



Natural tracers reveal population structure of albacore (*Thunnus alalunga*) in the eastern North Pacific

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Chemical signatures in otoliths and muscle tissue of albacore (*Thunnus alalunga*) from two regions of the North Pacific were characterized to examine population structure. Regions included northern (offshore northwest United States and Canada, $>40^{\circ}\text{N}$) and southern (offshore southwest United States and Mexico, $<40^{\circ}\text{N}$) areas where albacore have demonstrated region-specific differences in movement and size at age. Juvenile (ages 1–4 years) albacore were collected from each region through recreational and commercial fisheries over a 5-year period (2009–2013). Three different otolith chemistry assays were performed, including whole otoliths (proxy for lifetime signature), otolith edge (recent signature), and otolith core (nursery signature). Whole otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ showed similar $\delta^{13}\text{C}$ and enriched $\delta^{18}\text{O}$ ($\sim 0.5\text{‰}$) values for juvenile albacore collected in the southern region; classification success to the two regions ranged from 78 to 91% during each year (similar age classes). Otolith edge $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ showed similar results as whole otoliths, but no regional differences were found for otolith core chemistry. Incorporation of trace element concentrations from whole otoliths improved discrimination between regions to 90–100% classification success during each year of the study, with significantly higher Ba:Ca, Mg:Ca, and Mn:Ca in albacore otoliths from the northern region. Albacore from the southern region also displayed enriched muscle $\delta^{13}\text{C}$ ($\sim 1.21\text{‰}$) and $\delta^{15}\text{N}$ ($\sim 0.85\text{‰}$) values relative to fish of the same size range from the northern region. Discrimination success between the two regions across all years using muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was 91%. Ultimately, results from this study suggest regional separation of albacore in the eastern North Pacific warranting region-specific vital rates in future modelling efforts.

Keywords: albacore, otoliths, stable isotopes, *Thunnus alalunga*, tissue, trace elements.

Introduction

Albacore (*Thunnus alalunga*) is a circumglobal, highly migratory tuna species found throughout tropical, subtropical, and temperate regions of the world's oceans. In the North Pacific, albacore support an important fishery that is currently managed as a single stock. This stock spawns in the central and western tropical and subtropical regions centred on 15°N , after which many juveniles begin trans-oceanic migrations to forage in the highly productive California Current in the eastern North Pacific (ENP; Clemens and Craig, 1965). By age 1, albacore begin entering the troll and pole-and-line

fisheries in the ENP (Childers *et al.*, 2011). Upon arrival to the ENP, the distribution and relative abundance of juvenile albacore vary latitudinally (Wetherall *et al.*, 1987; Childers *et al.*, 2011) before they become sexually mature at around age 5 and migrate to the western and central Pacific (WCP) spawning grounds (Sund *et al.*, 1981; Childers *et al.*, 2011).

Accurate characterization of population structure and stock mixing of albacore is critical for effective management, and recent evidence suggests that the population structure of albacore in the North Pacific is more complex than indicated by the current

single-stock model (Laurs and Wetherall, 1981; Laurs and Powers, 2009). In the ENP, albacore show differences in size distributions (Laurs and Wetherall, 1981), size-at-age (Renck et al., 2014), and migration patterns (Laurs and Powers, 2009; Childers et al., 2011) between two distinct regions, a north region offshore of the northwest United States and Canada and a south region extending offshore of the southwest United States and Mexico. Results from tagging studies conducted by US commercial surface fleets between 1971 and 1978 indicate limited mixing of albacore north and south of 40°N at the Mendocino Escarpment (Laurs and Lynn, 1977). Furthermore, juvenile albacore demonstrate different migratory behaviours north and south of this latitude, with albacore in the northern region appearing to be more transient in contrast to more resident behaviours displayed by individuals in the southern region (Childers et al., 2011). In addition to limited north-to-south mixing in the ENP, regional size-at-age differences support smaller juvenile albacore in the northern compared with the southern region (Renck et al., 2014). Given documented regional differences, additional studies using methodologies such as natural tracers (i.e. genetics, otolith chemistry, tissue chemistry) are needed to determine whether exchange rates between the two regions are sufficiently limited to support the sub-stock concept of albacore in the ENP.

Otolith chemistry is often used to examine movement patterns of marine fish populations (Sturrock et al., 2012; McMahon et al., 2013), and the principal assumption of this approach is that the composition of otolith material is reflective of the inhabited water mass (Campana, 1999). Whole otolith analysis represents an integrated measure of an individual's entire life history, and this approach has been used to assess lifetime exposure to different environmental conditions (Campana et al., 2000; Wells et al., 2010). On a finer scale, the chemistry of the otolith core is often used to retrospectively determine an individual's natal origin (Thorrold et al., 2001; Rooker et al., 2008), while the otolith edge can be used as a proxy for recent habitat use (Woodson et al., 2013). Otolith chemistry has been a successful tool for movement and mixing studies in offshore environments (Darnaude et al., 2014) and on multiple tuna species in the Pacific (Wang et al., 2009; Shiao et al., 2010; Wells et al., 2012; MacDonald et al., 2013), but its application has not yet been used on albacore in the North Pacific.

Another approach for evaluating population structure, commonly used to investigate foraging ecology and migrations of consumers, is the use of naturally occurring stable isotopes in muscle tissue. This approach is predicated on the isotopic relationship between consumer and prey. As a consumer grows and turns over muscle tissue, the signature of the new tissue reflects the isotopic signature of its prey in a predictable way (DeNiro and Epstein, 1978). Depending on the rate of tissue turnover, stable isotopes in tissue can reflect a feeding period of several months to over a year (DeNiro and Epstein, 1978, 1981; Madigan et al., 2012). Utilizing this approach, it is possible to compare the isotopic composition of a single species collected from different environments with distinctive isoscapes to understand dietary differences and, hence, the degree of separation between the groups. This method has been successfully applied in the ENP, providing evidence for the separation of northern fur seals (*Callorhinus ursinus*) off southern California (<40°N) from those off Oregon and Washington (>40°N; Newsome et al., 2007). Many other studies have confirmed the use of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in muscle tissue of consumers as a way of effectively identifying either population separation (Graham et al., 2010; MacKenzie et al., 2011) or movement patterns of animals

across distinct ocean isoscapes (Cherel and Hobson, 2007; Seminoff et al., 2012), including tunas (Madigan et al., 2014).

