

NURSERY ORIGIN AND CONNECTIVITY OF SWORDFISH (*XIPHIAS GLADIUS*)

IN THE NORTH PACIFIC OCEAN

A Thesis

by

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ABSTRACT

Trace elements in otolith cores of young-of-the-year (YOY) swordfish, *Xiphias gladius*, were used as natural tracers to predict the nursery origin of sub-adult and adult swordfish sampled from three foraging grounds in the North Pacific Ocean (NPO). First, otolith core chemistry (proxy for nursery origin) was used to evaluate nursery-specific elemental signatures in YOY swordfish. Sagittal otoliths from YOY swordfish were collected from 2000 to 2005 among four regional nurseries in the NPO including Central Equatorial North Pacific Ocean (CENPO), Central North Pacific Ocean (CNPO), Eastern Equatorial North Pacific Ocean (EENPO), and Western North Pacific Ocean (WNPO). Otolith core trace element concentrations of calcium (^{43}Ca), magnesium (^{24}Mg), strontium (^{88}Sr), and barium (^{138}Ba) were measured and quantified using laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS). Univariate tests indicated that three element:Ca molar ratios (Mg:Ca, Sr:Ca, and Ba:Ca) were detectable and significantly different among nurseries. Sr:Ca ratios were higher in individuals collected from the CENPO while Mg:Ca ratios were higher in individuals from the CNPO. Overall nursery classification success from quadratic discriminant analysis of YOY swordfish to their nursery of collection was 72%. Next, otolith core chemistry of sub-adults and adults collected from three foraging grounds where targeted fisheries exist (Hawaii, California, and Mexico) was 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 $45.6 \pm$

13.2%; California $84.6 \pm 10.8\%$; Mexico $64.5 \pm 15.9\%$). Results from this study highlight the importance of the CENPO nursery to the NPO and provides researchers and fisheries managers new information on connectivity of the Pacific swordfish population in the NPO.

DEDICATION

I dedicate this thesis to my family. First, to my parents who have always encouraged me and who have taught me the value of hard work. I also dedicate this thesis to Grant Quesnell, my husband, who has provided invaluable support, love, and patience throughout this process. Lastly, this thesis is also dedicated to Abigail Marie, my amazing daughter, who has filled our lives with laughter and love.

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The raw LA-ICP-MS data for the young-of -the-year swordfish otolith cores analyzed was provided by Robert Humphreys of the Pacific Islands Fisheries Science Center (PIFSC).

All other work and analysis conducted for the thesis was completed by the student independently.

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1. INTRODUCTION

Swordfish, *Xiphias gladius*, is an epi- and mesopelagic species found throughout the world's oceans, ranging from 50°N to 35°S in tropical, subtropical, and temperate waters (Nakamura, 1985; Palko et al., 1981). In the North Pacific Ocean (NPO), swordfish migrate between temperate waters for feeding and warmer waters (20°-29°C) to spawn, although the timing of these migrations differs depending on the region (Nakamura, 1985). Spawning takes place in the boreal spring and summer months (March – July) in the central North Pacific, year-round in the equatorial Pacific, and during the austral spring (September – December) in the western South Pacific (Nakamura, 1985). Spawning generally occurs 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 and Ueyanagi, 1974). Swordfish larvae distributions are associated with major currents including the North Equatorial and Kuroshio currents in the NPO, and juvenile and adult swordfish are often found near upwelling areas with high productivity (Palko et al., 1981). Frontal zones also play a major role in the distribution of swordfish as sharp gradients of temperature and salinity create areas of rich production where small pelagic prey are abundant (Palko et al., 1981; Sakagawa, 1988; Holts & Sosa-Nishizaki, 1994).

Swordfish are a highly adaptable species that can tolerate substantial changes in their environment (i.e., depth and temperature) and target a variety of food sources from the epi-pelagic to the benthos (Palko et al., 1981). Numerous physiological adaptations,

such as specialized muscles to improve brain, eye, and cardiac function (Block, 1987; Carey, 1979; Fritsches et al., 2005; Galli et al., 2009), have enabled swordfish to withstand rapid temperature variations that occur with increasing depth, as well as between the warm and cold boundaries of oceanic water masses (Ward et al., 2000). These adaptations allow swordfish, a highly migratory species, to complete daily excursions below the mixed layer and long distance seasonal migrations (Molony, 2008). While it has been hypothesized that young-of-the-year (YOY) swordfish do not migrate far during their first year (Gorbunova, 1969 cited by Palko et al., 1981), results from tagging studies indicate that adult swordfish are capable of substantial horizontal and vertical migrations (Abascal et al., 2010; Abecassis et al., 2012; Carey and Robison, 1981; Dewar et al., 2011; Evans et al., 2014; Takahashi et al., 2003). Adults undertake considerable migrations from cool waters towards warm waters in order to spawn (Nakamura et al., 1985; Palko et al., 1981) and it has been hypothesized that swordfish migrate offshore to spawn (Kume and Joseph, 1969). Results from a number of tagging studies may provide some support for this hypothesis as some individuals have been observed migrating from temperate coastal foraging grounds towards the tropical open ocean (Abascal et al., 2010; Abecassis et al., 2012; Dewar et al., 2011; Evans et al., 2014; Takahashi et al., 2003); however, more research is needed in order to better establish links between spawning grounds and foraging grounds where swordfish are targeted by commercial fishing.

Swordfish is an economically important species that supports regional recreational fisheries and commercial fisheries worldwide. Swordfish catch in the

Pacific Ocean has increased steadily since the 1980s, with estimated landings from 15,160 t in 1980 to 61,692 t in 2014 (FAO Fish Stat, 2016). Most commercial fisheries target swordfish using pelagic longline fishing gear in areas of high prey concentration, such as convergence zones, strong thermoclines, and near seamounts and banks (Palko et al., 1981; Ward et al. 2000). In the NPO, U.S. commercial fisherman harvest swordfish using longline gear in the federal waters of Hawaii (between 3 – 200 nautical miles from shore) and the high seas (waters beyond the Exclusive Economic Zone (EEZ) of the U.S. and of any foreign nation), while commercial fisherman on the U.S. West Coast harvest swordfish using drift gill nets and harpoons (Fish Watch, 2014). The Hawaii based longline fishery is the largest producer of swordfish in the U.S. (Fish Watch, 2014) and targets swordfish within, and adjacent to, fronts of the Subtropical Convergence zone north of Hawaii (DeMartini et al. 2007). In 2012, swordfish was the third highest contributor to the total commercial fisheries ex-vessel revenue of Hawaii, with an ex-vessel revenue of \$6.7 million (Western Pacific Regional Fishery Management Council, 2014) and contributed \$2.1 million in ex-vessel revenue to West Coast commercial fisheries (Pacific Fishery Management Council, 2014).

Assessment and management of Pacific swordfish has been challenging due to the highly migratory nature of this species and its circumglobal distribution. In 2009, the Billfish Working Group of the International Scientific Committee (ISC) for Tuna and Tuna-like Species reviewed genetics research, catch per-unit effort (CPUE) data, and catch distribution data and concluded that there was evidence that Pacific swordfish stock structure in the NPO may no longer support a single-stock hypothesis, but rather a

two-stock hypothesis (ISC, 2009). By 2014, a swordfish population consisting of two-stocks in the NPO, the Western and Central North Pacific Ocean (WCNPO) and the EPO, had been widely adopted with the two stocks being separated by a diagonal boundary extending from Baja, California to the Equator (ISC, 2014). The EPO stock is managed internationally by the Inter-American Tropical Tuna Commission (IATTC) while the Western and Central Pacific Fishery Commission (WCPFC) manages the WCNPO stock. Stock assessments in the NPO are conducted by the ISC, with the most recent stock assessment indicating that the WCNPO stock is not being overfished or experiencing overfishing and that the EPO is not overfished but subject to overfishing (ISC, 2015). Despite the adoption of management plans based on a swordfish population comprised of two-stocks in the NPO, debate still continues regarding swordfish population structure in the Pacific Ocean. In fact, the ISC states that a major contributor of error and uncertainty in most recent stock assessments continues to be the uncertainty surrounding NPO swordfish stock structure (ISC, 2014), indicating that there is a need for research aimed towards answering questions about connectivity, exchange, and movement among regions.

Pacific swordfish stock structure hypotheses range from a single stock to a five-stock hypothesis (Hinton & Alvarado Bremer, 2007); with mounting evidence appearing to support that the Pacific swordfish population consists of multiple stocks, as opposed to one single panmictic population. A review on models based on fisheries catch data ranged from two-stock (Ichinokawa and Brodziak, 2008; Nakana, 1998), three-stock (Bartoo and Coan, 1989; Ichinokawa and Brodziak, 2008; Nakano, 1998; Bell, 1980),

and four stock hypotheses (Hinton, 2003; Hinton and Deriso, 1998; Sosa-Nishizaki, 1990; Sosa-Nishizaki and Shimizu, 1991). It is important to note, however, that models in agreement on the number of swordfish stocks often do not agree on latitudinal and longitudinal boundaries (Lu et al., 2016). Genetic studies also 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 and Takeyama, 2000; Rosel and Block, 1995), while others found evidence supporting subdivisions in the population (Bremer et al., 2006; Lu et al., 2016; Reeb et al., 2000; Sosa-Nishizaki et al., 1996; Ward et al. 2001). Results from age and growth studies of swordfish in the Pacific also appear to support a multi-stock hypothesis as differences in growth rates have been detected in swordfish sampled from Australia (Young and Drake, 2004), Chile (Cerna, 2009), Hawaii (DeMartini et al., 2007), and Taiwan (Sun et al., 2002). Additionally, tagging studies lend support to a multi-stock hypothesis as no trans-hemispheric or trans-oceanic migrations have been recorded, even though swordfish are capable of migrations of thousands of kilometers (Abascal et al., 2010; Abecassis et al., 2012; Dewar et al., 2011; Evans et al., 2014; Takahashi et al., 2003). Caution must be used in the interpretation of tagging studies as they are often of limited duration and do not provide insight into the origin or spawning locations of tagged fish.

