Rearing conditions and habitat use of white seabass (*Atractoscion nobilis*) in the northeastern Pacific based on otolith isotopic composition

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A B S T R A C T

White seabass, *Atractoscion nobilis*, is an important coastal resource throughout both California and Baja California, but whether this species comprises a single or multiple subpopulations in the northeastern Pacific is not known. The aim of this study was to infer larval rearing habitats and population structure of white seabass by sampling adults from three regions spanning a latitudinal temperature gradient and a distance of over 1000 km, and analyzing the isotopic composition (δ18O and δ13C) of otolith aragonite corresponding to the larval, juvenile and adult stages. Otolith cores revealed high isotopic variability and no significant differences among regions, suggesting overlapping rearing conditions during the larval stage, the potential for long distance dispersal or migration or selective mortality of larvae at higher temperatures. Back-calculated temperatures of aragonite precipitation derived using regional salinity-δ18O relationships and local salinity estimates also did not differ significantly. However, there were significant differences between the δ18O values of the first seasonal growth ring of age 0 fish as well as back-calculated aragonite precipitation temperatures, suggesting the presence of two potentially discrete subpopulations divided by Punta Eugenia (27°N) along the central Baja California peninsula. These findings are consistent with regional oceanographic patterns and are critical for understanding white seabass population structure, and provide information needed for the implementation of appropriate management strategies.

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1. Introduction

Assessing the role of dispersion, migration and the level of population connectivity is important for managing coastal fish populations and identifying ecologically important habitats (Gillanders, 2005; Cowen and Sponaugle, 2009). Sciaenid fishes have early life stages that can be found in various coastal habitat types (Cowan and Birdsong, 1985; Gray and McDonall, 1993). The larval stage can last several weeks (Donohoe, 1997), and drift distance is driven by a host of biological and physical processes (Largier, 2005; Cowen and Sponaugle, 2009). Juveniles can spend months to years in juvenile habitats (Griffiths and Hecht, 1995), and adults have the potential to migrate tens to hundreds of kilometers to form spawning aggregations (Aalbers and Sepulveda, 2015). Hence, the population structure of sciaenids and other marine species with similar life history strategies may reflect the processes influencing dispersion as well as migration patterns.

The white seabass, *Atractoscion nobilis*, is one the largest members of the family Sciaenidae, reaching 160 cm total length (TL) and more than 41 kg (Vojkovich and Reed, 1983). It is an important species for both the recreational and local commercial fisheries along the Pacific coast of California and Baja California (Allen and Franklin, 1992; Allen et al., 2007; Cartamil et al., 2011).
Few studies have provided information regarding spawning locations and migration patterns, and there is limited information on larval and juvenile ecology. The white seabass spawning period is during the spring and summer months (May to August), and spawning aggregations may be found in the interface between the sandy areas and shallow rocky reefs that support kelp forests (Thomas, 1968; Aalbers and Sepulveda, 2012).

Several studies focusing on different life stages have contributed to the current understanding of white seabass population structure. Moser et al. (1983) found that while the spawning centers are located off southern California and central Baja California, a higher abundance of white seabass larvae were caught in the inshore (<50 m from the surf zone) regions of San Sebastian Vizcaino Bay and the Gulf of Ulloa (Fig. 1). Allen and Franklin (1992) studied the distribution of newly settled juveniles in coastal waters and proposed that larvae transported from northern Baja California to southern California were a major source juveniles. Previous genetic studies have suggested a potentially continuous spawning population in the eastern Pacific (Bartley and Kent, 1990; Franklin, 1997; Coykendall, 2005), but the geographical range, sample size or number of genetic markers employed by these studies is limited. Tagging studies suggest limited (ca. <200) seasonal migrations along the California coastline (Hervás et al., 2010; Aalbers and Sepulveda, 2015). However, the absence of tagging studies in central and southern Baja California waters precludes the assessment of connectivity between the northern and southern range of white seabass in the Pacific. More recently, regional differences in otolith growth rates of age 1 fish have been found between southern California and southern Baja California, which are likely attributed to differences in environmental conditions (Romo-Curiel et al., 2015). These findings suggest limited mixing, at least during the first year of life. In summary, despite the recent work on movements and growth of this species, a clear understanding of its population structure remains lacking for this valuable bi-national resource. To build upon recent population structure hypotheses and better understand white seabass population dynamics, this study used otolith isotopic composition to assess population connectivity.

1.1. Isotopic analyses

The isotopic composition of otolith aragonite (δ18O and δ13C) has been used as a natural tracer to evaluate habitat use, population structure, migration, connectivity and mixing of fish populations, and for reconstructing their temperature and salinity history (Patterson et al., 1993; Valle and Herzka, 2008). Isotopic ratios are permanently imprinted in the otolith carbonate, recording ambient conditions experienced by an individual fish at the time of aragonite deposition (Campana, 1999). The stable isotopes of oxygen (18O/16O) in otolith aragonite are deposited near equilibrium with the isotopic composition of the ambient water (δw). However, there is isotope discrimination against 18O as a function of temperature, resulting in a negative relationship between δ18O values and temperature (Epstein et al., 1953; Iacumin et al., 1992; Patterson et al., 1993). It is possible to estimate the temperature at the time of aragonite deposition using δ18O values and estimates of δw (Campana, 1999; Darniade et al., 2014), and to thereby discriminate between fish living under different environmental conditions (Iacumin et al., 1992; Godisken et al., 2012). Regional salinity-δw relationships can be used to estimate the isotopic composition of seawater (Craig and Gordon, 1965; Paul et al., 1999), as predict δ18O values for particular regions (Rowell et al., 2005; Valle and Herzka, 2008).