In this work, we tested the use of different natural tracers to discriminate albacore collected from two regions in the ENP (north and south of 40°N). Previous work has shown regional differences in seawater chemistry (i.e. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$; Gruber et al., 1999; LeGrande and Schmidt, 2006) and otolith isotopic composition of congeners (Pacific bluefin tuna, *Thunnus orientalis*, Shiao et al., 2010; yellowfin tuna, *Thunnus albacares*, Wells et al., 2012) in the North Pacific, supporting the use of these natural tracers in the present study. Our questions included: (i) could regional differences be detected using whole otolith chemistry (representing a lifetime signature of environmental exposure) and muscle tissue (representing a shorter temporal signal) for albacore if migratory histories or residency periods of individuals differed between regions, (ii) does the otolith edge (proxy for recent habitat exposure) for individuals collected between regions differ, and (iii) assuming core chemistry reflects the origin of individuals, will unique signatures indicate different spawning/nursery grounds?

Material and methods

Sample collections

Sagittal otoliths and muscle tissue of albacore were obtained through recreational and commercial fishing operations in the ENP over a 5-year period (2009–2013). Two regions were sampled: north and south of 40°N at the Mendocino Escarpment (Figure 1). Samples from the northern region were collected by commercial troll (artificial-jig fishing gears) and pole-and-line (live-bait fishing) surface fisheries. Samples from the southern region were collected from recreational pole-and-line fishing vessels operating off southern California and Baja California, Mexico, as well as during research cruises using troll gear. All fish were collected during the fishing season (July–October) of each year sampled. All specimens were frozen and transported to the NOAA Southwest Fisheries Science Center in La Jolla, CA, for later processing. Fish were measured to the nearest centimetre straight fork length (L_F) on the boat or in the laboratory. Whole sagittal otoliths from a single individual were used for both bulk stable isotope and trace element analyses (one otolith for each), and another individual was used for both the otolith core and edge stable isotope analyses (Table 1). For samples in which muscle tissue was extracted, 37% of the fish matched corresponding otolith samples analysed. A total of 205 albacore were analysed for whole otolith stable isotopes, 169 for whole otolith trace elements, 134 otolith core, 123 otolith edge, and 225 for stable isotopes of muscle tissue.

Otolith stable isotope analysis

Sagittal otoliths were extracted from both fresh and frozen specimens ranging in size from 51 to 99 cm L_F , cleaned of biological residue, and stored dry in plastic vials. In the laboratory, whole otoliths were first soaked in doubly deionized water (DDIH_2O), moved to a 3% hydrogen peroxide solution for 5 min to eliminate any remaining biological material, and then transferred into a new DDIH_2O bath for 5 min to remove surface residue. For whole otolith stable isotope preparation, one otolith was ground down to a fine powder using a mortar and pestle before being sent to the University of Arizona's Environmental Isotope Laboratory for analysis. For otolith core and edge stable isotope preparation, otoliths were embedded in Struers epoxy resin (EpoFix) and sectioned using a low-speed ISOMET saw to obtain transverse sections that

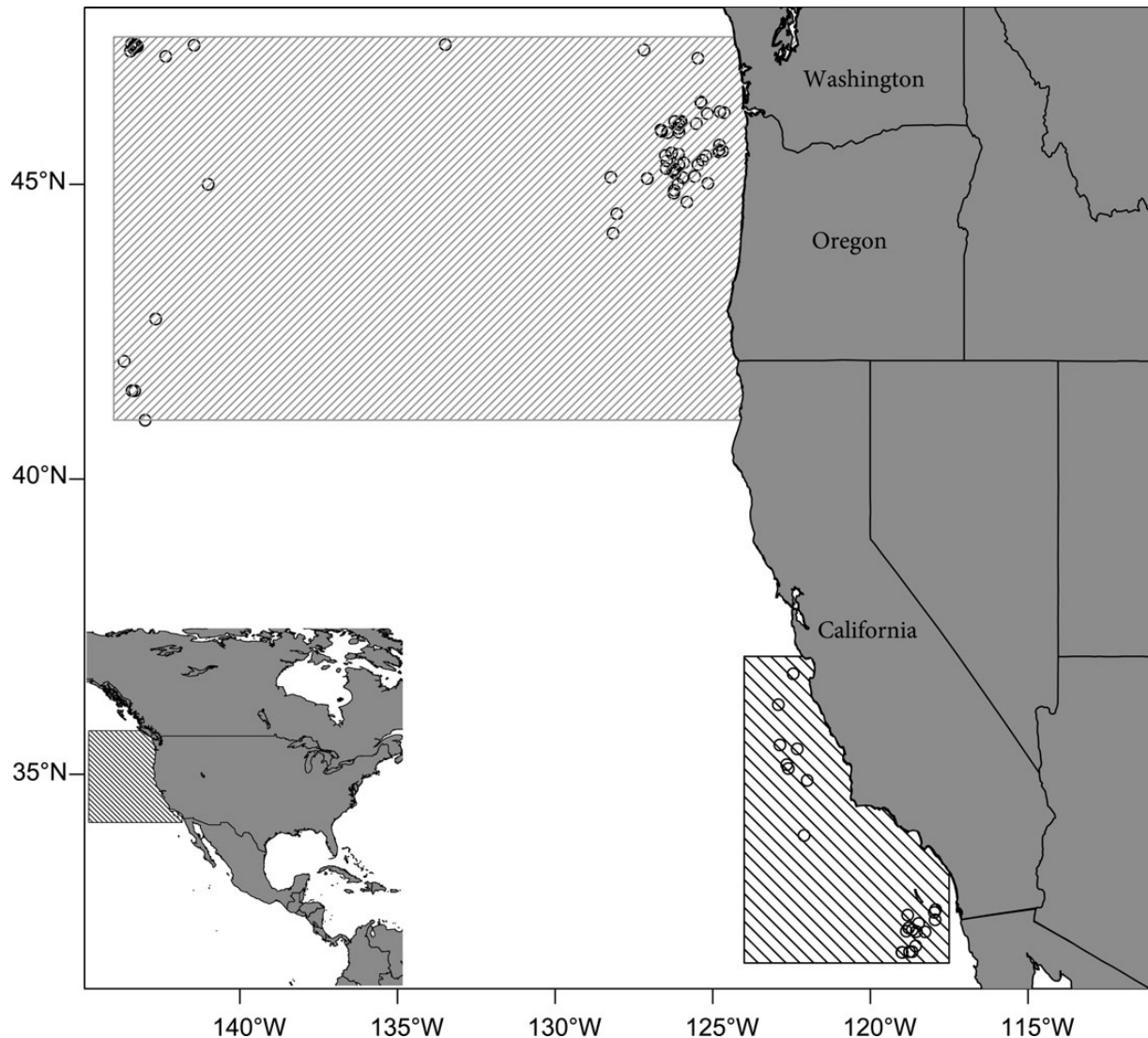


Figure 1. Map of the study regions located in the ENP where albacore were collected. The two study regions are separated at 40°N and consist of a northern region offshore Oregon and Washington, USA, and a southern region located offshore California, USA, and Baja, Mexico. Shaded areas depict general collection areas and circles are known locations where albacore samples were acquired.

