Seasonal movement patterns and temperature profiles of adult white seabass (*Atractoscion nobilis*) off California

Scott A. Aalbers (contact author)
Chugey A. Sepulveda

Email address for contact author: scott@pier.org

Pfleger Institute of Environmental Research (PIER)
2110 South Coast Highway, Unit F
Oceanside, California 92054

Abstract—To better understand the seasonal movement patterns of adult white seabass (*Atractoscion nobilis*), 173 depth- and temperature-sensitive data storage tags were deployed at various sites within the Southern California Bight during 2008–2011. Commercial and recreational fishing crews recaptured 41 tagged individuals (24%) between La Salina, Baja California Norte, Mexico (32°01′N, 116°53′W), and Half Moon Bay, California (37°28′N, 122°28′W). Tagged fish were at liberty for an average duration of 468 days (range: 9–1572 days), and mean net displacement between the points of release and recapture was 229 km (range: 2–624 km). Collectively, 9130 days of archived data revealed distinct seasonal trends in depth distribution, and significantly deeper profiles during the winter months. Minor differences in mean depth values were evident between daytime (14.9 m [±standard deviation (SD) 5.1]), nighttime (15.5 m [SD 5.1]), and twilight periods (16.8 m [SD 6.8]). However, the vertical rate of movement (VROM) was significantly greater during twilight hours (48.9 m h^{-1} [SD 12.3] when compared with day and night VROM values (39.6 m h^{-1} [SD 10.8] and 41.1 m h^{-1} [SD 13.2]). The greatest depth achieved by any individual was 245 m; however, 95% of all depth records were less than 50 m. Ambient water temperatures ranged from 8.7° to 23.6°C, and had a mean value of 15.2°C (SD 1.4°C). A vertical shift toward the surface as water temperatures increase during the spring and summer months contributes to heightened vulnerability during the spawning season, presenting management challenges toward the long-term sustainability of this resource.

The white seabass (*Atractoscion nobilis)* supports lucrative recreational and commercial fisheries throughout California and Baja California, Mexico (Vojkovich and Crooke, 2001; Rosales-Casian and Gonzalez-Camacho, 2003). Because of their high recreational and market value, white seabass are targeted opportunistically and fishing effort is influenced by local availability (Skogsberg, 1939; MacCall et al., 1976; CDFG, 2011). During periods of heightened abundance, persistent localized effort is directed toward white seabass by both recreational and commercial operations throughout much of the range of this species (Whitehead, 1929; MacCall et al., 1976).

Over the past century, landings and catch per unit of effort (CPUE) of white seabass in California have fluctuated dramatically, reaching peak levels in the early 1920s and late 1950s that were followed by troughs in the late 1920s and 1960s (Whitehead, 1929; MacCall et al., 1976; CDFG[1]). Vojkovich and Reed (1983) suggested that prolonged intervals of reduced landings off California are likely a response to periods of overexploitation and other

unknown factors. Collective landings and CPUE from California recreational and commercial fisheries have steadily increased since 1998, indicating a recent stock resurgence from levels of record-low abundance in the 1980s (Vojkovich and Reed, 1983; Allen et al., 2007; CDFG, 2011).

The majority of California's white seabass harvest typically occurs from April to September along the southern coast from Point Conception to San Diego and throughout the Channel Islands (Skogsberg, 1925; Thomas, 1968). Landings north of Point Conception have increased dramatically since 2008; commercial hook-and-line catches north of Point Arguello increased from 1% of the total California harvest in 2008 to 22% of annual state landings in 2010 (CDFG, 2009; 2011). Over the same period, recreational catches north of Point Arguello increased from 3% to 38% of total state landings. Heightened landings from the northern region have been coupled with a sharp increase (266%) in the numbers of vessels entering the white seabass fishery (CDFG 2011), rising from 93 permitted boats in 2009 to 254 commercial vessels in 2011 (CDFG[2]). A

---

[1] CDFG (Calif. Dep. Fish Game). 2002. Final white seabass fishery management plan (WSFMP), 161 p. [Available from https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=34195&inline=true, accessed March 2014.]

[2] CDFG (Calif. Dep. Fish Game). 2012. White seabass fishery management plan annual 2010–2011 review, 6 p. [Available from https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=75302&inline=true, accessed March 2014.]

comparable northward shift in fishing effort was documented from 1957 to 1961 and was also coupled with a sharp increase in the number of vessels that entered the fishery (Vojkovich and Reed, 1983). During this period, commercial landings of white seabass reached a record high of more than 1500 metric tons in 1959, 36% of which came from the waters north of Point Conception (Thomas, 1968; Vojkovich and Reed, 1983). Interannual shifts in the latitudinal distribution of white seabass have been suggested in the past (Skogsberg, 1939; Young[3]; Maxwell[4]); however, fishery-independent data on movement patterns and stock structure of white seabass have been limited.

Attempts to evaluate movement patterns of juvenile white seabass through a conventional tagging program in the mid-1970s were ineffective because of limited tag deployments ($n=58$) and no reported tag recoveries (Maxwell[4]). An evaluation of movement patterns based on historical fishery data indicates that white seabass occur off Baja California during winter and move northward along the coast of California as water temperatures increase during the spring and summer months (Skogsberg, 1939; Maxwell[4]; Vojkovich and Crooke, 2001). Spawning is thought to occur with northward advancement from March to July (Skogsberg, 1925; Thomas, 1968; Young[3]), although little information is available regarding spawning activity north of Point Conception. Fish harvested along California and Baja California are currently considered to be from a continuous spawning population with a high level of genetic diversity (Maxwell[4]; Coykendall, 1998; Rios-Medina, 2008). Discrepancies in this single-stock model have been indicated by Franklin (1997), and the existence of regionally discrete stocks with limited rates of mixing has been considered (Vojkovich and Crooke, 2001).

Despite a robust history of white seabass catch data since the 1890s, essential fishery information on the geographic distribution of stocks, habitat use, and seasonal movement patterns remains largely unavailable (Skogsberg, 1939; Vojkovich and Reed, 1983; CDFG[1]). Additional uncertainties on spatial and temporal aspects of white seabass depth distribution, residence periods, and exploitation rates present major challenges for effective fishery management, particularly for a population that is harvested by more than one nation (Thomas, 1968; Maxwell[4]; CDFG[1]). Regulations that reduce the likelihood of overexploitation are currently in place; however, additional research and adaptive management strategies are necessary for the sustainable use of this valuable fishery resource (Vojkovich and Reed, 1983; CDFG[1]). Fishery-independent information on fine- and course-scale fish movements has been identified as essential to adequately assess fishery impacts and address questions related to seasonal distribution and stock structure of white seabass (Thomas, 1968; CDFG[1]). Our objectives were to assess movement patterns, temperature preferences, and recapture rates of adult white seabass off the California coast.

Materials and methods

Tagging procedure and sampling regime

Cefas G5[5] and G5 long-life data storage tags (DSTs; Cefas Technology Limited, Lowestoft, UK) were surgically implanted in the peritoneal cavity of white seabass by using techniques modified from Stutzer (2004). Wild-caught white seabass were tagged and released around Santa Catalina Island ($n=107$) and along the southern coastline of California ($n=66$) during the spring and summer months of 2008–2011 (Table 1). After capture on hook and line, fish were brought alongside the vessel and transferred in a knotless nylon-mesh dip net (Duraframe, Viola, WI) to an onboard tagging cradle. A conventional identification marker (FIM-96; Floy Tag, Inc., Seattle, WA) was inserted into the dorsal musculature traversing the dorsal-fin pterygiophores. Upon securing the fish ventral-side up within a tagging cradle, a 2-cm incision was made with a scalpel through the dermal layer adjacent to the ventral midline approximately 8 cm anterior to the anal vent. A stainless steel trocar was used to penetrate the ventral musculature, and a DST was inserted into the peritoneal cavity. The incision was closed around an external identification stalk with a PDS II surgical-grade suture and a CP-1 reverse cutting needle (Ethicon, Somerville, NJ) along with a 35-wide stainless-steel skin stapler (PGX-35W; 3M, St. Paul, MN).

Fish total length (TL) was measured to the nearest centimeter, sex was recorded, and the hook was removed before release. Sex was determined by both the audible detection of low-frequency sound production by males during the capture and tagging process and the presence or absence of milt upon application of pressure to the abdominal region. All tagging was conducted during the spawning season when mature males are consistently running ripe and characteristically produce low-frequency sound upon handling (Aalbers and Drawbridge, 2008; Gruenthal and Drawbridge, 2012). Total handling time onboard the vessel ranged from 65 to 135 s.

Because postrelease survival of white seabass hooked in the visceral region has been shown to be

---

[3] Young, P. H. 1973. The status of the white seabass resource and its management. Calif. Dep. Fish Game Mar. Resour. Tech. Rep. 15, 10 p. [Available from http://aquaticcommons.org/756/1/Technical_Report_1973_No._15_A.pdf, accessed April 2014.]

[4] Maxwell, W. D. 1977. Progress report of research on white seabass, *Cynoscion nobilis*. Calif. Dep. Fish Game Mar. Resour. Admin. Rep. 77-14, 14 p. [Available from http://aquaticcommons.org/76/1/Marine_Resources_Administrative_Report_No[1]._77-14.pdf, accessed April 2014.]

Table 1

Tag deployment and recovery statistics for 41 adult white seabass (*Atractoscion nobilis*) recaptured between La Salina, Baja California Norte, Mexico, and Half Moon Bay, California, from June 2008 to July 2013. DAL=days at liberty, rec. hook-line=recreational hook and line, com. hook-line=commercial hook and line.

