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Movements and behaviors of swordfish *Xiphias gladius* in the United States Pacific Leatherback Conservation Area.

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Running head: Swordfish vertical distribution

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ABSTRACT

This study reports on the movements of swordfish tagged within the Pacific Leatherback Conservation Area (PLCA), an expansive region (>500,000 km^2) off the U.S. West Coast that has been seasonally restricted to drift-gillnet fishing since 2001 to reduce leatherback sea turtle (*Dermochelys coricea*) interactions. Thirteen swordfish were outfitted with satellite-linked archival tags scheduled for short (2-20 d, n=11) and longer-term (150 d, n=2) data collection. All tags were deployed on basking swordfish using traditional harpoon-based methods during the fall of 2012-2013, near offshore seamounts (35.6^o N/122.9^o W to 37.4^o N/123.5^o W). Depth and temperature data from 11 swordfish (~90 to 150kg) resulted in <251 days of movement information from the PLCA region. All tagged individuals exhibited surface-oriented nocturnal movements, spending >99% of the night above the average thermocline depth (37.5 m), with an average night depth of 8.3 ± 1.6 m. Daytime depth distribution was greater and more variable (mean 107.1 ± 21.2 m), with fish primarily displaying three behavioral patterns: (1) basking activity, 16.7% of the day; (2) a mixed-layer distribution between 3 m and the thermocline, (26.8% of the day); and (3) prolonged dives below the thermocline, 56.5% of the day. For seven of the tracks, daytime basking rates increased when thermocline depth was < 37 m. As fish moved offshore, there was less variability in vertical movements with a reduction in both basking activity and mixed layer occupancy, as well as an increase in average daytime depth. These data are discussed with respect to the potential development of alternative fishery options for the PLCA.

Key words: gillnet, fishery, depth, thermocline, sea turtle

INTRODUCTION

Swordfish landings from U.S. West Coast-based fishing vessels have severely declined over the past 30 years, with California landings, ex-vessel revenues, and fishery participation reaching historic lows in 2015 (PFMC, 2017). This decline is not linked to stock status, as recent stock assessments suggest that the Western and Central North Pacific Ocean (WCNPO) swordfish stock is not overfished and that overfishing is not occurring (Brodziak, 2010; WCPFC, 2014). Instead, the decline has been primarily attributed to strict bycatch mitigation measures that have severely reduced the core historic range of the fishery (Carretta et al., 2003, Benson et al 2009; Martin et al., 2015). Efforts to increase gear selectivity and reduce bycatch have taken a toll on the West Coast swordfish industry, especially since local production continues to compete directly with global imports that tend to operate under less oversight (Bartram et al., 2010; Martin et al., 2015). Despite these hurdles, sustainable fishery development continues to be a management priority of the Pacific Fisheries Management Council (PFMC) and provides the basis for this study.

Within the U.S. exclusive economic zone (EEZ) off the West Coast, swordfish are targeted by the California large-mesh drift gillnet (DGN) fleet, by the deep-set buoy gear fishery (which is currently in exempted status) and by a small southern California-based harpoon fishery (Bedford and Hagerman, 1983; Hanan et al., 1993; Sepulveda et al., 2015). Off California, DGN interactions with bycatch species of concern (e.g., marine mammals and sea turtles) have prompted numerous restrictions that have directly affected local fishers through gear modifications and time and area closures. The most dramatic management measure put in place to date was the implementation of the Pacific Leatherback Conservation Area (PLCA), a temporal restriction intended to further reduce interactions with endangered leatherback sea turtles (*Dermochelys coricea*; Federal Register, 2001). The PLCA was established in 2001 and restricts DGN operations from August 15-November 15 over a 500,000 km^2 area along the central coast of California during the peak swordfish season (Carretta et al. 2003; Martin et al., 2015). Contemporary DGN operations are now seasonally restricted to the waters of the Southern California Bight (SBC), a relatively small portion of the CA coastline. The implementation of the PLCA has negatively influenced DGN fishery participation and West Coast landings by limiting the historic fishery range and preventing fishers from tracking seasonal swordfish migrations into the PLCA (Hanan et al., 1993; Benson et al., 2009; Martin et al., 2015).

While DGN is the dominant gear used to target swordfish off California, shallow-set longline remains the principal mode of capture for swordfish globally (Ward et al., 2000). Within the West Coast EEZ, longline gear is not currently authorized by the state of California or under the Fishery Management Plan for Highly Migratory Species (PFMC, 2011). The longline prohibition off California was based primarily on potential interactions with endangered and sensitive species (i.e., leatherback and loggerhead sea turtles), spatial overlap with recreational fisheries, and the presence of a juvenile shark nursery in the Southern California Bight, SCB (O'Brien and Sunada, 1994; PFMC, 2011). Collectively, limitations on permissible gear options coupled with the decline of current DGN and harpoon operations, have resulted in an under-utilization of the West Coast swordfish resource (WCPFC, 2014). Unlike DGN, the rationale for the decline of California-based harpoon operations can likely be attributed to several factors including the unpredictable nature of the fishery, its dependence on ideal weather conditions, periods of reduced basking behavior, and high operational costs (Sepulveda et al., 2010).

The concern over protected species bycatch coupled with the decline in the West Coast swordfish operations has prompted efforts to characterize habitat overlap between target and non-target species and identify potential gear alternatives that can capitalize on habitat segregation (Benson et al., 2009; Sepulveda et al., 2010; 2014; Dewar et al., 2011; Abecassis et al., 2012). A comparison of the vertical movements of swordfish and leatherback sea turtles suggest that daytime depth segregation may offer an opportunity to target swordfish at depth (below the thermocline, >70m) while avoiding turtles that tend to remain predominantly within the upper-mixed layer (Benson et al., 2007; Sepulveda et al., 2010; Dewar et al., 2011). The potential for capitalizing on daytime habitat separation has been the motivation for other studies that have aimed to selectively target swordfish deep during the day (Beverly et al., 2009; Sepulveda et al., 2014; Sepulveda and Aalbers, submitted). However, because swordfish have been shown to display local differences in depth distribution (Carey and Robison, 1981; Carey, 1990; Sepulveda et al., 2010; Dewar et al., 2011; Abecassis et al., 2012; Abascal et al., 2015), regionally-specific movement information is needed. The present study focused on documenting habitat characteristics, movement patterns and depth distribution of swordfish tagged within the boundaries of the PLCA. These data are intended to assist in the development of alternative gears for targeting swordfish off the U.S. West Coast and to promote the sustainable harvest of an underutilized domestic resource.

METHODS

Location and tagging activities

All swordfish were tagged in the PLCA, a region that spans from approximately Point Sur, CA northward towards the Oregon border and out beyond the 200-nm U.S. EEZ (Fig. 1; Table 1). Tagging was conducted aboard the R/V *Malolo* with research operations based out of Monterey Bay, CA (36° 36'N/ 121° 53'W). Tagging activities were centered on areas of productivity and thermal convergence (i.e., chlorophyll concentration and sea surface temperature). Basking swordfish were spotted at the surface using stabilized binoculars or with the aid of a spotter plane and tagged from an extended (8m) bow pulpit using a modified harpoon following the protocol described by Sepulveda et al., 2010. Swordfish size estimates, geographic position and environmental conditions (i.e., sea state, water temperature and color) were documented for each tag deployment and recovery event.