Table 1. Summary table of sample sizes and associated range of lengths (cm L_F in parentheses) based on several different analytical techniques.

Year	Region	Stable isotopes (whole otolith)	Trace elements (whole otolith)	Outer edge (stable isotopes)	Core (stable isotopes)	Stable isotopes (muscle tissue)
2009	North	14 (52–69)	0	0	0	0
	South	20 (55–77)	0	0	0	0
2010	North	23* (62–84)	23* (62–84)	16 [†] (63–75)	23 [†] (63–75)	39 (56–84)
	South	25* (63–84)	25* (63–84)	22 [†] (62–80)	26 [†] (59–77)	14 (72–84)
2011	North	15* (51–74)	15* (51–74)	12 [†] (62–75)	12 [†] (65–75)	0
	South	12* (77–99)	10* (77–99)	14 [†] (55–99)	14 [†] (55–99)	0
2012	North	25* (53–80)	25* (53–80)	14 [†] (54–76)	14 [†] (54–76)	49 (53–80)
	South	25* (52–80)	25* (52–80)	15 [†] (54–84)	15 [†] (54–84)	48 (54–85)
2013	North	22* (53–90)	22* (53–90)	15 [†] (57–90)	15 [†] (57–90)	45 (56–82)
	South	24* (55–93)	24* (55–93)	15 [†] (55–84)	15 [†] (55–84)	30 (55–83)

Similar symbols indicate analyses were from the same fish.

included the core (Wells *et al.*, 2013). Following attachment to a sample plate, the portion of the otolith core corresponding to ca. the first 2 months of life was milled from the otolith section using

a New Wave Research MicroMill system. The preprogrammed drill path was made using a 500 μm diameter drill bit, and 14 passes each at a depth of 55 (770 μm total) were used to obtain

core material from the otolith. A small amount of material surrounding the core may have been incorporated into the isolated powdered core material, but likely represents a minimal amount that would not affect the overall results. Similar procedures were used to collect material for otolith edge, but the drill path was modified along the edge corresponding to the most recent month of life based on daily ring counts derived from Renck *et al.* (2014). Powdered core and edge material was transferred to silver capsules and later analysed for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ on an automated carbonate preparation device (KIEL-III) coupled to a gas-ratio mass spectrometer (Finnigan MAT 252) maintained at the University of Arizona's Environmental Isotope Laboratory. The isotope ratio measurement was calibrated based on repeated measurements of National Bureau of Standards (NBS) NBS-18 and NBS-19, with six standards run for every 40 samples. Precision was $\pm 0.11\text{‰}$ (s.d.) for $\delta^{18}\text{O}$ and $\pm 0.08\text{‰}$ (s.d.) for $\delta^{13}\text{C}$. Stable $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopes are reported relative to the Pee Dee belemnite (PDB) scale after comparison with an in-house laboratory standard calibrated to PDB.

Otolith trace element analysis

Elemental composition of whole otoliths was determined using solution-based inductively coupled plasma mass spectrometry (ICP-MS) from 4 years of collections (2010–2013). Before analysis, otoliths were weighed to the nearest milligramme, and laboratory equipment was cleaned by soaking in 3 M nitric acid (20%) for a 24 h period and rinsed with Milli-Q water and capped on a rack. Otoliths were first soaked in ultrapure water (Milli-Q water) to hydrate biological residue adhering to the surface of the sample. Next, otoliths were transferred to 3% hydrogen peroxide for 5 min to dissolve remaining biological residue and then immersed for 10 s in ultrapure 1% nitric acid to remove surface contamination. Finally, otoliths were washed with Milli-Q water twice for 5 min each to remove the acid, dried in a laminar flow fume hood, and saved in decontaminated Eppendorf vials. Otoliths were digested in 1 ml of 3 M nitric acid overnight at 70°C. Whole otoliths were analysed using a Thermo-Fisher ICP-MS at medium resolution setting ($m/\Delta m = 4000$) to minimize spectral interferences. Trace element concentrations were calculated by linear interpolation based on normalization with the internal standard to account for drift in addition to calibration curves from multiple element standards. Four elements (^{137}Ba , ^{24}Mg , ^{55}Mn , ^{88}Sr) were detectable and used for the analysis. Limits of detection were calculated from individual calibration curves ($\mu\text{g l}^{-1}$): ^{137}Ba (0.11), ^{42}Ca (30.20), ^{24}Mg (0.07), ^{55}Mn (0.01), and ^{88}Sr (0.07). Trace element concentrations ($\mu\text{g l}^{-1}$) were converted to element:Ca ratios ($\mu\text{mol mol}^{-1}$) for statistical analyses.

Muscle tissue stable isotope analysis

White muscle tissue was collected from albacore ranging from 55 to 85 cm L_{TL} when possible, samples were chosen from the same fish from which otoliths were extracted. Tissue was taken primarily from the dorsal musculature; however, when dorsal muscle was not available, samples were taken from deep-core muscle next to the vertebra or ventral regions of the fish. Duplicate or triplicate muscle samples were taken from 52 fish to allow for a comparative analysis of muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from different locations across the body. All tissue samples were stored frozen before being lyophilized. Samples were initially washed in purified Milli-Q water before lyophilization using a Virtis benchtop freeze-dryer and then ground to a powder using hand-held stainless steel micro lab spatulas. Lipids were extracted using a petroleum ether

solvent in a Dionex 200 Accelerated Solvent Extractor. Cells containing samples were injected with petroleum ether at 1500 psi, heated to 100°C for 5 min, held for 5 min to reach thermal equilibrium, and then flushed with fresh solvent and purged with nitrogen. This process was repeated three times for each cell. Samples were then stored in 2 ml cryogenic vials and shipped to the University of Arizona's Environmental Isotope Laboratory for analysis using a continuous-flow gas-ratio mass spectrometer (Finnigan Delta PlusXL) coupled to an elemental analyzer (Costech). Standardization was based on acetanilide for stable isotopes, NBS-22 and USGS-24 for $\delta^{13}\text{C}$, and IAEA-N-1 and IAEA-N-2 for $\delta^{15}\text{N}$. Precision was ± 0.10 (s.d.) for $\delta^{13}\text{C}$ and ± 0.15 (s.d.) for $\delta^{15}\text{N}$, based on repeated internal standards. The standard reference material was atmospheric nitrogen for N_2 , and PDB carbonate for CO_2 . Sample stable isotope ratios relative to the isotope standard are expressed in the following conventional delta (δ) notation in parts per mil (‰):

$$\delta = \left[\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1000,$$

where R_{sample} and R_{standard} are the corresponding ratios of heavy to light isotopes (e.g. $^{15}\text{N}/^{14}\text{N}$) in the sample and standard, respectively.

