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Insights into the horizontal movements, migration patterns, and stock affiliation of California swordfish

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Abstract

This study reports on the horizontal movements of swordfish (*Xiphias gladius* L.) tagged during deep-set fishery trials off the California coastline. Position estimates from several electronic tag types were used to better understand swordfish stock structure and regional affiliation with current boundary hypotheses used to manage swordfish in the eastern north Pacific. Swordfish were outfitted with (a) satellite-linked mark–recapture tags ($n = 66$), (b) electronic data storage tags that were recaptured ($n = 16$), (c) fin-mounted Argos transmitters ($n = 6$), and (d) satellite-linked archival tags ($n = 4$). Twenty-six percent of tagged swordfish reported close to (<225 km) their deployment location within the southern California Bight (SCB). Of the 50 swordfish that moved outside the SCB, 76% exhibited affiliation to the Eastern Pacific Ocean (EPO) management unit, 20% moved into the Western and Central North Pacific (WCNP) and 4% spent time within both the EPO and WCNP boundaries. Mean displacement between deployment and reporting locations was 1,250 ± 1,375 km, with daily rates of movement up to 55 km/day. Seasonal migrations ranged from the equator (0.8°N.132.4°W) to the Hawaiian Islands (17.0°N/154.2°W), with multiple individuals returning to the initial tagging locations the subsequent season. Seasonal site fidelity exhibited by several individuals highlights the importance of the SCB foraging grounds. While no evidence of trans-equatorial or trans-Pacific crossing was documented, extensive movements validate the highly migratory nature of California swordfish and support the need for future inclusion of spatial distribution data in management. Findings suggest that SCB swordfish may exhibit a higher level of EPO connectivity than previously proposed.

KEYWORDS

California, fishery, Pacific, population dynamics, stock, swordfish, tagging

1 | INTRODUCTION

The swordfish is a large, fast-growing pelagic species that supports lucrative fisheries around the globe (Demartini, Uchiyama, Humphreys, Sampaga, & Williams, 2007; Ward, Porter, & Elscot, 2000). Swordfish are highly migratory in nature and capable of extensive horizontal movements between tropical spawning areas and rich foraging grounds within the higher latitudes (~50°N to 50°S; Hinton, Bayliff, & Suter, 2005). Exploitation occurs over much of this range, with the bulk of commercial production in the Pacific Ocean coming from shallow-set longline operations that occur both along the continental margins as well as on the high seas (Hinton et al., 2005; ISC, 2014; Ward et al., 2000).

Although monotypic, past work has shown swordfish distribution and population structure to be complex, with structure evident across and within ocean basins (Alvarado Bremer, Hinton, & Greig, 2006; Reeb, Arcangeli, & Block, 2003; Smith et al., 2015). As shown in the Atlantic, swordfish in the Pacific have been proposed to segregate, with several different hypotheses proposed on the delineation and distribution of the different management units (Alvarado Bremer et al., 2006; Brodziak & Ishimura, 2009; Hinton et al., 2005; Lu, Smith, Hinton, & Alvarado Bremer, 2016; Reeb et al., 2003; Sosa-Nishizaki & Shimizu, 1991).

Based on recent assessments, swordfish in the eastern north Pacific are managed as two independent stocks that vary with respect to productivity, size, and current exploitation status (ISC, 2014, 2018). The larger of the two management units is the Western and Central North Pacific stock (WCNP), a management unit that is under the oversight of the International Scientific Committee, Billfish Working Group. Currently, the WCNP stock is proposed to be the larger and healthier of the two north Pacific management units, with recent assessments proposing fishing mortality and total removals to be at a sustainable level (Brodziak & Ishimura, 2010; ISC, 2014, 2018). In contrast, the Eastern Pacific Ocean stock (EPO) is proposed to be a smaller management unit that is managed by the Inter-American Tropical Tuna Commission (IATTC) and regional fishery management organizations [i.e., Pacific Fisheries Management Council (PFMC)]. Recent assessment of the EPO stock has proposed declining trends and that the stock was subject to overfishing (ISC, 2014).[1]

Although some degree of mixing has been suggested (reviewed by Hinton et al., 2005), the boundary currently used to delineate between the two eastern north Pacific stocks is considered to be based on the best available science derived from both historic longline operations and biological reference points (ISC, 2014). Although informative, swordfish spatial distribution and movement studies within this region have not been used to differentiate or inform on population structure. This is largely because of the lack of adequate movement data for incorporation into spatial analyses and the difficulty associated with incorporating tagging studies into assessment models (Goethel, Quinn, & Cadrin, 2011; Sippel et al., 2014).

Within the eastern north Pacific, several tagging studies have documented swordfish movements and depth distribution (Abecassis, Dewar, Hawn, & Polovina, 2012; Carey & Robison, 1981; Dewar et al., 2011; Sepulveda & Aalbers, 2018; Sepulveda, Knight, Nasby-Lucas, & Domeier, 2010). Despite advancements in electronic tag and geolocation technology, deep-diving behaviors and short tag retention times have made swordfish migration patterns difficult to quantify. Collectively, most of the available information on horizontal movements is from short-term tracks (1–6 months) that radiate out from southern California to the south and west with the onset of winter conditions (Abecassis et al., 2012; Dewar et al., 2011).

Although limited, these previous studies have shown that swordfish tagged off Southern California often enter into and spend significant time within the EPO stock boundary (Abecassis et al., 2012; Dewar et al., 2011; Sepulveda et al., 2010). These past studies also support the hypothesis that mature swordfish feed along the temperate latitudes of the west coast during the summer and fall months and return to the tropics to spawn during the winter and early spring (DeMartini, Uchiyama, & Williams, 2000; Hinton et al., 2005; Sosa-Nishizaki & Shimizu, 1991). Despite the continued reliance upon the eastern Pacific swordfish stocks by domestic and international fleets, annual migration patterns and seasonal movements of swordfish in this region continue to be poorly understood.

To better understand the horizontal movements of swordfish off the California coast, this study integrated multiple electronic tag technologies and deployed them on swordfish caught during deep-set gear development trials (Sepulveda & Aalbers, 2018; Sepulveda, Heberer, & Aalbers, 2014). The horizontal movements and annual migration patterns are also compared to existing management unit boundaries for the region.

2 | MATERIALS AND METHODS

2.1 | Tagging locations and protocols

All swordfish were tagged aboard the *R/V* Malolo during experimental fishing trials to test deep-set gear configurations designed for selectively targeting west coast swordfish within the SCB (Sepulveda & Aalbers, 2018; Sepulveda et al., 2014). Gear configurations, rigging, and set protocols were standardized to align with the terms and conditions outlined in the PIER deep-set buoy gear (DSBG) and linked-buoy gear (LBG) exempted fishing permits (EFPs) for highly migratory species (HMS) issued through the NOAA West Coast Regional Office and approved by the Pacific Fishery Management Council (PFMC). All capture and handling procedures followed guidelines of the Pfleger Institute of Environmental Research Ethics Protocol # 151.168.14-21 and California Department of Fish and Wildlife Scientific Collection permit no. SC-2471.

Swordfish were caught, tagged, and released using both DSBG and LBG configurations in accordance with EFP and published DSBG gear protocols. As described in detail in Sepulveda et al. (2014) and Sepulveda and Aalbers (2018), each vertical mainline was suspended from three inline floats including a 20-kg non-compressible buoy and associated surface and subsurface strike indicator floats. Surface buoys were actively monitored by the research vessel and immediately hauled with a hydraulic line puller (Custom Sea gear) upon visual detection of a strike (either when more than one buoy was submerged or all three surface buoys were floating). Set and tag deployment locations were centered around areas of productivity and thermal convergence (i.e., chlorophyll concentration and sea surface temperature) within

[1]http://www.pcouncil.org/wp-content/uploads/2015/08/G1a_NMFS_Rpt2_Stelle_to_Lowman_SEPT2015BB.pdf

the eastern portion of the SCB between Point Conception and the Mexico border, as well as off the coast of central California between the Farallon Islands and the Davidson Seamount (Figure 1a–c).

