Latin American Journal of Aquatic Research, 52(1): 90-106, 2024
DOI: 10.3856/vol52-issue1-fulltext-3090

Research Article

Insights into swordfish (*Xiphias gladius*) movement patterns and habitat utilization off the coast of northern Chile

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ABSTRACT. This study reports on the fine-scale movements of swordfish (*Xiphias gladius*) tagged off of the Antofagasta region of northern Chile, where harpoon fishing operations date back more than seven millenia. The study was conducted within a highly productive swordfish foraging area where movements and habitat use remain poorly characterized. Swordfish were outfitted with both data storage and satellite-linked archival tags scheduled for short (<30 days) and longer-term (>100 days) data collection. All tags were deployed on basking swordfish using harpoon-based methods across two field seasons in March 2019 and April 2022 around oceanic fronts and offshore seamounts. Fine-scale depth and temperature data were recorded over 145 days from four adult swordfish (100-200 kg). Swordfish exhibited regionally unique diurnal behaviors with greater average daytime depths than those recorded at night (78.0 ± 66.5 and 12.7 ± 4.9 m, respectively). The average daytime depths were shallower than those previously documented for other Pacific regions, including Chile's offshore waters. Daytime basking was observed on 76% of the daily records (110 out of 145 days) and accounted for approximately 12% of the collective daylight hours. Findings align with previous swordfish tagging studies and suggest that depth distribution patterns vary considerably depending on regional oceanographic conditions. Movement data are compared with previous studies, and we discussed relative to regional fishing operations.

Keywords: *Xiphias gladius*; harpoon tagging; oxygen minimum zone; depth distribution; southeastern Pacific

INTRODUCTION

The swordfish (*Xiphias gladius*) is a highly migratory species that supports commercial and artisanal fisheries in every major ocean basin (reviewed by Folsom et al. 1997). In the Eastern North Pacific (ENP), swordfish movement and habitat characterization studies have focused on both temperate foraging grounds along the USA west coast (Sepulveda et al. 2010, 2019), as well as subtropical spawning areas (Dewar et al. 2011, Abecassis et al. 2012). Existing data has shown that swordfish display relatively consistent diurnal movement patterns across regions, with daytime depths typically spent well below the thermocline and nights largely within the waters of the upper mixed layer (Carey & Robinson 1981, Carey 1990, Dewar et al. 2011). One exception to this pattern is the daytime surface basking behavior that forms the basis of traditional harpoon fisheries (Ward et al. 2000, Takahashi et al. 2003, Stoehr et al. 2018).

Although relatively consistent diurnal movement trends have been documented for swordfish across ocean basins, daytime depth distribution has been shown to vary by both region and oceanography

Associate Editor: Yassir Torres

(Sepulveda et al. 2010, Dewar et al. 2011). While offshore, swordfish in the North Pacific exhibited relatively consistent vertical movement patterns, with daytime depths ranging between 400-600 m (Dewar et al. 2011, Abecassis et al. 2012). In contrast, shallower daytime depths (250-400 m) have been recorded from tagged swordfish that move into productive foraging areas along the eastern margins of the basin, where average daytime depths approximate the upper reaches of the oxygen minimum zone (OMZ; Prince & Goodyear 2006, Sepulveda et al. 2010, Dewar et al. 2011).

Off California, the reduced average daytime depths have led to the development of a daytime fishery that targets swordfish below the thermocline (Sepulveda et al. 2014, Sepulveda & Aalbers 2018). The new deep-set fishery has resulted in high selectivity for swordfish and low levels of bycatch and has offered a way to circumvent fishery interactions with sensitive species (i.e. sea turtles and marine mammals), a common problem in shallow-set swordfish operations of the North Pacific (Carretta et al. 2003, Sepulveda et al. 2023).

Like California, Chile has one of the most productive coastal ecosystems in the world, which serves as a foraging ground for swordfish and other highly migratory species (Yáñez et al. 2008, Bakun et al. 2015, Lazo-Andrade et al. 2021). Similar to other eastern boundary current systems, Chilean surface waters exhibit exceptionally high levels of primary production, which, when coupled with low rates of midwater mixing, generates a shallow (<100 m) and pronounced OMZ (Morales et al. 1999, Stramma et al. 2010). The waters off the Chilean coast also support vast commercial fisheries, including an inshore harpoon and drift-gillnet (DGN) fishery that targets swordfish within the rich foraging grounds of the Humboldt Current System (Lazo-Andrade et al. 2021).

Previous electronic tagging efforts off South America have documented swordfish movements in offshore regions targeted by longline fisheries operating at night within the upper 100 m of the water column (Abascal et al. 2010). Abascal et al. (2010) reported that swordfish depth distribution within offshore areas of the South Pacific typically ranges from 400-600 m during the day, which directly aligns with findings from the North Pacific (Dewar et al. 2011, Abecassis et al. 2012) and the Atlantic (Neilson et al. 2009, Dewar et al. 2011). Given that swordfish movements have not been well documented throughout their entire range, it is not known if the daytime depth distribution trends observed in the ENP hold true for other areas in the Pacific, including other eastern boundary current systems like the one off South America (Pauly & Christensen 1995, Karstensen & Ulloa 2009).

Swordfish movements and habitat utilization off coastal Chile remain poorly understood despite its continued economic importance. Although Abascal et al. (2010) published a tagging study from the Southern Ocean, all swordfish were tagged offshore (>1000 km) and well outside of the Chilean Exclusive Economic Zone (EEZ). This work provides the first evaluation of adult swordfish movement patterns relative to regional fishery operations and oceanographic conditions within the productive coastal waters of northern Chile. Given that the eastern boundary current systems off California and Chile are both regional upwelling centers that serve as seasonal foraging grounds for swordfish, the following hypotheses were proposed: 1) swordfish off coastal Chile display a shallower daytime depth distribution compared to those documented within offshore waters, and 2) the coastal depth distribution will allow for additional opportunities to target swordfish during the daytime.

MATERIALS AND METHODS

Research location and permitting

Swordfish tagging operations were performed along the northern coast of Chile during the primary swordfish harpoon season (March-May), based aboard the fishing vessel FV "Rocio Lucilla 1" a 13 m artisanal harpoon vessel based out of the port of Taltal (25.4°S, 70.5°W). Electronic tagging efforts were focused within the coastal waters between 25 to 27°S and out to 71.5°W on two 10-day vessel charters in March 2019 and April 2022 (Fig. 2). All tagging activities were performed under permissions granted by the authority of the Undersecretary de Pesca y Acuicultura (Resolution EX. 776/2019 & Resolution EX. 109/2020).

Tag specifications and attachment

Multiple electronic tags were deployed on the same swordfish to maximize the collection of movement and environmental data from each individual. Tags used in this study included Wildlife Computers (WC) MiniPATs, WC Mark-Recapture (mrPAT) tags, and Cefas G5 data storage tags (DSTs). Satellite-based tags were programmed for 30-day deployments (WC MiniPATs) or 180-day schedules (mrPAT) to collect both fine-scale (5 min resolution) time series data and longer-term horizontal movement data. Following the scheduled deployment period or in the event of a premature release from the fish, time series and geolocation data were transmitted to the Argos satellite network and subsequently downloaded by the research team. Cefas G5 DSTs were programmed to record 1 min resolution depth and temperature data. The DSTs were used to secure additional data if a local fishing vessel recovered a tag. MiniPATs and DSTs were rigged using duplicate 100 kg monofilament tethers crimped to a plastic umbrella dart so DSTs remained implanted after PSATs were released (Sepulveda et al. 2018). Tag darts were inserted into the dorsal musculature of surface basking swordfish using extended harpoon poles affixed with modified tag applicator tips.