Statistical analyses

Multivariate analysis of variance (MANOVA) was used to test for differences in otolith stable isotopes ($\delta^{13}\text{C}_{\text{otolith}}$ and $\delta^{18}\text{O}_{\text{otolith}}$) and trace elements (Ba:Ca, Mg:Ca, Mn:Ca, Sr:Ca) between regions and among years and age classes. Albacore ages were estimated directly by examination of growth increments in sagittal otoliths (Wells *et al.*, 2013), which included samples from this study. A multivariate analysis of covariance (MANCOVA) was used to test for differences in muscle tissue $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between regions and across years with fish length as the covariate. Linear regressions were used to examine the relationship of muscle tissue $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with fish length. Pillai's trace statistic was used to test for significance due to its robustness to violations of the homogeneity of variance assumption (Wilkinson *et al.*, 1996). Univariate tests for individual stable isotopes and trace elements were then analysed using analysis of variance (ANOVA), and *a posteriori* differences among means were detected with Tukey's honestly significant difference (HSD) test. A separate MANOVA as well as individual ANOVAs for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were run on the 52 duplicate or triplicate sampled fish to test for significant differences of muscle tissue sampling locations across the body. Quadratic discriminant function analysis (QDFA) was used to evaluate classification accuracy of albacore according to collection region based on the jackknife reclassification. Jackknife reclassification was also used to examine the accuracy of discriminating between regions according to otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of core and edge. Statistical analyses were performed using SYSTAT 10.0 (SYSTAT Software Inc.) and the programming environment R (R Core Development Team, 2013), and significance was determined at the α -level of 0.05.

Results

A total of 205 individual albacore were analysed for whole otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. The mean otolith $\delta^{13}\text{C}$ was -7.92‰ (± 0.42 s.e.) in the southern region vs. -8.08‰ (± 0.43) in albacore collected from the northern region (Figure 2), and values were not significantly different. The mean otolith $\delta^{18}\text{O}$ from southern albacore was significantly enriched in each of the 5 years (ANOVA, $p < 0.05$) with an overall average of -1.05‰ (± 0.18) for albacore from

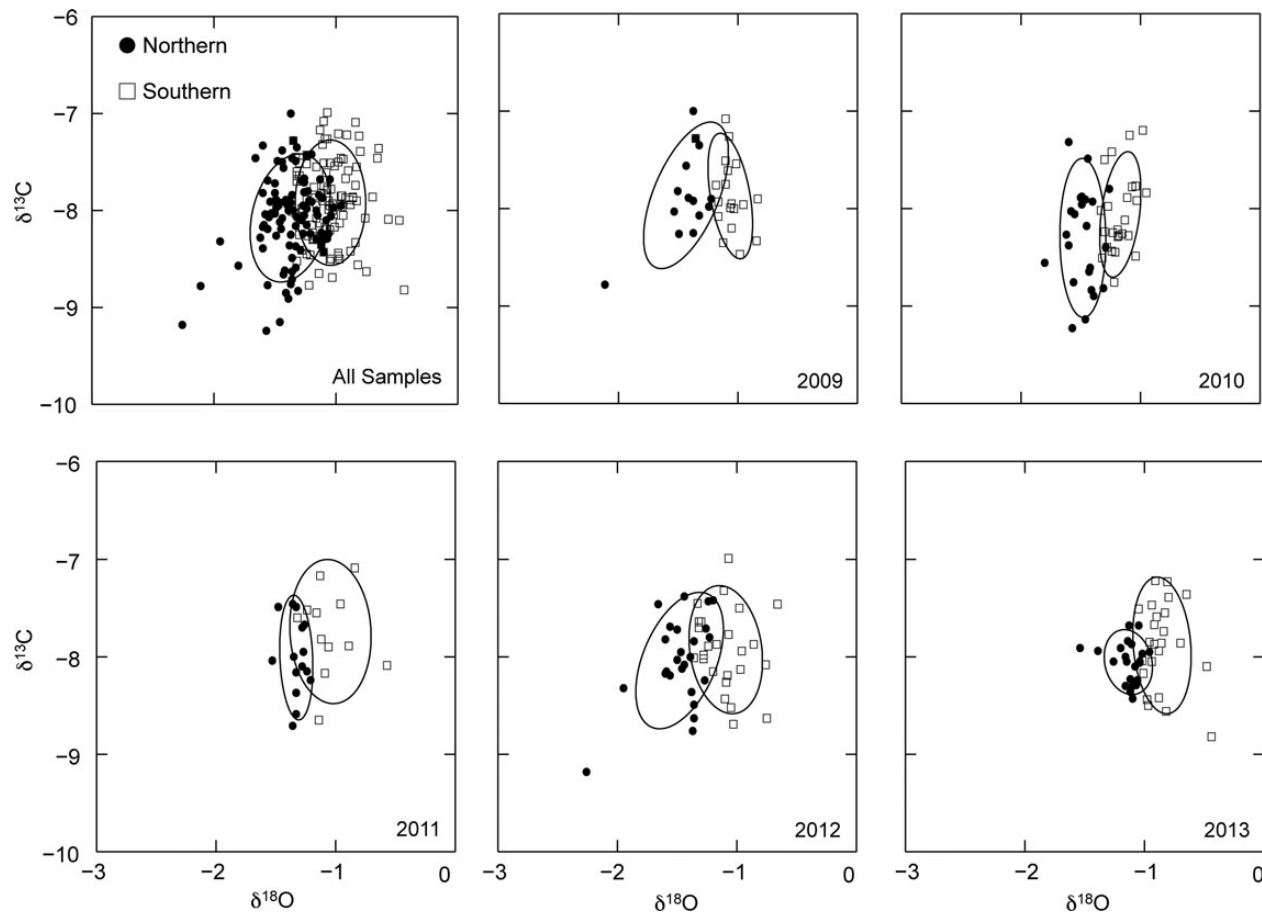


Figure 2. Whole otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ stable isotopes of albacore from two regions in the ENP (northern, black circles; southern, white squares). Top left graph shows all years combined. Confidence ellipses represent ± 1 s.d. around the mean.

the southern region vs. -1.37‰ (± 0.22) for fish from the northern region (Figure 2). Otolith $\delta^{18}\text{O}$ was enriched in albacore from the southern region by an average of $0.28\text{--}0.37\text{‰}$ each year. When looking at specific age classes, largest regional differences in $\delta^{18}\text{O}$ were found in the youngest age class, with age 1 albacore from the southern region enriched by an average of 0.44‰ relative to the northern region. The mean otolith $\delta^{18}\text{O}$ differences then progressively decreased from 0.33‰ for age 2 and 0.25‰ for age 3.