2.2 | Tag specifications and attachments

Multiple electronic tag types incorporating a variety of technologies, sampling parameters, and attachment techniques were employed to generate datasets and estimate swordfish horizontal movements off the California coast (Table 1). The type and number of tags deployed on each swordfish was based on various factors including fish size, tag availability, fish condition, hook position, and time of year. Cefas G5 data storage tags (DST; Cefas Ltd.), capable of logging fine-scale (60-s) depth and temperature records, have been consistently deployed on swordfish captured during the gear testing trials (n = 151; from 2011 to June of 2018). This study reports on the horizontal position reported by swordfish captains, observer records, and logbook entries for only those DST's that were recaptured prior to the end of this study (n = 16). Three different types of Wildlife Computers satellite tags (Wildlife Computers WC; Redmond, Washington, USA) were deployed to estimate position through the Argos satellite network (Table 1). Satellite-linked tag types included Wildlife Computers Mark-Report tags (mrPAT, n = 66), pop-up satellite archival tags (PSAT, [Mk-10 and miniPAT, n = 4]), and smart position or temperature Argos transmitters (SPOT-258A and SPOT-258F, n = 6). The two PSAT tag types used in this study (Mk-10 and miniPAT) were programmed for shorter duration (<30 days) deployments focused on physiological questions (Stoehr, St. Martin, Aalbers, Sepulveda, & Bernal, 2017); however, tag pop-up positions were also incorporated into this study.

Two generations of mrPAT's were used in the study, the first iteration was deployed in 2016–2017 and was slightly smaller than the second-generation models (13 × 3 cm) deployed during 2017–2018. The second-generation mrPAT's incorporated several improvements, including increased buoyancy, a fixed antennae, and a premature-release detection feature for enhanced data quality and reporting rates. Swordfish were either outfitted with a single mrPAT programmed for a 90–180 day deployment or with duplicate mrPAT's with different pop-up schedules (90–240 days) to document movements over the course of the season. Deployment schedule was determined so that the anticipated pop-off date would align with the period in which the fish are no longer within the SCB (i.e., proposed spawning season, March–July; DeMartini et al., 2000; Hinton et al., 2005). Fin-mounted SPOT-258 transmitters were programmed for up to 200 transmissions per day at either 45-s (n = 1) or 15-s (n = 5) intervals. Transmissions were set to be delivered upon activation of the wet–dry sensor when the dorsal fin was exposed to air during a basking event.

All mrPAT, PSAT, and Cefas G5 DSTs 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). In the event that swordfish could not be restrained alongside the vessel, tags were deployed using an extended pole affixed with a single (Figure 2a) or three-pronged applicator tip to facilitate simultaneous implantation (Figure 2b). To better achieve optimal tag placement, most of the swordfish captured in this study were tagged while restrained alongside the tagging vessel using a hand-held tagging stick (~40 cm; Figure 2c). In 2017–2018, a modified bill snooter was used to better control the fish and limit movement during tag application. Tag positioning was centered upon the base of the dorsal fin at an approximate 45° angle to the body midline. All applications attempted to traverse the dorsal fin pterygiophores and cross the dorsal midline. Electronic tags were also opportunistically deployed on surface basking swordfish encountered during the study period (n = 4) using a modified tagging harpoon from an extended bow pulpit as described by Sepulveda et al., (2010).

Argos transmitters (SPOT tags) were mounted to the primary spines of the dorsal fin. Transmitters were positioned along the anterior edge and above the base of the fin to ensure that the wet–dry sensor was exposed to air during basking events (Figure 3b). A water-resistant cordless drill and 3/16" drill bit was used to perforate fin spines and plastic cable ties or nylon bolts and stainless hardware were used to anchor the tag in place (Figure 3a). All excess material was removed before release.

Following tag application, swordfish were measured and fin clips were taken for genomic studies prior to hook removal and subsequent release. For unrestrained individuals, fish size and condition were estimated and hook location was recorded prior to release using an extended line cutter which was used to sever the monofilament leader adjacent to the hook.

2.3 | Data analysis

Data transmissions were received via the Argos satellite system and processed through the Argos CLS system platform and Wildlife Computers web portal. For PSATs and mrPATs, transmitted data summaries and pop-up locations were downloaded to determine if tags reported on schedule and for examination of daily data summaries. Changes in min–max daily temperatures were verified to determine if values were consistent with the daily vertical migration patterns of swordfish and to confirm that tags remained affixed throughout the deployment. Overall displacement, horizontal rate of movement (ROM), and heading calculations were based on initial release and pop-up locations. Geolocation was not estimated from transmitted light level and sea surface temperature data due to the limited number of PSAT's deployed, their limited deployment duration and the lack of adequate illumination at depth (Dewar et al., 2011). For double-tagged individuals (mrPAT), net displacement and heading values were calculated for both pop-up locations. Duplicate mrPAT deployments with matching regional affinities were used for displacement analyses while all location data were used for assessing regional affinity.

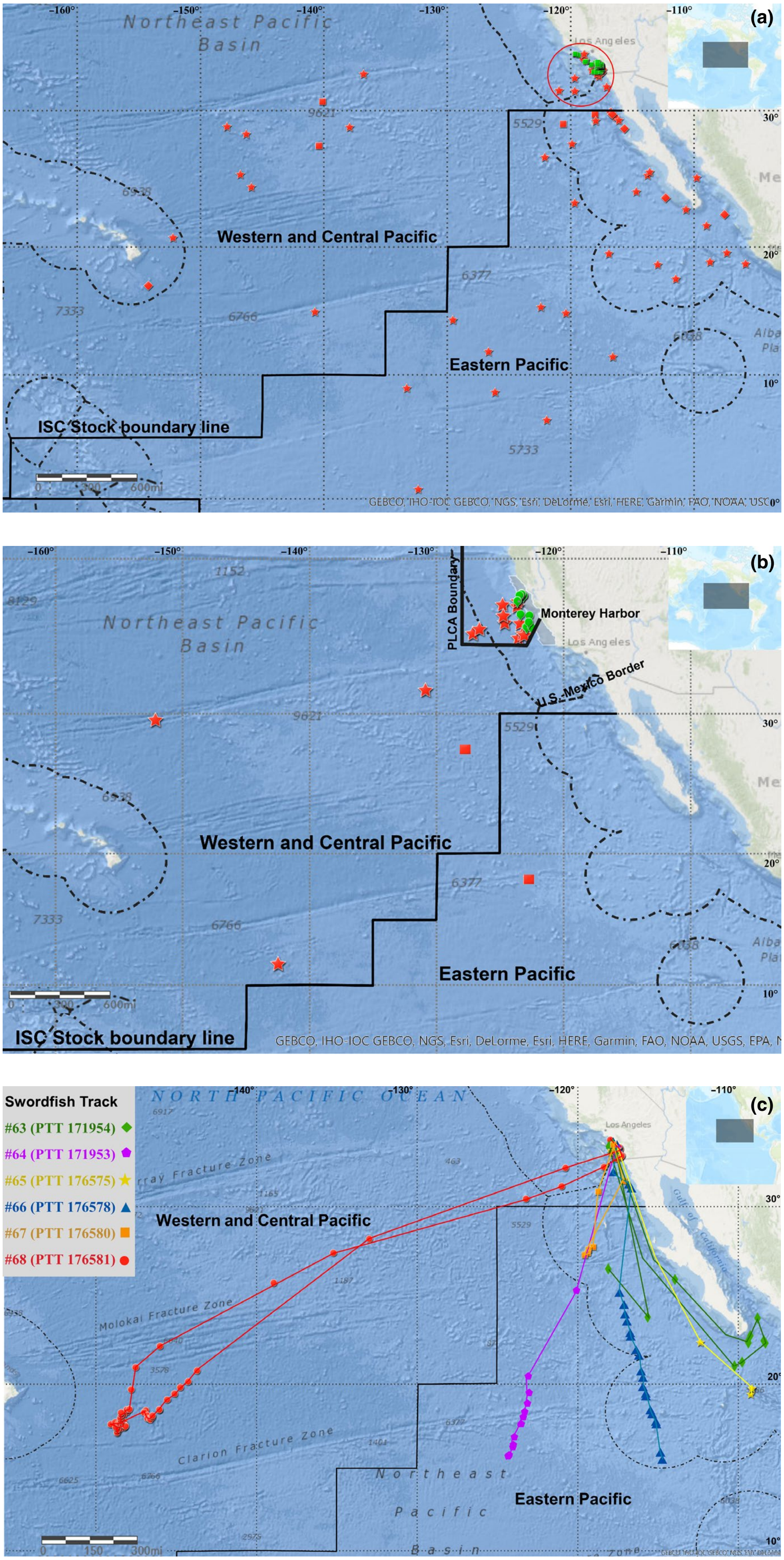

FIGURE 1 (a) Electronic tag deployment and reporting locations for 62 swordfish released within the Southern California Bight (green square = electronic tag deployments). Reporting locations are plotted relative to current ISC stock boundary designations in the North Pacific Ocean (red star = mrPAT reporting locations; red square = mrPATs with both EPO and WCNP reporting locations; red diamond = DST recovery; broken line represents exclusive economic zone boundaries). (b) Tag deployment and reporting locations for swordfish tagged in this study (n = 3) and in the fall of 2012–2013 (Sepulveda et al., 2018; n = 11) off central California within the Pacific Leatherback Conservation Area (PLCA) plotted in relation to current ISC and PLCA boundaries (green circles = electronic tag deployments; red stars = WCNP reporting locations; red squares = swordfish with both WCNP and EPO reporting locations; grey shaded area = leatherback sea turtle critical habitat. (c) Estimated track lines of six swordfish (#63–68) affixed with fin-mounted Argos transmitters tagged within the Southern California Bight in 2017–2018, relative to current ISC stock boundary designations

