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Nursery-specific contribution estimates of Pacific Bluefin Tuna to the eastern North Pacific Ocean

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Abstract

***Objective*: The Pacific Bluefin Tuna *Thunnus orientalis* is a highly migratory species currently managed as a single stock with two discrete spawning areas in the western Pacific Ocean: one extending from the Nansei Islands through Taiwan and the Ryukyu Archipelago (East China Sea) and the other in the Sea of Japan. While age-0 fish remain near Japan, an unknown portion of age-1 and age-2 Pacific Bluefin Tuna migrate to the eastern Pacific Ocean, returning to the western Pacific Ocean after several years. The dynamics and timing of these migrations are poorly understood, and questions remain about how many fish migrate to the eastern Pacific Ocean and from which spawning (i.e., nursery) area they originate. This study used natural tracers (i.e., otolith chemistry) to estimate the nursery origin of subadult and adult Pacific Bluefin Tuna (ages 4–7) from the eastern Pacific Ocean to provide a better understanding of Pacific Bluefin Tuna movement and connectivity.**

***Methods*: We analyzed otolith cores from age-0 Pacific Bluefin Tuna from the two western Pacific Ocean nursery areas for trace elements (Li, Mg, Mn, Sr, Zn, and Ba) and stable isotopes ($\delta^{13}C$ and $\delta^{18}O$) to establish baseline signatures spanning a 4-year period (2011–2014). These baseline signatures were then compared against otolith cores from subadult and adult Pacific Bluefin Tuna collected in the eastern Pacific Ocean to estimate the relative contributions of each nursery area and assess whether these contributions vary with age-class and year.**

***Results*: Distinct chemical signatures existed in the otolith cores of age-0 Pacific Bluefin Tuna collected from the two nursery areas. Subadult and adult Pacific Bluefin Tuna collected in the eastern Pacific Ocean over a 4-year period (2016–2019) were then age-class matched to baselines using two mixed-stock analysis approaches. Nurs-**

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ery-specific contribution estimates to the eastern Pacific Ocean were generally higher from the East China Sea averaging 61% (SD = 26%) versus 39% (26%) from the Sea of Japan. However, contribution estimates varied largely by year and age-class ranging from 18% to 91% from the East China Sea and 9–82% from the Sea of Japan.

***Conclusions*: This study expands upon the application of these natural tracers for population connectivity of this economically important species and highlights the importance of both nursery areas supporting Pacific Bluefin Tuna in the eastern Pacific Ocean. Results suggest that nursery-specific recruitment dynamics can shift substantially across cohorts. The high interannual variability in relative contribution estimates underscores that both the East China Sea and Sea of Japan support migratory Pacific Bluefin Tuna biomass in the eastern Pacific Ocean.**

Keywords: mixed-stock analysis, natal origin, otolith geochemistry, stable isotopes, *Thunnus orientalis*, trace elements

Lay summary

The Pacific Bluefin Tuna is an economically important and highly migratory species. This study used natural tracers to estimate the nursery origin of subadult and adult Pacific Bluefin Tuna collected in the eastern Pacific Ocean. Results highlight the importance of both nursery areas supporting Pacific Bluefin Tuna in the eastern Pacific Ocean.

Introduction

The Pacific Bluefin Tuna *Thunnus orientalis* is a highly migratory pelagic predator distributed across the North Pacific Ocean, playing a key ecological role as an upper-trophic-level predator while supporting valuable fisheries throughout its range (International Scientific Committee, 2024). Pacific Bluefin Tuna exhibit a complex life history characterized by spawning in the western Pacific Ocean across two primary nursery areas: the East China Sea (spawning April–June), extending from the Nansei Islands through Taiwan and the Ryukyu Archipelago, and the Sea of Japan (spawning July–August) (Itoh, 2009; Ohshimo et al., 2017; Shiao et al., 2017). From these coastal nurseries (i.e., spawning areas), juvenile Pacific Bluefin Tuna disperse widely to forage before eventually returning to spawn as adults (James et al., 2021). During their first 1 to 2 years of life, when juvenile Pacific Bluefin Tuna are particularly vulnerable to troll and purse-seine fisheries (Lin et al., 2025), a portion of juveniles undertake trans-Pacific migrations to the eastern Pacific Ocean, where they feed and grow for several years before returning to the western Pacific Ocean to eventually spawn (Inagake et al., 2001; Madigan et al., 2017). Within the western Pacific Ocean, sexual maturity varies by nursery area: Individuals from the East China Sea typically mature at age 9 or older (Ashida et al., 2015), whereas those from the Sea of Japan reach maturity between age 3 and age 5 (Okochi et al., 2016). This differentiation in life history traits, combined with extensive transoceanic connectivity, complicates stock assessment and management efforts. Integrated methodologies capable of resolving natal origin and movement patterns are therefore essential for developing spatially explicit management strategies for this economically and ecologically valuable species.

A suite of complementary analyses has significantly advanced our understanding of Pacific Bluefin Tuna migration and connectivity across the North Pacific Ocean (Fujioka, Fukuda, Tei, et al., 2018; Nakatsuka, 2020). Tagging studies, including archival and satellite tagging, have provided crucial information on size- and age-dependent movement patterns within the eastern Pacific Ocean (Boustany et al., 2010) and western Pacific Ocean (Fujioka, Fukuda, Tei, et al., 2018; Fujioka et al., 2021, 2025). Tagging data have also shed light on the timing, duration, and location of transoceanic migrations, revealing that these movements are shaped by a dynamic interplay of oceanographic conditions, thermal preferences, prey distribution, and physiological limitations (Fujioka et al., 2021, 2025; Kitagawa et al., 2007). Although archival and satellite tagging studies provide detailed individual-level information, these approaches are often constrained by small sample sizes due to financial limitations, low tag return rates, or both, limiting their ability to characterize population-level patterns of connectivity and natal origin.

