fisheries. Captain Dawie Erasmus and the crew of the *RV Ellen Khuzwayo* are thanked for their tireless assistance during longline operations. We would like to acknowledge Karen Evans for sharing her expertise and knowledge as well as Yann Tremblay for providing the particle model used to analyse the horizontal movement. Finally Bruce Mann from Oceanographic Research Institute (ORI) and staff of the Inshore research section of the Chief Directorate: Fisheries Research and Development of Department of Agriculture, Forestry and Fisheries (DAFF) are thanked for their assistance in the field.

References:

Abascal, F. J., Mejuto, J., Quintans, M., and Ramos-Cartelle, A. 2010. Horizontal and vertical movements of swordfish in the Southeast Pacific. – ICES Journal of Marine Science, 67: 466–474.

Beckett, J. S. (1974) Biology of swordfish, *Xiphias gladius* L., in the northwest Atlantic Ocean. In: Shomura RS, Williams F (eds) Proceedings of the International Billfish Symposium, part 2. Review and contributed papers. (NOAA tech Rep NMFS SSRF-675) U.S. Government Printing Office, Washington, D.C., pp103-106.

Bigelow, K.A., Boggs, C.H. and He, X. (1999) The environmental effects on swordfish and blue shark catch rates in the US North Pacific longline fishery. Fisheries Oceanography. 8(3): 178-198.

Bigelow, K.A., Musyl, M.K., Poisson, F. and Kleiber, P. (2006) Pelagic longline gear depth and shoaling. Fisheries. Research. 77:173–183.

Block, B.A., Dewar, H., Farwell, C.F. and Prince, E.D. (1999) Novel satellite technology for tracking the movements of Atlantic bluefin tuna. Proc. Natl Acad. Sci. USA 95:9384– 9389.

Boyce, D. G, Tittensor, D. P. and Worm, B. (2008) Effects of temperature on global patterns of tuna and billfish richness. Marine Ecology Progress Series, 355: 267-276.

Brill, R.W., Holts, D.B., Chang, R.K.C., Sullivan, S., Dewar, H. and Carey, F.G. (1993) Vertical and horizontal movements of striped marlin (*Tetrapturus audax*) near the Hawaiian Islands, determined by ultrasonic telemetry, with simultaneous measurement of oceanic currents. Marine Biology, 117: 567±574.

Brill, R. W, Block, B. A, Boggs, C. H., Bigelow, K. A, Freund, E. V. and Marcinek, D. J. (1999) Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands, recorded using ultrasonic telemetry: implications for the physiological ecology of pelagic fishes. Marine Biology, 133: 395-408.

Brown, C.A. (1995) Preliminary examination of size and location data for United States tagged and recaptured swordfish. Collect. Vol. Sci. Pap. ICCAT, 44 (3): 217-224.

Carey, F. G., and Robinson, B. H. (1981) Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. Fishery Bulletin US, 79: 277–292.

Collette, B. B. (1995) Xiphiidae. Peces espada. p. 1651-1652. In W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter and V. Niem (eds.) Guia FAO para Identificacion de Especies para lo Fines de la Pesca. Pacifico Centro-Oriental. 3 Vols. FAO, Rome.

Damalas, D., Megalofonou, P. and Apostolopoulou, M. (2007) Environmental, spatial, temporal and operational effects on swordfish (*Xiphias gladius*) catch rates of eastern Mediterranean Sea longline fisheries. *Fisheries Research*, 84: 233-246.

Dewar, H., and Polovina, J. 2005. Deploying satellite tags on swordfish using the California harpoon fleet. *Pelagic Fisheries Research Program Newsletter*, 10: 4–6.

Draganik, B. and Cholyst, J. (1987) Temperature and moonlight as simulators for feeding activity by swordfish. *ICCAT Col. Vol. Sci. Pap.* 27, pp. 305–314 (SCRS/87/080 Rev.).

Evans, K., Kolody, D., Abascal, F., Holdsworth, J., Maru, P. and Sippel, T. (2012) Spatial Dynamics of swordfish in the South Pacific Ocean Inferred from Tagging Data. Eighth regular session of the WCPFC. Busan, Republic of Korea, 7-15 December 2011. WCPFC-SC8-2012/ SA-IP-05.

Garcia-Cortes, B., Mejuto, J. and Quintans, M (2003) Summary of swordfish (*Xiphias gladius*) recaptures carried out by the Spanish surface longline fleet in the Atlantic Ocean: 1984-2002. *Collect. Vol. Sci. Pap. ICCAT*, 55(4): 1476-1484.

Holland K., Brill R., Chang R.K.C. (1990) Horizontal and vertical movements of Pacific blue marlin captured and released using sportfishing gear. *Fish Bull US* 88: 397±402.

Holts D. and Bedford D. (1990) Activity patterns of striped marlin in the southern California Bight. In: Stroud RH (ed) *Planning the future of billfishes*. National Coalition Marine Conservation, Savannah, Georgia, pp 81±93.

Hoolihan, J. P. (2005) Horizontal and vertical movements of sailfish (*Istiophorus platypterus*) in the Arabian Gulf, determined by ultrasonic and pop-up satellite tagging. *Marine Biology*, 146: 1015-1029.

IOTC-SC14 (2011) Report of the Fourteenth Session of the IOTC Scientific Committee. Mahe, Seychelles, 12-17 December 2011. *IOTC-2011-SC-14-R[E]*: 259pp.

Jolley J.W. Jr and Irby E.W. Jr (1979) Survival of tagged and released Atlantic sailfish (*Istiophorus platypterus*: Istiophoridae) determined by acoustical telemetry. *Bulletin of marine Science*, 29: 155±169.

Laurs, R.M., Fiedler, P.C. and Montgomery, D.R. (1984) Albacore tuna catch distributions relative to environmental features observed from satellites. *Deep-Sea Res.* 31:1085±1099.