TABLE 1 Description of electronic tag types used to document swordfish movements (9/2012 to 6/2018)

Tag model	Tag type	Attachment method	Anchor attachment	Data products
Cefas G5 DST	Data storage tag (DST)	Intramuscular	Nylon umbrella dart	Depth & temperature time series and reported recovery location[a]
WC mrPAT	Satellite-linked	Intramuscular	Nylon umbrella dart	Transmitted pop-up position & daily min-max temperature/tilt
WC SPOT (258A and 258F)	Argos transmitter	Dorsal fin mount	Nylon bolts & cable ties	Transmitted position estimates upon basking
WC PSAT (MINIPAT & MK-10)	Satellite-linked archival tag	Intramuscular	Nylon umbrella dart	Transmitted pop-up position and summarized depth & temperature profiles

[a]Data storage tags require recapture for reported position and data download.

For SPOT tags, consecutive transmissions received in a single Argos satellite pass were used to estimate swordfish position. Processed data containing valid position information were ranked by quality based on location class (LC = 3, 2, 1, 0, A, B, with 3 being the most accurate location estimate, B being the least) and plotted in ARCGIS Pro (ESRI) for further spatial analysis. The distance between each valid daily position estimate was calculated, with preference given to the highest quality LC, prior to summing all values to evaluate total displacement distance and horizontal ROM for each track. Because multiple messages need to be received during a single Argos satellite pass in order for a location to be calculated based on the transmission Doppler shift, the vast majority of transmissions did not generate valid geolocation estimates. To reduce potential error associated with geolocation estimates, only platforms with at least five location estimates were incorporated into movement analyses (n = 6). Despite continued transmission of SPOT tags (i.e., transmissions continued to be received from five swordfish as of this publication, 11/2019), this study only reports on position estimates up until the arbitrary data collection cutoff date of June 30, 2019. Further analyses of swordfish movements relative to oceanic conditions (i.e., bathymetry, sea surface temperature, chlorophyll concentration) as well as depth and temperature distribution are slated for incorporation into future analyses and publications.

Rates and direction of horizontal movement were calculated for each track to estimate annual migration routes relative to the ISC stock boundaries for eastern north Pacific swordfish (ISC, 2014). All values are indicated as mean ± 1 SD and $\alpha < 0.05$ was used to infer significance. Satellite-derived data were analyzed independently from archived depth and temperature records, which were not reported in this study. Fin clips from all tagged individuals were stored and archived to assess genetic differentiation of fish with known migrations and stock affiliation in a subsequent study.

3 | RESULTS

3.1 | Deployment duration and performance

Position estimates were consolidated from a suite of 92 electronic tags (66 mrPATs, 6 SPOT tags, 4 PSATs, and 16 DSTs) deployed on 71 individual swordfish off the California coast between September 2012, and December 2018 (Table 2). PSAT deployment durations ranged from 5 to 30 days; whereas mrPAT deployments ranged from 90 to 240 days (mean = 106 ± 29 days). Although SPOT tags continued to actively transmit over the study duration, data are presented up to June 30, 2019, the arbitrary cutoff date for inclusion in this study. Six SPOT tags collectively provided 293 position estimates from 1,522 Argos transmissions received during the study period (Table 3). The number of position estimates per individual ranged from 5 to 156 (mean = 48.2 ± 54.9) spanning transmission periods up to 569 days (mean = 278 ± 154 days; Table 3). Cefas DSTs were at liberty for 42–1,006 days prior to recapture, with a mean deployment period of 234 ± 245 days.

3.2 | Southern California Bight (SCB) deployments

In this study, 86 electronic tags were deployed within the SCB on 68 swordfish, ranging in size from ~122 to 214 cm (mean = 165 ± 21 cm, lower jaw fork length, LJFL). Collectively, 26% of the SCB swordfish later reported close to (<225 km) the initial release site within the SCB study area (n = 18). Swordfish that moved outside of the SCB study area predominantly travelled on a southerly heading (mean = 173 ± 24 range: 136°–216°), with 76% of the individuals (n = 38) moving into the EPO management unit (Figure 1a,c). Ten tagged swordfish (20%) travelled on a westerly heading (mean = 259 ± 11°; range: 253°–270°) from the initial tagging site and later reported within the WCNP region. Additionally, two of the double-tagged mrPAT swordfish (4%) from the SCB spent time in both the EPO and WCNP management units, with pop-up locations occurring on either side of the stock boundary line (Figure 1a).

3.3 | Pacific Leatherback Conservation Area (PLCA) deployments

Six satellite-linked tags were deployed off the coast of Central California on three swordfish that ranged from 196 to 218 cm LJFL (mean = 209 ± 12 cm LJFL). Tags were deployed within the boundaries of the PLCA, an expansive region (>500,000 km^2) off the U.S.

FIGURE 2 Electronic tag application protocols and placement. (a) shows the use of a single applicator positioned at the base of the dorsal fin, (b) shows the use of a multi-prong applicator for deploying up to three tags simultaneously, and (c) the preferred method which entailed the use of a hand-held applicator which ensured the cross-pterygiophore positioning of the tag anchor

West Coast that has been seasonally restricted to drift-gillnet fishing since 2001 to reduce leatherback sea turtle (*Dermochelys coricea*) interactions (Federal Register, 2001; Table 2). PLCA swordfish revealed movements to the southwest (203°–236° heading; mean: 219°), predominantly within the WCNP management unit (Figure 1a,b). One tagged swordfish outfitted with two mrPATs, a PSAT, and a Cefas DST crossed into the western portion of the EPO management area after spending at least 90 days within the boundaries of the WCNP (Figure 1b).

3.4 | Movements within the Southern California Bight

Eighteen of the swordfish tagged off southern California (18 out of 68 individuals) later reported within the SCB study area, with a mean displacement of only 99 ± 75 km from the initial tagging location. For these individuals, mean horizontal rate of movement was just 1.5 ± 2.4 km/day over a mean deployment duration of 105 ± 49 days. There was no apparent relationship between tag deployment duration and displacement distance or direction; however, short-duration PSAT deployments and prematurely released mrPATs (<30 days) generally resulted in limited horizontal movements and spatial information. Based on the 1st (90–120 days) and 2nd (180–240 days) mrPAT pop-up locations, six double-tagged swordfish initially exhibited limited horizontal displacement and ROM values within the SCB study area followed by extensive movements into the EPO or WCNP over the subsequent 60–90 days period. For example, a 120-day mrPAT (PTT# 164515) deployment on double-tagged swordfish #29 popped up 154 km west of its deployment site within the SCB on February 17, 2017, resulting in an initial ROM of just 1.3 km/day. However, over the next 60 days, swordfish #29 moved 2,740 km into the WCNP on a westerly heading with a mean ROM of 45.7 km/day before the 2nd mrPAT popped up east of the Hawaiian Islands.