Tagging procedures

Following tagging methods used off California (Sepulveda et al. 2010, 2018), basking swordfish were spotted at the surface using stabilized binoculars and tagged from an extended (2 m) bow pulpit using a modified harpoon. Two harpoons were used simultaneously by two different taggers to maximize productivity and deploy multiple tags on each swordfish, similar to the regional protocols used by the harpoon fleet out of Taltal (Fig. 1). To maximize the collection of vertical and horizontal movement data from each individual; there was an attempt to deploy three different electronic tags on each swordfish. Electronic tagging activities were centered along areas of thermal convergence and productivity targeted by other commercial harpoon vessels based out of Taltal and neighboring ports. Areas of convergence were identified using an onboard water temperature recorder and sea-surface temperature and chlorophyll concentration data obtained from Aqua and Terra earth-observing system satellites.

Environmental data

Swordfish size estimates were based on either the weight approximated by the tagging crew (Swordfish #1, 3) or the dressed weight reported by the captain upon recapture (Swordfish #2, 4). The geographic position and environmental conditions, including sea state, sea-surface temperature, and water color, were also recorded for each tagging event. The water column was sampled using an RBRconcerto[3] optical dissolved oxygen sensor (RBR Ltd. Ottawa, Canada) to obtain high-resolution (0.5 s) temperature/depth/oxygen profiles down to 300 m at each tagging site (Table 1). Although spatial and temporal scales varied between data sources, dissolved oxygen (DO) levels at depth (0.5 m resolution) recorded from each tagging location were compared with 1) depth (0.5 m resolution) and temperature (0.1°C) data recovered from tagged swordfish, 2) World Ocean Atlas data (5-25 m depth and 1° latitude-longitude resolution; Boyer et al. 2018), and 3) published literature from the Antofagasta region (Fuenzalida et al. 2009). DO data were used to characterize habitat utilization and identify environmental conditions that may influence swordfish vertical movements and regional fishery operations. Because there has been variability in the reporting of OMZ thresholds and measurement units (Levin 2003, Karstensen et al. 2008), depth DO levels were examined for both the 1.5 mg L^{-1} (~45 µmol kg^{-1}) and 0.7 mg L^{-1} (~22 µmol kg^{-1}) concentrations.

Data analyses

Downloaded files were formatted and imported into a Microsoft Access database with satellite-derived time series (5 min resolution) data analyzed independently from archived depth and temperature records (1-s and 1-min resolution). All records were converted (UTC-4) to Chile Standard Time (CLT) and classified as day, night, or twilight based on the mean monthly time of sunrise, sunset, and nautical twilight at the midpoint between tag deployment and recovery locations from the Astronomical US Naval Observatory (2022). Daytime values were assigned to all periods between sunrise and sunset. In contrast, nighttime was assigned for periods between the average time of nautical twilight at dusk and nautical twilight at dawn. Records were considered twilight if times occurred between the meantime of sunset and nautical twilight at dusk or from nautical twilight at dawn to sunrise. Paired t-tests were used to test for differences in diel depth distribution. Mean and standard deviation (SD) values were presented with significance inferred at <0.05.

The collective depth and temperature histograms were generated by calculating the percent occurrence at 30 m depth intervals and 1°C temperature bins for both day and nighttime periods. Sea-surface temperature (SST) values were derived from temperature records at depths ≤3 m, either from transmitted or recovered MiniPAT time-series data and longer-term DST records. Fine-scale data archives from recaptured swordfish were further analyzed to evaluate the vertical rate of movement (VROM) by calculating the absolute change in depth divided by descent and ascent times. Thermocline depth was calculated from 1-s resolution time-series records as the maximum temperature gradient (delta T) between subsequent 1-m depth bins and compared against the steepest portion of the temperature-at-depth curve. Calculated thermocline depths were verified against WC mixed-layer depth estimates generated from transmitted MiniPAT data

Figure 1. Double tagging a basking swordfish (178980) using satellite-based pop-up transmitters implanted using modified harpoons from the 2 m extended bow pulpit of the artisanal harpoon vessel "Rocio Lucilla 1". Techniques adapted from the local harpoon fleet based out of Taltal, Chile. (Photo credit: Ralph Pace).

Table 1. Deployment and recovery information from four swordfish outfitted with multiple electronic tags off the coast of northern Chile. TAL: time at liberty; SST: sea-surface temperature; OMZ depth: depth of oxygen minimum zone at which dissolved oxygen level settled below 1.5 mg L^{-1} from cast recorded at each tagging site; Est. wt.: swordfish whole weight estimated by tagging crew.

Fish #	Tag type	Tag number	Deploy date	Deployment location	Recovery date	Recovery location	TAL (d)	SST (°C)	OMZ depth (m)	Est.wt. (kg)
1	MiniPAT	178978	3/15/19	25.38°S/70.75°W	4/16/19	22.71°S/72.40°W	30	21.5	119	150
1	MrPAT	176955	3/15/19	25.38°S/70.75°W	3/19/19	24.99°S/71.50°W	4	21.5	119	150
2	MiniPAT	178979	3/17/19	25.51°S/70.79°W	4/18/19	24.75°S/72.78°W	30	19.6	135	100
2	Cefas DST	A15226	3/17/19	25.51°S/70.79°W	7/7/19	23.54°S/71.60°W	112	19.6	135	100
3	MiniPAT	178980	3/18/19	25.66°S/70.86°W	3/20/19	25.26°S/71.18°W	2	19.8	111	110
3	MrPAT	176963	3/18/19	25.66°S/70.86°W	4/06/19	24.08°S/70.74°W	18	19.8	111	110
4	MiniPAT	164529	4/29/22	26.66°S/71.18°W	4/30/22	26.56°S/71.09°W	1	17.8	115	270
4	Cefas DST	A18647	4/29/22	26.66°S/71.18°W	4/30/22	26.56°S/71.09°W	1	17.8	115	270

files and values in published literature from the study area during the fall season (Morales et al. 1999). The average thermocline temperature was calculated as the mean temperature value between subsequent 1-m depth bins spanning the maximum temperature gradient.

Net displacement and horizontal rate of movement (HROM) were determined from the distances and heading between initial release points and pop-up locations. For double-tagged individuals, net displacement and heading values were calculated for both MiniPAT and mrPAT pop-up locations and reported recapture locations. Estimated track lines were also generated through the WC proprietary GPE3 model and displayed in ArcGIS Pro (Version 10.7.1. Environmental Systems Research Institute [ESRI], Inc. Redlands, CA) for spatial analysis; however, geolocation estimates were not used for HROM analyses due to the limited deployment duration and the lack of adequate illumination at depth for generating accurate light curves.

RESULTS

Tagging

Electronic tags (n = 10) were deployed on four free-swimming swordfish within the Antofagasta region of northern Chile from the artisanal harpoon vessel FV "Rocio Lucilla 1" during two research cruises based out