Otolith edge (i.e. outer margin) was used as a proxy for recent habitat use, and results showed similar patterns as whole otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. Otolith edge $\delta^{13}\text{C}$ was similar in the outer margins of albacore otoliths from each region, with a mean of -7.86‰ (± 0.07) in the southern region vs. -7.93‰ (± 0.07) in albacore collected from the northern region (Figure 3a). Otolith edge $\delta^{18}\text{O}$ was significantly enriched in albacore from the southern (mean = $-1.04\text{‰} \pm 0.02$) relative to the northern region (mean = $-1.31\text{‰} \pm 0.02$, ANOVA, $p < 0.05$; Figure 3a). Moreover, otolith edge $\delta^{18}\text{O}$ from albacore in the southern region was significantly enriched by $0.15\text{--}0.35\text{‰}$ relative to fish from the northern region during each of the 5 years (ANOVA, $p < 0.05$). Otolith edge $\delta^{18}\text{O}$ was not significantly different from whole otolith $\delta^{18}\text{O}$ from each region, with a difference of 0.01‰ in the southern region and 0.06‰ in the northern region, suggesting the two methods provided similar results for the samples examined.

Otolith core $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ was used to investigate the potential for northern and southern fish coming from different nursery areas. Otolith core $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ were not significantly different for albacore from each region (Figure 3b). Otolith core $\delta^{13}\text{C}$ averaged -8.50‰ (± 0.08) for albacore in the northern region and -8.57‰ (± 0.08) in the southern region; otolith core $\delta^{18}\text{O}$ averaged -1.47‰ (± 0.03) for albacore in the northern region and -1.41‰ (± 0.02) in the southern region. Similar patterns were found when examining each year and age class separately.

Significant differences in whole otolith element:Ca ratios for albacore were observed between regions and among years (MANOVA, $p < 0.05$; Figure 4). Ba:Ca averaged $2.03 \mu\text{mol mol}^{-1}$ (± 0.10) in albacore from the northern region and $1.02 \mu\text{mol mol}^{-1}$ (± 0.11) in fish from the southern region. Similar regional trends were apparent during each of the 4 years examined, with the mean Ba:Ca significantly higher in the northern region by 0.58 (2010) to 1.49 (2011) $\mu\text{mol mol}^{-1}$ relative to the southern region ($p < 0.05$). Interannual comparisons indicate significantly lower Ba:Ca ratios in 2010 only in the northern region relative to 2011–2013 (ANOVA, $p < 0.05$), while Ba:Ca ratios were similar across years in the southern region. The mean overall Mg:Ca was significantly higher in the northern region ($p < 0.05$), averaging 60.79 (± 2.31) vs. $41.89 \mu\text{mol mol}^{-1}$ (± 2.55) in the southern region, and regional differences supported significantly higher Mg:Ca ratios in albacore from the north during 2 of the 4 years examined (2011, 2013;

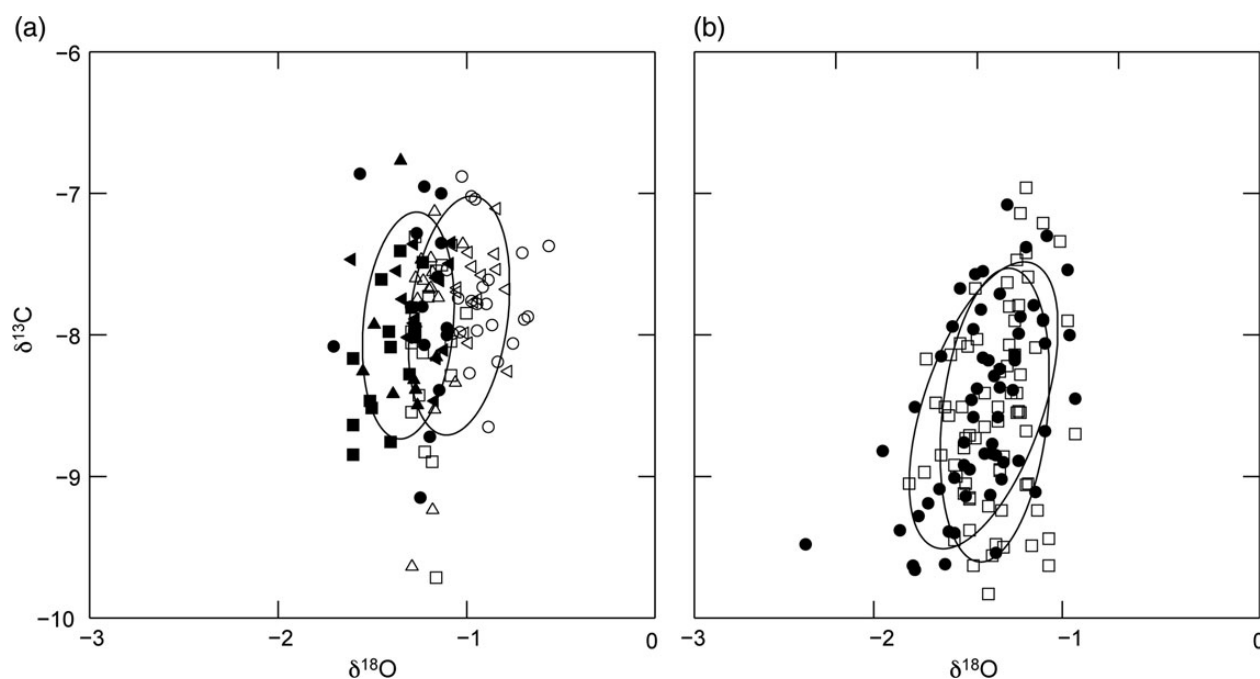


Figure 3. Otolith outer edge (a) and core (b) $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ stable isotopes of albacore from two regions in the ENP (northern, black; southern, white). Symbols for outer margin (a) represent years: 2010 (circles), 2011 (upright triangles), 2012 (sideways triangles), and 2013 (squares). Confidence ellipses represent ± 1 s.d. around the mean.