Tag no.	Fish total length	Deployment			DAL	Recapture			Net movement	Recapture gear
		Date	Latitude	Longitude		Date	Latitude	Longitude		
A02049	132 cm	5-19-08	33°18′ N	118°18′ W	1154	7-18-11	33°20′ N	118°29′ W	16 km	rec. hook-line
A02066	127 cm	5-19-08	33°18′ N	118°18′ W	1572	9-11-12	36°57′ N	121°57′ W	542 km	com. hook-line
A02055	119 cm	5-25-08	33°18′ N	118°18′ W	767	6-30-10	34°13′ N	119°20′ W	144 km	U.S. gill net
A02071	114 cm	5-25-08	33°18′ N	118°22′ W	31	6-25-08	34°14′ N	119°25′ W	144 km	U.S. gill net
A02143	97 cm	6-02-08	33°28′ N	118°36′ W	798	8-10-10	37°28′ N	122°28′ W	624 km	com. hook-line
A02054	124 cm	6-12-08	33°18′ N	118°18′ W	746	6-28-10	33°39′ N	118°12′ W	40 km	U.S. gill net
A02118	117 cm	6-12-08	33°18′ N	118°18′ W	1342	2-13-12	34°18′ N	119°27′ W	211 km	U.S. gill net
A02119	117 cm	6-12-08	33°18′ N	118°18′ W	377	6-24-09	33°40′ N	118°13′ W	19 km	rec. hook-line
A02159	119 cm	6-12-08	33°18′ N	118°18′ W	764	7-26-10	34°00′ N	118°48′ W	90 km	speargun
A02075	91 cm	6-26-08	33°18′ N	118°21′ W	371	6-30-09	34°14′ N	119°19′ W	125 km	U.S. gill net
A02105	122 cm	7-15-08	33°18′ N	118°21′ W	350	6-29-09	34°12′ N	119°19′ W	141 km	U.S. gill net
A02131	109 cm	5-06-09	33°24′ N	118°22′ W	76	7-21-09	36°58′ N	121°56′ W	576 km	rec. hook-line
A03604	152 cm	5-14-09	33°18′ N	118°21′ W	690	4-06-11	32°01′ N	116°53′ W	195 km	Mexico gill net
A02128	127 cm	6-05-09	33°24′ N	118°22′ W	896	11-21-11	36°58′ N	122°08′ W	600 km	com. hook-line
A03606	114 cm	6-08-09	33°18′ N	118°21′ W	490	10-12-10	36°37′ N	121°52′ W	512 km	com. hook-line
A03609	124 cm	6-16-09	33°18′ N	118°20′ W	741	6-27-11	33°40′ N	118°12′ W	45 km	U.S. gill net
A03613	79 cm	6-23-09	33°18′ N	118°21′ W	16	9-07-09	33°19′ N	118°25′ W	11 km	rec. hook-line
A02094	102 cm	6-29-09	33°20′ N	117°34′ W	820	9-27-11	32°01′ N	116°53′ W	192 km	Mexico gill net
A02325	112 cm	6-29-09	33°20′ N	117°34′ W	354	6-18-10	33°39′ N	118°12′ W	45 km	U.S. gillnet
A02161	132 cm	6-30-09	33°20′ N	117°34′ W	744	7-14-11	34°24′ N	119°49′ W	237 km	speargun
A03595	122 cm	7-09-09	33°20′ N	117°34′ W	722	7-01-11	33°17′ N	117°29′ W	6 km	speargun
A03596	124 cm	7-10-09	33°20′ N	117°34′ W	439	9-22-10	36°37′ N	121°54′ W	587 km	com. hook-line
A03591	152 cm	7-18-09	33°23′ N	117°37′ W	346	6-28-10	32°47′ N	117°17′ W	72 km	com. hook-line
A02109	109 cm	3-16-10	32°50′ N	117°18′ W	146	8-08-10	35°06′ N	120°39′ W	448 km	com. hook-line
A02111	104 cm	3-17-10	32°50′ N	117°18′ W	153	8-15-10	32°51′ N	117°18′ W	2 km	rec hook-line
A02133	114 cm	3-17-10	32°50′ N	117°18′ W	493	7-24-11	32°09′ N	116°54′ W	86 km	Mexico gill net
A06101	124 cm	5-05-10	33°17′ N	117°29′ W	17	5-22-10	32°51′ N	117°17′ W	56 km	speargun
A06097	135 cm	5-20-10	33°20′ N	117°34′ W	416	7-10-11	36°57′ N	121°57′ W	602 km	com. hook-line
A06065	137 cm	5-26-10	33°18′ N	118°22′ W	27	6-22-10	33°39′ N	118°15′ W	45 km	U.S. gill net
A06089	86 cm	5-26-10	33°19′ N	118°23′ W	386	6-16-11	34°13′ N	119°26′ W	120 km	U.S. gill net
A06101b	140 cm	5-26-10	33°18′ N	118°22′ W	155	10-28-10	36°37′ N	121°52′ W	520 km	com. hook-line
A06067	114 cm	5-27-10	33°18′ N	118°22′ W	97	8-31-10	36°32′ N	121°56′ W	506 km	com. hook-line
A06076	117 cm	5-27-10	33°18′ N	118°22′ W	385	6-16-11	34°15′ N	119°20′ W	120 km	U.S. gill net
A06117	130 cm	6-12-10	33°36′ N	117°58′ W	106	9-26-10	36°37′ N	121°52′ W	552 km	com. hook-line
A06122	104 cm	6-12-10	33°36′ N	117°58′ W	11	6-23-10	33°40′ N	118°17′ W	32 km	U.S. gill net
A06118	102 cm	6-13-10	33°36′ N	117°58′ W	8	6-22-10	33°39′ N	118°16′ W	29 km	U.S. gill net
A06120	130 cm	6-13-10	33°36′ N	117°58′ W	765	7-18-12	36°57′ N	121°57′ W	568 km	com. hook-line
A06107	130 cm	6-24-10	32°47′ N	117°17′ W	355	6-14-11	32°42′ N	117°16′ W	8 km	speargun
A06073	91 cm	6-07-11	33°18′ N	118°20′ W	110	9-24-11	33°23′ N	118°29′ W	19 km	speargun
A02143	127 cm	3-17-10	32°50′ N	117°18′ W	1155	5-17-13	32°42′ N	117°16′ W	12 km	speargun
A06108	135 cm	6-25-10	32°47′ N	117°17′ W	695	7-17-13	32°42′ N	117°16′ W	11 km	com. hook-line

compromised (Aalbers et al., 2004), only mouth-hooked individuals in good physical condition (e.g., no hook damage) were selected for tagging. Fish were captured at depths of 3–33 m. Most individuals were positively buoyant upon capture as a result of gas bladder expansion; however, artificial deflation of the gas bladder was unnecessary, and all tagged fish were able to return to depth after release.

Contact and reward information was printed upon

both the stalk and body of the DSTs as well as on externally affixed conventional tags. Information on recapture vessel, geographic location, fish size, sex, and general fish condition was documented upon communication with fishermen that reported tag recoveries. A $200 reward, tagging project T-shirt, and a summary of statistics for the recaptured individual were sent out to fishermen upon recovery of a DST.

DSTs were programmed by using 3 sampling re-

gimes to maximize fine-scale data acquisition within the constraints of tag memory capacity and battery life. In 2008, Cefas G5 DSTs were programmed to record depth (0.15 m resolution) every 2 min and temperature (0.1°C resolution) every 4 min. In 2009, Cefas G5 long-life DSTs stored depth and temperature records every 2 min, and tags in 2010 recorded depth at 1-min intervals and temperature every 2 min. Time-series data for cumulative analyses were standardized to a sampling regime of 2-min intervals for depth and 4-min intervals for temperature for all tag recoveries.

Upon recovery, fine-scale depth and temperature data were downloaded from all DSTs and complete time-series records over the entire deployment period were recovered from 22 DSTs. Battery life expired before recovery of 11 DSTs; however, the time-series data for the active recording life of these 11 DSTs were retrieved and provided by the tag manufacturer (Cefas Technology Limited). Four of the internally implanted DSTs were either shed through the incision site or incidentally discarded along with the viscera during fish processing, as only conventional identification markers were reported by fishermen. Subsequent investigations should incorporate 3 recovered data sets because recaptures were reported after completion of comprehensive data analyses, and 1 DST was lost in the mail.

Data analysis

Time-series data were formatted in Excel worksheets before export into an Access database (Microsoft Office 2010, Redmond, WA). All records were classified as *day*, *night*, or *twilight* values on the basis of the mean monthly time (Pacific Standard Time [PST]) of sunrise, sunset, and nautical twilight at the initial tagging location from the Astronomical Applications Department of the U.S. Naval Observatory data services portal (http://aa.usno.navy.mil/data/index.php). Daytime was defined as the average monthly time of sunrise until the average time of sunset; nighttime was assigned to all values between the mean time of nautical twilight at dusk until the mean time of nautical twilight at dawn; and twilight values included all data between mean time of sunset and nautical twilight at dusk as well as from nautical twilight at dawn until mean time of sunrise for each month.

Vertical rate of movement (VROM) was calculated for each fish (n=33) as the absolute difference of all subsequent records of depths taken every 2 min. Individual VROM values were converted to m h^{-1} before subsequent analyses. For all fish, VROM values that exceeded 150 m h^{-1} were binned by hour of the day to further evaluate daily periods of peak vertical activity. Depth values ≤5 m were binned by month and by hour to identify periods of surface-oriented behavior. Analyses did not control for autocorrelation in the mean comparisons and descriptive statistics used to characterize vertical data by time of day and season.

