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Movement patterns of white seabass *Atractoscion nobilis* tagged along the coast of Baja California, Mexico

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Abstract This study outfitted wild-caught white seabass (*Atractoscion nobilis*) with electronic data storage tags (DSTs) to evaluate subsequent movements of adult fish captured along Baja California, Mexico (BC). Cefas G5 DSTs were surgically implanted into 89 wild-caught white seabass ranging in size from 66 to 152 cm TL between La Salina (32.11°N/116.90°W) and San Quintin (30.25°N/115.83°W), BC. Twenty-four tagged individuals (27%) were recaptured between April, 2010 and May, 2017, following a mean time at liberty of 608 days (range = 18–1424 days) and a mean displacement of approximately 125 km (± 173 km; range = 3–720 km) between the point of release and recapture. Tagged white seabass were recaptured between Santa Rosalillíta, BC (28.66° N/114.27°W) and Monterey Bay, California (36.65°N/121.86°W), with four individuals reported above the U.S-Mexico border. Collectively, 8547 days of archived data revealed that white seabass spent 95% of the time at depths <60 m, with a maximum depth of 158 m. Ambient water temperature ranged from 10.2 to 24.1 °C, with a mean (± SD) of 15.2 ± 0.4 °C. Seasonal shifts in depth profiles to deeper waters during the winter months were comparable with findings from previous tagging studies performed off California. Relatively high recapture rates reaffirm the economic importance of this resource in both the U.S. and Mexico, while tag recoveries within close proximity to particular deployment sites suggest seasonal site fidelity to specific geographic areas. White seabass movements between BC and California further support the transboundary nature of the stock and suggest that future management would benefit from international fishery policies.

Keywords Sciaenidae · Vertical movements · Depth distribution · Electronic tagging

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Introduction

Species of the family Sciaenidae comprise a valuable group of marine finfish that are extensively harvested throughout Northwestern Mexico (Cota-Nieto et al. 2018; Ojeda-Ruiz et al. 2019). Regional landing summaries incorporate several sciaenid species, including *Cynoscion parvipinnis & C. xanthulum*, into a corvina aggregate, with approximately 4500 metric tons of corvinas landed along the northern Gulf of California and Pacific coastline of Baja California (BC) in 2017 (CONAPESCA, 2017). White seabass (i.e. curvina blanca; *Atractoscion nobilis*) constitute a valuable component of corvina aggregate landings by small-scale operations from more than 30 established fishing

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communities within the state of BC (Cartamil et al. 2011; Moreno-Báez et al. 2012; Romo-Curiel et al. 2015; Rubio-Cisneros et al. 2016).

The vast majority of white seabass landed in Mexico have traditionally been exported directly to the United States, with ex-vessel values ranging from \$2.75–\$3.64 USD/kg between 2000 and 2006 (Escobedo-Olvera 2009, Cartamil et al. 2011). More recently the export market to the U.S. has grown considerably, with market prices nearly doubling over the past decade (Pers. Comm. D. Rudie). Market growth and steady demand has led to an increase in directed fishing effort for white seabass along the coast of BC and California, despite declining trends in California landings and spawning stock biomass since 2008 (Valero and Waterhouse 2016).

Prior to 1982, a considerable proportion of the white seabass landed in California was harvested by 12 to 20 California-based gillnet vessels that fished along the Baja California Peninsula during the fall and winter months (August–March; Skogsberg 1925; Vojkovich and Reed 1983). In some years, as much as 80% of the annual U.S. commercial white seabass catch occurred in Mexican waters, until foreign gillnet permits were revoked by Mexico in 1982 (Vojkovich and Reed 1983; Escobedo-Olvera 2009). At the same time, Mexico began to explore the potential for harvesting white seabass using small set and drift gillnets, pulled by hand (Escobedo-Olvera 2009). The Mexican gillnet fishery for white seabass grew quickly and is now an important source of seasonal income for fishers operating small pangas, less than 10 m in length, out of fishing camps along the Baja California Peninsula (Escobedo-Olvera 2009; Cartamil et al. 2011; Cota-Nieto et al. 2018). White seabass harvest along the Baja California Peninsula now predominantly occurs from May–September, with a peak in June (Escobedo-Olvera 2009), much of which is still caught using hand-pulled gillnets near the surface. However, a recent increase in the use of hydraulic spools to haul larger gillnets has been noted within several BC fishing communities, a trend that may continue to elevate fishing effort.

Despite a strong bi-national reliance on white seabass stocks, population connectivity across their range remains uncertain. Based on range-wide genetic analyses, it has been proposed that white seabass harvested along the Pacific coast of California and BC are part of the same breeding population (Coykendall 2005; Ríos-Medina, 2008), however; alternative hypotheses suggest that genetically distinct subpopulations exist both along Baja California Sur (BCS) as well as within the Gulf of California, (Franklin 1997; Franklin et al. 2016). Regional differences in otolith microchemistry and growth rates of age 1 fish have also been identified, suggesting some level of distinction between fish from the Southern California Bight (SCB) and BCS (Romo-Curiel et al. 2015; Romo-Curiel et al. 2016). Recent tagging work has demonstrated transboundary movements between southern California and BC (Aalbers & Sepulveda 2015); however, it is unclear to what extent the resource is shared between nations due to overall uncertainties in white seabass stock structure. It has long been suggested that successful management of this transboundary resource is dependent upon understanding fish movements and whether fish harvested along California and Baja California Peninsula are part of one intermixing population (i.e. Panmixia) (Maxwell 1977; California Department of Fish and Wildlife 2002). The objectives of this study were to assess white seabass movement patterns and population connectivity through electronic tagging of wild-caught individuals captured along the Baja California coastline and compare results with recent tagging studies performed off southern California.

Materials and methods

Tagging procedure and sampling regime

A total of 89 Cefas G5 and G5 long-life data storage tags (DSTs; Cefas Technology Limited [CTL], Suffolk, UK) were surgically implanted into the peritoneal cavity of wild-caught white seabass captured aboard 5-9 m pangas for hire along the BC coastline (Table 1). Capture locations were dependent upon seasonal availability within day-trip range of BC fishing communities between La Salina (32.11°N/116.90°W) and San Quintin (30.25°N/115.83°W), (Table 1, Fig. 1). Male and female white seabass, ranging in size from 66 to 152 cm TL (mean = 102 ± 24 cm) were opportunistically tagged and released over five consecutive seasons from July 6, 2009 to July 23, 2013. The majority of tagging occurred during the white seabass spawning season (Aalbers, 2008), with deployments during the months of June ($n = 31$), July ($n = 29$) and August ($n = 21$), along with eight deployments in September. Specific procedures for fish capture, tagging and sex determination were based around protocols further detailed in Aalbers and Sepulveda (2015).