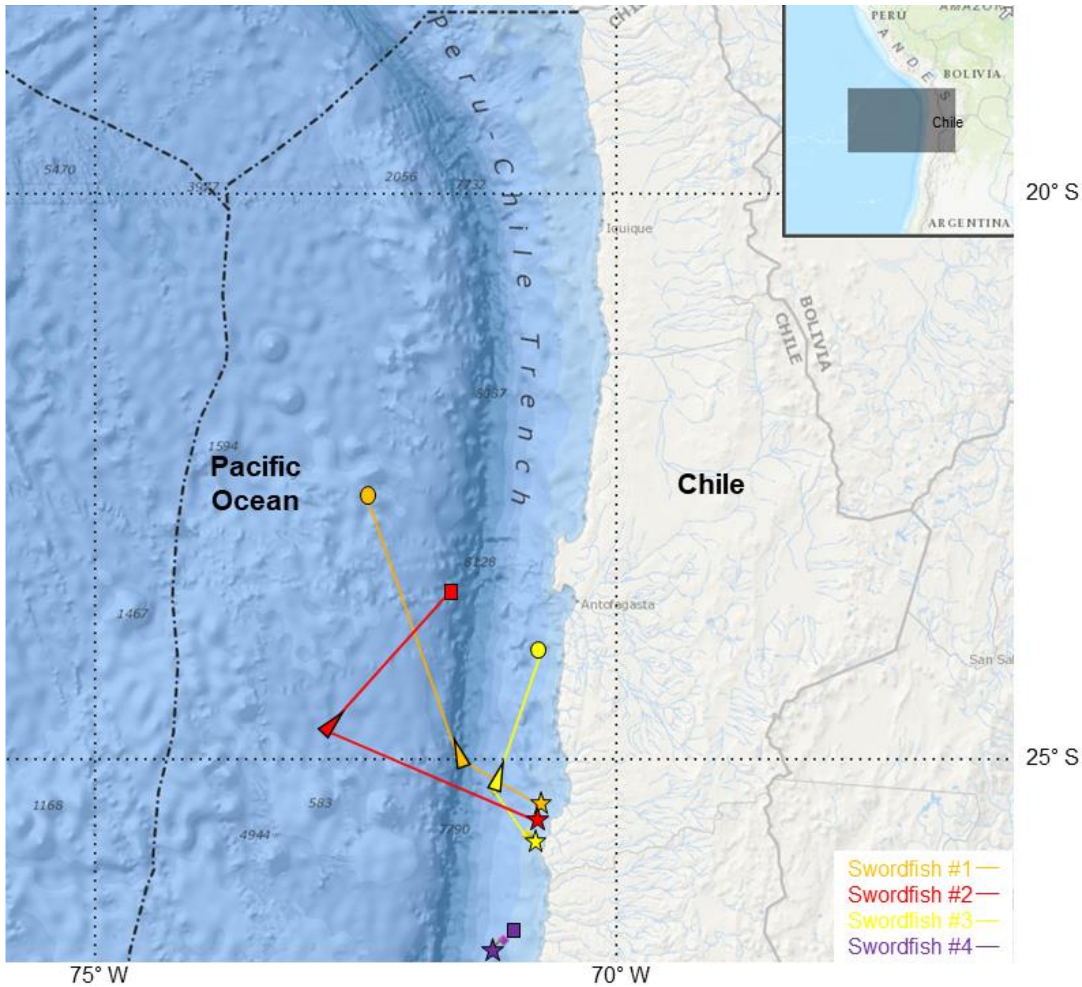

Figure 2. Map of the northern Chile coastal study area exhibiting the deployment (star), initial reporting (triangle), pop-up (circle), and recapture (square) locations for eight electronic tags deployed on four swordfish in the southeastern Pacific Ocean.

of the port of Taltal in 2019 and 2022 (Fig. 2). Tagged swordfish had an estimated weight range of 100-270 kg (Table 1). Fine-scale movement data were obtained from eight electronic tags deployed on four swordfish. Two of the DSTs have not yet been recovered as of this work.

Depth distribution

Swordfish exhibited regionally unique diurnal behaviors with significantly greater average daytime depths than those recorded at night (78.0 ± 66.5 and 12.7 ± 4.9 m, respectively). Based on transmitted time-series data (5-min resolution) from four miniPATs, swordfish spent 95% of the nighttime within the upper 50 m of the water column and 99% of the nighttime above 65 m (Fig. 3). Tagged swordfish occupied the upper mixed layer (<30 m) approximately 85% of the nighttime and occurred above 11 m over 37% of the night, with 12% of the nighttime spent in the upper 3 m of the water column. Similarly, daytime basking (≤3 m) occupied approximately 12% of the collective daylight records and varied between individuals in frequency and duration, with Swordfish #3 basking across 53% of the day. Surface basking occurred throughout the daylight hours, although most (51%) of overall time spent at the surface occurred between 14:00 and 18:00 h.

Although daytime dives to a maximum depth of 750 m were recorded, the overall mean daytime depth was much shallower (78.0 ± 66.5 m). Collectively, tagged swordfish spent less than 15% of the daytime at depths greater than 150 m (Fig. 4a), with most deeper daytime dives recorded during a single track (Swordfish #1). Swordfish #1 spent more than 27% of the daytime at depths exceeding 150 m, with multiple dives below 500 m

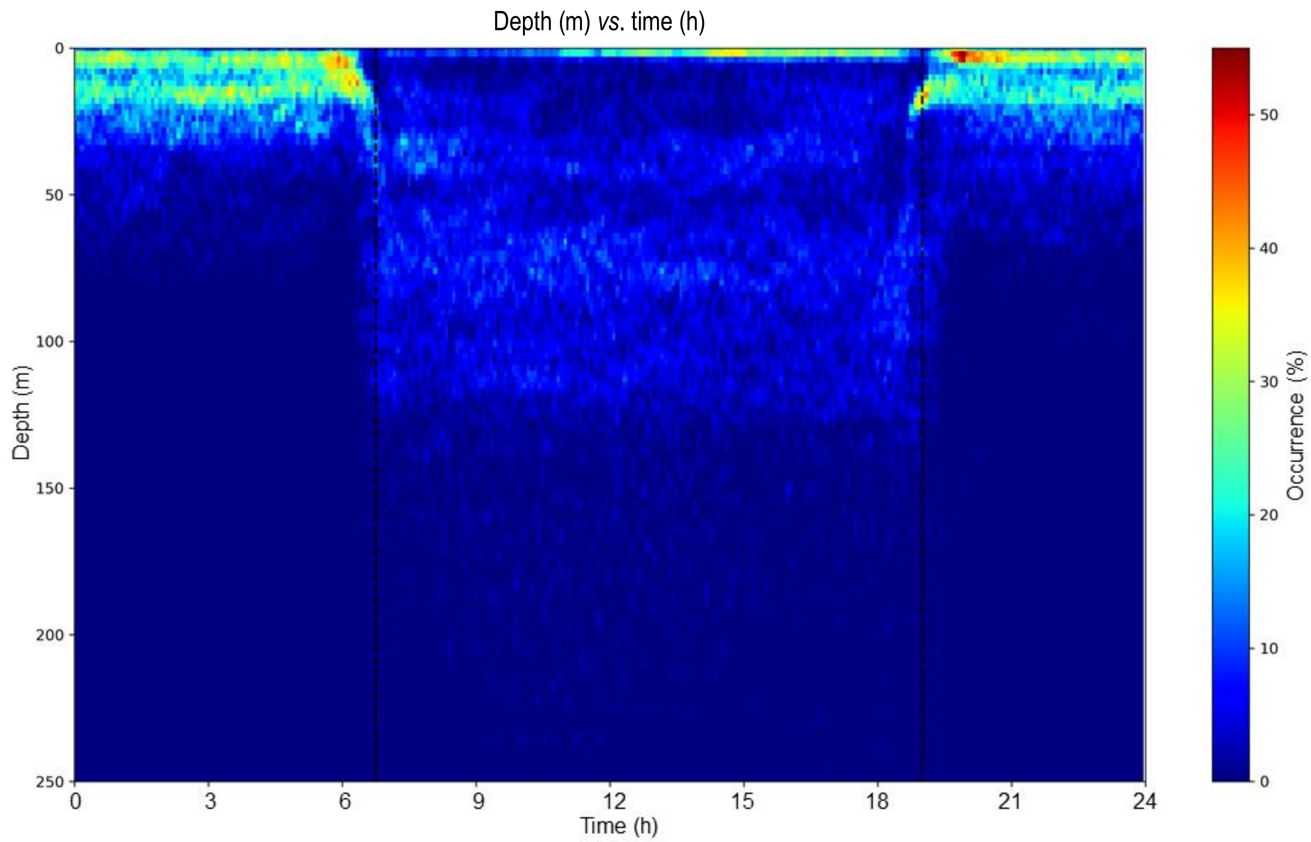

Figure 3. Joint 24 h depth probability plot (<250 m), which illustrates the cumulative probability of occurrence from four swordfish tracks along the coast of northern Chile. Vertical dotted lines indicate the approximate Chilean standard time (CLT) of sunrise and sunset.

(maximum depth = 750 m) for periods of up to 8 h in duration. In contrast, the other three tagged swordfish collectively spent less than 2% of the day below 150 m with brief and infrequent dives up to 742 m (Swordfish #2). Fine-scale (1-s) depth and temperature records from Swordfish #4 revealed that only 7 min of the day were spent deeper than 150 m, while Swordfish #3 did not dive deeper than 142 m during its 2-day track. Swordfish #4 exhibited a series of 11 daytime dives below 50 m to a maximum depth of 170 m, with a mean dive duration of only 10.5 ± 2.5 min. Vertical rates of movement (VROM) during consecutive dives ranged from 7.6-22.4 m min^{-1} ($\bar{x}$ = 12.0 ± 4.3 m min^{-1}) upon descent and increased to 28.6 ± 7.5 m min^{-1} on average (range: 16.6-38.8 m min^{-1}) during ascents from depth.

