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Nursery origin and population connectivity of swordfish *Xiphias gladius* in the North Pacific Ocean

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Abstract

Element:Ca ratios in the otolith cores of young-of-the-year (YOY) swordfish, *Xiphias gladius*, were used as natural tracers to predict the nursery origin of subadult and adult swordfish from three foraging grounds in the North Pacific Ocean (NPO). First, the chemistry of otolith cores (proxy for nursery origin) was used to develop nursery-specific elemental signatures in YOY swordfish. Sagittal otoliths of YOY swordfish were collected from four regional nurseries in the NPO between 2000 and 2005: (1) Central Equatorial North Pacific Ocean (CENPO), (2) Central North Pacific Ocean (CNPO), (3) Eastern Equatorial North Pacific Ocean (EENPO) and (4) Western North Pacific Ocean (WNPO). Calcium (^{43}Ca), magnesium (^{24}Mg), strontium (^{88}Sr) and barium (^{138}Ba) were quantified in the otolith cores of YOY swordfish using laser ablation inductively coupled plasma mass spectrometry. Univariate tests indicated that three element:Ca ratios (Mg:Ca, Sr:Ca and Ba:Ca) were significantly different among nurseries. Overall classification success of YOY swordfish to their nursery of collection was 72% based on quadratic discriminant analysis. Next, element:Ca ratios in the otolith cores of subadults and adults collected from three foraging grounds where targeted fisheries exist (Hawaii, California and Mexico) were examined to calculate nursery-specific contribution estimates. Mixed-stock analysis indicated that the CENPO nursery contributed the majority of individuals to all three foraging grounds (Hawaii 45.6 ± 13.2%, California 84.6 ± 10.8% and Mexico 64.5 ± 15.9%). The results from this study highlight the importance of the CENPO nursery and provide researchers and fisheries managers with new information on the connectivity of the swordfish population in the NPO.

KEYWORDS
North Pacific Ocean, nursery, otolith chemistry, swordfish, trace elements

1 | INTRODUCTION

Swordfish, *Xiphias gladius*, is an epi- and mesopelagic species found throughout the world's oceans, ranging from 50°N to 50°S in tropical, subtropical and temperate waters (Abecassis *et al.*, 2012; Nakamura, 1985; Palko *et al.*, 1981). In the North Pacific Ocean (NPO), swordfish migrate between temperate waters for feeding and warmer waters to spawn, although the timing of these migrations differs among regions (Grall *et al*., 1983; Nakamura, 1985). Spawning season in the central and western NPO coincides with the boreal spring and summer months (March–July), taking place as late as November. Similarly, in the western South Pacific spawning takes place in the austral spring and summer (September–January). In equatorial waters, spawning takes place year-round. Spawning generally takes place in waters where surface temperatures are greater than 20°C (Palko *et al*., 1981), with larvae most frequently encountered at temperatures above 24°C (Nakamura, 1985; Nishikawa & Ueyanagi, 1974). Swordfish larvae are often associated with major currents, including the North Equatorial and Kuroshio currents in the NPO. These frontal zones or areas of convergence also play a major role in the distribution of juvenile and adult swordfish as sharp gradients of temperature and salinity are associated with areas of high primary and secondary productivity, enhanced prey abundance and higher catch rates (Holts & Sosa-Nishizaki, 1998; Seki *et al*., 2002).

Determining the stock structure of swordfish is challenging in the NPO due to their highly migratory nature (Dewar *et al*., 2011). While young-of-the-year (YOY) swordfish do not appear to migrate far during their first year (Gorbunova, 1969), adult swordfish are capable of substantial horizontal migrations, including movements from temperate coastal foraging grounds to tropical open ocean areas for spawning (Abecassis *et al*., 2012; Dewar *et al*., 2011; Evans *et al*., 2014). A range of tools, including genetics, length at age data, tagging and catch data, have been used to assess the stock structure of swordfish in the NPO, and proposed stock structure ranges from a single stock to a five-stock hypothesis (Hinton, 2003; Ichinokawa & Brodziak, 2008). Genetic studies yield conflicting results, with some studies indicating that there is little to no evidence of genetic differentiation in swordfish throughout the Pacific Ocean basin (Chow & Takeyama, 2000; Rosel & Block, 1996), while others found evidence supporting subdivisions in the population (Alvarado Bremer *et al*., 2006; Lu *et al*., 2016). Results from age and growth studies of swordfish in the Pacific Ocean appear to support a multistock hypothesis as differences in growth rates have been detected in swordfish sampled from Australia (Young & Drake, 2004), Chile (Cerna, 2009), Hawaii (DeMartini *et al*., 2007) and Taiwan (Sun *et al*., 2002). Additionally, tagging studies lend support to a multistock hypothesis as no trans-hemispheric or trans-oceanic migrations have been recorded in the Pacific Ocean, even though swordfish are capable of migrations of thousands of kilometres (Dewar *et al*., 2011; Sepulveda *et al*., 2020; Takahashi *et al*., 2003). Currently, NPO swordfish are managed internationally by the Western and Central Pacific Fisheries Commission and in the eastern Pacific by the Inter-American Tropical Tuna Commission althoughuncertainty remains regarding population structure within each jurisdiction.