Tag specifications and attachment

Three different satellite-linked tag types were deployed, MK10 pop-off satellite archival tags (PSATs), SPLASH tags and MK10-AF transmitting fast-GPS tags (Wildlife Computers WC; Redmond, Washington, USA). The PSAT and SPLASH tags were programmed to record depth, ambient water temperature, and light level every 60s. PSATs were used for short-duration (2-20 days) deployments aimed at documenting fine-scale movements within the PLCA. Following release from the animal, most of the short-term tags were re-acquired with a signal direction finder (Sepulveda et al., 2010). The two fast-GPS tags were programmed to summarize temperature and depth data into 6h bins over longer-term deployments (<150 days) to assess behavior at greater spatial and temporal scales.

Tag tethers were rigged with an 11-cm section of 100 kg monofilament leader material, stainless steel crimps and black plastic umbrella anchors (Sepulveda et al., 2010). A secondary electronic 'hitchhiker' data storage tag (DST; Cefas Technology Limited, Lowestoft, UK) was tethered in line with PSATs to remain with the swordfish following the programmed PSAT pop-off date. Cefas G5 DSTs must be recovered from recaptured swordfish to obtain archived data. A stainless sled (Evans et al., 2014) was used to anchor the two fast-GPS tags without secondary DSTs. Archived time-series data were analyzed independently of satellite-derived data sets.

Archived data analyses

For the recovered PSATs (Table 1), fine-scale data were downloaded and summary statistics were calculated. Archived depth and temperature data were analyzed (as detailed below) to evaluate basking rates, vertical rates of movement, thermocline depth, dive duration and periodicity, as well as daytime versus nighttime depth and temperature distributions. All records were classified as *day*, *night*, or *twilight* values based on the mean Pacific Standard Time (PST) of sunrise, sunset, and nautical twilight for each deployment period at the initial tagging location from the Astronomical Applications Department of the U.S. Naval Observatory data services portal (http://aa.usno.navy.mil/data/index.php). For each deployment period, daytime was defined as the average time of sunrise until the average time of sunset; nighttime was assigned to all values between the mean time of nautical twilight at dusk until the mean time of nautical twilight at dawn; and twilight values included all data between mean time of sunset and nautical twilight at dusk as well as from nautical twilight at dawn until mean time of sunrise.

Depth statistics were quantified for each behavior type in relation to the depth of the thermocline for each track. Thermocline depth was estimated for each day of all archived data sets by determining the maximum gradient of temperature (ΔT) between 0.5 m depth bins. Mean thermocline temperature was estimated by averaging consecutive temperature records from subsequent 0.5 m depth bins spanning the maximum ΔT gradient. Thermocline values were also verified through visual inspection of depth-temperature plots for each swordfish and subsequently verified against published values for the study region (Palacios et al., 2004). The number and duration of all dives below the thermocline, as well as the descent and subsequent ascent rates, were enumerated for each fine-scale track. A dive was defined as a series of depth records that traversed the estimated daily thermocline depth for >5 min. Vertical ascent and descent rates in m min^{-1} were calculated for each of these dives. The initial and final times of dawn descents and dusk ascents were compared to the local times of sunrise and sunset for all dives that occurred within 48 h of a known location (tag deployment or pop-off). Relative light level data were summarized and compared between day, night, and twilight periods for archived data sets. Light level data were not used to estimate geolocation given that past studies have shown limited accuracy for species that exhibit extensive vertical movements during crepuscular periods (Musyl et al., 2003; Dewar et al., 2011). Because archived data sets did not span multiple lunar cycles, moon phase was not considered in analyses. Vertical rate of movement (VROM) was calculated for each fish as the mean absolute difference of all subsequent 1min depth records (Sepulveda et al., 2011).

Based on daytime dive characteristics and previous movement studies, three distinct behavior patterns were used to categorize daytime depth distribution; 1) basking periods, 2) time spent within the mixed layer, and 3) time spent below the thermocline (Sepulveda et al., 2010). Basking was defined as daytime periods in which the fish was at or within 3m of the surface, while mixed layer activity represents periods when depths ranged from >3m to the thermocline. The percent time below the thermocline was calculated using the estimated daily thermocline depth**.** Basking events were examined for both duration and time of occurrence (initiation). Individual basking events were differentiated by a change in depth in which the fish traversed the thermocline (Sepulveda et al., 2010).

Satellite-derived data analyses

To examine shift in behavior off-shore, a subset of five tags for which deployment durations were >2 weeks and horizontal distance was >100 km were analyzed (Table 1). Four of these tags were not recovered and thus provided no archival data. Consequently, for this comparison only transmitted data were used. Both PDT and time-series data were used to characterize the depth of the mixed layer when possible, as described above, by selecting the depths or depth bins where ΔT was the greatest. For examination of diel patterns, only histogram bins that excluded sunrise and sunset were used for analyses (Abecassis et al., 2012). For comparisons among tags, the same 6 h time period was used for all five tags, regardless of the binning interval which ranged from 1-6 h.

To characterize changes in habitat use with offshore movement, data from the beginning and end portions of individual fish tracks were compared. For PLCA5, the first and second weeks were compared and for fish #s PLCA 9, 10, 11, 13, the first and third weeks were compared (assuming that in the first week the fish remained closer to the tagging position compared to the last week of the deployment). Comparisons of temperature and depth, including basking behavior, were made using the time-series, PDT and histogram data.

Horizontal movements

Relative light data was collected by the archival tags once every minute, however it was not used to estimate geolocation due to both the limited duration of tag deployments as well as the lack of adequate illumination at depth (Musyl et al., 2003; Dewar et al., 2011). Given that this work focused on short-term movements within the PLCA, horizontal movements were solely evaluated for net displacement and direction between tag deployment and pop-off locations. The minimum rate of movement (km/day) was estimated for each fish as the net-displacement distance over the deployment duration. For the GPS tags a number of intermittent locations were obtained, however, all of these positions were from fish that had already moved offshore of the PLCA.

Statistical analysis and environmental data

Paired t-tests were conducted to identify differences in mean daytime and nighttime depth and VROM values. Pearson correlation coefficients were used to measure for dependence between the variables of mean daily thermocline depth, daytime basking rate, and maximum nighttime depth. All values are indicated as mean ± SE. Using archived data, daily depth probability plots were constructed with Matlab software vers. 6.0 [R12] (The MathWorks, Inc., Natick, MA) with depth bins of 1 h by 2 m to illustrate the cumulative probability of occurrence for each depth over a 24-h period. Sea surface temperature and chlorophyll concentration data were reviewed for both the tagging and pop-off locations of each swordfish using MODIS data obtained from Aqua and Terra EOS Satellites; processed by Terrafin Software, (www.terrafin.com).

RESULTS

A total of thirteen swordfish were tagged with electronic tags in the PLCA in September and October of 2012 and 2013 (Fig. 1 and Table 1). Tagged swordfish ranged in size from ~75 to ~170 kg (mean ~107 ± 8 kg). Of the thirteen tagged individuals, seven PSATs were recovered for fine-scale analyses; satellite transmitted depth and temperature data were received from four individuals, one PSAT failed to report, and one individual received only a 'hitchhiker' archival tag after the PSAT release pin severed upon application. The collective dataset included deployment durations ranging from 2 to 150 days and provided 251 days of depth, temperature and relative light level data (Table 1). No swordfish tagged with Cefas DSTs have been recaptured to date.

Vertical distribution

Analyses of vertical distribution and PLCA habitat use was principally derived from the archived data sets. For the seven archived data sets, overall depths ranged from 0 to 608 m (Figs. 2 & 3a). Significant differences were observed in the mean (± SE) day (107.1 ± 21.2 m) and night (8.3 ± 1.6 m) depths (paired *t*-test: t=11.37, P<0.001). The average daytime depth below the thermocline (not including basking or mixed layer periods) was 234.4 ± 15.2 m. Daytime dives below the thermocline ranged in duration from 9 to 884 min, with a mean dive duration of 172.6 ± 19.5 min. Swordfish consistently remained within the mixed layer throughout the night, with 99.9% of collective nocturnal records being shallower than the daily thermocline depth. The mean daily thermocline depth for the seven archived datasets was 37.5 ± 1.9 m (range 23-62 m), corresponding to mean temperatures ranging from 13.0 to 14.9°C, with a mean thermocline temperature of 13.9 ± 0.2°C. Overall, ambient temperatures experienced by swordfish tagged within the PLCA ranged from 5.1°C at depth to 20.1°C at the surface (Fig. 3B).

