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Bigeye thresher shark *Alopias superciliosus* movements and post-release survivorship following capture on linked buoy gear

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ABSTRACT

Off the US west coast, fishery development efforts have led to the recent recommendation for authorization of deep-set buoy gear (DSBG) and linked buoy gear (LBG), two commercial gear types for targeting swordfish at depth during the day. Because the new deep-set configurations interact with bigeye thresher sharks (*Alopias superciliosus*), a large pelagic species that is not typically retained for sale, this work has focused on documenting the fate of released catch. Bigeye thresher sharks (BETS) were captured and outfitted with pop-up satellite archival tags (Wildlife Computers sPATs and miniPATs) to assess movement trends and acute (30-d) post-release survival during exempted fishing trials authorized by National Marine Fisheries Service (NMFS) and the Pacific Fisheries Management Council (PFMC). Post-release survivorship was based on 14 BETS (~157−230 cm L_F) caught on LBG between August 2016 and December 2019 following fight times ranging from 17−300 min. Thirteen BETS survived the acute effects of capture, and one immediate mortality was documented following heavy entanglement in the monofilament leader. BETS were resilient to the acute effects of handling stress following capture on LBG, with an observed post-release survival rate of 93 %. Surviving BETS exhibited consistent diurnal dive patterns with sharks remaining well below the thermocline during the daytime (mean = 386 ± 62 m) and within the mixed layer at night (mean = 65 ± 25 m). With the exception of one tag that reported within close proximity of the SCB tagging location, BETS exhibited extensive southward movements (mean = 1235 ± 235 km) towards a potentially relevant migratory corridor for large pelagic sharks.

1. Introduction

Recent fishery development work off the U.S. West Coast has resulted in the recommendation for authorization of a deep-set fishery for swordfish that primarily operates within the Southern California Bight (SCB)[1] . The soon-to-be-authorized fishery will allow for the use of two gear configurations, deep-set buoy gear (DSBG) and linked-buoy gear (LBG), designs that were developed to reduce spacial overlap with protected species by positioning up to 30 baited hooks below the thermocline during the daytime (Sepulveda et al., 2015; Sepulveda and Aalbers, 2018b).

Similar catch composition has been reported between the two configurations following both research and exempted trials, with catch predominantly consisting of swordfish (*Xiphias gladius;* >75 %) and bigeye thresher sharks (*Alopias supercilliosus*; <12 %). Although occasionally retained for sale, the vast majority (~90 %) of bigeye thresher sharks (BETS) are released or discarded due to a limited market demand (Walsh et al., 2009; Sepulveda et al., 2019b). Given the need to better document the impact of a new deep-set fishery on the BETS resource, an initial study was conducted to quantify the post-release survival of BETS following capture on DSBG (Sepulveda et al., 2019b). Findings revealed a low post-release mortality rate, with ~90 % of BETS surviving the acute effects of capture.

Despite many functional similarities in the design of LBG and DSBG (i.e. target depth, number of baited hooks, strike-indicator buoy system), LBG incorporates a heavy weighting system and extended horizontal mainline that may further restrict vertical and horizontal movement of catch while on the line (Fig. 1). Given that BETS are obligate ram ventilators and LBG hook depths occur near the oxygen minimum zone (OMZ; Levin, 2003), restricting movement has the potential to impact post-release survival. Further, because the horizontal footprint of LBG may be up to 5 nm, increased catch processing times have the potential

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[1] PFMC Gear Authorization (p. 7−8) https://www.pcouncil.org/documents/2019/10/september-2019-decision-document.pdf (accessed 4/9/2020).

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to impact survival.

Considering the high vulnerability of BETS to over exploitation (Gruber and Compagno, 1981; Chen et al., 1997; Smith et al., 2008; Amorim et al., 2009) and the additional source of catch and effort likely to occur under the new California deep-set fishery, this work focused on assessing post-release fate of BETS following capture on LBG. Movement data for this poorly studied species were also used to characterize depth and temperature distribution and better assess how ongoing fishing operations may be tailored to further reduce future BETS interaction rates.

2. Methods

2.1. Location, permitting and data collection

Tag deployments were focused within the SCB from Santa Cruz Island (33.92, -119.63) to Oceanside, CA (33.24, -117.68) between August 2016 and December 2019 (Table 1; Fig. 2). Tagging activities were performed during LBG research trials conducted under a NOAA letter of authorization (LOA) as well as exempted fishing activities (EFP) sanctioned by the PFMC and NOAA West Coast Regional office (WCR). All cooperative fishers were trained on tagging and release protocols and had participated in previous survivorship studies (Sepulveda et al., 2019b). Handling time, hook position, and BETS size, condition and sex were noted prior to release. When accurate fork length (L_F) could not be measured, BETS size (kg) was estimated alongside the tagging vessel and converted to L_F values (Kohler et al., 1996).

2.2. Linked buoy gear configuration

LBG design was consistent across research and cooperative vessels, with all sets measured and constructed by the research team prior to deployment. Gear characteristics strictly followed EFP mandates outlined in the PIER-LBG EFP terms and conditions. Briefly, pre-measured sections of 3.2 mm monofilament mainline were deployed from a mini-28 longline reel coupled with a hydraulic line shooter (Lindgren-Pitman, Pompano Beach, Florida, USA). Daytime deployments occurred between sunrise and sunset comprising up to 10 serviceable sections with three gangions suspended at depths of 250−450 m between two 3.6 kg weights. LBG sets consisted of up to thirty 18/0 non-offset circle hooks (Mustad model 39960D) baited with jumbo squid (*Illex spp*.), mackerel (*Scomber japonicus*) or Pacific saury (*Cololabis saira*) on 8−10 m monofilament gangions (2.5 mm) affixed with illumination (power light; Fig. 1). Each section had two sets of strike indicator buoys that were used to signal when something was on the line (Sepulveda et al., 2019b). Similar to DSBG, a strike was determined when all three strike indicator buoys were either floating at the surface or when more than one buoy was submerged. Upon visual detection of a strike, specific sections were individually serviced using a hydraulic line puller (Custom Sea gear; Odessa, FL USA) and subsequently re-set. Strike time, haul-back duration, fight time and depth of capture were all determined from time-depth recorders that were affixed to each gangion (Cefas Technology Limited; Lowestoft, UK).

