



Movements and behaviors of swordfish in the Atlantic and Pacific Oceans examined using pop-up satellite archival tags

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ABSTRACT

Swordfish are highly specialized top-level predators that have been challenging to study. In this paper, data from 31 pop-up satellite archival tags attached to swordfish from (i) the eastern Pacific, (ii) central Pacific, and (iii) western North Atlantic-Caribbean were analyzed. Common across locations was a pronounced

diel vertical pattern with daytime hours spent primarily below the thermocline and nighttime hours spent in warmer waters, close to the surface. One exception to this pattern was periodic daytime basking events which were most common in cooler waters off California. Maximum daytime depths were significantly correlated with light penetration as measured by the diffuse attenuation coefficient at 490 nm. Temperature did not appear to influence daytime depths, and swordfish tolerated both extremely low temperatures (4°C) and rapid and dramatic temperature changes (>20°C). Temperature did appear to influence the nighttime depths in the Pacific where fish typically remained in the surface mixed layer. In contrast, in the warm tropical Atlantic this was not the case, and nighttime depths were much deeper. In all areas, nighttime depth increased around the full moon. Given the parallels between the vertical movement patterns of swordfish and those of the deep sound scattering layer we suggest that swordfish vertical distribution patterns, especially during daytime, are influenced largely by resource availability. At night, when swordfish are typically targeted by fisheries, both ambient light and temperature influence movements. Understanding vertical movement patterns of swordfish can help evaluate gear vulnerability, improve population assessments, and potentially reduce fisheries bycatch.

Key words: Atlantic Ocean, deep sound scattering layer, diel migration, Pacific Ocean, satellite tags, swordfish

INTRODUCTION

Shifts in the vertical distributions of fish can change their vulnerability to fishing gear and thus complicate population assessments based on catch-per-unit-effort (CPUE) data (Sharp, 1978; Brill and Lutcavage, 2001). Habitat-based models have been introduced that correct CPUE data to account for variability in gear vulnerability and improve stock assessments (Hinton and Nakano, 1996; Bigelow *et al.*, 2002; Maunder *et al.*, 2006; Bigelow and Maunder, 2007).

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These models, however, require an understanding of how environmental parameters influence both vertical and horizontal distribution patterns (Hanamoto, 1987; Brill and Lutcavage, 2001; Bigelow *et al.*, 2002; Bigelow and Maunder, 2007). Although swordfish (*Xiphias gladius*, Linnaeus, 1758) support large fisheries in all ocean basins (Nakamura, 1985; Folsom *et al.*, 1997; FAO, 2009), limited information is available on vertical movement patterns (Seki *et al.*, 2002). In this report, we present a comparison of data collected from three oceanographic regions where important swordfish fisheries exist or existed. The use of comparative data revealed important patterns in the vertical distribution of swordfish and provides insights into the possible factors underlying vertical habitat use, resulting in a more mechanistic understanding of movements.

Swordfish is a monogeneric species in the family Xiphiidae that diverged from the other istiophorid billfish (marlin, sailfish, and spearfish) around 3 million yr ago (Fierstein and Stringer, 2007). The swordfish is one of several large pelagic predators that have evolved the physiological capabilities necessary to function at extreme conditions of pressure and temperature (Carey, 1982; Van den Burg *et al.*, 2005). Numerous adaptations enable swordfish to maintain muscle, brain, eye and cardiac function in cool waters (Carey, 1982; Block, 1987; Dickson and Graham, 2004; Fritsches *et al.*, 2005; Galli *et al.*, 2009). In comparison to the other billfish and most tunas, swordfish spend protracted periods below the surface mixed layer during daily vertical migrations (Holland *et al.*, 1990a,b; Brill *et al.*, 1993; Block *et al.*, 1997; Pepperell and Davis, 1999; Schaefer and Fuller, 2002; Musyl *et al.*, 2003; Horodysky *et al.*, 2007). In addition, swordfish can tolerate low surface temperatures and have a broader latitudinal range (50°N–50°S) compared to other billfish species, which are generally limited to approximately 40°N–40°S in the Pacific and Atlantic Oceans (Nakamura, 1985; Sakagawa, 1989).

Swordfish support commercial fisheries throughout much of their geographic range, with over 100 000 mt harvested world-wide annually (Folsom *et al.*, 1997; FAO, 2009). Due to the commercial importance of swordfish, considerable effort has been expended to describe geographic distribution patterns (Nakamura, 1985; Sakagawa, 1989), stock structure (Rosel and Block, 1996; Hinton and Deriso, 1998; Nakano, 1998; Reeb *et al.*, 2000; Alvarado-Bremer *et al.*, 2004), spawning areas (Grall and de Sylva, 1983; Taylor and Murphy, 1992; DeMartini *et al.*, 2000; Mejuto *et al.*, 2008), and how oceanographic

features relate to abundance (Bigelow *et al.*, 1999; Seki *et al.*, 2002; Santos *et al.*, 2006). Although movement and distribution patterns vary considerably with season, gender, and ocean basin, a number of generalities are apparent. Swordfish spawn throughout the tropics where sea surface temperatures are 24°C or higher, and in some regions spawning occurs year-round (Grall and de Sylva, 1983; Nakamura, 1985). Following spawning, swordfish move to foraging grounds, with large females aggregating in cooler waters at higher latitudes and smaller males dominating the catch at lower latitudes (Nakamura, 1985; Taylor and Murphy, 1992; DeMartini *et al.*, 2000; Sperling *et al.*, 2005). Some of the largest fisheries for swordfish are concentrated in the foraging grounds in coastal boundary currents off California, Japan, Chile, New England, Australia, and New Zealand (Nakamura, 1985; Sakagawa, 1989; Carocci and Majkowski, 1996). In offshore areas, fisheries are concentrated at convergence zones with frontal features (Bigelow *et al.*, 1999; Sedberry and Loefer, 2001; Seki *et al.*, 2002), including the Gulf Stream isotherms (Sedberry and Loefer, 2001) and the frontal boundaries of the North Pacific Transition Zone (Bigelow *et al.*, 1999; Seki *et al.*, 2002).

Describing vertical habitat use for swordfish has been more challenging than describing geographic patterns. Catch data provide only limited insights into daily vertical movements, as most fishing occurs at night when swordfish are near the surface (Hanan *et al.*, 1993; Bigelow *et al.*, 2006). While electronic tagging studies have provided novel information on the vertical habitat use by swordfish, sample sizes have been small, the duration of experiments is often short, and the geographic coverage has generally been limited. Studies using pop-up satellite archival tags (PSATs) deployed off the U.S. East Coast and in the Mediterranean have provided limited insights into vertical movements (Sedberry and Loefer, 2001; Matsumoto *et al.*, 2003; Loefer *et al.*, 2007; Canese *et al.*, 2008; Neilson *et al.*, 2009). The most detailed information comes from acoustic telemetry studies (Carey and Robison, 1981; Carey, 1990; Holts *et al.*, 1994), but these studies tend to be on the order of days and are typically only nearshore. To date, there is little information on how swordfish vertical movement patterns vary geographically or how they are influenced by environmental conditions. In this study, we attempted to fill this gap by comparing the vertical habitat use of swordfish in three areas: the eastern Pacific Ocean (EPO), central Pacific Ocean (CPO) and tropical western North Atlantic-Caribbean (WNAC).

MATERIALS AND METHODS

Tagging

PSAT tags were used in all study regions. All PSAT tags were attached externally using an anchor placed near the dorsal fin as previously described (Block *et al.*, 1999; Prince *et al.*, 2002; Prince and Goodyear, 2006). Capture methods varied across locations (Table 1). When fish were caught using longline or recreational gear, they were brought alongside the vessel and the tag was inserted using a long tagging pole. The line was then cut close to the hook and the fish released. Four anchor types were used: medical grade nylon anchor (Prince and Goodyear, 2006), a black nylon dart resembling a squid jig (Domeier *et al.*, 2005), stainless steel dart (Block *et al.*, 1999) or a nylon head augmented with spear gun flopper-blades (developed by Musyl and Prince). The leaders connecting the anchors to the tags consisted of high-test monofilament or fluorocarbon and were secured using stainless steel crimps. Location (GPS) and estimated mass were recorded at the time of tagging.

Electronic tags

The PSATs used were model PTT 100 from Microwave Telemetry (Columbia, MD, USA; MT tags) or models PAT 2, 3 or 4 from Wildlife Computers (Redmond, WA, USA; WC tags). The tags were programmed to release on a specific date or after a specific duration and final locations at pop-up were estimated by Argos (Argos, 1989). Tags from both manufacturers included fail-safe features to initiate tag release and transmission if the tag was shed prematurely or the fish died (Arnold and Dewar, 2001; Domeier *et al.*, 2003).

PSATs were set to record temperature, depth, and relative light level indexed to an internal clock. The precision of temperature and depth of the MT tags was 0.1768°C and 5.4 m, respectively. For WC tags, the

precision of temperature measurements was 0.1°C between 12 and 26.95°C, and 0.2°C outside this range. The precision in depth measurements for WC tags was 1, 2, 4, 8, and 16 m over ranges of 0–99.5, 100–199.5, 200–299.5, 300–499.5, and 500–979.5 m, respectively, although depths are reported in 4-m increments in the temperature depth profiles (PDTs) to facilitate data compression. Depending on the manufacturer, the devices had different data-managing protocols. WC tags acquired temperature and depth data every 60 s that were then summarized into 12 user-defined bin intervals. Data were also assembled into PDTs. The PDTs provided the maximum and minimum temperature at eight depths ranging from the minimum to the maximum depths. The histogram and PDT recording intervals were set by the users at 2-, 3-, 8-, 12-, or 24-h. For the MT tags, temperature and depth data were acquired hourly. While light level data are collected by both tag types, light-based geolocation estimates were precluded by the swordfishes' dive patterns as observed in bigeye tuna (*Thunnus obesus*) (Musyl *et al.*, 2003).

Data analysis

Data from the first 24 h were not included in the analysis to reduce possible effects of capture and tagging (Dewar and Graham, 1994; Gunn and Block, 2001; Skomal and Chase, 2002). For both tag types, sea surface temperatures (SST) were taken from temperatures recorded at depths ≤8 m. Maximum, minimum, and average temperatures and depths for both day and night were calculated from the hourly data provided by the MT tags. In all but one MT tag, the depth change between successive measurements was constrained at ≈ 90 m (Arrizabalaga *et al.*, 2008) due to tag software limitations associated with data compression. Consequently, only data where the difference between subsequent values was <90 m were used.