While multiple methods have been employed to examine the population structure of swordfish in the Pacific Ocean, the use of otolith chemistry has been limited (Humphreys Jr *et al*., 2005). Otolith chemistry has provided key insights on the population structure, mixing and movement of several pelagic fishes (Rooker *et al*., 2008; Wells *et al*., 2010; Wells *et al*., 2015). In addition, application of otolith chemistry has been used to discriminate fish from nursery areas (Gillanders & Kingsford, 2000; Rooker *et al*., 2003; Thorrold *et al*., 1998) and to classify adults of unknown origin using established nursery baseline signatures (Rooker *et al*., 2016; Schloesser *et al*., 2010; Wells *et al*., 2012). A previous study (Humphreys Jr *et al*., 2005) found significant differences in otolith trace element concentrations of YOY swordfish sampled from several nurseries in the central Pacific Ocean, indicating that otolith chemistry may be a useful tool to investigate the connectivity of swordfish between nursery and foraging grounds in the NPO.

The aim of the present study was to use otolith chemistry to determine the nursery origin and population connectivity of swordfish in the NPO. First, otolith core chemistry of YOY swordfish sampled from putative nurseries in the NPO was analysed to determine if individuals from regional nurseries could be discriminated and to establish baseline nursery signatures. Next, subadult and adult swordfish were collected from three fishing regions in the NPO (Hawaii, California and Mexico) and the otolith core chemistry of these individuals was compared to YOY baseline signatures. Lastly, nursery-specific contribution estimates of subadults and adults from the three fishing regions were estimated using mixed-stock analysis.

2 | MATERIALS AND METHODS

2.1 | Sample collections

YOY swordfish were opportunistically collected during commercial fishing trips and through fishery independent sampling operations in the NPO over a 5 year period (2000–2005). Four regional nurseries were sampled: Central Equatorial NPO (CENPO; between 0–7°N and 159–168°W), Central NPO (CNPO; between 18–33°N and 154–168°W), Eastern Equatorial NPO (EENPO; between 0–5°N and 84–96°W) and Western NPO (WNPO; between 27–40°N and 143–164°E) (Figure 1). In total, 109 YOY swordfish were sampled (Table 1). Swordfish <100 cm eye-to-fork-length (EFL) were classified as YOY and swordfish >100 cm EFL were classified as subadult or adult based on previous age and growth studies of swordfish in the central NPO (DeMartini *et al*., 2007). It has been hypothesized that YOY swordfish do not migrate far from their spawning grounds during the first year of life (Gorbunova, 1969), thus we assumed that swordfish <100 cm EFL captured in the four regions corresponded to their respective spawning ground. On collection, swordfish heads were removed, frozen and transported to the National Oceanic and Atmospheric Administration (NOAA) Pacific Islands Fisheries Science Center for otolith extraction and processing.

Sagittal otoliths of subadult and adult swordfish (>100 cm EFL, hereafter collectively referred to as adult) were opportunistically collected by NOAA fishery observers on commercial vessels during longline and gill net operations from 2012 to 2015. Three regions were targeted for sampling where established fisheries exist: CNPO and Hawaiian Islands (HI; between 17–32°N and 144–168°W), offshore California (CA; between 31–40°N and 117–126°W) and offshore Baja California, Mexico (MX; between 23–27°N and 111–115°W)

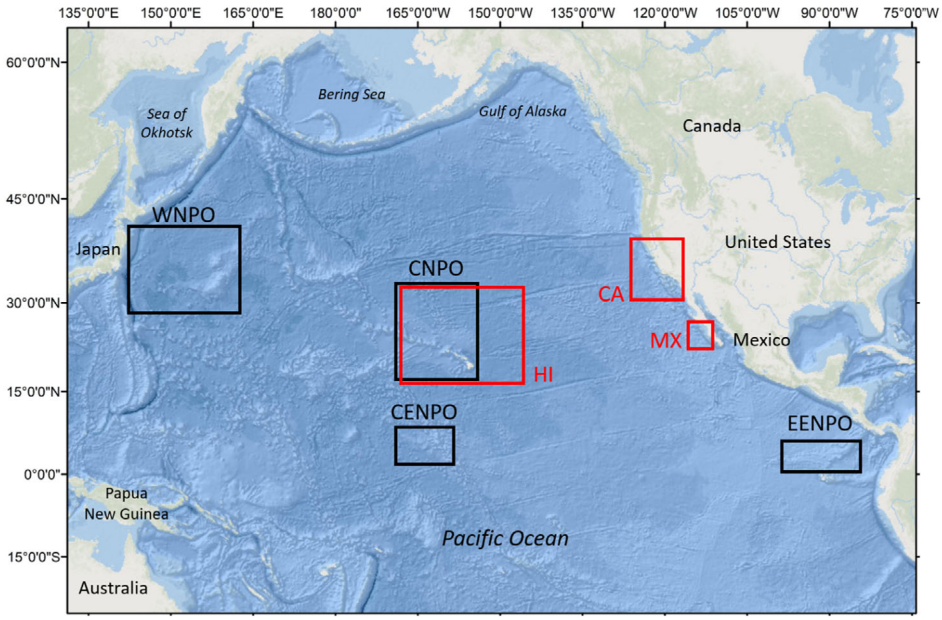

FIGURE 1 Map of the study regions located in the NPO where YOY and adult swordfish were collected. Regional nurseries are indicated by boxes outlined in black and adult fishing regions are indicated by boxes outlined in red

TABLE 1 Regional nursery locations, sample size and year of sample collections for YOY swordfish