Although this study was primarily focused on the movements of adult white seabass, a portion of the tagged females may have been immature considering that existing information on white seabass size of maturity data remains uncertain (Maxwell 1977; Ragen 1990). Based on preliminary findings from an inadequate study that macroscopically examined gonads from a limited number ($n = 3$) of females between 70 and 85 cm (Clark 1930), it was assumed that tagged females greater than 79 cm TL were mature and that all males tagged in this study were mature. Thus, approximately 10% of the females ($n = 7$) or unidentified individuals ($n = 2$) tagged in this study may have been immature, while three (13%) of the recaptured females (<79 cm TL) were assumed to be immature (Table 1). All identified males were assumed to be mature given their smaller size of maturity (~65 cm; Clark 1930; Thomas 1968).

All individuals selected for electronic tagging were mouth-hooked and in good physical condition (e.g., no hook damage) to minimize the potential for post-release mortalities caused by hooking injuries (Aalbers et al. 2004; Stutzer 2004). An external conventional tag (FIM-96; Floy Tag Inc. Seattle, WA, USA) was inserted into the dorsal musculature (traversing the primary dorsal fin pterygiophores) of all white seabass for secondary identification. Contact and reward information were printed in Spanish and English upon both the stalk and body of the DSTs as well as on externally affixed conventional tags. A $200 cash reward was distributed to fishers upon recovery of a DST along with recapture specifics. Metrics (i.e. fish size [TL], sex, date, geographic location, general fish condition) were recorded upon tag deployment and recovery. Net displacement values and bearings were calculated between initial tag deployment positions and reported recapture locations. To maximize fine-scale time series data acquisition within memory capacity and battery constraints, Cefas G5 standard DSTs were programmed to record depth (±0.15 m; 50-bar pressure sensor) at 2-min intervals and temperature (±0.1 °C) every 4 min at 10-bit resolution over a 2-year period. Programming regimes were modified in 2010 to record depth every min and temperature every 2 min on G5 long-life DSTs with upgraded memory and battery-capacity.

Data analysis

All archived data sets were summarized at 2-min depth and 4-min temperature intervals to normalize time series among different sampling regimes (Aalbers and Sepulveda 2015). Time series data generated from each tag recovery were formatted to Pacific Standard Time (PST) prior to generating summary statistics. Vertical rate of movement (VROM) was calculated for each set of recovered data ($n = 20$) as the absolute difference of all subsequent 2-min depth records. The number of records of depth ≤ 5 m were calculated for each monthly period to identify seasonal differences in the frequency of occurrence of surface-oriented behavior. Mean daily sea surface temperatures were derived from temperature values recorded by each DST at depth values <5 m. Temperature profiles were generated by pooling all data and calculating the percent occurrence by 1 °C bins for each month.

Daily mean, min and max depth and temperature values were calculated for each fish and plotted using a 7-day running average for smoothing and ignoring fractions of first and last deployment days. Daily depth probability plots were constructed for each month using one hour by 2 m depth bins to illustrate the probability of occurrence across the depth range (MATLAB, R12). Fourier analyses were conducted using linear interpolated data to identify diurnal signals in the frequency range 0.5–8 cycles per day (cpd). Power spectra were generated from daily averaged time series that exceeded 250 days ($n = 17$) based on spectral density of depth values over the range of 5–50 cycles per year (cpy).

Summary statistics were generated for each track by month and year to identify individual, seasonal and inter-annual differences in mean depth and temperature values. Individual mean depth values from the months of December, January and February were compared against data from the months of June, July and August using a paired t-test to identify seasonal differences in depth profiles. All values are indicated as mean ± 1 SD and $\alpha < 0.05$ was used to infer significance.

Results

Tag recoveries

To date, 24 of the 89 tagged individuals (27%) have been recaptured between Santa Rosalillíta, BC (Lat

Table 1 White seabass data storage tag deployment and recovery specifics for 24 individuals recaptured between Santa Rosalillíta, BC and Monterey, CA between May, 2010 and May, 2017

DST #	TL (cm)	Sex	Deployment date	Deployment location (°N, °W)	Recapture date	Recapture location (°N, °W)	Days at liberty	Displacement (km)
A02168	124	F	6/20/2009	32.10, 116.90	6/28/2010	32.85, 117.28	373	91
A02165	132	F	6/20/2009	32.10, 116.90	9/11/2010	36.65, 121.86	448	680
A02132	91	NA	7/28/2009	31.22, 116.34	7/12/2010	31.82, 116.81	349	80
A02147	91	NA	7/28/2009	31.22, 116.34	1/31/2013	31.20, 116.36	1283	3
A02169	104	NA	7/29/2009	30.73, 116.05	4/25/2010	30.10, 115.83	270	73
A06053	84	F	8/9/2010	32.10, 116.90	5/15/2011	32.15, 116.91	279	5
A06055	130	F	8/9/2010	32.10, 116.90	4/27/2012	31.98, 116.80	627	17
A06048	130	NA	8/9/2010	32.10, 116.90	8/30/2013	31.57, 116.70	1117	62
A06052	109	F	8/12/2010	32.10, 116.90	7/9/2011	32.02, 116.88	331	9
A06046	119	F	8/12/2010	32.10, 116.90	9/25/2011	32.18, 116.92	409	9
A09239	104	F	8/29/2012	30.35, 115.88	8/19/2014	30.37, 115.96	720	7
A09240	112	M	9/21/2012	30.25, 115.83	8/10/2014	29.91, 115.76	688	38
A06056	66	M	9/21/2012	30.25, 115.83	5/3/2016	29.32, 115.12	1320	124
A09671	74	F	6/22/2013	31.39, 116.57	6/2/2014	31.41, 116.52	345	5
A09659	76	M	6/23/2013	31.40, 116.56	7/11/2013	31.52, 116.66	18	16
A09662	76	F	6/23/2013	31.37, 116.56	7/14/2015	32.55, 117.20	751	144
A06055b	81	F	6/23/2013	31.40, 116.56	7/5/2015	28.66, 114.27	742	377
A09667	91	M	6/23/2013	31.37, 116.57	6/6/2016	28.90, 114.47	1080	341
A09657	76	F	6/23/2013	31.39, 116.57	2/20/2015	31.02, 116.36	607	46
A03613	97	F	6/23/2013	31.40, 116.56	5/17/2017	31.11, 116.33	1424	39
A09979	88	F	7/19/2013	30.49, 116.10	7/17/2014	33.80, 118.41	363	427
A09976	81	M	7/19/2013	30.49, 116.10	7/19/2014	30.88, 116.27	365	46
A09975	86	NA	7/21/2013	30.49, 116.10	6/17/2014	28.66, 114.27	331	270
A09971	79	M	7/21/2013	30.49, 116.10	7/4/2014	31.20, 116.36	348	83

28.65°N, Long 114.21°W) and Monterey, California (36.61°N, 121.87°W), following periods at liberty ranging from 18 to 1424 days (mean = 608 ± 381 days; Fig. 1). A 27% recapture rate was reported from local gillnetters ($n = 17$), purse seiners (Sardineros; $n = 2$) and sportfishers (n = 1) operating proximal to prominent BC fishing communities, as well as California-based gillnetters (n = 1), spearfishers (n = 1), hook-and-line commercial (n = 1) and recreational fishers (n = 1). With the exception of one tag recovery in January and one in February, all additional recaptures occurred between late April and September. Complete time-series records from ten DSTs were directly downloaded at the PIER lab upon recovery. Another ten DSTs were retrieved after the battery expired, but CTL engineers were able to recover time series data for the active battery life of the tag. Two DSTs were lost by fishers/processors following recapture and two DSTs contained very little data following redeployment with minimal remaining battery life and were not used in subsequent analyses. Recovered DSTs with sufficient information provided 8547 days of time series data consisting of 6.56×10^6 depth and 3.28×10^6 temperature records at 2-min and 4-min resolution, respectively. Depth and temperature records from at least one tagged individual were available over a 6-year time period spanning from June 20, 2009 through June 17, 2015, with the exception a 66-day gap between June 23 and August 29, 2012 (Fig. 2a and b).