Multiple methods have been employed to examine population structure of Pacific swordfish, though, the use of otolith chemistry methodology has been limited. Otoliths are calcified structures in teleost fishes which are used to maintain equilibrium and for hearing (Campana and Nielson, 1985; Pannella, 1971). Material is deposited on the

otolith daily (Pannella, 1971) and, once deposited, is metabolically inert, meaning that it is neither resorbed or reworked (Campana and Nielson, 1985). Approximately 90% of the otolith is composed of calcium carbonate and trace elements that are derived from the water mass the fish inhabits; thus, it can be hypothesized that otoliths from fish inhabiting water bodies with differing environmental characteristics will have differing elemental composition (Campana et al., 1995; Campana, 2005). Otolith composition is influenced in part by the ambient environment as well as by factors such as salinity, temperature, pH, dissolved oxygen concentrations, and availability of trace elements (Campana, 1999; Mayer et al., 1994; 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). Utilization of otolith chemistry as a natural tag has proven useful in the study of pelagic fish species to make inferences on population structure, mixing, and movement (Baumann et al., 2015; Campana et al., 1999; MacDonald et al., 2013; Rooker et al., 2008; Secor et al., 2001; Wells et al., 2010, 2015). In addition, application of otolith chemistry has been used to discriminate fish from nursery areas (Gillanders and Kingsford, 2000; Humphreys et al., 2005; Rooker et al., 2001b, 2003; Thorrold et al., 1998), and to classify adults of unknown origin using established nursery baseline signatures of pelagic species (Carlson et al., 2016; Rooker et al., 2008; Schloesser et al., 2010; Walther et al., 2008; Wells et al., 2012). To date, there has been one study examining the otolith chemistry of Pacific swordfish in the NPO (Humphreys et al., 2005). With a goal of testing the feasibility of using otolith chemistry to discriminate

among swordfish nursery grounds throughout the Hawaiian Islands, Humphreys et al. (2005) examined the trace elements in swordfish otoliths sampled from several nurseries surrounding the Hawaiian Islands and the Central Pacific Ocean. Differences in elemental concentrations were detected among nurseries, indicating otolith chemistry may be an appropriate approach to investigate population structure of swordfish in the NPO.

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

2. METHODS

2.1 Sample Collections

Sagittal otoliths of YOY swordfish were opportunistically collected by National Oceanographic and Atmospheric Administration (NOAA) fishery observers and field researchers during commercial and fishery independent fishing operations in the NPO over a 5-year period (2000 – 2005). Swordfish <100 cm eye-to-fork length (EFL) were classified as YOY and swordfish >100 cm EFL were classified as sub-adult or adult based on previous age and growth studies of swordfish in the central NPO (DeMartini et al., 2007). Swordfish larval distribution has been observed and documented throughout the northwest and north central Pacific as well as throughout the central equatorial Pacific and the eastern equatorial Pacific (Grall et al., 1983; Nishikawa and Ueyanagi, 1974; Nishikawa et al., 1985). Furthermore, it has been hypothesized that YOY swordfish do not migrate far from their spawning grounds during the first year of life (Gorbunova, 1969), thus it can be assumed that swordfish <100 cm EFL are captured close to their spawning grounds. Based on this information, four nursery grounds were sampled: the central equatorial NPO (CENPO; between 0-7°N and 159-168°W), the central NPO (CNPO; between 18-33°N and 154-168°W), the eastern equatorial NPO (EENPO; between 0-5°N and 84-96°W), and the western NPO (WNPO; between 27-40°N and 143-164°E) (Figure 1.) In total, 112 YOY swordfish were sampled (Table 1). Upon collection, swordfish heads were removed, frozen and transported to the NOAA Pacific Islands Fisheries Science Center (Hawaii) for otolith extraction and processing.

Sagittal otoliths of sub-adult and adult swordfish (>100 cm EFL) were opportunistically collected by NOAA fishery observers and field researchers during commercial and research longline fishing and gill net operations from 2012 to 2015. Three foraging grounds where targeted fisheries exist, hereafter referred to as fishing regions, were sampled: the CNPO and Hawaiian Islands (HI; between 17-32°N and 144-168°W), Coastal California (CA; between 31-40°N and 117-126°W), and Coastal Baja California, Mexico (MX; between 23-27°N and 111-115°W) (Figure 1) (Table 2). Whole heads were collected, frozen, and transported to a regional lab 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 in order to establish a sample of individuals that could have originated from the nursery grounds during the 2000 to 2005 period when YOY swordfish were sampled (52% of total samples) (Table 2). In order to increase sample sizes, additional individuals not meeting the EFL/age requirements were analyzed; of the added individuals, 35% were approximately aged to within 1 year of the 2000 to 2005 period when YOY swordfish were sampled (Table 2).

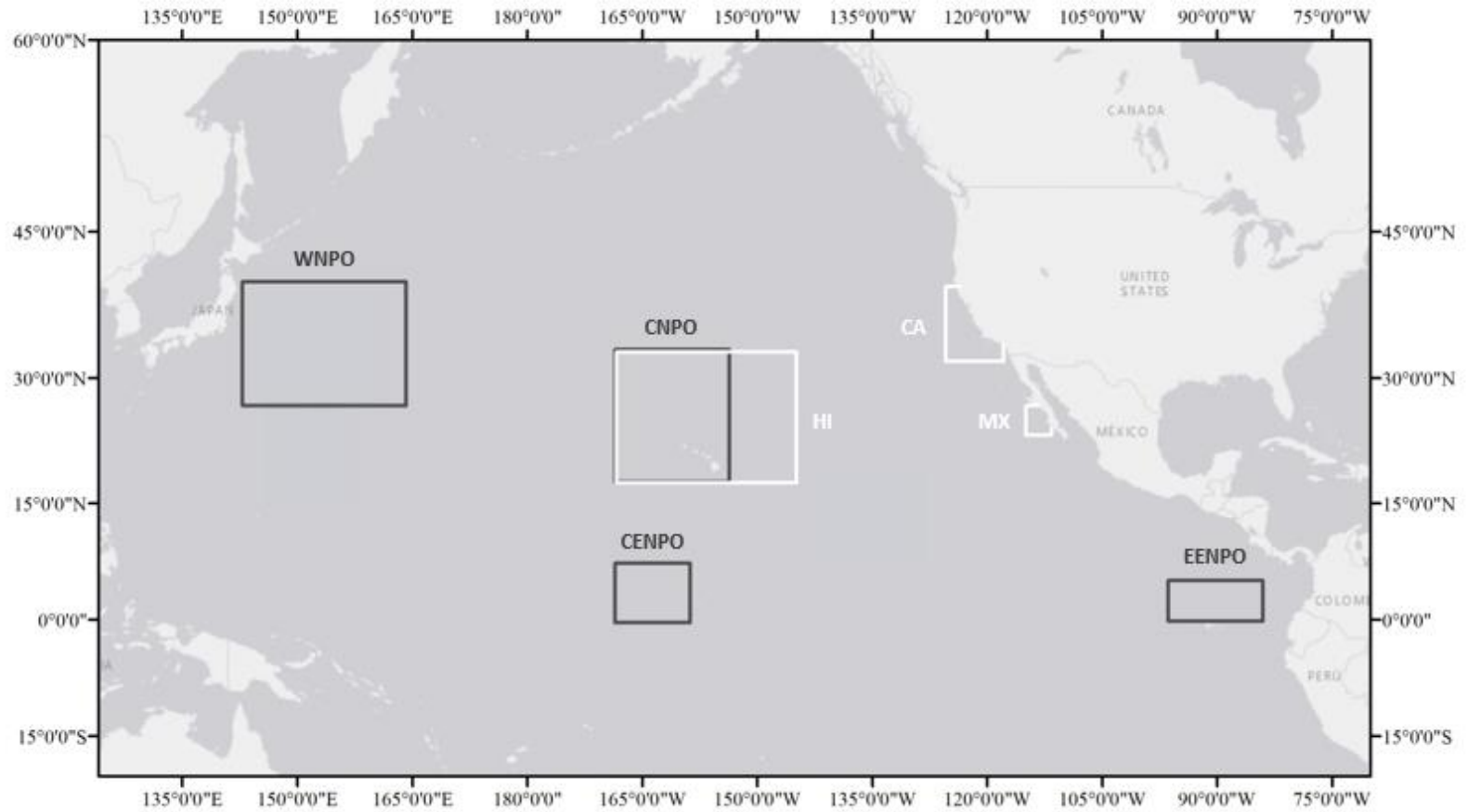


Figure 1. Map of the study regions located in the NPO where YOY and adult swordfish were collected. Nurseries are indicated by boxes outlined in gray and adult fishing regions are indicated by boxes outlined in white.

Table 1. Nursery locations, sample size, and years of sample collections for YOY swordfish.

Nursery	Acronym	n	Latitude	Longitude	Sampling years
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 years of collection for sub-adult and adult swordfish.

Region	Acronym	n	Latitude	Longitude	Sampling years
CNPO and Hawaiian Islands	HI	22	17-32°N	144-168°W	2014, 2015
Coastal California, United States	CA	22	31-40°N	117-126°W	2012, 2013, 2014
Coastal Baja California, Mexico	MX	21	23-27°N	111-115°W	2013
	Total	65			

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 hours. Due to the pronounced curvature, minute size, and delicate nature of swordfish otoliths, otoliths were not cleansed with hydrogen peroxide or nitric acid in order to prevent breakage and to save material for analysis. Otoliths were embedded in Crystalbond™509 sulcal side down and mounted on 9mm x 9mm quartz glass pieces. The otolith core was exposed by hand-polishing the sagittal plane against MARK V Laboratory 30M, 9M, and 3M 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). This technique uses a focused laser to vaporize or “ablate” solid materials and the ablated material is then transferred to a plasma mass spectrometer for analysis. Mounted YOY swordfish otoliths were processed at the Keck Collaboratory for Plasma Spectrometry, at Oregon State University (OSU). Upon arrival at the Keck Collaboratory, mounted YOY otoliths were transferred to a clean room where they were cleansed and sonicated for 10 minutes in ultra-pure water to avoid trace element contamination. Six individual 9mm x 9mm glass mounted YOY otoliths were attached to an acid-washed quartz slide (25 mm x 50 mm) using double-sided tape.