Mitchum, G. and Polovina, J. (2001) Evaluation of Remote Sensing Technologies for Identification of Ocean Features Critical to Pelagic Fishes. *JIMAR/PFRP Annual Report*. (www.soest.hawaii.edu/PFRP).

- Nakamaru, I. (1985) FAO species catalogue. Vol. 5. Billfishes of the world. An annotated and illustrated catalogue of marlins, sailfishes, spearfishes and swordfishes known to date. FAO Fish. Synop. 125(5):65 p.
- Neilson, J. D., Smith, S., Royer, F., Paul, S. D., Porter, J. M. and Lutcavage, M. (2009) Investigations of Horizontal Movements of Atlantic Swordfish Using Pop-up Satellite Archival Tags. In Tagging and Tracking of Marine Animals with Electronic Devices, Reviews: Methods and Technologies in Fish Biology and Fisheries 9, pp 145-159.
- Nishikawa, Y., Honma, M., Ueyanagi, S. and Kikawa, S. (1985) Average distribution of larvae of oceanic species of scombrid fishes, 1956±1981. Far Seas Fisheries Research Laboratory, Shimizu.
- Palko, B.J, Beardsley, G. L., Richards, W. J. (1981) Synopsis of the biology of the swordfish, *Xiphias gladius* Linnaeus. (NOAA Tech Rep) NMFS Circ 441:2-11.
- Podesta, G.P., Browder, J.A. and Hoey, J.J. (1993) Exploring the relationship between swordfish catch rates and thermal fronts on U.S. longline grounds in the western North Atlantic. Cont. Shelf Res. 13:253±277.
- Pepperell, J. G and Davis, T. L. O. (1999) Post-release behaviour of black marlin, *Makaira indica*, caught off the Great Barrier Reef with sportfishing gear. Marine Biology, 135: 369-380.
- Poisson, F. (2006) Synopsis of the reproductive dynamics of swordfish in Indian Ocean and areas for future studies, IOSSS Workshop, La Reunion.
- Potier, M., Bach, P., Ménard, F., Marsac, F. (2012) Influence of mesoscale features on micronekton and top predators in the Mozambique Channel. In press.
- Reeb, C. A., Arcangeli, L. and Block, B. A. (2000) Structure and migration corridors in Pacific populations of the swordfish *Xiphias Gadius*, as inferred through analyses of mitochondrial DNA. Marine Biology, 136: 1123-1131.
- Rosel, P. E. and Block, B. A. (1996) Mitochondrial control region variability and global population structure in the swordfish, *Xiphias Gladius*. Marine Biology, 125 (1) 11-22.
- Sabarros, P. S, Ménard, F., Lévénez, J-J., Tew-Kai, E., Ternon, J-F. (2009) Mesoscale eddies influence distribution and aggregation patterns of micronekton in the Mozambique Channel. Marine Ecology Progress Series, 395: 101-107.
- Sedberry, G.R. and Loefer, J. K. (2001) Satellite telemetry tracking of swordfish , *Xiphias gladius*, off the eastern United States. Marine Biology, 139: 355-360.

Seki, M. P., Polovina, J. J., Kobayashi, D. R., Bidigare, R. R and Mitchum, G. T. (2002) An oceanographic characterization of swordfish (*Xiphias gladius*) longline fishing grounds in the springtime subtropical North Pacific. *Fisheries Oceanography*, 11(5): 251-266.

Sepulveda, C., Knight, A., Nasby-Lucas, N. and Domeier, M.L. (2010) Fine-scale movements of the swordfish *Xiphias gladius* in the Southern California Bight. *Fish. Oceanogr.* 19:279– 289.

Skomal, G. B. (2007) Evaluating the physiological and physical consequences of capture on post-release survivorship in large pelagic fishes. *Fisheries Management and Ecology*, 14: 81-89.

Takahashi, M., Okamura, H., Yokawa, K., and Okazaki, M. (2003) Swimming behaviour and migration of a swordfish recorded by an archival tag. *Marine and Freshwater Research*, 54: 527–534.

Tal Sperling, A., Neilson, J. D., Carruthers, E. H., and Stone, H. H. (2005) Compilation and analyses of Canadian conventional tagging data for swordfish (*Xiphias gladius*), 1961-2004. *Collect. Vol. Sci. Pap. ICCAT*, 58(4): 1483-1494.

Tew Kai, E. and Marsac, F. (2010). Influence of mesoscale eddies on spatial structuring of top predators' communities in the Mozambique Channel. *Progress in Oceanography*, 86: 214-223.

Yuen HSH, Dizon AE, Uchiyama JH (1974) Notes on the tracking of the Pacific blue marlin, *Makaira nigricans*. In: Shomura R, Williams F (eds) *Proceedings of the International Billfish Symposium 1972*. Part 2. US Department of Commerce, Kailua, Hawaii, pp 265±268 (NOAA tech Rep NMFS SSRF-675) 380.

Young, J., Lansdell, M., Riddoch, S. and Revill, A. (2006) Feeding ecology of broadbill swordfish, *Xiphias gladius*, off eastern Australian in relation to physical and environmental variables. *Bulletin of Marine Science*, 79(3): 793-809.