For the WC tags, it was not possible to examine day/night patterns from tags programmed for 12- or

Table 1. Summary of pop-up satellite archival tag deployments and data recovery for the four studies including tag manufacturer, data intervals and tagging method.

| Study | Tags deployed | Tags reported | Tag type | Data intervals | Tagging method |
|----------------------------------|---------------|----------------|----------|----------------|--------------------------------|
| Western North Atlantic-Caribbean | 9 | 9 (2 M, 1 AR) | WC | 2/3/8 h | Recreational or longline |
| Central Pacific | 30 | 11 (2 ND) | MT | 0.5–1 h | Research Longliner |
| Eastern Pacific | | | | | |
| CA 1 | 15 | 13 (5 M, 1 AR) | WC | 2 h | Commercial longline or harpoon |
| CA 2 | 8 | 8 (1 ND) | MT, WC | 12/24 h | Harpoon |
| Total | 62 | 31† | | | |

M, mortalities, ND, no data, AR, archival record. †While 41 tags reported seven represented mortalities and three tags provided no useful depth or temperature data.

24-h bins. For PSATs programmed with 2-, 3-, and 8-h bins, the time of civil twilight at the tag deployment and pop-up locations were determined (<http://www.usno.navy.mil/USNO/astronomical-applications/data-services/>) and bins that included sunrise and sunset were excluded from analysis. For two WNAC fish for which bin widths were set at '250–350, 350–450' rather than '200–300, 300–400', the widths were standardized to allow for broad comparisons. The time spent in each bin was divided by two and assigned to 50-m increments from which the desired 100-m bins were created. This standardization was only necessary for bins deeper than 200 m and may introduce some bias if depths are not equally distributed across the bin.

The timing and speed of ascent and descent were calculated from two archival records obtained from the recovered WC tags. We compared the time at which the fish reached 40 m in the EPO and 200 m in WNAC to the time of local civil twilight. These depths were selected as triggers because they were slightly deeper than the typical nighttime depths and because fish did not always leave from, or return to, the surface in the morning and evening. The average rate of depth change was determined by dividing the depth difference between two successive sampling intervals by the corresponding time interval (1 or 2 min). These values were then averaged over each ascent and descent, for each basking event, and during sunrise and sunset. Basking events were defined as any daytime ascent from depth to the surface followed by a subsequent descent prior to sunset.

Vertical habitat envelopes (VHE, i.e., the percent time spent in a given temperature-depth-bin) were calculated as described in Luo *et al.* (2006). The VHE were only calculated for time intervals where both the PDT and depth histograms were available. The relationship between nighttime depth and lunar illumination, uncorrected for cloud cover (<http://www.usno.navy.mil/USNO/astronomical-applications/data-services/>), was examined by linear regression analysis.

Depth and/or temperature data from both tag types were used to assess the location of the fish in relation to the surface mixed layer and thermocline. For both tags types, SST was compared to the minimum temperature over a given period. For the WC tags, the depth of the bottom of the surface mixed layer was visually approximated using the PDT data (see below; Fig. 4) when the point of inflection was apparent. Straight-line distances and speeds were estimated from the deployment and pop-up locations. Magnetic compass bearings were calculated when horizontal displacements were >60 km (Table 2).

The tag deployment and pop-up locations were linked to oceanography using two methods. First, a MATLAB program (<http://coastwatch.pfel.noaa.gov/xtracto/>) was used to extract the diffuse attenuation coefficient (K490). The K490 indicates how strongly light intensity at 490 nm is attenuated within the water column (e.g., $K490 = 0.1 \text{ m}^{-1}$ indicates that light intensity is reduced by one natural log per 10 m of depth). Non-linear regression analysis was used to characterize the relationship between the maximum depth and the K490. The K490 was subsequently used to estimate the top of the deep sound scattering layer (DSL) applying the equation provided by Tont (1976) and the conversion between Secchi disc depth and attenuation reported by Matciak (1997). To estimate oxygen concentration at the maximum depth, the World Ocean Atlas, model-derived climatological data were queried (<http://www.nodc.noaa.gov/OC5/SELECT/woaselect/woaselect.html>).

RESULTS

PSATs were deployed on 62 swordfish in the EPO, CPO and WNAC between April 2001 and November 2006 (Tables 1 and 2, Fig. 1). Deployments in the EPO were a part of two studies conducted in the Southern California Bight, CA1 (H. Dewar) and CA2 (C. Sepulveda). From all tag deployments, 31 data records (>1 day) were obtained. Mortalities were identified for seven fish using the transmitted depth records (Domeier *et al.*, 2003; Moyes *et al.*, 2006; Swimmer *et al.*, 2006). Two WC tags were recovered providing records of temperature, depth and light levels recorded every 1 or 2 min.

The mean (\pm SD) straight-line distance swordfish traveled was 878 ± 750 km (Table 2). The longest distance recorded was from a fish released in the Windward Passage between Cuba and Haiti that traveled 2632 km in 62 days. The estimated minimum rate of travel for all fish ranged from 0.2 to 59 km day^{-1} (mean $21 \pm 17 \text{ km day}^{-1}$). The fastest speed was documented for a fish released off California that traveled 1126 km in 19 days. The mean rate of travel was not significantly different ($P > 0.05$ Kruskal–Wallis test) in the three areas: EPO 25 km day^{-1} , CPO 14 km day^{-1} and WNAC 21 km day^{-1} .

While comparisons of the complete temperature and depth histograms computed over 24 h were complicated by the different data collection strategies, some patterns were evident. Consistent across all study areas was a bimodal distribution for both temperature and depth, reflecting a pattern of diel vertical movements (Fig. 2). The relative amount of time spent in

Table 2. Summary of the pop-up satellite archival tags (PSATs) deployments >1 day. Days-at-liberty (DAL)/programmed pop-up period. The straight-line distance and speed and bearing were calculated from deployment and pop-up locations.

| Tag number | Estimated mass (kg) | Date deployed | DAL/Pop-up period | Distance (km) | Speed (km day ⁻¹) | Direction |
|----------------------------------|---------------------|-------------------|-------------------|---------------|-------------------------------|-----------|
| Western North Atlantic-Caribbean | | | | | | |
| 42719 | 11 | 13 September 2003 | 30/30 | 176 | 6 | NE |
| 23397† | 27 | 8 May 2003 | 15/27 | 355 | 24 | NE |
| 42720 | 45 | 13 September 2003 | 30/30 | 1543 | 51 | SE |
| 46102 | 59 | 6 May 2004 | 62/60 | 2632 | 42 | NE |
| 46103 | 77 | 6 May 2004 | 65/63 | 1411 | 22 | NW |
| 66696 | 27 | 18 July 2006 | 90/90 | 45 | 0.5 | |
| 66697 | 23 | 18 July 2006 | 120/120 | 24 | 0.2 | |
| Central Pacific | | | | | | |
| 13082 | 45 | 2 April 2001 | 10/181 | 163 | 16 | SE |
| 13099 | 90 | 5 April 2001 | 100/395 | 982 | 10 | NE |
| 13102 | 64 | 4 April 2001 | 5/395 | 39 | 8 | |
| 13103 | 68 | 5 April 2001 | 29/395 | 680 | 23 | SW |
| 13115 | 135 | 17 April 2002 | 11/183 | 440 | 40 | SW |
| 13217 | | 7 April 2002 | 93/245 | 590 | 6 | SW |
| 13229 | 20 | 10 April 2002 | 187/245 | 898 | 5 | NE |
| 29146 | 90 | 11 April 2002 | 60/245 | 860 | 14 | SW |
| 45676 | | 22 May 2004 | 245/245 | 883 | 3.6 | NE |
| Eastern Pacific | | | | | | |
| CA1 | | | | | | |
| 19203 | 68 | 11 September 2002 | 42/42 | 1822 | 43 | SW |
| 19910 | 65 | 16 November 2002 | 65/65 | 690 | 11 | SW |
| 30319‡ | 45 | 9 February 2003 | 19/60 | 691 | 36 | SW |
| 30410 | 114 | 4 November 2003 | 41/60 | 120 | 3 | SW |
| 40560 | 90 | 19 November 2003 | 40/60 | 1478 | 37 | SW |
| 30321 | 90 | 19 November 2003 | 19/60 | 1126 | 59 | SW |
| 30406 | 80 | 16 December 2003 | 60/60 | 2404 | 40 | SW |
| 8832† | 80 | 31 October 2004 | 24/305 | 61 | 2.5 | |
| CA2 | | | | | | |
| 6065 | | 17 September 2003 | 41/91 | 10 | 0.2 | |
| 6066 | | 2 October 2003 | 61/61 | 1456 | 24 | SW |
| 6067 | | 12 September 2003 | 61/61 | 1384 | 23 | S |
| 448 | 68 | 7 November 2005 | 106/108 | 599 | 6 | SW |
| 616 | 60 | 29 August 2005 | 82/122 | 687 | 8 | SE |
| 635 | 82 | 13 November 2006 | 10/10 | 444 | 47 | SW |
| 657 | 68 | 1 December 2005 | 90/90 | 2528 | 28 | SW |

†Tags that were recovered. ‡Tag that was deployed north of the Hawaiian Islands.

waters <12°C (36–39%) was also similar across areas. One notable difference was the time spent above 60 m (Pacific >45%, WNAC ≈ 22%).

Minimum and maximum temperatures and maximum depths for all fish are reported in Table 3. The minimum depth over a given day was always 0 m. The maximum depths experienced by individuals ranged from 210 to >980 m (average 646 ± 210 m). The full temperature range across all swordfish was 4 to 31°C, while SST ranged from 14 to 31°C; the warmest temperatures were in the WNAC and coolest in the

EPO. The mean minimum temperatures reached were similar across individuals and locations (mean minimum temperature $7 \pm 3^\circ\text{C}$) although overall minimum temperatures ranged from 4 to 18°C.