2.3. Survivorship estimates

Upon capture, BETS were outfitted with either a satellite-linked miniPAT (n = 4) or survivorship pop-up archival tag (sPAT; n = 9; Wildlife Computers; Redmond, Washington, USA) rigged with a monofilament leader and plastic umbrella dart (Sepulveda et al., 2019b). Tags were positioned in the dorsal musculature proximal to the base of the dorsal fin with a hand-held tagging stick. In addition to transmitting Argos positions and daily summary data (min/max depth & temperature and change in relative light level) to infer survival (Hutchinson et al., 2015), 2nd generation sPATs incorporated proprietary software to also transmit depth records (10-min resolution) over the final five days of tracks. MiniPATs additionally transmitted 5-min resolution depth, temperature, relative light level and daily summary data for the entire 30-d track. Survivorship was assessed from depth and temperature records following protocols previously used to infer mortality (Horodysky

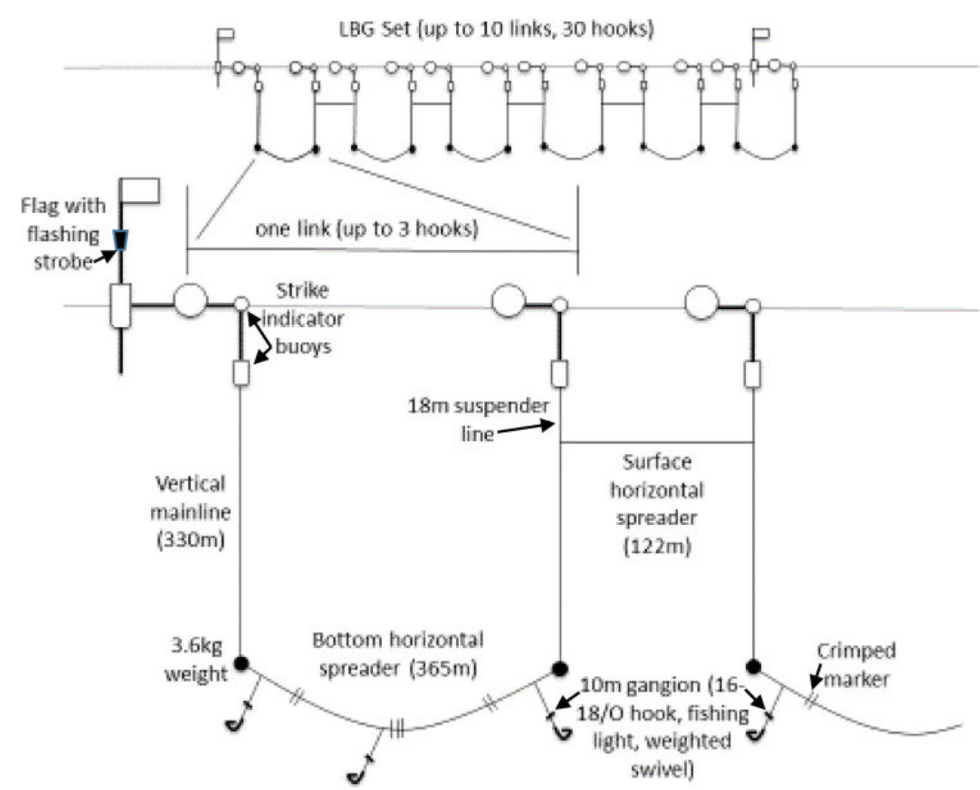

Fig. 1. Depiction of linked buoy gear (LBG) configuration developed by authors to target California swordfish at depth during the daytime.

Table 1
Satellite tag deployment and pop-up specifics for thirteen bigeye thresher sharks released following capture on linked buoy gear off the coast of southern California.

PSAT Type	PTT #	Date Deploy	Deploy Lat Long	Pop-up Date	Pop-up Lat Long	Distance (km)	ROM (km/day)	Heading (° true)	Est. L_F (cm)	Mortality
MiniPAT	164533	8/25/16	33.10 -117.77	9/25/16	22.30 -122.46	1286	41.5	203	213	No
MiniPAT	164539	8/29/16	33.31 -117.96	9/29/16	23.68 -122.72	1167	37.6	205	191	No
sPAT	171543	7/10/17	33.08 -117.48	8/10/17	22.55 -126.38	1460	47.1	219	194	No
sPAT	171540	8/8/17	33.47 -117.83	9/7/17	26.94 -118.86	733	23.6	188	226	No
sPAT	171544	8/8/17	33.48 -117.85	9/7/17	22.86 -125.45	1394	45.0	214	187	No
MiniPAT	164535	8/29/17	33.89 -119.59	9/28/17	24.90 -116.45	1045	34.8	162	168	No
MiniPAT	164534	8/30/17	33.91 -119.62	9/29/17	24.19 -120.27	1083	36.1	184	177	No
sPAT	172424	8/24/18	33.27 -117.76	9/24/18	25.11 -127.53	1311	42.3	228	220	No
sPAT	171563	11/28/18	33.17 -117.55	12/29/18	33.11 -117.37	18	0.6	45	157	No
sPAT	171545	11/28/18	33.19 -117.56	12/29/18	22.57 -127.37	1523	49.1	221	189	No
sPAT	172421	11/28/18	33.16 -117.54	12/28/18	23.01 -125.12	1351	45.0	216	181	No
sPAT	172423	8/20/19	33.23 -117.82	9/21/19	25.00 -124.63	1167	36.4	217	230	No
sPAT	171556	12/5/19	33.14 -117.66	1/5/20	22.74 -124.70	1460	43.4	213	200	No