In contrast, carbon isotope ratios reflect both dietary sources via metabolic processes as well as the dissolved inorganic carbon (DIC) pool (Thorrold et al., 1997; Hoie et al., 2003). The contribution of carbon deposited in the otoliths from metabolic sources varies and has been estimated at 20—30% of the total (Kalish, 1991; Weidman and Millner, 2000), and the remainder presumably reflects the isotopic composition of DIC (Campana, 1999). Nevertheless, geographic variations in the carbon isotopic ratios of the otolith aragonite have been successfully used as natural tags to differentiate between fish subpopulations (Newman et al., 2010; Steer et al., 2010; Correia et al., 2011).

Data from the otolith core (the central portion of otoliths that is deposited during early life) can provide information regarding natal origin and spawning areas, while data corresponding to specific ages may indicate changes in fish habitat over time (Gao et al., 2004, 2013; Steer et al., 2010; Gao et al., 2013). The isotopic analysis of subsamples from specific sections of adult otoliths corresponding to specific time periods enables the reconstruction of each individual’s environmental history as a function of age, date and other life history considerations (Gillanders, 2005, Weidman and Millner, 2000). Central to the robust interpretation of the isotopic composition of biogenic carbonates and the calculation of robust temperature estimates based on δ18O values is the explicit consideration of the processes that underlie its variability (Thorrold et al., 1997; Campana, 1999; Elsdon and Gillanders, 2002). Thus, oceanographic data should be incorporated into the analysis and interpretation of isotope ratios (Ashford and Jones, 2007).

The isotopic composition of the otolith core of adult white seabass collected from three regions of the northeastern Pacific, encompassing a distance of over 1000 km, was measured to infer larval rearing habitats and population structure. We also analyzed the isotopic composition of subsamples from seasonal translucent and opaque otolith growth rings corresponding to the juvenile (age 0.5–2 yr) and adult (age 8–10 yr) stages to infer ontogenetic
movement patterns and the level of mixing between different life stages. Back-calculated aragonite precipitation temperatures were compared to regional coastal SSTs and in situ measurement of temperature and salinity to evaluate whether the $\delta^{18}O$ values of otolith core and growth rings were consistent with regional oceanographic conditions. Differences in the oxygen and carbon isotopes values in otolith core and growth rings of adult white seabass from different locations would indicate that adult fish were reared under different environmental conditions, and would suggest limited connectivity between subpopulations. Further, given that there is a sharp latitudinal gradient in SST throughout the distribution of white seabass in Pacific waters, we hypothesized that fish sampled in more southern waters would present $\delta^{18}O$ values consistent with higher aragonite precipitation temperatures.

2. Methods

2.1. Sample collection

Otoliths were obtained opportunistically from commercial and recreational catches of white seabass from April through August of 2009–2011. Commercial fishing activities were conducted aboard small (5–7 m), outboard-powered fishing boats, within 5–20 km of coastal fishing camps along Baja California. Samples were also obtained from recreational fishing tournaments targeting white seabass within southern California, as well as from PIER research vessels (SCP ID NUMBER: 002471). A total of 117 samples were collected in three regions: southern California (SC; n = 40), USA, San Sebastian Vizcaino Bay (VB; n = 36) and the Gulf of Ulloa (GU; n = 41) off the central and southern Baja California peninsula, Mexico, respectively (Fig. 1).

2.2. Isotopic analysis

One sagittal otolith from each fish was embedded in epoxy resin and sectioned transversely using a low speed diamond saw (Buehler, ISOMET™) to cut through the otolith core. The section containing the core was mounted on a microscope slide using epoxy resin and polished using abrasive paper of decreasing grit size. Age estimates of all otoliths sections were evaluated in a previous study (Romo-Curiel et al., 2015), and the spawning year for each fish was back-calculated based on catch date. White seabass born between 1999 and 2006 (age range 4–12 yrs; n = 32 for SC, n = 36 for VB and n = 32 for GU) were selected for isotopic analysis of the otolith core. This period excludes El Ninño years, which has been shown to influence the isotopic composition of fish otoliths in the California Current region due to the abnormally high water temperatures (Dorval et al., 2011).