Diel patterns in depth and temperature

While evidence of the diel pattern is seen in the 24-h histograms (Fig. 2), it is more apparent in the archival records and the hourly data from the MT tags (Fig. 3). The archival records revealed that fish 8832 (EPO) and 23397 (WNAC) descended below their typical

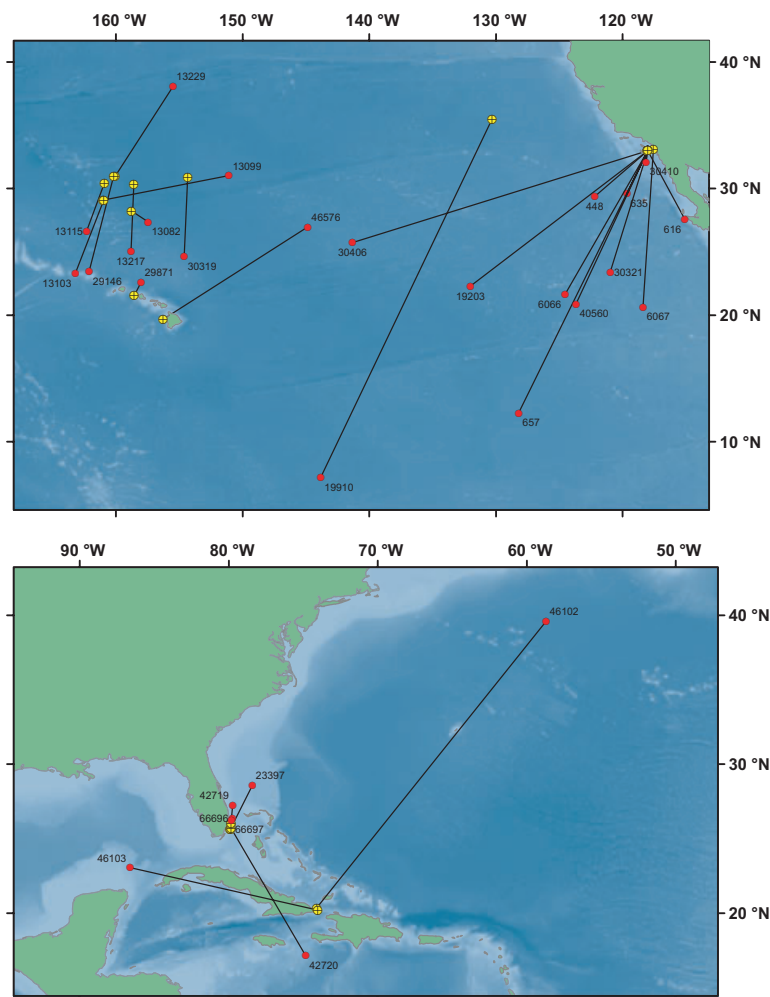


Figure 1. Maps of the Pacific (top) and Atlantic (bottom) Oceans showing both the tagging (yellow circles) and pop-up (red circles) locations for all tags where deployments were longer than 1 day.

nighttime depths prior to morning civil twilight and did not return until after evening civil twilight. The EPO fish descended to below 40 m an average of 7 min (± 4 min) before morning civil twilight and returned an average of 13 min (± 2 min) after evening civil twilight. For this fish, the mean rates of descent and ascent at dawn and dusk were $14 (\pm 1.8)$ and $9 (\pm 0.4)$ m min⁻¹, respectively. The WNAC fish reached 200 m an average of 4 min (± 3 min) before morning civil twilight and 9 min (± 3 min) after evening civil twilight. The mean rates of descent and ascent at dawn and dusk were $8.2 (\pm 0.2)$ and $8.7 (\pm 0.2)$ m min⁻¹, respectively. Note that there was little variation in the relative light measurements other than during basking events (Fig. 3).

Diel patterns were also apparent in the transmitted data when daytime and nighttime hours could be separated for analyses. Due to overlap with civil twilight, it was not possible to examine the 8-h histograms for one WNAC fish during the night and for

two WNAC fish during the day. Comparing day and night PDT data across all study areas (Table 3), the average maximum depth was significantly deeper during the day (450 ± 173 m versus 78 ± 61 m night) and the average temperature cooler ($10 \pm 4.3^\circ\text{C}$ versus $21 \pm 3^\circ\text{C}$ night; $P < 0.05$, t-test). One exception was for a fish tagged in the EPO that remained above 60 m over a 3-day period. This was bounded by periods of typical diel movements (e.g., Takahashi *et al.*, 2003; Sepulveda *et al.*, 2010).

A comparison of the daytime and nighttime depth across locations revealed a number of patterns. For daytime hours, trends were apparent in basking events, proximity to shore and oceanography (e.g., fish 30406, Fig. 4a). For nighttime hours, trends were associated with mixed layer temperature and depth, lunar illumination and oceanography. Given the distinct diel pattern, data collected during the day and night were examined separately with the first comparisons made across locations.

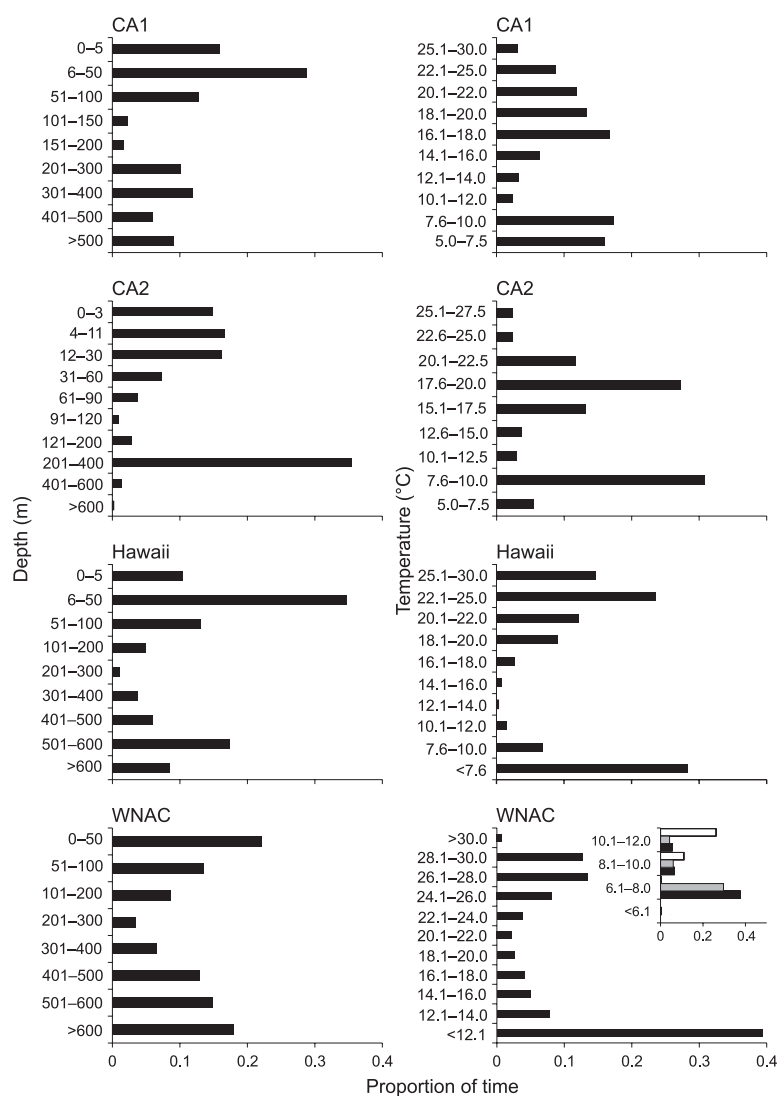


Figure 2. Temperature and depth histograms over 24 h for each of the four studies. For the western North Atlantic-Caribbean (WNAC), three tags had bins assigned below 12°C. The data for these three tags are shown in the inset. The CA1 and CA2 studies could not be combined due to differences in binning strategies.

Daytime-Basking

One exception to the typical daytime distribution was basking events that were best observed in the archival records. These basking events ($N = 7$) were characterized by rapid movements from depth to the surface, surface intervals of 7 min to 2.8 h (median 35 min), and rapid return to depth. The mean rate of ascent ($38 \pm 9 \text{ m min}^{-1}$) was slower than the mean rate of descent ($57 \pm 17 \text{ m min}^{-1}$; $P < 0.05$ *t*-test) with a maximum mean speed for one descent of 107 m min^{-1} . All basking events for these two fish occurred between 9:03 and 13:38 h local time.

Basking events were also apparent in the transmitted data from the WC tags when the bounds of the histograms and PDTs included only daytime hours (EPO $N = 8$ fish, WNAC $N = 5$ fish; in the Pacific-only events at SST $< 24^\circ\text{C}$ were included, see below). A total

of 75 days were identified with basking events (EPO = 65, WNAC = 10). Only two fish showed no basking events, one tagged in the Windward Passage (WNAC) and the other tagged immediately north of the main Hawaiian Islands. The average time spent at the surface in a given day across all tags ranged from 10 min to 4.7 h (average 1.6 ± 1.3 h). The percent of days in which an individual showed one or more basking events ranged from 0 to 80% (median 15%) and was significantly less in the WNAC (median = 0.2%, range 0–14%) than in the Pacific (median 36%, range = 0–80%) ($P < 0.05$, Mann–Whitney rank sums test).