Seasonal depth statistics were evaluated for the 16 individual fish for which time-series data was collected for each month of the calendar year. Daily depth and temperature means were calculated and plotted with a 7-day running mean for smoothing. Daily depth probability plots were constructed with Matlab software vers. 6.0 [R12] (The MathWorks, Inc., Natick, MA) for each month with depth bins of 1 h by 2 m to illustrate the cumulative probability of occurrence for each depth. Spectral analysis by use of the fast Fourier transform (FFT) algorithm was conducted to show the diurnal signal and associated harmonics dominating in the frequency range of 0.5–8.0 cycles per day (cpd), and a Hanning window was used to reduce overlap between adjacent spectral peaks (Shepard et al., 2006). Data on mean daily depths were used to remove the diurnal cycle before long-period oscillations in the frequency band of 0.02–0.14 cpd were calculated for the 3 longest time series (721–741 days).
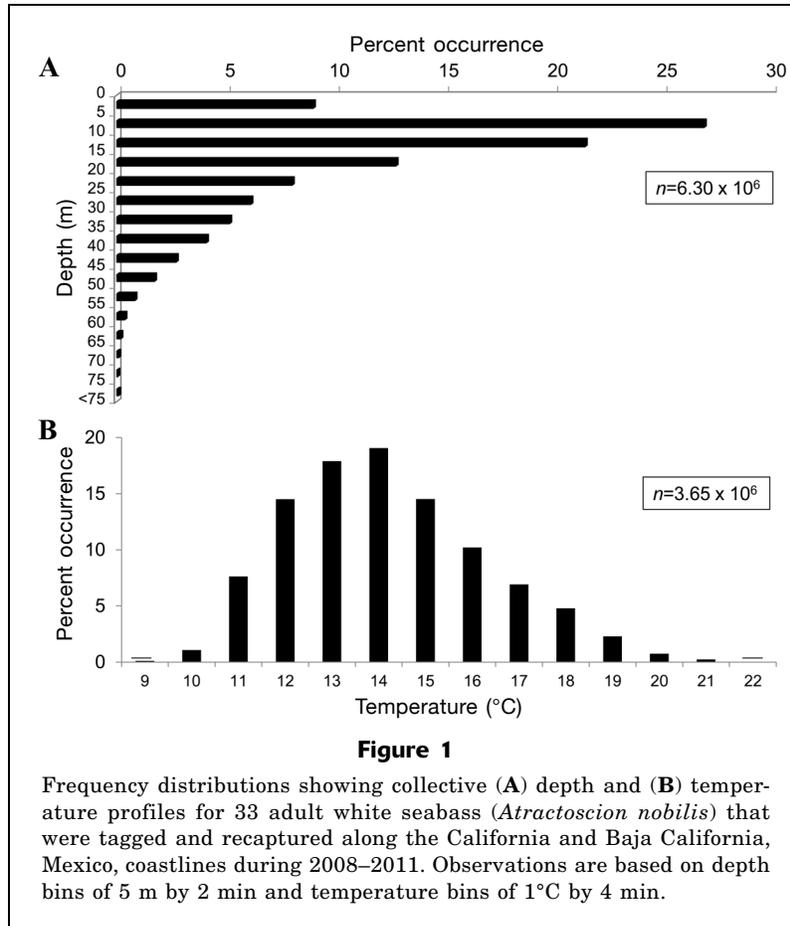
A paired *t*-test was conducted from mean depth values of 16 data sets that contained time-series records for each month of the calendar year to determine if seasonal differences were apparent between winter months (October–March) and summer months (April–September). Paired *t*-tests were also employed for all white seabass (n=33) to identify differences in VROM values: daytime versus nighttime periods, daytime versus twilight periods, and nighttime versus twilight periods. All mean values are indicated as means with standard deviations (SD) in parentheses, and α<0.05 was used to infer significance.

Results

Tag deployments and recoveries

Between April 24, 2008, and June 8, 2011, 173 adult white seabass, ranging in size from 71 to 152 cm TL (mean=118 cm TL), were affixed with DSTs. Of the 95 individuals for which sex was determined during tagging, 76% were identified as females and 24% were sound-producing males. Commercial and recreational crews recaptured 41 tagged individuals (77% female) during the study period, an overall recapture rate of 24% (Table 1). Annual recapture rates varied from a low of 6% (1 of 17) for 2011 deployments to a high of 29% (17 of 58) for 2010 deployments. Collectively, the largest number of tag recoveries also occurred in 2010, with 17 of the 41 tag recoveries (41%) reported during that year. Between the months of April and October, 95% of tag recaptures occurred. Of the 41 recaptured individuals, 13 were harvested by California gillnetters, 3 were reported by Mexican gillnetters, 13 were taken by California commercial hook-and-line vessels, 5 were caught by California recreational anglers, and 7 were recovered by California spear fishermen (Table 1).

Collectively, 9130 days of time-series data compiled from 33 DSTs provided 6.30×10^6 depth and 3.65×10^6

Figure 1

Frequency distributions showing collective (**A**) depth and (**B**) temperature profiles for 33 adult white seabass (*Atractoscion nobilis*) that were tagged and recaptured along the California and Baja California, Mexico, coastlines during 2008–2011. Observations are based on depth bins of 5 m by 2 min and temperature bins of 1°C by 4 min.

temperature records at resolutions of 2 min and 4 min. Fish at liberty for periods of up to 1572 days (mean=468 days) provided comprehensive multiyear data sets for an evaluation of seasonal and interannual patterns of depth distribution and habitat use.
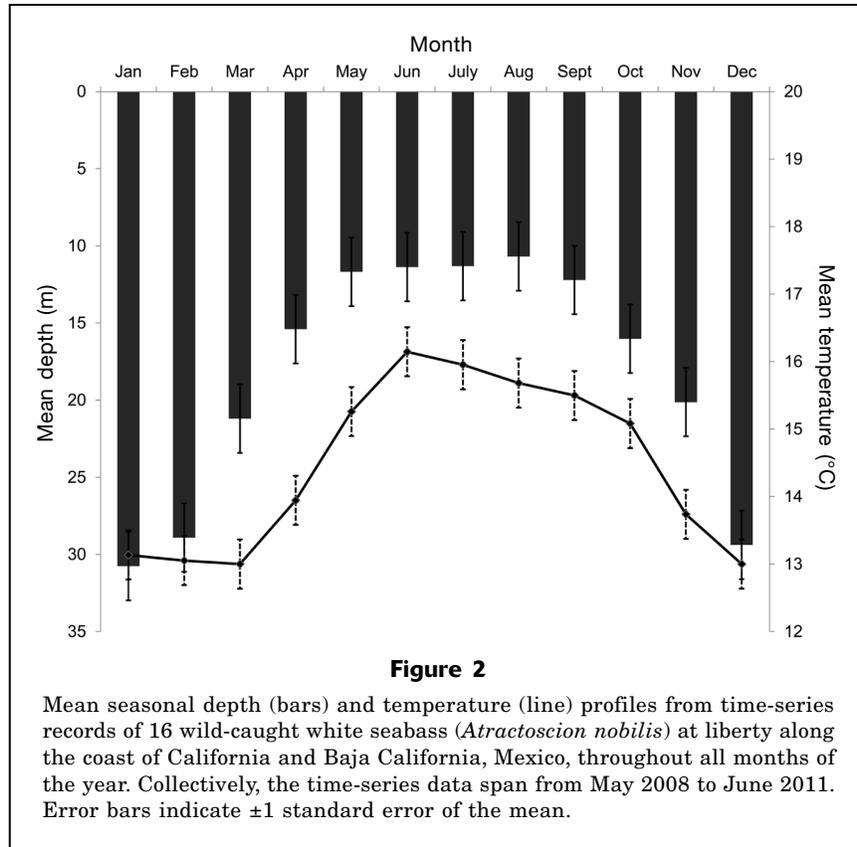
Vertical movements

The cumulative mean depths during the daytime, nighttime, and twilight periods were 14.9 m (SD 5.1), 15.5 m (SD 5.1), and 16.8 m (SD 6.8), respectively. Brief vertical excursions to depths up to 245 m were recorded; however, 95% of all the recorded depths were <50 m (Fig. 1A). Monthly mean depth values of tagged fish revealed that the fish remained significantly deeper in the water column between October and March (paired t-test: t=14.41, $P<0.0001$) than between April and September, reaching a maximum mean depth of 31.1 m (SD 13.2) in January (Fig. 2). Depth profiles were shallower on average as water temperatures increased during the spring and summer months, reaching a minimum mean depth of 10.5 m (SD 7.3) in August (Fig. 2).

Although diel and seasonal depth patterns were consistent among most fish, individual variability and interannual trends were apparent from mean daily depth and temperature profiles (Fig. 3, A and B). For example, fish A06097 remained consistently deeper (27.0 m [SD 13.5]) than all other white seabass (9.4 m [SD 4.5], n=4) during the summer months of 2010. In comparison, fish A03591 occurred at roughly half (14.4 m [SD 3.7]) of the mean depth observed for all other fish (28.9 m [SD 4.5], n=7) during the winter months of 2009–2010. Although A03591 was the largest female (152 cm TL) tagged during this study, a consistent correlation was not found between fish size and mean depth, fish size and mean temperature, or sex and mean depth. Mean depth and temperature from August to October in 2010 were considerably less for 5 individuals recaptured within Monterey Bay than for all other fish recaptured in other areas: 8.7 m and 13.6°C versus 13.0 m and 15.4°C.