Table 1. Deployment and tagging details for swordfish tagged with pop-up satellite archival tags (n=11). Catch locations, release positions, release times and release conditions are shown for each fish as well as pop-up date, programmed pop-up date and actual number of days where data were collected. The lower jaw fork length (LJFL) of each swordfish was estimated to the nearest cm.

| PTT nr | Tag date | Latitude | Longitude | Time Released | Estimated LJFL (cm) | Release condition | Pop-up date | Programmed cut-off | Actual days |
|--------|------------|------------|-----------|---------------|---------------------|------------------------|-------------|--------------------|-------------|
| 57663 | 2011/10/18 | -28 17.136 | 34 54.419 | 03:32 | 140 | Good | 2012/01/16 | 90 | 91 |
| 57675 | 2011/10/19 | -28 23.454 | 34 47.152 | 07:15 | 170 | Good | 2011/10/21 | 180 | 2 |
| 57670 | 2011/10/19 | -28 35.30 | 34 43.40 | 04:15 | 150 | Floating and thrashing | 2011/10/19 | 180 | 1 |
| 57678 | 2011/10/25 | -27 45.017 | 38 01.692 | 03:50 | 170 | Sluggish | 2011/10/30 | 90 | 5 |
| 57668 | 2011/10/25 | -27 49.625 | 38 02.582 | 06:11 | 220 | Sluggish | 2011/10/29 | 90 | 4 |
| 57679 | 2011/10/25 | -27 50.556 | 38 01.016 | 06:40 | 220 | Good | 2011/10/25 | 180 | 1 |
| 57673 | 2011/10/26 | -27 48.617 | 38 53.004 | 03:41 | 160 | Sluggish | 2011/10/21 | 180 | 60 |
| 57664 | 2011/10/26 | -27 49.325 | 38 03.543 | 04:02 | 180 | Good | 2011/10/28 | 90 | 64 |
| 57657 | 2011/10/27 | -27 45.306 | 38 01.469 | 04:51 | 160 | Good | 2011/10/29 | 180 | 2 |
| 57658 | 2011/10/28 | -28 34.531 | 35.23.421 | 05:08 | 169 | Good | 2011/10/29 | 180 | 1 |
| 57571 | 2011/11/02 | -35 49.062 | 18 56.815 | 04:35 | 170 | Sluggish | 2012/01/25 | 90 | 80 |

Table 2. Data on horizontal and vertical movements of the four swordfish tagged with pop-up archival tags during a period of 13 weeks. Average swimming speeds (km.h⁻¹) and average depths with standard deviation at calculated locations during different moon phases were calculated for each week. The number of observations as well as the percentage of time in shallow waters (0-400m) and deep waters (>401 m) were calculated. The movement between shallow (0-400m) and deep (>401m) waters were calculated for each swordfish per week. In instances where no data were available this was denoted by ‘-’.

| 57663 | Swimming speed | | Swimming depth | | | Movements from shallow to deep | | | Bathymetry | | Moon phase |
|-------|--------------------------------------|--|--------------------------------|-------------------------------|--------|--------------------------------|--------|-----------|------------|---------------|------------|
| | Average speed (km.hr ⁻¹) | | Number of observations 0-400 m | Number of observations >401 m | % Deep | % Shallow | % Deep | Avg depth | Std dev | | |
| 1 | 0.64 | | 11 | 3 | 79 | 21 | 6 | -2.489 | 352 | Last Quarter | |
| 2 | 0.73 | | 12 | 5 | 71 | 29 | 10 | -2.621 | 53 | New moon | |
| 3 | 1.11 | | 10 | 6 | 63 | 38 | 8 | -2.558 | 228 | First Quarter | |
| 4 | 1.81 | | 15 | 6 | 71 | 29 | 9 | -4.065 | 1.152 | Full moon | |
| 5 | 1.89 | | 17 | 5 | 77 | 23 | 9 | -3.524 | 441 | Last Quarter | |
| 6 | 2.15 | | 12 | 3 | 80 | 20 | 6 | -3.902 | 701 | New moon | |
| 7 | 1.66 | | 13 | 5 | 72 | 28 | 10 | -4.929 | 206 | Full moon | |
| 8 | 1.22 | | 12 | 4 | 75 | 25 | 8 | -5.223 | 210 | Last Quarter | |
| 9 | 2.01 | | 14 | 4 | 78 | 22 | 8 | -5.141 | 394 | New moon | |
| 10 | 1.84 | | 8 | 3 | 73 | 27 | 4 | -3.080 | 984 | First Quarter | |
| 11 | 2.21 | | 13 | 4 | 76 | 24 | 8 | -3.960 | 705 | First Quarter | |
| 12 | 2.40 | | 14 | 5 | 74 | 26 | 10 | -4.559 | 436 | Full Moon | |
| 13 | - | | - | - | - | - | - | - | - | New Moon | |

| 57664 | Swimming speed | | Swimming depth | | | Movements from shallow to deep | | | Bathymetry | | Moon phase |
|-------|--------------------------------------|--|--------------------------------|-------------------------------|--------|--------------------------------|--------|------------------|------------|---------------|------------|
| | Average speed (km.hr ⁻¹) | | Number of observations 0-400 m | Number of observations >401 m | % Deep | % Shallow | % Deep | Average depth(m) | Stdev | | |
| 1 | 0.66 | | 0 | - | - | - | 0 | -4.734 | 101 | Last Quarter | |
| 2 | 0.79 | | 6 | 1 | 86 | 14 | 2 | -4.686 | 193 | New moon | |
| 3 | 0.79 | | 3 | 0 | 100 | 0 | 0 | -4.686 | 193 | First Quarter | |
| 4 | 0.80 | | 0 | 0 | - | - | 0 | -3.666 | 883 | Full moon | |
| 5 | 0.40 | | 0 | 0 | - | - | 0 | -2.100 | 131 | Last Quarter | |
| 6 | 0.81 | | 1 | 1 | 50 | 50 | 2 | -2.002 | 129 | New moon | |
| 7 | 1.20 | | 3 | 5 | 38 | 63 | 4 | -1.798 | 164 | Full moon | |

| | | | | | | | | | |
|----|------|---|---|----|----|---|--------|-----|---------------|
| 8 | 1.80 | 7 | 6 | 54 | 46 | 5 | -2.450 | 222 | Last Quarter |
| 9 | 1.89 | 3 | 2 | 60 | 40 | 2 | -2.295 | 558 | New moon |
| 10 | 2.47 | - | - | - | - | 0 | -2.621 | 488 | First Quarter |
| 11 | - | - | - | - | - | 0 | - | - | First Quarter |
| 12 | - | - | - | - | - | 0 | - | - | Full Moon |
| 13 | - | - | - | - | - | 0 | - | - | New Moon |