Chemical and structural analysis of hard parts, including otoliths and vertebrae, have also emerged as powerful tools for inferring movement patterns and identifying nursery origins of Pacific Bluefin Tuna, often providing cost-effective alternatives to tagging studies that can accommodate larger sample sizes. Uematsu et al. (2024) investigated the natal origin of Pacific Bluefin Tuna populations by measuring the radius of the first annulus in vertebrae. Because spawning occurs earlier in the East China Sea than in the Sea of Japan, the first vertebral annulus forms at a larger size in early hatched individuals from the East China Sea, allowing discrimination between the two spawning cohorts. Otolith chemistry has also been used extensively to infer population connectivity and natal origin in Pacific Bluefin Tuna (Mohan et al., 2022; Rooker et al., 2021; Shiao et al., 2021; Wells et al., 2020). Trace element analysis exploits the fact that elements incorporated into otoliths during early life reflect the ambient water chemistry of natal environments. Chemical "fingerprints" unique to each nursery can be established by analyzing otolith cores of age-0 fish collected directly from the East China Sea and Sea of Japan. These fingerprints are then compared against Pacific Bluefin Tuna of any age captured throughout the western Pacific Ocean and eastern Pacific Ocean to infer their natal origin (Wells et al., 2020). Similarly, stable isotopes of oxygen and carbon in otoliths provide complementary information about migratory patterns. Oxygen isotope values ($\delta^{18}O$) reflect the water temperature experienced during otolith formation and can distinguish

between Pacific Bluefin Tuna that overwinter in different nursery areas based on the timing and position of the first winter signal in the otolith (Shiao et al., 2010). Carbon isotope values ($\delta^{13}C$) vary between the western Pacific Ocean and eastern Pacific Ocean due to regional differences in dissolved inorganic carbon, enabling reconstruction of trans-Pacific migration history (Kawazu et al., 2020).

These geochemical and tagging approaches are frequently combined with modeling frameworks to understand stock structure, and Nakatsuka (2020) concluded that current evidence supports managing Pacific Bluefin Tuna as a single stock due to high intermixing throughout the population. Despite this single-stock framework, understanding the relative contribution of each nursery area to different regions and age-classes remains essential for effective management, particularly as populations recover and demographics shift. Following severe declines in spawning stock biomass during the 1990s, stricter management measures implemented through the Western and Central Pacific Fisheries Commission and the Inter-American Tropical Tuna Commission have led to a notable rebound in Pacific Bluefin Tuna abundance (International Scientific Committee, 2024; Lin et al., 2025). Concurrent with this recovery, eastern Pacific Ocean fisheries historically dominated by younger individuals (ages 1–3) have shown an increasing presence of larger and older fish in recent years (James et al., 2021). Understanding nursery-specific contributions across age-classes is therefore important for characterizing how each contributes to different demographic components of the eastern Pacific Ocean population and for informing spatially explicit management strategies.

Several studies have examined the natal origin of Pacific Bluefin Tuna in the eastern Pacific Ocean using otolith-based approaches. Wells et al. (2020) analyzed otolith trace element chemistry from the cores of age-1 Pacific Bluefin Tuna collected in the California Current Large Marine Ecosystem (CCLME) and detected substantial contributions from both the East China Sea and Sea of Japan, demonstrating that juveniles from both nurseries recruit to the eastern Pacific Ocean. More recently, Uematsu et al. (2024) used vertebral annuli analysis to suggest that juvenile Pacific Bluefin Tuna (ages 1–2) in the eastern Pacific Ocean predominantly originated from the East China Sea (70–77%). However, contribution estimates for older age-classes (ages 4+) in the eastern Pacific Ocean remain limited despite the increasing presence of subadult and adult Pacific Bluefin Tuna in eastern Pacific Ocean fisheries. The purpose of this study was to determine the natal origin of subadult and adult Pacific Bluefin Tuna (ages 4–7) collected in the eastern Pacific Ocean using a combination of otolith trace element chemistry and stable isotope analysis. We established baseline signatures by analyzing element : Ca ratios and stable isotopes ($\delta^{13}C$ and $\delta^{18}O$) from otolith cores of age-0 Pacific Bluefin Tuna collected from both known nursery areas (East China Sea, Sea of Japan) over a 4-year period. These baseline signatures were then compared against otolith cores from subadult and adult Pacific Bluefin Tuna collected in the eastern Pacific Ocean to estimate the relative contributions of each nursery area and assess whether these contributions vary with age-class and year.

Methods

Sample collection

Samples of age-0 Pacific Bluefin Tuna (<34 cm fork length [FL]) were collected in both nursery areas over a 4-year period (2011–2014) by the Japan Fisheries Research and Education Agency. Within each nursery area, 10 individuals were sampled equally across nurseries and years at multiple collection dates (June–December) and locations during each year to obtain a representative baseline sample, for a total of 80 samples (Table 1). Subadult and adult Pacific Bluefin Tuna (ages 4–7, 134–185 cm FL) were collected in the eastern Pacific Ocean over a 4-year period (2016–2019) for age-class matching to age-0 baselines (Table 1). All subadult and adult Pacific Bluefin Tuna from the eastern Pacific Ocean were collected through recreational fisheries across a range of locations and dates (June–September) throughout the CCLME. Ages of subadult and adult Pacific Bluefin Tuna were derived from previous length–age relationships reported in Shimose et al. (2009).

Otolith preparation and analysis

Following extraction and cleaning, one sagittal otolith from each age-0 Pacific Bluefin Tuna was embedded in Struers EpoFix resin and sectioned using a low-speed diamond blade saw to obtain a 1.5-mm transverse section that included the otolith core. Otolith sections were polished to the core and then attached to a sample plate using Crystalbond thermoplastic glue. A single otolith from each individual was used for both trace element and stable isotope analysis.