Carbonate was extracted from three different regions along the sectioned otolith surface with a high precision micromill (ESI New Wave Micromill) at the Marine Science Institute, University of Texas in Austin and at the Center for Scientific Research and Higher Education of Ensenada (CICESE). Each otolith core sample was obtained from a 300 $\times$ 300 $\mu$m square centered on the core using a raster pattern with parallel lines separated by 100 $\mu$m and with a depth setting of 100 $\mu$m. The raster area was designed to coincide with the dimensions of the otolith core (Fig. 2). The limited dimensions of the area from which aragonite was extracted in the otolith core was designed to reduce the potential for contamination with aragonite precipitated during other life stages (e.g. Begg et al., 1999). Fishes of at least 10 years of age (mean age of 13 yrs) were selected for isotopic analysis of annual growth rings. Isotopic analysis of annual growth rings was only conducted for white seabass samples collected from the two distal regions (SC and GU) with the most contrasting environmental conditions. The otolith core and four growth rings corresponding to the juvenile stage were sampled: the first and second summer growth seasons (opaque rings corresponding to the first and second year of life, hereafter referred as 0.5 and 1.5 yrs) and the first and second winters (translucent rings, hereafter age 1 and 2 yrs). Likewise, five growth rings corresponding to the adult stage were sampled (8.5, 9.5, and 10.5 yrs, corresponding to the summer opaque growth rings and 9 and 10 yr, corresponding to the winter translucent rings). Each growth ring was sampled by drilling a single curve (650 long $\times$ 150 $\mu$m wide and 100 $\mu$m set depth). After the collection of each sample, the microdrill bit and work surface were cleaned with compressed air.

Between 30 and 60 $\mu$g of aragonite were weighed on a microbalance. Analysis of otolith powder was performed in the Stable Isotope Laboratory of the University of California at Santa Cruz using a Kiel IV carbonate device coupled to a Thermo Scientific MAT253 Isotope Ratio Mass Spectrometer under certified standards (CM12, Atlantis II, NBS-18 and NBS-19). Precision measurements (SD) of $\delta^{18}O$ values were 0.03‰ for CM12, and 0.02‰ for Atlantis II, NBS-18 and NBS-19. For $\delta^{13}C$, the precision was 0.06‰ for CM12 and Atlantis II, 0.02‰ for NBS-18 and 0.05‰ for NBS-19. All isotopic analysis and measurements are reported in standard $\delta$ notation ($\%$) using VPDB (Vienna PeeDee Belemnite) as the international standard:

$$\delta = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000$$ (1)

where R is the abundance of the heavy to light isotope ratio of the sample or standard.

The time period integrated by each core sample was estimated based on the analysis of the otolith core. White seabass (4–12 cm TL; n = 20) otolith samples collected during a trawl survey along the coast off Camp Pendleton, California on July 19–21, 2010. Each sagittal otolith from young-of-the-year white seabass was mounted sulcus-side up on a glass slide and polished using abrasive paper of decreasing grit and 0.05-micron alumina to enhance the visibility of daily growth increments. Polished otoliths were viewed with a microscope (Leica DMLS; 10–40 × magnification) and photographed with a digital camera (Leica DFC 450). Daily growth increments were counted twice for each individual by two independent readers, starting from the focus of the core and core diameter was measured using the Image J software package (National Institutes of Health, Bethesda, MD, USA).

2.3. Regional SST and salinity

To obtain temperature estimates representative of white seabass larval habitat, sea surface temperatures (SST) during the spawning season (April–September) were obtained by downloading oceanographic data from the Scripps Photobiology Group of Scripps Institution of Oceanography, University of California San Diego (http://spg.ucsd.edu/Satellite_data/California_Current/) viewed on October 2014). The SSTs represent an integration of water masses, and are available with high resolution (approx. 1 km$^2$). Monthly mean SST data were compiled for near-coastal waters from April 2000–September 2006 (Fig. 1). Salinities at 10 m were obtained from reports and publications derived from in situ measurements conducted during quarterly CalCOFI and Investigaciones Mexicanas de la Corriente de California (IMECO-CAL) cruises off the coast of the Baja California peninsula (http://www.calcofi.org/ccpublications/ccreports.html). Salinities were obtained for two periods: summer (April to September) and winter (October to March) for the same regions used to estimate SST
values. To evaluate the degree of similarity between monthly average SSTs and salinity very near the coast (not covered by CalCOFI or IMECOCAL cruises), the SST and salinity records were compared with in situ measurements made at the Scripps Institution of Oceanography Pier in southern California (http://www.sccoos.org/data/piers). For the waters off the Baja California peninsula regions, the comparisons were made with the seasonal climatology provided by Durazo et al. (2010).