3.5 | Movements from the SCB to the WCNP management unit

Among those swordfish that reported from outside of the SCB tagging area, ~20% of the individuals moved to the west and reported within the WCNP management unit. Similar to that described for several double mrPAT-tagged swordfish, SPOT-tagged individuals initially remained within the SCB study area prior to making wide-ranging migrations into the WCNP and EPO management areas. For example, a 180-cm swordfish (#68) was tagged with SPOT#17U2507 (PTT

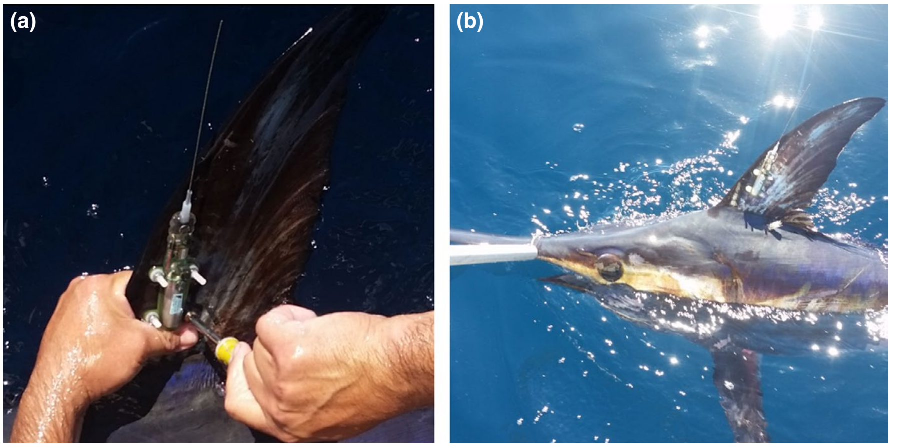

FIGURE 3 Image showing the position and placement of Argos transmitters on the dorsal fin of swordfish. (a) SPOT tags were fastened through swordfish dorsal fin spines using either nyloc hardware or plastic zip ties. (b) Image showing the position of the SPOT body and antennae relative to the dorsal fin. Upon surfacing during a basking event the tag wet/dry sensor dries and transmissions are sent to the Argos network

#176581) on October 24, 2018, and remained close to its SCB tagging site over the next 10 weeks before moving offshore at a 249° heading beginning on January 8, 2019. Over the next 10 weeks, swordfish #68 moved nearly 3,700 km toward an area around 17.5°/−149° within the WCNP management unit before returning to the SCB study area in June of 2019, where it subsequently reported near the initial deployment location. Mean displacement and ROM values were greater for tagged individuals that moved into the WCNP management unit (2,298 ± 1,915 km; 25.0 ± 15.0 km/day) when compared with EPO-affiliated swordfish (1,606 ± 1,033 km; 16.8 ± 11.7 km/day).

3.6 | Movements from the SCB to the EPO management unit

The majority of swordfish (76%) that moved outside of the SCB study area later reported within the EPO management unit. Five of the six SPOT-tagged swordfish of this study travelled into the EPO management unit with at least two individuals returning to the SCB study area following extensive movements along Baja California. For example, swordfish #63 (PTT# 171954) travelled southeast along the coast of Baja California in November, 2017, and entered the Sea of Cortez during the spring of 2018 before returning to the SCB study area in August, 2018. Over a nine-month period, this 152-cm LJFL swordfish travelled a roundtrip distance of 3,971 km within the EPO before returning to within 15 km of its original release site on August 20, 2018. Upon returning to the SCB, daily ROM decreased considerably with seasonal movements confined to a relatively small section of the SCB (Figure 1c). The greatest mrPAT displacement distance (3,877 km) was observed for a 161 cm LJFL swordfish (Tag #16U0979) that travelled into the EPO toward the equator (0.8°N/132.0°W) at an average rate of 21.5 km/day over the 180-day mrPAT deployment.

3.7 | Archival tag recaptures

Cefas G5 DSTs have been deployed on all swordfish tagged during experimental gear trials performed by the PIER team (n = 151 from August, 2011, to June, 2018). This work reports on sixteen (>10%) recaptured individuals, half of which were reported by California drift gillnet (n = 5) and deep-set buoy gear (n = 3) fishers operating within the SCB. All of the SCB recoveries (n = 8) were reported within 150 km of the initial tagging location between August and January, with a mean time at liberty of 234 ± 245 days. Seven of the recovered DSTs (44%) were reported by Mexican flagged longline vessels operating within the EPO management unit (Figure 4). Swordfish recaptures off the coast of Baja California occurred between October and March, with an average time at liberty of 113 ± 56 days. Additionally, one DST (A13138) was reported by a U.S. flagged longline vessel fishing within the WCNP management area, south of the Hawaiian Islands. This individual (DST # A13138) had a time at liberty of 307 days and was recaptured 4,061 km from the initial release site at a 253° heading.

4 | DISCUSSION

This work focused on better understanding the horizontal movements and management unit affiliation of swordfish captured and tagged off the California coast. Findings from this work largely support those of previous movement studies (Abecassis et al., 2012; Dewar et al., 2011; Sepulveda et al., 2010) and validate that swordfish exhibit wide-ranging migrations from the eastern margins of the Pacific Basin to the equator and out beyond the Hawaiian Islands. Contrary to that reported in some of the existing stock structure hypotheses, the vast majority of tagged swordfish that ventured outside of the SCB entered into and remained seasonally within the EPO management unit (76%). Similarly, seven of the eight (88%) DSTs that were recovered outside of the southern California study area were reported by Mexican flagged longline vessels operating within the boundaries of the EPO management unit (Figure 4). Although future deployments are needed to further assess seasonal migration patterns, this work suggests that SCB swordfish may exhibit a stronger affiliation for the EPO management unit than that previously reported.

TABLE 2 Tag deployment and recovery statistics for 92 electronic tags affixed to 71 swordfish off California from September, 2012, through December, 2018

Swordfish #	LJFL (cm)	DST #	Tag type	PTT #	Tag deployment				Tag recovery				Displacement	Direction	ROM
					Date	Region	Latitude	Longitude	Latitude	Longitude	Affiliation	Duration			
1	152	A12887a	mrPAT	164519	1/31/17	SCB	32.68	−118.14	15.39	−122.41	EPO	90	1,971	193	21.90
2	152	A12890	mrPAT	164505	11/3/16	SCB	33.19	−117.82	31.42	−120.90	SCB	120	249	237	2.94
3	142	A13123	mrPAT	164470	9/27/16	SCB	33.12	−117.49	25.62	−113.59	EPO	90	915	155	10.17
4	169	A13124	mrPAT	164482	9/8/16	SCB	32.73	−117.56	32.84	−118.27	SCB	180	68	277	0.38
5	205	A13128	mrPAT	164467	8/18/16	SCB	33.13	−117.77	8.96	−133.28	EPO	90	3,123	214	34.71
6	161	A13132	mrPAT	164472	8/30/16	SCB	33.35	−117.85	17.57	−111.47	EPO	240[a]	1,866	159	7.71
7	161	A13143	mrPAT	164481	9/15/16	SCB	32.78	−117.58	0.81	−132.35	EPO	180	3,877	206	21.54
8	152	A13144	mrPAT	164468	9/15/16	SCB	32.77	−117.61	23.34	−119.67	EPO	115[a]	1,068	188	9.28
9	142	A13146	mrPAT	164524	10/12/16	SCB	33.05	−117.46	18.68	−112.94	EPO	120	1,660	163	13.83
10	165	A13149	mrPAT	164525	10/12/16	SCB	33.05	−117.46	6.40	−121.93	EPO	120	2,999	190	24.99
11	133	A13322	mrPAT	164523	1/3/17	SCB	32.68	−117.89	28.37	−146.29	WCNP	90	2,754	268	30.60
12	208	A13330	mrPAT	164488	12/1/16	SCB	33.09	−117.69	27.66	−119.89	EPO	90	639	200	7.10
13	182	A13332	mrPAT	164527	8/30/17	SCB	33.90	−119.62	11.47	−116.58	EPO	90	2,513	173	27.92
14	161	A13335	mrPAT	171682	12/13/17	SCB	33.17	−118.30	21.65	−108.99	EPO	120	1,575	143	13.12
15	208	A13336	mrPAT	164520	12/13/16	SCB	33.38	−118.75	24.18	−114.68	EPO	150[a]	1,097	161	7.31
16	136	A13524	mrPAT	171690	11/30/17	SCB	33.09	−117.54	31.68	−117.08	SCB	90	161	166	1.79
17	176	A13525	mrPAT	164503	11/30/17	SCB	33.06	−117.53	22.86	−110.65	EPO	90	1,320	147	14.66
18	152	A13528	mrPAT	164494	11/30/17	SCB	33.06	−117.53	32.28	−119.67	SCB	90	218	247	2.42
19	165	A13529	mrPAT	164522	11/30/17	SCB	33.06	−117.53	25.45	−146.77	WCNP	90	2,949	261	32.77
20	147	A13530	mrPAT	171695	11/30/17	SCB	33.06	−117.53	8.64	−126.13	EPO	90	2,855	200	31.73
21	166	A14627	mrPAT	171709	8/24/18	SCB	33.27	−117.76	33.20	−118.12	SCB	180	34	258	0.19
22	165	A14629	mrPAT	171692	8/14/18	SCB	33.01	−117.80	31.38	−119.66	SCB	180	252	224	1.40
23	196	A15199	mrPAT	177054	11/28/18	SCB	33.15	−117.52	14.91	−120.38	EPO	45[a]	2,049	189	45.53
24	181	A15205	mrPAT	176961	12/12/18	SCB	33.05	−117.53	15.01	−140.72	WCNP	120	3,080	235	25.67
25	142	A15207	mrPAT	176964	12/11/18	SCB	33.01	−117.71	18.88	−108.70	EPO	120	1,809	148	15.07
26	160	A15208	mrPAT	176662	12/19/18	SCB	33.01	−117.49	18.74	−105.82	EPO	90	1,967	140	21.85
27	122	A15214	mrPAT	176661	12/20/18	SCB	32.92	−117.45	20.73	−152.22	WCNP	90	3,686	257	40.96
28	122	A15223	mrPAT	176665	1/9/19	SCB	33.19	−117.53	19.58	−107.34	EPO	90	1,820	149	20.22
29	159	A12891	mrPAT	164515	10/19/16	SCB	33.28	−117.87	32.79	−119.42	SCB	120	154	249	1.29
			2nd mrPAT	164495	10/19/16	SCB	33.28	−117.87	28.90	−147.85	WCNP	+60	2,740	268	45.67
30	189	A13129	mrPAT	164463	8/29/16	SCB	33.30	−117.98	33.08	−117.73	SCB	90	34	137	0.37
			2nd mrPAT	164479	8/29/16	SCB	33.30	−117.98	32.93	−117.42	SCB	+27[a]	34	140	1.25