Trace elements in otolith cores were analyzed using a PQ Excell LA-ICP-MS. Nine elements of interest were analyzed: calcium (^{43}Ca), magnesium (^{24}Mg), aluminum

(²⁷Al), silicon (²⁹Si), manganese (⁵⁵Mn), zinc (⁶⁶Zn), strontium (⁸⁶Sr, ⁸⁸Sr), barium (¹³⁸Ba), and lead (²⁰⁸Pb). National Institute of Standards and Technology (NIST) glass 610 (*n* = 60) and 612 (*n* = 48) were used as the standard and analyzed after every 6 otolith samples to maintain instrument precision. Estimates of instrument analytical precision, as % relative standard deviation (%RSD) for NIST610 (*n* = 60) were: ²⁴Mg = 5.84 ± 0.84%; ²⁷Al = 3.61 ± 1.44%, ²⁹Si = 3.96 ± 1.44%, ⁴³Ca = 5.56 ± 0.97%, ⁵⁵Mn = 4.66 ± 1.21%, ⁶⁶Zn = 7.75 ± 0.69%, ⁸⁸Sr = 4.07 ± 1.45%, ¹³⁸Ba = 4.31 ± 1.38 %, ²⁰⁸Pb = 6.36 ± 0.86% while the RSDs for NIST612 (*n* = 48) were: ²⁴Mg = 14.25 ± 3.9%, ²⁷Al = 3.85 ± 0.21%, ²⁹Si = 4.14 ± 0.26%, ⁴³Ca = 6.21 ± 0.8%, ⁵⁵Mn = 10 ± 2.19%, ⁶⁶Zn = 22.72 ± 4.04%, ⁸⁸Sr = 6.94 ± 1.1%, ¹³⁸Ba = 10.41 ± 1.92%, ²⁰⁸Pb = 13.6 ± 3.23%. NIST 610 and 612 were also used to create calibration curves for each element of interest. Four elements (²⁴Mg, ⁸⁸Sr, ¹³⁸Ba, and ⁴³Ca) 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., 2001b), 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 outward towards the dorsal outer edge (Figure 2). Transects were ablated with at least 45 degrees of angular separation. Elemental concentrations were measured and reported

at approximately 1 – 2 μm intervals throughout the duration of each 250 μm transect. These values were then averaged to provide a single elemental concentration value (for each element, for each transect). The elemental concentration values from each transect were then averaged to provide a single element concentration value (for each element, for each individual otolith core). Element concentration values were then transformed into element:Ca ratios using the same methodology as used for the standards.

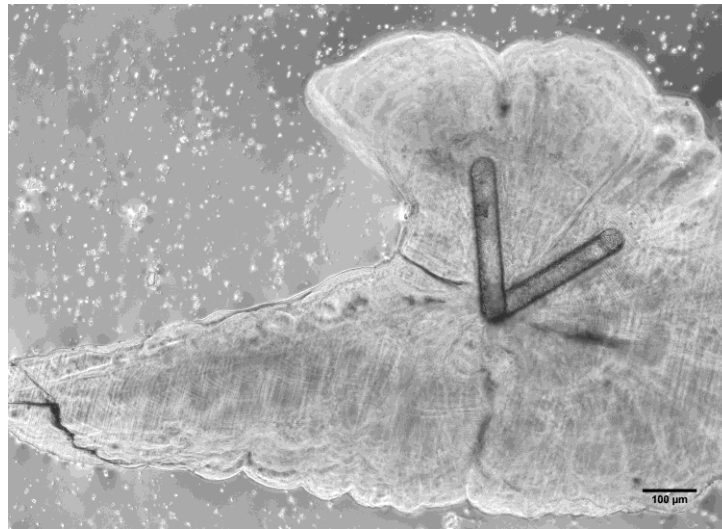


Figure 2. Swordfish sagittal otolith ground on the sagittal plane with two transects, originating from the core, radiating distally.

Estimates of the age range covered by the ablations were made in order to assess what range of days during the early life stage were being analyzed. Five otoliths were selected and growth rings within 250 μm of the core were counted in order to determine an approximate age. It was estimated that the ablation analyzed material incorporated into the otolith during the first 56 days of life.

2.4 Trace Element Analysis: Adult Swordfish

Adult otoliths were processed at Texas A&M University, Galveston (TAMUG). Twelve individual 9mm x 9mm glass mounted sub-adult and adult otoliths were attached to a non-corrosive glass slide (27 mm x 46 mm) using double-sided tape. Trace elements in otoliths were assessed using a Thermo Scientific XSeries II ICP-MS. Methods were identical to the YOY methods with the following exceptions. Repeat rates were adjusted from 8 Hz to 10 Hz when analyzing 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. National Institute of Standards and Technology (NIST) glass 614 was used as the standard and was analyzed after every 2 otolith samples. Estimates of instrument analytical precision, as % relative standard deviation (%RSD) for NIST614 was: ^{24}Mg : $11.89\pm 1.21\%$, ^{44}Ca : $11.59\pm 1.06\%$, ^{88}Sr : $11.64\pm 1.288\%$, ^{138}Ba : $24.2\pm 1.58\%$. Trace element contamination was avoided by pre-ablating transects and standards with a laser spot size of 80 μm using laser energy, repeat rates, and ablation speeds of 30%, 10 Hz, and 10 $\mu\text{m/s}$, respectively.

To compare results between facilities, a sub-sample ($n = 6$) of YOY otoliths processed at the Keck Collaboratory were selected and a transect was ablated from each

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 analyzed in order to compare decontamination procedures. Of these pairs, one otolith was decontaminated using the sonicating method used for the nursery otoliths while the other otolith was decontaminated using the pre-ablate method used for the adult otoliths.

2.5 Statistical Analysis

A total of 109 YOY swordfish otoliths from four nurseries in the NPO were analyzed for 3 trace element:Ca ratios (Mg:Ca, Sr:Ca, and Ba:Ca) present at levels above detection limits. Nurseries were examined for outliers (otoliths with element:Ca ratios $>$ 3 standard deviations from the mean), and 1 sample from the CNPO was removed, leaving a sample size of 44 from that nursery and an overall sample size of 108. Nursery was used as a fixed factor in a multivariate analysis of variance (MANOVA) model to test for nursery-specific differences in otolith core element:Ca ratios. Pillai's trace statistic was used to test for significance as it is the most robust to deviations from assumption of homogeneity of variance and covariance (Quinn and Keough, 2002). Univariate tests for each element:Ca ratio was performed using analysis of variance (ANOVA) and *post hoc* differences among sample means were detected with Tukey's honestly significant difference (HSD) test. Year of sample collection was used as a fixed factor in MANOVA and ANOVA models to test for temporal differences in otolith core element:Ca ratios within nurseries consisting of samples collected over multiple years, to include the CENPO (2001, 2002) and the CNPO (2000, 2002, 2004, 2005).

Post hoc differences were detected with Tukey's honestly significant difference (HSD) test. Quadratic discriminant analysis (QDA) was then used to evaluate the classification accuracy of individual YOY Pacific swordfish to nurseries based on jackknife reclassification. Variances were not homogenous across nurseries for Sr:Ca molar ratios, thus appropriate transformations were applied to the data by cubing Sr:Ca ratios and tests were recalculated. Additionally, non-parametric and robust tests were conducted using Kruskal-wallis for univariate analysis and functions within R's rrcov package (Todorov & Filzmoser, 2009) for multivariate analysis (robust MANOVA utilizing classic Wilks' Lambda statistic using the Wilks.test function) and to assess classification accuracy (robust QDA using the QdaCov function). Transformations, non-parametric tests, and robust MANOVA and QDA analyses did not alter the significance of any tests, thus only results from MANOVA and QDA using the untransformed data are presented here. 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-ablating). Mg:Ca, Sr:Ca, and Ba:Ca ratios were not significantly different for transects of otoliths analyzed 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-ablating) 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 ($248 \pm 65 \mu\text{mol}:\text{mol}$) when otolith surfaces were decontaminated by preablating 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 preablation 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 ($\alpha / \#$ 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 contribution estimates of Pacific swordfish recruits to the fishing regions of HI, CA, and MX were obtained using the maximum likelihood mixed-stock analysis program HISEA developed by Millar (1990). The baseline data set used for mixed-stock analysis consisted of element:Ca ratios from otolith cores of YOY swordfish originating from the four NPO nurseries and included only those element:Ca ratios deemed significantly different among nurseries by ANOVA. Element:Ca ratios of otolith cores of adult samples collected from the fishing regions of HI, CA, and MX were used to estimate the origin of these adults in the bootstrap mode of HISEA with 1000 simulations. Nursery specific contribution estimates were calculated four times for each of the three adult fishing regions. The initial analysis (n) included the element:Ca ratios from otolith cores of all adult otoliths analyzed (Table 3). The remaining analyses separated total sample size (n) into three subgroups, (A, B, and C) based on the

estimated birth year of each individual. The second analysis (A) 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 sampling YOY (2000-2005) (Table 3). The third analysis (B) included only the element:Ca ratios obtained from the otolith cores of adult fish that were within one year of the 2000 – 2005 sample period (Table 3). Lastly, the fourth analysis (C) included only the element:Ca ratios obtained from otolith cores of adult fish that could not have originated from the nurseries during the 2000 – 2005 sample period (Table 3).

Table 3. Adult swordfish sample sizes for Millar’s HISEA mixed stock analysis. Total sample sizes are denoted in the table under the n column, while A represents the number of individuals that could have originated from the nurseries during the 2000-2005 YOY sample period, B represents the number of individuals that were within one year of the 2000-2005 sample period, and C represents individuals that did not originate from the nurseries during the 2000-2005 sample period.

Region	n	A	B	C
HI	22	3	2	17
CA	22	12	8	2
MX	21	19	1	1
Total	65	34	11	20

2.6 Environmental Data

Environmental data for each nursery was extracted from open access resources using the marine geospatial ecology toolbox in ArcGIS (Roberts et al., 2010). Sea

surface salinity (SSS) and sea surface temperature (SST) annual averages from 2005 were extracted using ROMS-CoSiNE, a tool that accesses the Pacific ROMS-CoSiNE 12.5 km 3-day analyses published by the University of Maine Ocean Modeling Group (Table 4).