Temperature profiles

Daytime water temperatures reached a maximum of 23.0°C near the surface and a minimum of 5.4°C at depth ($\bar{x}$ = 15.0 ± 4.4°C). Water temperatures at night ranged from 21.9 to 12.4°C with an overall mean nighttime temperature of 19.4 ± 1.8°C (Fig. 4b). At the surface (depths above 3 m), swordfish occurred within SSTs that ranged from 14.0 to 23.0°C, with an overall mean SST of 20.3 ± 1.0°C. Mean SST values were lower ($\bar{x}$ = 17.0°C) for the short-duration track of Swordfish #4, where SST values ranged from 16.3 to 17.4°C, with a mean thermocline temperature of approximately 15.4°C.

Electronic tag recaptures

The depth and temperature-sensitive DSTs recovered from two recaptured swordfish provided fine-scale time series data throughout the time at liberty. On July 7, 2019, Swordfish #2 was recaptured aboard a Chilean DGN vessel weighing 108 kg, providing four months of depth and temperature data (1-min resolution). Dives up to 742 m were recorded, and archived data records indicated that 95% of daytime dives were to depths of less than 125 m, and 95% of the nighttime was spent at depths above 50 m.

Additionally, Swordfish #4 was recaptured by an artisanal harpoon vessel on April 30, 2022, at a dressed weight of 215 kg, providing the return of both the

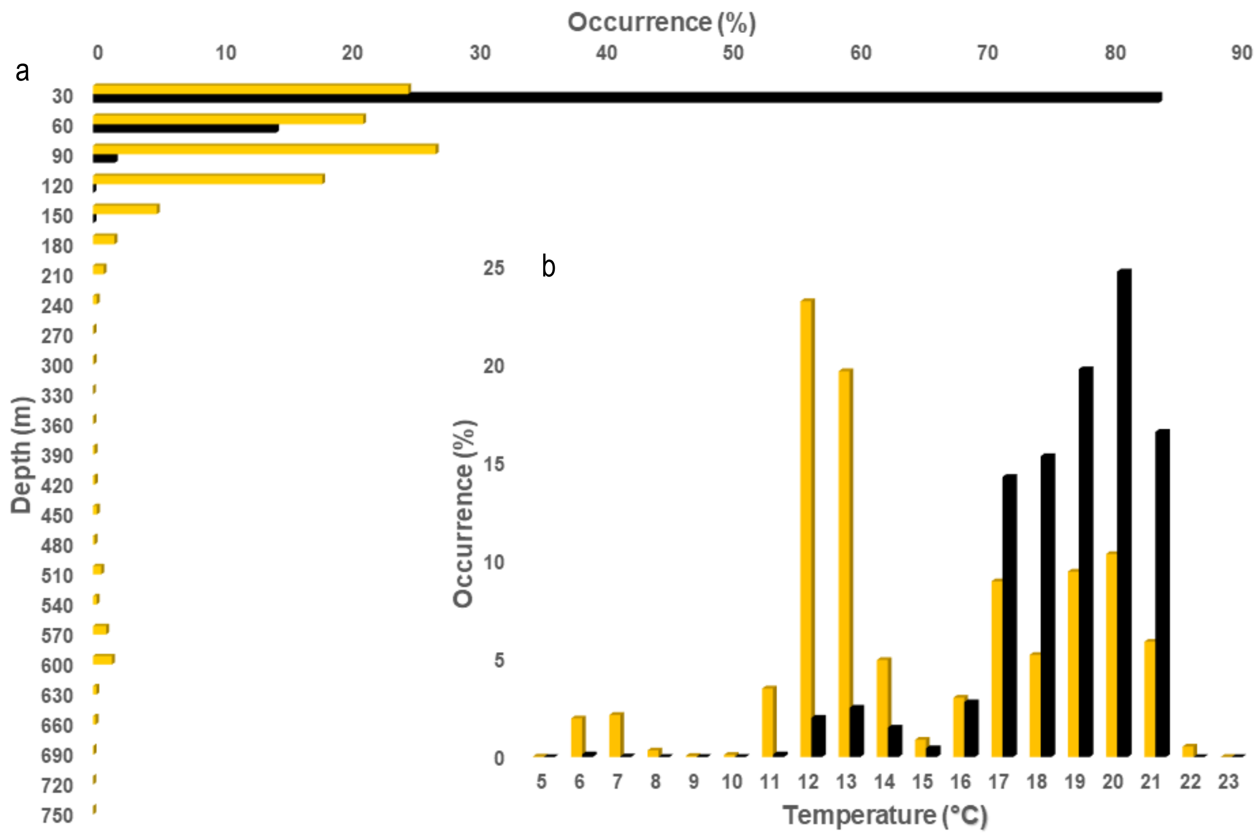

Figure 4. a) Cumulative depth and b) temperature distribution for both daytime (yellow bars) and nighttime (black bars) periods binned from collective tag data obtained from four swordfish tracked off the coast of northern Chile.

MiniPAT and Cefas DST. The recovery of both electronic tags provided fine-scale depth and temperature data over 24 h (Fig. 5) at both 1-s and 1-min resolution. Water temperature ranged from 11.4 to 17.4°C between the surface and 170 m during this short-term track. High-resolution (1-s) data from Swordfish #4 revealed a thermocline depth of approximately 30 m, with more than 99% of the nighttime spent within the upper mixed layer (Figs. 6a-b). Swordfish #4 spent 95% of the daytime hours at depths less than 115 m and 99% of the day above 150 m.

Dissolved oxygen (DO)

DO levels remained above 6.0 mg L^{-1} throughout the upper mixed layer at depths above the thermocline, which ranged from 25-50 m across tracks. Water column profiles recorded immediately after each successful tagging event revealed similar trends between tag deployment sites. For two of the tagging site casts (Swordfish #2, 4), DO concentrations abruptly dropped to 1.5 mg L^{-1} (~45 µmol kg^{-1}) at depths as shallow as 80 m and then increased slightly (1.6-2.0 mg L^{-1}) between 80 and 100 m before settling below 1.5 mg L^{-1} at depths of 105-115 m and below 0.7 mg L^{-1} (~22 µmol kg^{-1}) between 125 and 155 m (Fig. 7). Daytime depth distributions aligned closely with DO profiles, as the track data show that swordfish collectively spent less than 5% of the daytime within the portion of the water column (125-400 m) at DO concentrations of less than 1.5 mg L^{-1} (Fig. 8). Whereas, Swordfish #3 spent less than 1% of the daylight hours at depths below 111 m, where the recorded DO contour dropped below 1.5 mg L^{-1} (Table 1).