(Continues)

TABLE 2 (Continued)

Swordfish #	LJFL (cm)	DST #	Tag type	PTT #	Tag deployment				Tag recovery						
					Date	Region	Latitude	Longitude	Latitude	Longitude	Affiliation	Duration	Displacement	Direction	ROM
31	214	A13134a	mrPAT	164461	9/26/16	SCB	33.03	−117.75	30.97	−116.94	SCB	90	241	162	2.68
			2nd mrPAT	164471	9/26/16	SCB	33.03	−117.75	25.21	−109.78	EPO	+90	950	135	10.56
32	161	A13133	mrPAT	164501	10/13/16	SCB	32.92	−117.43	29.05	−120.61	EPO	120	526	216	4.38
			2nd mrPAT	164510	10/13/16	SCB	32.92	−117.43	27.51	−140.41	WCNP	+60	2,283	270	38.05
33	157	A13137	mrPAT	164459	8/25/16	SCB	33.10	−117.77	32.54	−117.48	SCB	90	68	157	0.76
			2nd mrPAT	164475	8/25/16	SCB	33.10	−117.77	19.52	−116.89	EPO	+46[a]	1,449	179	31.50
34	182	A13138a	mrPAT	171700	10/19/17	SCB	33.37	−118.71	11.88	−126.66	EPO	90	2,522	201	28.02
			2nd mrPAT	171708	10/19/17	SCB	33.37	−118.71	22.32	−113.98	EPO	+90	1,777	46	19.74
35	165	A13142	mrPAT	164492	9/27/16	SCB	33.10	−117.47	26.31	−113.88	EPO −148.53	90	831	154	9.23
			2nd mrPAT	164473	9/27/16	SCB	33.10	−117.47	25.39	−113.77	EPO	+90	103	156	1.15
36	142	A13145	mrPAT	164480	9/26/16	SCB	33.02	−117.81	33.36	−117.88	SCB	90	39	350	0.43
			2nd mrPAT	164487	9/26/16	SCB	33.02	−117.81	29.35	−116.09	EPO	+60[a]	478	161	7.97
37	182	A13317	mrPAT	171694	10/18/17	SCB	33.40	−118.74	32.92	−131.55	WCNP	90	1,193	271	13.26
			2nd mrPAT	171688	10/18/17	SCB	33.40	−118.74	24.52	−145.87	WCNP	+90	1,646	241	18.29
38	169	A13319	mrPAT	164493	8/29/17	SCB	33.89	−119.63	33.91	−119.88	SCB	90	24	280	0.26
			2nd mrPAT	171701	8/29/17	SCB	33.89	−119.63	32.56	−136.78	WCNP	+90	1,600	270	17.78
39	182	A13324	mrPAT	164521	1/3/17	SCB	32.68	−117.89	30.81	−129.40	WCNP	90	1,107	252	12.30
			2nd mrPAT	164504	1/3/17	SCB	32.68	−117.89	28.86	−137.91	WCNP	+60	849	257	14.15
40	181	A13327	mrPAT	164517	12/1/16	SCB	33.11	−117.69	32.87	−117.72	SCB	180	27	177	0.15
			2nd mrPAT	164502	12/1/16	SCB	33.11	−117.69	32.39	−117.71	SCB	180	80	180	0.45
41	189	A13328	mrPAT	164512	12/13/16	SCB	33.37	−118.83	30.64	−140.11	WCNP	90	2,025	267	22.51
			2nd mrPAT	164513	12/13/16	SCB	33.37	−118.83	29.95	−118.04	EPO	+60	2,112	85	35.20
42	161	A13333	mrPAT	164509	8/30/17	SCB	33.90	−119.62	33.54	−118.02	SCB	90	153	106	1.70
			2nd mrPAT	171707	8/30/17	SCB	33.90	−119.62	32.56	−117.87	SCB	+90	110	30	1.22
43	147	A13533	mrPAT	164497	10/25/17	SCB	33.35	−117.80	33.21	−118.77	SCB	90	92	33	1.02
			2nd mrPAT	171697	10/25/17	SCB	33.35	−117.80	26.70	−122.09	EPO	+90	847	211	9.41
44	142	A13536	mrPAT	171681	11/28/17	SCB	33.10	−117.48	19.16	−114.13	EPO	90	1,585	167	17.61
			2nd mrPAT	171706	11/28/17	SCB	33.10	−117.48	14.38	−129.55	EPO	+90	1,724	254	19.16
45	169	NA	PSAT	164530	8/28/17	SCB	33.84	−119.40	33.22	−117.99	SCB	30	148	116	4.95
46	161	A13327	PSAT	173781	12/28/17	SCB	33.17	−117.65	29.31	−117.96	EPO	30	430	184	14.34
47	208	A11605	PSAT	84791	8/7/15	SCB	32.88	−117.88	32.36	−117.65	SCBE	5	62	160	12.40
			G5 DST	NA	8/7/15	SCB	32.88	−117.88	29.57	−116.42	EPO	57	394	159	6.91

(Continues)

TABLE 2 (Continued)