Horizontal movements

Tagged white seabass were at liberty for a mean duration of 608 days (range = 18–1424 days), with a mean

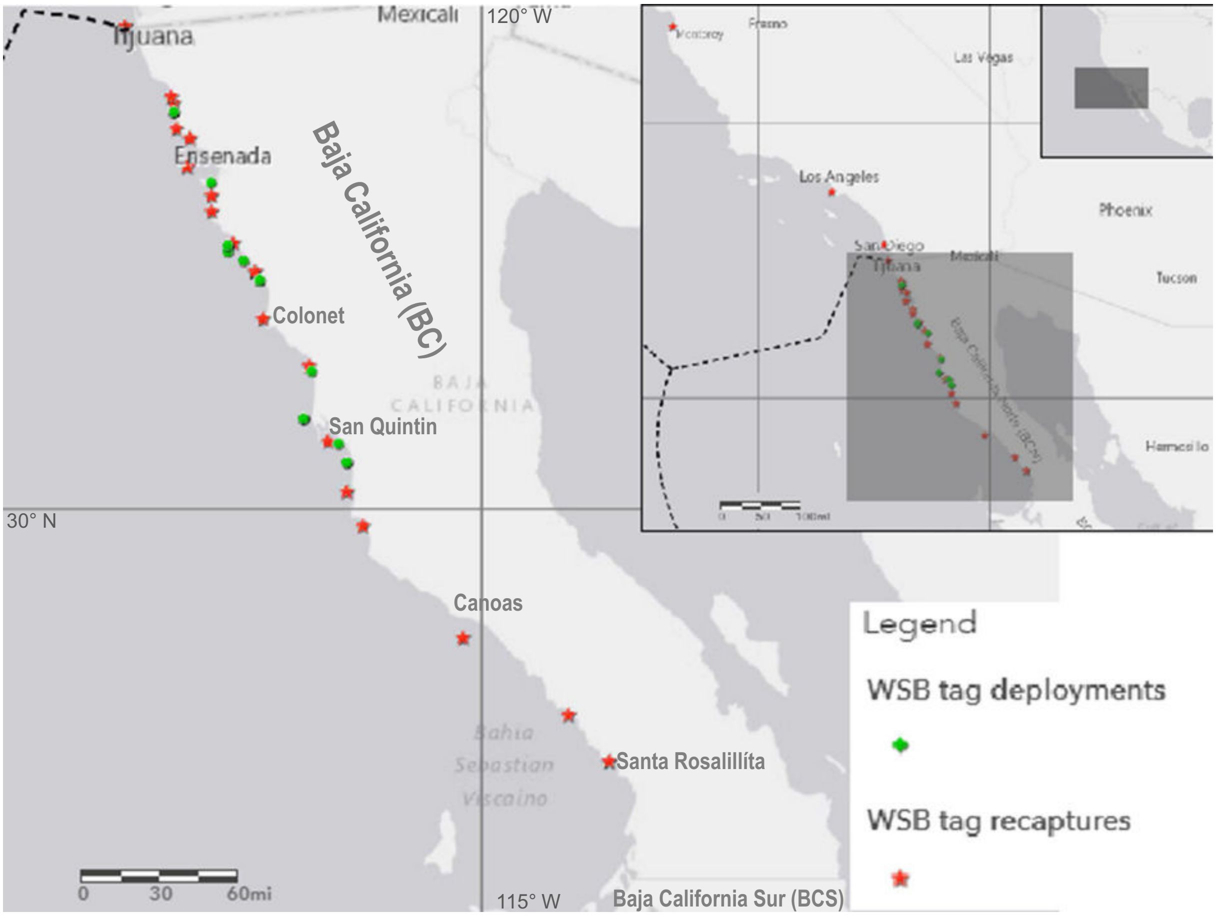

Fig. 1 Inset maps (shaded) displaying data storage tag deployments from July, 2009 through July, 2013 and recovery locations from May, 2010 to May, 2017 for 24 white seabass. Dashed line indicates U.S. Mexico border and exclusive economic zone; solid lines represent 5° latitude and longitude contours

horizontal distance of 125 km (± 173 km) between the point of tag deployment and recovery. Twelve individuals were recovered within 50 km of their initial tagging site after a mean time at liberty of 591 (± 409 days). Of the tagged fish with a net displacement of more than 50 km ($n = 12$), half of the recaptured individuals moved southeast of their initial tagging location (138–163° heading; mean 150°), while the other six individuals moved in a northwesterly direction (327–331° heading; mean 329°). Four of the recaptured white seabass (17%) were recovered above the U.S./Mexico border after moving NW over a mean distance of 327 km. There was no apparent trend in the direction of movement from specific tagging locations, irrespective of release date. Additionally, there was no relationship between fish size and net displacement nor time at liberty and net displacement (Table 1). However, there was an apparent relationship between displacement distance and mean depth, with an increased mean depth for white seabass that were recaptured more than 50 km from tag deployment sites (mean = 23.5 ± 16.7 m) than for individuals recaptured close to initial tag deployments (mean = 13.0 ± 9.0 m).

Vertical movements and temperature profiles

Although depths of up to 158 m were recorded, 95% of the records were < 60 m (Fig. 3). Mean depth values ranged from 3.5 to 33.4 m between individuals with an overall mean depth of 18.3 ± 12.9 m. Tagged fish reached a maximum monthly average (±SD) depth of 31.1 ± 13.2 m in January and a minimum mean depth of 8.0 ± 5.9 m in July (Fig. 4). Surface-oriented movements were infrequent (<2% occurrence) and sporadic