For all EPO fish that moved offshore, a subset of data over the first and last 10 days were used as a proxy for near- and offshore locations, respectively (Table 4). As seen in the raw PDT data for fish 30406 (Fig. 4a), the number of basking events (minimum

Table 3. Summary of the temperature (T; °C) and depth (D; m) obtained for all deployments including the mean sea surface temperature (SST) and range, mixed layer depth (MLD), difference between average minimum nighttime temperature and SST (ΔT), the overall minimum temperature and maximum depth, and temperature and depth data separated into day and night.

| Tag No. | Mean SST | SST range | MLD/ ΔT | Min T | Max D | Day | | Night | | |
|----------------------------------|----------|-----------|-----------------|-------|-------|------------|------------|------------|------------|-------|
| | | | | | | Max D mean | Min T mean | Max D mean | Min T mean | Min T |
| Western North Atlantic-Caribbean | | | | | | | | | | |
| 42719 | 30 | 29–30 | 52/12 | 6 | 724 | 491 | 7 | 183 | 17 | 10 |
| 42720 | 30 | 29–31 | 48/7 | 8 | 808 | 690 | 10 | 186 | 23 | 19 |
| 46102 | 26 | 25–28 | 52/6 | 7 | 864 | 690 | 12 | 177 | 21 | 19 |
| 46103 | 28 | 27–30 | 70/8 | 6 | 880 | 740 | 7 | 207 | 20 | 10 |
| 23397 | 28 | | 77/4 | 7 | 708 | 605 | 11 | 127 | 24 | 20 |
| 66696 | 30 | 29–31 | 42/10 | 6 | 800 | 541 | 8 | 151 | 19 | 9.4 |
| 66697 | 29 | 28–30 | 54/8 | 6 | 856 | 614 | 9 | 141 | 21 | 10 |
| Central Pacific | | | | | | | | | | |
| 13082 | 29 | 21–29 | /1.3 | 18 | 210 | 76 | 26 | 6 | 27 | 20 |
| 13099 | 23 | 22–25 | /1.9 | 5 | 640 | 436 | 9 | 24 | 23 | 10 |
| 13103 | 23 | 20–24 | /0.4 | 5 | 732 | 565 | 8 | 37 | 22 | 19 |
| 13115 | 21 | 18–22 | /1.6 | 8 | 425 | 127 | 18 | 54 | 20 | 15 |
| 13217 | 23 | 19–27 | /2.2 | 4 | 974 | 598 | 6 | 45 | 23 | 18 |
| 13229 | 24 | 22–25 | /0.8 | 5 | 570 | 454 | 7 | 27 | 22 | 9 |
| 46576 | 25 | 22–26.7 | /1.4 | 4.7 | 888 | 492 | 8 | 39 | 24 | 19 |
| 29146 | 24 | 18–27 | /3.5 | 5 | 629 | 504 | 6 | 33 | 22 | 16 |
| Eastern Pacific | | | | | | | | | | |
| CA1 | | | | | | | | | | |
| 8832 | 18 | 17–18.5 | 33/0.7 | 7.1 | 489 | 400 | 8 | 31 | 17.3 | 17 |
| 19910 | 25 | 18–28 | /1.0 | 6 | 568 | 262 | 13 | 76 | 21 | 14 |
| 30406 | 17 | 14–21 | 73/0.2 | 5 | 688 | 429 | 7 | 60 | 18 | 14 |
| 19203 | 20 | 15–23 | /1.0 | 4 | 980 | 389 | 8 | 63 | 18 | 8 |
| 30410 | 17 | 16–19 | 34/0.3 | 8 | 376 | 277 | 10 | 27 | 17 | 14 |
| 30321 | 18 | 16–20 | 48/0.9 | 7 | 436 | 289 | 10 | 47 | 17 | 14 |
| 40560 | 20 | 17–23 | 62/0.8 | 7 | 480 | 390 | 8 | 59 | 19 | 14 |
| 30319 | 22 | 20–23 | /0.5 | 5 | 716 | 602 | 6 | 82 | 20 | 17 |
| CA2 | | | | | | | | | | |
| 6065 | 20 | 15–22 | | 7 | 355 | 336 | 9 | 15 | 20 | 16 |
| 6066 | 19 | 16–21 | | 6 | 451 | 248 | 9 | 19 | 20 | 10 |
| 448 | 17 | 16–19 | <60/ | 6 | 620 | | | | | |
| 616 | 20 | 16–22 | <50/ | 6 | 484 | | | | | |
| 635 | 19 | 17–19 | <50/ | 7 | 396 | | | | | |
| 657 | 22 | 15–26 | | 4 | 980 | | | | | |

depth = 0 m) declined significantly as the fish moved offshore ($P < 0.05$, Mann–Whitney rank sums test). Basking events were also noted in the CPO (range 0–12% of days), although given the ≈ 90 m cap on most successive depth changes and the 1-h sampling interval in the MT tags, basking could easily have been missed. It was not possible to compare near- and offshore trends in the WNAC.

Daytime-Pacific offshore versus nearshore movements

In the Pacific, during the day, an increase in depth and decrease in temperature was apparent as fish moved

offshore (Fig. 4a, Table 4). The mean maximum depth increased from 287 ± 42 to 457 ± 118 m, and the mean minimum temperature decreased from 8.8 ± 1.0 to $7.3 \pm 1.0^\circ\text{C}$ (Table 4). This pattern is also seen in the vertical habitat envelope (VHE) and histograms for near- and offshore areas (Figs 5 and 6). As fish moved away from the coast, the time spent above 50 m decreased from 32 to <1%, whereas time spent below 400 m increased from 2 to 72%. Likewise, the average time spent below 7.5°C increased from 5 to 60% (Figs 5 and 6). The differences in depth and temperature distributions between nearshore and

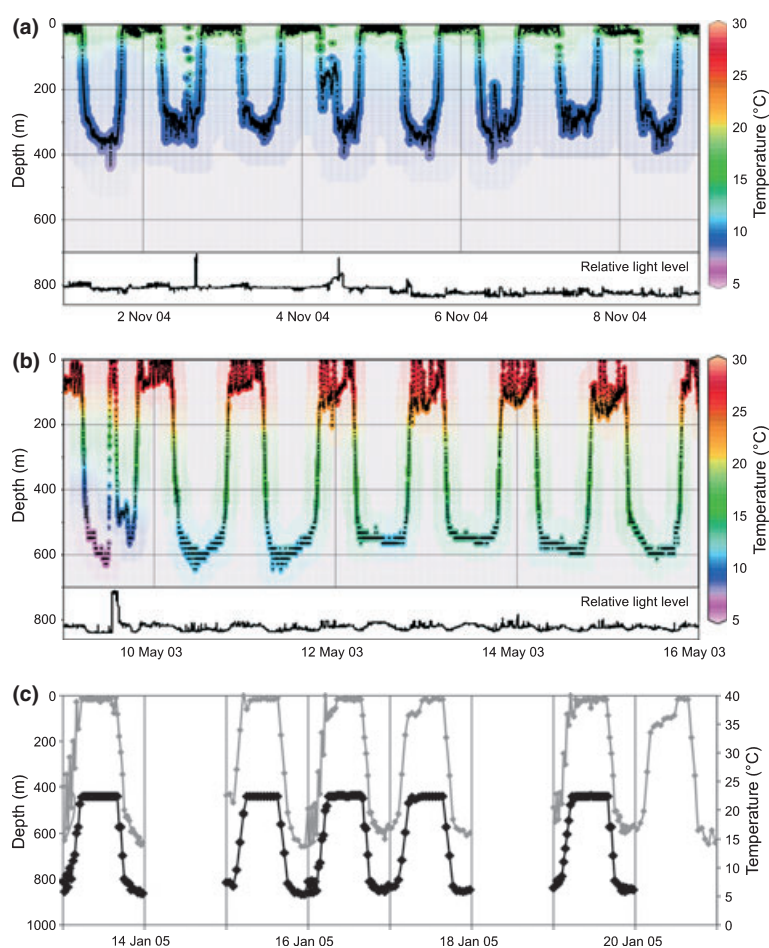


Figure 3. Temperature (coded in color), depth and light data (lower panel) obtained from the two tags recovered off (a) California and (b) Florida. Note the increase in light associated with basking; this provides a reference for daytime light levels. (c) The hourly record for the transmitted depth and temperature data for one Microwave Telemetry tag (depth changes on this tag were not constrained to $\Delta 90$ m).

offshore areas were significant [$P < 0.05$, Kolmogorov–Smirnov (K-S) goodness-of-fit test].

The daytime vertical distribution pattern for swordfish in offshore areas of the EPO was similar to that for fish tagged in the CPO, although the daytime depth range for the CPO fish was broader, and more time was spent below 500 m (56 versus 47%; Figs 5 and 6). The daytime temperature distributions were not significantly different ($P > 0.05$, K-S goodness-of-fit test) nor were the average maximum depths ($P > 0.05$, Mann–Whitney rank sums test).

While general trends are apparent in the Pacific when moving offshore, there was some variability in the records from both the EPO and CPO. For example, considerable variability in depth was seen in the longest record (245 days, tag 45676) where daytime depths ranged from approximately 300–800 m (Fig. 4c). In the EPO, the one fish that moved southeast (tag 616, Fig. 1), showed a pattern opposite to that of fish that moved offshore. Comparing values over the first and last 10 days, the mean maximum

depth decreased from 432 to 308 m, the mean minimum temperature increased from 7 to 9°C (Table 4).

Daytime – western North Atlantic-Caribbean

Possibly due to the range of movements observed, there was no consistent pattern in depth or temperature over the course of the tracks for the five fish released near the southeastern coast of Florida (Fig. 4d). In contrast, the two individuals tagged in the Windward Passage, while moving in different directions, did show consistent changes in temperature and/or depth across their tracks. Fish 46102 traveled to the North Atlantic Ocean and showed a decrease in the maximum daytime depth (≈ 800 –600 m) and an increase in the minimum temperature (≈ 7 –14°C). In contrast, fish 46103 moved NW into the Gulf of Mexico and showed a decrease in the maximum daytime depth (≈ 850 –700 m), with no change in the minimum temperature.

In general, swordfish in the WNAC spent more time at greater depths than fish in the Pacific (Figs 4d,

Table 4. Comparison of the depths and basking events for near and offshore in the eastern Pacific Ocean. Included are the percentage of days on which basking events occurred, and the average daily maximum depth and minimum temperature. Values are calculated over the first 10 days (nearshore) and last 10 days (offshore) when possible.

| | Nearshore basking (% days) | Nearshore depth (m) | Nearshore temp (°C) | Offshore basking (% days) | Offshore depth (m) | Offshore temp (°C) |
|-------|----------------------------------|------------------------|------------------------|---------------------------------|-----------------------|-----------------------|
| CA1 | | | | | | |
| 8832† | 20 | 400 (305) | 8 (9) | NA‡ | | |
| 30410 | 56 | 260 | 10 | NA | | |
| 30321 | 67 | 295 | 10 | NA | | |
| 30406 | 82 | 257 | 9 | 0 | 621 | 6 |
| 19203 | 55 | 255 | 10 | 50 | 477 | 7 |
| 40560 | 50 | 327 | 8 | 30 | 426 | 8 |
| 30319 | NA | | | 0 | 615 | 6 |
| 19910 | NA | | | 0 | 470 | 7 |
| CA2‡ | | | | | | |
| 635 | | 289 | 9 | | | |
| 6065 | | 272 | 8 | | 306 | 9 |
| 6066 | | 251 | 10 | | 317 | 8 |
| 448 | | 379 | 8 | | 424 | 7 |
| 616 | | 432 | 7 | | 308 | 9 |
| 657 | | 313 | 8 | | 294 | 12 |

NA, data not available for respective region.