2.4. Isotopic composition of seawater (δw) and back-calculated temperature

The isotopic composition of seawater (δw) was calculated from regional salinity estimates using the Craig and Gordon (1965) equation for north Pacific surface waters:

\[
\delta_w = -18.5 + 0.54 \text{ Salinity}
\]  

(2)

There is an absence of detailed regional data on the isotopic composition of seawater, particularly for the waters off central and southern Baja California. The processes that contribute to changes in the salinity and δw of surface waters are rainfall, freshwater inflow, melting ice, evaporation and freezing, as well as vertical mixing and horizontal advection (Schmidt, 1998; Sharp, 2007). However, the waters off southern California and Baja California are not subject to freezing and are limited in freshwater inflow due to the region’s arid nature (Wilkinson et al., 2009). The primary factors driving variations in salinity in the coastal waters inhabited by white seabass are therefore upwelling events, evaporation and the mixing of different water masses. The slope of Craig and Gordon (1965) equation is similar to the one reported by Paul et al. (1999) for mid-latitudes and the one derived from GEOSecs data (δw = −17.95 + 0.50 Salinity; see also Valle and Herzka, 2008), supporting the use of relationship for deriving estimates of δw. The isotopic composition of the water was corrected (−0.22‰) to account for the difference in the standards used to report oxygen isotope ratios of water and biogenic carbonates (Sharp, 2007).

Back-calculated temperatures were estimated from oxygen isotope ratios (δ18Owater) at the otolith core from SC, VB and GU and along juvenile growth rings of fish caught in SC and GU by applying the aragonite equation proposed by Campana (1999) in an extensive review of the literature:

\[
\delta^{18}O_{\text{oalto}} = \delta_w + 3.71 - 0.206 T \degree \text{C}
\]  

(3)

where δ18Owater is the isotopic composition measured from otolith subsamples. The isotopic composition of the water was estimated based on mean salinity estimates of the region where the corresponding adult was caught (see results).

Predicted δ18Owater values for aragonite for temperatures and salinities of each region were calculated based on δw estimates derived using the Craig and Gordon (1965) equation for north Pacific surface waters and Campana (1999) aragonite equation. Measured δ18Owater values were compared to predicted δ18Owater values to evaluate whether there was overlap in the environmental conditions typical of each sampling region and the stage-specific oxygen isotopic composition of fish otoliths.

2.5. Statistical analysis

Using the Quartile Method based on median distribution values (Zar, 1999), all outliers were identified and excluded from statistical analysis. One-way analysis of variance (ANOVA) was used to test whether δ13C and δ18O values of otolith cores differed between sampling regions. The non-parametric Kolmogorov–Smirnov test (K–S) was used to compare the distribution of isotopic values among regions. Back-calculated temperatures were compared between regions using a one-way ANOVA. The post-hoc multiple comparisons between isotopic values among regions were performed using Scheffe’s test. Age-specific δ13C and δ18O values from juvenile and adult growth rings were compared between regions with a two-way repeated measures analysis of variance (RM ANOVA); the data corresponding to juvenile and adult growth rings were treated separately. Holm-Sidak post-hoc tests for pairwise comparisons were used to identify whether there were differences in isotopic values between ages and regions. All data compiled with parametric assumptions of normality (Shapiro–Wilk’s test) and homoscedasticity (Levene’s test). Data were analyzed using the Systat 13 and plotted using Sigma Plot 12.5 software packages.

3. Results

3.1. Isotopic analysis of otolith cores

Stable isotopes values were obtained for 100 white seabass otolith cores (Fig. 3). Two outliers were identified in two different GU samples with values of −5.37‰ for δ13C and −1.88‰ for δ18O; both fish were excluded from further analysis. The average δ13C value was −2.66 ± 0.60 for SC (mean ± SD; range −3.73 to −1.54‰), −3.73 ± 0.78‰ for VB (−4.74 to −1.92‰) and −2.81 ± 0.64 for the GU (range −4.17 to −1.28‰). The δ18O values were also variable, ranging from −1.52 to −0.02‰ for SC (mean ± SD = −0.61 ± 0.31‰), −1.57 to 0.01‰ for VB (−0.75 ± 0.35‰) and −1.49‰ to −0.09 (−0.71 ± 0.34) for GU.

There was a significant difference in δ13C values between regions (ANOVA F(2,95) = 27.47, P < 0.001); the mean carbon isotope composition of VB differed from SC and GU (Scheffe’s test,
showed a high level of dispersal, even when the number of individuals analyzed for a particular year was limited (Fig. 4).

3.2. Regional SST and salinity

Comparison of mean monthly SSTs between regions indicated a marked latitudinal gradient (Supplementary Fig. 1), and there was a similar pattern in SSTs during the spawning period (April–September) from 1999 to 2006. Monthly average temperatures from April to September were similar between SC and VB (ranging from 15.8 to 21.0°C and 16.3–21.8°C, respectively). Higher temperatures were observed for GU (17.3–26.6°C). During the summer, SSTs at GU were 3 to 6°C higher than at SC and 4 to 5°C greater than VB. In SC the highest monthly SST was observed during August (21.0°C on average). In both VB and the southern region the highest SST occurred during September (21.8°C and 26.6°C, respectively, on average).

Regional salinity at 10 m depth during the spawning season (April–September) and winter (October–March) months of 1999–2006 also showed a latitudinal gradient (Table 1). Given the linear relationship between salinity and δ_o, estimates of the isotopic composition of seawater in GU exhibited lighter values than that from SC and VB (Supplementary Fig. 2). Within a region, average δ_o values showed limited temporal variability, varying by <0.02‰ between seasons in SC and VB, and by 0.25‰ in GU.