Horizontal movements

Given the limited time at liberty and because the main focus of this work was aimed at quantifying vertical movements, only cursory analyses were performed on swordfish horizontal movements. All tagged swordfish moved northward (40-302° true heading) from initial tagging locations, with movements of up to 357 km along the coast of Chile over 30 days (Fig. 2). Daily

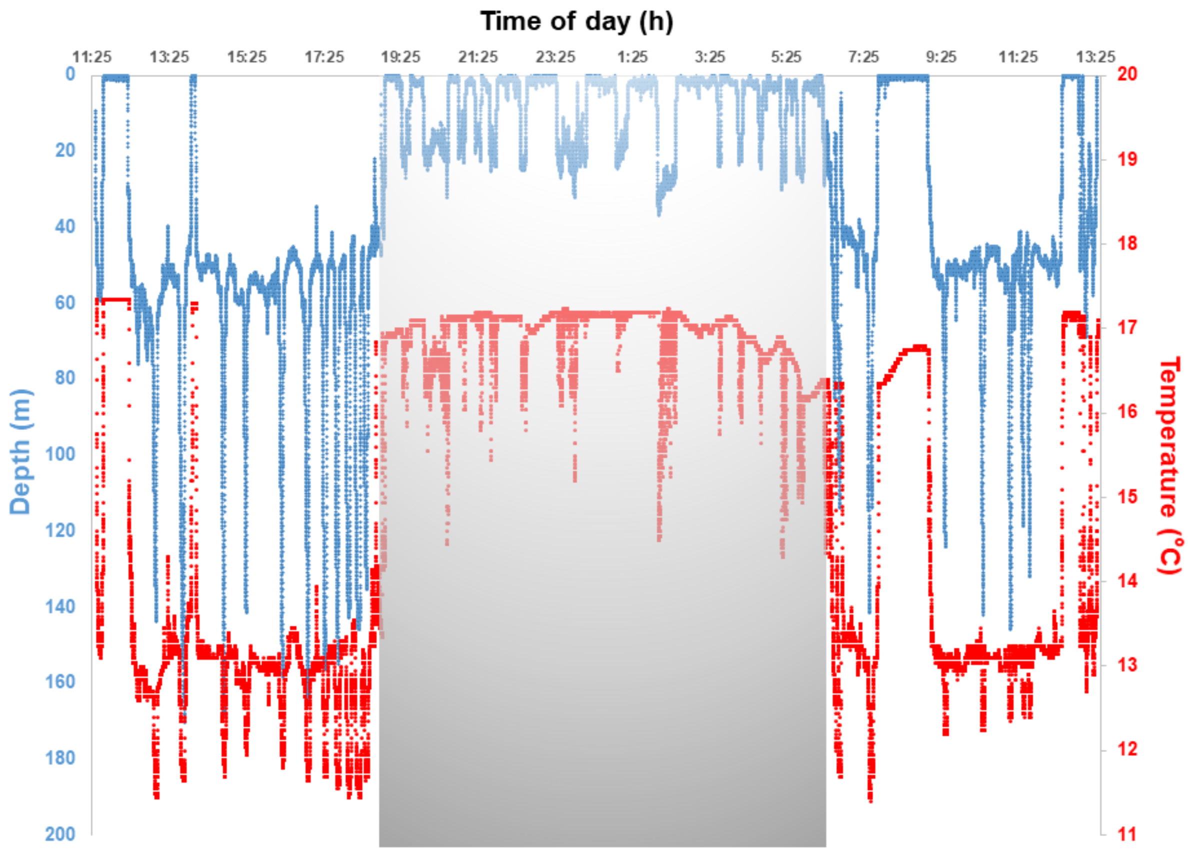

Figure 5. Twenty six hour depth (blue) and water temperature (red) profiles for a 270-kg swordfish 164529 that was tagged off the coast of northern Chile. The shaded box represents nighttime.

rates of horizontal movement (HROM) based on net displacements ranged from 2.2-17.6 km d^{-1} between individuals, with a collective mean HROM of 9.9 km d^{-1}.

DISCUSSION

This work documents the first movements of swordfish tagged along the coastal margin of the Eastern South Pacific. Similar to findings in the ENP (Carey & Robison 1981, Dewar et al. 2011, Sepulveda et al. 2018), the swordfish tagged off the coast of northern Chile revealed daytime depths that were much shallower than those documented for offshore waters (Abascal et al. 2010). The daily depth records also showed considerable basking activity, a behavior that has supported the use of harpoon methods in this region since the sixth millennium BCE (Béarez et al. 2016, Biton-Porsmoguer et al. 2022). The relatively shallow daytime existence aligns with areas of low DO levels. Also, it supports previous hypotheses that suggest oxygen content may restrict depth distribution and compress suitable habitats for pelagic species (Prince & Goodyear 2006, Abascal et al. 2010, Lam et al. 2015). Habitat compression can also impact prey movements, influencing predator depth distribution (Prince & Goodyear 2006, Leung et al. 2019). Although temporally and spatially limited, the daily movement data collected in this study provides insight into swordfish depth distribution and habitat use in the region. The data also provides insight into the spatial overlap of swordfish and existing commercial fisheries of the region, which may further our ability to improve fisheries and increase gear selectivity.

Depth distribution

Like previous studies, the swordfish tagged off northern Chile exhibited a wide range of vertical movements, spanning from the surface to depths more than 700 m (Dewar et al. 2011). However, the daytime dive profiles recorded in this study were considerably shallower and more variable than swordfish depths observed in other regions, including a previous tagging study performed further offshore (Abascal et al. 2010). Previous authors have proposed that the extensive

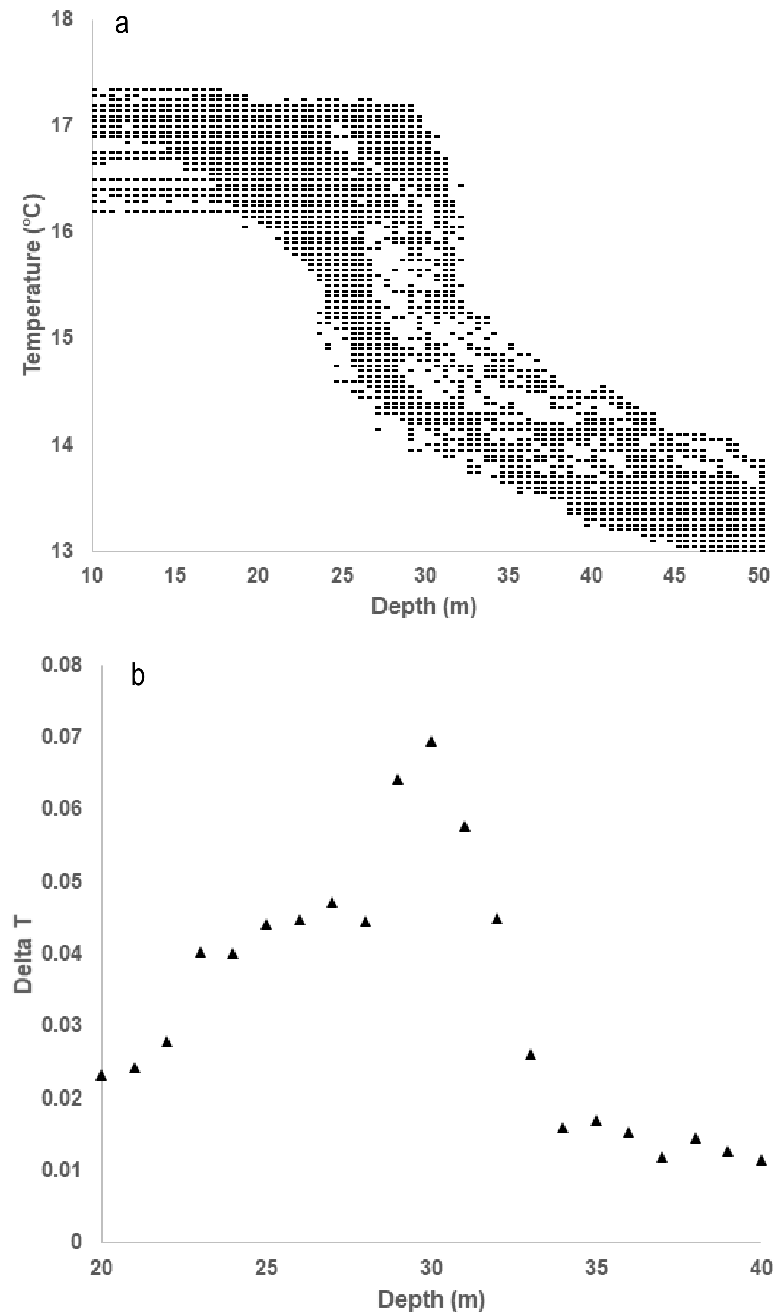

Figure 6. Fine-scale (1-s resolution) temperature at depth data obtained from swordfish 164529. a) Temperature at depth plot, and b) delta T at depth plot showing a thermocline depth of approximately 30 m.

vertical movements of swordfish are related to foraging activity focused on prey associated with the deep scattering layer (Carey 1990, Dewar et al. 2011, Sepulveda et al. 2018). The unique ability to tolerate extreme temperature fluctuations and reduced oxygen levels at depth enables swordfish to follow vertically migrating prey from the surface waters at night to the cold waters below the OMZ during the daytime (Wegner et al. 2009, Stoehr et al. 2018).