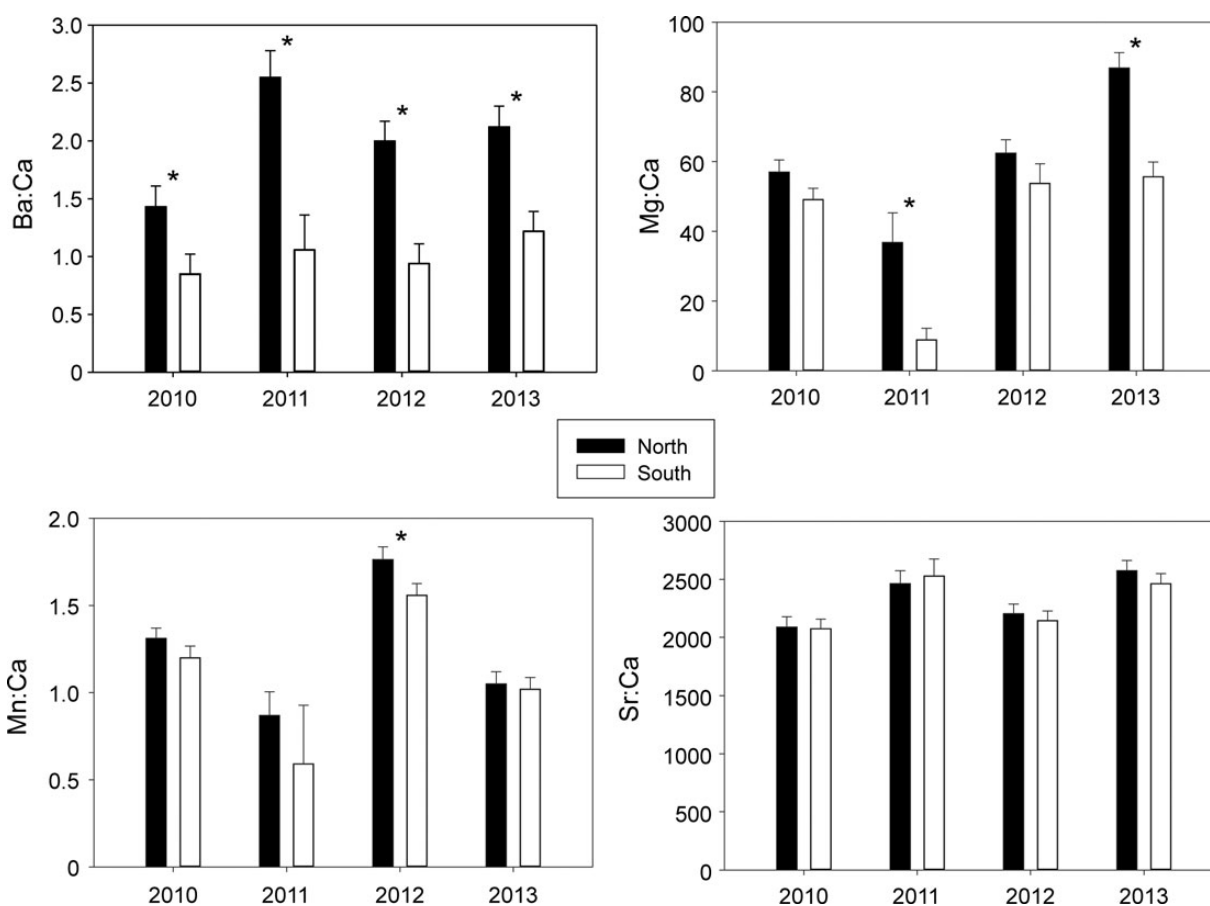


Figure 4. Elemental ratios ($\mu\text{mol mol}^{-1} \pm 1$ s.e.) in whole otoliths of albacore from two regions in the ENP (northern, black; southern, white). Asterisks depict significant regional differences ($p < 0.05$).

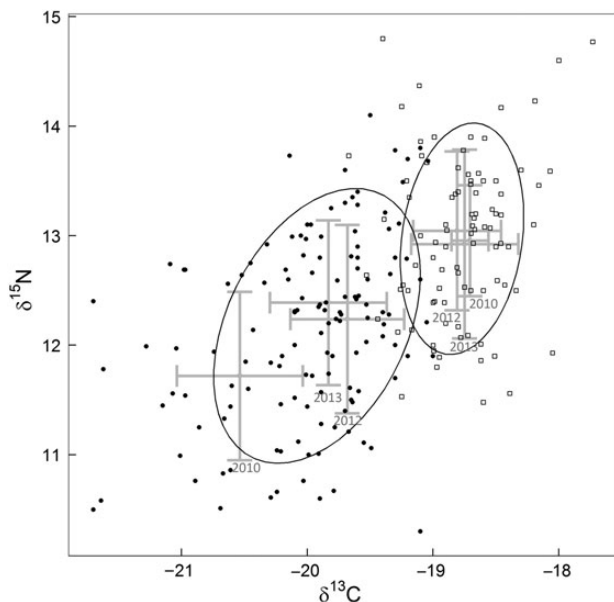


Figure 5. Muscle tissue $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes of albacore from northern (black circles) and southern (white squares) regions in the ENP. Ellipses indicate 75% confidence intervals for each region. Error bars represent ± 1 s.d. for each sample year within each region.

ANOVA, $p < 0.05$). A significant year effect was also detected for Mg:Ca, with ratios significantly lower in both regions in 2011 relative to the other 3 years (ANOVA, $p < 0.05$) and significantly higher in the northern region in 2013 averaging $86.85 (\pm 4.37) \mu\text{mol mol}^{-1}$. For Mn:Ca, ratios were significantly higher in the northern region (1.25 ± 0.04) relative to the southern region (1.09 ± 0.04) (ANOVA, $p < 0.05$), and Mn:Ca ratios were significantly lower in 2011 relative to other years (ANOVA, $p < 0.05$, Figure 4). The mean Sr:Ca ratios in albacore otoliths were similar between regions (ANOVA, $p = 0.34$) averaging $2333.91 (\pm 45.99)$ in the northern region and $2304.65 (\pm 50.78) \mu\text{mol mol}^{-1}$ in the southern region. Significantly, higher Sr:Ca ratios were recorded in both regions during 2011 and 2013 compared with 2010 and 2012 (ANOVA, $p < 0.05$, Figure 4); however, no regional differences were detected between years of high or low Sr:Ca.

The combination of otolith stable isotopes and trace elements was used to discriminate between regions. While discrimination was high irrespective of the year (78–91%) using whole otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, classification success increased to 90–100% during each year with the addition of trace elements (2010, from 90 to 96%; 2011, from 89 to 100%; 2012, from 78 to 90%; 2013, from 91 to 100%). Age-specific classification success using whole otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ improved with increasing age from 73% for age 1, 76% for age 2, and 88% for age 3. Addition of trace elements improved age-specific classification success to 88% for age 1, 86% for age 2, and 92% for age 3 between regions.

Muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ indicated that albacore from the southern region were significantly enriched in both tracers (MANCOVA, $p < 0.05$; Figure 5). The mean muscle $\delta^{13}\text{C}$ for albacore from the southern region was $-18.77\text{‰} (\pm 0.35)$ compared with $-19.98\text{‰} (\pm 0.59)$ for fish collected from the northern region. The mean muscle $\delta^{15}\text{N}$ measured $12.99\text{‰} (\pm 0.74)$ for fish collected in the southern region and averaged $12.14\text{‰} (\pm 0.84)$ in the northern region. Discriminant analysis success was similar when using

muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, with an overall jackknife classification success of 91% (88–100%). Trends of enriched muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in albacore from the southern region were consistent across all years examined (MANCOVA, $p < 0.05$; Figure 5). The interaction between year and region was significant for muscle $\delta^{13}\text{C}$ (MANCOVA, $p < 0.05$), but not for $\delta^{15}\text{N}$, indicating that $\delta^{13}\text{C}$ values differed from year to year. In the northern region, significantly depleted muscle $\delta^{13}\text{C}$ was measured in 2010 ($-20.52\text{‰} \pm 0.52$) compared with 2012 ($-19.66\text{‰} \pm 0.40$) and 2013 ($-19.93\text{‰} \pm 0.58$). Albacore length had a significant effect on both muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for fish captured in the southern region ($p < 0.05$), while fish from the northern region did not show a significant length effect ($\delta^{13}\text{C}$, $p = 0.13$; $\delta^{15}\text{N}$, $p = 0.08$). Linear regression indicated that, for southern fish, a positive correlation existed between fish length and muscle $\delta^{13}\text{C}$ ($y = 212.7 + 7.621 \times x$, $r^2 = 0.06$) and $\delta^{15}\text{N}$ ($y = 3.163 + 5.116 \times x$, $r^2 = 0.12$). Both MANOVA and ANOVA results for tissue samples taken from multiple body locations were non-significant ($p > 0.05$), indicating the ability to directly compare isotopic values of muscle tissue sampled from different locations of the body.

Discussion

Multiple tracers produced results supporting differences in albacore collected from two regions in the eastern Pacific. Both tracers of recent environmental conditions, otolith edge (ambient water chemistry) and muscle tissue (diet) as well as longer term surrogates of environmental exposure (whole otoliths) were different for albacore from the two regions, indicating that two subgroups of juvenile albacore exist in the California Current with limited regional movement or mixing. These results complement previous studies showing regional differences in size-at-age, growth rates, and migratory patterns of albacore from southern and northern regions of the ENP (Laurs and Wetherall, 1981; Childers *et al.*, 2011; Renck *et al.*, 2014). However, the lack of regional differences in otolith core chemistry (proxy for spawning/nursery areas) provides little evidence to support separate production zones of albacore in the ENP.

Results from this study provide insight into the utility of both stable isotopes and trace elements for distinguishing regional signatures for albacore that may also be applied to other species. Otolith $\delta^{18}\text{O}$ was the most useful tracer for discriminating albacore from the two regions, and the similarities between the results using whole otoliths or otolith edge material suggest that both applications are capable of discriminating region-specific signatures in the otoliths of albacore from the regions investigated. Regional differences in otolith $\delta^{18}\text{O}$ are in accord with known differences in the oceanography and seawater chemistry in the southern and northern reaches of the California Current. Surface seawater $\delta^{18}\text{O}$ (upper 50 m) from the south region averages -0.1‰ in contrast to depleted values of -0.8‰ from the north region (Schmidt *et al.*, 1999), paralleling our results for otolith $\delta^{18}\text{O}$ in albacore, though the regional difference in seawater $\delta^{18}\text{O}$ (0.7‰) is larger than regional differences measured in both whole otolith and otolith edge $\delta^{18}\text{O}$ ($0.2\text{--}0.4\text{‰ year}^{-1}$). Incorporation of elements into the otolith is a three-step process involving branchial uptake (from water to blood plasma), cellular transport (blood to endolymph), and crystallization (endolymph to otolith). The lack of a direct match between seawater and otolith $\delta^{18}\text{O}$ is likely attributed to this complex process (Campana, 1999; Darnaude *et al.*, 2014).

Similar otolith $\delta^{13}\text{C}$ was found for both short- (otolith edge) and long-term (whole otolith) measures of environmental history, suggesting this tracer may not be useful for distinguishing albacore from

different regions of the ENP. While spatial differences in seawater $\delta^{13}\text{C}$ have been documented in the ENP (Ruiz-Cooley and Gerrodette, 2012), the relationship between seawater and otolith $\delta^{13}\text{C}$ is not always consistent because the majority (>80%) of otolith-derived carbon may be from dissolved inorganic carbon (DIC) of surrounding seawater (Solomon et al., 2006). In addition, results using $\delta^{18}\text{O}$ often differ, while those using $\delta^{13}\text{C}$ do not. In a study on population structure of Pacific cod (*Gadus macrocephalus*) in the northern region, a clear separation was found between estuarine vs. coastal fish using otolith $\delta^{18}\text{O}$, but no differences were detected for otolith $\delta^{13}\text{C}$ (Gao et al., 2005). Similarly, discrimination of regional nurseries of yellowfin tuna (*T. albacares*) throughout the WCP was driven primarily by otolith $\delta^{18}\text{O}$ rather than otolith $\delta^{13}\text{C}$ (Wells et al., 2012). Moreover, Rooker et al. (2014) used otolith $\delta^{18}\text{O}$ to discriminate yearling Atlantic bluefin tuna (*Thunnus thynnus*) from regional spawning/nursery areas (Gulf of Mexico and Mediterranean Sea), but found no significant differences in otolith $\delta^{13}\text{C}$ between the two regions.

Trace elements improved the discrimination of albacore to regions, and usually, matched expected patterns based on regional oceanography and freshwater input into the ENP. In general, both salinity and temperature are lower in the northern region than in the southern region (Hickey and Banas, 2003). Barium generally displays an inverse relationship with salinity (Walther and Limburg, 2012), consistent with the higher otolith Ba:Ca ratios observed for albacore samples from the northern region. Barium is also higher in recently upwelled water, which can translate into higher levels in otoliths (Elsdon et al., 2008; Woodson et al., 2013). Observed otolith Ba:Ca ratios, however, showed the opposite trend, with higher values in the northern region where upwelling rates are lower. Peak upwelling indices reported by the Pacific Fisheries Environmental Laboratory (PFEL) indicated upwelling rates exceeding $300 \text{ m}^3 \text{ s}^{-1}$ per 100 m of coastline within the southern region of this study in contrast to upwelling rates rarely exceeding $100 \text{ m}^3 \text{ s}^{-1}$ per 100 m of coastline in the north. The difference may be linked to the fact that albacore in the northern region spend a larger percentage of the year in offshore waters compared with albacore in the southern region (Childers et al., 2011). Previous studies have demonstrated higher Ba concentrations in otoliths of fish in open oceanic environments relative to coastal upwelling regions (Ashford et al., 2007, 2011). Local oceanography in the northern region may, therefore, affect Ba:Ca ratios in seawater and otoliths, including the extent of the Columbia River plume, seasonal movement of water masses associated with the California Current, and offshore eddy dynamics (Hickey and Banas, 2003). Alternatively, previous studies have shown dietary contributions of Ba in otoliths (Buckel et al., 2004), which may be a product of regional differences in feeding patterns of albacore (Glaser, 2010; Glaser et al., 2014).