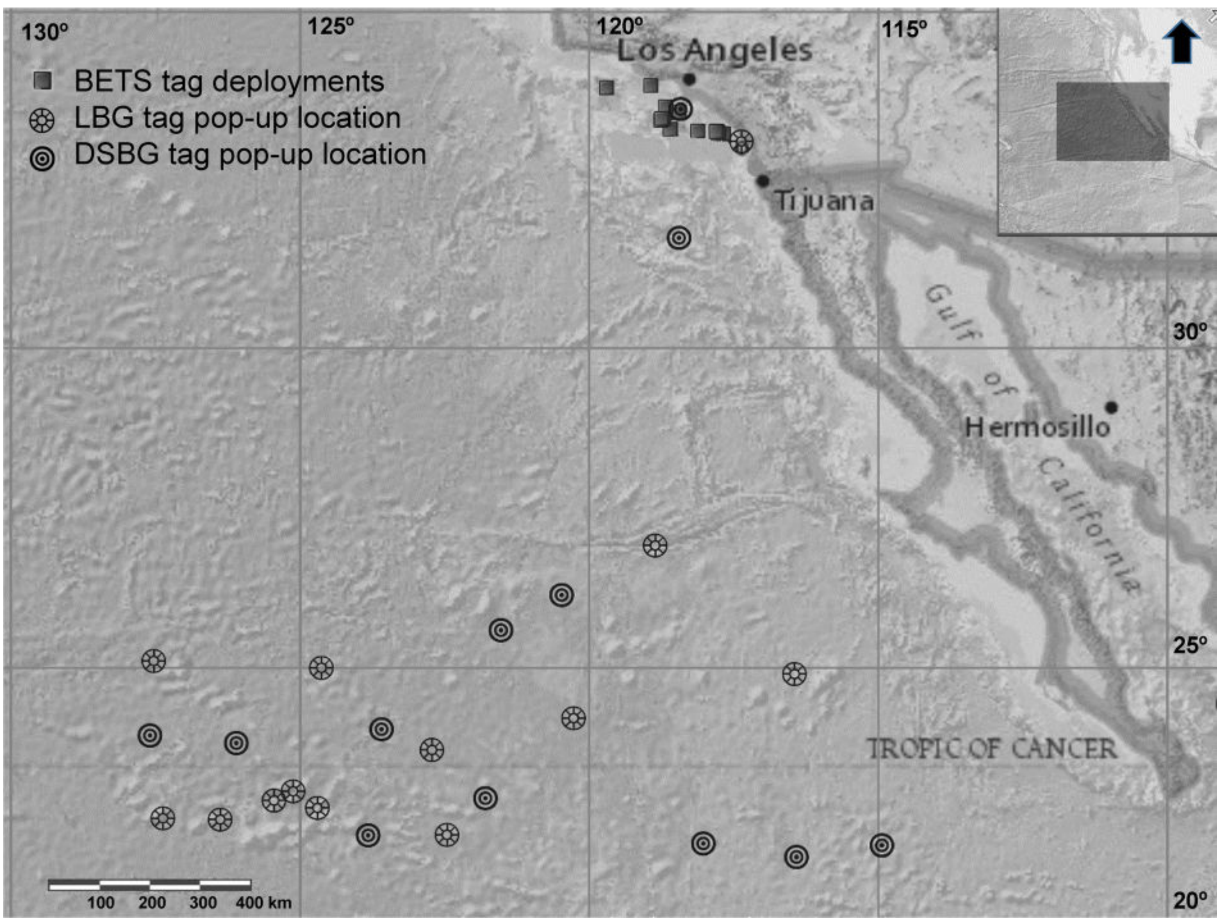

Fig. 2. Map of the North Pacific Ocean illustrating tag deployment and 30-d pop-up locations for bigeye thresher sharks (*Alopias superciliosus*) that survived following capture and release on **(a.)** linked buoy gear (this study; n = 13) and **(b.)** deep-set buoy gear (Sepulveda et al., 2019b; n = 12) from 2016–2019.

and Graves, 2005; Heberer et al., 2010), while relative light level data was used to confirm that tagged sharks had not been preyed upon during the deployment (Goldsmith et al., 2017; Sepulveda et al., 2019b).

2.4. Data analyses

Because consistent vertical movements during twilight hours impeded the use of light curves to effectively estimate specific geolocations; net displacement, direction and rate of horizontal movement were measured based on tag deployment and pop-up locations (Musyl et al., 2011; Sepulveda et al., 2018a). Transmitted time series data were converted to Pacific Standard Time and categorized into day, night, and twilight periods based on the time of sunrise/sunset and nautical twilight for specified tag deployment or pop-up locations (Sepulveda et al., 2018a). Vertical rate of movement (VROM) was calculated as the difference in the minimum and maximum depth values during each morning descent and evening ascent divided by the duration of twilight periods for miniPAT time series data (5-min resolution).

To assess regional differences in BETS depth distribution between the southern California Bight (SCB) tagging area and offshore pop-up locations along Baja California Sur (BCS), transmitted time series data (5-min resolution) from four miniPAT deployments were split into an initial 5-d period (Days 2–6) for comparison with the final 5-d period (Days 26–30). The first day of time series data were omitted to avoid initial disparities in BETS dive patterns resulting from potential capture and handling stress (Heberer et al., 2010). Paired t-tests were used to test for differences in depth distribution across regions and diel periods. Mean and standard deviation (SD) values were presented with significance inferred at <0.05.

2.5. Additional analyses

Additional regional assessments were based on transmitted depth data from this study (n = 13) combined with comparable sPAT and miniPAT data from BETS tagged during previous DSBG survivorship work (n = 12; Sepulveda et al., 2019b). All transmitted depth records were standardized to 10-min resolution and parsed by time of day (day vs night) as well as by region (SCB vs BCS) to generate comparative plots and summary statistics.

BETS depth data during periods of SCB occupancy were also plotted and compared against depth data from six swordfish that were at liberty during the same time frame within the SCB to assess potential differences in daytime habitat utilization between the two species. Interspecific comparisons incorporated time-series data recovered from data storage tags affixed to the six swordfish (Cefas G-5 DSTs) that were recaptured within the SCB between September 2016 and December 2019.

Physical recovery of one sPAT (#171563) off southern California allowed time-series data (1-s resolution) from the entire deployment to be downloaded for assessment of fine-scale movements and thermocline depth. Sea-surface temperatures (SST) and mixed layer depth estimates were generated from summaries of transmitted daily data.