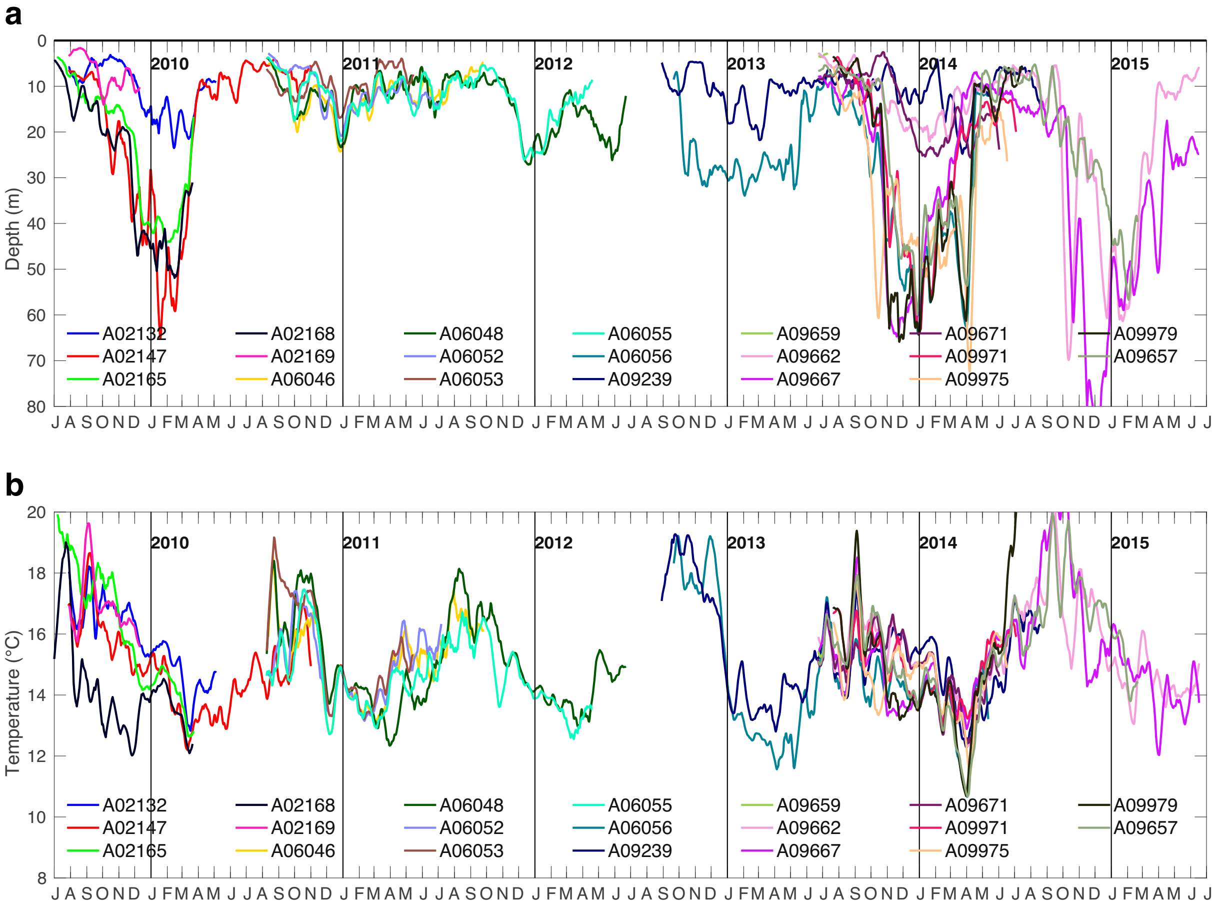

Fig. 2 Mean daily (a.) depth and (b.) temperature profiles from 20 tagged white seabass that were at liberty from June, 2009 through June, 2015, with a 66-day gap in data between June 23 and August 29, 2012

during the winter months, whereas movements towards the surface were more common from June to September when tagged fish collectively spent 30% of the time within the upper 5 m of the water column. Despite considerable individual and inter-annual variation among white seabass tracks (Fig. 2a), significant differences in depth were apparent between the winter (December–February; mean = 29.8 ± 15.2 m) and summer months (June–August; mean = 9.2 ± 3.5 m; *p* value<0.0001). Seasonal shifts to deeper water were most pronounced during the winter months of 2009–10 (mean = 37.0 ± 11.0 m), 2013–14 (37.6 ± 11.3 m) and 2014–15 (50.5 ± 16.2 m), with shallower mean depths observed during the winter periods of 2010–11 (mean = 15.6 ± 5.5 m), 2011–12 (mean = 21.6 ± 6.0 m) and 2012–13 (mean = 21.8 ± 5.7 m). Although depth values were considerably greater during the winter months of 2009–10, 2013–14 and 2014–15 (mean = 40.0 ± 15.7 m), temperature records did not reflect such a shift. Mean temperature (14.6 ± 1.0 °C) during the winter months of 2009–10, 2013–14 and 2014–15 was slightly higher than the collective mean temperature (mean = 14.1 ± 0.9 °C) from the winter months of 2010–11, 2011–12 and 2012–13, when depth profiles were collectively shallower (mean = 18.3 ± 5.7 m).

Two smaller females (DST #A09662 & A09671) exhibited a shallower depth distribution throughout the winter months of 2013–14, while two smaller males (DST #A06056 & A09971) remained considerably deeper during the same period; however, there was not a consistent relationship between fish size and mean depth distribution. For individuals with tracks extending more than one year, several tagged fish (i.e. DST #A06056, A09657 and A09667) exhibited deeper profiles during two consecutive winter periods, whereas the mean depth for DST #A09662 was nearly 3 times

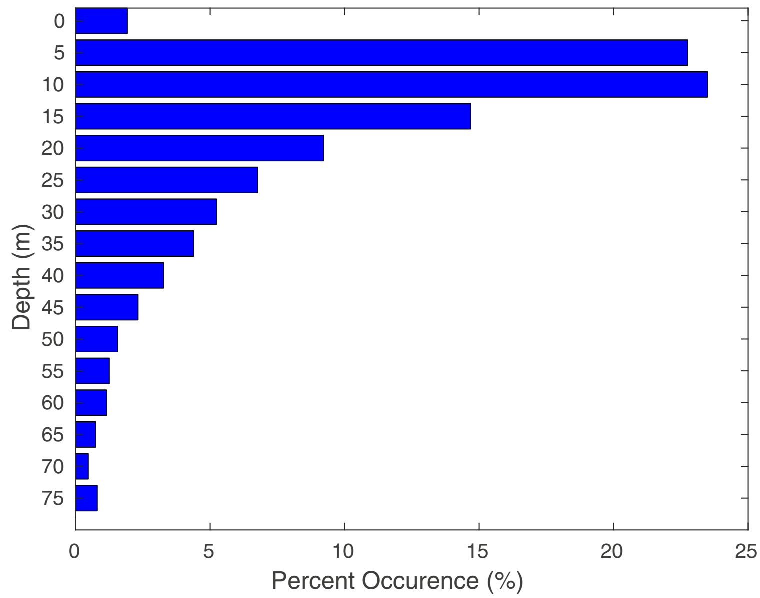

Fig. 3 Depth histogram by 5-m bins based on 20 tagged white seabass at liberty between June, 2009 and June, 2015

greater during the winter of 2014–15 (50.5 ± 14.5 m) when compared with mean depth during the winter of 2013–14 (19.2 ± 14.7 m).

Depth probability plots constructed for each month further exhibited seasonal shifts in depth, with shallower distributions evident from April through October, transitional periods during March and November, and deeper profiles from December through February (Figs. 5a-d). Depth probability plots also substantiated heightened vertical rates of movement around dawn and dusk throughout all months of the year (Figs. 5a-d). Consistent daily (24 h) and semi-daily (12 h) peaks in spectral density were evident from Fourier analyses of depth data for multiple tracks ($n = 19$) along with discrete peaks at 3,4 and 5 cycles per day (Fig. 6). Longer-term periodicities (5–50 cycles per year), on the scale of 1 week to 2.5 months were highly variable and not persistent among all individuals.