For trace element analysis, elemental concentrations were quantified using an Elemental Scientific NWR193UC (193-nm wavelength, <4-ns pulse width) laser ablation system coupled to an Agilent 7500ce inductively coupled plasma mass spectrometer at the University of Texas at Austin. For age-0 samples, five ablation spots were placed first at the otolith core (defined as the narrowest part of the section), followed by two equally spaced spots on each side of the core, corresponding to approximately the first month of life based on previous estimates of otolith accretion rates (Kitchens et al., 2018). Prior to analysis, ablation spots on otolith samples and standards were preablated (fluence of 2.97 ± 0.03 J/cm^2, 20 Hz, 75-μm spot, 2-s dwell) to remove potential surface contamination. Ablation parameters during spot sample acquisition included a fluence of 2.97 ± 0.03 J/cm^2, 20 Hz, 50-μm spot, 30-s dwell. For subadult and adult samples, life history profiles were analyzed by ablating laser scans from the otolith core (narrowest part of the section; start of life) outwards along the growth axis to the otolith edge. Again, prior to analysis, life history transects on otolith samples and standards were preablated (fluence of 2.85 ± 0.01 J/cm^2, 20 Hz, 10 Hz, 75-μm spot, 5-μm/s scan rate) to remove potential surface contamination. Ablation parameters during line transect acquisition included fluence of 2.85 ± 0.01 J/cm^2, 10 Hz, 50-μm spot, 5-μm/s scan rate. For both methods unknown samples were bracketed hourly by standard measurements on the laser ablation inductively coupled plasma mass spectrometer (MACS-3 and NIST 612, measured in triplicate for 60 s). The quadrupole time-resolved method measured 10 masses

Table 1 Summary statistics of Pacific Bluefin Tuna collected from both spawning areas (East China Sea [ECS] and Sea of Japan [SoJ]) and adults (ages 4–7) collected from the eastern Pacific Ocean (EPO), showing average size (cm fork length), mean element : Ca ratios, and mean stable $\delta^{13}C$ and $\delta^{18}O$ isotope values in otolith cores. Standard deviations are show in parentheses.

Year	Area	*n*	Size	Li:Ca µmol/mol	Mg:Ca µmol/mol	Mn:Ca µmol/mol	Zn:Ca µmol/mol	Sr:Ca mmol/mol	Ba:Ca µmol/mol	$\delta^{13}C$	$\delta^{18}O$
Age 0											
2011	ECS	10	20.2 (1.64)	5.18 (0.70)	347.93 (40.67)	4.51 (1.71)	2.36 (0.74)	1.81 (0.10)	1.27 (0.59)	−10.66 (0.39)	−2.45 (0.22)
	SoJ	10	27.4 (1.47)	5.79 (0.51)	416.39 (26.22)	4.47 (1.08)	2.77 (0.61)	1.79 (0.10)	0.52 (0.08)	−10.31 (0.38)	−2.72 (0.20)
2012	ECS	10	20.3 (1.80)	4.91 (0.62)	359.08 (45.14)	2.52 (0.72)	2.84 (0.99)	1.75 (0.12)	0.71 (0.26)	−11.03 (0.41)	−2.51 (0.17)
	SoJ	10	32.6 (0.66)	5.29 (0.48)	372.55 (27.66)	6.78 (3.58)	2.91 (1.24)	1.83 (0.16)	1.08 (0.60)	−10.52 (0.70)	−2.76 (0.36)
2013	ECS	10	20.3 (1.94)	5.39 (0.88)	403.84 (75.98)	3.17 (1.49)	2.28 (0.49)	1.75 (0.11)	0.69 (0.19)	−10.94 (0.54)	−2.48 (0.36)
	SoJ	10	27.3 (1.41)	5.22 (0.71)	401.61 (47.53)	4.20 (0.90)	2.36 (0.80)	1.71 (0.08)	0.78 (0.20)	−9.98 (0.40)	−3.03 (0.13)
2014	ECS	10	20.2 (1.80)	5.20 (0.67)	429.38 (45.28)	3.07 (1.88)	2.10 (0.86)	1.86 (0.11)	0.57 (0.20)	−10.81 (0.26)	−2.54 (0.19)
	SoJ	10	27.3 (1.48)	5.22 (0.69)	335.74 (36.78)	7.26 (2.84)	2.49 (0.52)	1.63 (0.11)	0.69 (0.32)	−10.05 (0.47)	−2.26 (0.19)
Age 4											
2016	EPO	22	141.1 (4.04)	5.91 (3.15)	248.71 (81.42)	3.27 (1.22)	2.79 (1.99)	1.70 (0.13)	0.81 (0.80)	–	–
2017	EPO	25	142.8 (4.43)	5.39 (2.43)	231.75 (46.36)	3.95 (1.50)	3.40 (2.55)	1.76 (0.17)	0.73 (0.32)	–	–
2018	EPO	8	143.2 (6.54)	6.44 (1.27)	275.30 (78.65)	3.48 (2.10)	2.59 (0.76)	1.84 (0.09)	0.93 (0.33)	–	–
2019	EPO	8	141.5 (8.49)	5.35 (3.26)	189.30 (35.86)	1.94 (0.70)	1.15 (0.43)	1.76 (0.12)	0.73 (0.27)	–	–
Age 5											
2016	EPO	11	158.2 (5.60)	3.73 (2.23)	287.85 (102.0)	3.94 (1.78)	5.41 (4.98)	1.61 (0.17)	0.89 (0.53)	–	–
2017	EPO	10	157.0 (4.95)	5.37 (1.93)	220.59 (53.54)	3.03 (0.77)	2.19 (1.27)	1.67 (0.13)	0.58 (0.31)	–	–
2018	EPO	26	160.4 (3.84)	6.33 (1.86)	227.84 (65.93)	3.27 (2.14)	2.68 (2.29)	1.74 (0.16)	0.09 (0.97)	–	–
2019	EPO	4	156.1 (7.03)	6.02 (2.12)	196.45 (40.64)	2.52 (0.91)	1.47 (1.03)	1.61 (0.12)	0.45 (0.13)	–	–
Age 6											
2017	EPO	12	167.2 (1.85)	5.37 (2.48)	218.57 (41.42)	2.81 (1.54)	2.88 (1.39)	1.72 (0.13)	0.82 (0.64)	–	–
2018	EPO	24	168.9 (1.86)	4.08 (2.17)	216.89 (42.12)	3.85 (1.87)	2.95 (3.31)	1.74 (0.14)	0.79 (0.28)	–	–
2019	EPO	8	171.2 (2.31)	4.59 (1.19)	208.21 (61.32)	2.93 (1.49)	2.98 (2.60)	1.70 (0.09)	0.82 (0.41)	–	–
Age 7											
2018	EPO	8	181.2 (3.83)	5.54 (2.07)	204.54 (42.60)	2.72 (1.87)	1.86 (0.82)	1.64 (0.11)	0.63 (0.25)	–	–
2019	EPO	22	179.4 (2.70)	5.99 (2.19)	222.43 (75.60)	3.01 (1.30)	3.64 (4.06)	1.74 (0.15)	0.88 (0.48)	–	–