| 57671 | Swimming speed | | Swimming depth | | | | Movements from shallow to deep | | | Bathymetry | | Moon phase |
|-------|--------------------------------------|------------------------|--------------------------------|-------------------------------|-----------|--------|--------------------------------|-------------------|--------|------------|-------|---------------|
| | Average speed (km.hr ⁻¹) | Number of observations | Number of observations 0-400 m | Number of observations >401 m | % Shallow | % Deep | Number of observations | Average depth (m) | Stddev | | | |
| Week | | | | | | | | | | | | |
| 1 | 2.32 | - | - | - | - | - | - | - | - | 2.986 | 1.269 | Last Quarter |
| 2 | 2.26 | - | - | - | - | - | - | - | - | 4.685 | 744 | New moon |
| 3 | 2.11 | 5 | 1 | 83 | 17 | 2 | 2 | 2 | 2 | 3.528 | 624 | First Quarter |
| 4 | 2.26 | 15 | 3 | 83 | 17 | 4 | 4 | 4 | 4 | 4.685 | 744 | Full moon |
| 5 | 2.11 | 12 | 5 | 71 | 29 | 8 | 8 | 8 | 8 | 3.528 | 624 | Last Quarter |
| 6 | 1.93 | 12 | 10 | 55 | 45 | 9 | 9 | 9 | 9 | 4.200 | 139 | New moon |
| 7 | 1.85 | 10 | 8 | 56 | 44 | 11 | 11 | 11 | 11 | 4.196 | 134 | Full moon |
| 8 | 1.96 | 8 | 9 | 47 | 53 | 3 | 3 | 3 | 3 | 4.703 | 572 | Last Quarter |
| 9 | 1.81 | 6 | 7 | 46 | 54 | 1 | 1 | 1 | 1 | 5.209 | 199 | New moon |
| 10 | 3.54 | 11 | 3 | 79 | 21 | 4 | 4 | 4 | 4 | 4.235 | 686 | First Quarter |
| 11 | 3.66 | 14 | 0 | 100 | 0 | 0 | 0 | 0 | 0 | 4.845 | 373 | First Quarter |
| 12 | 3.14 | 28 | 0 | 100 | 0 | 0 | 0 | 0 | 0 | 4.736 | 202 | Full Moon |
| 13 | 1.83 | 11 | 1 | 92 | 8 | 0 | 0 | 0 | 0 | 3.119 | 776 | New Moon |

| 57673 | Swimming speed | | Swimming depth | | | | Movements from shallow to deep | | | Bathymetry | | Moon phase |
|-------|--------------------------------------|------------------------|--------------------------------|-------------------------------|-----------|--------|--------------------------------|-------------------|--------|------------|-----|---------------|
| | Average speed (km.hr ⁻¹) | Number of observations | Number of observations 0-400 m | Number of observations >401 m | % Shallow | % Deep | Number of observations | Average depth (m) | Stddev | | | |
| Week | | | | | | | | | | | | |
| 1 | - | - | - | - | - | - | - | - | - | - | - | Last Quarter |
| 2 | 1.31 | 5 | 2 | 71 | 29 | 4 | 4 | 4 | 4 | 4.987 | 23 | New moon |
| 3 | 1.31 | 7 | 3 | 70 | 30 | 5 | 5 | 5 | 5 | 4.987 | 23 | First Quarter |
| 4 | 1.11 | 6 | 5 | 55 | 45 | 7 | 7 | 7 | 7 | 4.929 | 69 | Full moon |
| 5 | 1.24 | 11 | 5 | 69 | 31 | 7 | 7 | 7 | 7 | 4.628 | 142 | Last Quarter |
| 6 | 1.17 | 4 | 1 | 80 | 20 | 2 | 2 | 2 | 2 | 3.861 | 252 | New moon |
| 7 | 1.14 | 11 | 2 | 85 | 15 | 3 | 3 | 3 | 3 | 3.188 | 259 | Full moon |
| 8 | 1.13 | 1 | 2 | 33 | 67 | 2 | 2 | 2 | 2 | 2.630 | 464 | Last Quarter |
| 9 | 1.35 | - | - | - | - | 1 | 1 | 1 | 1 | 2.837 | 51 | New moon |
| 10 | - | - | - | - | - | - | - | - | - | - | - | First Quarter |
| 11 | - | - | - | - | - | - | - | - | - | - | - | First Quarter |

12
13

-

-

-

Full Moon
New Moon

Figure 1. Typical post-release behaviour of an unsuccessful swordfish release followed by mortality. The pop-up archival tag attached to this swordfish (PTT 57668) popped off 3 days after release.