3. Results

3.1. Survivorship

Survival rate was estimated from a total of 14 bigeye thresher sharks (157−230 cm L_F) that were captured on 90 LBG sets (737 LBG sections; 2211 baited hooks) soaked over 646 h from August 25, 2016 through December 5, 2019. Fight times ranged from 17 to 300 min (mean = 64 + 77 min; Table 1) with haul-back times (included in overall fight time) ranging from 8 to 30 min (mean = 13.5 ± 4.5 min). Time depth recorders revealed a mean capture depth of 304 ± 20 m (range = 265−327 m) on LBG sets within the SCB tagging area. Most BETS captured during this study were hooked in the mouth (n = 10) with the exception of three foul-hooked sharks (pectoral-fin hooked) and one deeply-hooked individual.

One of the fourteen BETS captured on LBG incurred mortality following a 50-min fight time. The single mortality arrived at the vessel severely entangled in monofilament, with the tightly wrapped gangion constricting the anterior portion of the shark (i.e. mouth, eyes and gill slits) (Fig. 3). An sPAT was initially implanted alongside the tagging vessel; however, prior to release it was apparent that the shark was experiencing rigor mortis. An immediate mortality event was recorded and no sPAT was deployed after verifying a lack of active swimming or physical response upon contact with the nose and eyes.

Transmitted depth, temperature and light level records from the 30-d deployments were used to validate survival of the remaining 13 BETS captured and released from LBG. All sPATs popped up on schedule and transmitted complete 30-d data summaries and 5-d time series records, while miniPATs transmitted full summary data of which 85–88 % of 30-d time series data was successfully decoded. One of the sPATs (BETS #171563) that popped up within the SCB tagging area was physically recovered when it washed ashore along San Onofre, California and 1-s time series data were downloaded for the entire 30-d track.

3.2. Vertical movements

Bigeye thresher sharks remained significantly deeper (paired *t*-test $t = 24.5$, $P < 0.0001$) throughout the daytime (mean=386±62 m) than at night (mean=65±25 m), with increased rates of vertical movement during twilight periods. Typical diel movement patterns entailed BETS diving to depths exceeding 200 m during the morning twilight period, where sharks remained throughout the daytime before ascending into the mixed layer after sunset (Fig. 4a). For 12 of the BETS tracks, more

Fig. 3. Bigeye thresher shark recorded as an immediate mortality resulting from severe entanglement in monofilament gangion following capture on linked buoy gear (LBG).

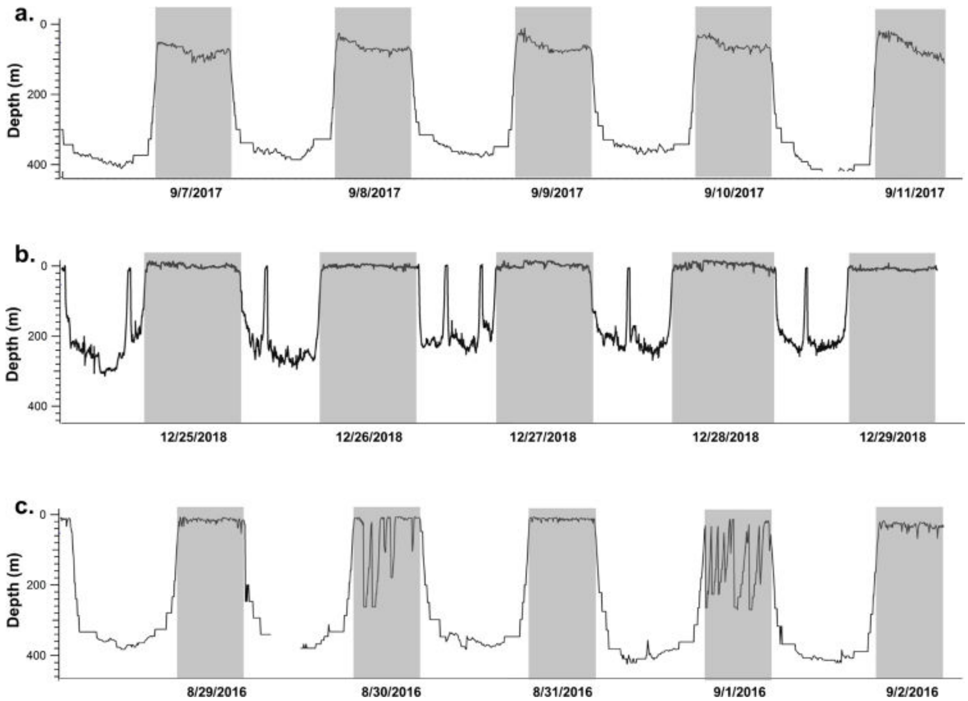

Fig. 4. Five-day time series of depth plots showing **(a.)** typical diel movement patterns exhibited by most tagged bigeye thresher sharks (e.g. BETS #164535) occurring at depths <200 m throughout the daytime and >100 m during the night, **(b.)** shallower daytime depth distribution unique to BETS #171563 during a 5-d period of occupancy within the southern California Bight (SCB) in December 2018 and **(c.)** deeper nighttime dives exhibited to depths of nearly 300 m by BETS #164533 along the coast of Baja California Sur (BCS). Shaded areas represent nighttime periods.

than 99 % of daytime depth records ranged from 200 to 500 m (mean = 398 ± 45 m). However, the smallest tagged individual (BETS #171563; 157 cm L_F) exhibited a considerably shallower daytime depth distribution (mean = 238 ± 61 m; range = 1−370 m) off southern California during December 2018. BETS #171563 spent 21 % of the day at depths >200 m and exhibited intermittent midday ascents towards the surface (Fig. 4b). Although these daytime ascents into the mixed layer were relatively brief in duration (<90 min), surface-oriented movements occurred on 24 (77 %) of the 31 days in the track record, with multiple midday ascents on three dates.