Table 4. Mean annual sea surface salinity (SSS in PSU) and sea surface temperature (SST in °C) from 2005 extracted from ROMS-CoSiNE.

Nursery	Mean SSS	SSS Range	Mean SST	SST Range
CENPO	35.1	35.0 - 35.3	26.8°C	25.5 - 25.6°C
CNPO	35.4	34.8 - 35.7	23.6°C	19.9 - 26.1°C
EENPO	34.3	33.9 - 34.8	25.1°C	21.6 - 26.4°C
WNPO	34.7	34.2 - 35.4	20.7°C	13.7 - 25.4°C

3. RESULTS

Trace element signatures of YOY swordfish varied significantly among nurseries (MANOVA $df = 3$, Pillai's trace = 0.93, $F = 15.41$, $p < 0.05$) with all three individual element:Ca ratios being significantly different among nurseries (ANOVA Mg:Ca: F value = 14.18, $p < 0.05$; Sr:Ca: F value = 24.77, $p < 0.05$; Ba:Ca: F value = 6.41, $p < 0.05$). Tukey's HSD tests indicated that not all nursery individual element:Ca ratios were significantly different from the other nurseries. For example, Mg:Ca and Sr:Ca ratios were not significantly different between the EENPO and WNPO, Sr:Ca and Ba:Ca ratios were not significantly different between the WNPO and CNPO, and Ba:Ca ratios were not significantly different between the CENPO and EENPO (Figure 3). Nurseries in the central Pacific Ocean (CENPO and CNPO) had higher mean Mg:Ca and Sr:Ca ratios than the eastern and western Pacific Ocean nurseries (Table 5). The highest Mg:Ca ratios were observed in the CNPO (mean \pm SD: $73.084 \pm 21.368 \mu\text{mol}:\text{mol}$) and the lowest were observed in the WNPO ($44.973 \pm 9.21 \mu\text{mol}:\text{mol}$). The highest Sr:Ca ratios were observed in the CENPO ($1344.723 \pm 96.568 \mu\text{mol}:\text{mol}$), with the EENPO exhibiting the lowest ($1019.953 \pm 225.369 \mu\text{mol}:\text{mol}$) and highest regional variability (SD: $225.369 \mu\text{mol}:\text{mol}$). Ba:Ca ratios were higher with increasing latitude, with higher Ba:Ca ratios found in the northern nurseries (CNPO and WNPO) than in the equatorial nurseries (CENPO and EENPO; Figure 3). Ba:Ca ratios were highest and more variable in the WNPO ($1.771 \pm 1.105 \mu\text{mol}:\text{mol}$), with the CENPO exhibiting the lowest ratios ($1.1001 \pm 0.524 \mu\text{mol}:\text{mol}$). The CENPO and CNPO nurseries exhibited greater

regional variability in Mg:Ca ratios (SD: 21.258 and 21.368 $\mu\text{mol}:\text{mol}$, respectively), while the EENPO and WNPO nurseries exhibited greater regional variability in Sr:Ca (SD: 225.369 and 136.882 $\mu\text{mol}:\text{mol}$, respectively) and Ba:Ca (SD: 0.876 and 1.105 $\mu\text{mol}:\text{mol}$, respectively) ratios.

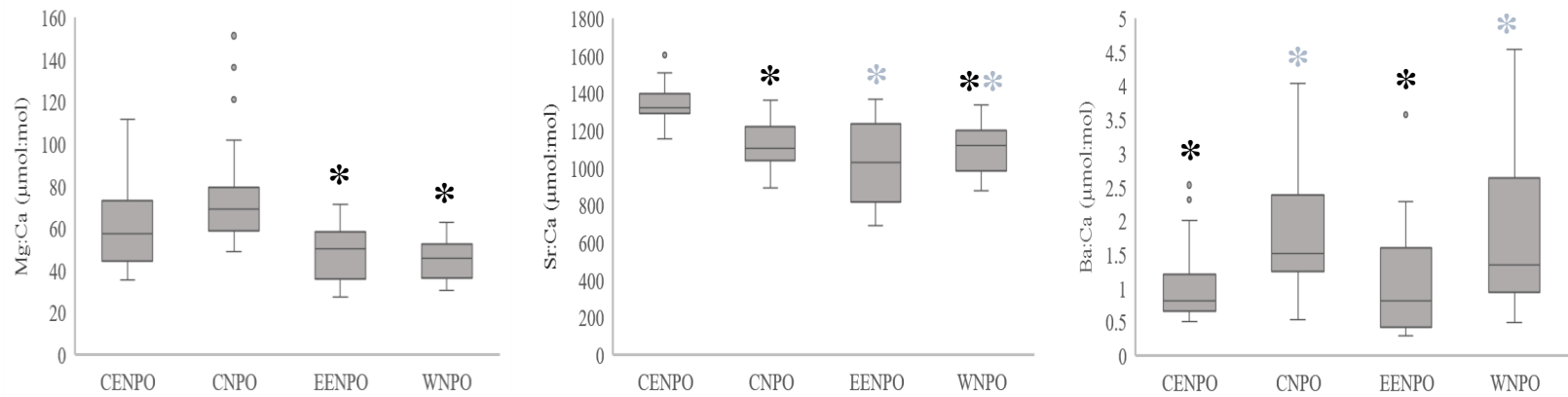


Figure 3. Element:Ca ratios measured at the otolith core for YOY swordfish sampled from the CENPO, CNPO, EENPO, and WNPO nurseries. Lack of significant differences in element:Ca ratios are denoted by asterisks (*) and color; nurseries of the same color did not display significant differences (Tukey's HSD $p > 0.05$).

Table 5. Element:Ca ratios measured in the sagittal otolith cores of YOY swordfish from 4 nurseries in the NPO. Data are in mean \pm SD $\mu\text{mol}:\text{mol}$.

Element:Ca Ratio	CENPO	CNPO	EENPO	WNPO
Mg:Ca	61.634 \pm 21.258	73.084 \pm 21.368	48.141 \pm 13.058	44.973 \pm 9.210
Sr:Ca	1344.723 \pm 96.568	1117.071 \pm 122.629	1019.953 \pm 225.369	1089.277 \pm 136.882
Ba:Ca	1.001 \pm 0.524	1.785 \pm 0.870	1.105 \pm 0.876	1.771 \pm 1.105

Interannual variability was nursery and element specific. Interannual variability was not detected for overall element:Ca ratios for any nursery during the period of sample and was only detected for Sr:Ca ratios in one of the nurseries. Interannual comparisons in the CENPO nursery indicated that there were not significant differences in overall element:Ca signatures during the period of collections (2001, 2002; MANOVA, $p > 0.05$). A significant year effect was detected for Sr:Ca ratios between 2001 and 2002 (ANOVA, $p < 0.05$), with a lower mean Sr:Ca ratio in 2001 than in 2002 (Table 6). Interannual comparisons in the CNPO nursery indicated that there were not significant differences in overall element:Ca signatures (MANOVA, $p > 0.05$) or among individual element:Ca ratios (ANOVA, $p > 0.05$) during the period of sample (2000, 2002, 2004, 2005). An investigation of interannual variability in both the EENPO and WNPO was not conducted as sampling occurred over a one-year period for each nursery (2005 and 2004, respectively).

Table 6. Comparison of element:Ca ratios measured in the sagittal otolith cores of YOY swordfish by year within the CENPO and CNPO nurseries. Data are in mean \pm SD $\mu\text{mol}:\text{mol}$.

Region	Year	Mg:Ca Range	Mg:Ca Mean \pm SD	Sr:Ca Range	Sr:Ca Mean \pm SD	Ba:Ca Range	Ba:Ca Mean \pm SD
CENPO	2001	35.729 - 111.933	66.034 \pm 25.626	1154.759 - 1420.921	1290.534 \pm 68.281	0.549 - 2.532	1.001 \pm 0.559
	2002	38.137 - 95.633	58.333 \pm 17.457	1248.965 - 1604.755	1385.365 \pm 96.205	0.507 - 2.312	1 \pm 0.515
CNPO	2000	51.428 - 102.041	69.924 \pm 14.498	895.476 - 1364.993	1110.464 \pm 130.372	0.530 - 3.531	1.504 \pm 0.939
	2002	50.408 - 79.819	63.015 \pm 9.285	1004.921 - 1263.329	1142.964 \pm 91.327	1.351 - 4.039	2.423 \pm 0.991
	2004	48.850 - 151.330	83.755 \pm 28.868	897.675 - 1361.455	1105.504 \pm 134.387	0.901 - 2.980	1.760 \pm 0.643
	2005	55.045 - 68.830	63.231 \pm 7.247	974.283 - 1265.729	1136.325 \pm 148.439	1.290 - 1.615	1.505 \pm 0.187

Discriminant analysis based on all three element:Ca ratios produced moderate separation of the CENPO and CNPO nurseries, and lesser separation between the EENPO and WNPO nurseries (Figure 4). Canonical variable 1 (x axis) moderately separated the CENPO from the other nurseries and accounted for 74.6% of the total dispersion. The second canonical variable 2 (y axis) separated the CNPO from the other nurseries, with the first and second canonical variables accounting for 96.7% of the total dispersion. Results of discriminant analysis showed separation of swordfish nurseries in the NPO with a 72.2% overall classification success rate (Figure 4). 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%). Classification success of this model was far better than if an attempt had been made to classify individuals randomly (chance of correctly classifying an individual randomly, per nursery: CENPO 26.9%, CNPO 39.8%, EENPO 14.8%, and WNPO 18.5%). The majority of misclassified individuals originating from the CENPO were classified as EENPO fish (7.1%). The majority of misclassified individuals originating from the CNPO were classified as WNPO fish (11.4%). Individuals originating from the EENPO were mainly misclassified to the CENPO (18.8%) and CNPO (25%) nurseries, while individuals originating from the WNPO were mainly misclassified to the CNPO (30%) and EENPO (20%). In order to determine possible effects of interannual variability on discriminant analysis results, the model was rerun 6 additional times; each rerun sequentially excluded samples of individual years from nurseries sampled over multiple

years. Classification success from the discriminant analysis reruns ranged from 65.2 – 70.7%.