using integration times of 10 ms (^{24}Mg, $^{43–44}$Ca, ^{88}Sr), 20 ms (^{25}Mg, ^{55}Mn), and 50 ms (^{7}Li, ^{66}Zn, $^{137–138}$Ba). Time-resolved intensities were converted to concentration (ppm) equivalents using Iolite software, with ^{43}Ca as the internal standard and a Ca index value of 38.3 weight percent. U.S. Geological Survey MACS-3 was used as the primary reference standard, and accuracy and precision were assessed from replicates of NIST 612 analyzed as an unknown. The NIST 612 analyte recoveries ($N = 72$) were typically within 2% of GeoREM preferred values (http://georem.mpch-mainz.gwdg.de). Concentrations were converted to element : Ca molar ratios (R_E; μmol/mol) based on the molar mass of each element (M_E; g/mol) and calcium (M_{Ca} = 43 g/mol):

$$R_E = \frac{[E]}{1{,}000}\left(M_E \frac{0.38}{M_{Ca}}\right)^{-1}.$$

To characterize the core signature of the subadult and adult samples, the first 200 μm of the life history transect was averaged, corresponding to approximately the first months of life as analyzed by the ablation spots of the age-0 samples. Comparing ablated spots to line transects was confirmed valid, as it was determined that no significant difference exist between values obtained by the two methods (Zapp Sluis et al., 2025).

For stable isotope analysis (δ^{13}C and δ^{18}O), the portion of the otolith core corresponding to the first months of life was milled from the otolith section using a New Wave Research MicroMill system. Prior to milling, each otolith section was polished to remove the laser-ablated transect line. A preprogrammed drill path was made using a 350-μm diameter drill bit, and 14 passes each at a depth of 55 μm were used to obtain core material from the otolith. Powdered core material was transferred to silver capsules and later analyzed for δ^{13}C and δ^{18}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-19 and NBS-18, with six standards run for every 40 samples. Precision was ±0.11‰ (SD) for δ^{18}O and ±0.08‰ (SD) for δ^{13}C. Stable isotopes are reported relative to the PeeDee Belemnite scale after comparison to an in-house laboratory standard calibrated to PeeDee Belemnite.

Statistical analysis

Multivariate analysis of variance was used to test for differences in both trace elements and stable isotopes of age-0 Pacific Bluefin Tuna between nurseries; Pillai's trace statistic was used to test for significance. Two-way univariate tests were also performed using analysis of variance, with nursery, year, and nursery × year interactions as fixed factors. A posteriori differences among means were detected with Tukey's honestly significant difference (HSD) test. Quadratic discriminant function analysis was used to determine the classification accuracy of Pacific Bluefin Tuna to each nursery area based on jackknife reclassification. Estimates of nursery origin for Pacific Bluefin Tuna collected in the eastern Pacific Ocean were derived by comparing element : Ca ratios in the otolith cores of subadult and adult Pacific Bluefin Tuna to the corresponding baseline data of age-0 Pacific Bluefin Tuna. Statistical significance for all tests was set at $\alpha = 0.05$, and SYSTAT (version 13) was used for all analyses.

Nursery area (East China Sea versus Sea of Japan) of subadult and adult Pacific Bluefin Tuna collected in the eastern Pacific Ocean was predicted using the maximum likelihood mixed-stock analysis program HISEA (Millar, 1987). Mixed-stock analyses included bootstrapping with 1,000 simulations to obtain estimates of uncertainty. In addition, multinomial logistic regression (MLR) was used as a second classification framework (Rooker et al., 2019). Multinomial logistic regression is an extension of binary logistic regression that allows for more than two categories of outcome variables (Hosmer & Lemeshow, 2000). Recent applications of MLR using otolith chemistry demonstrate its potential for classifying mixed stocks of Bluefin Tuna (also known as Atlantic Bluefin Tuna) *Thunnus thynnus* by predicting stock origins of individuals and proportions of mixed stocks (Rooker et al., 2019). The MLR model in this study was developed with element : Ca ratio baseline data and then used to predict the probability of unknown individuals originating from the two nursery areas. While model parameters in MLR are also estimated using a maximum likelihood estimator, MLR is fundamentally different from HISEA in that it does not directly estimate the proportion of each population and does not assume a classification matrix where the probability of individuals being randomly selected from a specific population in the mixed sample is known from the baseline. Instead, MLR predicts the probability for individuals randomly sampled from the mixed sample, assigns them to a category, and then estimates the proportions of each population. One potential advantage of MLR is that it can be applied to a mixed sample that may not include all potential sources or nurseries by establishing probability thresholds that assign individuals with lower predicted probabilities to an undetermined source that may not be represented in the baseline. Classification in MLR is based on a vector of conditional probability, and here we applied a series of probability thresholds for positive predictions, with all modeling performed in R (R Core Team, 2018).