†Parenthetical values show the average daytime depth and temperature for the archival record.

‡Basking could not be determined for the CA2 tags because the programming interval did not allow for separation of data into daytime and nighttime hours.

5 and 6). During the day, the former spent 83% of the time below 500 m, whereas fish in the EPO and CPO spent 47 and 56%, respectively. The maximum daytime depths (Table 3) were also significantly deeper in the WNAC ($P < 0.05$, Mann–Whitney rank sums test). However, there was little difference in the daytime temperatures across regions. The average minimum daytime temperatures in the EPO (10°C), CPO (11°C) and WNAC (9°C) were not significantly different ($P < 0.05$, Mann–Whitney rank sums test, Table 3), nor was the time spent below 12°C (offshore EPO 82%, CPO 84% and WNAC 74%). Fish occupying the nearshore areas of the EPO spent only 59% of the daytime below 12°C.

Daytime – maximum depth and light attenuation

Maximum daytime depths at all beginning and end-points were matched to light penetration using the satellite derived K490 when it was available. The K490 (m^{-1}) was significantly correlated with maximum daytime depth (Fig. 7, $P < 0.05$, $R^2 = 0.57$). The majority of the time (22 of 27 measurements) the maximum depth fell below the depth corresponding to the top of the DSL during the day. The median difference between the estimated top of the DSL and the maximum depth was 98 m.

Daytime – vertical shift at SST >24°C in the Pacific

The three swordfish in the Pacific Ocean that entered areas with SST >24°C showed significant and rapid shifts in depth and temperature ($P < 0.05$ K-S goodness-of-fit test) (Fig. 8). Daytime depths shifted from >400 to <200 m. For example, fish 19910 decreased the time spent below 200 m from 85 to 5% (Fig. 8) with a corresponding increase in temperature. In contrast, there was little to no shift at night. Although all WNAC fish experienced temperatures >24°C, similar vertical patterns were not observed.

Nighttime – Pacific offshore versus nearshore movements

Similar to daytime depths, the PDT and histogram data reveal that nighttime depths also increased as fish moved offshore (Figs 4b, 5 and 6). Both the mean maximum depth (onshore 40 ± 12 , offshore 75 ± 15 m) and the mean minimum temperature (onshore 16.4 ± 1 , offshore $19.5 \pm 0.5^\circ\text{C}$) increased significantly ($P < 0.05$, Mann–Whitney rank sum test). Likewise, the time spent in the top 5 and 50 m decreased.

Swordfish in the Pacific, regardless of location, appear to remain primarily within the surface mixed layer at night. In the EPO, the estimated surface mixed layer depth was consistently deeper than the average maximum nighttime depth and the average difference

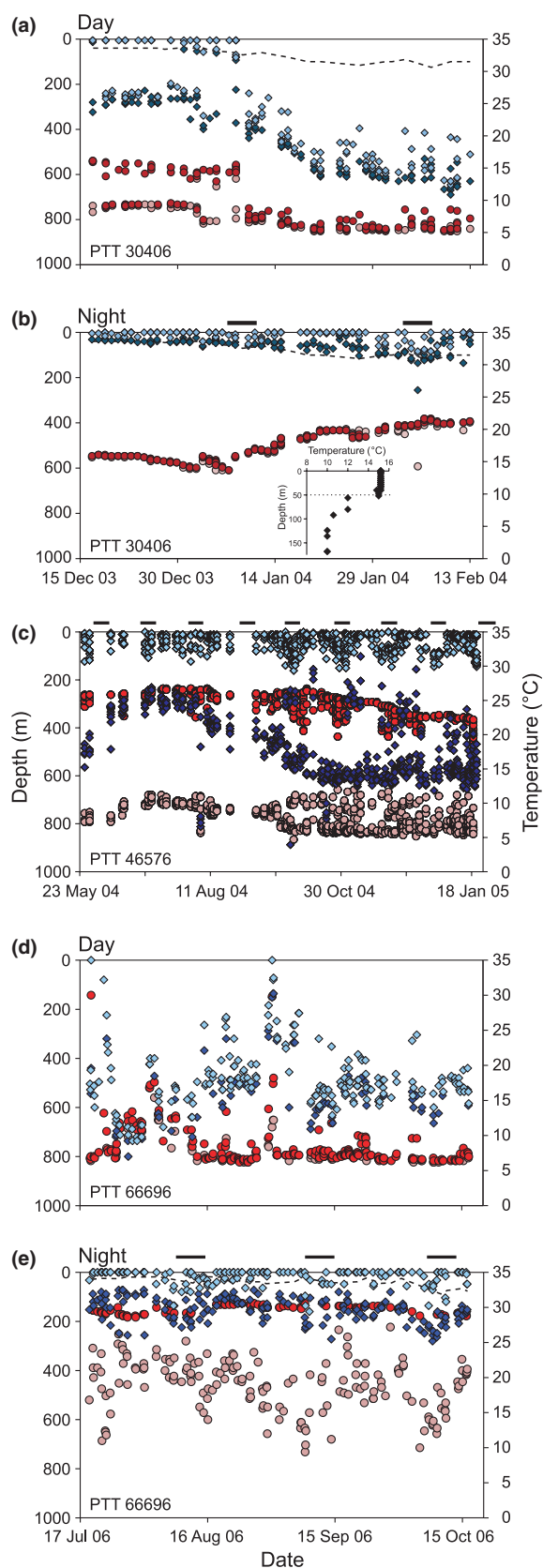


Figure 4. Temperature/depth data from three tags are shown: (a, b) 30406, eastern Pacific Ocean; (c) 46576, Central Pacific Ocean; (d, e) 66696, western North Atlantic-Caribbean. For all but (c), the PDT data are shown including the maximum (dark blue) and minimum (light blue) depth, sea surface temperature (red) and minimum temperature (pink) with day and nighttime values in the top panel and bottom panels, respectively. The estimated depth of the uniform temperature surface layer (dashed line) is also shown. The inset in (b) shows an example of how the PDT data were used to approximate the mixed layer depth. For (c) the hourly daytime temperature (pink) and depth (dark blue) and nighttime temperature (red) and depth (light blue) are shown. For all panels, the horizontal black bars indicate the time of the full moon.

between the minimum temperature and SST was only $0.7 \pm 0.1^\circ\text{C}$ (Table 3, Fig. 4b). While the actual surface mixed layer depth could not be determined from the MT tags, the shallow average nighttime depths (33 ± 8 m) and the similarity between SST and average minimum temperatures (mean difference $1.6 \pm 0.4^\circ\text{C}$, Table 3) suggest that these fish also remained primarily within the surface mixed layer at night.

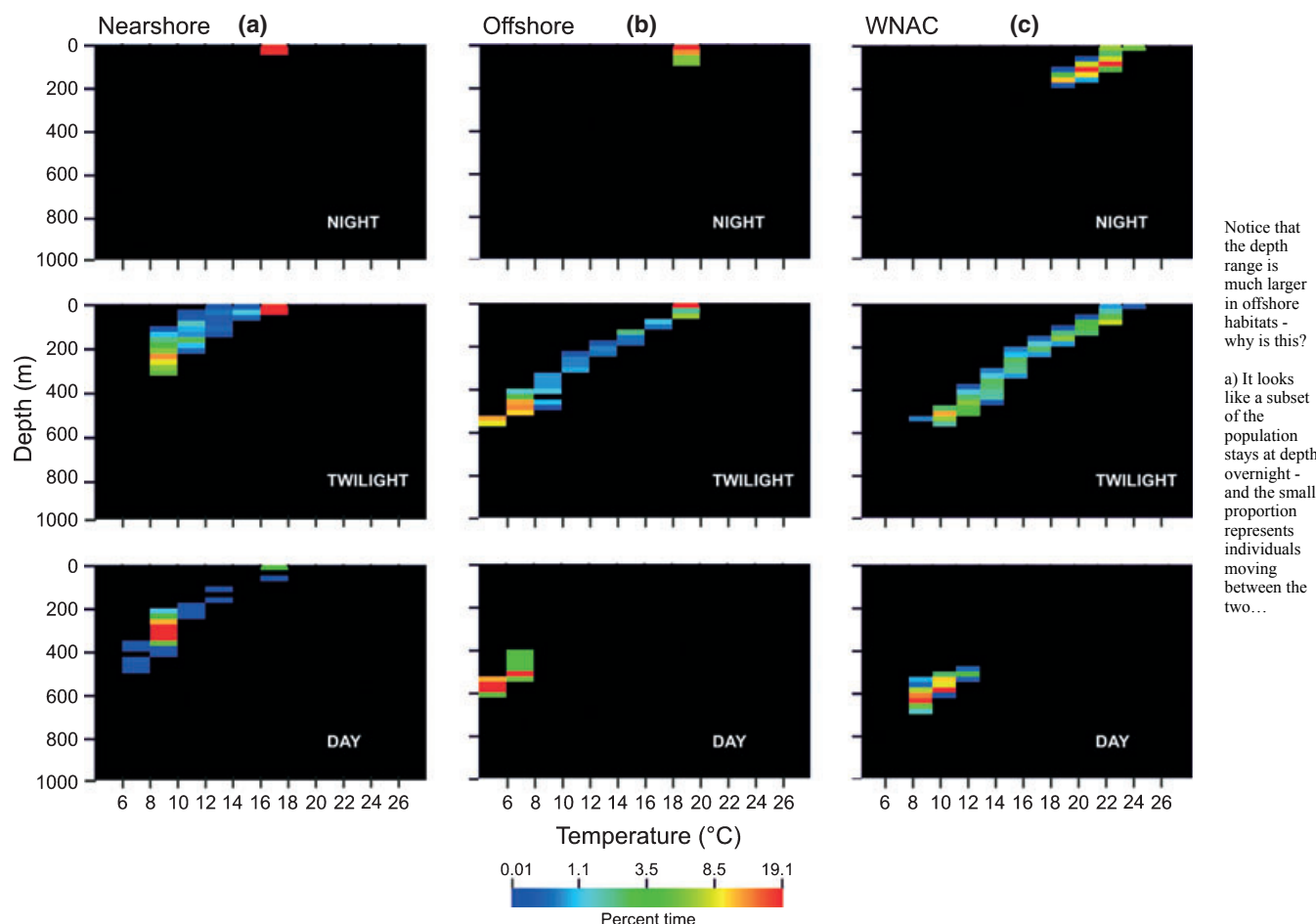
Nighttime – western North Atlantic-Caribbean