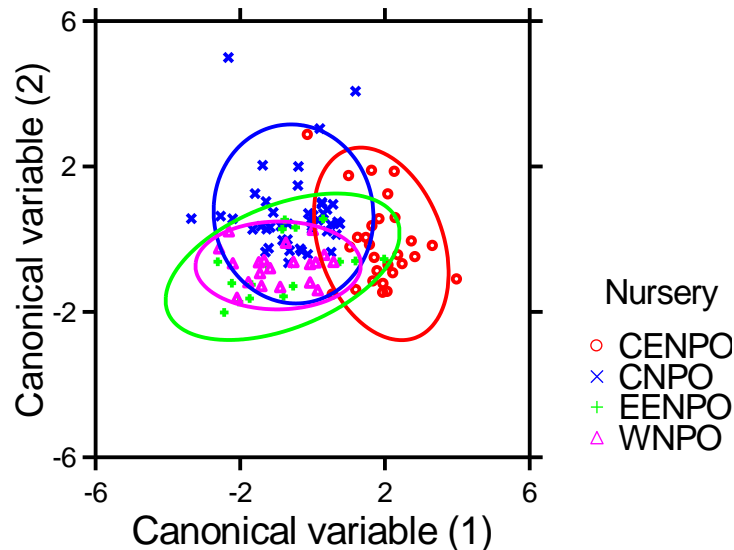


Figure 4. Canonical plot scores and 90% confidence ellipses from discriminant analysis of otolith cores of YOY swordfish sampled from 4 nurseries in the NPO. Discriminant analysis based on 3 element:Ca ratios (Mg:Ca, Sr:Ca, Ba:Ca).

Element:Ca ratios of otolith cores from the adult fishing grounds were also examined. Mean Mg:Ca ratios of the three adult fishing grounds were similar (HI: $41.96 \pm 1.7 \mu\text{mol:mol}$; CA: $43.57 \pm 2.44 \mu\text{mol:mol}$; MX: $45.04 \pm 2.03 \mu\text{mol:mol}$) and were well within Mg:Ca ratio ranges of the CENPO (mean: 61.22, range: 35.7 – 111.9 $\mu\text{mol:mol}$), EENPO (mean: 48.14, range: 27.6 – 71.3 $\mu\text{mol:mol}$), and WNPO (mean: 4.97, range: 30.4 – 62.9 $\mu\text{mol:mol}$). Mean Mg:Ca ratios of the three adult fishing grounds were lower than the ratio range of the CNPO (mean: 73.27, range: 48.9 – 151.3 $\mu\text{mol:mol}$). CA and MX otoliths exhibited the similar mean Sr:Ca ratios while HI

otolith ratios were lower (CA: 1339.9 ± 31.06 $\mu\text{mol}:\text{mol}$; MX: 1338.1 ± 41.17 $\mu\text{mol}:\text{mol}$; HI: 1253.7 ± 29.87 $\mu\text{mol}:\text{mol}$), however, all three adult fishing regions' mean Sr:Ca ratios were above the mean ratios of the CNPO (1116.62 $\mu\text{mol}:\text{mol}$), EENPO (1019.95 $\mu\text{mol}:\text{mol}$), and WNPO (1089.28 $\mu\text{mol}:\text{mol}$) nurseries. MX otolith cores exhibited the highest Ba:Ca ratios (1.73 ± 0.22 $\mu\text{mol}:\text{mol}$), followed by HI and CA (1.38 ± 0.18 $\mu\text{mol}:\text{mol}$ and 1.13 ± 0.13 $\mu\text{mol}:\text{mol}$, respectively). All three adult fishing ground mean Ba:Ca ratios fall between the lowest mean ratios of the CENPO and EENPO (0.99 and 1.10 $\mu\text{mol}:\text{mol}$, respectively) and the highest mean ratios of the CNPO and WNPO (1.77 $\mu\text{mol}:\text{mol}$ for both).

Mixed stock analysis suggested that the CENPO may be a major contributor of swordfish recruits to the fishing regions of HI, CA, and MX (Figures 5, 6, 7). Mixed stock analysis results for the HI fishing region were variable (Figure 5), with contribution estimates and associated error rates fluctuating among groups n (all adults), A (adults that may have originated from the nurseries during the period of YOY sample), B (adults aged to within 1 year of originating from the nurseries during the period of YOY sample), and C (adults that could not have originated from the nurseries during the period of YOY sample) (Table 7). As sample sizes were small for groups A and B, and associated error rates were high, results from sample n will be used for discussion. Local production appears to be negligible in the HI fishing region (CNPO: $0.05 \pm 0.80\%$), with the majority of recruits originating from both the CENPO ($45.59 \pm 13.21\%$) and the WNPO ($45.51 \pm 18.64\%$). Mixed stock analysis results for the CA and MX fishing regions were less variable and more consistent than those of the HI fishing

region (Figures 6 and 7), with contribution estimates and associated error rates fluctuating very little among groups n, A, B, and C (Tables 8 and 9). As results were fairly consistent among groups n, A, B, and C (with the exception of MX group C, which had a small sample size and large error rates), results from sample n for both CA and MX will be used for discussion. Adult swordfish caught in the CA fishing region are mainly derived from CENPO recruits ($84.6 \pm 10.05\%$), followed by small contributions from the WNPO ($10.93 \pm 10.11\%$). Similarly, adult swordfish caught in the MX fishing region were largely recruits from the CENPO ($64.46 \pm 15.93\%$), followed by the WNPO ($30.87 \pm 18.00\%$).

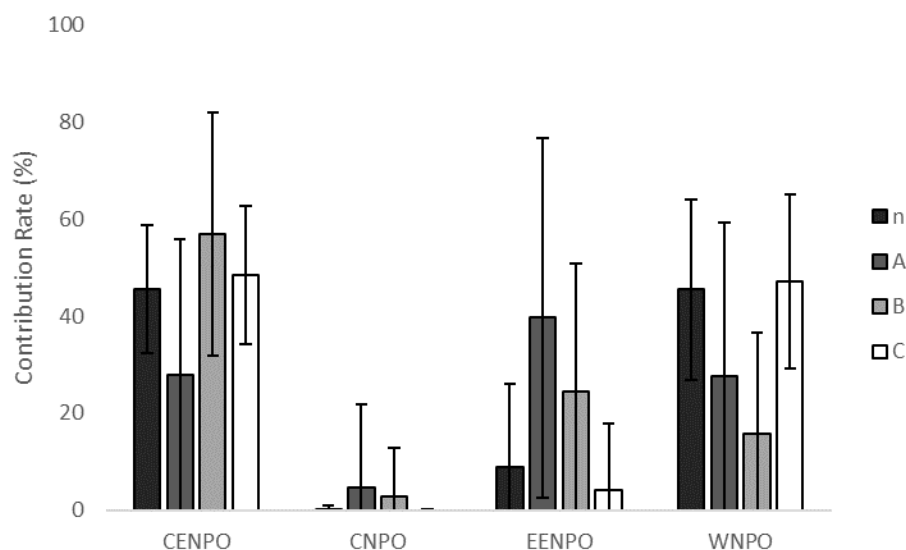


Figure 5. Nursery contribution estimates (\pm SD) to the HI fishing region. Total sample sizes are denoted by n, while A represents the number of individuals that could have originated from the nurseries during the 2000-2005 YOY sample period, B represents the number of individuals that were within one year of the 2000-2005 sample period, and C represents individuals that could not have originated from the nurseries during the 2000-2005 sample period.

Table 7. Nursery contribution estimates (\pm SD) to the HI fishing region. Total sample sizes are denoted by n, while A represents the number of individuals that could have originated from the nurseries during the 2000-2005 YOY sample period, B represents the number of individuals that were within one year of the 2000-2005 sample period, and C represents individuals that could not have originated from the nurseries during the 2000-2005 sample period.

Nursery	Contribution Estimate: n	Contribution Estimate: A	Contribution Estimate: B	Contribution Estimate: C
CENPO	45.59 \pm 13.21	27.94 \pm 28.02	56.97 \pm 25.17	48.53 \pm 14.31
CNPO	0.05 \pm 0.80	4.78 \pm 16.97	2.79 \pm 10.17	0.00 \pm 0.14
EENPO	8.85 \pm 17.14	39.66 \pm 37.02	24.42 \pm 26.53	4.22 \pm 13.64
WNPO	45.51 \pm 18.64	27.62 \pm 31.65	15.82 \pm 20.90	47.25 \pm 17.99

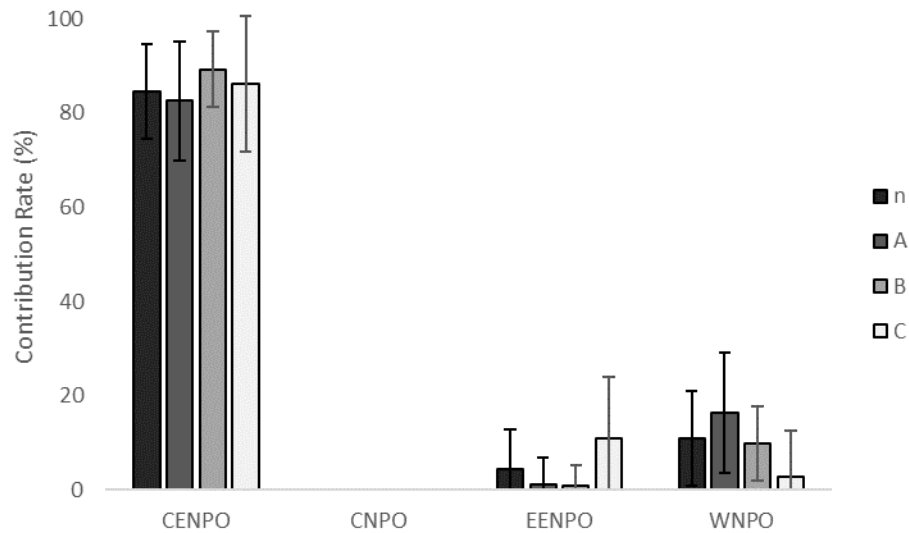


Figure 6. Nursery contribution estimates (\pm SD) to the CA fishing region. Total sample sizes are denoted by n, while A represents the number of individuals that could have originated from the nurseries during the 2000-2005 YOY sample period, B represents the number of individuals that were within one year of the 2000-2005 sample period, and C represents individuals that could not have originated from the nurseries during the 2000-2005 sample period.