Additional information on overall vertical habitat use was obtained from the transmitted datasets where data were examined over the first and second or first and third weeks of the deployment as described above. Overall depths ranged from 0-616 m. While data are of lower resolution, a similar overall diel pattern was apparent with deeper depths during the day than at night. Overall mean daytime depths averaged 327 ±39 m compared to 49 ±12 m at night. Mixed layer depths ranged from 21-72 m and increased with distance offshore (near-shore mean 31 ± 5 m; offshore mean 44± 10 m).

Description of behavioral patterns

Following previous studies on West Coast swordfish (Sepulveda et al., 2010), daytime behaviors were sub-divided into three categories based on depth distribution: (1) basking

(<3m), (2) mixed layer (>3m and above the thermocline), and (3) below the thermocline. Collectively, basking activity accounted for 16.7% of all daytime records. Within individuals, as many as four independent basking events were exhibited in a single day. When compared among individuals, basking activity was highly variable, ranging from 3.5 to 55.2% of the daytime records. A mixed-layer distribution was observed in 26.8% of the daytime records and periods beneath the thermocline accounted for 56.5% of the day. Similarly, time below the thermocline also varied among individuals (13.4% to 63.3%).

Swordfish depth distribution and behavior were found to vary with thermocline depth. The average thermocline depth was 31.8 ± 1.7 m during basking behavior, 38.3 ± 3.6 m during mixed layer activity and 43.9 ± 3.6 m when swordfish were predominantly below the thermocline. For the seven archival records, time spent basking per day decreased significantly as thermocline depth increased (Fig. 4a) (r = -0.531, P-value = 0.001). Similarly, the number of days when basking was observed decreased with increased thermocline depth (Fig. 4b). Increased thermocline depth also coincided with offshore movements and no basking behavior was recorded in any of the tracks when thermocline depth exceeded 70 m. Maximum nighttime depth was also significantly correlated with thermocline depth for seven archival records (r = 0.421, P-value = 0.011) and for all but one of the transmitted records.

Basking was documented in all seven archived datasets with a total of 58 individual events over 29 independent days. At least one basking event was observed on 77% of the days included in the archived dataset. The mean duration of each basking event was 73 ± 11 min with a range from one to 362 min, but increased to 105.1 ± 12 min when only basking events >3 min were considered (n=40). Although basking events occurred over all portions of the day, a peak was observed between 14:00 and 15:00 PST, while daytime basking activity was rarely observed prior to 09:00 PST or after 17:30 PST (Fig. 5). Afternoon basking events were typically followed by evening dives below the thermocline prior to the dusk ascents. Surface oriented activity (<3m) was also prevalent during the nighttime hours (range, 9.9% to 77.7%), with swordfish spending on average 35.4% ± 8.8% of the night at depths of <3m.

Diel comparisons of VROM indicated significantly greater values during the day (4.5 ± 0.2 m/min) than at night (2.3 ± 0.1 m/min) (paired t-test: t=9.69, P<0.001), and highest during twilight periods (5.5 ± 0.3 m/min). For individuals with a proximate known location, descent rates (calculated over individual dives) were greater during midday dives (11.9 ± 0.5 m/min) than those associated with dawn descents (5.3 ± 0.3 m/min). Similarly, mean midday ascent rate (14.2 ± 0.8 m/min) was greater than mean VROM at dusk (5.2 ± 0.3 m/min). Dawn and dusk VROMs did not differ. Dawn descents were initiated within 20 min PST of civil twilight (mean = 12.7 ± 2.4 min) and dusk ascents were initiated within 14 min PST of sunset (mean = 5.2 ± 1.1 min) (Fig. 6). Mean relative light level decreased from 54.8 ± 0.7 to 24.8 ± 2.3 during dawn descents and increased from 36.3 ± 3.0 to 57.8 ± 3.5 during dusk ascents, with a peak around civil twilight. Mean relative light level at depth (>200m) during the daytime (39.5 ± 1.5) was lower than that recorded at night (43.5 ± 1.0) and during the twilight periods (48.9 ± 2.7).

Shifts in vertical distribution may have been associated with mixed layer depth, along with distance travelled offshore. For two fish (PLCA9 and 10) that remained within 180 km of the deployment site and for which the average mixed layer depth (MLD) was shallower than 31 m, basking was still prevalent throughout the tracks and daytime depths showed no substantial change. For the three remaining swordfish, all of which moved more than 400 km from the tagging location and experienced mean MLD of 40 m or greater (PLCA 5, 11 and 13), basking declined dramatically and increases in both daytime and nighttime depths were observed (Table 2).

Temperature

Collectively, swordfish were tagged at sea surface temperatures (SST) ranging from 16.1 to 19.6°C with an average SST of 17.7 ± 0.3°C. The average temperature experienced below the mean thermocline depth was 8.3 ± 0.3°C (Fig. 3B). Average SST values fluctuated by month and by year (13.6 to 20.1°C), with higher average surface temperatures in 2013 (17.9 ± 0.2°C) relative to 2012 (16.2 ± 0.2°C). Basking activity occurred over the entire range of sea-surface temperatures (mean 17.8 ± 0.5°C), with peak occurrence around 18°C. For the two transmitted datasets with the greatest net displacement from the PLCA, recorded SST was within the range of values recorded for the archived datasets [15.2 - 22°C (mean 18.5 ± 5°C)] with similar mean daily minimum temperatures (8.2 ± 7°C).

DISCUSSION

Increasingly, fishery management decisions have been influenced by concerns over bycatch impacts rather than the population dynamics of target species. Off the U.S. West Coast, conservation concerns over endangered leatherback sea turtles have led to the steady decline of a once productive swordfish fishery (Martin et al., 2015). In an attempt to identify opportunities for reducing interactions and re-opening areas currently closed to California fishers, this work focused on documenting the vertical movements of swordfish tagged within the Pacific Leatherback Conservation Area. Fine-scale vertical movements were analyzed to assess depth distribution trends within the PLCA and the degree to which swordfish vertical distribution overlaps with species of concern (i.e., leatherback sea turtles). This work suggests that swordfish within the PLCA are capable of exhibiting highly variable movements during the day with a consistently shallow (within the upper mixed layer) distribution at night. Although similar swordfish movement patterns have been described in other studies (Carey and Robison, 1981; Takahashi et al., 2003; Sepulveda et al., 2010; Dewar et al., 2011), heightened variability in daytime depth distribution distinguishes PLCA movements from other regions studied to date. The varied daytime depth distribution may provide additional challenges for swordfish fisheries that operate within the PLCA during the day. Nonetheless, swordfish daytime depths were consistently greater than those exhibited by leatherback sea turtles tracked within the PLCA (Benson et al., 2007), suggesting that daytime deep-set techniques may reduce turtle interactions when compared to more traditional methods that operate near the surface at night (i.e., DGN, shallow-set longline). Findings from this work can be applied towards fishing gear innovations and the development of alternative methods for harvesting swordfish within the PLCA. As demonstrated previously (Carretta et al., 2003; Eguchi et al., 2016), spatial overlap and similarities in nighttime depth distribution between swordfish and other pelagic species will continue to be a hurdle in the development of nocturnal swordfish fisheries (i.e., shallow-set longline, DGN) off California.