Results

A total of 80 age-0 Pacific Bluefin Tuna were used to establish baseline otolith geochemical values in the two nursery areas over a 4-year period (2011–2014). Average size of age-0 Pacific Bluefin Tuna was 24.5 cm FL (SD = 4.8) and ranged from 17.1 to 33.6 cm FL (Table 1). A total of 188 subadult and adult Pacific Bluefin Tuna collected from 2016 to 2019 ranged in size from 133.8 to 188.4 cm FL, with an average size of 159.0 cm FL (SD = 14.4) (Table 1).

Pacific Bluefin Tuna core chemistry by nursery area

Collectively, element : Ca ratios and stable isotope signatures of age-0 Pacific Bluefin Tuna otolith cores were significantly different between nursery areas and across years

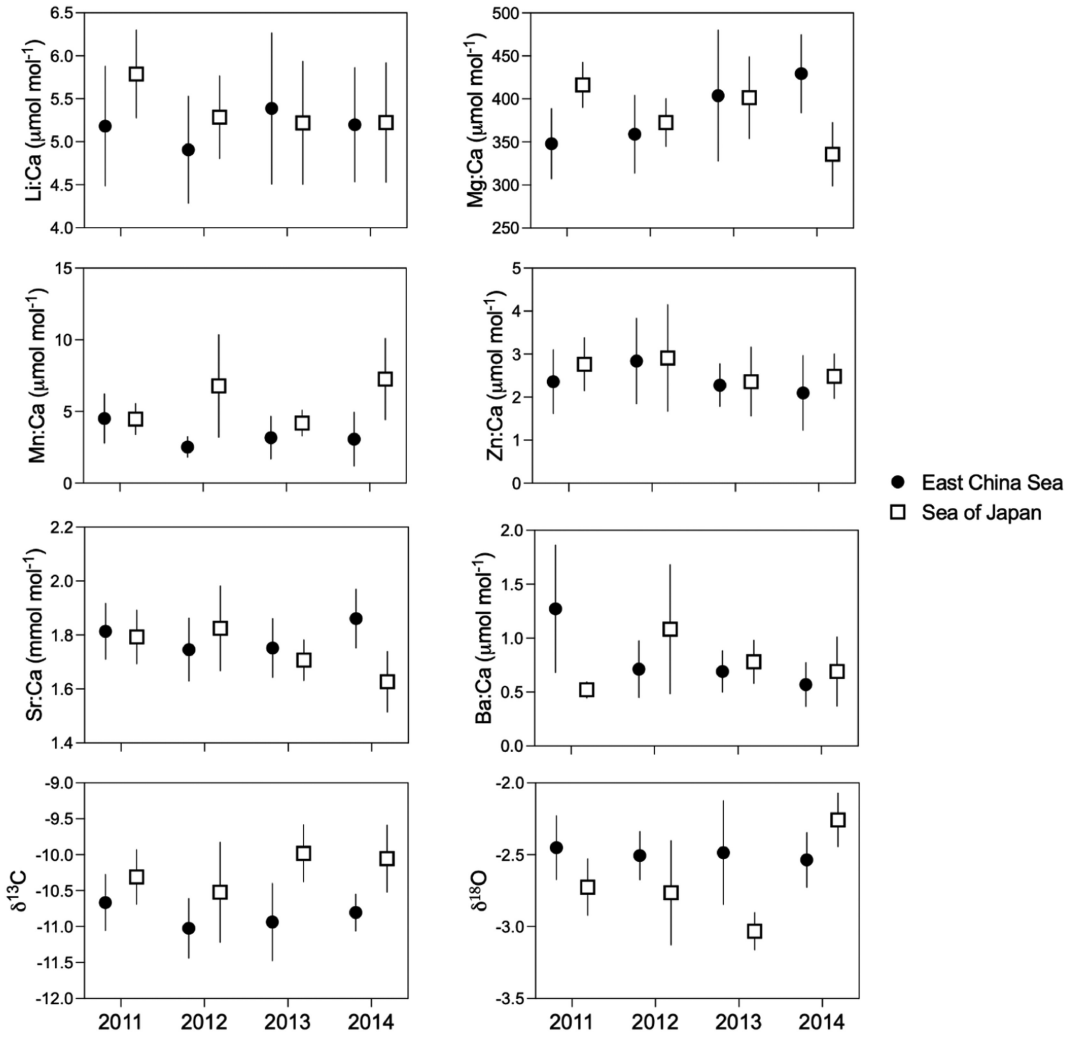

Figure 1 Mean (error bars show SD) otolith core element : Ca ratios and stable $\delta^{13}C$ and $\delta^{18}O$ isotopes of age-0 Pacific Bluefin Tuna from the two nursery areas, East China Sea (black circles) and Sea of Japan (white squares). Elemental ratios include Li:Ca, Mg:Ca, Mn:Ca, Zn:Ca, Sr:Ca, and Ba:Ca and stable $\delta^{13}C$ and $\delta^{18}O$ isotopes.

(multivariate analysis of variance; $P < 0.001$). Individual element : Ca ratios and stable isotopes in otolith cores were variable across years within both nursery areas (Figure 1). Otolith Mg:Ca, Mn:Ca, Sr:Ca, Ba:Ca, $\delta^{13}C$, and $\delta^{18}O$ each showed a significant main effect by nursery area; however, each also had a significant nursery × year interaction ($P < 0.001$). The ratio of Mg:Ca was significantly lower in Pacific Bluefin Tuna otolith cores from East China Sea samples in 2011 relative to Sea of Japan (Tukey's HSD; $P = 0.026$) and significantly higher in East China Sea samples in 2014 (Tukey's HSD; $P < 0.001$) (Figure 1). The ratio of Mn:Ca was significantly higher in Pacific Bluefin Tuna otolith cores from Sea of Japan samples relative to East China Sea in 2 of the 4 years (2012, 2014; Tukey's HSD; $P < 0.001$) (Figure 1). The ratio of Sr:Ca was significantly higher in otolith cores from East China Sea samples in 1 of the 4 years (2014; Tukey's HSD; $P = 0.031$). The ratio of Ba:Ca was significantly higher in otolith cores from East China Sea samples relative to Sea of Japan in 2011 (Tukey's HSD; $P < 0.001$). The level of $\delta^{13}C$ was significantly higher in otolith cores from Sea of Japan samples relative to those from the East China Sea in 2013 (Tukey's HSD; $P < 0.001$) and 2014 (Tukey's HSD; $P = 0.011$; Figure 1). Lastly, $\delta^{18}O$ was significantly higher in East China Sea samples relative to Sea of Japan samples during 1 of the 4 years (2013; Tukey's HSD; $P < 0.001$; Figure 1). The elements Li and Zn showed no differences between nursery areas.