BETS predominantly remained within the upper mixed layer throughout the night, with mean nighttime depth distributions ranging from 22−103 m among individuals (n = 13). While 84 % of nighttime depth records were <100 m, BETS #164533 and 164534 exhibited repetitive bounce dives to depths of nearly 300 m on several nights (Fig. 4c). Although the deepest single nighttime dives were outside of the full moon phase, the greatest mean nighttime depths (mean = 78−116 m; n = 4) all occurred during full moon phases. However, there was no apparent relationship between mean daytime depth and lunar phase for any of the miniPAT tagged individuals.

Overall, BETS exhibited consistent timing of both morning descents and evening ascents. Morning descents from the mixed layer to the waters below the thermocline were consistently initiated around nautical twilight, with BETS reaching a mean depth of 281 ± 38 m by the time of local sunrise (mean VROM = 4.2 ± 0.9 m/min). Vertical ascents into the upper mixed layer were initiated around local sunset, with a mean VROM of 4.6 ± 0.8 m/min.

Increases in mean daytime depth, nighttime depth, SST and mixed layer depth occurred between the SCB tagging area (Fig. 5a) and offshore BCS pop-up locations (Figs. 5, 6). Daytime depths within the SCB tagging area (mean = 339.0 ± 34.9 m) increased significantly (paired *t*-test $t = 2.96$, $P = 0.0296$) to a mean daytime depth of 404.5 ± 67.2 m during the final 5-d period off BCS (Fig. 6). Similarly, mean nighttime depth increased from 34.8 ± 17.5 m during the initial 5-d period to 51.6 ± 21.9 m during the final five days of miniPAT tracks (Fig. 6). In addition, estimated sea-surface temperature (SST) and mixed layer depth increased from a mean value of 20.1 ± 1.1 °C to 23.6 ± 0.6 °C and from 20 to 48 m, respectively between SCB and BCS regions. Inter-specific depth comparisons suggested that BETS remained slightly deeper than swordfish both during the daytime (339.0 ± 34.9 m vs. 322.9 ± 39.4 m) and at night (34.8 ± 17.5 m vs. 14.3 ± 7.5 m) within the SCB (Fig. 7).

3.3. Temperature

Temperature at depth reached a minimum of 4.6 °C on the single deepest dive to a daytime depth of 1013 m by BETS #164535. Otherwise, minimum daily temperature ranged from 6.1 to 10.3 °C, corresponding to maximum daily depth values that ranged from 262 to 521 m. A significant difference (paired *t*-test $t = 24.1$, $P < 0.0001$) in the mean daytime (7.9 ± 0.9°C) and nighttime (19.3 ± 3.0°C) temperature was evident. Sea-surface temperature ranged from 17.2 to 23.1°C at SCB tag deployment sites and from 21.0 to 25.3°C at pop-up locations within the lower latitudes off BCS. Ninety-nine percent of SST's were greater than 17°C.

3.4. Horizontal movements

BETS #171563 was the only tag that popped up within the SCB, just 17 km from its deployment location. The remaining twelve satellite-based tags transmitted 375−1,350 km off the coast of BCS, between 22−27 °N latitude and 118−128 °W longitude (Fig. 2). Mean displacement for these twelve BETS was 1235 ± 235 km (range = 733−1,523 km) over the 30-d period at liberty. Tags popped-up to the S-SW (162−228° true heading) of deployment location with a mean horizontal ROM of 40.2 ± 7.0 km day^{-1} (range = 23−49 km day^{-1}).

4. Discussion

This study offers insight into the post-release fate, movements and habitat utilization of a poorly known species that is routinely caught in a novel deep-set fishery for swordfish. The high rate of survivorship observed on both LBG and DSBG (Sepulveda et al., 2019b) suggests that BETS are remarkably resilient to capture stress and that overall fishing mortality rates in the new fishery may be considered low. Distinct vertical profiles were consistent with reports from previous bigeye thresher