3.3. Back-calculated temperature of otolith cores

The back-calculated temperatures derived from δ^{18}O_{oto} values of the otolith cores of white seabass ranged from 14°C to 23°C (Fig. 5). The back-calculated temperatures for fish captured in each region were highly variable, reflecting the variability in δ^{18}O_{oto} values. For SC, the average back-calculated temperature was 17.8°C (range 15.3–21.9°C), 18.6°C for VB (range 14.9–22.5°C) and 18.9°C for GU (range 16.0–22.2°C). Despite the overlapping back-calculated temperatures between regions, there were significant differences in δ^{18}O_{oto} values (F(2, 95) = 3.979, P = 0.026); the mean back-calculated temperature in GU was significantly higher than SC (Scheffe's test, MS = 2.572, P = 0.032). There were no significant differences between the mean back-calculated temperature for SC vs VB and between VB vs GU (Scheffe's test, P > 0.05).

3.4. Comparison of predicted vs. measured δ^{18}O values

The range of predicted aragonite δ^{18}O values obtained by considering regional summer SSTs and salinities had a broader range for the GU than SC and VB, and showed overlap between regions (Table 1; Fig. 6). For SC the predicted δ^{18}O values ranged from −0.10‰ to −1.40‰; the range for VB was similar (from −0.15‰ to −1.50‰). In contrast, the range of predicted δ^{18}O values was greatest for GU (−0.17‰ to −2.30‰). Comparison of the range of predicted δ^{18}O values with δ^{18}O_{oto} measurements indicated that almost all δ^{18}O_{oto} measures were within the range of the predicted isotopic values for a given region. For SC and VB, the range of predicted δ^{18}O values was greater than the measured δ^{18}O_{oto} values; none of the otolith cores had isotope ratios <−1.6‰.

3.5. Isotopic analysis of juvenile and adult growth rings

The δ^{13}C values of individual juvenile and adult white seabass otolith growth rings collected in SC and GU exhibited an increasing level of variability as a function of age; the range of values increased from 2 to 3‰ during the juvenile stage to ca. 4.5‰ for the adult

Fig. 3. Carbon and oxygen isotope ratios measured in the otolith cores of White Seabass (A. nobilis) sampled off Southern California (SC), Vizcaino Bay (VB) and in the Gulf of Ulloa (GU). White circles indicate outliers that were excluded from statistical analyses.

Fig. 4. δ^{13}C (a) and δ^{18}O (b) values of otoliths cores of White Seabass plotted as a function of their spawning year and by sampling region: Southern California (SC), Vizcaino Bay (VB) and Gulf of Ulloa (GU). The numbers above the boxplot represent the sample size for each year.
stage (Supplementary Fig. 3a and c). In contrast, the $\delta^{18}O$ values of juvenile growth rings showed a consistent pattern between opaque (summer growth, more depleted isotope ratios) and translucent (winter growth, more enriched isotope ratios) rings and a much narrower range than $\delta^{13}C$ values. However, the seasonal pattern was no longer observed during the adult stage (Supplementary Fig. 3b and d).

The mean carbon and oxygen isotope ratios for white seabass otolith growth rings showed distinct patterns when comparing the juvenile and adult life stages (Fig. 7). While mean isotope ratios showed distinct seasonal shifts during the juvenile stage, these were not evident during the adult stage. Two-way repeated measures ANOVA indicated that there were no significant differences in mean $\delta^{13}C$ and $\delta^{18}O$ values between regions during either the juvenile or adult stage (Supplementary Table 1). However, for the juvenile stage, mean $\delta^{13}C$ and $\delta^{18}O$ values differed significantly between ages for fishes sampled in both regions (Supplementary Table 1).

### Table 1
Regional salinities (minimum, maximum and average), estimated oxygen isotopic composition of the water ($\delta w$), and summer SSTs obtained from satellite images for Southern California (SC), Vizcaino Bay (VB) and Gulf of Ulloa (GU).

<table>
<thead>
<tr>
<th>Region</th>
<th>Salinity</th>
<th>$\delta w$ (%)</th>
<th>SST (°C)</th>
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<tr>
<td></td>
<td>Summer</td>
<td>Winter</td>
<td>Summer</td>
</tr>
<tr>
<td>SC</td>
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<td>GU</td>
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Fig. 5. Frequency distribution of back-calculated temperatures obtained from $\delta^{18}O_{ot}$ values of otolith cores of White Seabass, *A. nobilis*, adults collected in Southern California (SC), Vizcaino Bay (VB) and Gulf of Ulloa (GU).

Fig. 6. Isotopic map of predicted $\delta^{18}O$ values for aragonite as a function of salinity and temperature. Rectangles represent the range of predicted $\delta^{18}O$ values for three regions of the California current system in which white seabass were sampled, based on regional sea surface temperature and salinities during their summer spawning season. Diagonal lines indicate the full range of isotopic values measured in the otolith cores for each region: Southern California (line with dots), Vizcaino Bay (dashed line) and Gulf of Ulloa (dots).