Depth probability plots constructed for each month represented seasonal shifts in depth, indicating more surface-oriented distributions evident from April to October, transitional periods during March and November, and deeper profiles from December to February (Fig. 4, A–D). Fish showed more of a bimodal depth distribution during transitional periods, with peaks in cumulative probability near 10 m as well as at depths between 15 and 30 m (Fig. 4, B and D).

Figure 2

Mean seasonal depth (bars) and temperature (line) profiles from time-series records of 16 wild-caught white seabass (*Atractoscion nobilis*) at liberty along the coast of California and Baja California, Mexico, throughout all months of the year. Collectively, the time-series data span from May 2008 to June 2011. Error bars indicate ±1 standard error of the mean.

Depth probability plots summarized for 16 fish over a 24-h period also exhibited increased vertical activity around dawn and dusk throughout all months of the year (Fig. 4, A–D).

Consistent daily (24-h) and semidaily (12-h) peaks in spectral density were evident from FFTs of depth data for multiple individuals ($n=16$), indicating strong diel periodicities in vertical movement patterns (Fig. 5A). Longer-term periodicities (0.02–0.14 cpd), on the scale of days to months, were not persistent among individuals (Fig. 5B). Although variability in harmonic frequencies (cpd) was apparent between individuals ($n=16$), spectral density peaks were perceptible for 9 individuals between 0.044 and 0.048 cpd (21–23 days). Five individuals also showed predominant peaks in spectral density at 0.033 cpd (30 days); however, correlation (coefficient of correlation [r]=0.01–0.19) between depth and lunar luminosity values were low.

There was no significant difference in mean values of VROM between day and night (paired t-test: $t=0.49$, df=32, $P=0.625$). However, the mean VROM was significantly greater during the twilight hours (48.9 m h^{-1} [SD 12.3] than during the day (39.6 m h^{-1} [SD 10.8]; paired t-test: $t=8.16$, df=32, $P<0.0001$) and nighttime (41.1 m h^{-1} [SD 13.2]; paired t-test: $t=5.30$, df=32, $P<0.0001$). Similarly, VROM values exceeded 150 m h^{-1} most frequently around 0500 and 1900 PST (Fig. 6A). In contrast, surface-oriented behavior (depths ≤5

m) reached a minimum during twilight periods, and increased surface activity occurred from 0900 to 1600 PST and from 2300 to 0300 PST (Fig. 6B). Collectively, surface-oriented behavior was heightened from May to September, with a peak in July, but was rarely observed from November to February (Fig. 7).

Horizontal movements

The locations of tag recoveries spanned an 820-km stretch of coastline between La Salina, Baja California Norte (32°01′N, 116°53′W), and Half Moon Bay, California (37°27′N, 122°28′W) (Table 1). The majority of tagged fish ($n=22$) moved in a northwesterly direction (300–330° heading; mean: 317°) along the California coastline during their time at liberty. Five recaptured individuals moved southeast of their initial tagging location (135–158° heading; mean: 151°), 3 of which were recovered below the border of the United States and Mexico. The reported locations for more than half of the tag recoveries ($n=22$) were >100 km from the tagging site, and 21% of fish were recaptured between 20 and 100 km from the point of release. After a mean time at liberty of 433 days (range: 9–1154 days), 11 individuals were recovered within 20 km of their initial tagging site. There was no relationship between fish size and net displacement or between time at liberty and net displacement (Table 1).
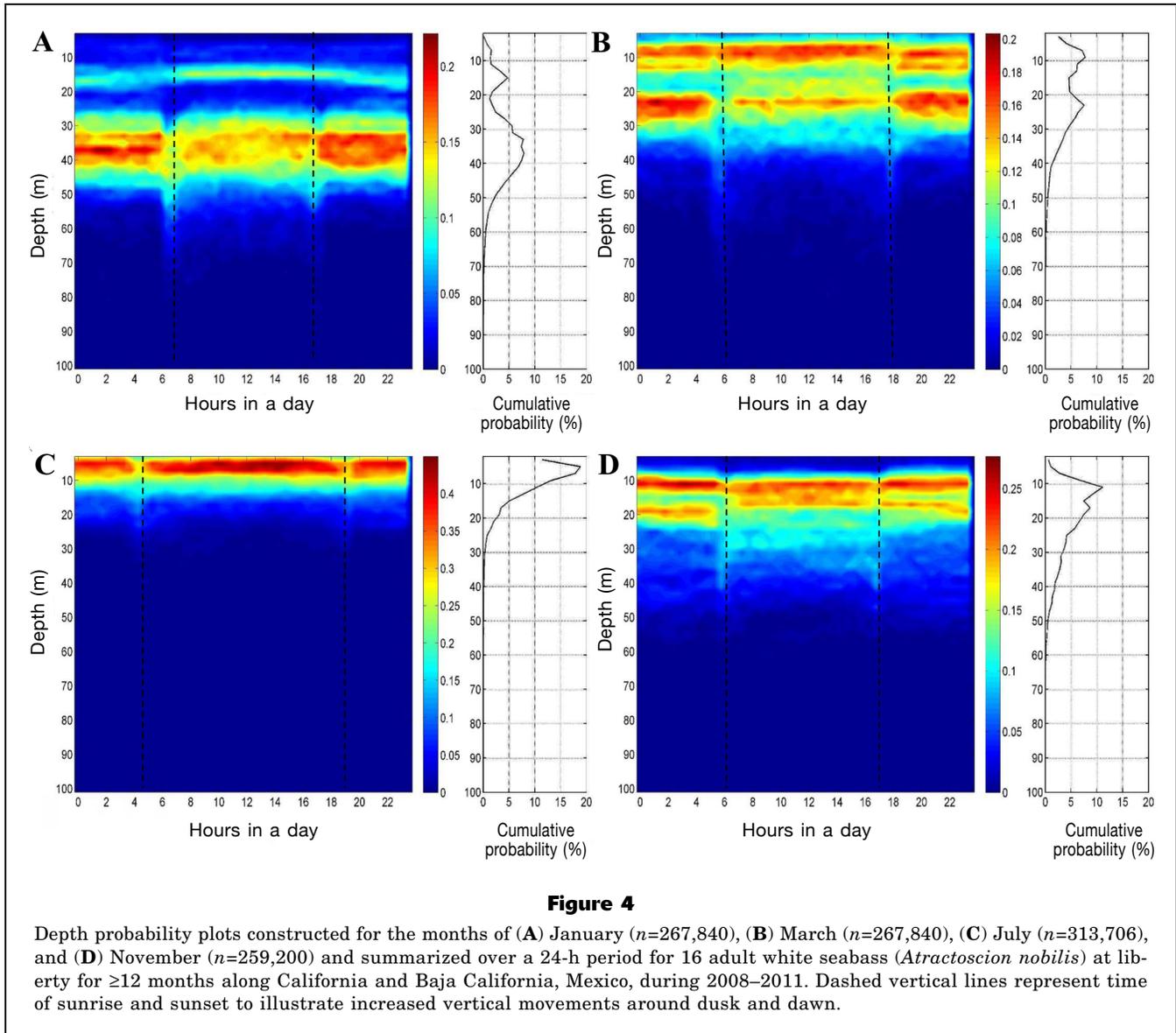
Figure 3