Nursery	Acronym	*n*	Latitude	Longitude	Sampling year
Central Equatorial North Pacific Ocean	CENPO	28	0–7°N	159–168°W	2001, 2002
Central North Pacific Ocean	CNPO	45	18–33°N	154–168°W	2000, 2002, 2004, 2005
Eastern Equatorial North Pacific Ocean	EENPO	16	0–5°N	84–96°W	2005
Western North Pacific Ocean	WNPO	20	27–40°N	143–164°E	2004
	Total	109			

TABLE 2 Adult fishing region locations, sample size and year of collection for adult swordfish

Region	Acronym	*n* (all)	*n* (baseline)	Latitude	Longitude	Sampling year
CNPO and Hawaiian Islands	HI	22	3	17–32°N	144–168°W	2014, 2015
Offshore California, United States	CA	22	12	31–40°N	117–126°W	2012, 2013, 2014
Offshore Baja California, Mexico	MX	21	19	23–27°N	111–115°W	2013
	Total	65	34			

Note. Sample sizes (*n*) include all adult samples and adult samples that matched the YOY baseline.

(Figure 1 and Table 2). Whole heads of adults were collected, stored frozen and transported to a regional laboratory for extraction. EFL was used to approximate an age for each individual (DeMartini *et al*., 2007) and otoliths were selected for core chemistry analysis based on the individual's approximate age to establish a sample of individuals with birth years that matched up with the YOY baseline; 52% of the adult swordfish in our sample matched the 2000 to 2005 baseline (Table 2).

2.2 | Otolith preparation

To prepare otoliths for elemental analysis, otoliths were stripped of remaining tissues, cleansed in ultrapure (Super-Q) water and air dried under a Class 100 laminar flow hood for at least 24 h. Due to the pronounced curvature, minute size and delicate nature of swordfish sagittal otoliths, otoliths were not cleansed with hydrogen peroxide or nitric acid to prevent breakage and to save material for analysis. Otoliths were embedded in Crystalbond™509 sulcal side down and mounted on 9 × 9 mm quartz glass pieces. The otolith core was exposed by hand-polishing the sagittal plane against MARK V Laboratory 30 M, 9 M and 3 M lapping films.

2.3 | Trace element analysis: YOY swordfish

Trace elements in otolith cores were quantified using laser ablation–inductively coupled plasma mass spectrometry (LA-ICP-MS) at the Keck Collaboratory for Plasma Spectrometry at Oregon State University (OSU) and analysed using a PQ Excell LA-ICP-MS. Prior to analysis, embedded otoliths were transferred to a clean room where they were cleansed and sonicated for 10 min in ultrapure water to avoid trace element contamination. Six individual 9 × 9 mm glass-mounted YOY otoliths were attached to an acid-washed quartz slide (25 × 50 mm) using double-sided tape. Nine elements of interest were analysed: calcium (^{43}Ca), magnesium (^{24}Mg), aluminium (^{27}Al), silicon (^{29}Si), manganese (^{55}Mn), zinc (^{66}Zn), strontium (^{86}Sr, ^{88}Sr), barium (^{138}Ba) and lead (^{208}Pb). National Institute of Standards and Technology (NIST) glass 610 and 612 were used as the standard and analysed after every six otolith samples to maintain instrument precision. Estimates of instrument analytical precision, as percentage relative standard deviation (%RSD) for NIST610 (n = 60) were ^{24}Mg = 5.84 ± 0.84%, ^{27}Al = 3.61 ± 1.44%, ^{29}Si = 3.96 ± 1.44%, ^{43}Ca = 5.56 ± 0.97%, ^{55}Mn = 4.66 ± 1.21%, ^{66}Zn = 7.75 ± 0.69%, ^{88}Sr = 4.07 ± 1.45%, ^{138}Ba = 4.31 ± 1.38% and ^{208}Pb = 6.36 ± 0.86%. Relative standard deviations for NIST612 (n = 48) were ^{24}Mg = 14.25 ± 3.9%, ^{27}Al = 3.85 ± 0.21%, ^{29}Si = 4.14 ± 0.26%, ^{43}Ca = 6.21 ± 0.8%, ^{55}Mn = 10 ± 2.19%, ^{66}Zn = 22.72 ± 4.04%, ^{88}Sr = 6.94 ± 1.1%, ^{138}Ba = 10.41 ± 1.92% and ^{208}Pb = 13.6 ± 3.23%. NIST 610 and 612 were also used to create calibration curves for each element of interest. Four elements (^{24}Mg, ^{88}Sr, ^{138}Ba and ^{43}Ca) were detectable and used for further analysis. Calcium was used as an internal standard and assumed to be evenly distributed across the otolith at a concentration of 38% (Rooker *et al.*, 2001a), thus calcium was used to correct variations in ablation yield and counting efficiencies (Baumann *et al.*, 2015). Elemental concentrations were transformed into element:Ca molar ratios based on the molar mass of each element and calcium (see Baumann *et al.*, 2015).

Two 250 μm transects were ablated from each otolith with a laser spot size of 50 μm using laser energy, repeat rates and ablation speeds of 50%, 8 Hz and 3 μm/s, respectively. Transects originated from the primordium, or core, and progressed outwards towards the dorsal outer edge (Figure 2). Transects were ablated with at least 45° of angular separation. Element concentrations were measured and reported at approximately 1–2 μm intervals throughout the duration of each 250 μm transect. The element concentrations from each transect were then averaged to provide a single element concentration value (for each element, for each individual otolith core). Element concentrations were then transformed into element:Ca ratios using the same methodology as used for the standards.