Fig. 7. Mean $\delta^{13}C$ and $\delta^{18}O$ values (±standard error) measured in seasonal otolith growth rings of juvenile and adult of white seabass, *A. nobilis*. Samples were collected in Southern California (SC; white circles dots) and Gulf of Ulloa (GU; black circles). N — otolith core; S — summer growth ring; W — winter growth ring; subscripts correspond to the estimated age of each growth ring.
Table 1. The Holm-Sidak post-hoc pairwise comparison test indicated significant differences in $\delta^{18}O$ values between summer (S) and winter (W) growth rings of juveniles (Fig. 7; Supplementary Table 2). The only significant differences in $\delta^{18}O$ values between ages was for S0.5, which corresponds to summer growth during the first year of life (the difference between mean isotope ratios was 0.65‰), with significant differences at that age among regions (RM ANOVA, $t = 2.663$, $P = 0.010$).

3.6. Back-calculated temperature for core and seasonal growth rings of juveniles

The back-calculated temperatures for the seasonal growth rings sampled during the juvenile stage showed a broad range and overlapped between ages and seasons (Fig. 8). The limited variability in salinity (and hence $\delta_w$ estimates) led to temperature differences of $<2^\circ C$ for individual growth rings. Higher temperatures coincided with the summer aragonite precipitation and lower temperatures corresponded to the winter rings. Back-calculated temperatures were higher in fish captured in GU than those from SC, with a difference around 1 $^\circ C$ for the same age among regions. However, the temperature of the first summer opaque ring (S0.5) was higher in the GU than SC by about 4.5 $^\circ C$ on average.

4. Discussion

Findings of this study provide evidence to support the presence of two potentially discrete subpopulations of white seabass divided by Punta Eugenia in the Baja California peninsula. The isotopic analysis of the first otolith growth ring indicated that white seabass collected in southern California must consistently experience different environmental conditions than individuals reared within the Gulf of Ulloa. These results agree with the differences in growth rates reported by Romo-Curiel et al. (2015) for the first year of life in adult white seabass from the same regions, and have significant management implications.

4.1. Isotopic composition of otolith cores and back-calculated larval rearing temperatures

The estimated time interval represented by otolith core subsamples was 18–25 days, consistent with the 2–3 week duration of the white seabass larval period reported by Donohoe (1997). The $\delta^{13}C$ and $\delta^{18}O$ values of the otolith cores of adult white seabass captured within each sampling region were highly variable across spawning years and age classes (up to 2‰; Fig. 3). The variability in isotopic ratios were persistent through time and thus representative of the white seabass population, allowing for robust inferences into its population structure.

The $\delta^{13}C$ values of the carbon precipitated in fish otoliths is a function of the dissolved inorganic carbon (DIC) as well as the byproducts of an individual’s metabolism (Kalish, 1991; Weidman and Millner, 2000; McMahon et al., 2013). The $\delta^{13}C$ value of the DIC in surface waters of the Pacific off North America is approximately 0.8–0.9‰ as a result of upwelling events along the coast, and those values do not change substantially at spatial scales dominated by isolated physical processes (Kroopnick, 1985; McMahon et al., 2013). In contrast, the relative contribution of metabolically derived carbon to the $\delta^{13}C$ values of otolith carbonate varies between species and even among individuals of the same species (Jacumin et al., 1992; Weidman and Millner, 2000; Nelson et al., 2011). Estimating the percent contribution of each source of carbon to the $\delta^{13}C$ values of white seabass otoliths was beyond the scope of this study. However, the $\delta^{13}C$ values measured in otolith core of white seabass from each sampled region were highly variable and lighter (ca −1.5 to 5‰) than regional DIC values (ca. 1‰; Fig. 3a), suggesting that the contribution of metabolic carbon is likely important, albeit variable. The difference in average $\delta^{13}C$ in VB relative to those from SC and GU suggests that larval white seabass from VB probably relied on a different food source, or that the relative contribution of food-based carbon varied between regions.

The isotopic composition of seawater ($\delta_{wo}$) varied seasonally between regions, mirroring regional shifts in surface salinities. Craig and Gordon (1965) reported $\delta_{wo}$ values between −0.5 and −0.4‰ for the northeastern Pacific surface waters based on samples taken between 20°N, 130°W and 32°N, 120°W. For the summer season during which white seabass spawn, the range of $\delta_{wo}$ values reported by Craig and Gordon (1965) is only 0.12 and 0.19‰ more enriched in $\delta^{18}O$ than the mean values applied to back-calculated temperature estimates of fish caught in SC and VB, respectively, and similar to the estimates for the GU (−0.58 to −0.31‰). Limited variability in regional salinity (<1, equivalent to 0.5‰ in $\delta_{wo}$) indicates regional temperature is the most important factor influencing $\delta^{18}O$ values observed in white seabass otoliths. The high variability in $\delta^{18}O$ values measured in otolith core (range 2‰) was reflected in a wide range of back-calculated temperatures for each sampling region, which overlapped. Aalbers (2008) reported an
ambient water temperature of 11.3–21.7 °C in coastal waters off southern California during spawning events of wild white seabasses. The highest frequency of spawning activity was recorded between 15 and 18 °C, similar to the back-calculated temperatures estimated for otolith cores of adults caught in SC waters. The broad range of back-calculated temperatures might reflect seasonal changes in the environmental conditions prevalent during the long spawning period of white seabass (Thomas, 1968; Aalbers, 2008). The differences in average back-calculated temperature between SC and GU likely reflects the well-documented latitudinal temperature gradient found along the southern California and Baja California peninsula during summer months (e.g. Lynn and Simpson, 1987; Durazo et al., 2010; Supplementary Fig. 1). Alternatively, the differences in the estimates of average temperature could be biased due to variations in the region-specific salinity estimates. The higher temperature found in the GU compared to SC could in fact be offset by the higher salinity found in more southern waters. However, the salinity differed by a maximum of 0.55, which would lead to a limited impact in back-calculated temperature estimates.