Comparison of the nighttime data between ocean basins revealed a significant increase in the depths in the WNAC versus the Pacific. The average maximum nighttime depth (176 ± 30 m) and overall depth distributions were shifted to deeper waters (Table 3, Figs 3, 4e, 5, and 6). Despite these depth differences, the mean minimum temperatures occupied at night were not significantly different ($P > 0.05$ KW Rank Sum Test; EPO $14 \pm 3^\circ\text{C}$, CPO $16 \pm 4^\circ\text{C}$, WNAC $14 \pm 5^\circ\text{C}$; Table 3) and very little time ($<2\%$) was spent below 12°C . Both the average maximum depth in comparison with estimates of the depth of the surface mixed layer (42–77 m; Table 3, Fig. 4e) and the substantial difference between minimum temperature and SST (mean $7.9 \pm 1.1^\circ\text{C}$) indicate that, unlike in the Pacific, swordfish in the WNAC are not constrained to the surface mixed layer at night.

Nighttime – depth and lunar illumination

A significant increase in nighttime depths around the full moon was observed in all regions (Figs 4b,c,e and 9) ($P < 0.05$ regression analysis). The minimum depths were similar across locations, increasing from the surface around the new moon to ≈ 20 m at the full moon. Around the full moon, the mean nighttime depths ranged from 70 to 220 m, with the deepest values in the WNAC. An examination of minimum

Figure 5. The vertical habitat envelopes are shown for three representative days for fish (a) near- and (b) offshore in the Pacific and (c) in the western North Atlantic-Caribbean (WNAC).



temperatures showed only a 1°C change comparing the 0–10% and 90–100% illumination intervals, indicating that position in relation to the surface mixed layer did not change substantially.

Oxygen

Oxygen concentration at maximum depths ranged from 0.5 to 5.1 ml L⁻¹ (0.7–6.9 mg L⁻¹, or 7–84% saturation, converted using temperatures at depth) with the two lowest values encountered at lower latitudes off Baja California, Mexico and in the CPO. In the EPO, nine of 21 estimates were 1 mL L⁻¹ or less (1.2 mg L⁻¹, or 13% saturation).

DISCUSSION

Horizontal movements

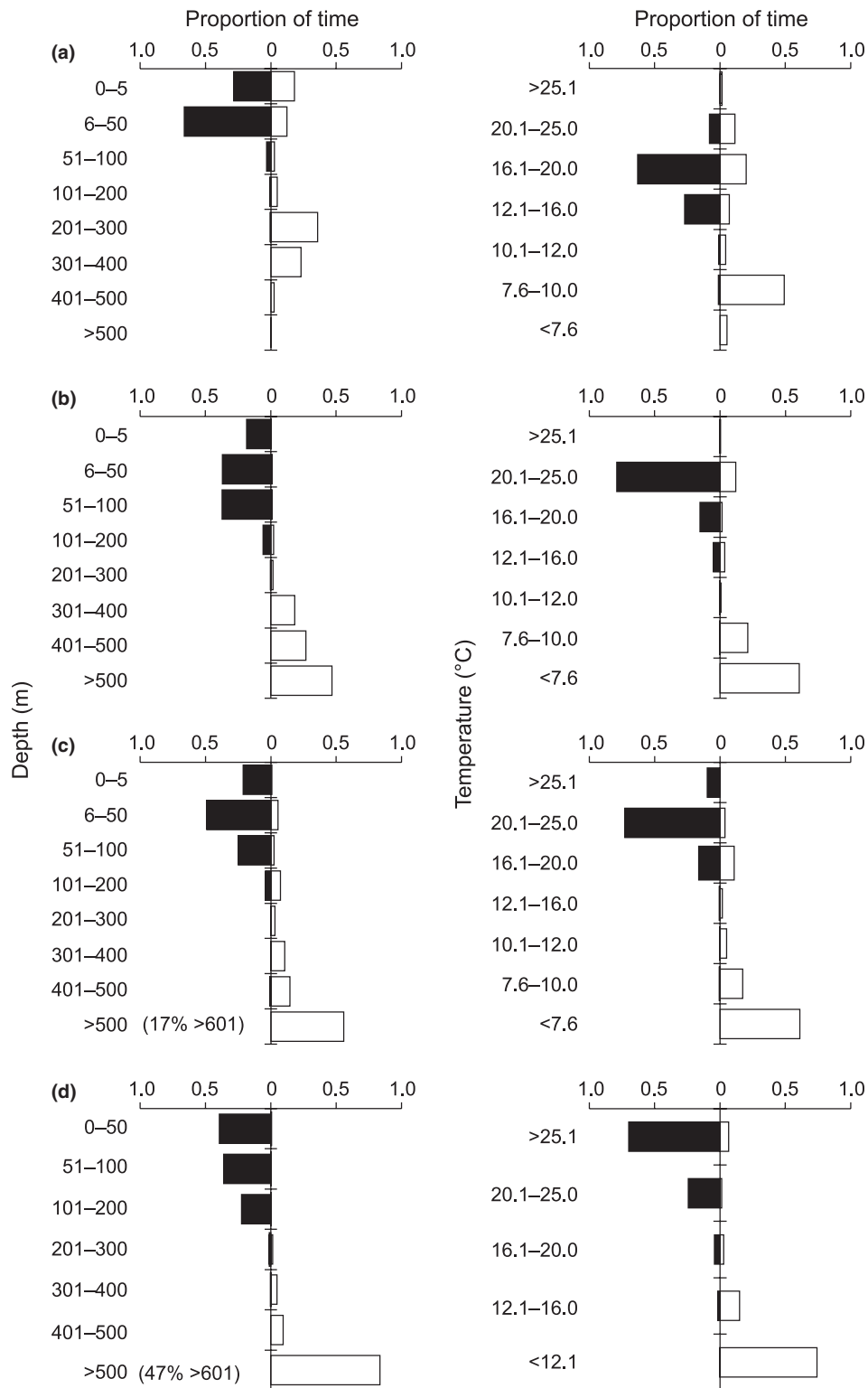
The PSATs used in our study functioned essentially as fisheries-independent, short-term conventional tags

(Block *et al.*, 2005; Bolle *et al.*, 2005). The rapid speeds for some fish suggest directed movement away from the tagging location. Our highest estimated straight-line speed (59 km day⁻¹, or 1.3 knots) is comparable to 'sustained speeds' reported for swordfish (Carey and Robison, 1981; Carey, 1990), and other large pelagic predators (summarized in Block *et al.*, 1992). Given the relatively low sample size and short deployment durations the utility for examining migratory patterns or stock structure is limited.

Vertical movements

Vertical diving records from both oceans revealed consistent diel patterns. Swordfish leave near-surface waters before sunrise, descend slowly to depth, and then return slowly to the surface after sunset. Thus, other than during **basking events**, swordfish expose themselves to little solar illumination. These results are consistent with those of previous studies, and

Figure 6. The depth and temperature histograms (showing relative frequency of time spent) that represent the entire dataset for each region; (a) nearshore, (b) offshore (both CA1), (c) offshore (central Pacific) and (d) western North Atlantic-Caribbean (WNAC). Data are separated into daytime (open bars) and nighttime (closed bars).



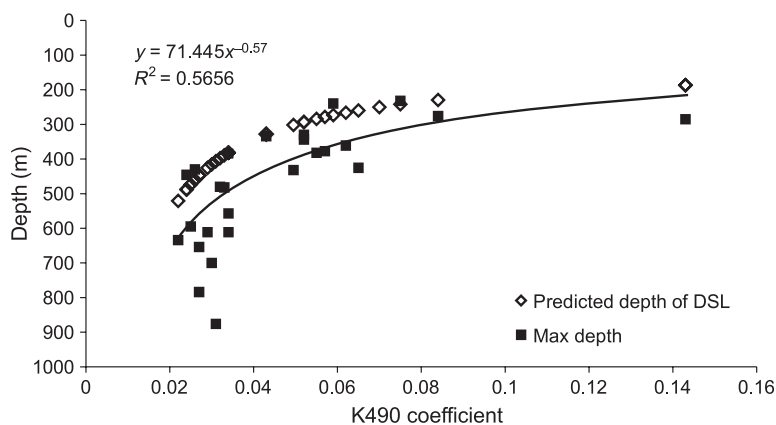
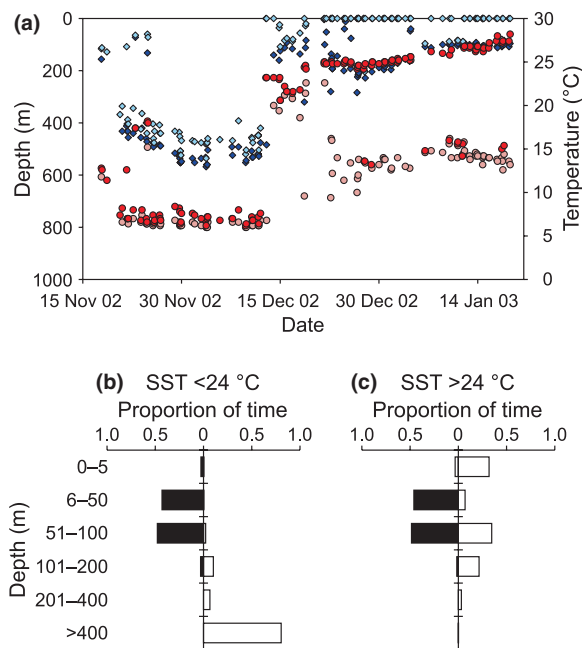


Figure 7. Plot of the maximum depth as a function of the K490 (m^{-1}) attenuation coefficient. Also shown are the estimated depths of the top of the deep scattering layer (DSL) as a function of the K490 determined using the equation provided by Tont (1976) and the conversion between Secchi disc depth and attenuation reported by Matciak (1997).