Classification accuracy

Classification success of age-0 Pacific Bluefin Tuna to the respective nursery areas when combining across all 4 years was 83% when using all element : Ca ratios and stable isotopes combined and 71% when using only element : Ca ratios. Results of classification success varied by year and by combining both element : Ca ratios and stable isotopes versus using only element : Ca ratios. In 2011, 95% classification success was found using both types of markers, and similarly, there was 80% classification success in 2012. In 2013, classification success was 95% using both versus 90% using only element : Ca ratios. In contrast, classification success in 2014 was 90% using both approaches and improved to 95% using only element : Ca ratios. Even though Li and Zn showed no significant differences between nursery areas, both were useful in overall

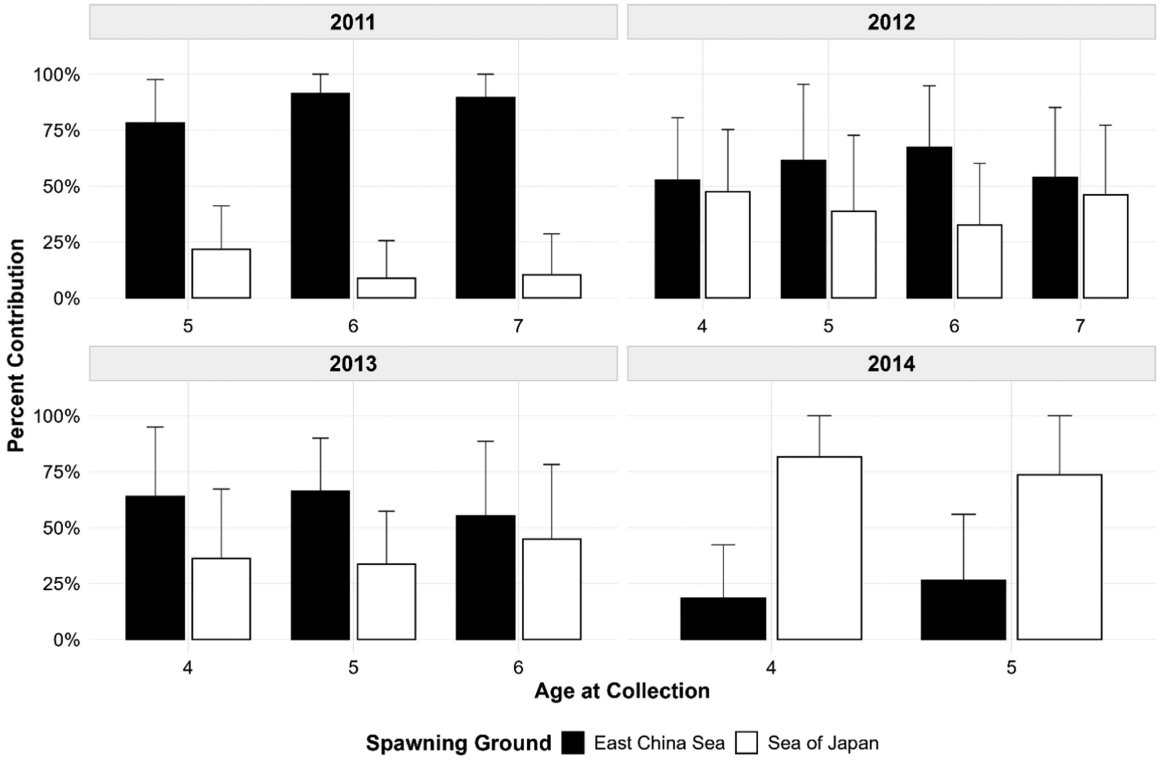

Figure 2 Percent contribution estimates (mean ± SD) of age-4 to age-7 (subadult and adult) Pacific Bluefin Tuna collected in the eastern Pacific Ocean using the analysis program HISEA, based on spawning year.

discrimination between the two nurseries, with improved performance in overall classification success of age-0 Pacific Bluefin Tuna. Stable isotopes only improved classification success in 1 year (2013) of the 4-year baseline by 5%; consequently, only element : Ca ratios were used to assign nursery origin to subadult and adult Pacific Bluefin Tuna from the eastern Pacific Ocean.

Mixed-stock contribution estimates

Results from mixed-stock analysis support that subadult and adult Pacific Bluefin Tuna recruits to the eastern Pacific Ocean originate from both the East China Sea and Sea of Japan nurseries. Overall, a higher percentage of subadult and adult Pacific Bluefin Tuna recruits in the eastern Pacific Ocean originated from the East China Sea, with an overall combined average of 61.2% (SD = 30.0) relative to 38.8% (26.0) from the Sea of Japan based on the HISEA models (Figure 2). Similar results were found using the MLR models, with higher overall contributions from the East China Sea for each of the four model frameworks (Figure 3). As the confidence threshold increases (from 0.5 to 0.8), the MLR model requires greater certainty before assigning an individual to either the East China Sea or Sea of Japan, causing more individuals with intermediate predicted probabilities to go unassigned. This trade-off between assignment confidence and coverage explains the growing percentage of unassigned fish at higher thresholds.