Table 8. Nursery contribution estimates (\pm SD) to the CA fishing region. Total sample sizes are denoted by n, while A represents the number of individuals that could have originated from the nurseries during the 2000-2005 YOY sample period, B represents the number of individuals that were within one year of the 2000-2005 sample period, and C represents individuals that could not have originated from the nurseries during the 2000-2005 sample period.

Nursery	Contribution Estimate: n	Contribution Estimate: A	Contribution Estimate: B	Contribution Estimate: C
CENPO	84.60 ± 10.08	82.59 ± 12.68	89.32 ± 8.06	86.18 ± 14.34
CNPO	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.04	0.00 ± 0.00
EENPO	4.47 ± 8.45	1.17 ± 5.63	0.84 ± 4.22	11.00 ± 12.9
WNPO	10.93 ± 10.11	16.24 ± 12.79	9.83 ± 7.80	2.81 ± 9.75

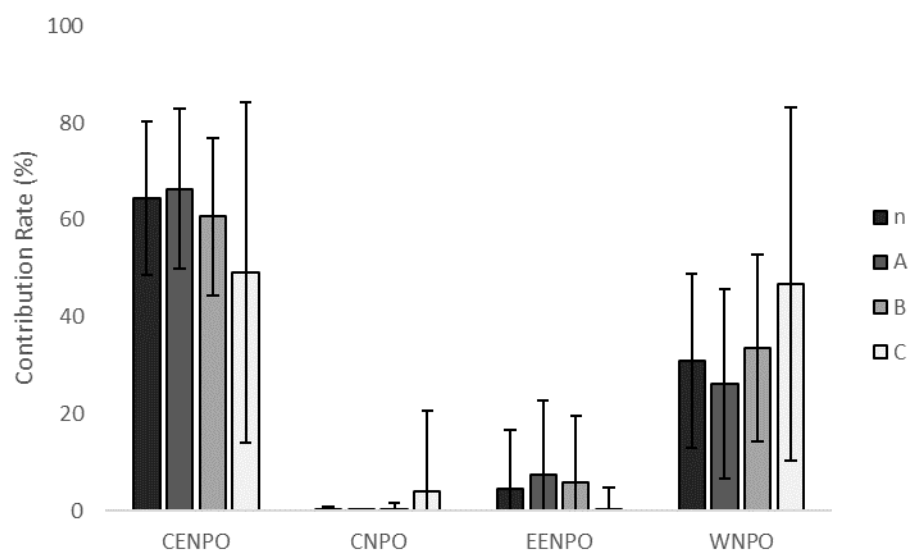


Figure 7. Nursery contribution estimates (\pm SD) to the MX fishing region. Total sample sizes are denoted by n, while A represents the number of individuals that could have originated from the nurseries during the 2000-2005 YOY sample period, B represents the number of individuals that were within one year of the 2000-2005 sample period, and C represents individuals that could not have originated from the nurseries during the 2000-2005 sample period.

Table 9. Nursery contribution estimates (\pm SD) to the MX fishing region. Total sample sizes are denoted by n, while A represents the number of individuals that could have originated from the nurseries during the 2000-2005 YOY sample period, B represents the number of individuals that were within one year of the 2000-2005 sample period, and C represents individuals that could not have originated from the nurseries during the 2000-2005 sample period.

Nursery	Contribution Estimate: n	Contribution Estimate: A	Contribution Estimate: B	Contribution Estimate: C
CENPO	64.46 \pm 15.93	66.42 \pm 16.45	60.66 \pm 16.19	49.02 \pm 35.12
CNPO	0.06 \pm 0.78	0.01 \pm 0.21	0.13 \pm 1.50	3.93 \pm 16.78
EENPO	4.61 \pm 12.07	7.42 \pm 15.38	5.74 \pm 13.92	0.30 \pm 4.49
WNPO	30.87 \pm 18.00	26.15 \pm 19.57	33.46 \pm 19.24	46.75 \pm 36.43

4. CONCLUSION

Analysis of trace elements within the core of YOY swordfish otoliths revealed unique nursery signatures in the NPO, which were then used to calculate nursery-specific contribution estimates to three adult fishing regions. In this study, Mg:Ca, Sr:Ca, and Ba:Ca ratios within YOY swordfish otolith cores varied significantly among nurseries. Specifically, Mg:Ca and Sr:Ca ratios were highest in the otolith cores of YOY swordfish sampled from the central Pacific nurseries (CENPO and CNPO) and Ba:Ca ratios were highest in the northern Pacific nurseries (CNPO and WNPO). Overall trace elemental signatures sufficiently differed among nurseries with overall classification success of 72.2%, with Sr:Ca molar ratios primarily driving discrimination followed by Mg:Ca and Ba:Ca, respectively. Using these nursery element:Ca molar ratios as a baseline, nursery-specific contribution estimates suggested that the CENPO nursery was the main contributor to the adult fishing grounds of HI, CA, and MX. These results complement a previous study that detected regional differences in otolith chemistry of swordfish sampled from several nurseries surrounding the Hawaiian Islands and in the Central Pacific Ocean (Humphreys et al., 2005).

Trends in Mg:Ca, Sr:Ca, and Ba:Ca otolith core ratios among the four nurseries may have been influenced, in part, by ambient water chemistry, sea surface salinity (SSS) and sea surface temperature (SST). Studies have indicated that temperature and salinity generally have a positive relationship with otolith Sr concentrations (Bath et al., 2000; Elsdon and Gillanders, 2002; Elsdon and Gillanders, 2003; Elsdon et al., 2008;

Kalish, 1989; Secor and Rooker, 2000). In this study, otolith core mean Sr:Ca ratios appeared to exhibit a positive relationship to both SSS and SST as ratios were higher in the CENPO and CNPO than in the EENPO and WNPO. 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 and Wuenschel, 2006; Morse et al., 1997), otolith core mean Mg:Ca ratios also appeared to exhibit a positive relationship to SSS in this study. YOY swordfish otolith cores of individuals sampled from the CNPO exhibited the highest mean Mg:Ca ratios, while the WNPO exhibited the lowest mean Mg:Ca ratios. The CENPO and CNPO are generally characterized by higher mean SSS (35.1 and 35.4 PSU, respectively) than the EENPO and WNPO (34.3 and 34.7 PSU, respectively). Both the EENPO and WNPO are located within regions influenced by freshwater contributions. The low SSS of the EENPO is due to a number of factors, including a “fresh pool” formed by heavy precipitation associated with the northward movement of the ITCZ and atmospheric moisture imported from the Atlantic Ocean over the Central America land barrier by the North Atlantic Trade Winds (Alory et al., 2012; Tomczak and Godfrey, 2013) as well as high riverine fresh water inputs from Central and northern South America during periods of intense seasonal rainfall (Fielder and Talley, 2006). Modern rivers have lower Mg:Ca ratios than seawater (Coggon et al., 2010) and the EENPO nursery may be influenced by riverine inputs from the San Juan and Patia rivers of Columbia and the Esmeraldas and Chone rivers of Ecuador which discharge approximately 260 km³ freshwater in the Pacific Ocean annually (Crossland et al., 2005). SSS of the WNPO is affected by multiple currents, including the

convergence of the cool, low salinity subarctic fresh waters of the Oyashio Current and the warm, high salinity equatorial waters of the Kuroshio Current (Tomczak and Godfrey, 2013). Moreover, the Amur River discharges approximately 390 km³ of fresh waters and sediments into the Sea of Okhotsk (Zhabin et al., 2010), which is carried through the Kuril Island straits and mixes with the Oyashio current (Talley and Nagata, 1995). Higher Mg:Ca ratios in the CNPO than in the CENPO, despite similar SSS, may indicate that swordfish otolith Mg:Ca ratios are negatively related to SST as SST was higher in the CENPO than in the CNPO (26.8°C and 23.6°C, respectively). Additionally, a combination of low SSS and high annual SST (25.1°C) may also have been a contributing factor to the EENPO's relatively low Mg:Ca otolith core ratios. Temperature has been shown to affect otolith Ba concentrations (Fowler et al., 1995; Elsdon and Gillanders, 2002, 2004; Miller, 2009, 2011) and in this study, mean otolith Ba:Ca ratios were highest in the CNPO and WNPO, which are generally characterized by lower SST (23.6°C and 20.7°C, respectively) than the CENPO and EENPO (26.8°C and 25.1°C, respectively). A previous otolith chemistry study of YOY swordfish also demonstrated this latitudinal trend, with otoliths sampled from regions located in higher latitudes having higher Ba concentrations than otoliths sampled from regions located in lower latitudes (Humphreys et al., 2005).

Differences in regional oceanographic conditions among the nurseries appears to have an effect on the trace element signatures of swordfish otoliths in the NPO; however, there are multiple factors that may also influence the incorporation of trace elements into the otolith. Analysis of environmental effects on otolith chemistry are

often complicated by the effects of growth rate on otolith deposition, interactions amongst environmental factors, and species specific environmental tolerances and differences in maintaining hydro-mineral balance (Elsdon et al., 2008; Kalish, 1989; Martin and Wuenschel, 2006). Swordfish, specifically, are known to complete vertical migrations (Palko et al., 1981). As the otolith transects analyzed on the YOY swordfish otoliths equate to the first ~60 days of life, it is unlikely that larval swordfish have developed the morphological features necessary to complete significantly deep dives this early in life (Bremer, 1994); thus it is unlikely that dives to deeper waters may affect YOY swordfish otolith core trace element signatures in this study. Diet has also been shown to affect otolith Sr and Ba concentrations (Buckel et al., 2004), although it has been estimated that 83-88% of Sr and 98% of Ba otolith concentrations are derived from the surrounding water (Farrell and Campana, 1996; Walther and Thorrold, 2006). Additionally, some studies have demonstrated that not only do temperature and salinity affect otolith elemental concentrations, but that interactions between these two factors, as well as between concentrations of the elements themselves, also have an effect on otolith elemental concentrations (Devries et al, 2005; Elsdon and Gillanders, 2004; Miller, 2011). Despite uncertainty as to how the ambient environment may specifically affect otolith chemistry, trace elements within the core of YOY swordfish otoliths show promise as a natural marker for retrospectively determining an individual's place of origin.