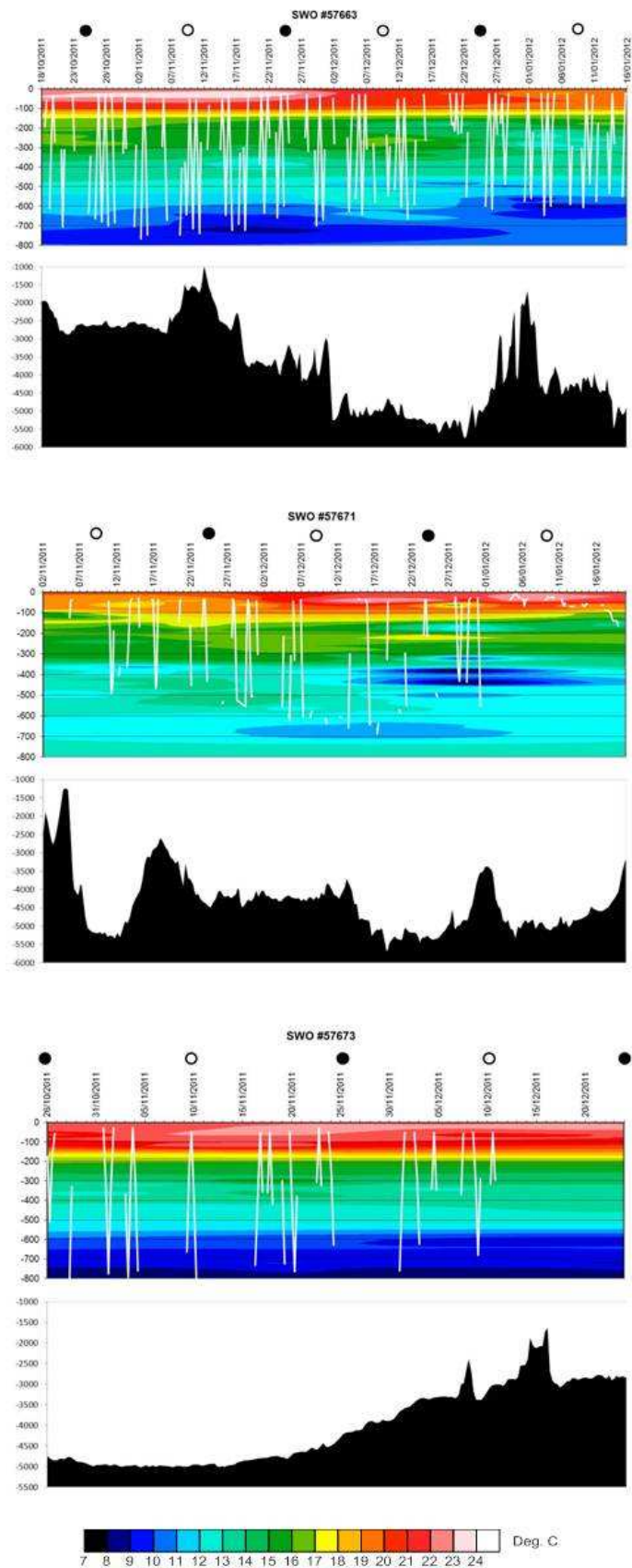
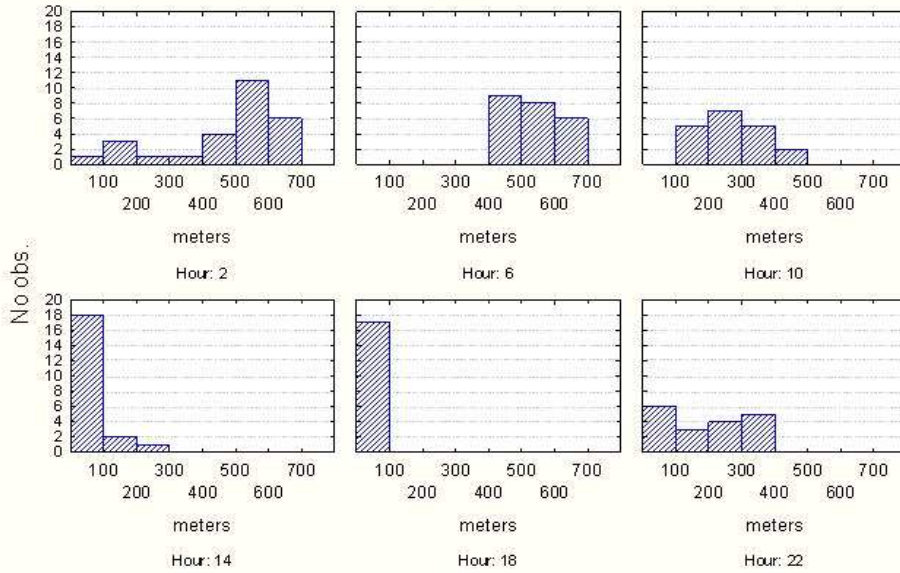


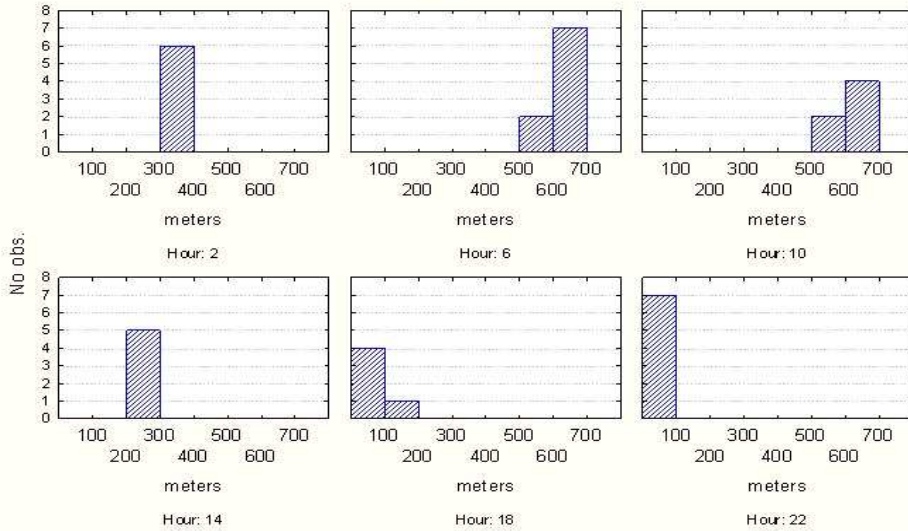
Figure 2. The vertical movement of three swordfish tagged with pop-up archival tags are shown superimposed on temperature ranges at different moon phases. The depth profiles at each location and experienced by each fish is shown in the bottom panel.