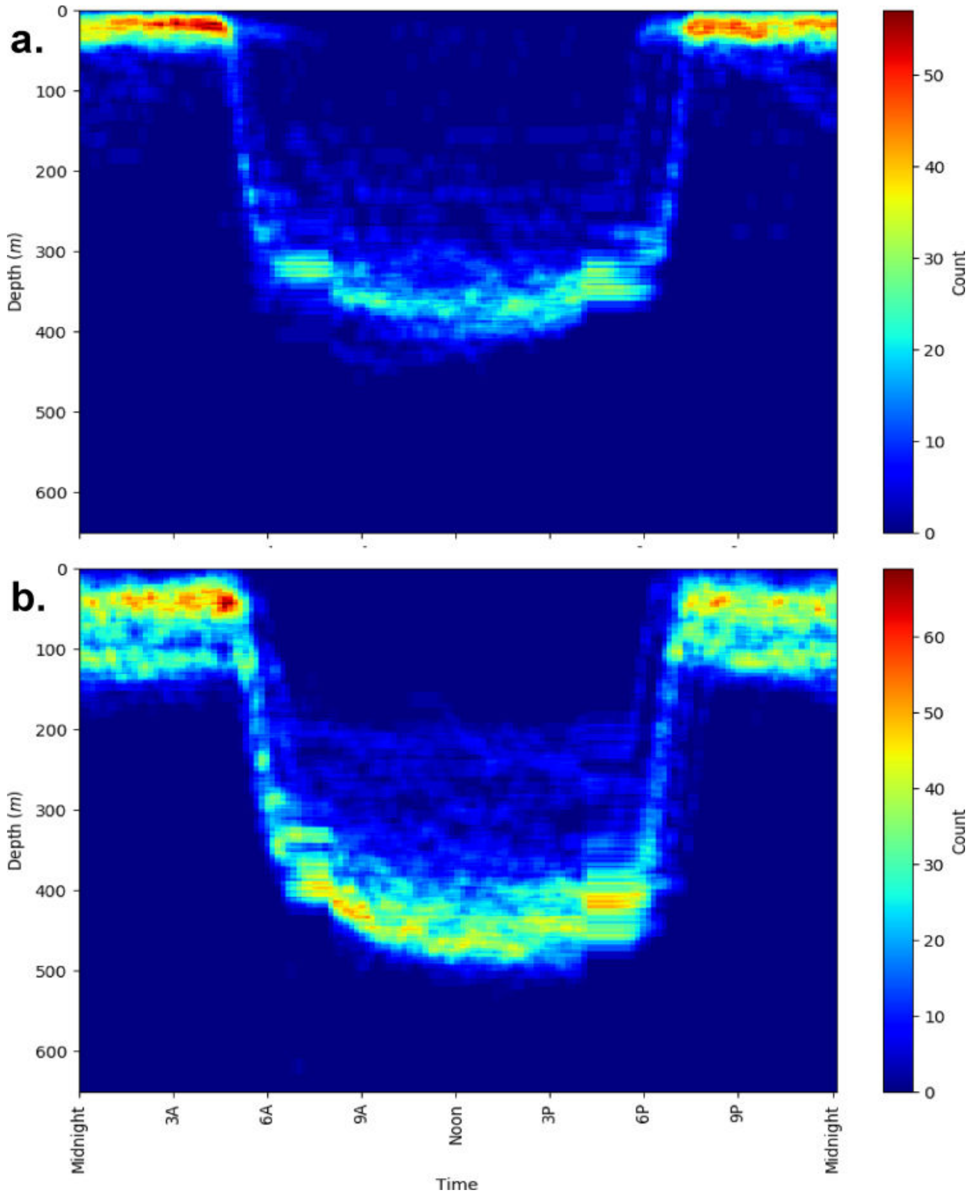

Fig. 5. Diurnal depth probability plots constructed for tagged bigeye thresher sharks **(a.)** during periods of occupancy within the southern California Bight (SCB) and **(b.)** during the 5-day period prior to tags popping up off the coast of Baja California Sur (BCS) between 22 and 27 degrees North latitude and 118 to 128 degrees West longitude.

shark tagging studies and closely overlap with swordfish diel movement patterns within the SCB. Extensive horizontal movements off the coast of BCS validate the highly migratory nature of this shared pelagic resource and offer insights into a common migratory pathway in the eastern north Pacific.

4.1. Survivorship

After fight times up to 300 min, all but one (93 %) of the BETS caught and released from LBG survived the acute effects of capture. Immediate mortality observed for a single individual was likely the result of impaired forward movement and reduced potential for ram ventilation following severe entanglement in monofilament. The observed 7% mortality rate on LBG was similar to post-release mortality estimates for BETS that were caught and released on DSBG (8–14 %), both of which are considered low (Muoneke and Childress, 1994; Sepulveda et al., 2019b). Although long-term survival and fitness cannot be fully assessed from short-term tagging studies, it has been suggested that monitoring fish movements and survival for 30 d may be sufficient to document most capture-induced mortality events (Muoneke and Childress, 1994; Moyes et al., 2006).

Despite the low dissolved oxygen levels at LBG capture depths, post-release mortality rates in this study were considerably lower than the reported 25 % BETS mortality rate following capture on shallow-set longline gear (Musyl et al., 2011), where capture depths were <100 m and soak time averaged 15 h. Based on fishery observer estimates derived from Hawaii-based longline operations, higher immediate mortality rates were reported for BETS captured on both shallow-set (22.6 %) and deep-set (16.5 %) longline gear from 2004 to 2006 (Walsh et al., 2009; Musyl et al., 2011). Immediate mortality rates on pelagic longline gear (observed at the point of release) were further extrapolated to minimum mortality estimates of 31.6 % for shallow-set and 24.1 % for deep-set operations, with minimum mortality rates approaching 50 % for both Hawaiian longline fisheries during periods when shark finning was more prevalent in U.S. waters (Walsh et al., 2009). In the Atlantic, Coelho et al. (2012) reported an immediate

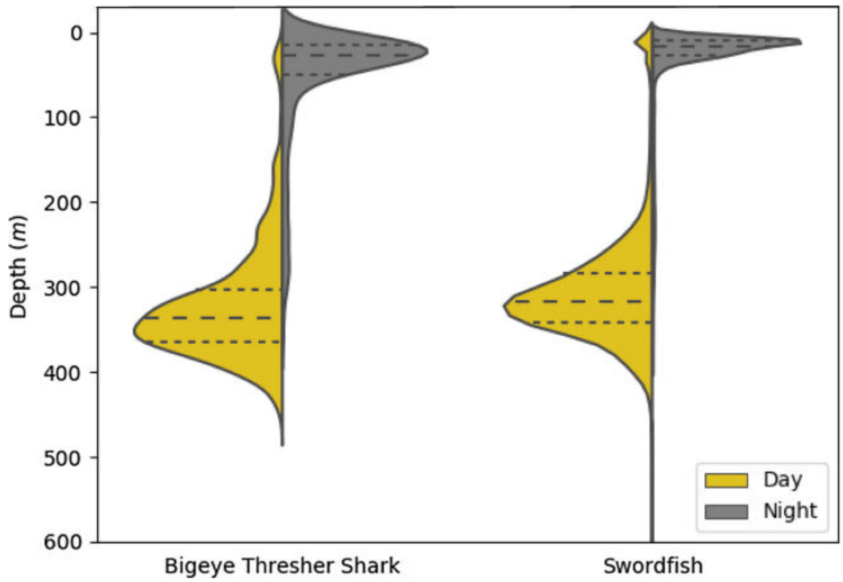

Fig. 6. Kernel density estimation of day (yellow area) and nighttime (gray area) depth distribution probability with mean (± 1 SD; dashed lines) for tagged bigeye thresher sharks during 5-d periods of residence within both **(a.)** the southern California Bight (SCB) and **(b.)** offshore regions along Baja California Sur (BCS) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