Time-series plots for 16 adult white seabass (*Atractoscion nobilis*) at liberty off California and Baja California, Mexico, between May 2008 and June 2011 (duration ≥12 months), illustrating (**A**) mean daily depth ($n=5.21\times10^6$ observations) and (**B**) mean daily temperature ($n=2.61\times10^6$ observations) values calculated with a 7-day running mean for smoothing.
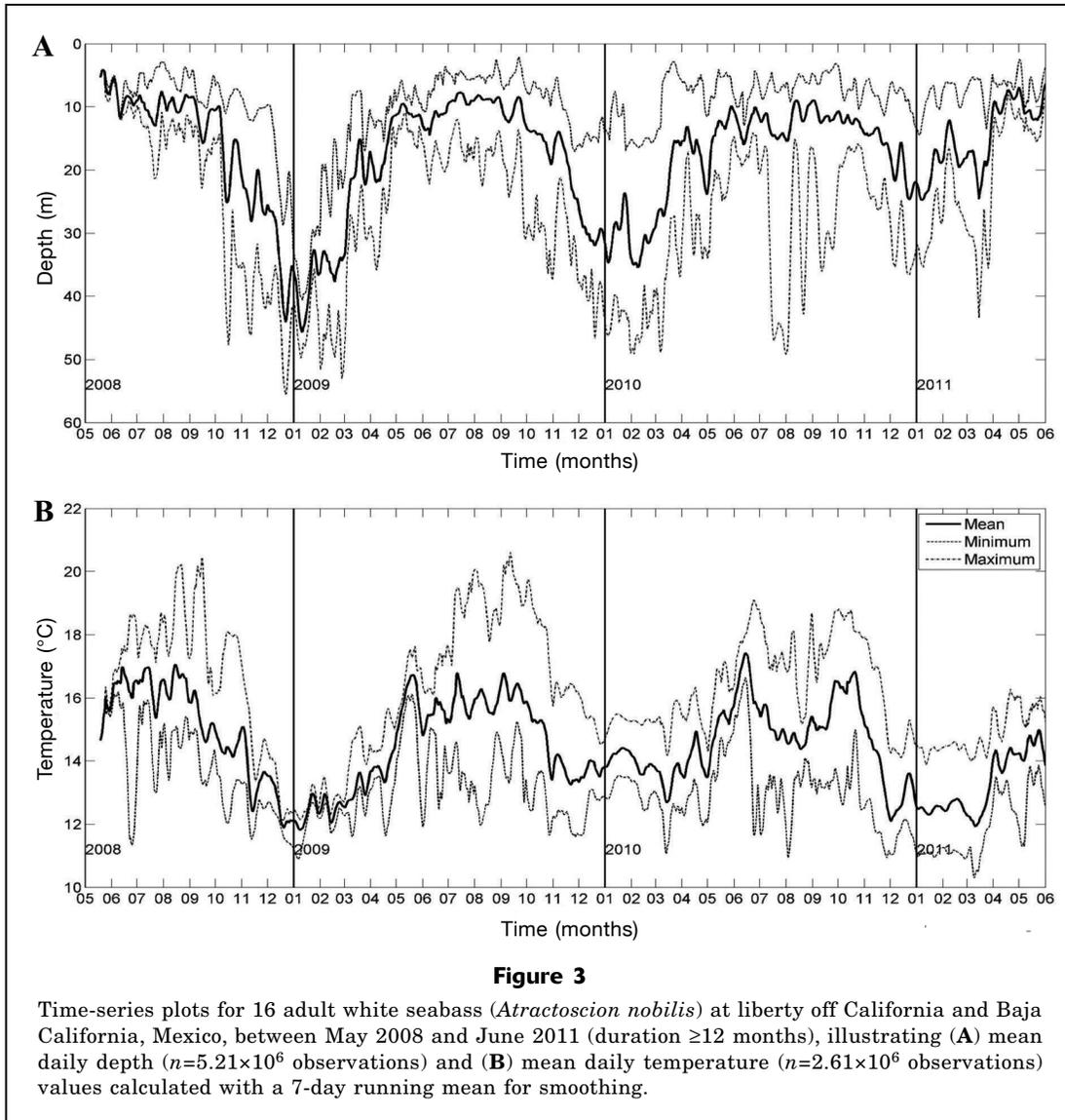
Temperature profiles

Tagged white seabass experienced water temperatures from 8.8°C to 23.6°C but spent the majority (52%) of time between 13 and 16°C with a peak around 14°C (Fig. 1B). Temperatures ranged between 11°C and 19°C for 95% of all records (Fig. 1B), and 95% of the time that fish spent at depths ≤5 m (i.e., in surface-oriented behavior) occurred at ambient temperatures between 12°C and 19°C. Mean monthly temperatures reached a minimum of 13.0°C in December and a maximum of 16.0°C in June (Fig. 2).

Discussion

This study revealed a relatively high tag recovery rate, providing an extensive data set from fish both tem-

porally and spatially distributed along the California and Baja California coastlines. Despite differences in deployment times and locations, depth and temperature profiles were markedly similar among most fish, and all individuals exhibited seasonal shifts in depth distribution. A significantly shallower and less variable distribution from April to September (than in winter months) contributes to greater vulnerability to most gear types and validates seasonal fishery trends that were suggested nearly a century ago (Skogsberg, 1939). Seasonal and diel shifts in depth distribution, VROM values, and surface-oriented behavior are all indicative of increased feeding and spawning-related activities as water temperatures increase in the spring and summer months. These data provide insight into the migratory nature of the white seabass, along with the first evidence of transboundary movements across the border
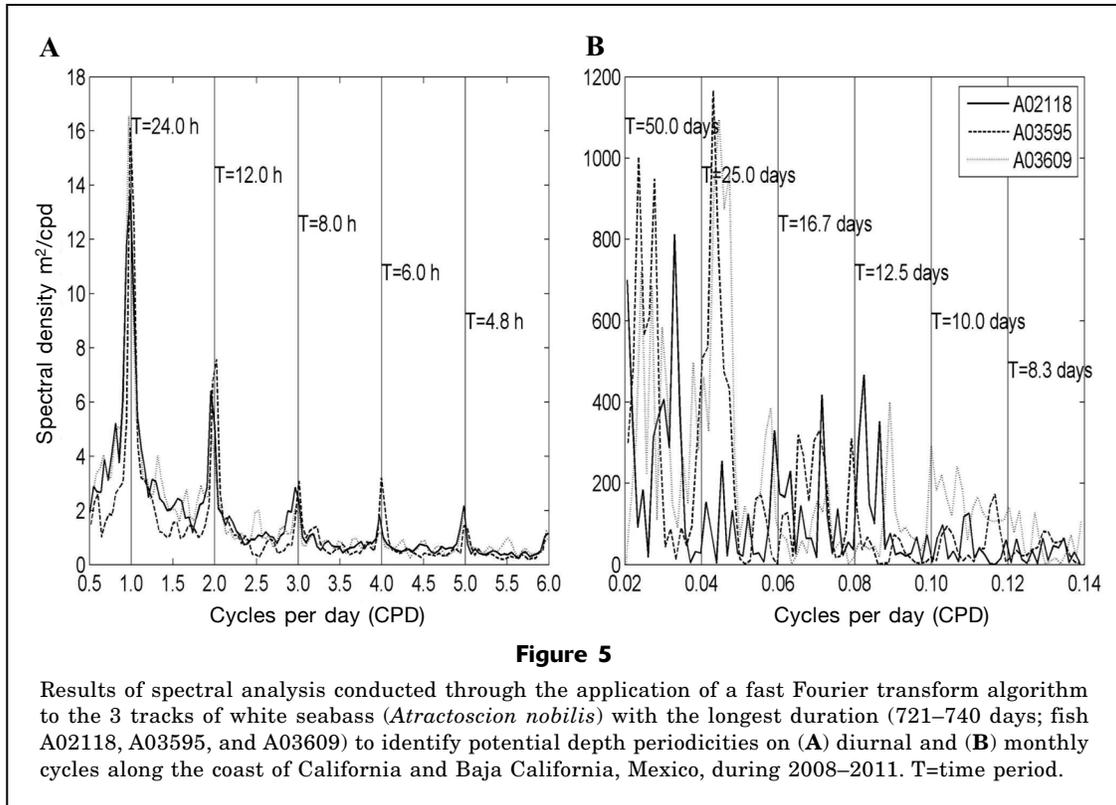
Figure 4

Depth probability plots constructed for the months of (**A**) January (*n*=267,840), (**B**) March (*n*=267,840), (**C**) July (*n*=313,706), and (**D**) November (*n*=259,200) and summarized over a 24-h period for 16 adult white seabass (*Atractoscion nobilis*) at liberty for ≥12 months along California and Baja California, Mexico, during 2008–2011. Dashed vertical lines represent time of sunrise and sunset to illustrate increased vertical movements around dusk and dawn.

of the United States and Mexico, further supporting the need for a cohesive international management regime for this species.

Tag recoveries

All recaptured white seabass were reported in good physical condition. The dissection of a 125-cm-TL female recaptured 17 days after release revealed that the tagging incision was completely healed and that there was no infection or postrelease trauma. Similarly, in a controlled study to evaluate the effects of surgically implanting V-16 tags (Vemco, Halifax, Nova Scotia, Canada) in wild-caught white seabass (75–124 cm TL), incision sites healed within 90 days, and there were no indications of necrosis or infection (Stutzer, 2004).

Stutzer (2004) also found no long-term (450 days) effects on growth, feeding behavior, or survival for the adult white seabass that received tag implants (*n*=30), versus fish in control (*n*=20) and sham surgery groups (*n*=20). Although survival of white seabass was not likely influenced by the capture, handling, or tagging processes, it is possible that other factors (e.g., predation and barotrauma) influenced postrelease survival in the study described here. At least 2 tagged individuals were observed to have been preyed upon by California sea lions (*Zalophus californianus*) directly after release. Increased vulnerability to predation directly after release likely was associated with the effects of exertion, gas bladder inflation, and equilibrium loss experienced during the capture process (Danylchuk et al., 2007).
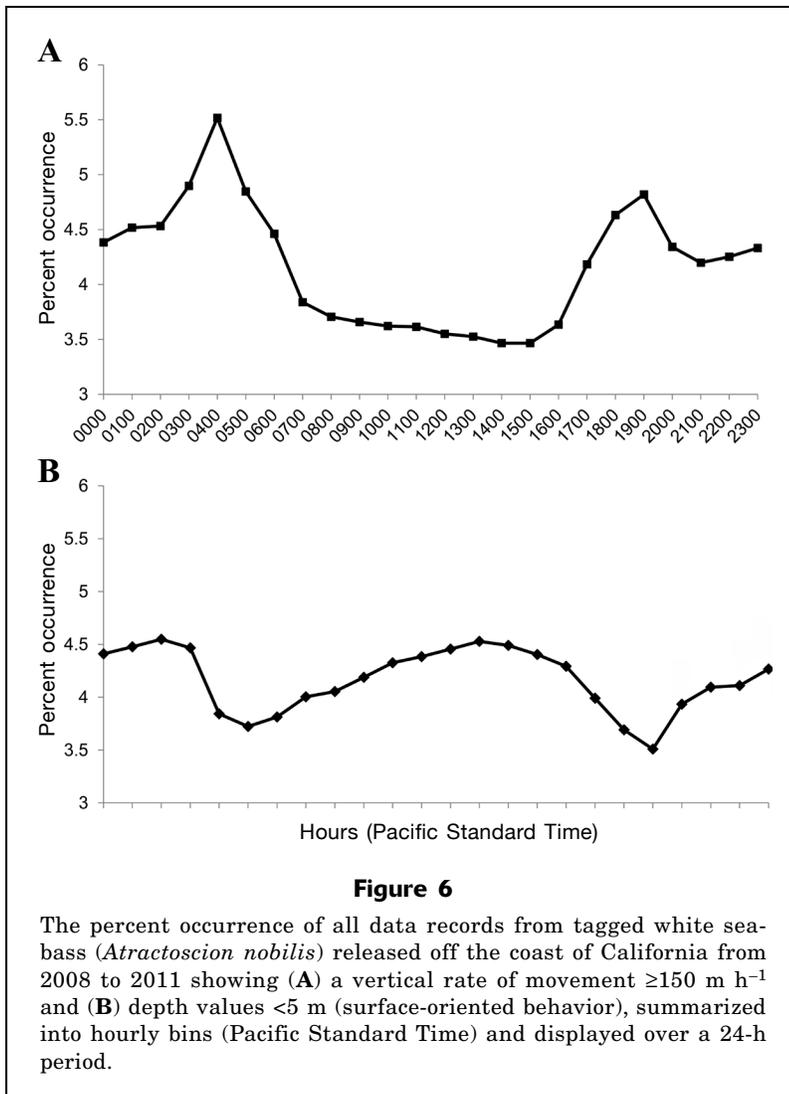
Figure 5