Tagging operations

All swordfish movements described in this study were obtained from fish that were tagged using harpoon-based techniques, a method that has been used to tag swordfish successfully in multiple regions (Carey and Robison, 1981; Sepulveda et al. 2010; Dewar et al., 2011). Other studies have tagged swordfish using longline capture techniques with less success (Dewar et al 2011). Harpoon techniques provide a relatively non-invasive tag attachment method that has been shown to result in minimal post-tagging mortality (Sepulveda et al., 2010). In the present study, only one swordfish tag did not report any information (tag #12A0138). Although post-tagging disposition cannot be verified, it is possible that the additional mass of the trailing data storage tag may have hindered floatation and prevented transmission, particularly if the tags were shed prior to the programed release date.

Although harpoon-based tagging techniques are ideal with respect to minimizing capture and handling stress, these methods require the swordfish to be basking, a behavior not commonly observed when swordfish occur offshore (Table 2; Dewar et al., 2011). The majority of the tagging operations were performed in areas that have been historically associated with basking and commercial harpoon operations (i.e., sea mounts, canyons, ridges) (Pers. Comm. Mike McCorkle, Santa Barbara). Thus, the short-term behaviors and movement patterns reported in this study may be more representative of swordfish that occur within areas or conditions with a higher propensity for basking.

Depth distribution

The average daytime depths exhibited by the swordfish in this study were slightly shallower, 234 m versus 273 m than those reported for previous studies off Southern California (Sepulveda et al., 2010; Dewar et al., 2011). Despite regional differences, the collective range of depths reported for California swordfish are much shallower than those reported for other ocean basins (~400-1000 m, Dewar et al., 2011; Abascal et al., 2010). The shallower daytime depths off California have been attributed to several factors, including high stratification and thermocline depth (~70 m Palacios et al., 2004) as well as the depth range of the oxygen minimum layer (~300-500 m; OML defined as <0.5 mL L^{-1} dissolved oxygen; Levin, 2003; Bograd et al., 2008; Netburn and Koslow, 2015). At depth, low dissolved oxygen levels have been shown to influence the lower boundaries of several pelagic species, as it can limit favorable habitat and also influence the distribution of mesopelagic prey (Prince and Goodyear, 2006; Bograd et al., 2008; Netburn and Koslow, 2015).

In this study, the range of daytime depths exhibited by PLCA swordfish (<180 km from shore) were also shown to be much more variable than those reported off Southern California (Sepulveda et al., 2010; Dewar et al., 2011). This variability may be in response to the distribution of prey (Dewar et al., 2011; Evans et al., 2014), as the California Current system (including the PLCA) has been shown to be an important foraging area for swordfish (Markaida and Hochberg, 2005; Sepulveda et al., 2010; Dewar et al., 2011). Understanding regional vertical distribution is, however, complicated by both the variety and distribution of potential swordfish prey along the California coast. Based on stomach content analyses, swordfish have been shown to be opportunistic feeders that forage on a variety of fish and squid that are epipelagic, benthic or associated with the deep scattering layer (DSL) (Stillwell and Kohler, 1985; Markaida and Hochberg, 2005; Young et al., 2006). Swordfish diving and prolonged existence below the thermocline has been linked to foraging on DSL associated prey, with both diurnal ascent and descent times closely corresponding to the vertical migration of DSL organisms (Carey, 1990, Carey and Robison, 1981; Dewar et al., 2011; Sepulveda et al., 2010). Further, the time and rate of dawn descents (±20 min civil twilight; 5.3 ± 0.3 m/min) and dusk ascents (±14 min sunset; 5.2 ± 0.3 m/min) of swordfish in this study were similar to DSL migrations observed on the sonar (Furuno, CH-250; Camas, WA) aboard the R/V *Malolo* during the tagging cruises. Vertical movements were also comparable to diel DSL migrations documented within other regions of the eastern North Pacific [i.e., Gulf of California; (Mean ascent time: ±9 min sunset; avg. max ascent rate: 5.2 ± 1.9 m/min) Cade and Benoit-Bird, 2015]. A number of factors can influence the depth of the DSL and associated prey during the day, including light attenuation, temperature, oxygen concentration (Netburn and Koslow, 2015; Cade and Benoit-Bird, 2015) as well as the presence of bathymetric features (Porteiro and Sutton, 2007; Musyl et al., 2003). A combination of these factors likely played a role in the highly variable daytime depth distribution reported in this study.

The nocturnal depth trends and movements of PLCA swordfish were found to be similar to those reported for swordfish tracked off Southern California, with movements largely confined to the upper mixed layer (Sepulveda et al., 2010; Dewar et al., 2011). Of particular interest was the high propensity for surface activity at night, with some individuals spending more than 50% of the night hours at or near the surface. Reduced dive activity at night may be a way for swordfish to more efficiently transit from one area to another, a strategy that has been proposed for explaining prolonged periods of surface swimming off Southern California (Sepulveda et al., 2010). In the case of this study, increased surface activity may also suggest limited feeding at night and/or a higher reliance upon daytime foraging activity. Off the U.S. East Coast, nocturnal surface activity or night basking has been capitalized upon by harpoon fishers that target swordfish under bright lights at night, an activity referred to as "night jacking" (Pers. Comm. Andrew White, swordfish spotter pilot, San Diego CA). It is not known whether nocturnal harpooning is a feasible option for harvesting swordfish within the PLCA region.

Other differences between PLCA swordfish and those previously tracked within the SCB include the amount of time spent above the thermocline [43% (this study) versus ~32% Dewar et al., 2011] and the percent time basking at the surface during the day [16.7% (this study) versus 8% Sepulveda et al., 2010]. Despite individual variability, this work was able to identify a potential link between thermocline depth and basking activity (Figs. 4a, b). Dewar et al., (2011) identified a similar finding for swordfish tagged off Southern California, which exhibited reduced basking activity as fish moved offshore into areas with a deeper thermocline. Similarly, commercial fishers off California have historically used their echo-sounders to identify thermocline depth while searching for productive fishing areas during the harpoon and drift-net seasons. Off the California coast, we propose that thermocline depth may be responsible for some of the seasonal and inter-annual variability of basking activity, which directly influences the success of harpoon operations (Coan et al., 1998; Sepulveda et al., 2014). Understanding the conditions that influence basking rates may help identify specific areas or periods of increased basking activity, a scenario that could augment future harpoon operations off Southern California and within the PLCA.

Basking behavior in swordfish has been most commonly associated with behavioral thermoregulation (i.e., returning to the surface to warm and speed metabolic processes) following successful foraging events at depth (Takahashi et al., 2003; Sepulveda et al., 2010; Dewar et al., 2011). Other hypotheses proposed for swordfish basking activity include the recovery from prolonged exposure to environmental stressors experienced at depth (Carey and Robison, 1981). Carey and Robison (1981) proposed that swordfish routinely bask during times of the day when they dive to the greatest depths, or following prolonged exposure to reduced oxygen concentration. At the depths commonly frequented by swordfish (below the thermocline) oxygen concentration and temperature both impose physiological constraints and basking activity has been proposed to be a behavior associated with recovery from prolonged exposure to these harsh conditions.