Median depth by time of the day
Swordfish # 57671



a)

Median depth by time of the day
Swordfish # 57664



b)

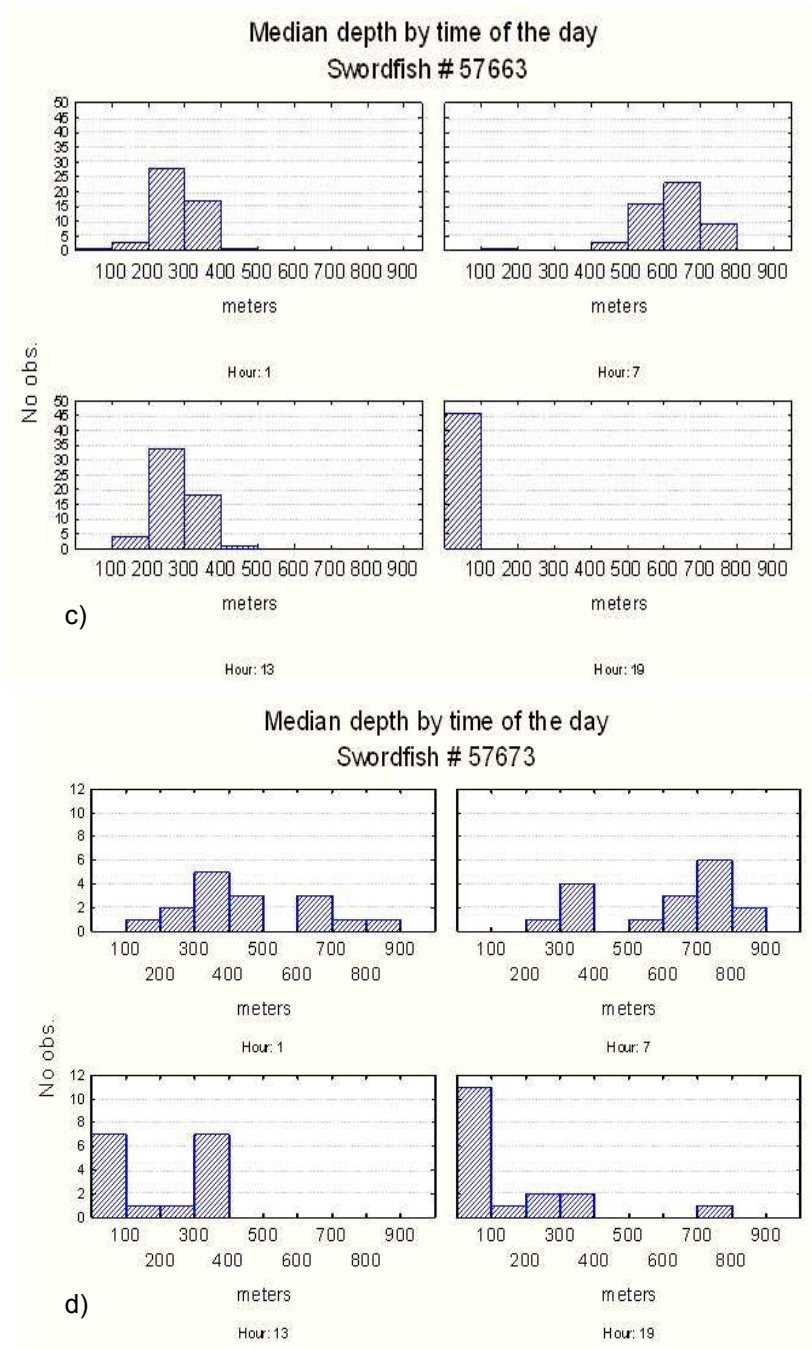


Figure 3. The median swimming depth at the time of the day for swordfish a) #57671 , b) #57664, c) #57663 and d) #57673.