Tagged individuals experienced water temperatures from 10.2 to 24.1 °C, with an overall mean of 15.2 ± 0.4 °C. Despite a relatively broad temperature tolerance, tagged white seabass spent 73% of the time within a temperature range of 13–16 °C, with peak occurrence around 14 °C (Fig. 7). Ninety-five percent of all temperature records were between 12 and 19 °C, while 95% of SSTs occurred between 13 and 19 °C. The mean SST for all tag deployments was 16.5 ± 1.1 °C (range = 11.1–24.1 °C). Mean monthly temperatures reached a

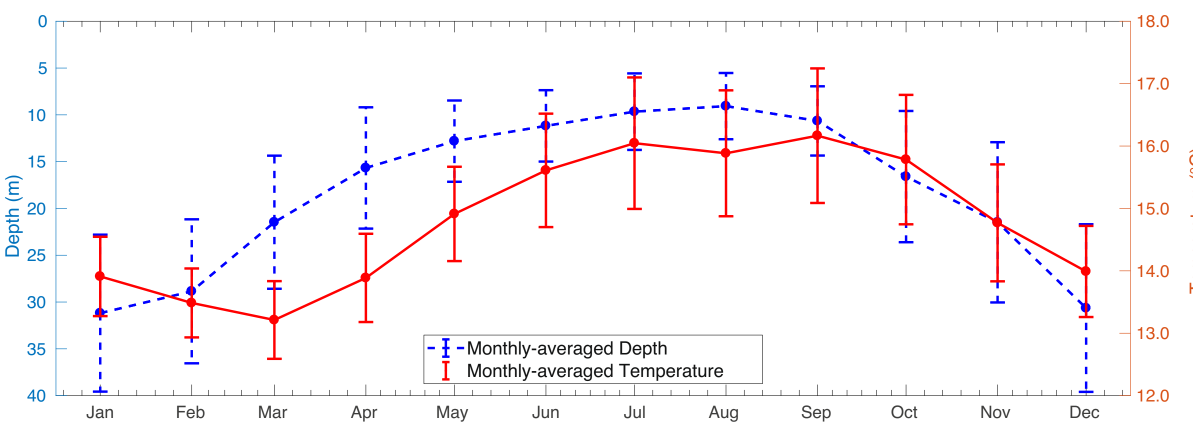

Fig. 4 Mean (± 1 SD) monthly depth and temperature values summarized from 20 white seabass tagged along the coast of Baja California

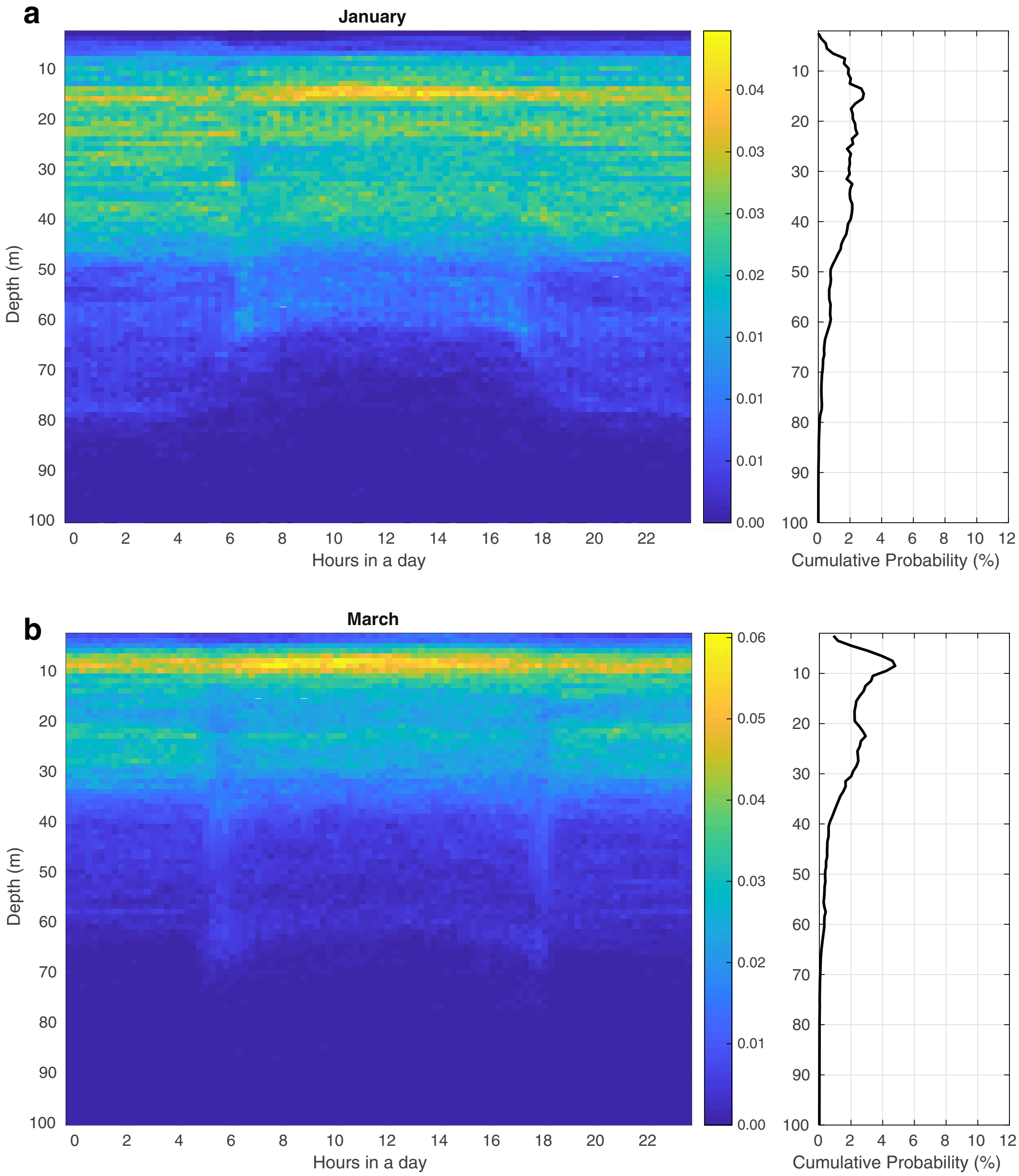

Fig. 5 Joint probability of depth plots summarized into a 24-h period for the months of (a.) January, (b.) March, (c.) June, and (d.) November consolidated from white seabass data storage tags deployed off the coast of Baja California

maximum of 16.5 °C in July, with a minimum of 13.3 °C in March (Fig. 4).