Swordfish #	LJFL (cm)	DST #	Tag type	PTT #	Tag deployment				Tag recovery			Duration	Displacement	Direction	ROM
					Date	Region	Latitude	Longitude	Latitude	Longitude	Affiliation				
48	148	A06061	G5 DST	NA	9/17/12	SCB	33.06	−117.86	32.20	−119.07	SCB	471	150	230	0.32
49	165	A11536	G5 DST	NA	7/10/14	SCB	32.68	−117.49	32.70	−117.53	SCB	420	10	280	0.02
50	202	A11540	G5 DST	NA	9/3/15	SCB	33.07	−117.45	29.77	−116.68	EPO	179	374	156	2.09
51	173	A11604	G5 DST	NA	9/4/15	SCB	33.08	−117.45	23.70	−112.31	EPO	168	1,158	151	6.89
52	153	A11591	G5 DST	NA	11/23/15	SCB	33.35	−117.73	28.73	−115.65	EPO	42	551	155	13.12
53	153	A11590	G5 DST	NA	11/23/15	SCB	33.32	−117.72	33.22	−117.66	SCB	1,006	10	124	0.01
54	185	A12878	G5 DST	NA	1/26/16	SCB	32.88	−117.73	33.57	−118.90	SCB	323	133	305	0.41
55	161	A12887	G5 DST	NA	7/19/16	SCB	32.77	−117.51	33.50	−118.83	SCB	96	148	303	1.54
56	173	A13135	G5 DST	NA	8/3/16	SCB	32.88	−117.72	29.90	−116.74	EPO	112	344	157	3.07
57	175	A13134	G5 DST	NA	8/3/16	SCB	32.88	−117.72	32.67	−117.47	SCB	49	34	120	0.69
58	153	A11540	G5 DST	NA	8/9/16	SCB	33.27	−117.68	29.75	−116.63	EPO	120	403	160	3.36
59	173	A13127	G5 DST	NA	8/17/16	SCB	33.12	−117.47	32.87	−117.42	SCB	58	28	169	0.48
60	157	A13138	G5 DST	NA	9/14/16	SCB	32.66	−117.55	17.03	−154.23	WCNP	307	4,061	253	13.23
61	177	A14631	G5 DST	NA	8/21/18	SCB	33.12	−117.87	22.46	−107.53	EPO	205	1,560	136	7.61
62	175	A13323	G5 DST	NA	8/28/17	SCB	33.83	−119.39	33.57	−118.93	SCB	139	51	123	0.37
			mrPAT	164518	8/28/17	SCB	33.83	−119.39	33.91	−118.89	SCB	90	47	75	0.52
63	153	A13538	SPOT−258	171954	10/25/17	SCB	33.30	−117.81	26.59	−118.11	EPO	317	5,302	140	16.73
64	139	A13540	SPOT−258	171953	12/06/17	SCB	33.17	−117.54	15.84	−124.27	EPO	43	2,072	200	48.19
65	188	A15204	SPOT−258	176575	12/12/18	SCB	33.05	−117.54	19.42	−109.22	EPO	46	1,792	149	38.96
66	131	A14623	SPOT−258	176578	10/5/18	SCB	33.09	−117.88	16.01	−114.85	EPO	135	2,629	170	19.47
67	136	A13323	SPOT−258	176580	8/24/18	SCB	33.31	−117.78	27.80	−119.04	EPO	249	1,511	195	6.07
68	180	A15201	SPOT−258	176581	10/24/18	SCB	33.32	−117.78	17.68	−148.53	WCNP	188	8,520	249	45.32
69	218	A13313	mrPAT	171685	9/7/17	PLCA	37.48	−123.31	36.48	−124.74	WCNP	90	169	229	1.88
			2nd mrPAT	171698	9/7/17	PLCA	37.48	−123.31	11.67	−142.47	WCNP	+60	3,280	219	54.67
70	196	A13309	mrPAT	171684	9/12/17	PLCA	37.36	−123.17	27.53	−127.76	WCNP	90	1,175	203	13.06
			2nd mrPAT	171699	9/12/17	PLCA	37.36	−123.17	18.13	−122.71	EPO	+90	2,138	179	11.88
			PSAT	37524	9/12/17	PLCA	37.36	−123.17	35.95	−123.69	WCNP	5	164	196	32.76
71	214	A13310	mrPAT	164496	9/7/17	PLCA	37.46	−123.31	35.64	−126.62	WCNP	90	358	236	3.98

Note: 2nd mrPAT rows refer to double-tagged individuals; + duration value for double-tagged swordfish equates to the number of days after the first mrPAT reported; DST # with alpha value indicates that tag was recovered and subsequently redeployed.

Abbreviations: Est. LJFL, estimated lower jaw fork length (cm); PLCA, Pacific Leatherback Conservation Area; ROM, horizontal rate of movement (km/day); SCB, Southern California Bight.

[a]Tags that released from fish prematurely.

TABLE 3 Performance metrics of ARGOS transmitters affixed to the dorsal fin of six swordfish tagged within the Southern California Bight

Swordfish number	PTT ID number	Deploy date	Last location	Duration	Last transmission	Duration	No. of transmissions	# Received ARGOS messages	No. of positions	Displacement (km)
63	171954	10/25/17	5/17/19	569	05/17/19	569	4,610	393	44	5,302
64	171953	12/6/17	1/18/18	43	06/30/18	206	3,342	162	26	2,072
65	176575	12/12/18	1/27/19	46	06/27/19	197	1,205	125	5	1,792
66	176578	10/5/18	2/17/19	135	02/20/19	138	4,390	243	42	2,629
67	176580	8/24/18	6/30/19	310	06/30/19	310	1,833	84	20	1,511
68	176581	10/24/18	6/30/19	249	06/30/19	249	7,521	515	156	8,520

Note: Between October, 2017, and June 30, 2019, with active transmissions received in 2019 from five of the transmitters.

4.1 | Tagging procedures

Although past studies have largely relied upon harpoon or shallow-set longline operations for tagging swordfish, this study capitalized on concurrent deep-set gear trials off California (Sepulveda & Aalbers, 2018; Sepulveda et al., 2014). Prior to this study, most of the swordfish tagging within the SCB was accomplished using harpoon methods (Dewar et al., 2011; Sepulveda et al., 2010). Although ideal with respect to minimizing stress induction, harpoon methods often result in poor tag placement and are subject to availability constraints, as basking activity is intermittent and condition dependent (Dewar et al., 2011; Palko, Beardsley, & Richards, 1981; Sepulveda et al., 2010). Although shallow-set longline is the most widely used method for harvesting swordfish worldwide, long soak times (i.e., overnight), and rapid haul back speeds can result in high rates of post-release mortality (Ito, Dollar, & Kawamoto, 1998). Unlike most longline operations, the California deep-set fishery occurs during the daytime and incorporates a strike indicator system that allows swordfish to be hauled immediately upon detection of a strike (Sepulveda et al., 2014). Reduced fight times and rapid processing of catch minimizes capture stress and increases post-release survivorship, a critical factor given the high cost of electronic tags (Musyl et al., 2015).

4.2 | Horizontal movement data

In this study, most electronic tags were deployed within the SCB (n = 86), a large portion of the California coastline that includes waters from the U.S./Mexico border to Point Conception and out to 300 km (Dailey, Reish, & Anderson, 1993). Previous swordfish tagging work has been centered around this region of the eastern north Pacific, primarily because of the calm waters and the presence of a traditional harpoon fishery (Coan, Vojkovich, & Prescott, 1998; Dewar et al., 2011; Sepulveda et al., 2010). Due to constraints in both the number of electronic tags deployed and deployment duration (~1–6 months) of previous studies, data on swordfish migration routes and horizontal movements patterns remain limited (Carey & Robison, 1981; Dewar et al., 2011; Holts, Bartoo, & Bedford, 1994; Sepulveda et al., 2010). Further, swordfish deep-diving behavior impacts the precision of light-based geolocation and limits the accuracy of position estimates based on the time of sunrise and sunset (Dewar et al., 2011). Nonetheless, previous tagging data suggest that swordfish seasonally enter the SCB during the summer months, and subsequently leave with the onset of winter conditions (Abecassis et al., 2012; Dewar et al., 2011; Sepulveda et al., 2010). The movement data collected in this study align with previous works and support the hypothesis that swordfish feed throughout the temperate latitudes off the west coast and return to lower-latitude spawning areas during the winter and spring (DeMartini et al., 2000; Hinton et al., 2005; Sosa-Nishizaki & Shimizu, 1991).

It is evident from past studies that the direction and timing of swordfish departures from the US west coast are variable, with migration paths extending into both the EPO and WCNP management units (Dewar et al., 2011). Findings from Dewar et al. (2011) showed that approximately 70% of tagged swordfish that departed from the SCB between 2002 and 2008 entered into the EPO management unit, a finding that is similar to the results from this work. Abecassis et al. (2012) also showed that the majority (56%) of swordfish that departed from the southern California tagging area moved into the EPO region. Although informative, most of the past work remains limited due to short tag retention periods, a factor that has hindered the development of interannual migration hypotheses. Despite these data, and previous hypotheses proposed by Hinton et al. (2005), California swordfish are currently considered to be solely affiliated with the WCNP management unit (ISC, 2014).