Estimates of the age range covered by the ablations were made to assess the number of days during the early life stage being analysed. Daily growth increments within 250 μm of the core were counted for five specimens to determine an approximate age. It was estimated that the 250 μm transect represented the first 56 days of life ±4 days (mean ± S.D.).

2.4 | Trace element analysis: adult swordfish

Adult otoliths were processed using a Thermo Scientific XSeries II LA-ICP-MS at Texas A&M University at Galveston (TAMUG). Methods for analysing adult otoliths followed the protocols described for the YOY otoliths with the following exceptions. Due to morphological differences between the YOY and adult swordfish otoliths, adult otoliths could not withstand the sonicating cleansing process. Instead, adult otoliths were gently scrubbed with brushes and soaked in ultrapure water to remove tissues and contaminants. Pre-ablation transects and standards with a laser spot size of 80 μm were performed using laser energy, repeat rates and ablation speeds of 30%, 10 Hz and 10 μm/s, respectively. Repeat rates were adjusted from 8 to 10 Hz when analysing the adult samples as the software would not allow for a lower setting. The four elements that were detectable in the otoliths of YOY swordfish (^{24}Mg, ^{88}Sr, ^{138}Ba and ^{43}Ca) were used for analysis. NIST glass 614 was used as the standard and analysed after every two otolith samples. Estimates of instrument analytical precision, as %RSD for NIST614, were ^{24}Mg 11.89 ± 1.21%, ^{44}Ca 11.59 ± 1.06%, ^{88}Sr 11.64 ± 1.288% and ^{138}Ba 24.2 ± 1.58%.

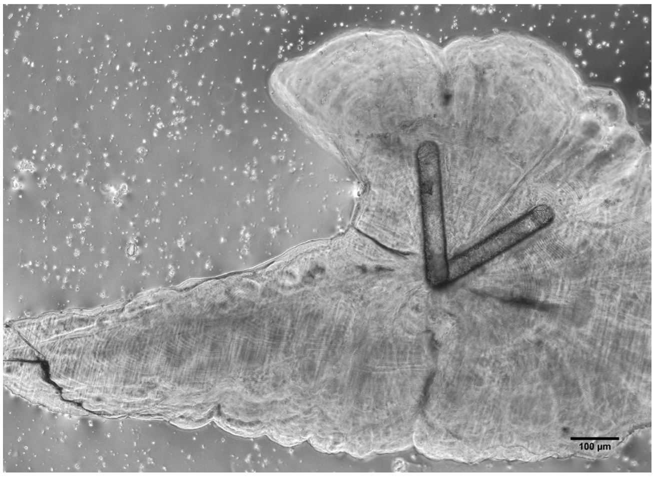

FIGURE 2 Swordfish sagittal otolith ground on the sagittal plane with two transects, originating from the core, radiating distally across the dorsal side of the otolith

To determine whether the elemental fingerprints obtained at the two facilities were comparable, a subsample (n = 6) of YOY otoliths processed at the Keck Collaboratory were also run at the TAMUG facility. Additionally, as elemental incorporation between the left and right sagittal otoliths has been shown to be symmetrical in another highly migratory pelagic species (Rooker *et al.*, 2001b), sagittal pairs from adult swordfish (n = 10) were analysed to compare decontamination procedures. Of these pairs, one otolith was decontaminated using the sonicating method used for the YOY otoliths while the other otolith was decontaminated using the pre-ablation method used for the adult otoliths.

2.5 | Statistical analysis

Paired (dependent) t-tests were used to compare element:Ca ratios for samples processed at the two facilities as well as decontamination methods (sonicating *vs.* pre-ablation). Mg:Ca, Sr:Ca and Ba:Ca ratios were not significantly different for transects of otoliths analysed at both the Keck Collaboratory and the TAMUG laboratories (*t*-test with Bonferroni correction, $P > 0.025$), indicating that measurements were comparable between LA-ICP-MS machines and facilities. Comparisons of decontamination methods (sonicating *versus* pre-ablation) indicated that both Mg:Ca and Ba:Ca ratios were similar between methods (*t*-test with Bonferroni correction, $P > 0.025$); however, significant differences were detected when comparing mean Sr:Ca ratios (*t*-test with Bonferroni correction, $P < 0.025$). Mean Sr:Ca ratios were significantly higher (248 ± 65 μmol:mol) when otolith surfaces were decontaminated by pre-ablating transects, as opposed to sonicating. Differences in Sr:Ca ratios were not always consistent and ranged from +10% to +27% among otolith pairs. Given that a number of factors could affect Sr:Ca ratios, such as morphological differences between otolith pairs or the angle of otolith planar section, and that differences were not consistent, Sr:Ca ratios of adult otoliths decontaminated by pre-ablation were not transformed. Significance was determined at the α-level of 0.05 for all tests, with the exception of the paired *t*-tests, where a Bonferroni adjustment (α/# of comparisons) was used to control for type I error. Statistical analyses were performed using the R Project for Statistical Computing (version 3.2.3) and SYSTAT version 13 (SYSTAT software).