Figure 8. The shift in depth at temperatures $>24^{\circ}\text{C}$ for fish 19910. (a) The raw temperature/depth profile (PDT) data showing daytime minimum and maximum depth (light and dark blue respectively) and temperature (pink and red, respectively). The depth histograms for both day (open bar) and night (black bars) for periods when sea surface temperatures (SST) were (b) $<24^{\circ}\text{C}$ and (c) $>24^{\circ}\text{C}$.

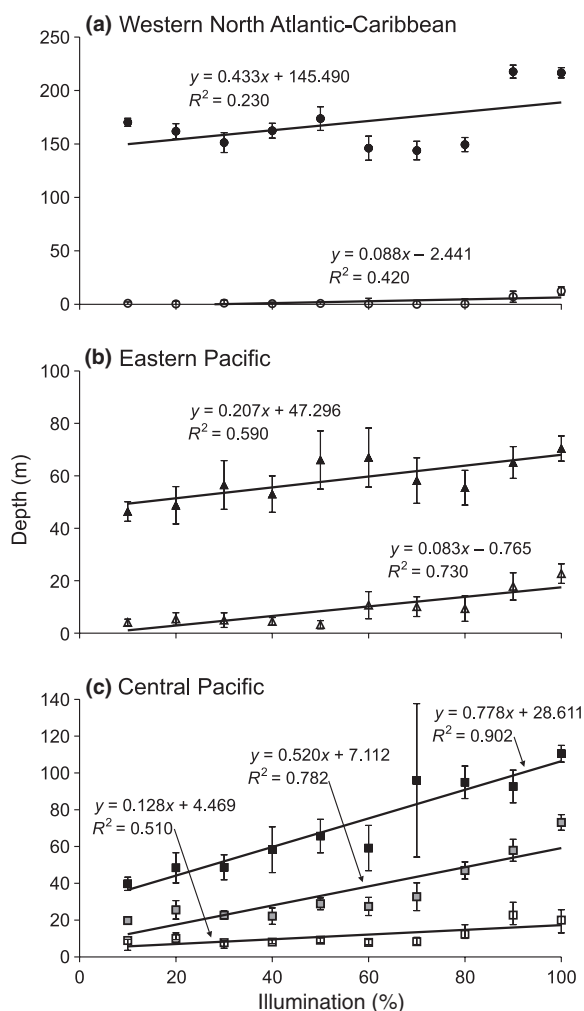


where data overlap geographically, the depths observed are similar (Carey and Robison, 1981; Carey, 1990; Holts *et al.*, 1994; Sedberry and Loefer, 2001; Takahashi *et al.*, 2003; Musyl *et al.*, 2004; Loefer *et al.*, 2007; Canese *et al.*, 2008; Sepulveda *et al.*, 2010). This study does extend observations to two new regions: the CPO and WNAC. In both areas, the depths are the deepest reported for swordfish, >800 m. Our results also greatly increase the data available for the EPO.

There is a general consensus that the diel vertical movements of swordfish and other large pelagic predators are associated with foraging in the DSL (Josse *et al.*, 1998; Dagorn *et al.*, 2000; Schaefer and Fuller, 2002; Musyl *et al.*, 2004; Gilly *et al.*, 2006). Although specific feeding events cannot be identified with the PSATs, the stomach contents of swordfish reveal a mix of benthic, epipelagic, and mesopelagic fishes and squids (Scott and Tibo, 1968; Markaida and Sosa-Nishizaki, 1998; Moteki *et al.*, 2001; Markaida and Hochberg, 2005; Young *et al.*, 2006). In addition, the daytime depths of animals tagged in this study were primarily within the DSL. The ability to target the organisms of the DSL during the day has certain advantages. Prey organisms are concentrated over a relatively narrow range of depths during the day, versus during the night, when they are more dispersed (Clark *et al.*, 2000). The activity of the prey is also likely to be slowed in the cooler waters at depth (Fry, 1971; Donnelly and Torres, 2004). Swordfish, on the other hand, have a suite of adaptations that enhance the function of their visual, locomotor, circulatory and neural systems in the cold dark waters at depth, providing them with a predatory advantage (Carey, 1982, 1990; Block, 1987; Dickson and Graham, 2004; Fritsches *et al.*, 2005; Lisney and Collin, 2006; Warrant, 2008; Galli *et al.*, 2009; Kröger *et al.*, 2009).

Our results show that the depths swordfish occupy during the day and night vary geographically. Daytime depths, other than while basking, are linked to light attenuation, increasing as light penetrates deeper into the water column. The shift to deeper waters is most likely linked to parallel increases in the depth of the DSL which has been shown to increase as light penetrates deeper (Kampa and Boden, 1954; Dickson, 1972; Tont and Wick, 1973; Tont, 1976; Frank and Widder, 2002). Carey and Robison (1981) were the first to suggest, based on individual fish, that light

Figure 9. The nighttime depths as a function of lunar illumination are shown, calculated over 10 separate 10% illumination intervals. For the Wildlife Computers PSAT tags in both the (a) western North Atlantic-Caribbean and (b) the eastern Pacific, the average maximum and minimum depth are shown for each 10% illumination interval. (c) For the microwave telemetry tags deployed in the central Pacific, the average of the maximum, minimum and average nighttime depths are shown. These are calculated from the hourly values. Bars show the standard error.



levels influence swordfish vertical movements (Carey, 1990). Our data show that a similar shift exists across individuals over a range of oceanographic regimes. Indirectly, solar illumination appeared to have the greatest impact on the daytime depths of swordfish.

Depths occupied by swordfish at night were also influenced by light levels. Individuals spent more time in deeper waters as lunar illumination increased, most likely again reflecting the behaviors of the organisms of the DSL (Tont and Wick, 1973; Linkowski, 1996).

The increase in depth with increasing moon phase was greatest in the tropical WNAC, as expected given the lower attenuation coefficient in these waters. The positive correlation between maximum depth and lunar illumination is consistent with results from previous studies on other pelagic predators [e.g., Humboldt squid (*Dosidicus gigas*) and bigeye tuna] thought to forage on the DSL (Schaefer and Fuller, 2002; Musyl *et al.*, 2003; Gilly *et al.*, 2006). In addition to light, temperature appeared to impact the nighttime depths of swordfish, which may be related to physiological constraints on movements (described more fully below) rather than shifts in resource distribution.

Ambient temperature and oxygen concentration

While examination of vertical distribution is useful for assessing gear vulnerability, depth *per se* is not a relevant parameter from a physiological perspective nor can it be predictive (Brill and Lutcavage, 2001; Bigelow and Maunder, 2007; Bernal *et al.*, 2009).

Rather, temperature and oxygen concentrations are likely two of the main environmental factors limiting both the vertical and geographic distribution of large pelagic fishes (Sund *et al.*, 1981; Carey, 1990; Brill, 1994; Prince and Goodyear, 2006). Therefore, understanding the effects of temperature and oxygen improves prediction of behaviors and distributions, and should improve population assessment models based on CPUE (Hanamoto, 1987; Brill and Lutcavage, 2001; Bigelow *et al.*, 2003; Brill *et al.*, 2005; Bigelow and Maunder, 2007; Damalas *et al.*, 2007). Comparing the behaviors of a single species across regions with different oceanographic conditions is particularly useful in determining environmental limitations (e.g., Block *et al.*, 1997; Brill *et al.*, 1999). Insights into the impact of oxygen on vertical movements would be advanced by *in situ* measurements of ambient oxygen by the tags instead of relying on model-derived, climatological data.

Our data confirm that swordfish clearly inhabit a broad range of temperatures, encountering SSTs ranging from 14 to $\approx 30^{\circ}\text{C}$, and subjecting themselves to rapid temperature changes over 20°C during their daily vertical movements. The suggestion by Takahashi *et al.* (2003) that swordfish diel movements are limited below SST of 20°C is not apparent in our results. These authors reported only short forays below the thermocline during the days when SST fell to between 13.8 and 18.3°C . In contrast, we found that even at SSTs of 14°C , swordfish were capable of spending most of, if not the entire, day in cool water. While the overall minimum daytime temperatures observed across locations ($\approx 7^{\circ}\text{C}$) might indicate a

thermal limit, this may also be associated with resource distribution. Even colder minimum temperatures (2°C) have been reported (Takahashi *et al.*, 2003) and considerable variability was apparent within and among individuals in this study. Based on our observations, **daytime vertical movements appear to be dictated by resource distribution rather than by temperature.**

Some influence of temperature on vertical distributions was apparent at night. Fish in the EPO, where the coolest surface temperatures were experienced, remained in the surface mixed layer at night. While the estimates of the mixed layer depth were not possible in the CPO, the temperature and depth recorded as well as CPUE data (Seki *et al.*, 2002) suggest that a similar pattern exists here. This was not the case in the WNAC, where SST was $\approx 10^\circ\text{C}$ warmer and **night-time diving depth extended deep into the water column.** The similarity in minimum temperatures across locations (14–16°C), despite the differences in water column structure, is suggestive of some thermal optimum at night. Also similar across locations was the time spent below 12°C when averaged over a day. It may be important for fish to spend a minimum amount of time in warmer waters to enhance physiological functions such as growth and digestion.

Warm temperature can also constrain the vertical movements of large pelagic fishes (Teo *et al.*, 2007), which may help explain the nighttime vertical distribution patterns in the WNAC. Swordfish here did not remain in the surface mixed layer at night, but descended into the cooler waters below the thermocline, possibly to behaviorally thermoregulate. A similar mechanism was used in the Gulf of Mexico by adult bluefin tuna (*Thunnus thynnus*) that only made brief forays into the surface mixed layer ($\approx 26^\circ\text{C}$), presumably to spawn (Teo *et al.*, 2007). **Additional information on swordfish body temperatures would help to identify thermal limits and whether swordfish are actively trying to reduce body temperature, as do tunas** (Dewar *et al.*, 1994).