The increased time that PLCA swordfish spent in the mixed layer may also be explained by increased foraging opportunities on shelf species, such as Pacific hake (*Merluccius productus*). Historic DGN fishers operating within the PLCA have long proposed Pacific hake to be a key forage species of swordfish within the central California region (M. McCorckle, Pers. Com., Santa Barbara, CA). Similarly, gut content studies off western Baja California have also documented the importance of Pacific hake in the diet of West Coast swordfish (Markaida and Sosa-Nishizaki, 1994). Pacific hake have a broad depth distribution and have been shown to school and associate near the areas examined in this study (Bailey et al., 1982). Alternatively, foraging opportunities may be heightened near seamounts, as submarine features are known to have increased productivity and may aggregate a range of taxa across trophic levels or influence the depth of DSL associated organisms (Porteiro and Sutton, 2007; Morato et al., 2010). The diverse bathymetry of the PLCA region likely influences the movement patterns and foraging ecology of swordfish, further highlighting the importance of this area for future fishery development.

How these data relate to future PLCA fisheries

California drift gillnet (DGN): Based on the results from this study, the optimal time and depth to target swordfish within the PLCA would be near the surface at night when swordfish are concentrated within the mixed layer. This consistent diel movement pattern is likely responsible for the effectiveness and high productivity of the DGN gear type within the PLCA prior to its seasonal closure in 2001 (Hanan et al., 1993; Carretta et al., 2003; PFMC, 2013). In the early years of the fishery, the CA DGN fleet moved up and down the coast with effort largely dependent upon oceanic conditions, swordfish availability and weather. Early in the season, efforts focused along central and northern California, progressing southward as water temperatures declined in the fall and early winter (Hanan et al., 1993). The seasonal prohibition of DGN activities within the PLCA consequently reduced the fishery range, preventing domestic fishers from following resource migrations through the central and northern portions of California (Carretta et al., 2004; Gjertsen et al., 2014; Martin et al., 2015).

Given the overlap in nighttime depth distribution for many pelagic species, the potential to modify DGN gear to reduce bycatch while maintaining target species catch is limited. For example, based on leatherback movement data from the PLCA, a marked decrease in sea turtle interactions would likely occur if the minimum DGN depth were doubled from the current requirement of 11 m to 22 m (Benson et al., 2007). However, based on the swordfish depth data collected in this study, a doubling of the minimum net depth would consequently result in an estimated 33% reduction in swordfish catch. Thus, for this dataset the altering of the minimum net depth to 22-m would result in swordfish swimming above the net and not getting caught approximately 84% of the time, a scenario that would not likely be economically viable.

Harpoon: All swordfish tagged in this study exhibited surface basking behavior, suggesting that swordfish are vulnerable to harpoon-based capture within the PLCA. Although harpoon operations are not currently common above Point Conception, the harpoon fishery was once a vibrant industry that exploited the West Coast swordfish resource throughout the northern ports of California (Coan et al., 1998). Most of the PLCA harpooning operations were performed concurrently with DGN activity, a scenario that provided fishers with an opportunity to fish for swordfish both during the day and at night (G. Burke DGN fisher, Pers. Com., Santa Barbara, CA). Given the relatively low average catch rate of harpoon operations (~<1.0 fish/day; Coan et al., 1998) and the practice of combining harpoon and DGN activities, the seasonal prohibition of DGN activity within the PLCA also inadvertently reduced PLCA harpoon operations. Swordfish availability, basking rates, as well as optimal oceanic and weather conditions continue to be essential for the success and long term viability of harpoon operations. Elevated sea states, wind and large swell affect the ability to locate swordfish at the surface and also pose significant navigational and safety issues given the length of the extended bow pulpits (6-9 m) used in harpoon operations (Coan et al., 1998). Collectively these factors help explain why harpoon operations have declined across all ocean basins (Ward et al., 2000).

The rate of basking observed in this study (16.7%) was more than double than that reported for swordfish off southern California, further suggesting that a harpoon fishery may be viable within the PLCA (Sepulveda et al., 2010). However, factors such as market dynamics and high operational costs (i.e., slip fees, diesel, and insurance) must be considered for artisanal gear types to be successful. Because of the low catch per unit effort (CPUE) associated with harpoon fisheries (Bedford and Hagerman, 1983; Coan et al., 1998), fish must be received at a high price-point in order for operations to be economically viable. However, because harpoon-caught swordfish is bycatch free and typically received at a premium market price, this art of fishing continues to be an option for smaller-scale operations within the PLCA, particularly if coupled with additional fishing opportunities.

Shallow-set longline: Globally, shallow-set longline operations continue to be the most common technique used to harvest swordfish (Ward et al., 2000). These techniques capitalize on the shallow distribution of swordfish at night, with vessels deploying hundreds (500-1,000) of baited hooks within the mixed layer nightly. Although shallow-set longline operations are prohibited within the California EEZ, several fleets, including the Hawaiian longline fleet, target the waters adjacent to the PLCA (DeMartini et al., 2007; Brodziak, 2010). Given the spatial overlap between leatherback sea turtles and swordfish at night, it is likely that shallow-set fishing within the PLCA would pose some additional risk for leatherback turtle interactions, especially if fishing were to occur during periods of peak leatherback abundance (Eguchi et al., 2016). However, as demonstrated previously, several bycatch mitigation measures can collectively be used to reduce protected species interaction rates (Gilman et al., 2007; Gilman and Huang, 2017). An additional hurdle to a potential shallow-set longline operation is the high density of juvenile blue (*Prionace glauca*) and mako sharks (*Isurus oxyrinchus*) present within the PLCA during the peak swordfish season (Hanan et al., 1993). Although blue and mako sharks are not protected species, bait predation, gear loss and reduced selectivity are factors that influence the productivity of any longline fishery (Kumar et al., 2016).

Daytime deep-set operations: The use of depth to selectively target swordfish and avoid non-target species has been explored in several fisheries around the world (Gilman et al., 2006; Beverly et al., 2009), with recent research trials focused within the SCB (Sepulveda et al., 2014; Sepulveda and Aalbers, submitted). The SCB work suggests that daytime deep-setting may be an option for harvesting swordfish with minimal non-target interactions (Sepulveda et al., 2014). Although swordfish movements in this study were shown to be more variable than those of the SCB (Sepulveda et al., 2010; Dewar et al., 2011), the findings did reveal that the majority (57%) of the daytime records were composed of a consistent sub-thermocline distribution. The daytime depth distribution also revealed a deeper and more consistent depth regime when fish moved offshore, further suggesting the potential of selective targeting with deep-set techniques. Further, when compared to other regions, the average daytime depths of PLCA swordfish are well within a range that can be readily targeted using deep-set gear (Beverly and Robinson, 2004; Dewar et al., 2011; Sepulveda et al., 2014). Given the recent interest in increasing domestic production of West Coast swordfish and the heightened concern over potential protected species interactions, it is likely that any future PLCA fishery option will need to couple depth with proven gear modifications (i.e., circle hooks) to selectively target catch (Watson et al., 2005; Gilman et al., 2006). Because the use of deep-set techniques within the PLCA have not been fully explored, we feel that this is the next step towards identifying a harvest option for this underutilized region.

Conclusions

This work provides the first steps towards understanding swordfish movements within the U.S. Pacific Leatherback Conservation Area. In the case of the West Coast swordfish fishery, the protection of a critically endangered species has led to the underutilization of a domestic resource, economic loss and an increased reliance on foreign imports (Rausser et al., 2009; Gjertsen et al., 2014). Imported swordfish are primarily harvested by traditional shallow-set longline fisheries that incur higher rates of turtle and shark bycatch (Bartram et al., 2010; Chan and Pan, 2016). In addition to having increased environmental impacts, these imports also result in reduced employment opportunities for domestic fishers and directly affect local market dynamics. The use of proven gear innovations (i.e., circle hooks and bait type) in combination with species specific movement patterns and depth tailoring offer an opportunity for well managed domestic operations to thrive and exploit healthy stocks (Watson et al. 2005). Innovative, science-based harvest methods are key to the revitalization of the West Coast swordfish fisheries. The data collected in this study provides a first step towards identifying low-impact methods that may enable domestic fisheries to resume operations within the PLCA.