Nursery-specific differences in otolith core element:Ca ratios (Mg:Ca, Sr:Ca, Ba:Ca) were tested using a multivariate analysis of variance (MANOVA) model with nursery as a fixed factor. Wilks' lambda test statistic was used to test for significance as it is the most robust to deviations from assumption of homogeneity of variance and covariance (Ates *et al*., 2019). Univariate tests for each of the three element:Ca ratios were performed using analysis of variance (ANOVA). *Post hoc* differences were examined with Tukey's honestly significant difference (HSD) test. Quadratic discriminant analysis (QDA) was then used to evaluate the classification accuracy of individual YOY swordfish to nursery of collection based on jackknife reclassification. Given that element:Ca ratios in the otoliths of YOY swordfish were based on different sampling years from 2000 to 2005 among the four regional nurseries, we tested for temporal differences in otolith core element:Ca ratios within two nurseries that included multiple collections years: CENPO (2001, 2002) and the CNPO (2000, 2002, 2004, 2005). Although interannual variation in the otolith chemistry has been reported previously for pelagic fishes, significant variation in the year classes of YOY swordfish was only detected for Sr:Ca ratios in otoliths from the CENPO between 2001 and 2002 (ANOVA, $P < 0.05$), with a lower mean Sr:Ca ratio in otoliths collected from 2001 relative to 2002 (Supporting Information Table S1). Interannual variability for individual element:Ca ratios was not significant otherwise and was not detected for overall element:Ca ratios. Due to sampling constraints for YOY swordfish from each region, our analysis is based on the assumption that year-to-year variation from 2000 to 2005 was negligible.

Nursery contribution estimates of NPO swordfish recruits to the fishing regions of HI, CA and MX were obtained using the maximum likelihood mixed-stock analysis program HISEA (Millar, 1987). Baseline data used for mixed-stock analysis consisted of Mg:Ca, Sr:Ca and Ba:Ca ratios from otolith cores of YOY swordfish originating from the four regional nurseries, and the same element:Ca ratios in the otolith cores of adult swordfish from the three fishing regions were used to estimate their origin using HISEA in bootstrap mode with 1000 simulations. Nursery-specific contribution estimates were calculated two separate ways for each of the three adult fishing regions. The first analysis included the element:Ca ratios from otolith cores of all adult otoliths analysed and the second analysis included only the element:Ca ratios obtained from the otolith cores of adult fish that could have originated from the nurseries during the period of baseline sampling YOY (2000–2005) (Table 2).

2.6 | Ethical statement

The collection and use of experimental animals in this study complied with U.S. animal welfare laws, guidelines and policies, and was approved by the Institutional Animal Care and Use Committee of Texas A&M University.

3 | RESULTS

Trace element signatures in otolith cores of YOY swordfish varied significantly among nurseries (MANOVA d.f. = 3, $F = 15.41$, $P < 0.05$; Supporting Information Table S2). Each of the three individual element:Ca ratios differed significantly among nurseries (ANOVA Mg:Ca $F = 14.18$, $P < 0.05$; Sr:Ca $F = 24.77$, $P < 0.05$; Ba:Ca $F = 6.41$, $P < 0.05$). Otoliths from nurseries in the central Pacific Ocean (CNPO, CENPO) had higher mean Mg:Ca and Sr:Ca ratios than samples from the eastern and western Pacific Ocean nurseries (EENPO, WNPO). Mg:Ca ratios were significantly higher in otoliths collected from the CNPO compared to the CENPO, with samples from both nurseries being significantly higher than those from the EENPO and WNPO (Tukey's HSD test, $P < 0.05$; Figure 3). Sr:Ca ratios were significantly higher in otoliths from the CENPO when compared to all other nurseries (Tukey's HSD test, $P < 0.05$; Figure 3). Lastly, Ba:Ca ratios in otoliths were significantly higher in the CNPO and WNPO than in samples from the CENPO and EENPO (Tukey's HSD test, $P < 0.05$; Figure 3).

Results of discriminant analysis based on element:Ca ratios of otolith cores had a 72.2% overall classification success rate for regional swordfish nurseries in the NPO. Individual YOY swordfish collected from the CENPO had the highest classification success (89.3%), followed by the CNPO (79.6%), and the EENPO and WNPO (each 50.0%).

Element:Ca ratios of otolith cores from the adults sampled among three fishing regions were also examined. Otolith core Mg:Ca ratios of otoliths collected from the three fishing regions were similar (Hawaii 41.96 ± 1.7 μmol:mol, California: 43.57 ± 2.44 μmol:mol, Mexico: 45.04 ± 2.03 μmol:mol) and were well within Mg:Ca ratio ranges of YOY baseline samples from the CENPO (mean 61.63, range 35.7–-111.9 μmol:mol), EENPO (mean 48.14, range 27.6–71.3 μmol:mol) and WNPO (mean 44.97, range 30.4–62.9 μmol:mol), but were lower than the CNPO (mean 73.08, range 48.9–151.3 μmol:mol). Adult swordfish collected off California and Mexico had similar otolith