Contribution estimates by nursery area varied according to both year and age-class of Pacific Bluefin Tuna collected in the eastern Pacific Ocean (Figure 2). For example, contribution estimates from the East China Sea ranged from a low of

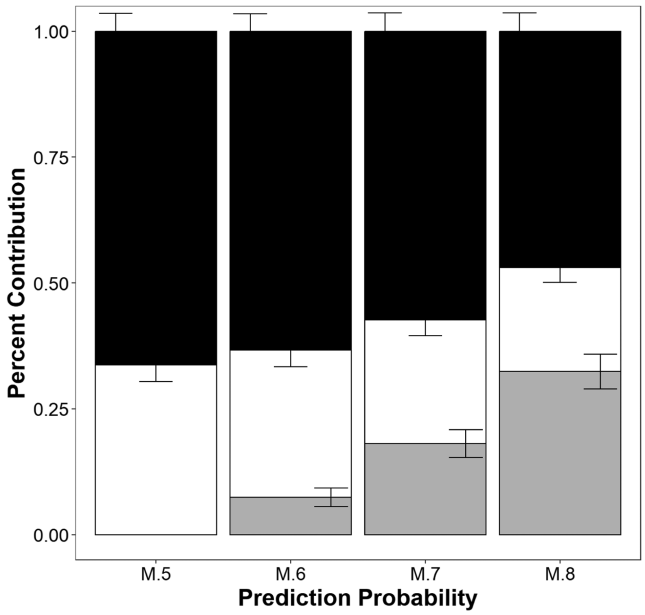

Figure 3 Percent contribution estimates (mean ± SD) of subadult and adult Pacific Bluefin Tuna collected in the eastern Pacific Ocean using multinomial logistic regression frameworks. Estimates from multinomial logistic regression are shown as M.5, M.6, M.7, and M.8 to represent the four different probability thresholds (0.5–0.8) from East China Sea (black), Sea of Japan (white), and undetermined sources (gray).

18.5% (SD = 23.8) for age-4 Pacific Bluefin Tuna collected in 2018 to a high of 91.2% (16.8) for age-6 Pacific Bluefin Tuna collected in 2017. Contribution estimates from the Sea of

Japan ranged from 8.8% (16.8) for age-6 Pacific Bluefin Tuna collected in 2017 to a high of 81.6% (23.8) for age-4 Pacific Bluefin Tuna collected in 2018. In 11 of the 13 age-class × year combinations, mixed-model results supported higher numbers of subadult and adult Pacific Bluefin Tuna in the eastern Pacific Ocean sourced from the East China Sea; however, in two instances, Pacific Bluefin Tuna in the eastern Pacific Ocean had higher probabilities of originating from the Sea of Japan (Figure 2). These included age-4 Pacific Bluefin Tuna from 2018 and age-5 Pacific Bluefin Tuna from 2019 (both from the 2014 cohort).

Discussion

Using otolith geochemistry from age-0 baseline samples collected over 4 years, we estimated the nursery-specific contributions of subadult and adult Pacific Bluefin Tuna (ages 4–7) collected in the eastern Pacific Ocean. Overall, the East China Sea contributed 61% of Pacific Bluefin Tuna to the eastern Pacific Ocean compared with 39% from the Sea of Japan; however, contributions varied by year and age-class, ranging from 18% to 91% for the East China Sea and from 9% to 82% for the Sea of Japan. Notably, age-4 Pacific Bluefin Tuna collected in 2018 and age-5 Pacific Bluefin Tuna collected in 2019, both from the 2014 year-class, showed higher contributions from the Sea of Japan (82% and 73%, respectively). These findings align with previous geochemical analyses of otolith (Rooker et al., 2021; Wells et al., 2020) and vertebrae (Uematsu et al., 2024) studies demonstrating that both nurseries contribute to eastern Pacific Ocean populations, with a larger fraction of the individuals analyzed in each study produced from the nursery in the East China Sea. Similar to these earlier assessments, our current study suggests that nursery-specific recruitment dynamics can shift substantially across cohorts. The high interannual variability in relative contribution estimates underscores that both the East China Sea and Sea of Japan play a significant role in Pacific Bluefin Tuna biomass to the eastern Pacific Ocean.

The higher overall contribution from the East China Sea nursery aligns with several lines of evidence suggesting that this is the more productive of the two spawning areas. The East China Sea is characterized by a longer spawning season (April–June versus July–August in the Sea of Japan), higher larval abundance, and greater spawning stock biomass (Ishihara et al., 2022; Itoh, 2009; Okochi et al., 2016). Additionally, Pacific Bluefin Tuna spawning in the East China Sea mature at larger sizes with higher batch fecundity compared with Pacific Bluefin Tuna spawning in the Sea of Japan (Okochi et al., 2016; Shiao et al., 2021), potentially contributing to higher overall recruitment from this nursery. Most Pacific Bluefin Tuna spawned in the East China Sea move north into the Pacific coast of Japan; however, some may enter the Sea of Japan and could have been classified as being spawned there (Watai et al., 2018). Geographic and oceanographic factors may also influence trans-Pacific migration rates from each nursery. Juvenile Pacific Bluefin Tuna migrating to the eastern Pacific Ocean are transported by the Kuroshio Current from the southern coast of Japan eastward across the Pacific (Fujioka, Fukuda, Furukawa, et al., 2018; Fujioka, Fukuda, Tei, et al., 2018; Madigan et al., 2017), a pathway more accessible to fish originating in the East China Sea. These seasonal movements progress fish eastward through their first year until they reach the Kuroshio–Oyashio transition zone, where exposure to cold waters is thought to trigger the onset of trans-Pacific migration (Fujioka, Fukuda, Furukawa, et al., 2018; Fujioka, Fukuda, Tei, et al., 2018). In contrast, the semi-enclosed geography of the Sea of Japan may promote higher residency, with a lower proportion of Sea of Japan–origin juveniles undertaking trans-Pacific migrations (Uematsu et al., 2024).