The impact of low oxygen concentration on the vertical distribution of many epipelagic organisms is increasingly recognized, **especially in the EPO with its shallow oxygen minimum zone** (Wyrteki, 1962; Carey and Robison, 1981; Gilly *et al.*, 2006; Prince and Goodyear, 2006; Vetter *et al.*, 2008; Nasby-Lucas *et al.*, 2009). While concentrations of $3.5 \text{ mL O}_2 \text{ L}^{-1}$ are suggested as the lower limit for a number of tuna and marlin (Ingham *et al.*, 1977; Brill and Bushnell, 1991; Brill, 1994; Prince and Goodyear, 2006), swordfish, similar to bigeye tuna, appear to be able to tolerate lower oxygen concentrations (Carey and

Robison, 1981; Hanamoto, 1987; Lowe *et al.*, 2000; Brill *et al.*, 2005). Carey and Robison (1981) reported that while the vertical movements of swordfish were constrained off Baja California Mexico, fish did occupy relatively hypoxic waters (10–20% of surface values, ≈ 0.5 to $1.1 \text{ mL O}_2 \text{ L}^{-1}$). In our study, nine of 21 measurements from the EPO fell within the same range and all swordfish here encountered concentrations below $2.15 \text{ mL O}_2 \text{ L}^{-1}$. The ability to tolerate hypoxic waters will allow for foraging over a greater range of depths, which may be of particular importance in the EPO. **Many DSL organisms are hypoxia-tolerant** (e.g., Childress, 1971; Childress and Nygaard, 1974; Belman and Childress, 1975; Sanders and Childress, 1990), including the Humboldt squid, which tolerates oxygen concentrations of 5–10% of saturation (Gilly *et al.*, 2006).

The ability of fish to maintain oxygen uptake and delivery is key to hypoxia tolerance (Gamperl and Driedzic, 2009; Wells, 2009). Although the blood oxygen binding characteristics of swordfish are not known, their **gill surface area is twice that of a similar size striped marlin, suggesting an increased tolerance for hypoxia.** Gill surface area is increased by the unique branching of the distal gill filaments that increases the number of secondary lamellae (Wegner *et al.*, 2009). Any efforts to assign accurate oxygen limits for swordfish will require more precise information on blood oxygen binding characteristics, oxygen concentrations at depth, and time spent at depth over a range of physical conditions (Brill *et al.*, 2005; Wells, 2009).

Basking

Exceptions to the typical diel vertical movement pattern were basking events. Basking behavior has been reported in swordfish in previous electronic tagging studies (Carey and Robison, 1981; Carey, 1990; Holts *et al.*, 1994; Takahashi *et al.*, 2003; Sepulveda *et al.*, 2010) and by fishers around the world (Nakamura, 1985; Brewster-Geisz *et al.*, 1997; Coan *et al.*, 1998). Although different definitions have been used to describe surface basking in swordfish, the present study characterized basking as a rapid ascent from depth, a surface period ranging from minutes to hours, then followed by a rapid descent. **The ascent and descent rates were much faster than those occurring at dawn and dusk** when the fish were presumably following the DSL. The rates of descent were consistently faster than ascent, the reverse of what is expected if fish are bursting and gliding to conserve energy (Weihs, 1973), suggesting that swordfish were actively swimming downward.

Most reports of basking are from the coastal waters of Japan, Chile, California, the Baja Peninsula of Mexico, New England and Canada (Carey and Robison, 1981; Sakagawa, 1989; Carey, 1990; Holts *et al.*, 1994; Coan *et al.*, 1998; Takahashi *et al.*, 2003; Neilson *et al.*, 2009; Sepulveda *et al.*, 2010). Our observations indicate that swordfish basking behaviors occur predominantly in cooler, coastal waters and then decrease as fish move offshore. While basking was also apparent in warm tropical waters of the WNAC and CPO, it was less frequent. Even in the EPO (Southern California Bight), where we recorded the majority of basking events, fish did not surface daily. This will effectively reduce the availability of swordfish to the harpoon fishery in comparison with drift gillnet and longline fisheries, which target swordfish at the surface at night.

There has been considerable speculation about the motivations for basking. Based on an increase in surface behavior in areas with a pronounced oxygen minimum zone, Carey and Robison (1981) suggested that basking allowed recovery from anaerobic debt after foraging in oxygen-poor water. Takahashi *et al.* (2003) reported that basking was more prevalent during the first days after fish entered cooler waters, suggesting that swordfish return to the surface to thermally recharge. The relationship we observed between basking and temperature was complex. Basking was observed in both warm tropical and cool temperate waters, did not always occur daily under similar thermal conditions, decreased in frequency as minimum daytime temperatures dropped and fish moved offshore, and did not occur in a regular pattern as do the thermoregulatory ascents to the warm surface waters observed in bigeye tuna and other species (Carey and Scharold, 1990; Holland *et al.*, 1992; Schaefer and Fuller, 2002; Musyl *et al.*, 2004; Schaefer *et al.*, 2007).

One possible explanation for the variability in basking behavior is potential links to foraging success (Takahashi *et al.*, 2003; Sepulveda *et al.*, 2010). Interestingly, harpooners in the Southern California Bight report that landed swordfish typically have full stomachs (D. Mauer, pers. comm.). Swordfish may be coming to the surface to speed digestion, which could in turn increase the frequency of foraging events. Possible explanations for the reduction in basking offshore may have to do with the increased distance to the surface or the generally higher concentration and diversity of prey in coastal waters, where swordfish apparently forage both in the water column and on banks (Carey and Robison, 1981; Carey, 1990; Holts *et al.*, 1994).

Putative spawning

In the Pacific, three swordfish occupied significantly shallower daytime depths in areas where the surface water temperature was 24°C and greater, possibly due to spawning. PSATs cannot record spawning activity *per se*, although spawning behavior has been inferred from electronic tagging data (Seitz *et al.*, 2005; Teo *et al.*, 2007). We suggest that the shallower daytime depths may be related to spawning behavior, based on the following:

1 The swordfish tagged in the EPO were large enough to be reproductively mature regardless of their sex (DeMartini *et al.*, 2000).

2 Swordfish spawn primarily in waters 24°C or warmer (Grall and de Sylva, 1983; Nakamura, 1985) and the shift in vertical movement occurred at or close to this temperature.

3 The swordfish were in known spawning locations (DeMartini *et al.*, 2000; Mejuto *et al.*, 2008).

Although spawning is thought to occur at night in most pelagic fish (Taylor and Murphy, 1992; Teo *et al.*, 2007), it was the vertical distribution during the day that changed. Presumably, occupying warmer waters enhances the development of eggs and sperm, although swordfish are clearly not seeking out the warmest waters available, similar to bluefin tuna in the Gulf of Mexico (Teo *et al.*, 2007). It is also possible that daytime behaviors are related to courtship, which has been observed in swordfish during the daytime in the Mediterranean (Romeo *et al.*, 2009).

Independent validation of spawning activity is required to determine whether the vertical shifts are associated with reproduction or some other factor such as oxygen concentration at depth or prey distribution. Interestingly, no similar patterns were observed in the WNAC despite the fact that swordfish were tagged on known spawning grounds during the spawning season (April through July) (Taylor and Murphy, 1992). Based on the size estimates, most of the swordfish tagged in the WNAC would be mature if they were males, but not if they were females (Taylor and Murphy, 1992). The ability to identify spawning from vertical behavior would improve our ability to locate spawning sites, examine the dynamics of spawning, and establish links between spawning and foraging grounds.

Implications of PSAT results for fisheries, population assessments and bycatch reduction

Understanding how environmental factors influence vertical distribution patterns is important for marine resource management and conservation. Based on our

results, temperature, oxygen, ambient light levels, and the associated depth of the DSL should be considered when assessing vertical distributions of swordfish and most likely other species that follow the DSL.

Some inferences about changes in catchability can be drawn from the vertical distributions at night when swordfish are typically targeted. In the CPO, the average depth of the shallow-set longline is 60 m (Bigelow *et al.*, 2006) and the swordfish vertical distribution is shallower than this depth until approximately 5 days before the full moon ($\approx 70\%$ illumination). Thus, there is likely more overlap with the longline gear around the full moon. In fact, catch rates in the Hawaii-based, shallow-set longline do increase around the full moon (Bigelow *et al.*, 1999). In the Southern California Bight, the drift gillnet fishery is required to set their nets 12 m below the surface to avoid protected species (PFMC, 2003). Our data suggest that swordfish may swim over the top of the net when the moon is 80% illuminated or less. In the Caribbean, one study using time-depth recorders found that the modal depth of hooks regardless of hook position was 40 m, although hooks did go as deep as 150 m (Rice *et al.*, 2007). The modal depth of swordfish at night (between 0 and 50 m) overlaps the modal hook depth.

One factor that complicates efforts to predict catchability from electronic tagging data is whether and by how much behavior is altered by the presence of the fishing gear, including light sticks (Broadhurst and Hazin, 2001). Nonetheless, the relationship between depth and environmental light levels (light attenuation and lunar phase) suggests the potential for modeling swordfish depths based on regional oceanography. For daytime depths, ambient oxygen levels and periods spent spawning or foraging on banks would also need to be considered.

The bycatch of sea turtles in longline fisheries targeting swordfish has received considerable attention in recent years (Gilman *et al.*, 2007; Howell *et al.*, 2008; Benson *et al.*, 2009; Gjertsen, 2011). Loggerhead (*Caretta caretta*) and leatherback sea turtles (*Dermochelys coriacea*) tend to remain in the top 100 m of the water column (Polovina *et al.*, 2003; Benson *et al.*, 2007) and swordfish are typically targeted at night, when the overlap with turtles is the greatest. It is, however, also possible to catch swordfish with longlines during the day at depth (Beverly and Robinson, 2004), which could reduce sea turtle bycatch. Our results could increase the success of daytime fisheries because of the ability to predict the daytime depths of swordfish.

CONCLUSIONS

Our results covering diverse habitats provide new insights into the biology of swordfish and how vertical distributions during the day and night are influenced by a range of environmental conditions with implications for gear vulnerability. The diel variability highlights the need for detailed temporal studies when linking habitat preferences to fisheries data. Additional information on the swordfish hypoxia tolerance, oxygen concentrations at depth, and the composition and dynamics of the DSL in relation to meso-scale environmental features would help improve our understanding of the foraging ecology of swordfish and further define essential habitat. Although challenging to synthesize, larger comparative studies combining results across a range of habitats have the potential to advance our biological understanding of species beyond those focused on smaller regions.

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