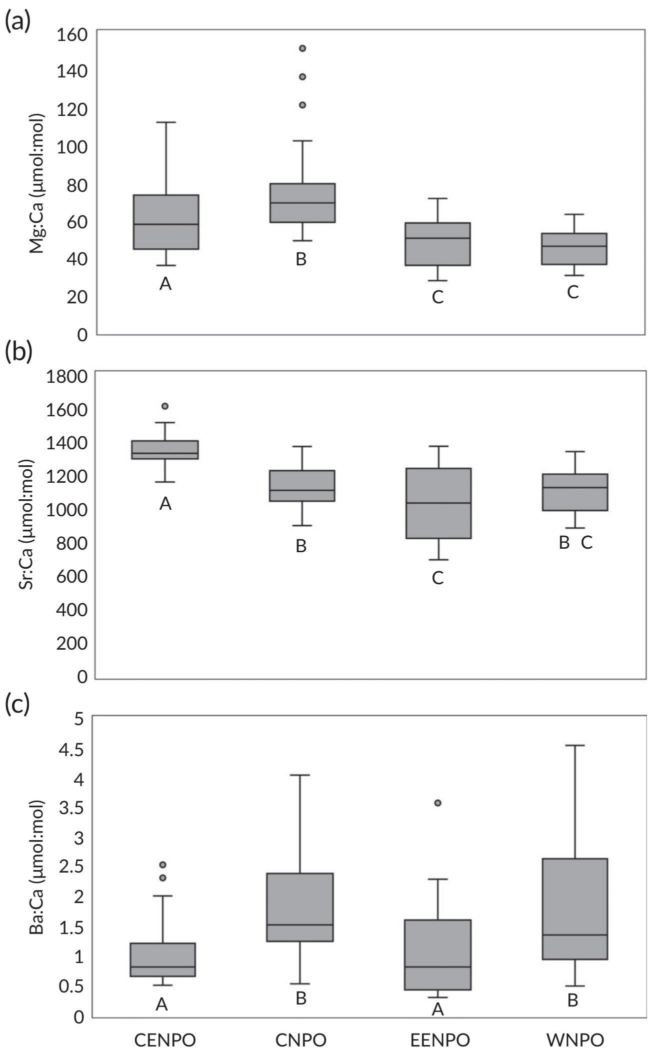

FIGURE 3 Box plots of element:Ca ratios measured at the otolith core for YOY swordfish sampled from the CENPO, CNPO, EENPO and WNPO nurseries. Boxes represent 25th and 75th percentiles, bars 5th and 95th percentiles, the line is the median and outliers are represented with dots. Significant differences in element:Ca ratios are denoted by different letters (Tukey's HSD $P > 0.05$)

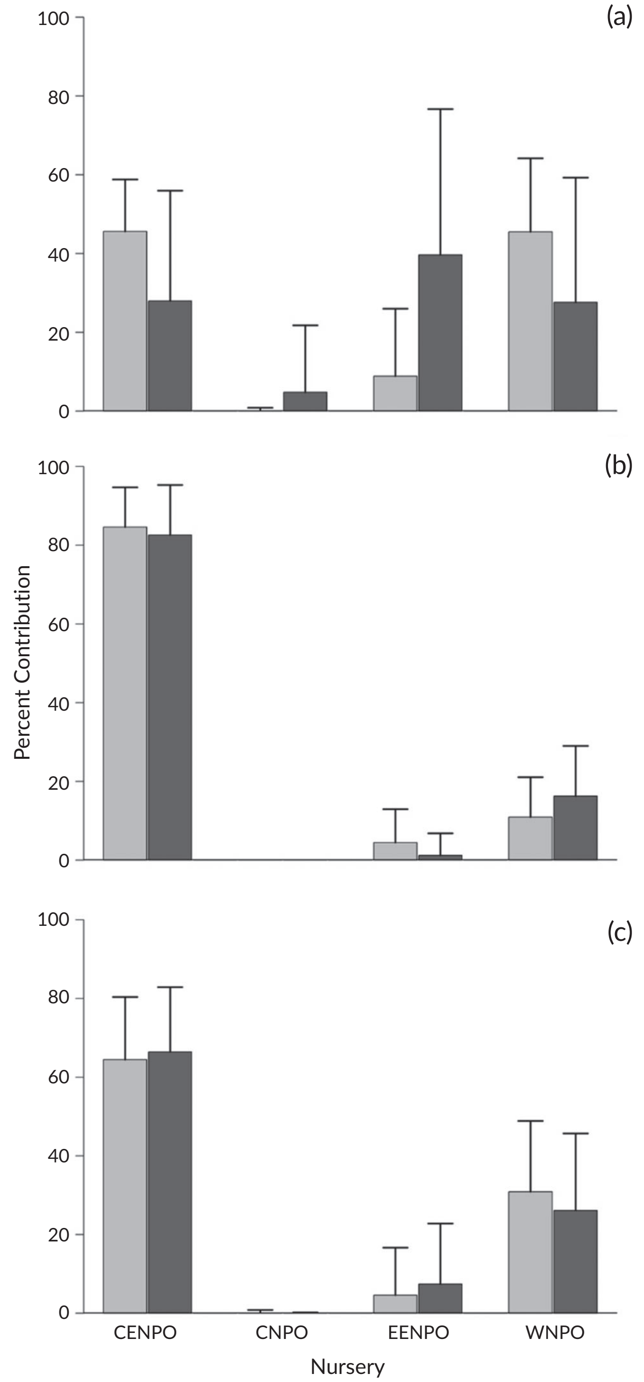

FIGURE 4 Nursery contribution estimates (± S.D.) to the (a) HI, (b) CA and (c) MX fishing regions. (□) all samples; (■) samples with matching baselines. 'All samples' represents contribution estimates based on all adult samples collected and 'Samples with matching baseline' represents the contribution from adult samples that originated from the nurseries during the 2000–2005 YOY sampling period