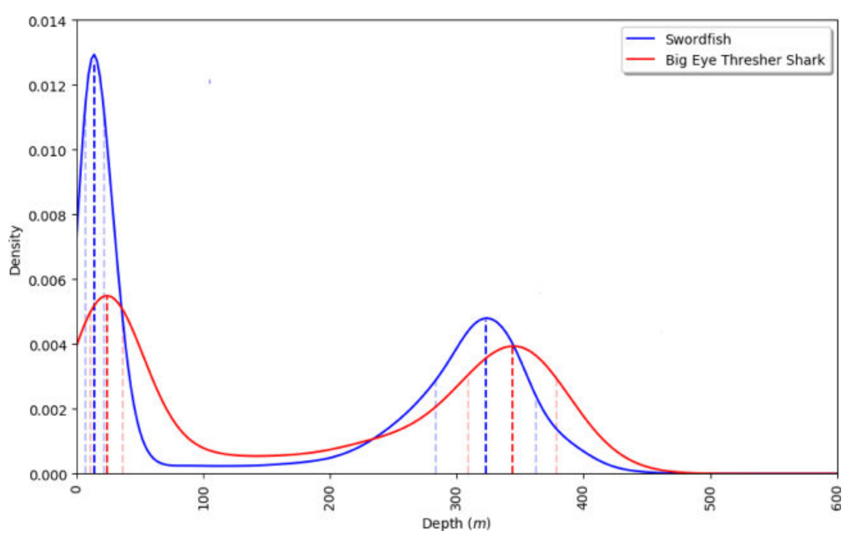

Fig. 7. Kernal density plot comparing depth profiles of swordfish (n = 6) and bigeye thresher sharks (n = 9) during periods of residency within the southern California Bight (SCB). Dashed lines represent mean ± 1 SD.

mortality rate of more than 50 % for BETS captured in a shallow-set swordfish longline fishery.

It has been suggested that shorter soak times could significantly reduce post-release mortality rates in longline fisheries (Diaz and Serafy, 2005; Carruthers et al., 2009), considering the cumulative physiological effects of capture stress, injury and oxygen deprivation (Musyl et al., 2011). The capacity to actively tend LBG and readily service individual sections upon detection of a strike can effectively reduce the amount of time on the line and may be a primary factor for the reduced post-release mortality rate observed in this study.

LBG was developed specifically for the U.S. west coast as a low-impact alternative to surface oriented fisheries that have historically seen high rates of bycatch and entanglements (Hanan et al., 1993; Ward et al., 2000; Carretta et al., 2004). Several key bycatch mitigation features, including strike detection, depth segregation, rapid descent rates and a taught mainline were incorporated into the deep-set gear design to reduce the rate of unintended interactions and discard mortalities. Strike detection serves as a visual indication as to when and where something is on the line, a design feature that enables both rapid servicing of target catch and the live release of bycatch. The use of heavy weights facilitates segregation from target and non-target species, while rapidly descending hooks to target depth and maintaining a taught mainline.

The use of circle hooks has been reported to enhance post-release survivorship of various marine species (Aalbers et al., 2004; Carruthers et al., 2009; Musyl et al., 2011) and is currently mandated in several U.S. pelagic longline fisheries, as well as in the new California deep-set fishery (Federal Register, 2004, 2019). Considering the low incidence of deeply hooked individuals recorded both in this study (7%) and by Sepulveda et al. (2019b; 0%), the mandated use of non-offset circle hooks may reduce the potential for hook damage to BETS in the new deep-set fishery. Although the hook was not visible when sPAT #172423 was deployed on a large (230 cm L_F) female that was recorded as deeply hooked, movement patterns were similar to other BETS and there was no indication of impaired behavior from hook damage.

Similarly, there were no apparent differences in the depth profiles of the three foul-hooked BETS tagged in this study. A relatively high incidence of foul-hooked BETS caught in longline fisheries has been attributed to the use of the caudal fin to initially strike baited hooks, leading to hooks becoming embedded in the enlarged upper lobe of the caudal or pectoral fins (Stillwell and Casey, 1976; Gruber and Compagno, 1981; Nakano et al., 2003; Aalbers et al., 2010). Although hooking location has been shown to be a primary factor influencing post-release survival rates in many species (Muoneke and Childress, 1994; Heberer et al., 2010), there was no indication of reduced survival from hook damage for deeply or foul-hooked BETS in this study.

4.2. Vertical movements

Regular diurnal movement patterns were resumed by all BETS within 24 h of release and were consistent with those of previous BETS tagging studies (Nakano et al., 2003; Weng and Block, 2004; Musyl et al., 2011; Sepulveda et al., 2019b). Both Nakano et al. (2003) and Musyl et al. (2011) also reported comparable daytime depths centered between 200 and 500 m, with nighttime depths predominantly around 80–130 m. Two BETS tracks within the Gulf of Mexico and around the Hawaiian Islands also showed similar depth (modal daytime depth ~300−500 m; 80 % of night <100 m) and temperature trends (6−12 °C during the day and 20−26 °C at night; Weng and Block, 2004), despite vast differences in bathymetry and oceanography from the eastern north Pacific area investigated in this study. Distinct vertical movement patterns were consistent with diel migrations of organisms associated with the deep scattering layer (DSL) and suggest that BETS may be capable of exploiting high-biomass aggregations of prey throughout the day, night and twilight periods (Cade and Benoit-Bird, 2015; Benoit-Bird et al., 2017; Sepulveda et al., 2018a, b). Stomach contents sampled from BETS collected within the SCB verified the presence of taxa associated with the DSL, including Pacific hake (*Merluccius productus*), barracudinas (*Paralepididae spp.*), lancetfishes (*Alepisaurus spp.)* and various species of cephalopods (Stillwell and Casey, 1976; Gruber and Compagno, 1981; Preti et al., 2008). Significant increases in nighttime depths around the full moon observed by four BETS tracks in this study are consistent with vertical movement behaviors of DSL organisms and other pelagic predators in response to lunar illumination (Musyl et al., 2003, 2011; Benoit-Bird et al., 2009; Orbesen et al., 2017).