High-resolution datasets from electronic and satellite-based tag technologies revealed relatively shallow daytime depths, with movements largely confined to the upper 150 m of the water column. Although periodic deep-dives to over 700 m were

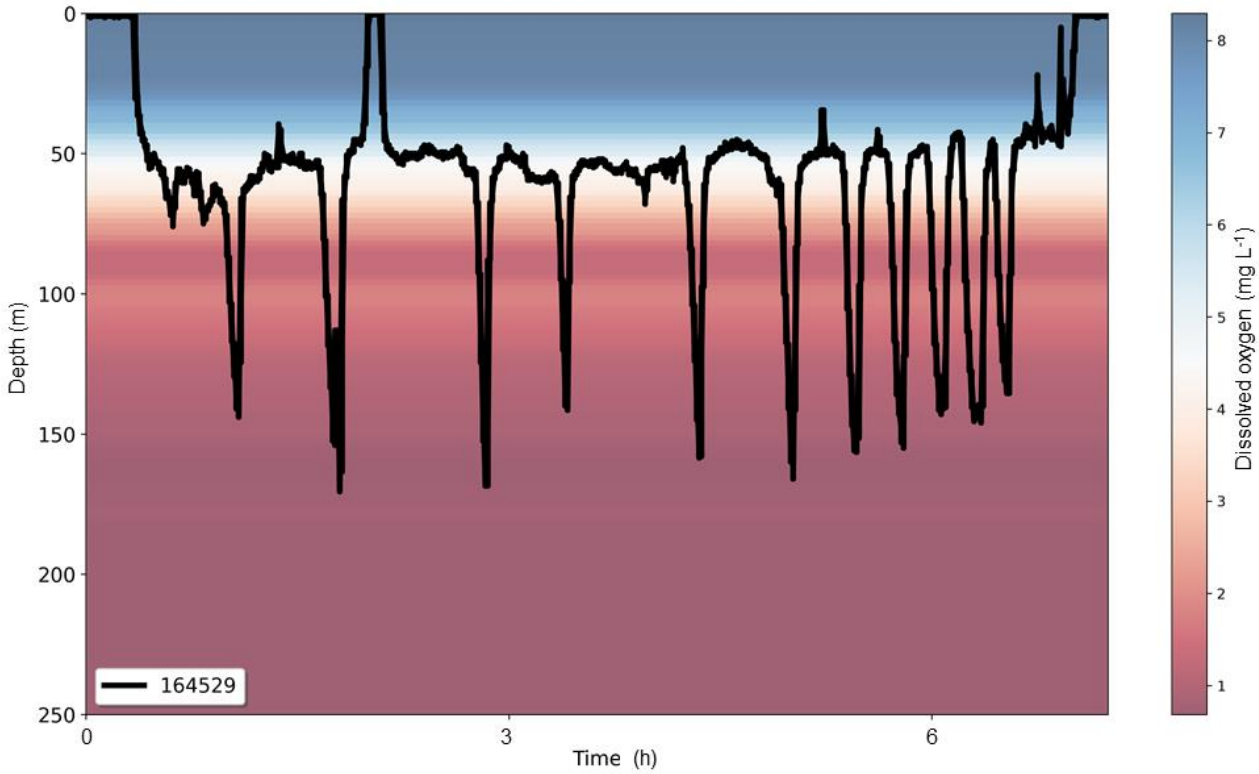

Figure 7. Daytime depth records from an 8 h period from swordfish 164529. Depth distribution is plotted over the dissolved oxygen concentration (mg L^{-1}) measured at the tagging site.

occasionally observed, most of the time spent below 150 m was observed from the single track of a 150-kg individual (Swordfish #1). Swordfish #1 may have ventured further offshore, outside the hypoxic shelf waters, or pushed beyond the OMZ to depths with higher DO concentrations. Regional World Ocean Atlas (WOA) data (25.5°S, 71.5°W) support the presence of a shallow OMZ within the study area, with DO concentrations dropping below 0.7 mg L^{-1} (<22 µmol kg^{-1}) at approximately 150 m during March (Boyer et al. 2018). Although the depth, thickness, and intensity of hypoxic areas vary considerably across different seasons and locations along northern Chile (Fuenzalida et al. 2009), mean annual DO levels within the study area (25.5°S, 71.5°W) remained relatively low between 150 and 400 m. Based on WOA data, DO concentrations increased above 1.5 mg L^{-1} (~45 µmol kg^{-1}) at around 400 m and up to approximately 3.0 mg L^{-1} (~90 µmol kg^{-1}) at 600 m (Boyer et al. 2018). Considering that regional DO concentrations at a depth of 600 m were reported at more than three times greater than those at 150 m, it may be that deeper waters may be more habitable for swordfish compared to the waters of the OMZ.

Depth, temperature, and DO data from water column profiling performed after each swordfish tagging event revealed a relatively shallow OMZ (0.7 mg L^{-1} at 155 m), which aligned with published DO estimates and WOA data sources for the region (Fig. 7; Fuenzalida et al. 2009, Abascal et al. 2010, Boyer et al. 2018). These data additionally support previous swordfish tagging studies in other parts of the Pacific that are also known to have a shallow OMZ (Carey & Robison 1981, Trucco-Pignata et al. 2019). For example, Carey & Robison (1981) showed that swordfish tracked off Baja California Sur (BCS), a region with a similarly shallow OMZ, exhibited limited vertical movements, largely restricted to the upper 100 m (Trucco-Pignata et al. 2019). Carey & Robison (1981) also proposed that areas of high stratification (temperature and oxygen) may contribute to increased basking activity, a behavior common off BCS as well as the waters off coastal Chile (Vega & Licandeo 2009). Similar vertical movement patterns observed between swordfish tagged off BCS and in this study may be related to the comparable oceanographic conditions of the two regions, considering that both eastern boundary current systems are highly productive areas with similar