4.3 | Deployment locations

Given that the vast majority of the tag deployments in this study were within the SCB, swordfish tagging data remain sparse for the waters off Central and Northern California, an area that historically supported significant fishing activity prior to the temporal restrictions of 2001 (PLCA; Federal Register, 2001). Similar to findings from the only other tagging study performed within the PLCA (Sepulveda, Aalbers, Heberer, Kohin, & Dewar, 2018), most of the swordfish tagged in this study subsequently reported within the WCNP management area (Figure 2). Only one of the double-tagged swordfish crossed into the EPO management area after remaining within the WCNP region for the initial few months of the track. The predominant pattern for swordfish tagged within the PLCA consisted of movements in a south-westerly direction with the onset of winter conditions (sea surface temperature cooling to <14°C) and subsequent movements into offshore areas near the North Pacific Transition Zone, an area that is targeted widely by several international fleets, including US-flagged longline vessels operating out of Hawaii (Bigelow, Boggs, & He, 1999; DeMartini et al., 2000; Ito & Childers, 2014). The Hawaiian longline fleet primarily operates along the frontal boundaries of the north Pacific transition zone, an expansive area north and east of the Hawaiian Islands that extends toward the west coast of the U.S. (Ito et al., 1998; Sakagawa, 1989). Hawaii-based longline vessels typically follow the swordfish resource as it moves eastward toward the U.S. west coast as the summer season progresses. In recent years, several of the Hawaiian-based vessels have shifted operations to focus solely out of California ports (i.e., San Francisco, Los Angeles) due to the proximity of fishing grounds and markets (Pers. Comm. Jim Heflin Commercial swordfish buyer, San Diego, CA). Although additional swordfish tagging efforts are underway off Central California, movement data collected to date suggest that PLCA swordfish have a relatively high affinity for the waters of the WCNP (Sepulveda et al., 2018).

4.4 | Phenotypic differences

Although phenotypic differences among Pacific swordfish have been suggested by seasoned fishers, no studies have been conducted to systematically evaluate morphological variance within the California fishery (Pers. Comm; M. McCorkle, Santa Barbara, CA). However, observed differences in average fish size (LJFL and girth), physical appearance, and parasite loading continue to suggest that there may be some separation between southern and central California swordfish stocks. Additionally, movement data from more than 150 electronic tag deployments by our group have yet to show any directed movements from southern California into the waters above Point Conception, an area that has been reported to be a biogeographic boundary for various California coastal species (Burton, 1998). Although it is well documented that swordfish can tolerate a wide range of temperatures and are highly migratory in nature, the level of mixing between swordfish stocks off southern and central California remains uncertain. In this study, fish tagged off central California (mean = 200 ± 21 cm LJFL) were considerably larger on average than those tagged within the SCB (mean = 167 ± 14 cm LJFL), however; size discrepancies may also be attributable to differences in latitudinal range, sex ratio, or related to a possible ontogenetic shift in migration patterns and diet. Sakagawa (1989) suggested that larger swordfish extend their latitudinal range higher into cooler waters as they increase in size. Since female swordfish grow larger than males, the composition of catches at higher latitudes may consist of a higher proportion of females, as has been reported in other areas (reviewed by Mejuto, 2018). Similarly, Hinton et al. (2005) discussed sex-specific segregation in certain areas of the Pacific, a factor that could also be used to explain regional differences in size and phenotypes, especially since the fish in this study were not sacrificed and sexed. Apparent differences in size and location may also be a function of increased thermal inertia and heightened tolerance of larger fish for cooler surface waters (Bernal, Sepulveda, Musyl, & Brill, 2009). Future work focused on genetic comparisons of tagged individuals along with additional movement data may help clarify questions pertaining to potential differences in size, morphology, parasite loading, and stock structure in this region.

4.5 | Physical tag recoveries, growth, and site fidelity

The physical recovery of swordfish tags in this study was ~10%, a value higher than that reported in most billfish tagging studies to date (~1%–3%; Ortiz et al., 2003) and similar to a recent archival tagging study on striped marlin *Kajikia audax* (Domeier, Ortega-Garcia, Nasby-Lucas, & Offield, 2018). The observed recapture rate for this study was, however, much less than that documented in a previous short-term tagging study in the same study region (55%; Sepulveda et al., 2010). Four of the sixteen DST recaptures of this study (25%) were likely attributable to localized fishing effort within the SCB, as they were reported within close proximity to the initial tagging location (<150 km) during the same season (<140 days at liberty) by California DGN or DSBG fishing vessels. Nearly half of the archival tag recoveries were reported by Mexican flagged longline vessels (n = 7) operating along the coast of Baja California during the winter and spring (<180 days at liberty) as fish moved outside (>225 km) the SCB (Figure 4). One of the tagged swordfish travelled more than 4,000 km to the west before it was recaptured by a longline vessel south of the Hawaiian Islands after 307 days at liberty (Figure 1a). Four of the tagged swordfish were recaptured by CA DGN or DSBG vessels fishing within the SCB during subsequent seasons, with the longest duration at liberty being >1,000 days. Some of the longer-duration recaptures were reported within the SCB the following year, a finding that provides additional support for seasonal site fidelity for the productive foraging grounds of the SCB.

The longest deployment duration recapture (1,006 days) was initially tagged off southern California (33.32°/−117.72°) at an estimated weight of 45 kg on November 23, 2015. Swordfish #53 (DST #11590) was subsequently recaptured approximately 10 km from the initial tagging site by a member of the same PIER DSBG exempted fishery team (*FV Chula*). The swordfish was estimated to have gained more than 90 kg over the 33-month time at liberty. Similar growth and mass gain was observed for swordfish #48 (DST #A06061), an estimated 60-kg swordfish tagged in September, 2012, by the PIER team. This individual was landed by the *F/V Gold Coast* (another member of the same EFP group) after 15 months at liberty with a dressed weight of 136 kg (Pers. Comm. Donald Krebs; San Diego, CA). DST #A06061 was also recaptured within 150 km of the initial southern California tag deployment site after 471 days at liberty. A similar level of site fidelity was previously described for a swordfish tagged with an archival tag off the coast of Japan, which was subsequently recaptured ~ 100km from the original tagging site nearly one year later (Takahashi, Okamura, Yokawa, & Okazaki, 2003). Additional findings have also been reported by Beckett (1972) on feeding area fidelity in the Atlantic. Further, Neilson et al. (2009) have also reported on a tagged swordfish off Nova Scotia that was eventually recaptured only five kilometers from its point of release after traveling to the waters off the Caribbean.

For the longer-term recaptures (>323 days), SST and day length estimates based on crepuscular activity (i.e., time of dawn descents and dusk ascents) were used to verify that the swordfish departed from the SCB and subsequently returned to the original tagging area after traveling to tropical latitudes (Carmody, Mariano, & Kerstetter, 2017; Lam, Galuardi, & Lutcavage, 2014). Additional analyses of fine-scale depth and temperature data from all recovered DST's and associated SPOT tags will be used to further examine seasonal and regional differences in vertical movement patterns, specific habitat utilization, and site fidelity hypotheses.

Although SPOT tags have been used to track the movements and migration rates of several marine species (Hammerschlag, Gallagher,