The use of otolith element signatures as natural markers of a region is at least partially dependent upon those signals remaining consistent among years. Multiple

studies on the otolith chemistry of other pelagic species have indicated that regional signatures may vary among years. Rooker et al. (2001) found that trace element signatures in the otoliths of juvenile Pacific bluefin tuna (*Thunnus orientalis*) varied among 3 annual cohorts collected in the East China Sea. Wells et al. (2012) also detected inter-annual variability in YOY yellowfin tuna (*Thunnus albacares*) otolith $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ in samples collected from the Philippines between two consecutive years, while samples collected from regions throughout the Pacific did not display inter-annual variability. More recently, Rooker et al. (2016) detected temporal variability in otolith $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ in YOY bigeye tuna (*Thunnus obesus*) in the far west Pacific Ocean as well as in otolith $\delta^{18}\text{O}$ in YOY yellowfin tuna in the far west and western equatorial Pacific Ocean between 2 consecutive years of sample. In this study, inter-annual variability was not significant for the overall element signature or for any of the individual element:Ca ratios in the CNPO during the years of collections (2000, 2002, 2004, 2005). Inter-annual 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), however, there was inter-annual variability in Sr:Ca between 2001 and 2002. This is 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 ratios tend to have a positive relationship with sea surface temperature and salinity, thus mean ratios may differ between years affected by ENSO. In this study, the CENPO experienced an ENSO El Nino warm period in 2002 and the mean otolith Sr:Ca ratio in 2002 was, in fact, higher than that of 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 are at least 150 $\mu\text{mol}:\text{mol}$ greater than the mean Sr:Ca ratios from the CNPO, EENPO, and WNPO. Additionally, classification success for the four nurseries was 68.5% when CENPO 2002 samples were excluded from analysis and 69.8% when CENPO 2001 samples were excluded from analysis. An investigation of inter-annual variability was not conducted on the EENPO and WNPO nurseries as these nurseries contain samples from only a single year. Overall inter-annual variability was also not investigated as samples were fisheries dependent, leading to unbalanced sampling among years, which did not allow for the testing of temporal stability of trace element signatures from all nurseries over all years of collections (2000 – 2005).

Mixed stock analysis predicted the nursery origin of the majority of adult individuals sampled from the fishing grounds of HI, CA, and MX were the CENPO and WNPO nurseries, although the percent composition of the HI fishing ground samples and the CA and MX fishing ground samples differ. Estimates of nursery origin using Mg:Ca, Sr:Ca, and Ba:Ca for adult swordfish samples collected from the HI fishing region suggest that the HI adult swordfish samples were sourced equally from the CENPO and WNPO, with negligible inputs from the CNPO and EENPO nurseries. This is particularly interesting as much of the HI fishing ground is located within the CNPO

nursery, suggesting that retention in this region may be low. Limited tagging data supports that swordfish are capable of large-scale migrations from the western North Pacific towards the central NPO (Takahashi, 2003) and that swordfish tagged in the central North Pacific have completed southbound migrations, although they were not tracked as far south as the equator (Dewar et al., 2011). These findings may also be supported by a study that detected genetic differences between swordfish larvae and swordfish adults collected from the CNPO, suggesting that mixing may occur within the Hawaiian Archipelago (Lu et al., 2016). Estimates of nursery origin for adult swordfish collected from the CA and MX fishing regions suggest that adult swordfish in our samples were sourced primarily from the CENPO, with minimal inputs from the WNPO and negligible inputs from the CNPO and EENPO nurseries. Tagging data supports these findings as swordfish movement between the west coast of the United States and the Baja California Peninsula towards the central NPO as well as the central equatorial Pacific have been observed (Dewar et al., 2011). Additionally, genetic studies may support that the CNPO may not contribute recruits to the MX fishery as differences were detected between swordfish sampled from Hawaii and Mexico (Sosa-Nishizaki et al., 1996). Lastly, our findings that the CNPO and EENPO may have contributed little to the adult samples of the CA and MX fisheries may be supported by a study which found that adult swordfish sampled from temperate waters off of the west coast of California and Mexico exhibited genetic differences from both larval swordfish from the tropical waters of the CNPO and adult swordfish sampled from the eastern NPO (ENPO) (Lu et al., 2016).

There are a number of potential sources of uncertainty in this study. First, not all swordfish spawning areas in the NPO were sampled and thus could not be included in the mixed stock model nursery baseline signatures. Accurate delineation of swordfish spawning seasons and grounds has not been accomplished for a number of reasons, including difficulties associated with sampling large areas of the Pacific Ocean, inconsistencies with sampling methods, and unequal sampling effort throughout the Pacific (Grall et al., 1983). The distribution of swordfish larvae in the Pacific Ocean appears to be closely associated with the 24°C isotherm, and ichthyoplankton surveys have found swordfish larvae throughout the northwest, north central, and central equatorial Pacific Ocean (Grall et al., 1983; Nishikawa et al., 1985) as well as the western and eastern equatorial Pacific Ocean (Palko et al., 1981, Nishikawa and Ueyanagi, 1974). Additionally, swordfish larvae have been found far offshore of Mexico in the EPO (Nishikawa and Ueyanagi, 1974) and studies of gonadal indices from mature female swordfish have indicated that there is reproductive activity in the vicinity of Baja California, Mexico (Hinton and Deriso, 1998). Missing baseline samples of YOY swordfish from other potential nurseries, such as the western equatorial Pacific Ocean, and specifically from a potential spawning and nursery area located near Baja California given its close proximity to the adult fishing grounds, may have an impact on the results of this study. The inclusion of additional nursery baselines could potentially alter the predictions of mixed stock analysis, either by indicating that the samples collected from the HI, CA, and MX fishing grounds originate from additional nurseries or by shifting predictions away from the CENPO and WNPO nurseries. Although it has

been assumed that swordfish do not migrate far during their first year of life (Gorbunova, 1969), there remains uncertainty as to how far swordfish larvae could have relocated from their respective natal grounds during the first ~60 days of life (the approximate age of the fish for the otolith material analyzed) and how far they may have relocated prior to sample. The unbalanced sampling design among years is also a source of uncertainty as the effects of interannual variability were unable to be evaluated for the EENPO and WNPO or for the nurseries overall. As both EENPO and WNPO YOY swordfish were sampled in one year, it was not possible to investigate whether trace element signatures from those regions were stable or not. Regional variability in trace element signatures could also have an impact on the results of this study as baseline signatures could be shifted, potentially leading to altered contribution estimates. Additionally, due to the unbalanced sample design among years, swordfish adults sampled from the fishing grounds of HI, CA, and MX were unable to be age class matched to the nurseries as all nurseries were not sampled during any year of the 2000 – 2005 YOY swordfish sampling period. 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 fishing grounds of HI, CA, and MX were used as representatives for large adult groups. Additionally, adult samples used in mixed stock analysis included individuals whose estimated ages indicate that they likely did not originate from the nurseries during the 2000 -2005 period of sample, particularly for the adult swordfish sampled from the HI fishing grounds.

Obtaining a better understanding of swordfish population structure in the NPO is essential for the effective management of this species. It has been hypothesized that swordfish adults may exhibit site fidelity to foraging grounds, with migrations towards shared spawning areas (Lu et al., 2016; Kolody and Davies, 2008); the gene flow between adults migrating from foraging areas separated by great distances and spawning in shared locations may explain why some genetic studies have indicated little to no genetic differences among groups sampled throughout the NPO (Chow and Takeyama, 2000; Reeb et al., 2000; Rosel and Block, 1995). Results of this study may lend support to this hypothesis as adults appear to originate from shared spawning areas, the CENPO in this instance. Results also suggest that the CENPO and WNPO nurseries may be important contributors to the adult fishing grounds of HI, CA, and MX. Additionally, this study highlights the potential importance of the central equatorial swordfish nursery as a source of swordfish recruits to all three fishing regions sampled in the NPO in this study. The central equatorial Pacific Ocean has also been referred to as a zone of high swordfish abundance (Hinton and Deriso, 1998) and the observation that swordfish reproduction occurs year-round in the equatorial Pacific Ocean (Palko et al., 1981) lends support to the hypothesis that the CENPO nursery may be a large contributor of swordfish recruits to the NPO. There were no substantial differences in the source of adult CA and MX swordfish, suggesting that these two fishing grounds may largely consist of recruits from the same nurseries. While this study resulted in moderate classification success among nurseries, this technique would likely benefit from the addition of stable isotope analysis and a more balanced nursery sample collection over a

span of multiple years to facilitate interannual comparisons. Furthermore, the inclusion of otoliths sampled from additional nursery grounds and the inclusion of additional adult fishing grounds may greatly improve classification accuracy and provide further insight into nursery contribution rates of swordfish recruits to adult fishing grounds in the NPO.