4.3. Comparative movements

Based on tagging data from this study (n = 13) in combination with depth records from twelve BETS tagged within the SCB following catch and release on DSBG (Sepulveda et al., 2019b), both day and nighttime depth distribution were considerably greater around offshore pop-up locations when compared to inshore depth profiles. Mean daytime depth was 309 ± 59 m for BETS (n = 8) that remained inside of the 120° longitude line compared to a five-day mean depth of 414 ± 28 m for BETS carrying tags that popped up outside of 120 °W (n = 17). Increased depth distribution has also been reported for swordfish between nearshore tagging locations and offshore pop-up areas along the California coast (Sepulveda et al., 2018a), and may be attributed to regional differences in the OMZ and mixed layer depths (Cairns and LaFond, 1966; Bograd et al., 2008). A relatively shallow oxygen minimum layer has been identified off the coast of southern California (Bograd et al., 2008; Booth et al., 2014; Netburn and Koslow, 2015), thus both BETS and swordfish exhibited daytime depths that were extended into the upper reaches of the OMZ. A reduced and relatively consistent depth distribution within the SCB for both swordfish and BETS has enhanced the effectiveness of deep-set gear designs, while similar approaches may not be as successful further offshore.

BETS predominantly remained at depths exceeding 200 m throughout the daytime, with the exception of BETS #171563, which exhibited intermittent surface-oriented movements during the daytime while off southern California in December 2018 (Fig. 4a,b). The surface-oriented activity exhibited in this track had not previously been documented during the daytime for BETS, although similar behavior has been observed for swordfish tagged along the California coast (Sepulveda et al., 2010, 2018a). Archived depth records from six swordfish recaptured within the SCB tagging area similarly revealed that the majority of the daytime hours were spent below 200 m, with intermittent vertical ascents towards the surface throughout the day. Surface-oriented basking behavior occurred during approximately 8% of the daytime hours for swordfish tagged within the SCB from 2003 to 2006 (Sepulveda et al., 2010). It has been suggested that behavioral thermoregulation drives daytime swordfish excursions towards the surface following heavy foraging at depth (Sepulveda et al., 2010). It may be possible that localized or seasonal shifts in OMZ depth could also influence daytime depth distribution or the occurrence of rapid vertical ascents. Seasonal shifts in depth distribution may be in response to vertical movements of prey or changes in oceanographic conditions within the SCB during the late fall and winter months, with similar reductions in depth distribution observed in swordfish that remain within the SCB throughout the winter months (PIER unpublished data). As the smallest individual tagged during this study (157 cm FL), BETS #171563 was likely immature based on size of maturity estimates reported by Chen et al. (1997) and may have resided within the SCB during the winter months rather than undertaking an extensive breeding migration.

Overall, BETS day and nighttime depth profiles within the SCB were slightly deeper than those reported for swordfish, a species that has received considerable study within the SCB (Sepulveda et al., 2010; Dewar et al., 2011; Sepulveda et al., 2019a). Individual mean daytime depths ranged from 306 ± 30 m to 367 ± 35 m for BETS tagged within the SCB tagging area, with an overall mean depth of 339 ± 35 m. Because BETS occur deeper on average than the target hook depth for both DSBG and LBG, BETS catch rates as currently observed in the new deep-set fishery may already be reduced under existing gear configurations. Shoaling target hook depths may further reduce the rate of BETS interactions in LBG and DSBG fisheries, however; BETS are visual predators that possess enlarged eyes specialized for low-light vision and focused upwards to effectively silhouette prey species from below. Therefore, BETS may be attracted to gear from a considerable distance, particularly considering the use of a light source to illuminate baited hooks. Additional gear trials designed to test different hook depths and bait types throughout the season may be valuable towards evaluating their effect on catch rates and composition.

4.4. Horizontal movements

Directed movements of BETS towards a relatively confined region off Baja California points to a common migratory pathway and suggests a strong regional affinity to this series of bathymetric features and seamounts off of the Mexican coastline. Given the rapid and consistent southward movements from 22 BETS tagged between this study and Sepulveda et al. (2019b), we propose that this offshore corridor may be an area of considerable biological importance for large pelagic sharks of the Eastern North Pacific. Rapid departures from the SCB tagging area may have initially been in response to the stress of capture, however consistent rates and direction of horizontal movements suggest the presence of a relevant migratory pathway. Interestingly, two BETS tagged off the Hawaiian Islands in 2002−04 travelled more than 3000 km to this same region while at liberty for 180–240 d before PSATS popped up approximately 1,600−1,900 km off the coast of BCS, between 16.5 and 20 N latitude and 125–130 W longitude (Musyl et al., 2011). Given that very little information is available on the life history of this species, the offshore region along BCS may be important for mating or pupping activity. It may also be the case that this region of the eastern north Pacific is an important foraging zone with a prolific DSL, particularly considering that similar migratory routes have been documented for white sharks (*Carcharodon carcharias*) tagged off of California (Domeier and Nasby-Lucas, 2008; Jorgensen et al., 2009).

4.5. Fishery implications

Although most elasmobranchs caught in Mexican fisheries are retained for the sale of shark meat and fins, BETS catches off California are primarily discarded from fisheries that target swordfish and other highly migratory species (Hanan et al., 1993; Sepulveda et al., 2019b). Considering the high retention rates of elasmobranchs in the longline fishery off Mexico and high discard mortality rates of U.S.-based longline and DGN fisheries (Holts et al., 1998; Coelho et al., 2012), these collective interactions likely comprise the majority of BETS fishing mortality in the ENP. Given the low discard mortality rates estimated for both LBG and DSBG (Sepulveda et al., 2019b) along with the <20 % retention rates estimated from exempted fishery trials since 2015, the new deep-set fishery likely comprises a minor component of the total BETS fishing mortality for the ENP.

4.6. Conclusion

Collective findings on the fate of BETS following capture on both LBG and DSBG may better inform discussions related to HMS management and permitting criteria for the developing deep-set fishery along California. Results can also be extended to better inform seafood ranking programs towards a more accurate evaluation of the developing deep-set fishery, which has the potential to positively impact domestic swordfish markets and stimulate ex-vessel values under a sustainable classification. Additional gear trials designed to evaluate catch composition at various capture depths will assist in validating regional and interspecific differences documented with electronic tagging studies to better optimize catch and further reduce bycatch rates in the developing daytime deep-set fishery.

CRediT authorship contribution statement

Scott A. Aalbers: Writing - original draft, Investigation, Formal analysis, Data curation. **Michael Wang:** Validation, Methodology, Writing - review & editing. **Charles Villafana:** Project administration, Resources. **Chugey A. Sepulveda:** Funding acquisition, Conceptualization, Visualization, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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