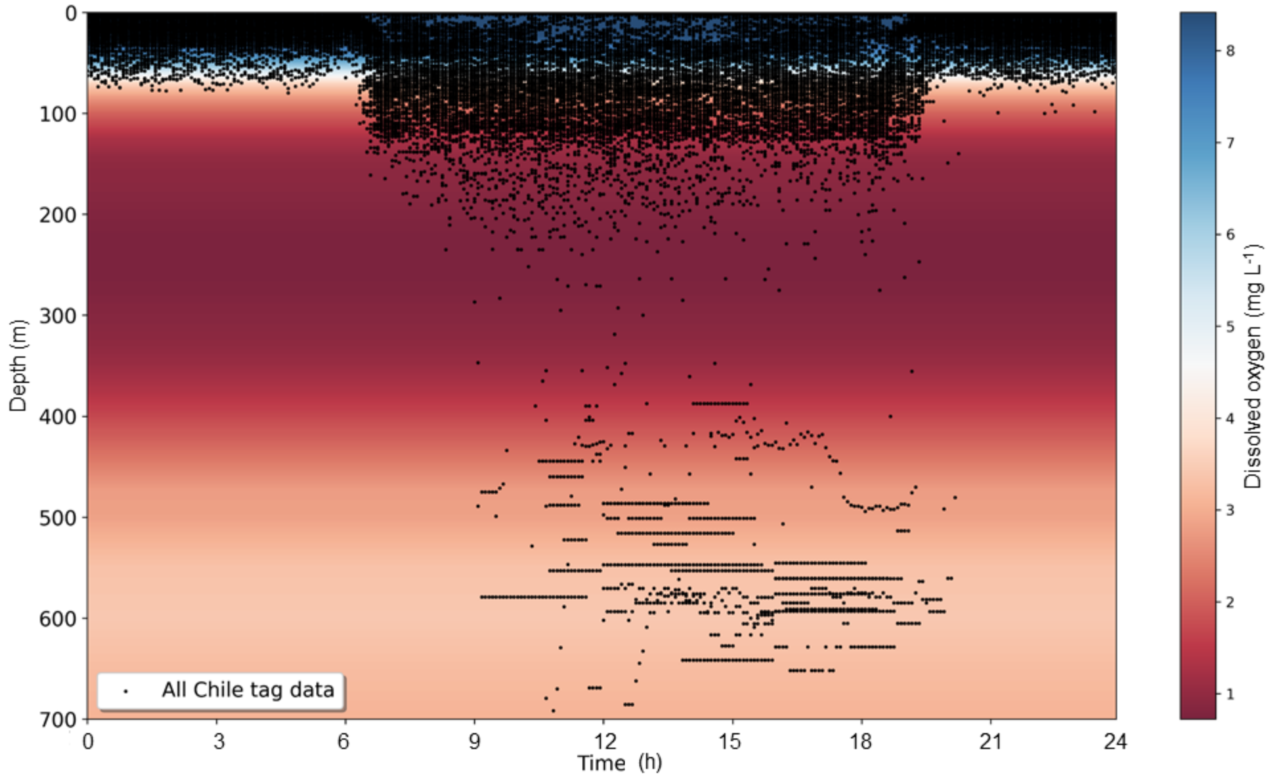

Figure 8. Jointed 24-h depth distribution of four swordfish tagged off of northern Chile in relation to dissolved oxygen concentration (mg L^{-1}) converted from the statistical means of available O_2 data collected over multiple years (1960-2018) for the corresponding season, 1° study area grids (25.5°N, 71.5°W), and depth range (0-750 m) from the 2018 World Ocean Atlas (Boyer et al. 2018).

latitudes, temperatures, and DO profiles (Fuenzalida et al. 2009, Boyer et al. 2018, Trucco-Pignata et al. 2019).

The data presented in this study also align with those from one of the tagged swordfish (tag 73552) in the Abascal et al. (2010) study. Despite uncertainty on the exact location of Swordfish 73552, the fish was tracked during a similar time of year (March-April) and exhibited a much shallower track than the rest of the swordfish in the Abascal et al. (2010) study. Abascal et al. (2010) proposed that daytime depths correlate with distance from shore. They were likely influenced by regional DO levels at depth, as OMZ depth has been shown to increase in this region with distance from the coast (Fuenzalida et al. 2009, Boyer et al. 2018).

Similar movement trends have been documented off California, where swordfish depth distribution has also increased with distance from shore (Sepulveda et al. 2010, 2018, Dewar et al. 2011). Although the upper reaches of the OMZ off California are much deeper than that described for coastal Chile, it may be that oxygen concentration at depth is a determining factor in predicting the vertical distribution of swordfish or possibly the prey distribution that influences swordfish movements. As previous authors suggested, regional oceanography and the depth distribution of the local forage base must be considered potential drivers of swordfish depth distribution (Abascal et al. 2010, Sepulveda et al. 2010, Evans et al. 2014).

Temperature at depth

Swordfish have been shown to possess several adaptations that help buffer the effects of extreme temperature change (Carey 1982, Block 1986), including an eye and brain warming system as well as modifications to their red aerobic swimming musculature (RM, RM is in a medial position) and circulation (the presence of heat exchanging retia associated with the RM) (Carey 1982, Block 1986, Stoehr et al. 2018). These adaptations have been proposed to enable swordfish to buffer rapid thermal changes and exploit waters often considered inaccessible to other fish (Stoehr et al. 2018). Despite being able to withstand extremely low ambient temperatures for prolonged periods, the average daytime temperatures encountered in this study ($\bar{x}$ = 15.0 ± 4.4°C) were considerably elevated compared with temperatures at depth reported for swordfish in nearby waters (Abascal et al. 2010) as well as those in other ocean basins (Dewar et al. 2011). The lack of consistent temperature-related trends recorded in this study suggests that water temperature did not significantly influence either day or nighttime movements. The vast majority (>90%) of daytime basking activity occurred within SST ranging between 19 and 22°C, and all swordfish consistently remained above the mean thermocline temperature of 15.4°C throughout the night.

Basking activity

The Taltal region of Chile is home to one of the oldest documented harpoon fisheries in the Pacific, with cave art showing harpoon techniques for swordfish dating back more than 7000 years (Béarez et al. 2016). The region where the tagging operations were performed continues to support a viable harpoon fleet dominated by small, artisanal vessels with a limited range. Although largely replaced by more industrial methods (longline, DGN), harpoon techniques continue to support artisanal fisheries in the Pacific, Atlantic, and Mediterranean seas (Coan et al. 1998, Ward et al. 2000, Vega et al. 2008, Neilson et al. 2009). Harpoon fisheries depend highly on relatively calm oceanic conditions and consistent seasonal basking activity. This behavior has been proposed to increase digestion rates (i.e. behavioral thermoregulation) as well as the recovery from oxygen debt (Carey & Robison 1981, Ward et al. 2000, Takahashi et al. 2003, Sepulveda et al. 2010, Evans et al. 2014). Similar to reports off California, harpoon fishers reported that basking swordfish off Taltal have stomachs commonly full of jumbo squid (*Dosidicus gigas*) or hake (*Merluccius* spp.) upon harvest, which further supports hypotheses that basking may be related to digestion (*pers. comm*. Cpt. Damian Leyton; Sepulveda et al. 2010).

Similar to previous swordfish tagging studies, this work capitalized on regional basking activity to deploy tags and document fine-scale movements (Neilson et al. 2009, Sepulveda et al. 2010). Because harpoon-based methods have been proposed to minimize the post-capture stress response typically induced by other gear types (i.e. hook and line, Wells et al. 1986), this study was able to record natural movements from the proximate tagging area without the swordfish immediately departing (Sepulveda et al. 2010). Whereas swordfish caught and tagged by hook and line have a tendency to immediately depart the tagging area with reduced diving/feeding activity, likely in response to stress associated with the capture event, precluding the collection of natural short-term movement data (Carey & Robison 1981, Sepulveda et al. 2010, Dewar et al. 2011). However, because basking swordfish often remain near the surface after being tagged by harpoon (Carey & Robison 1981, Sepulveda et al. 2010), they are often more likely to be recaptured by other fishing vessels operating within the area, which is the case for Swordfish #4, which was tagged on April 29, 2022, and subsequently harpooned by another fishing vessel near the tag deployment site the following day.

Although harpoon-based tagging may provide fine-scale movement data for a specific location, tag positioning and retention rates are often compromised compared to the tagging of restrained fish (Sepulveda et al. 2010, 2019). Swordfish tag retention rates increase when tag anchors are positioned near the base of the dorsal fin, which has a robust network of tendons and pterygiophores (Potthoff & Kelly 1982). Because harpoon tag placement is more variable and often only within the epaxial musculature, prematurely shedding is common and likely the reason for the early tag release from Swordfish #3 (Wilson et al. 2005).

Harpoon fishery

Harpoon fishing continues to be one of the most selective harvest methods for targeting swordfish worldwide (Coan et al. 1998). Although extremely effective at times, harpoon fishing relies upon both calm conditions and consistent basking activity, factors that limit the locations and reliability of successful operations (Ward et al. 2000). Artisanal vessels primarily harvested swordfish off Chile using harpoons before 1984, with operations largely restricted to periods from January through May, when good weather and oceanic conditions as well as basking swordfish were present (Barbieri et al. 1998).

Based on the short-term tracks recorded in this study, swordfish spent up to 53% of the daytime either at or near the surface, with a collective basking rate of approximately 12%. The amount of time that swordfish remained at the surface was greater than the 8% basking rate reported from swordfish tagged off of southern California (Sepulveda et al. 2010) and slightly lower than that reported for fish off central California (16%; Sepulveda et al. 2018). Although traditional harpoon operations continue to be carried out along the north Chilean coast, data from this study suggests that the resource is not accessible to fishers most of the day (88%). Most basking activity was documented from 14:00 to 18:00 h CST, coinciding with increased periods of prevailing winds during the afternoon in this region. Heightened sea-state from strong winds and large swells throughout northern Chile may further inhibit the success of sight-based fisheries. Other logistical constraints, including high operating costs relative to returns and resource proximity to fishing ports, may further limit the economic feasibility of harpoon operations.