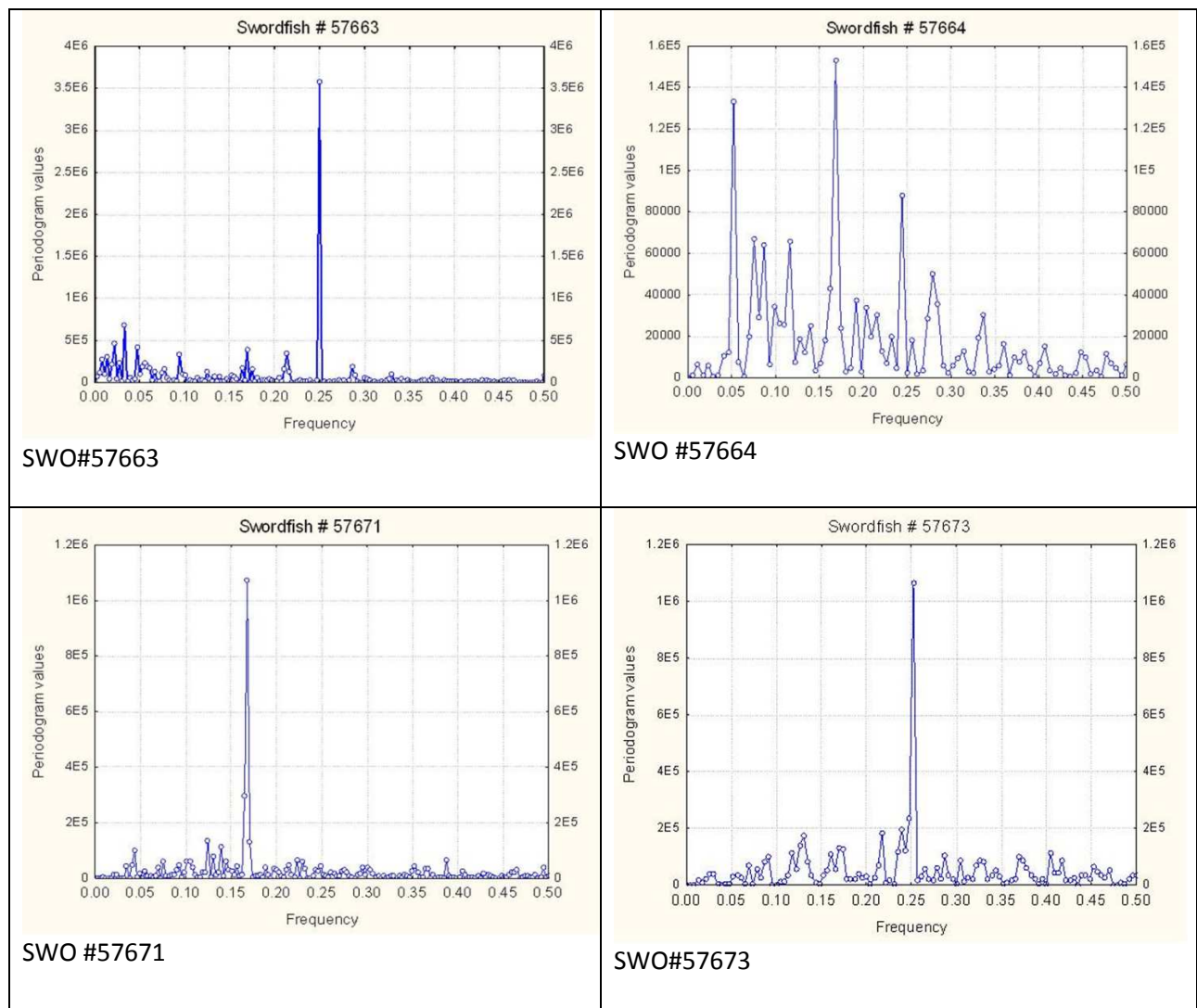
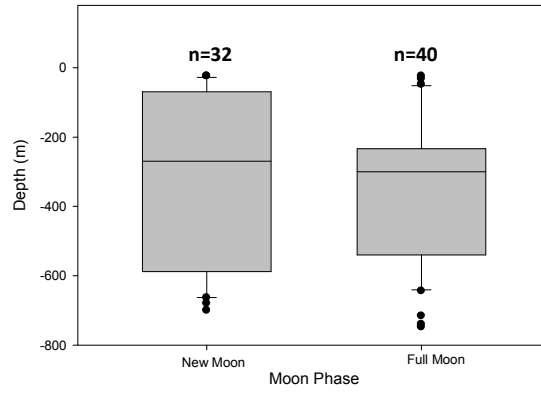
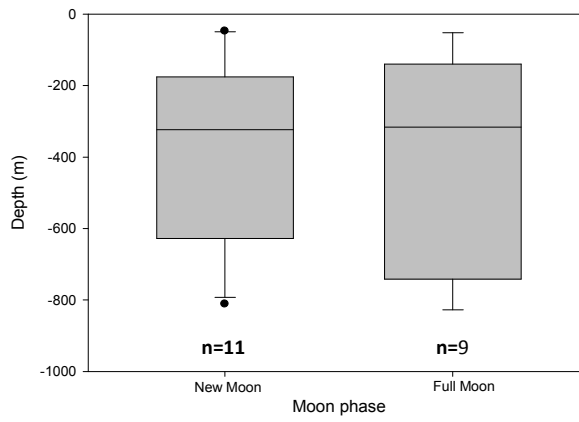


Figure 4. Results from spectral analysis of the four swordfish tagged with pop-up archival satellite tags. Periodogram values showed a peak in periodicity of 0.25 for swordfish 57663 and 57673 (4 measures in 24 hours), 0.05 for swordfish 57664 (6 measurements in 24 hours) and 0.17 for swordfish 57671 (6 measurements in 24 hours).

Swordfish # 57663



Swordfish # 57673



Swordfish # 57671

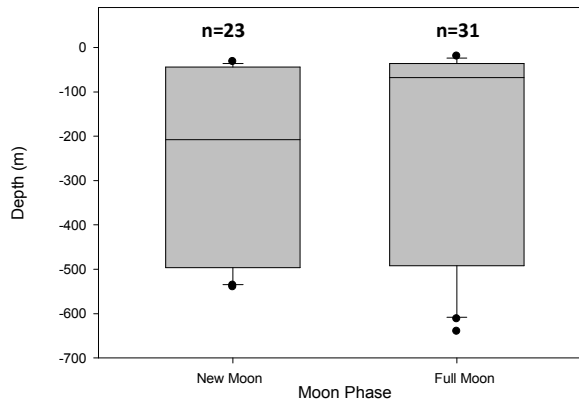


Figure 5. Diving depths (m) of swordfish tagged with pop-up archival satellite tag two days before and after full moon, n represents the number of observations for each moon phase.