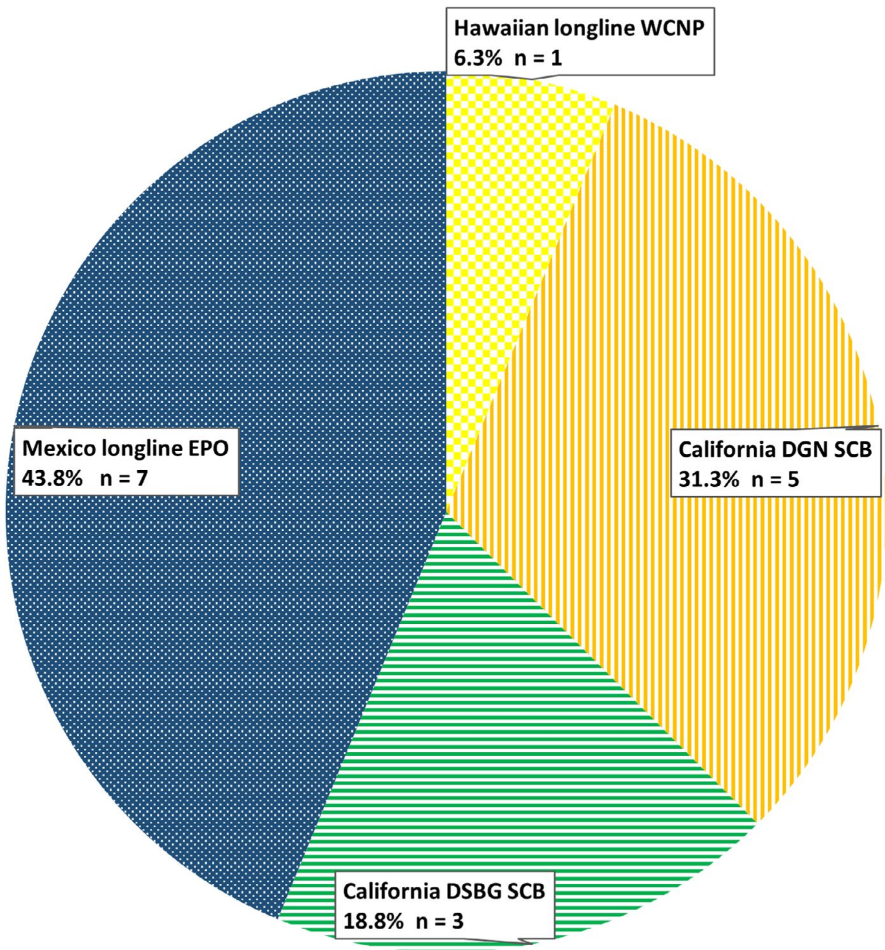

FIGURE 4 Illustration showing the corresponding number and percent (in parentheses) of all recaptured electronic tags in this study. Tags were reported from multiple fleets throughout the north Pacific Basin (n = 16)

& Lazarre, 2011; Holdsworth, Sippel, & Block, 2009), this work is among the first to successfully offer extended, year-long tracks on swordfish in the Pacific. The interannual roundtrip tracks for at least three individuals outfitted with fin-mounted SPOTs validate the usefulness of this technology on this species. These data are critical for effective management especially on a shared stock that exhibits a high degree of seasonal site fidelity (Nielsen & Seitz, 2017). Fidelity to the SCB tagging area was also demonstrated by swordfish #63 (PTT #171954), a SCB-caught swordfish that was released at 33.30°/−117.81° on October 25, 2017. Based on the Argos position data, this individual moved around the southern tip of Baja California and into the Sea of Cortez during April 2018 (Figure 1c). Following an extensive journey to the south, swordfish #63 resurfaced within 15 km (33.13/−117.88) of its initial tagging location on August 20, 2018, where it transmitted for two consecutive weeks within the SCB. The path taken by swordfish #63 shows that it had likely crossed within <1 km of the original tagging location. Additional Argos transmissions from swordfish #63 along the coast of southern and then central Baja California in May 2019, show a second seasonal loop into the EPO (Figure 1c). Similarly, swordfish #68 (PTT #176581) returned to within 75 km of the original tag deployment location following an estimated 8,540 km seasonal roundtrip within the WCNP management unit. Swordfish #68 exhibited one-way displacement distances of approximately 3,700 km over 8–10 week periods during directed offshore and return movements. The heightened displacement rates (~50 km/day) are similar to the maximum rates documented for swordfish in previous tagging studies (Dewar et al., 2011), as well as those of several mrPAT's deployed in this study.

Heightened ROM values during offshore and onshore migrations were interspersed with 6–10 week periods of reduced average ROM (~1.1 km/day) both within the SCB (~32.5°/−117.6°) and around an offshore area centered around 18.0° × −147.0°. Although it was not yet possible to determine if spawning occurred during this period, future work will focus on assessing vertical rates of movement in the offshore tropical areas and proposing hypotheses on potential spawning areas.

4.6 | Movements in relation to stock structure

Although this work offers the most comprehensive horizontal movement dataset for swordfish in this region, stock structure and seasonal migrations remain uncertain. This is primarily because of the complex and widespread movements reported in this study as well as the relatively limited number of tag deployments made to date. Although these initial findings are not sufficient to differentiate stock structure in the eastern north Pacific, they do provide insight and a starting point to develop and refine stock structure hypotheses based on fishery-independent data. We are hopeful that these and future movement pattern studies can be incorporated into regional assessment models. Nonetheless, the results from this study support several past stock structure hypotheses and clearly demonstrate a connection between California swordfish and the EPO management unit (reviewed below).

In alignment with this work, Kume and Joseph (1969) used catch records to propose that swordfish along Baja California migrate into California waters during the summer and fall months. Similarly, Bedford and Hagerman (1983) reported a link between swordfish off Baja California (Mexico) and California. Following suite, several stock structure hypotheses based off catches and biological reference points have also proposed that swordfish of the eastern north Pacific region collectively fall into a larger management unit that encompasses both the Eastern North Pacific as well as portions of the western and Central North Pacific (Hinton, 2003; Hinton & Deriso, 1998; Nakano, 1994; Sosa-Nishizaki, 1990; Sosa-Nishizaki & Shimizu, 1991).

Given the disparities and continued uncertainty regarding swordfish stock structure in the north Pacific, the International Scientific Committee performed additional model runs in 2009 that included a combined north Pacific stock hypothesis (EPO and WCNP single stock hypothesis) as well as an EPO and WCNP segregated population model (Brodziak & Ishimura, 2010; ISC, 2014). Additionally, in 2014 and 2018, the ISC again indicated a continued need for alternative swordfish stock structure hypotheses given the uncertainty associated with the distribution of Pacific swordfish. Collectively, we propose that the current line of tagging research, with an emphasis on the use of SPOT-tag technology, are needed to fully elucidate annual migration patterns and test stock structure hypotheses. Further, the incorporation of additional ongoing genomic analyses may provide relevant information that can be incorporated into future swordfish stock assessments in the north Pacific.

4.7 | Relevance to current management

In the eastern north Pacific, current management and harvest estimates suggest that swordfish harvested off California are solely comprised of individuals from the WCNP stock (ISC, 2014). For this reason, significant effort has been focused on fishery development and increasing yield from what has been proposed to be an underutilized west coast resource (Sepulveda & Aalbers, 2018; Sepulveda et al., 2014). Unfortunately, stock boundary designations have not been tested using movement or spatial tagging data, as current boundaries are largely the product of fishery-dependent observations and biological reference points (ISC, 2014, 2018). These data-gaps are common in HMS fisheries given the difficulty and cost associated with collecting movement data and the subsequent incorporation of such data into existing production models (Lynch, Graves, & Latour, 2011; Sippel et al., 2014). Despite such hurdles, the refinement of management unit boundaries and stock structure hypotheses with movement data is now common practice and recommended for HMS fisheries across the globe whenever spatial data is available (Goethel et al., 2011; Maunder & Piner, 2017; Sippel et al., 2014).

Findings from this work lend support to a two-stock hypothesis, but possibly one that does not directly adhere to the stepped line along the eastern margin. Further, considering the potential issues associated with the use of fishery-dependent observations (Maunder & Piner, 2017), it may be that there are some other, possibly biologically or ecologically relevant boundaries that better describe the separation of these two management units. For example, Point Conception remains a natural break in the distribution of numerous marine species along California, including various nearshore and migratory fishes (Burton, 1998). Although regional tagging and genetic data are still needed to determine interannual movement patterns both above and below Point Conception, data currently suggest an increased affiliation with the EPO management unit for swordfish tagged below this biogeographic zone (Sepulveda & Aalbers, 2018).

5 | SUMMARY

Based on this work as well as previous studies, it is evident that Southern California is a foraging ground that seasonally aggregates swordfish from various regions of the eastern and central north Pacific. Of particular interest is the relatively strong site fidelity recorded in this work, with several individuals returning to specific locations within the SCB following extensive seasonal movements to tropical latitudes within both the EPO and WCNP management units. This topic is deserving of future study given its potential impacts on fishing operations and regional productivity. Findings provide initial insight into the complex movement patterns exhibited by swordfish off the California coast and introduce future questions on stock affiliation and existing management unit boundaries.

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CONFLICT OF INTEREST

All authors acknowledge that there are no conflicts of interest with their involvement and publication of this work.

AUTHOR CONTRIBUTION

All authors have made a significant contribution to the development and production of this work.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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