Our estimates of nursery-specific contributions are consistent with previous geochemical studies of Pacific Bluefin Tuna. Wells et al. (2020) examined age-1 juveniles in the CCLME and found East China Sea contributions ranging from 40% to 80% across 4 years, demonstrating substantial interannual variability similar to our findings for older age-classes. Studies of adult Pacific Bluefin Tuna in the western Pacific Ocean have generally reported higher East China Sea contributions: Rooker et al. (2021) found 66% East China Sea origin in Taiwan fisheries using otolith element : Ca ratios, while Shiao et al. (2021) estimated 84% East China Sea contribution using $\delta^{18}O$ analysis. Further, Uematsu et al. (2024) used vertebral annulus measurements to estimate 70–77% East China Sea origin for juvenile Pacific Bluefin Tuna (ages 1–2) in the eastern Pacific Ocean, and Ku et al. (2026) used otolith $\delta^{18}O$ and $\delta^{13}C$ analysis to estimate 91% East China Sea origin among CCLME fish. The consistency across studies using different geochemical approaches and examining different life stages suggests that the East China Sea may be the dominant source nursery for Pacific Bluefin Tuna in the eastern Pacific Ocean, though both nurseries make important contributions.

Significant contributions of Pacific Bluefin Tuna from the Sea of Japan existed from the 2014 year-class, demonstrating that recruitment to the eastern Pacific Ocean may be related to oceanographic conditions. Relatively normal ocean conditions existed in the North Pacific Ocean during most years of this study, with the exception of 2014, which is the same cohort of Pacific Bluefin Tuna estimated to originate from the Sea of Japan nursery area. A unique set of oceanographic events persisted in 2014 with the onset of El Niño conditions and a shift from the cool to warm phase of the Pacific Decadal Oscillation collectively associated with a marine heatwave known as the “Blob” (Bond et al., 2015; Chen et al., 2023). This set of conditions affected the distribution and abundance of marine organisms throughout the food web, including the catch of Pacific Bluefin Tuna in the eastern Pacific Ocean (Runcie et al., 2019). The Blob heatwave led to higher catches and a northward shift in Pacific Bluefin Tuna catch that may be a product of temperature preferences, prey distributions, or both (Runcie et al., 2019). Similarly, Ohshimo et al. (2017) found a northward shift in distribution of Pacific Bluefin Tuna larvae possibly caused by ocean warming from the 1990s to 2010s. Predictions of Pacific Bluefin Tuna distribution and nursery origin may be improved by incorporating ocean conditions and increased sample size for more confident prediction estimates.

The interannual variability in nursery-specific contributions likely reflects a complex interplay of biological

oceanographic processes. Polovina (1996) demonstrated that trans-Pacific migration propensity tracked decadal changes in prey abundance off Japan, with sardine-rich conditions promoting residency in the western Pacific Ocean, while Matsukawa (2006) proposed that migration represents an evolutionary response to population density approaching habitat carrying capacity. Muhling et al. (2018) further showed that sea surface temperatures near both nursery areas explained more interannual variance in Pacific Bluefin Tuna recruitment than spawning stock biomass and that environmental conditions in the two nurseries do not always covary. Collectively, these studies suggest that nursery-specific contributions to the eastern Pacific Ocean are likely shaped by dynamic and potentially independent variation in prey availability, habitat carrying capacity, and recruitment success across the two spawning areas. The elevated Sea of Japan contribution observed in the 2014 cohort likely reflects some combination of these factors, potentially compounded by the anomalous oceanographic conditions associated with the marine heatwave (Bond et al., 2015; Chen et al., 2023).

The combination of otolith element : Ca ratios and stable isotopes provided effective discrimination between the two nursery areas. Six of the eight measured tracers (Mg, Mn, Sr, Ba, $\delta^{13}C$, and $\delta^{18}O$) differed significantly between nurseries, though the magnitude and direction of these differences varied across years, resulting in significant nursery × year interactions. The interannual variability in otolith chemistry, also documented in previous studies (Rooker et al., 2001; Wells et al., 2020), likely reflects interannual changes in environmental or biological factors such as temperature, salinity, diet, physiology, and water chemistry at each nursery, as these factors influence otolith elemental incorporation (Campana, 1999). The consistently higher $\delta^{13}C$ values observed in Sea of Japan otolith cores may be attributed to elevated terrestrial carbon input in this semi-enclosed marginal sea, which increases dissolved inorganic carbon $\delta^{13}C$ in seawater (Michener & Schell, 1994). The interannual variability we observed underscores the importance of collecting baseline samples annually from both nurseries to accurately age-match and classify older individuals.

Both mixed-stock analytical approaches, HISEA and MLR, yielded comparable estimates of nursery-specific contributions, with overall East China Sea contributions of approximately 60% using both methods. As probability thresholds increased from 0.5 to 0.8 in the MLR framework, the proportion of individuals classified as undetermined increased from ~5% to ~30%, while the relative contributions from East China Sea versus Sea of Japan among classified individuals remained relatively consistent with HISEA estimates. The agreement between methods strengthens confidence in our nursery contribution estimates, while the presence of some individuals with low assignment probabilities may reflect baseline limitations, natural overlap in otolith chemistry between nurseries, or individual variation in otolith incorporation rates.

These findings add to the growing body of evidence from otolith chemistry, stable isotope analysis, and vertebral annulus studies demonstrating that both nursery areas contribute to Pacific Bluefin Tuna populations in the eastern Pacific Ocean, with the East China Sea generally dominant but with substantial interannual variability (Rooker et al., 2021; Shiao et al., 2021; Uematsu et al., 2024; Wells et al., 2020). The extension of nursery contribution estimates to older age-classes (ages 4–7) in the eastern Pacific Ocean provides additional support for current single-stock management approaches while highlighting the dynamic nature of trans-Pacific migration. The consistency of results across multiple geochemical tracers and analytical approaches strengthens confidence in these contribution estimates and highlights the value of otolith chemistry for resolving population connectivity in highly migratory species. As Pacific Bluefin Tuna populations continue to rebuild, continued monitoring of nursery-specific migratory patterns will contribute to effective management of this ecologically and economically important species.

Data availability

Data are available from the authors upon request.

Ethics statement

We followed ethical guidelines for animal treatment associated with collections.

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Conflicts of interest

None declared.

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