The predicted range of δ18O values for each region was calculated based on the full range of local salinity and SST estimates for the larval rearing period. A broader range of potential aragonite precipitation temperatures (including lighter δ18O values corresponding to warmer temperatures) was predicted for GU than SC and VB; however, there was a high degree of overlap between regions. Even though the predicted δ18O values for GU included lighter isotope ratios, the isotopic values measured in fish caught in GU covered roughly the same range as those of SC and VB. This may suggest that (1) white seabass have a behavioral preference for more temperate waters and avoid the warmer nearshore temperatures found in GU late in the summer season, (2) larvae spawned toward the end of the season didn’t survive, and (3) that the spawning period is shorter in GU, and that it occurs prior to the warming of nearshore waters. In addition, the warmer and more saline waters found in the southern sampling region yielded a similar range of predicted δ18O values than the more northern waters that are colder and less saline (Fig. 6). Whatever the cause, the high degree of overlap in the δ18O values of otolith cores did not allow for discrimination between regions.

4.2. Causes driving variability in δ13C and δ18O of otolith core of adults

The predicted regional δ18O values calculated from regional temperature and salinity measurements did not yield sufficient differences to ensure the conclusive discrimination of larval rearing habitats (i.e., there was a high degree of overlap in predicted oxygen isotope ratios). In addition, there was a high variability in δ18O ato values measured in the cores of adult white seabass collected in SC, VB and GU which could be attributed to different causes. Off southern California, white seabass have a long spawning season that extends from March to August (Thomas, 1968; Aalbers, 2008); SST increases by around 5 °C in SC waters, 6 °C in VB and 10 °C in the GU throughout the season. Hence, the mixing of larvae reared at different times during the spawning season could drive the large variation in core δ18O ato and δ13C values. Adult white seabass can migrate relatively long distances to feeding or spawning grounds, in which case adults may spawn in different regions than those where they were born (Overstreet, 1989). When otolith samples are collected opportunistically from adults captured by local fishing vessels, as was done in this study, it is possible that fish had migrated from different rearing grounds, contributing to the variability in the isotopic composition of otolith cores. In addition, along protected coastal areas of southern California and Baja California, temperatures are typically higher in shallower waters than offshore, and some exposed coastlines or points are prone to local intense upwelling (Graham and Lagier, 1997; Marín et al., 2003; Tapia et al., 2009). Given that the local temperature regime near the coast is highly dynamic and variable, it could generate high variability in the oxygen isotope composition of larval otoliths. White seabass larvae are also epipelagic during the late larval phase, which may be related with seeking preferential temperatures or their predator-avoidance capabilities (Margulies, 1989). In addition, off southern California white seabass larvae change from a pelagic distribution to a demersal environment following the 12–21 d larval period (Margulies, 1989; Donohoe, 1997). Selective mortality of larvae at the higher temperatures found in southern waters late in the spawning season, may explain the lack of adults with otolith cores with relatively negative isotope ratios in the Gulf of Ulloa. Unfortunately, there are no ecological studies of white seabass larvae or juveniles off the Baja California peninsula.

In summary, the results of this study do not clearly identify the processes that produce the high variability in δ18O ato from otolith cores of adult white seabass. However, the high degree of overlap in predicted and measured δ18O ato values between regions coupled with the potential for long-distance adult migration indicate that connectivity among potential subpopulations could occur during the adult stage.

4.3. Isotopic composition of juvenile otolith growth rings

The variation in δ13C values of juvenile otolith aragonite between translucent and opaque growth rings may be due to differences in the isotopic composition of food sources and changes in metabolic rate; the latter is considered the most important factor and varies with temperature (Kalish, 1991; Gauldie et al., 1994). White seabass exhibit significant phenotypic plasticity in terms of growth rates and size-at-age (Romo-Curiel et al., 2015), suggesting that individuals of the same age may have different food sources due to size-related feeding preferences, as has been documented for other sciaenid species (Stickney et al., 1975; Peters and McMichael, 1987). The most depleted δ13C values were measured in the growth rings laid down during the summer, when growth rates, water temperature, and respiration rates are higher, while the most enriched values corresponded to the winter growth rings, when growth and metabolic rates are reduced (Gauldie, 1996; Hoie et al., 2003; Portner et al., 2008). This suggests that the relative contribution of metabolically derived carbon to the carbon isotope ratios of the otoliths may be higher during the summer, a period of increased growth.