core Sr:Ca ratios (1339.9 ± 31.06 and 1338.1 ± 41.17 μmol:mol, respectively) while individuals from Hawaii were lower (1253.7 ± 29.87 μmol:mol); however, otolith core Sr:Ca ratios were above observed ratios of YOY swordfish from the CNPO (1117.07 μmol:mol), EENPO (1019.95 μmol:mol) and WNPO (1089.28 μmol:mol) nurseries. The highest otolith core Ba:Ca ratios were observed for adult swordfish from Mexico (1.73 ± 0.22 μmol:mol) followed by Hawaii and California (1.38 ± 0.18 μmol:mol and 1.13 ± 0.13 μmol:mol, respectively). Otolith core Ba:Ca ratios measured in adult swordfish from Mexico were most similar to YOY swordfish from the CNPO and WNPO (1.79 and 1.77 μmol:mol) while those collected off California were most similar to YOY swordfish from the CENPO and EENPO (1.00 and 1.11 μmol:mol, respectively), and mean ratios measured in adults from Hawaii were not closely matched to any nursery.

The results of mixed stock analysis support the finding that the CENPO contributes swordfish recruits to all three fishing regions investigated (Figure 4). As sample sizes were small for mixed stock analysis, including only age class matched samples, results from all sample collections are used for discussion. Local production appears to be negligible in the HI fishing region (CNPO 0.05 ± 0.80%), with the majority of recruits originating from both the CENPO (45.59 ± 13.21%) and the WNPO (45.51 ± 18.64%). Mixed stock analysis results for the CA and MX fishing regions were less variable and more consistent than those of the HI fishing region (Figure 4). Adult swordfish caught in the CA fishing region are mainly derived from CENPO recruits (84.6 ± 10.05%), followed by small contributions from the WNPO (10.93 ± 10.11%). Similarly, adult swordfish caught in the MX fishing region were largely recruits from the CENPO (64.46 ± 15.93%), followed by the WNPO (30.87 ± 18.00%).

4 | DISCUSSION

Use of otolith chemistry provided the first insights into the connectivity between spawning and foraging grounds for swordfish in the NPO. Analysis of trace elements within the otolith cores of YOY swordfish revealed four distinguishable nursery signatures in the NPO. These signatures were then used to calculate nursery-specific contribution estimates to three adult fishing regions. In this study, otolith Mg:Ca, Sr:Ca and Ba:Ca ratios of YOY swordfish varied significantly among nurseries. Specifically, otolith Mg:Ca and Sr:Ca ratios were highest for YOY swordfish sampled from nurseries located in the central NPO (CENPO and CNPO), while otolith Ba:Ca ratios were highest for individuals collected from northern nurseries (CNPO and WNPO). Overall trace element signatures sufficiently differed among nurseries with overall classification success of 72.2%, with Sr:Ca ratios primarily driving discrimination followed by Mg:Ca and Ba:Ca, respectively. Using nursery element:Ca ratios as a baseline, nursery-specific contribution estimates support the CENPO nursery as the main contributor to the adult fishing regions of HI, CA and MX.

Trends in otolith Sr:Ca, Mg:Ca and Ba:Ca for YOY swordfish from the four nurseries are likely linked to sea surface salinity (SSS) and sea surface temperature (SST). Studies have indicated that salinity and temperature generally have a positive relationship with otolith Sr concentrations (Elsdon *et al*., 2008; Kalish, 1989; Secor & Rooker, 2000), while studies investigating the effects of temperature and salinity on Mg concentrations in otoliths have had conflicting results (Elsdon *et al*., 2008; Fowler *et al*., 1995; Martin & Wuenschel, 2006). Both otolith Mg:Ca and Sr:Ca ratios of YOY swordfish appear to exhibit a positive relationship with a combination of high SSS and SST as values for both ratios were highest in the central NPO (CENPO and CNPO), nurseries characterized by moderate to high SSS and SST (Supporting Information Table S3). Otolith Mg:Ca and Sr:Ca ratios of YOY swordfish were lower in the WNPO (characterized by low SSS and SST) and the EENPO (characterized by high SST but low SSS) nurseries (Supporting Information Table S3). Temperature has been shown to affect otolith Ba concentrations (Elsdon & Gillanders, 2002, 2004; Fowler *et al*., 1995; Miller, 2009, 2011) and in this study otolith Ba:Ca ratios were highest in the CNPO and WNPO, which are generally characterized by lower SST than the CENPO and EENPO (Supporting Information Table S3). A previous otolith chemistry study of YOY swordfish demonstrated similar trends, with swordfish sampled from the CNPO having higher otolith Ba and lower otolith Sr concentrations than individuals from the CENPO (Humphreys Jr *et al*., 2005). Aside from SSS and SST, factors such as pH, dissolved oxygen concentration and the availability of trace elements in the water column influence otolith elemental composition (Campana, 1999; Sturrock *et al*., 2012). Additionally, regional variability due to riverine discharge, precipitation and evaporation, upwelling, volcanic activity and biological activity can further influence otolith chemistry (Campana, 1999). Despite uncertainty as to how the ambient environment may specifically affect otolith chemistry, trace elements within the otolith cores of YOY swordfish show promise as a natural marker for retrospectively examining an individual's environmental history.