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Figure Legends

Figure 1. Map of the North Pacific Ocean with inset of central California coastline to illustrate tag deployment (circle, ○) and pop-off (diamond, ◊) locations for eleven swordfish tagged in the fall of 2012-13 in relation to Pacific Leatherback Conservation Area boundaries and leatherback sea turtle critical habitat.

Figure 2. Depth probability plot summarized over a 24-h period using one hour by 2-m depth bins to illustrate the cumulative probability of occurrence (10*log10) from archived data (n=51,306) for seven swordfish tagged off the coast of central California (35°.6 N / 122°.9W to 37°.4N / 123°.5W). Approximate Pacific Standard times of sunrise and sunset are indicated by vertical dotted lines.

Figure 3. Daytime and nighttime (A.) depth and (B.) temperature distribution by 30-m and 1° C bins from archived data records for 7 swordfish tagged within the Pacific Leatherback Conservation Area (PLCA).

Figure 4. (A.) Percent of the daytime period that seven swordfish spent basking from archived tag records (n=45 days) and (B.) the percent of days in which swordfish basking events occurred from four satellite transmitted tag records (n=206 days) versus days in which no basking activity was observed, plotted against mean daily thermocline depth summarized into 10-m bins.

Figure 5. Frequency distribution of hourly daytime basking activity for 7 swordfish tagged off Central California in the fall of 2012-2013.

Figure 6. Depth plot overlay for three swordfish at liberty over the same 24-h period in October, 2012 (symbols are used to differentiate the three individuals; Δ, ◊, □). The vertical movements show consistent dawn descent and dusk ascent rates and the timing of movements relative to sunrise and sunset.

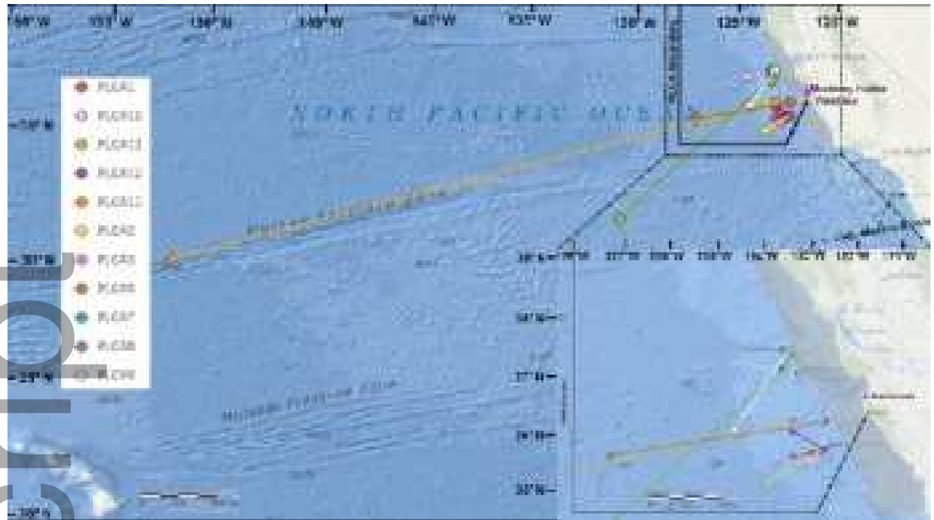
Table 1. Summary of pop-up satellite archival tag (PSATs) deployments within the Pacific Leatherback Conservation Area off the coast of California (2012-2013). PSAT No. with _b indicates tag was recovered and redeployed in 2013. Net displacement, direction, and rate of movement were calculated from taking the straight-line distance between deployment and pop-up locations.

Swordfish No.	**PSAT No.**	**Date deploy**	**Est. size (kg)**	**Deployment location**	**Pop-off location**	**Recovered PSAT**	**Net displacement**	**Direction (Heading)**	**Tag duration**	**Rate of movement**
PLCA1	05A0197	10/4/2012	105	35°38'N/ 122°58'W	35°34'N/123°23'W	Y	38 km	258°	2 days	19.0 km/day
PLCA2	05A0258	10/4/2012	75	35°36'N/122°54'W	35°06N/123°56'W	Y	110 km	240°	3 days	36.7 km/day
PLCA3	05A0217	10/7/2012	118	35°36'N/122°54'W	35°25'N/123°10'W	Y	32 km	231°	2 days	16.0 km/day
PLCA4	12A0138	10/18/2012	91	36°15'N 122°49'W	Did not report	-	-	-		-
PLCA5	12A0102	10/18/2012	114	36°10'N 122°42'W	35°35'N/127°14'W	N	415 km	262°	15 days	27.7 km/day
PLCA6*	A06052	10/18/2012	82	36°12'N/122°43'W	-	-	-	-	-	-
PLCA7	05A0217_b	9/1/2013	148	37°19'N/123°25'W	37°05'N/123°40'W	Y	37 km	217°	2 days	18.5 km/day
PLCA8	05A0258_b	9/1/2013	171	37°21'N/123°25'W	37°24'N/123°37'W	Y	18 km	289°	2 days	9.0 km/day
PLCA9	05A0313	9/2/2013	81	37°23'N/123°28'W	36°02'N/124°38'W	N	180 km	216°	20 days	10.8 km/day
PLCA10	12A0136	9/3/2013	109	37°02'N/123°38'W	37°11'N/124°48'W	Y	108 km	280°	20 days	5.4 km/day
PLCA11	11A0712	9/3/2013	100	37°01'N/123°38'W	31°38'N/130°52'W	N	955 km	233°	25 days	38.2 km/day
PLCA12	05A0197_b	10/6/2013	90	35°41'N/122°45'W	36°00'N/123°25'W	Y	69 km	300°	10 days	6.9 km/day
PLCA13	11A0716	10/16/2013	100	36°11'N/123°24'W	29°59'N/152°12'W	N	2827 km	255°	150 days	18.8 km/day

* PSAT pin broke upon deployment, deployed Cefas archival tag only.

Table 2. Data summaries for five swordfish that travelled offshore more than 100 km after being tagged within the PLCA. Depth and temperature statistics for the first (onshore) and last week (offshore) of the tracks are provided including the average maximum depth, day and night, the minimum daytime temperature, the daytime modal depth and the % time near the surface.

Swordfish No.	PSAT No.	Date deploy	Tag duration	Km/day	Day max (m) on/off	Night max (m) on/off	Day min (°C) on/off	Day mode (m) on/off	Percent time near surface (<5 m)
PLCA5	12A0102	10/18/12	15 days	27.7	282/367	24/42	8.8/7.2	250-300/ 350-400	19/1
PLCA9	05A0313	9/2/13	20 days	10.8	206/205	16/24	10.6/10.5	300-350/ 300-350	35/34
PLCA10	05A0313	9/3/13	20 days	5.4	231/244	19/28	10.0/10.0	300-350/ 250-300	30/16
PLCA11	11A0712	9/3/13	25 days	38.2	363/412	99/120	6.5/6.4	300-350/ 400-500	10/0
PLCA13	11A0716	10/16/13	150 days	18.8	390/571	50/60	6.5/5.3	300-350/ 400-500	12/0