Results of spectral analysis conducted through the application of a fast Fourier transform algorithm to the 3 tracks of white seabass (*Atractoscion nobilis*) with the longest duration (721–740 days; fish A02118, A03595, and A03609) to identify potential depth periodicities on (**A**) diurnal and (**B**) monthly cycles along the coast of California and Baja California, Mexico, during 2008–2011. T=time period.

Other factors that may have resulted in an underestimate of the recapture rate include tag shedding and nonreporting of recaptured individuals. Although a $200 reward was offered for the return of DSTs, it is possible that some recoveries were not reported. Four of the tags recovered in this study were not returned for up to 15 months after the recapture date, further indicating the possibility of under reporting. Therefore, the reported 24% recapture rate is conservative because it does not account for tags that were shed or recaptures that were not reported by the time of the analyses for this study. Given that the average time at liberty was 468 days, the recapture rate may increase further with additional tag recoveries.

The age and size structure of the fish tagged in this study were representative of fish captured in the commercial fishery, as more than 50% of white seabass harvested in California in 2010–2011 were >10 years of age (>112 cm TL) (CDFG[2]). Given that the mean size of white seabass captured in this study was 118 cm TL, all individuals were mature and most tagged fish were >10 years old, and some individuals exceeded 20 years of age (>150 cm TL) (Clark, 1930; Thomas, 1968; Romo-Curiel et al., in press). The ratio of commercial (67%) to recreational (33%) landings in California in 2010 was consistent with the ratio of recaptured white seabass observed in this study, with 68% of tags recovered by commercial fisheries and 32% from recreational anglers (in U.S. waters) (CDFG, 2011).

Of the white seabass tag recaptures, 95% occurred from April to October, a period that directly aligns with seasonal decreases in depth distribution (Fig. 2) and heightened surface-oriented behavior (Fig. 7). Only a single individual was recaptured from December to March, indicating that white seabass are less vulnerable to exploitation upon their dispersal to deeper waters during the winter months. The associations between fish depth distribution and catchability observed in this study are consistent with conclusions on seasonal fishery dynamics from Skogsberg (1939) and others (McCorkle[6]), who have reported that gill nets traditionally were deployed near the surface until mid-October and then set along the bottom from mid-October to December as fish retired to deeper waters. After December, landings were reduced substantially because fishermen were often unable to locate white seabass until the following summer (Skogsberg, 1939). Seasonal recapture trends align with historical fishery data, which indicate that the majority of white seabass landings in California occur from April to September (Skogsberg, 1925; Thomas, 1968). All tag deployments occurred from March to July and peaked in June, a period that directly aligns with the white seabass spawning season (Aalbers, 2008) and validates a heightened vulnerability to capture when fish aggregate to spawn.

---

[6] McCorkle, M. 2010. Personal commun. Commercial fisherman, Santa Barbara, CA 93109.

Figure 6

The percent occurrence of all data records from tagged white sea-bass (*Atractoscion nobilis*) released off the coast of California from 2008 to 2011 showing (**A**) a vertical rate of movement ≥150 m h^{-1} and (**B**) depth values <5 m (surface-oriented behavior), summarized into hourly bins (Pacific Standard Time) and displayed over a 24-h period.

Upon harvest, 77% of recaptured individuals were identified as female, indicating that white seabass sex can be adequately determined on the basis of the detection of sound production during the spawning season. The skewed sex ratio of 3.1:1.0 observed in this study may be related to temporal or size-related segregation among sexes; however, practical inferences cannot be made without a suitable sex-ratio estimate for the wild population.

Vertical movements

The observed shift of white seabass to deeper waters during the winter months may be in response to decreased thermal stratification or possibly to the interrelated effects that these conditions have on prey distribution and availability. As reported for other species, multiple factors, such as changes in oceanographic conditions and prey distribution, contribute to the ver-

tical movements displayed by a species at different times and locations (Hinke et al., 2005; Shepard et al., 2006; Schaefer et al., 2007; Sepulveda et al., 2010). Annual cycles of surface productivity and temperature structure off the coast of California have been shown to influence the vertical distribution of Chinook salmon (*Oncorhynchus tshawytscha*), with deeper profiles documented during the winter months (Hinke et al., 2005). Seasonal shifts in vertical distribution have also been described for Atlantic cod (*Gadus morhua*) (Neat et al., 2006) and yellowtail flounder (*Limanda ferruginea*) (Walsh and Morgan, 2004) in the northwest Atlantic.

Given the interannual variability in the depth and temperature profiles observed for multiple tagged individuals (Fig. 3, A and B), it is likely that seasonal trends in vertical distribution are closely related to localized oceanic conditions. Interannual variation between consecutive winter seasons was evident from the 723-day track of fish A03595, which transitioned from a mean depth of 31.8 m (SD 13.2) in the winter months of 2009–2010 to a mean depth of 8.4 m (SD 3.6) during the winter months of 2010–2011. Similarly, 5 tracks that extended throughout the winter months of 2010–2011 exhibited a considerable reduction in mean depth (18.4 m [SD 7.3]) compared with the 6 tracks recorded in the winter of 2008–2009 (30.8 m [SD 13.0]), but mean temperature values remained consistent (12.8°C) for both sets of time-series data.

Spectral peaks at 1 and 2 cpd may represent increased vertical movements around dawn and dusk, and harmonic peaks at 3 and 4 cpd may indicate weaker movement patterns surrounding daily tidal fluctuations (Fig. 5A). Periodic oscillations in the vertical thermal gradient within the coastal waters off San Diego have been shown to cycle at 6, 8, 12, and 24 h (1, 2, 3, and 4 cpd) relative to internal tidal fluctuations (Cairns, 1968), which typically lag 3 to 5 h behind mixed semidiurnal surface tides (Cairns and LaFond, 1966). Therefore, consistent daily shifts in depth distribution of white seabass may correspond with semidiurnal fluctuations in coastal thermocline depth. Diel and circatidal rhythms in the vertical movement patterns of basking sharks (*Cetorhinus maximus*) also were identified in the northeast Atlantic on the basis of spectral peaks in fine-scale depth records at periods of 1 and 2 cpd (Shepard et al., 2006). In the study described here, inconsistent harmonics in longer period (0.02–0.14 cpd) spectral density plots (Fig. 5B) indicate that the time-series data did not continuously

Figure 7

The percent occurrence of all depth values <5 m plotted by month to illustrate periods of surface-oriented behavior for 33 adult white seabass (*Atractoscion nobilis*) tagged and released off California and Baja California, Mexico, from 2008 to 2011.
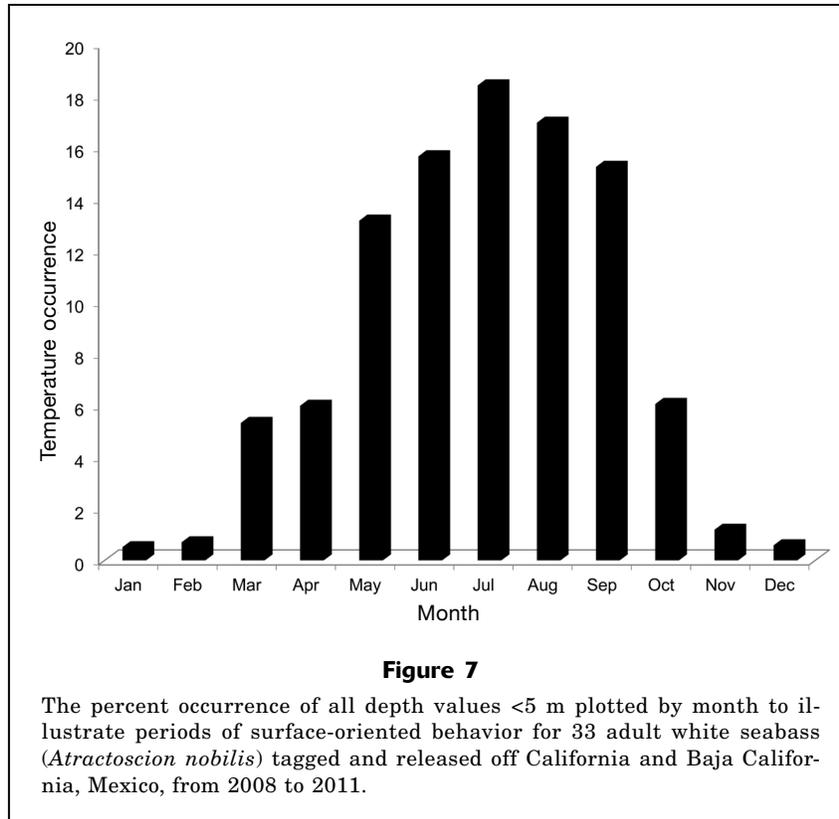
cycle at regular intervals over prolonged time periods (days to months). If this basic assumption of the FFT algorithm has not been met, then discontinuity would disperse energy throughout all frequencies (cpd), causing considerable noise in the spectral density plots. Additional analyses from tracks of multiple individual fish with extended time-series records may further identify rhythms in vertical movements on a monthly (lunar) or seasonal scale.