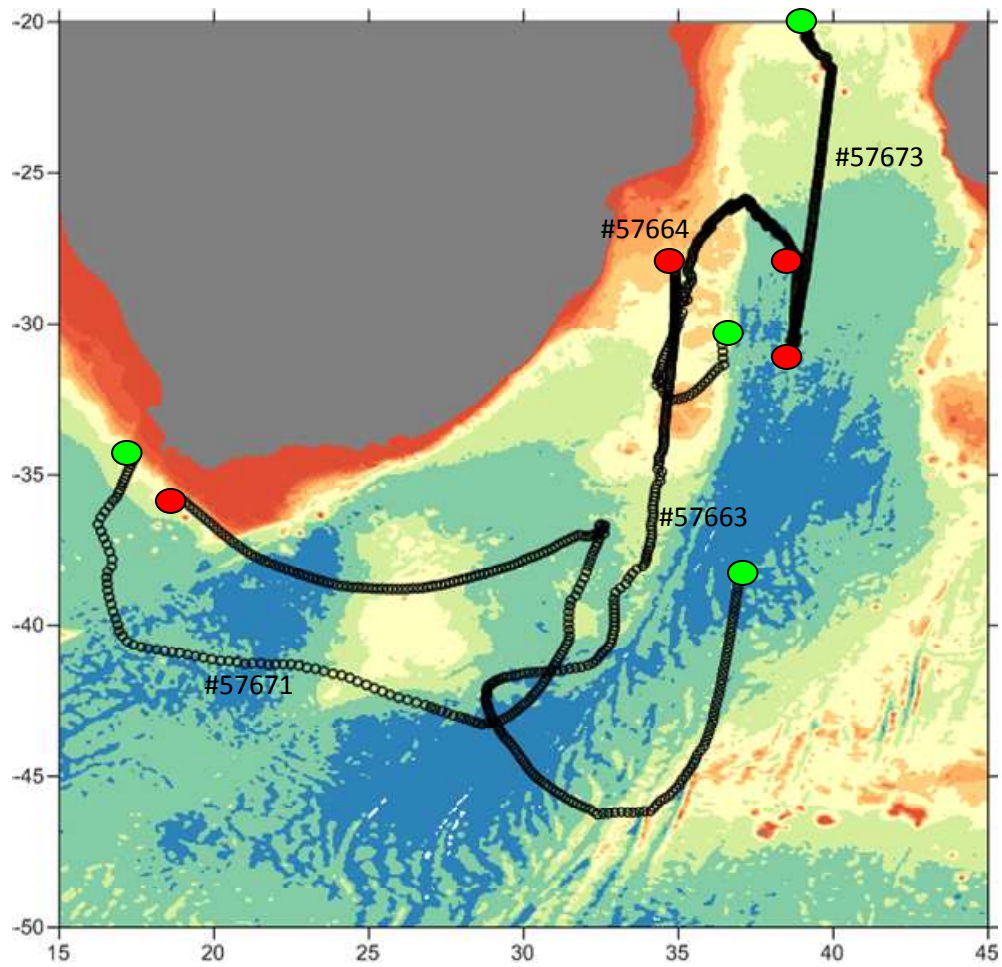


Figure 6. Horizontal movements across bathymetric features of swordfish tagged with pop-up archival satellite tags between the 16th October 2011 and 24th January 2012. The red dots indicate the tagging location and the green dots indicate the tag pop-off location.

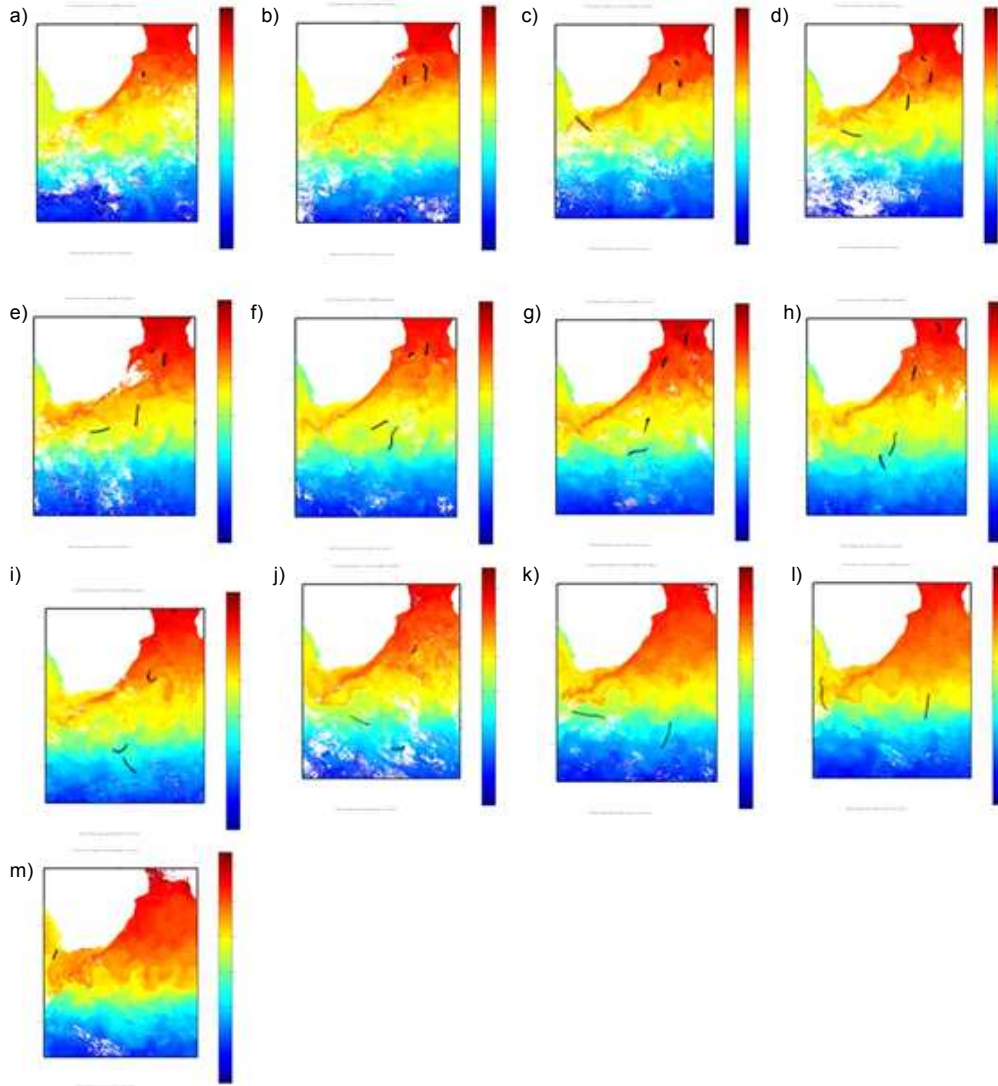


Figure 7. Horizontal movements of swordfish (n=4) tagged with pop-up archival satellite tags on a weekly basis from 16 October to the 24 January 2012 showing sea surface temperatures ($^{\circ}\text{C}$).