Discussion

This electronic tagging study further substantiates white seabass transboundary movements and provides the first direct evidence of northward migrations from BC into California, as inferred by Skogsberg (1939). Southward movements across the U.S.-Mexico international border were recently documented in a white seabass tagging study conducted on wild-caught adults captured along southern California (Aalbers and Sepulveda 2015), findings that collectively validate some level of mixing between white seabass off of California and BC. Vertical movement patterns and temperature profiles of white seabass tagged in this study were consistent with tracks

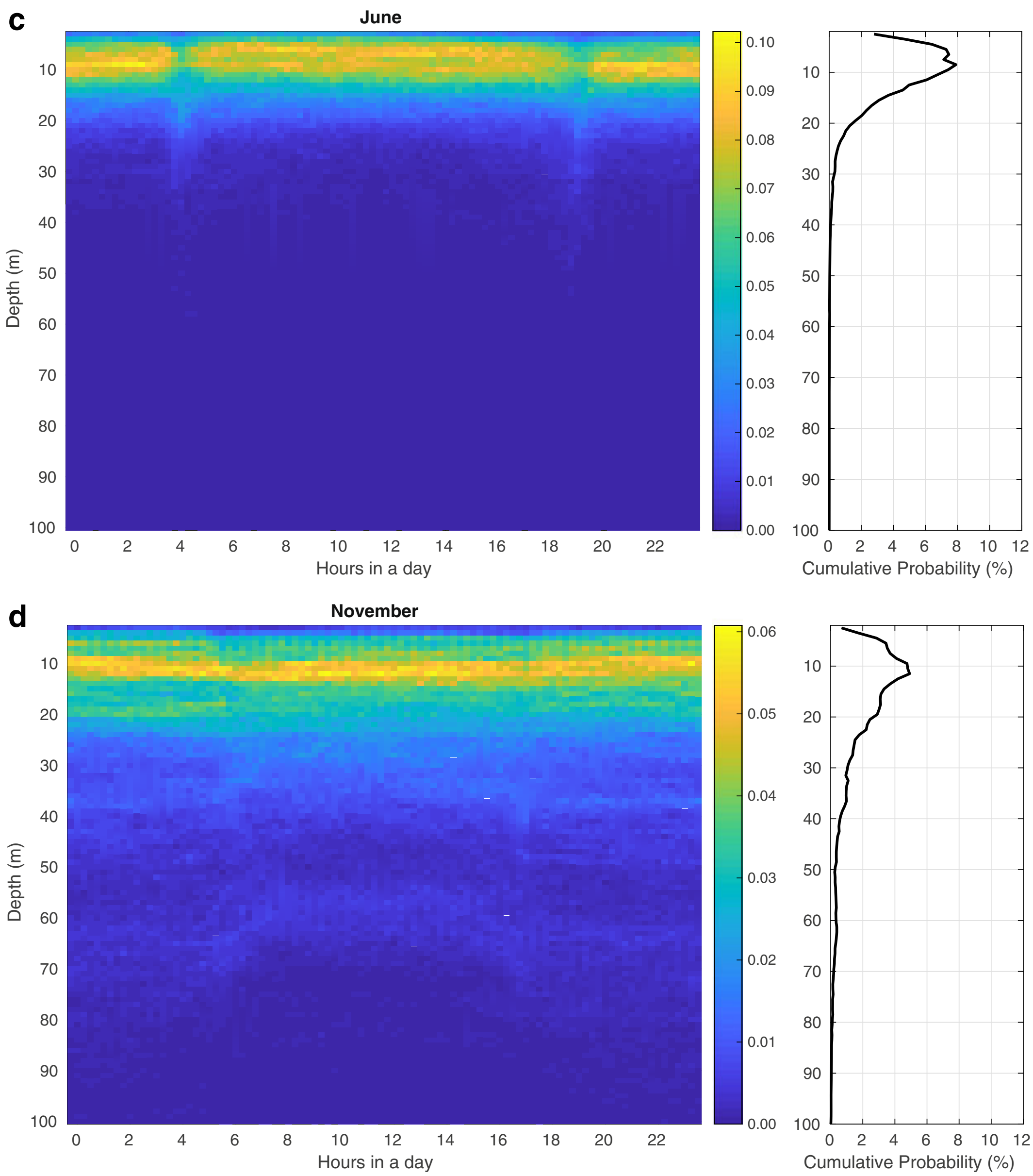

Fig. 5 (continued)

from fish tagged along California (Fig. 8; Aalbers and Sepulveda 2015), suggesting similar habitat utilization and providing further support for an interrelated stock. However, a lack of tag recoveries reported south of Punta Rosalillíta, BC support the need for additional movement studies across BCS to further investigate the potential for a disjunct white seabass subpopulation across the southern extent of their range.

Stock structure and biological parameters

Conflicting findings from genetic and otolith microchemistry studies also warrant additional work to further assess the level of white seabass subpopulation structure (Coykendall 2005; Ríos-Medina, 2008; Franklin 1997; Franklin et al. 2016; Romo-Curiel et al. 2016). Although previous work has not revealed consistent

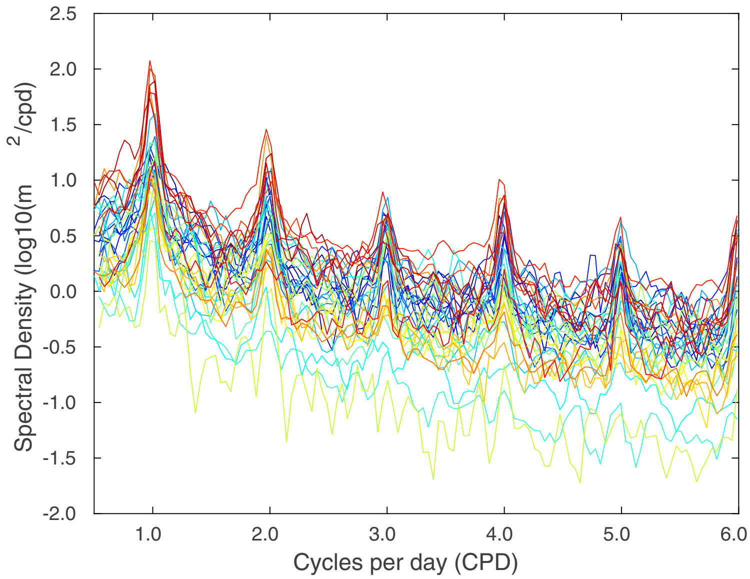

Fig. 6 Spectral analysis of white seabass depth periodicities displayed in cycles per day (CPD) to indicate high-frequency diurnal cycles for 19 sets of time series data ranging in duration from 135 to 730 days upon application of a fast Fourier transform algorithm

genetic differences across California and BC sampling regions (Coykendall 2005; Ríos-Medina, 2008), Franklin (1997) concluded that the white seabass stock is composed of a northern (Point Conception to central Baja California), southern (BCS), as well as a Sea of Cortez component based on microsatellite DNA analysis. More recently, Romo-Curiel et al. (2016) found ontogenetic differences in the isotopic composition of otolith growth rings, suggesting that the environmental conditions experienced by larval and juvenile white seabass reared along BCS may be different from individuals sampled off southern California and BC.