Drift gillnet fishery

Over the past two decades, DGN has remained the primary gear for harvesting swordfish within the Chilean Economic Exclusive Zone (Barbieri et al. 1998, IATTC 2022). The Chilean DGN fishery seasonally begins operations in January between 37 and 40°S, moving north with the resource towards 27 to 30°S by the end of the season in October (Barbieri et al. 1998). The Chilean DGN fishery operates predominantly at night, where fishers target swordfish within the near-surface waters along productive frontal zones throughout the region. DGN gear can be particularly effective in shallow and strong thermocline areas, as the stratification helps consolidate marine resources within the upper mixed layer at night (Hanan et al. 1993).

Based on the standard DGN net depth in the Chilean fishery (55 m; Barbieri et al. 1998) and the data obtained from the thermal profiling casts of this study, DGN gear deployed within the study area extends throughout the entire upper mixed layer. Using these data, we estimated swordfish vulnerability to Chilean DGN gear, which shows potential capture during >95% of the nighttime hours.

Because most other pelagic species also occur within the compressed upper mixed layer at night, the DGN fishery off the US West Coast implemented a minimum net depth of 11 m to reduce non-target catch (Hanan et al. 1993, Carretta et al. 2003, Sepulveda et al. 2004, Eguchi et al. 2016). Although a useful bycatch mitigation tool, the minimum net depth restriction can also significantly reduce target catch. For instance, using the swordfish movement data from this study and the 11 m restriction, swordfish would have remained outside of capture depth for 37% of the night hours. The potential loss of target catch associated with this type of net depth tailoring may not be an economically viable option for increasing gear selectivity. Tagging data also suggests that DGN is likely less effective for targeting swordfish during the daytime due to the deeper and more variable depth distribution exhibited. Although we acknowledge that the depth distribution patterns presented in this study are from short-term tags and may not persist throughout the year, the continued productivity of the DGN gear type for targeting swordfish in Chilean waters suggests that the upper mixed layer plays a central role in the movements of swordfish off the Chilean coast (Barbieri et al. 1998).

Longline fishery

Like DGN fisheries, shallow-set longline (SSLL) has been used to target swordfish at night along the Chilean coastline since 2001 (Ward et al. 2000, Vega & Licandeo 2009, Donoso & Dutton 2010); the Chilean SSLL vessels set between 1000 and 2000 hooks (depending on gear configuration) at night, spanning up to 80 km (Vega & Licandeo 2009). The fishery uses illuminated gangions that soak squid or fin bait (i.e. mackerel) in the surface waters at night, resulting in swordfish, tuna, and shark catch. Although SSLL remains the most common industrial gear used to harvest swordfish throughout the Pacific (Ito et al. 1998, IATTC 2022), the Chilean longline fleet declined to complete cessation in 2019 (IATTC 2022). Despite the recent trend, SSLL continues to be used by foreign fleets in the waters outside the Chilean EEZ (Abascal et al. 2010, IATTC 2022). It has been suggested that Chilean SSLL operations were less cost-effective than DGN operations due to high distances traveled, bait costs, and reduced swordfish landings (*pers. comm.* Cpt. Damian Leyton, Taltal, Chile). This study shows that shallow set operations within the upper 50 m of the water column at night should overlap with the swordfish resource. However, given that the shallow thermocline compresses other pelagic predators into the upper mixed layer, bycatch and bait predation from jumbo squid and sharks may complicate selective targeting and swordfish harvest rates.

Deep-setting for swordfish

Although not as common as industrial DGN and longline gears, deep-set fisheries for swordfish have recently expanded to several regions in the Pacific (Beverly & Robinson 2004, Onoda et al. 2006, Sepulveda & Aalbers 2018). Deep-set operations require understanding swordfish movement trends, with gear designed to target the resource at depths well below the thermocline during the day. Off California, deep-set gear configurations were developed using data similar to those collected in this study (Sepulveda et al. 2010, 2014, 2018). Because the efficiency of deep-set operations is reduced as swordfish daytime depths increase beyond 400 m, deep-setting is not economically viable in all parts of the Pacific (Boggs 2004). Further, because deep-set operations typically operate on a smaller horizontal footprint than shallow-set fisheries, they are most common in regions where the resource is either aggregated horizontally or within a narrow daytime depth range (250-350 m; Boggs 2004, Sepulveda et al. 2014, Sepulveda & Aalbers 2018). The daytime depth distribution of swordfish in this study was relatively variable and shallow (<150 m) compared to those reported from areas where deep-setting has been successfully trialed (250-350 m, Sepulveda et al. 2023). Based on the depth range reported in this study, an intermediately positioned hook and line fishery (i.e. ~100 m) could be designed to target swordfish during the day. However, there may be limited spatial segregation between swordfish and other non-target species, which could also influence effectiveness and selectivity. Additionally, given the abundance of jumbo squid found at similar depths within the region, targeting swordfish with illuminated baits may also lead to increased predation. This issue has also likely contributed to the decline of the Chilean SSLL fishery.

Regional ecology

This study was situated within an extremely productive region that has been proposed to be one of the most prolific upwelling centers in the world (Daneri et al. 2000, Carr & Kearns 2003, Ibáñez et al. 2015). In addition to supporting vast fisheries, the Chilean coastal waters also serve as an important foraging area for the South Pacific swordfish stock, with published and anecdotal reports suggesting that jumbo squid and South Pacific hake (*Merluccius gayi*) comprise a major part of the swordfish diet in this region (Letelier et al. 2009). Jumbo squid (locally known as jibia) are among the most abundant cephalopods in the Eastern Pacific Ocean and have been well-documented as an important prey item for swordfish (Alarcón-Muñoz et al. 2008, Ibáñez et al. 2015, Acosta-Pachón & Ortega-García 2019, Preti et al. 2023). Although the feeding ecology, movements, and seasonal distribution of these intermediate-trophic level predators is complex and largely unknown, it has been shown that *D. gigas* prey heavily upon the southern hake and that the regional biomass of both species is often correlated (Alarcón-Muñoz et al. 2008). Although regional catches and abundance of jumbo squid have fluctuated greatly over the years, with extended periods of absence off the Chilean coast, *D. gigas* has occurred with increasing abundance since 2001 and remains a very important fishery resource off Chile (Ibáñez et al. 2015). During the tagging cruises, neighboring vessels reported the presence of large *D. gigas* in the gut contents of swordfish that were harvested adjacent to the tagging locations, further supporting the importance of jumbo squid in the diet and movement patterns of swordfish along the coast of northern Chile.

CONCLUSION

This study provides insight into the fine-scale movements and habitat utilization of swordfish off the coast of northern Chile. This productive eastern boundary current system supports vast fishery production. Although limited, the data presented in this study reveal several similarities to swordfish movements reported off BCS, Mexico (Carey & Robison 1981), a region that is also situated within a productive eastern boundary current system with a shallow OMZ (Trucco-Pignata et al. 2019). These findings suggest that DO levels limit swordfish diving capacity or possibly aggregate prey resources such that daytime movements are largely confined to the upper 150 m of the water column. Based on the movement trends reported in this study, daytime sets with hooks positioned near the upper reaches of the OMZ (100-150 m) could provide local fishers with an additional swordfish targeting opportunity. However, gear selectivity may be limited given the proximity of baits to the upper mixed layer, and other factors, such as bait predation and gear overlap with the vast jumbo squid resource of the region, may also compromise target catch rates.

ACKNOWLEDGMENTS

This project was primarily conducted under support from The Nature Conservancy (TNC). The George T. Pfleger Foundation, the Offield Family Foundation, and the William H. and Mattie Wattis Harris Foundation provided additional support. Special thanks are offered to Ralph Pace, Damian Leyton, and the FV "Rocio Lucilla 1" crew. We also want to acknowledge the strong support and collaboration from the Instituto de Fomento Pesquero (IFOP) and Subsecretaría de Pesca (SUBPESCA), Chile.

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Received: May 16, 2023; Accepted: September 19, 2023

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