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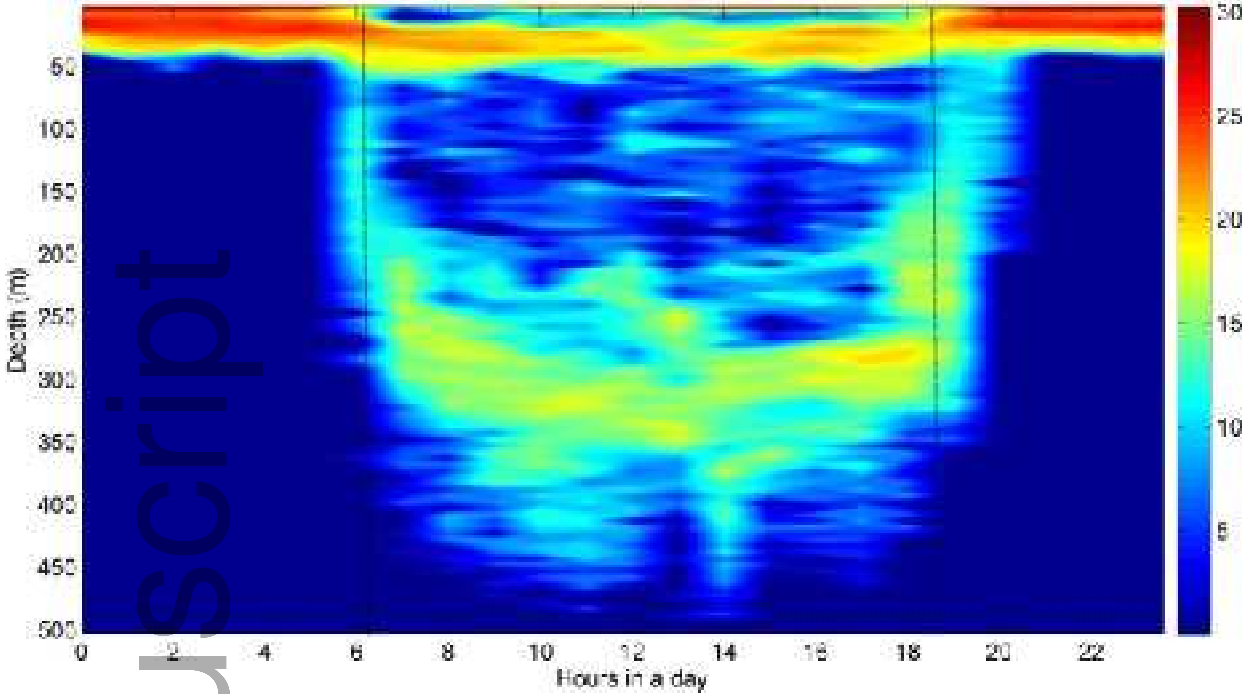

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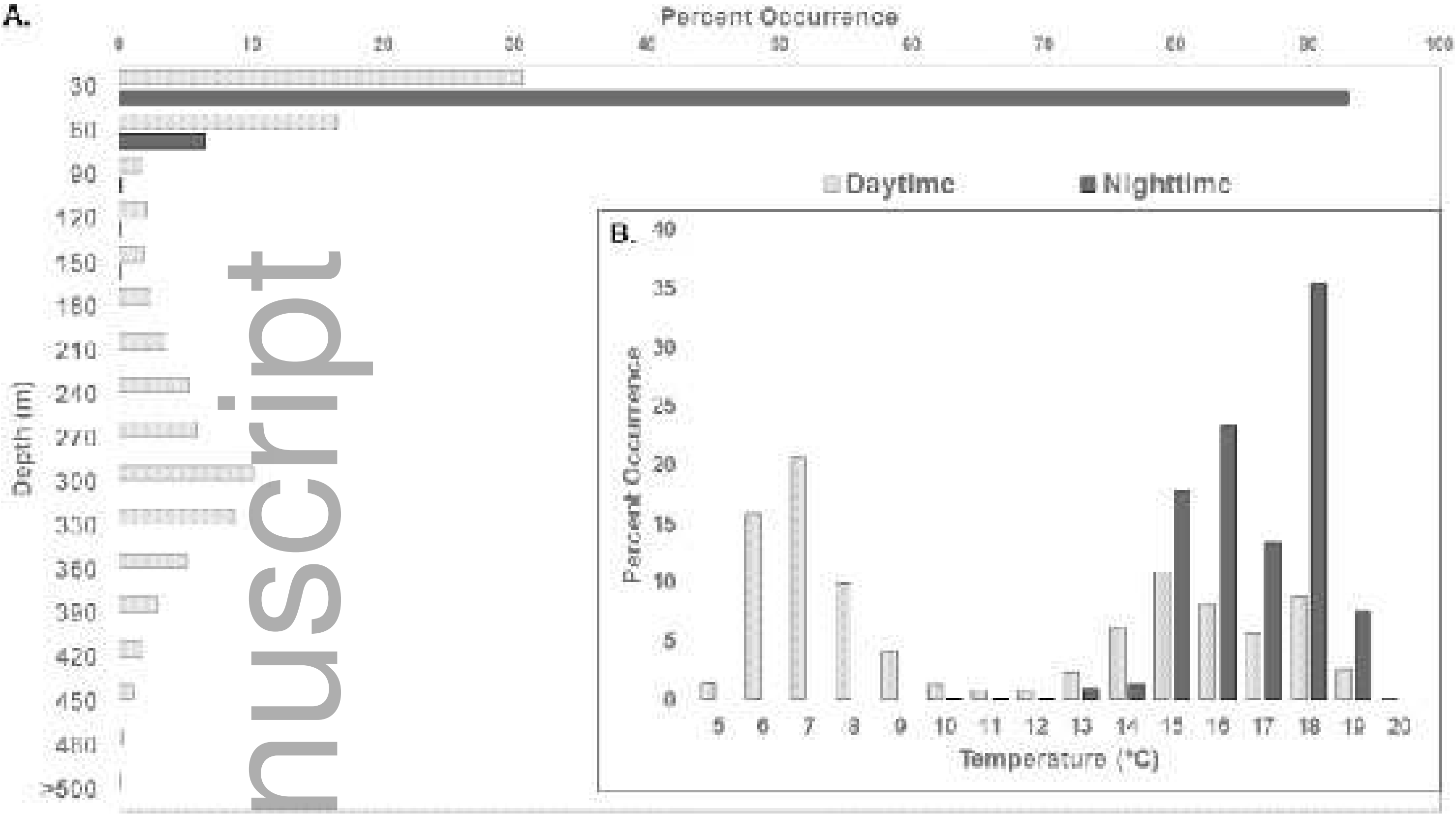