Interannual variability was not significant for the overall element signature or for Mg:Ca and Ba:Ca in the CENPO during the years of collection (2001, 2002), but there was interannual variability in Sr:Ca between 2001 and 2002. This may be a result of variability in climactic and oceanographic conditions resulting from the El Nino Southern Oscillation (ENSO), which affects sea surface temperatures, sea surface salinity and precipitation in the equatorial Pacific. A moderate El Nino warming period occurred between May of 2002 and March of 2003 (Climate Prediction Center, 2015). Typically, sea surface temperatures, salinity and evaporation rates increase over the central equatorial Pacific during an ENSO warm phase. As discussed, otolith Sr:Ca concentrations tend to have a positive relationship with sea surface temperature and salinity, thus mean concentrations may differ between years affected by ENSO. In this study, the CENPO experienced an ENSO El Nino warm period in 2002 and mean otolith Sr:Ca concentrations in 2002 were in fact higher than those from 2001. Despite interannual variability observed in Sr:Ca ratios in the CENPO, the mean Sr:Ca ratio from the CENPO from both 2001 and 2002 was at least 150 μmol:mol greater than the mean Sr:Ca ratios from the CNPO, EENPO and WNPO.

Mixed stock analysis predicted the CENPO and WNPO nurseries were the primary sources for adults sampled from the three fishing regions investigated. In the Hawaii fishing region specifically, estimates of nursery origin suggest that adult swordfish samples were equally from the CENPO and WNPO, with negligible inputs from the CNPO and EENPO nurseries. These results are particularly interesting as much of the Hawaii fishing region is located within the CNPO. Some corroboration of this result comes from a study which detected genetic differences between swordfish larvae sampled off the Kona coast of Hawaii Island and swordfish adults collected from two locations in the HI fishing grounds within the CNPO (Lu *et al*., 2016). Plankton net captures of swordfish larvae are predominantly concentrated along the Kona coast from May to July (Hyde *et al*., 2005). As they become juveniles, these HI swordfish extend their range along the Hawaiian Archipelago and into offshore waters where they overlap with the CNPO swordfish grounds. However, YOY swordfish are predominantly captured on deep longline sets that target bigeye tuna, but infrequently captured in the shallow set longline fishery that targets adults farther to the north (Sculley *et al*., 2018) where the contribution of the CNPO was very low. Additional research is needed to determine the recruitment corridor between foraging and spawning grounds for swordfish spawning in the CNPO.

As mentioned, the primary contributors to the California and Mexico fishing regions were also the CENPO and WNPO rather than spawning regions that are in closer proximity to these fisheries, the CNPO and EENPO. This finding appears to be supported by the genetic study of Lu *et al*. (2016) which found adult swordfish sampled from temperate waters off the west coast of California and Mexico differentiated from swordfish sampled from the EENPO. Furthermore, a separate study detected genetic differences between swordfish sampled from Hawaii and Mexico (Sosa-Nishizaki *et al*., 1996), also providing support for our findings that the CNPO provides limited recruits to the fishery in Mexico.

One question that remains is whether swordfish return to their natal spawning grounds. While this question cannot be addressed with the data collected here, electronic tagging studies provide some insight into the potential for fidelity and movements between fishing and spawning grounds. Two studies (Dewar *et al*., 2011; Sepulveda *et al*., 2020) demonstrated a connection between the foraging grounds and nursery grounds examined in this study, although tracks tend to be limited in duration and do not indicate spawning behaviour. In the largest study, Sepulveda *et al*. (2020) also reported that some swordfish returned to the same foraging grounds in subsequent years, exhibiting site fidelity. In addition, a comparison of deployments north and south of Point Conception, California revealed that the majority of fish tagged to the south moved into the waters off Mexico whereas most of the fish tagged north of Point Conception remained in the regions including the CNPO and CENPO. These findings reveal differences in movements away from foraging grounds even across small spatial scales in the California Current as reported between California and Mexico.

One of the most important findings of this study is that it highlights the importance of the central equatorial swordfish nursery as a potential source of swordfish recruits to the three fishing regions investigated. The CENPO has been referred to as a zone of high swordfish abundance (Hinton & Deriso, 1998; Su *et al*., 2020) and the observation that swordfish reproduction occurs year-round in the equatorial Pacific Ocean (Nishikawa *et al*., 1985; Palko *et al*., 1981) indicates that the CENPO nursery has the potential to be a large contributor of swordfish recruits to the NPO. This is of particular interest for future stock assessments and management as the Hawaiian fishery provides some 38% of the domestic catch of swordfish (Ito & Childers, 2014).

Caution must be used in the interpretation of the mixed stock analysis results as the small sample sizes (<25) of adult swordfish otoliths from the three fishing regions investigated were used as representatives for large adult groups. Additionally, adult samples included individuals whose estimated ages indicated that they likely did not originate from the baseline during the 2000–2005 sample period, particularly for the adult swordfish sampled from the HI fishing regions. Despite these limitations, multiple analyses using adults assessed to have originated from the baseline years, as well as adults that did not originate from the baseline, produced similar results.

Despite the limitations, the results presented here provide a proof of concept for the use of otolith chemistry to determine the nursery origin of subadult and adult swordfish in the North Pacific. Additional research sampling more larvae and spawning fish, as well as characterizing the outer margin of the otolith over time would be valuable next steps. Patterns over time in both the otolith core and outer margin will provide important information on the stability of recruitment patterns and site fidelity between spawning and foraging grounds. Understanding temporal and spatial patterns in recruitment is an important step towards understanding variability in abundance on the foraging grounds where targeted fisheries are focused.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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