Increased VROM values around dusk and dawn indicate heightened crepuscular activity throughout the year. Heightened feeding activity in other fishes and sharks has been associated with crepuscular periods as well as with instances of increased vertical activity (Kitagawa et al., 2004, Sepulveda et al., 2004, Bestley et al., 2008). Higher rates of crepuscular activity indicate that white seabass are effective low-light predators and support fishery information that white seabass are targeted most effectively by hook-and-line fishermen during crepuscular periods (Pfleger[7]). Because the spawning activity of white seabass peaks just after sunset during the spring and summer months (Aalbers, 2008), the increased VROM around dusk may also correspond with vertical excursions as-

sociated with spawning-related behavior and broadcast spawning events (Aalbers and Drawbridge, 2008). In contrast, diel surface-oriented behavior was observed most consistently during the midday (0900–1600 PST) and predawn (2300–0300 PST) hours, timing that coincided with periods of reduced vertical activity (Fig. 6, A and B). Surface-oriented behavior has also been described for white seabass during courtship periods within the hours preceding sunset (Aalbers and Drawbridge, 2008), periods when fish may be more vulnerable to spear fishermen and surface gill nets.

Horizontal movements

It was not uncommon for individuals to move more than 500 km from their initial point of release, verifying that white seabass are a highly mobile coastal species. A 109-cm-TL female travelled a net distance of 555 km over a 76-day period from Santa Catalina Island to Monterey Bay, California, at a rate of 8 km day^{-1}. Collectively, a mean displacement of 229 km from the initial tagging location indicates that white seabass are capable of extensive seasonal migrations. Widespread horizontal movements during the spawning season are consistent with recent data that indicate limited residency periods at distinct spawning sites along the southern coast of California (Aalbers and Sepulveda, 2012). The broad movements docu-

[7] Pfleger, T. 2010. Personal commun. Pfleger Institute of Environmental Research, 2110 South Coast Hwy., Oceanside, CA 92054.

mented in our study contrast with the limited home ranges that have been observed in other coastal fishes (Holland et al., 1996; Lowe et al., 2003; Neat et al., 2006). Although 11 of the tagged white seabass were recaptured within close proximity to their release sites after periods of up to 1154 days, interim movements away from the area during their time at liberty may have been substantial. Because fisheries-related information indicates that white seabass tend to reoccur within specific areas from year to year (Thomas, 1968) and considering the mean time at liberty for recaptures with short displacements was near 1 year in our study, it is possible that white seabass maintain an affinity for distinct sites or habitats that are revisited annually for feeding or spawning.

Although the majority of tag deployments occurred around Santa Catalina Island, most tags were recovered within the near-coastal waters. Only 2 tagged fish were recaptured around Santa Catalina Island, and interisland movements were not documented in this study. Seven individuals that were tagged around Santa Catalina Island were subsequently recaptured off the coast of Ventura, indicating a consistent route between Catalina Island and the Ventura flats. An additional 7 fish that were tagged around Santa Catalina Island in May and early June were later caught in the vicinity of Monterey Bay during late July and August of the same or following year, indicating that a portion of the stock traveled up the California coast during the summer months of some years. The high incidence of white seabass tag recaptures in Monterey Bay (26%) corresponds with the recent observed increase in recreational (38%) and commercial landings (22%) north of Point Arguello (CDFG, 2011).

Trends from tag deployments and recaptures indicated that white seabass moved seasonally in a north and westerly direction from July to September, as sea-surface temperatures (SSTs) increased throughout Southern California. Similar movement patterns based on fisheries-related data for Pacific barracuda (*Sphyraena argentea* [see Pinkas, 1966]) and yellowtail jack (*Seriola lalandi* [see Baxter, 1960]) have been suggested for other predatory species of the Southern California Bight. Northward movements of white seabass correspond with latitudinal shifts in SST maxima that follow a seasonal relaxation of coastal wind-driven upwelling and occur later (September–October) to the north of Point Arguello than SST peaks within the eastern Southern California Bight (August) (Legaard and Thomas, 2006; Garcia-Reyes and Largier, 2012). The observed drop in mean temperature values during the months of July–October (Fig. 1B), after a peak in June, may represent decreased SSTs when fish moved above Point Arguello during the summer and fall months, where ambient temperatures are consistently lower than those off the southern coast of California (Reid, 1988). An observed decline in mean depths, temperatures, and VROM values during the late summer and autumn months supports the Skogsberg (1939) hypothesis that white seabass progress northward along thermal fronts as temperatures increase within the Southern California Bight; however, additional data from light-sensitive archival tags with external temperature sensors are necessary to better assess annual migration routes and seasonal trends.

Temperature profiles

Although white seabass occurred across a broad temperature range (8–24°C), data indicate that white seabass occupy a relatively narrow thermal gradient, spending more than half of their time at temperatures between 13° and 16°C (Fig. 1B). Chinook salmon have also been reported to predominantly inhabit a narrow temperature range (8–12°C), indicating that fish may alter their depth in the water column to maintain a persistent thermal experience (Hinke et al., 2005). The relatively consistent temperature profiles from annual time-series records indicate that white seabass may alter spatial and temporal behavior patterns to occupy a particular thermal niche.

Periods of heightened surface-oriented behavior directly aligned with the months in which waters in Southern California exhibit the greatest degree of thermal stratification, with a relatively strong and shallow thermocline present from May to September throughout the region (Cairns and LaFond, 1966). Additionally, a peak in white seabass temperature records (Fig. 1B) corresponds with the 14°C isotherm that is commonly used to identify thermocline depth along the southern coastline of California (Cairns, 1968). However, because tag sensors were implanted within the peritoneal cavity of white seabass, thermal inertia prevented accurate measurement of thermocline depth from tag records. Further, because white seabass occurred over a broad stretch of coastline within areas of high mixing (i.e., upwelling zones and offshore islands) it is difficult to ascertain how thermocline depth influenced vertical distribution in this study.

Future research and management

Heightened fishing effort in conjunction with considerable limitations in essential fishery information warrants the continued need for fishery-independent data sources and active management practices for this species (MacCall et al., 1976; CDFG[1]). Supplementary long-term tagging data, including archived light-level and external temperature records, are currently being collected to provide more specific information on white seabass migration patterns relative to seasonal and interannual variations in oceanic conditions. Additional time-series records from multiple years across the geographic range of white seabass are needed to provide a more comprehensive understanding of fish habitat use, transboundary movements, and temporal shifts in distribution. Furthermore, complementary studies on white seabass stock structure along with a formal

stock assessment with currently available data sources would better enhance our understanding of the population dynamics of this species and facilitate the development of long-term management strategies.

In conclusion, this work provides insight into the seasonal movement patterns, habitat use, and depth distribution of wild-caught white seabass off the coast of California. Distinct seasonal depth distributions were identified with significantly deeper profiles during the winter months. Despite interannual variability, tagged adults spanned a narrow thermal gradient (13–16°C) centered around the 14°C isotherm, indicating the importance of environmental temperature on horizontal and vertical movements. A vertical shift to shallower waters during the spring and summer months directly coincides with the white seabass spawning period and with peak landings and fishing effort. Because of the diverse harvesting methods and seasonally high levels of fishing effort over a broad geographic range, all fisheries must be considered for the effective management and long-term sustainability of this resource.