Portions of BCS, including Sebastian Viscaino Bay and San Juanico Bay have been shown to support peak concentrations of larval white seabass during the months of May–August of 1950–1978, suggesting regionally important spawning areas (Moser et al. 1983). Peak abundance of 20–30 day-

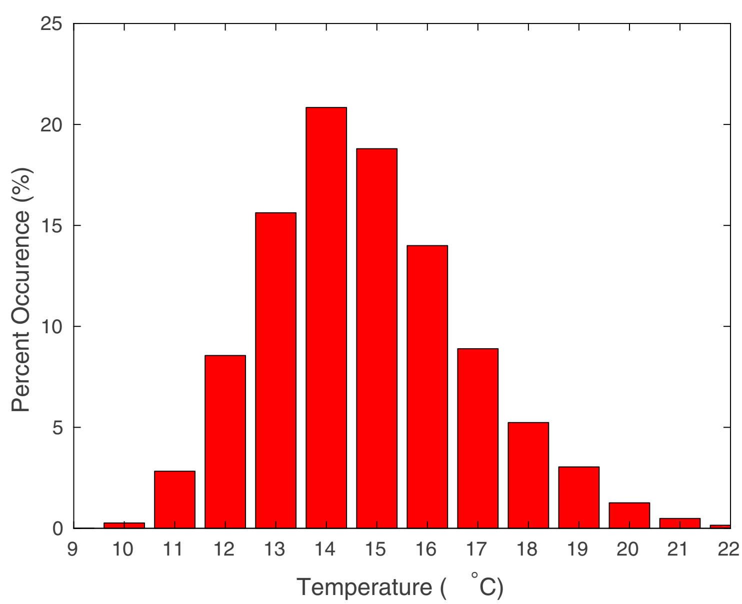

Fig. 7 Summarized temperature data by 1 degree C bins recovered from 20 tagged white seabass at liberty between June, 2009 and June, 2015

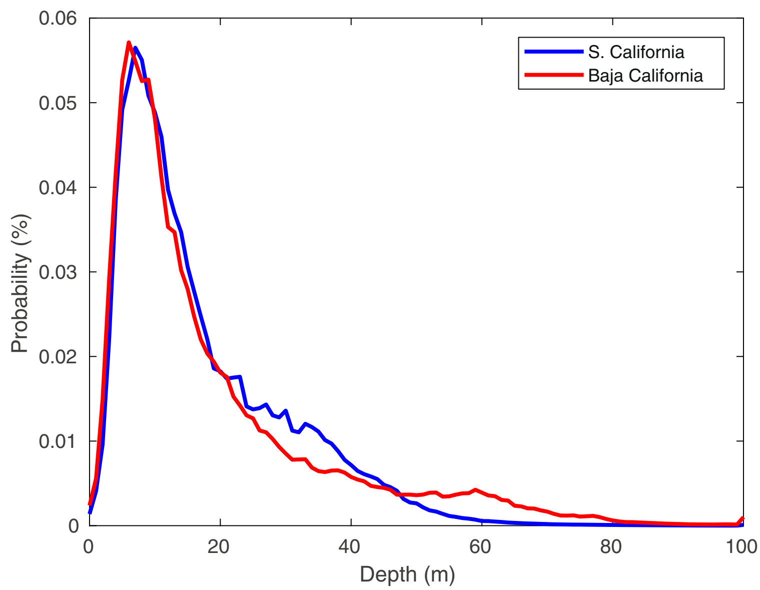

Fig. 8 Kernal density plot of time-series data comparing collective depth profiles from 19 white seabass tags recovered following deployment off Baja California and from 16 white seabass tags recovered following deployment off of southern California (Aalbers and Sepulveda, 2015)

old larvae have been identified in July along BCS, suggesting a later spawning peak than the May peak in spawning reported off of southern California (Aalbers 2008). Additional range-wide differences in the size structure (i.e. length frequency) and seasonality of peak harvest have been identified (Romo-Curiel et al. 2015), all potential indicators of differentiated stocks or spawning areas.

Tag recoveries

Ninety-two percent of tag recoveries occurred from late April–September, confirming that peak harvest throughout the region occurs during the spring and summer spawning season (Escobedo-Olvera 2009; Cota-Nieto et al. 2018). The seasonality of tag deployments and recoveries aligned with periods when California gillnetters target white seabass near the surface (July–October) (Skogsberg 1939). Similarly, gillnets are floated at the surface along the BC coastline during the summer months to target surface-oriented white seabass (aboyados), whereas bottom set nets are generally a more effective harvest method during the winter and early springtime (Escobedo-Olvera 2009).

More than 70% of the recaptured white seabass in this study were reported by small-scale gillnetters operating along BC; however, tags were also recaptured by all other pertinent gear types used in the region. Although it was apparent that gillnets were the most prominent gear type used to harvest white seabass along BC, two archival tag returns from commercial sardine purse-seine vessels (sardineros) confirm that purse-seining represented a notable source of white seabass fishing mortality. Whether captured as bycatch or directly targeted by purse seiners, it has been well documented that purse-seining for white seabass is both effective and unsustainable, as this method rapidly led to overexploitation in the early fishery off California (Whitehead 1929). It was estimated that prior to 1925, purse seiners and other round haul nets landed more than 50% of the total white seabass harvest off California (Croker 1937). A steep reduction in California landings throughout the 1930s–40s is thought to have resulted from excessive targeting of white seabass spawning aggregations with purse-seine nets. Directed purse seine sets during the white seabass spawning season can be very effective and may contribute to a considerable level of underreported harvest.

One of the white seabass tagged along BC was recaptured by a California gillnet fisher. A small fleet of approximately 20 gillnet vessels still actively target white seabass along California, however; gillnetting practices were restricted in 1994 to waters outside of three miles from the coastline or one mile of the Channel Islands (or > 128 m in depth; California Department of Fish and Wildlife 2019). Harvest levels and participation in the California gillnet fishery for white seabass have been in decline since 2010, with annual landings steadily declining below 100 metric tons from approximately 30 active vessels in recent years (Valero and

Waterhouse 2016; California Department of Fish and Wildlife 2019).

Both U.S. and Mexican recreational fishers also recaptured tagged white seabass in this study. White seabass are seasonally targeted by a large fleet of private, charter, and commercial passenger fishing vessels that generate a high level of recreational fishing effort off California. Over the past two decades, southern California recreational fishing vessels have contributed to a significant proportion of the statewide white seabass landings, occasionally exceeding annual commercial harvest levels (Aalbers et al. 2004; Valero and Waterhouse 2016). Additionally, small pangas for hire opportunistically target white seabass on hook-and-line from coastal towns throughout BC and BCS; however, recreational catch and effort is not well documented and considered to be low (Romo-Curiel et al. 2015). One tagged white seabass was also recovered by a California spearfisher, a more prominent method of take in recent years from an increasing number of free divers that effectively target large individuals from seasonal spawning aggregations across California and BC coastal waters (Valero and Waterhouse 2016).