Along with upwelling and differences in salinity, differences in riverine input may also account for regional differences in otolith element:Ca ratios observed in our albacore samples. The Columbia River discharge located in the northern region accounts for 77% of the coastal drainage of the US west coast (Barnes et al., 1972). The seaward extent of the Columbia River plume can extend as far as 400 km offshore (Barnes et al., 1972). Lithogenic sediment from the Columbia River can, therefore, be transported offshore to the mid- and outer shelf (Nitttrouer, 1978) and contribute to higher concentrations of the alkaline earth elements (Ba, Mg, Sr) in albacore otoliths from the northern region. In addition, otolith Sr:Ca shows a negative correlation with ambient temperature

(Radtke et al., 1990; Ikeda et al., 1999), consistent with the slightly higher concentrations (though not statistically significant) in albacore otoliths in the northern region during 3 of the 4 years examined.

Otolith core $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ was similar between albacore collected from the two study regions. Given the large geographic range and extended spawning season of albacore (Otsu and Uchida, 1959; Nishikawa et al., 1985; Chen et al., 2010), it may be difficult to separate region-specific nursery signals due to spatial and temporal variability in environmental conditions across spawning grounds in the WCP. Results show depleted otolith core $\delta^{18}\text{O}$ compared with whole otolith and otolith edge values. A similar westward depletion of otolith core $\delta^{18}\text{O}$ was reported in young-of-the-year yellowfin tuna in the WCP and attributed to environmental differences such as salinity and temperature across the regions investigated (Wells et al., 2012). These depleted otolith core $\delta^{18}\text{O}$ values appear to indicate that individuals may have been produced in nursery grounds west of our two study regions; however, no evidence was found for unique region-specific nurseries. Additional studies are needed to determine whether the two subgroups of albacore in the ENP originate from the same area and recruit to different regions along the California Current or are truly two separate stocks with distinct spawning grounds.

In addition to otolith chemistry, muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ proved effective for discriminating albacore from the two regions. Stable isotopes in the muscle tissue of consumers are affected by both their trophic position and the local signatures of producers that support the food web (Popp et al., 2007; Seminoff et al., 2012; Madigan et al., 2014). Dietary studies on albacore in the California Current have shown that fish in the northern and southern regions, as defined in this study, have generally overlapping diets, but differ in terms of their most important prey species. Albacore in the northern region have been observed to prey heavily on decapods, euphausiids, and fish, whereas the diets of albacore collected in the southern region are comprised primarily of squid and fish (Glaser et al., 2014). These patterns change as prey availability shifts (Glaser, 2010), but have been observed to be relatively stable across short periods (Glaser et al., 2014). Despite having notable differences in primary prey, a number of important prey species were shared by albacore in both regions, including anchovies and hake (Glaser et al., 2014). When this overlap in dominant prey species is compared with the high discrimination rate observed in albacore muscle tissues (91%), it is unlikely that prey species alone were responsible for the average muscle $\delta^{13}\text{C}$ enrichment of 1.2‰ in albacore from the southern region. Other factors that likely impact muscle $\delta^{13}\text{C}$ include distinct carbon isoscapes between $\delta^{13}\text{C}$ -enriched southern California (<40°N) and the $\delta^{13}\text{C}$ -depleted Pacific Northwest (>40°N), as observed by Newsome et al. (2007) in pinnipeds. Similar processes may affect albacore because movement patterns are region-dependent, with northern fish spending a larger proportion of time in $\delta^{13}\text{C}$ -depleted offshore waters compared with fish in the southern region (Childers et al., 2011). It is also possible that faster growth rates of albacore in the southern region (Laurs and Wetherall, 1981; Renck et al., 2014) may contribute to this difference because higher $\delta^{13}\text{C}$ values have been associated with rapid growth rates (Goericke and Fry, 1994).

Differences in regional prey availability and basal $\delta^{15}\text{N}$ values likely contribute to the mean muscle $\delta^{15}\text{N}$ difference of 0.9‰ for albacore between regions. Albacore in the northern region consumed larger amounts of decapods and euphausiids and had corresponding depleted muscle $\delta^{15}\text{N}$ compared with conspecifics in the

southern region, which forage on higher-trophic-level prey such as squid and fish (Glaser, 2010; Glaser *et al.*, 2014). Using compound-specific nitrogen isotope analysis of individual amino acids, Popp *et al.* (2007) found that differences in $\delta^{15}\text{N}$ values of yellowfin tuna were the result of spatial variations in $\delta^{15}\text{N}$ at the base of the food web across the eastern tropical Pacific and not distinct trophic feeding levels. Similarly, Madigan *et al.* (2014) found significant differences in muscle $\delta^{15}\text{N}$ of Pacific bluefin tuna that recently migrated from the western Pacific compared with those that had been in the California Current for more than a year. Spatial differences in $\delta^{15}\text{N}$ at the base of the food web are likely driven by variations in water chemistry and different nitrogen-cycling regimes. Limited oxygen can greatly affect $\delta^{15}\text{N}$ values because in the absence of adequate dissolved oxygen, denitrification causes the preferential removal of $\delta^{15}\text{N}$ -depleted NO_3^- leaving behind a strongly $\delta^{15}\text{N}$ -enriched environment (Graham *et al.*, 2010). The lower latitudes of the California Bight in the ENP that are in proximity to the Eastern Tropical Pacific oxygen minimum zone and the mixing of waters from this oxygen-depleted source with the southern waters of the California Current (Castro *et al.*, 2001; Voss *et al.*, 2001; Graham *et al.*, 2010) may, therefore, contribute to the enriched $\delta^{15}\text{N}$ values of albacore collected from the southern region.

This study combined natural tracers in otoliths and muscle tissue to assess the population structure of albacore in the ENP. Other than otolith $\delta^{13}\text{C}$, all tracers indicated separation between the two regions, with the strongest discrimination obtained by combining otolith $\delta^{18}\text{O}$ and three element:Ca ratios (Ba:Ca, Mg:Ca, Mn:Ca). Separation between regions indicates that vital rates should be region-specific in modelling efforts, and additional research into whether this represents two distinct stocks or recruitment of the same stock to different foraging grounds should be the focus of future efforts that will require a combination of tools, including genetics.

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