Acknowledgments

Literature cited

Aalbers, S. A., G. M. Stutzer, and M. A. Drawbridge.
   2004.   The effects of catch-and-release angling on the growth and survival of juvenile white seabass captured on offset circle and j-type hooks.   N. Am. J. Fish. Manage. 24:793–800.   doi: 10.1577/M03-034.1.
Aalbers, S. A.
   2008.   Seasonal, diel, and lunar spawning periodicities and associated sound production management of the white seabass (*Cynoscion nobilis*) in California waters. Fish. Bull. 106:143–151.
Aalbers, S. A., and M. A. Drawbridge.
   2008.   White seabass spawning behavior and sound production.   Trans. Am. Fish. Soc. 137:542–550.   doi: 10.1577/T04-058.1.
Aalbers, S. A., and C. A. Sepulveda.
   2012.   The utility of a long-term acoustic recording system for detecting white seabass *Atractoscion nobilis* spawning sounds.   J. Fish. Biol. 81:1859–1870.   doi: 10.1111/j.1095-8649.2012.03399.x.
Allen, L. G., D. J. Pondella, and M. A. Shane.
   2007.   Fisheries independent assessment of a returning fishery: abundance of juvenile white seabass (*Atractoscion nobilis*) in the shallow nearshore waters of the Southern California Bight, 1995–2005.   Fish. Res. 88:24–32.   doi: 10.1016/j.fishres.2007.07.012.
Baxter, J. L.
   1960.   A study of the yellowtail *Seriola dorsalis* (Gill). Fish Bull. Calif. Dep. Fish Game 110:1–91.
Bestley, S., T. A. Patterson, M. A. Hindell, and J. S. Gunn.
   2008.   Feeding ecology of wild migratory tunas revealed by archival tag records of visceral warming.   J. Anim. Ecol. 77:1223–1233.   doi: 10.1111/j.1365-2656.2008.01437.x.
Cairns, J. L.
   1968.   Thermocline strength fluctuations in coastal waters.   J. Geophys. Res. 73:2591–2596.   doi: 10.1029/JB073i008p02591.
Cairns, J. L., and E. O. LaFond.
   1966.   Periodic motions of the seasonal thermocline along the southern California coast.   J. Geophys. Res. 71:3903–3915.   doi: 10.1029/JZ071i016p03903.
CDFG (Calif. Dep. Fish Game).
   2009.   Review of selected California fisheries for 2008: coastal pelagic finfish, market squid, ocean salmon, groundfish, California spiny lobster, spot prawn, white seabass, kelp bass, thresher shark, skates and rays, Kellet's whelk, and sea cucumber.   CalCOFI Rep. 50:14–42.
   2011.   Review of selected California fisheries for 2010: coastal pelagic finfish, market squid, ocean salmon, groundfish, highly migratory species, Dungeness crab, spiny lobster, spot prawn, Kellet's whelk, and white seabass.   CalCOFI Rep. 52:13–35.
Clark, F. N.
   1930.   Size at first maturity of the white seabass (*Cynoscion nobilis*).   Calif. Fish Game 16:319–323.
Coykendall, D. K.
   1998.   Population structure and dynamics of white seabass (*Atractoscion nobilis*) and the genetic effect of hatchery supplementation on the wild population.   Ph.D. diss., 106 p.   Univ. Calif., Davis, CA.
Danylchuk, S. E., A. J. Danylchuk, S. J. Cooke, T. L. Goldberg, J. Koppelman, and D. P. Phillip.
   2007.   Effects of recreational angling on the post-release behavior and predation of bonefish (*Albula vulpes*): the role of equilibrium status at the time of release.   J. Exp. Mar. Biol. Ecol. 346:127–133.   doi: 10.1016/j.jembe.2007.03.008.
Franklin, M. P.
   1997.   An investigation into the population structure of white seabass (*Atractoscion nobilis*), in California and Mexican waters using microsatellite DNA analysis. Ph.D. diss., 109 p.   Univ. Calif., Santa Barbara, CA.
Garcia-Reyes, M., and J. L. Largier.
   2012.   Seasonality of coastal upwelling off central and northern California: new insights, including temporal and spatial variability.   J. Geophys. Res. 117, C03028.   doi: 10.1029/2011JC007629.
Gruenthal, K. M., and M. A. Drawbridge.
   2012.   Toward responsible stock enhancement: broadcast spawning dynamics and adaptive genetic management

in white seabass aquaculture. Evol. Appl. 5:405–417. doi: 10.1111/j.1752-4571.2011.00234.x.

Hinke, J. T., D. G. Foley, C. Wilson, and G. M. Watters.
    2005. Persistent habitat use by Chinook salmon *Oncorhynchus tshawytscha* in the coastal ocean. Mar. Ecol. Prog. Ser. 304:207–220. doi: 10.3354/meps304207.

Holland, K. N., C. G. Lowe, and B. M. Wetherbee.
    1996. Movements and dispersal patterns of blue trevally (*Caranx melampygus*) in a fisheries conservation zone. Fish. Res. 25:279–292.

Kitagawa, T., S. Kimura, H. Nakata, and H. Yamada.
    2004. Diving behavior of immature, feeding Pacific bluefin tuna (*Thunnus thynnus orientalis*) in relation to season and area: the East China Sea and the Kuroshio–Oyashio transition region. Fish. Oceanogr. 13:161–180. doi: 10.1111/j.1365-2419.2004.00282.x.

Legaard, K. R., and A. C. Thomas.
    2006. Spatial patterns in seasonal and interannual variability of chlorophyll and sea surface temperature in the California Current. J. Geophys. Res. 111, C06032. doi: 10.1029/2005JC003282.

Lowe, C. G., D. T. Topping, D. P. Cartamil, and Y. P. Papastamatiou.
    2003. Movement patterns, home range, and habitat utilization of adult kelp bass *Paralabrax clathratus* in a temperate no-take marine reserve. Mar. Ecol. Prog. Ser. 256:205–216. doi: 10.3354/meps256205.

MacCall, A. D., G. D. Stauffer, and J.-P. Troadec.
    1976. Southern California recreational and commercial marine fisheries. Mar. Fish. Rev. 38:1–32.

Neat, F. C., P. J. Wright, A. F. Zuur, I. M. Gibb, F. M. Gibb, D. Tulett, D. A. Righton, and R. J. Turner.
    2006. Residency and depth movements of a coastal group of Atlantic cod (*Gadus morhua* L.). Mar. Biol. 148:643–654. doi: 10.1007/s00227-005-0110-6.

Pinkas, L.
    1966. A management study of the California barracuda *Sphyraena argentea* Girard. Fish Bull. Calif. Dep. Fish Game 134:1–58.

Reid, J. L.
    1988. Physical oceanography, 1947–1987. CalCOFI Rep. 29:42–65.

Rios-Medina, K.
    2008. Analisis de diversidad y estructura genetica de la corvina blanca (*Atractoscion nobilis*) de las costas de la Peninsula de Baja California (Mexico) y California (EE.UU.) como primera aproxamacion para evaluar el impacto de su programa de repoblacion. Tesis, 65 p. Universidad Autonoma De Baja California, Ensenada, Baja California Norte, Mexico.

Romo-Curiel, A. E., S. Z. Herzka, O. Sosa-Nishizaki, C. A. Sepulveda, and S. A. Aalbers.
    In press. Otolith-based growth estimates and insights into population structure of white seabass, *Atractoscion nobilis*, off the Pacific coast of North America. Fish. Res. 161:374–383. doi: 10.1016/j.fishres.2014.09.004.

Rosales-Casian, J. A., and J. R. Gonzalez-Camacho.
    2003. Abundance and importance of fish species from the artisanal fishery on the Pacific coast of northern Baja California. Bull. South. Calif. Acad. Sci. 102:51–65.

Schaefer, K. M., D. W. Fuller, and B. A. Block.
    2007. Movements, behavior, and habitat utilization of yellowfin tuna (*Thunnus albacares*) in the northeastern Pacific Ocean, ascertained through archival tag data. Mar. Biol. 152:503–525. doi: 10.1007/s00227-007-0689-x.

Sepulveda, C. A., S. Kohin, C. Chan, R. Vetter, and J. B. Graham.
    2004. Movement patterns, depth preferences, and stomach temperatures of free-swimming juvenile mako sharks, *Isurus oxyrhinchus*, in the Southern California Bight. Mar. Biol. 145:191–199. doi: 10.1007/s00227-004-1356-0.

Sepulveda, C. A., A. Knight, N. Nasby-Lucas, and M. L. Domeier.
    2010. Fine-scale movements of the swordfish *Xiphias gladius* in the Southern California Bight. Fish. Oceanogr. 19:279–289. doi: 10.1111/j.1365-2419.2010.00543.x.

Shepard, E. L. C., M. Z. Ahmed, E. J. Southall, M. J. Witt, J. D. Metcalfe, and D. W. Sims.
    2006. Diel and tidal rhythms in diving behaviour of pelagic sharks identified by signal processing of archival tagging data. Mar. Ecol. Prog. Ser. 328:205–213. doi: 10.3354/meps328205.

Skogsberg, T.
    1925. Preliminary investigation of the purse seine industry of southern California. Fish Bull. Calif. Fish Game Comm. 9:1–95.
    1939. The fishes of the family Sciaenidae (croakers) of California. Fish Bull. Calif. Div. Fish Game 54:1–62.

Stutzer, G. M.
    2004. Effects of intraperitoneal implantion of ultrasonic transmitters on the feeding activity, growth, tissue reaction, and survival of adult white seabass (*Atractoscion nobilis*). M.S. thesis, 57 p. Calif. State Univ., San Marcos, CA.

Thomas, J. C.
    1968. Management of the white seabass (*Cynoscion nobilis*) in California waters. Fish Bull. Calif. Dep. Fish Game 142:1–33.

Vojkovich M., and S. Crooke.
    2001. White seabass. *In* California's living marine resources: a status report (W. S. Leet, C. M. Dewees, R. Klingbeil, and E. J. Larson, eds.), p. 206–208. Calif. Dep. Fish Game, Sacramento, CA. [Available from http://www.dfg.ca.gov/marine/status/status2001.asp.]

Vojkovich M., and R. J. Reed.
    1983. White seabass, *Atractoscion nobilis*, in California-Mexican waters: status of the fishery. CalCOFI Rep. 24: 79–83.

Walsh, S. J., and M. J. Morgan.
    2004. Observations of natural behaviour of yellowtail flounder derived from data storage tags. ICES J. Mar. Sci. 61:1151–1156. doi: 10.1016/j.icesjms.2004.07.005.

Whitehead, S. S.
    1929. Analysis of boat catches of white sea bass (*Cynoscion nobilis*) at San Pedro, California. Fish Bull. Calif. Div. Fish Game 21:1–27.