Horizontal movements

A maximum displacement of 720 km between tag deployment and recovery sites suggests that white seabass have the potential to move extensively; however, the mean displacement distance of 125 km was weighted by twelve individuals that were recaptured within 50 km of their initial release site. One of the fish recaptured close to the tag deployment site was only at liberty for 18 days, yet the mean time at liberty for the other eleven individuals was 639 ± 385 days (Range = 279–1283 days). Four of the individuals with net movements <30 km were recaptured during the same month of the subsequent year or after two years at liberty, suggesting that white seabass may return seasonally to specific sites along BC.

It may be the case that certain individuals did not migrate far and exhibited longer-term periods of regional fidelity. Certain individuals with reduced horizontal movements may have remained within shallower coastal waters throughout the winter months, considering the reduced mean depth for white seabass that were recaptured within 50 km of the initial tagging location. Little information is available on the movement patterns of juvenile white seabass, although recently settled individuals have been shown to reside within shallow coastal waters (Donohoe 1997) and it is likely that overall movements are relatively limited during their first few years of life (Maxwell 1977). Considering that existing information on white seabass size of maturity remains inconclusive (Clark 1930; Thomas 1968), it may be that some of the smaller females tagged in this study (e.g. DST #A09662, A09671) were immature and did not exhibit broad horizontal or vertical movements. Although it is unknown how far individuals may have traveled during their time at liberty, migratory fish may have shifted deeper along the continental shelf as oceanic conditions changed across latitudes. Additional deployments of geolocating archival tags along California and BC are underway, data which may better address questions related to seasonal site fidelity, annual migratory pathways and regional depth distributions (Aalbers and Sepulveda, unpublished data).

Vertical movements and temperature profiles

Extensive time-series data accumulated over the six-year study period reflect many similarities to the depth and temperature profiles reported for white seabass tagged off southern California (Aalbers and Sepulveda 2015), with significant increases in wintertime depth profiles documented in both studies. Inter-annual differences in depth profiles were equivalent during the two-year period that these tagging studies overlapped, with increased mean depths during the 2009–10 winter months relative to the winter period of 2010–11. For this study, inter-annual depth shifts were collectively greater in magnitude during the winter months of 2009–10, 2013–14 and 2014–15 (mean = 40.0 ± 15.7 m) relative to wintertime depths from 2010 to 11, 2011–12 and 2012–13 (mean = 18.3 ± 5.7 m). Inter-annual variability in depth profiles was likely influenced by temporal changes in oceanic conditions, considering that mean temperature at depth values were unexpectedly higher during the years with deeper wintertime profiles (mean = 14.6 ± 0.6 °C) than during the winter months of 2010–11, 2011–12 and 2012–13 (mean = 14.1.0 ± 0.3 °C).

Fluctuations in the thermal structure of the water column in relation to changing environmental conditions has been associated with shifts in vertical movement patterns for various species of marine fishes and elasmobranchs (Hinke et al. 2005; Sibert et al. 2006;; Coffey et al. 2017; Andrzejaczek et al. 2018). Vertical movement patterns of chinook salmon *Onchorhynchus tshawytscha* were attributed to behavioral thermoregulation in response to local thermal conditions, based on temperature at depth measurements in the 8–12 °C range recorded by subsurface buoys off Monterey Bay, California (Hinke et al. 2005). Similarly, white seabass temperature profiles remained within a narrow range (13–16 °C) more than 70% of the time (Fig. 7), despite significant seasonal changes in depth (Fig. 2a). Thus, white seabass movement patterns may be dependent upon regional temperature at depth profiles, suggesting that changing ocean conditions and temperature regimes may influence white seabass migratory pathways.

Although fine-scale rates of vertical ascents and descents were highly variable between tracks, FFT analyses revealed diel patterns of vertical movement, with spectral peaks identified at one and two cycles per day (Fig. 6). Diel movement patterns were also identified in adult white seabass tagged off California, along with comparable harmonic peaks at 3 and 4 cycles per day that were attributed to vertical movements around the mixed semi-diurnal tidal fluctuations and associated shifts in thermocline depth typical for this region of the eastern north Pacific (Cairns and LaFond 1966; Aalbers and Sepulveda 2015). Diel and tidal periodicity identified in basking shark vertical movements was attributed to cyclical foraging activity targeting concentrations of prey that aggregated at daily and semi-daily intervals, particularly during periods of increased tidal amplitude and current intensity (Shepard et al. 2006). Similarly, consistent vertical movement patterns have been recognized on diurnal scales in relation to foraging activity for a variety of other marine predatory species with diets consisting of small fishes and squid (Holland et al. 1992; Lam et al. 2014; Afonso et al. 2014), comparable to that of adult white seabass (Thomas 1968). White seabass movement patterns on a daily time scale may also be related to foraging activity during periods when prey species tend to aggregate or vertically migrate around dusk and dawn or following shifts in current direction surrounding tidal changes. Although longer-term periodicities were not evident from FFT analyses, shifts in depth observed across seasons align with reports of higher white seabass catchability in bottom-set gillnets during the winter months when fish are more closely associated with benthic habitats (Escobedo-Olvera 2009, Pers. Comm. M. McCorkle).

Management applications

Historical white seabass catch statistics for Baja California are difficult to aggregate for various reasons, however; the collection of additional information on spatial, temporal and biological components of directed fishery operations will continue to benefit future stock assessments and sustainable management practices throughout the region (Moreno-Báez et al. 2012; Valero and Waterhouse 2016). California landings data have exhibited dramatic fluctuations since the early 1900's, with several prominent peaks in catches during periods of heavy exploitation followed by subsequent declines (Whitehead 1929; Skogsberg 1939; Thomas 1968; Vojkovich and Reed 1983; Valero and Waterhouse 2016). Findings from the first formal white seabass stock assessment indicate that spawning stock biomass has been in decline since 2007 and has been reduced to less than 24% of the potential spawning stock biomass (Valero and Waterhouse 2016). Relatively high tag recovery rates documented along both California (24.3%; Aalbers and Sepulveda 2015) and Baja California (27.0%; this study) corroborate high rates of fishing mortality (*F*) first reported by Thomas (1968). Consistently high rates of electronic tag recoveries since 2009 confirms that both U.S. and Mexican fishers rely heavily on this valuable international resource. When coupled with declining catch trends, findings support the need for an updated stock assessment that incorporates relevant data sources from both U.S. and Mexico-based fishery operations. Extensive northerly and southerly movements documented during tagging studies collectively suggest a shared white seabass stock that seasonally migrates between California and BC. Confirmation of transboundary movements reinforces the need for collaboration between international government agencies and the collective development of cohesive fishery management policies.

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Availability of data and material The data used to produce this manuscript has been uploaded to an online data repository and may be made available upon reasonable request to the corresponding author.

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Declarations

Animal Ethics Approval All live-fish capture and handling procedures were approved by the Pfleger Institute of Environmental Research Animal Handling and Ethics Committee (Protocol #146–155.14-21).

Conflict of interest All authors declare that there are no known conflicts of interest or competing financial interests that may have influenced the material in this publication. All authors certify that they have no affiliations with entities that have interest in the subject matter or financial interests in the material discussed in this manuscript.

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