The linear relationship between carbonate δ18O ato values and temperature has been used to validate the seasonality of ring deposition in otoliths (e.g. Weidman and Milner, 2000). Samples taken from the translucent rings (summer growth season) of juvenile white seabass had the lightest δ18O ato values. Opaque growth rings had more enriched δ18O ato values, consistent with the lower temperatures of the winter season. Similar to other sciaenid species, previous age and growth studies of white seabass suggest that this species has an annual ring deposition rate (Romo-Curiel et al., 2015); however, a rigorous validation of the deposition of annuli remained lacking. The clearly seasonal pattern in δ18O ato values found in juveniles implies that one opaque and one translucent growth ring is deposited every year, further validating the yearly deposition assumed by Romo-Curiel et al. (2015).

There was a significant difference in the isotopic composition of the first summer growth ring (S0, S1) between SC and GU. The absolute difference in mean δ18O ato values of 0.65‰ is equivalent to a 4 °C back-calculated temperature difference. Southern California and the Gulf of Ulloa are located toward the northernmost and southernmost extent of the distribution of white seabass in Pacific
waters, and along a well-documented latitudinal temperature gradient (e.g. Lynn and Simpson, 1987; Durazo et al., 2010). Given that in this study the otoliths came from fish collected in SC and GU over the course of several years and belonged to different age groups, the significant difference in the δ18O values of the first summer growth ring indicates that there is likely limited mixing between the northernmost and southernmost sampled populations.

4.4. Isotopic composition of adult growth rings

While seasonal variations in the carbon and oxygen isotopic composition were evident during the juvenile stage, this was less evident for the growth rings corresponding to the adult stage. Aalbers and Sepulveda (2015) reported that adults tagged in southern California were found at a mean depth of 30 m during the winter, at average temperatures between 13 and 14 °C. During the spring and summer months, these same fish were primarily found in surface waters at depths of less than 10.5 m, and at mean temperatures between 16 and 18 °C. Hence, white seabass, like many other pelagic species, may actively select their thermal distribution throughout the year (Morita et al., 2010; Aalbers and Sepulveda, 2015), which is consistent with the more limited range of isotopic values that were measured during the adult stage. In addition, the smaller ring widths in adult otoliths may lead to a less recognizable seasonal cycle in isotope ratios of carbonate subsamples (Rowell et al., 2005). Specifically, the absence of a more marked seasonal pattern in the carbon and oxygen isotope ratios of growth rings sampled during the adult stage could also be due to a limitation in the spatial resolution of the milling procedure. The narrowing of the growth rings with age increased the possibility of sampling more than one growth season. Lastly, some studies have shown an uncoupling between seasonal patterns of ring deposition and growth in adult fishes which could also dampen the seasonal signal recorded in the isotope ratios of adult stage growth rings (Hoie and Folkvord, 2006; Sturrock et al., 2015).

4.5. Population structure of white seabass relative to oceanographic conditions

Although past studies of larval white seabass speculated that dispersal could occur over large distances (over hundreds of kilometers, e.g. Allen and Franklin, 1992; Donohoe, 1997), recent studies suggest that localized larval retention may be more common than previously thought (reviewed by Cowen et al., 2007). In species with nearshore spawning and relatively short larval stages (<month), evidence suggests that larval dispersal occurs over a much more limited spatial scale and that larval behavior and local retention zones may be important (<100 km, Cowen et al., 2007; see also review by Pineda et al., 2007). The large geographical separation between the potential subpopulations analyzed in this study (up to 1000 km) makes it unlikely that connectivity between SC and GU may occur during the larval stage. In addition, SC and the GU tend to show large-scale cyclonic circulation during at least part of the spawning season of white seabass, while the circulation in VB tends to be anticyclonic (e.g. Lynn and Simpson, 1987; González-Rodríguez et al., 2012; Durazo, 2015). This divergent circulation limits the potential for larval dispersal across the Punta Eugenia region, which is the southern limit of distribution for a variety of temperate species, as well as the northern limit of distribution for tropical species characteristic of the subtropical equatorial Pacific (e.g. Bernardi et al., 2003; Lluch Belda et al., 2003). There is therefore independent evidence that the Punta Eugenia region is a natural barrier to connectivity.

5. Conclusions

In conclusion, the isotopic composition of the otolith core of adult white seabass vary substantially but did not differ sufficiently to discriminate between potential subpopulations of larvae reared in three different potential spawning regions. However, there were differences between the oxygen isotopic composition and back-calculated temperature of the first seasonal growth ring of fish captured in SC and GU, suggesting the presence of two potentially discrete subpopulations divided by Punta Eugenia along the central Baja California peninsula (27°N).

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2016.01.016.

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