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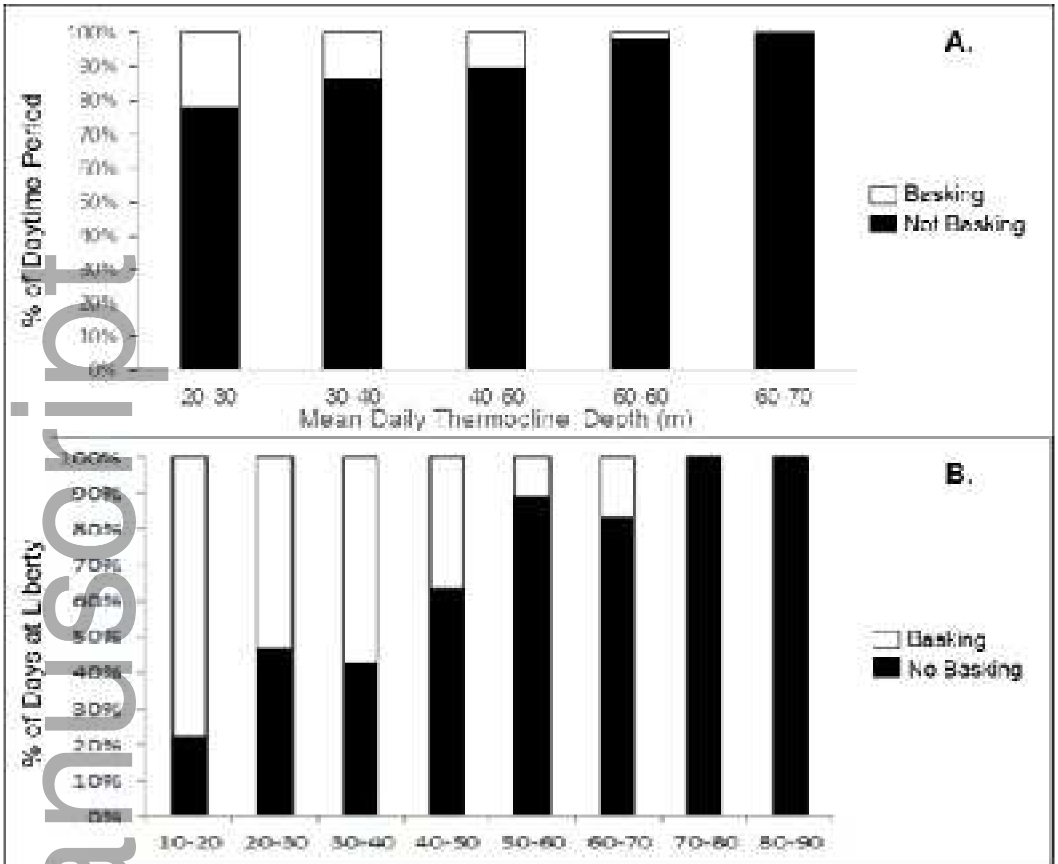

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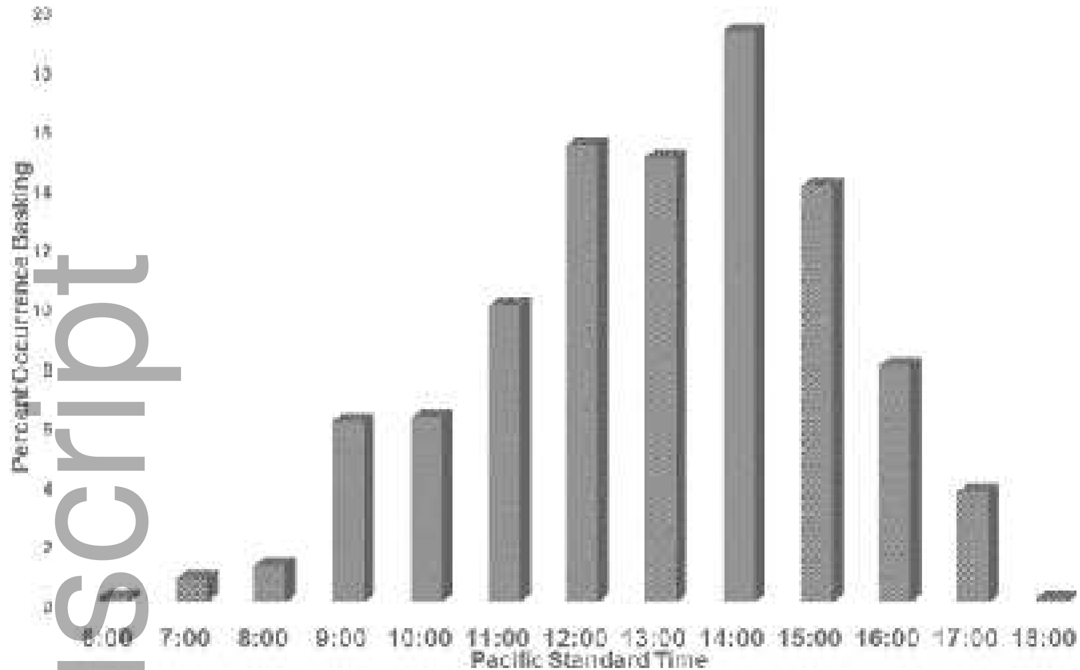

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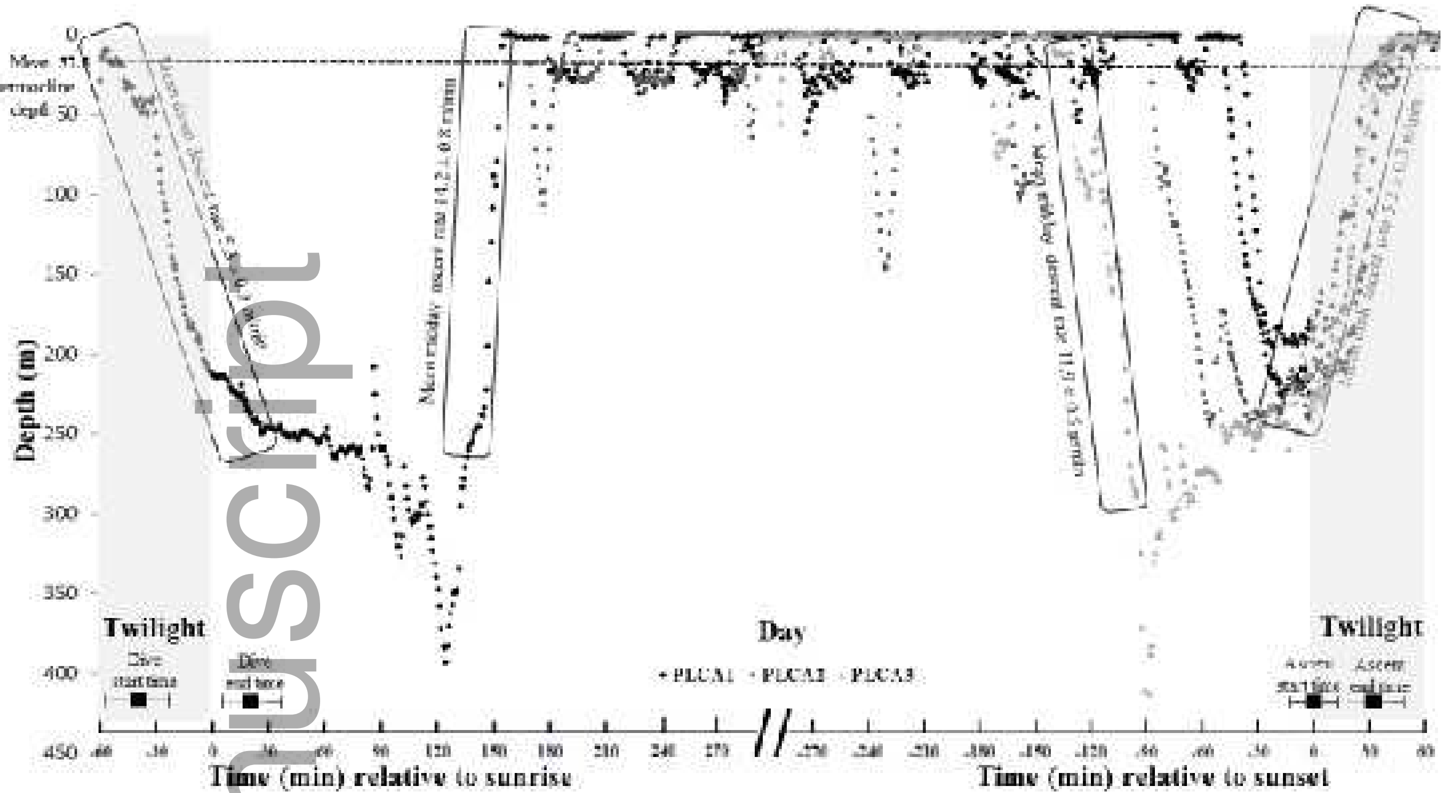

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