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APPENDIX A: YOY SWORDFISH RAW DATA

NURSERY	LACIPMS ID	MONTH	DAY	YEAR	Mg:Ca	Sr:Ca	Ba:Ca	EFL (CM)	SEX	LAT	LONG	ORIGINAL SAMPLE ID	VESSEL
CEPO	EQ10c	3	22	2002	38.137	1333.410	0.529	52.9	M	5° 32.4'N	161° 39.5'W	AD-0001	N/A
CEPO	EQ12Rc	3	18	2002	42.203	1311.855	0.799	61.7	F	6° 19.0'N	159° 06.5'W	AMC-0013	N/A
CEPO	EQ13Rc	3	11	2002	95.633	1401.378	2.008	61.5	F	2° 39.4'N	164° 55.3'W	BAL-0002	N/A
CEPO	EQ14Rc	3	15	2002	61.662	1507.165	0.825	55.3	F	6° 47.5'N	161° 17.2'W	BAL-0003	N/A
CEPO	EQ15Rc	3	15	2002	46.219	1389.905	0.890	63.1	M	6° 47.5'N	161° 17.2'W	BAL-0004	N/A
CEPO	EQ16Rc	3	16	2002	78.600	1318.045	0.507	51.6	M	6° 41.6'N	160° 45.0'W	BAL-0005	N/A
CEPO	EQ17c	3	22	2002	55.800	1444.649	0.773	55.8	F	6° 40.3'N	162° 16.6'W	BAL-0006	N/A
CEPO	EQ18Rc	3	22	2002	43.806	1604.755	0.770	61.1	M	6° 40.3'N	162° 16.6'W	BAL-0007	N/A
CEPO	EQ19Lc	3	25	2002	46.139	1358.219	1.087	56.4	F	6° 19.3'N	161° 36.9'W	GHF-0001	N/A
CEPO	EQ20L	3	15	2002	40.520	1356.894	0.859	60.9	F	6° 56.0'N	160° 42.0'W	GJG-0003	N/A
CEPO	EQ21c	2	13	2002	48.316	1482.792	1.390	58.3	F	6° 08.0'N	161° 15.0'W	GMB-0001	N/A
CEPO	EQ22Rc	3	4	2002	58.006	1270.317	1.257	64.4	M	7° 00.8'N	161° 15.6'W	CLJ-0038	N/A
CEPO	EQ23Rc	7	22	2001	63.307	1291.702	1.253	57.7	M	6° 45.3'N	161° 47.5'W	RWK-0001	N/A
CEPO	EQ24Lc	6	15	2001	64.436	1420.921	0.754	67.7	F	6° 31.7'N	164° 48.4'W	LLS-0002	N/A
CEPO	EQ25Rc	6	13	2001	75.347	1318.357	0.950	60.4	F	5° 00.1'N	162° 35.6'W	RXC-0002	N/A
CEPO	EQ26Lc	6	15	2001	61.005	1302.366	0.976	64.9	M	6° 31.7'N	164° 48.4'W	LLS-0001	N/A
CEPO	EQ27Lc	7	23	2001	54.257	1321.514	0.939	57.3	F	6° 41.2'N	161° 55.3'W	RWK-0002	N/A
CEPO	EQ28Lc	6	13	2001	102.144	1327.548	0.804	56.6	F	5° 00.1'N	162° 35.6'W	RXC-0003	N/A
CEPO	EQ29Lc	6	30	2001	52.284	1327.390	0.570	61.1	F	6° 07.2'N	165° 04.5'W	LMS-0008	N/A
CEPO	EQ30Lc	3	19	2002	66.540	1248.965	0.689	64.1	F	6° 40.5'N	163° 47.6'W	KJG-0002	N/A
CEPO	EQ31Rc	3	18	2002	63.617	1472.812	2.312	66	M	6° 43.7'N	163° 45.4'W	JWB-0009	N/A
CEPO	EQ32Lc	3	14	2002	57.203	1372.888	0.697	60.4	M	5° 46.3'N	161° 26.7'W	QJB-0003	N/A
CEPO	EQ35c	4	23	2002	90.930	1291.796	0.608	56.1	F	0° 45'S	160° 12.7'W	MKZ-0011	N/A
CEPO	EQ36Rc	6	9	2001	111.933	1220.445	2.532	56.4	F	6° 10.2'N	163° 23.2'W	RXC-0001	N/A
CEPO	EQ6Rc	10	6	2001	37.475	1320.924	0.549	55.3	M	5° 38.0'N	164° 39.8'W	CDM-0001	N/A

NURSERY	LACIPMS ID	MONTH	DAY	YEAR	Mg:Ca	Sr:Ca	Ba:Ca	EFL (CM)	SEX	LAT	LONG	ORIGINAL SAMPLE ID	VESSEL
CEPO	EQ7Rc	7	31	2001	95.764	1253.491	1.471	53.5	F	5° 05.6'N	162° 27.3'W	DCS-0032	N/A
CEPO	EQ8Lc	6	8	2001	38.732	1226.992	0.575	56	M	5° 14.5'N	161° 34.4'W	JAM-0003	N/A
CEPO	EQ9Lc	8	21	2001	35.729	1154.759	0.645	73.4	M	2° 45.1'N	167° 05.2'W	JAM-0004	N/A
CNPO	C10R	11	5	2000	92.008	1041.181	1.200	63.5	M	20° 52.1'N	163° 12.7'W	RZM-0002	N/A
CNPO	C11Ra	10	5	2000	51.798	1284.250	1.878	62	F	19° 38.2'N	160° 08.9'W	BLB-0004	N/A
CNPO	C12R	9	21	2000	56.055	1054.680	1.252	62.3	M	23° 48.1'N	156° 56.5'W	JWD-0040	N/A
CNPO	C13Ra	10	4	2000	63.051	1257.762	1.606	66.6	F	19° 47.5'N	160° 25.8'W	BLB-0003	N/A
CNPO	C14R	9	22	2000	69.311	1065.538	1.500	56.5	F	24° 41.1'N	156° 23.6'W	JWD-0041	N/A
CNPO	C15Ra	10	1	2000	72.646	1364.993	2.974	74.9	M	19° 57.3'N	160° 00.6'W	CWG-0001	N/A
CNPO	C16R	10	26	2000	84.116	1088.127	0.828	61.2	F	18° 44.8'N	159° 08.1'W	ADS-0002	N/A
CNPO	C1Rp	10	27	2000	70.674	895.476	0.744	67.1	F	20° 48.6'N	163° 48.5'W	BLB-0005	N/A
CNPO	C2Ra	10	27	2000	58.930	1051.133	0.943	60.4	M	20° 48.6'N	163° 48.5'W	BLB-0006	N/A
CNPO	C3La	10	27	2000	54.436	1204.868	3.531	62.5	F	20° 48.6'N	163° 48.5'W	BLB-0007	N/A
CNPO	C4R	12	24	2000	73.080	929.921	0.631	67.7	M	22° 21.2'N	161° 16.0'W	JET-0009	N/A
CNPO	C5La	11	20	2000	80.571	1061.848	0.530	62.2	F	21° 44.5'N	166° 16.6'W	RMB-0001	N/A
CNPO	C6R	9	30	2000	73.123	1184.458	1.059	69	M	19° 54.4'N	159° 19.1'W	BLB-0001	N/A
CNPO	C7L	9	25	2000	51.428	1012.876	0.904	71.1	M	21° 58.0'N	154° 19.0'W	JWD-0043	N/A
CNPO	C8	10	1	2000	102.041	1040.262	1.260	63.7	F	19° 21.8'N	160° 11.5'W	BLB-0002	N/A
CNPO	C9Ra	9	25	2000	65.515	1230.046	3.229	61.1	M	21° 58.0'N	154° 19.0'W	JWD-0044	N/A
CNPO	NP10Lc	9	14	2002	68.335	1238.696	2.019	56.5	M	28° 41.7'N	156° 58.7'W	MDC-0002	N/A
CNPO	NP18c	3	U	2004	100.458	959.120	1.625	82.6	F	28° 24'N	167° 04'W	5/28-15	Koshin Maru No. 7
CNPO	NP19Lc	3	U	2004	81.424	974.080	1.490	71	M	29° 07'N	167° 04'W	4/19-07	Koshin Maru No. 7
CNPO	NP1Lc	9	1	2002	70.044	1199.548	1.351	65.1	F	29° 02.5'N	157° 35.4'W	AMC-0015	N/A
CNPO	NP22Lc	3	U	2004	71.325	1140.506	1.482	75.8	M	29° 12'N	167° 13'W	4/19-1	Koshin Maru No. 7
CNPO	NP23Lc	3	U	2004	77.427	1073.789	0.901	88	F	29° 00'N	166° 58'W	4/19-6	Koshin Maru No. 7
CNPO	NP24Rc	3	U	2004	48.850	1255.690	2.477	78.2	F	29° 22'N	167° 39'W	5/28-10	Koshin Maru No. 7
CNPO	NP25Lc	3	U	2004	61.889	1046.486	1.296	83.5	F	29° 19'N	167° 36'W	4/19-4	Koshin Maru No. 7
CNPO	NP27Rc	3	U	2004	61.893	1288.094	2.112	80.5	M	29° 13'N	167° 10'W	4/19-3	Koshin Maru No. 7
CNPO	NP28Rc	3	U	2004	151.330	952.164	2.980	76	M	29° 16'N	167° 39'W	5/28-11	Koshin Maru No. 7
CNPO	NP29Lc	3	U	2004	71.132	897.675	0.928	86.5	F	29° 12'N	167° 41'W	4/19-5	Koshin Maru No. 7

NURSERY	LACIPMS ID	MONTH	DAY	YEAR	Mg:Ca	Sr:Ca	Ba:Ca	EFL (CM)	SEX	LAT	LONG	ORIGINAL SAMPLE ID	VESSEL
CNPO	NP2Lc	9	11	2002	56.150	1004.921	1.456	63.9	F	28° 36.6'N	157° 06.1'W	LAJ-0015	N/A
CNPO	NP30Rc	3	U	2004	136.199	1361.455	2.500	73.4	M	29° 10'N	167° 24'W	5/28-8	Koshin Maru No. 7
CNPO	NP31Lc	3	U	2004	81.620	1182.314	1.243	78.1	M	29° 13'N	167° 21'W	5/28-14	Koshin Maru No. 7
CNPO	NP32Rc	3	U	2004	68.031	1152.388	1.499	85.4	M	29° 18'N	167° 17'W	5/28-2	Koshin Maru No. 7
CNPO	NP34Lc	3	U	2004	121.166	1131.588	1.542	76.6	F	29° 16'N	167° 24'W	5/28-3	Koshin Maru No. 7
CNPO	NP35Lc	3	U	2004	75.922	1227.735	1.740	78.4	M	29° 14'N	167° 50'W	5/28-13	Koshin Maru No. 7
CNPO	NP36Lc	3	U	2004	63.923	1043.365	2.875	92	M	29° 13'N	167° 33'W	5/28-4	Koshin Maru No. 7
CNPO	NP37Lc	3	U	2004	67.494	1001.622	1.477	76.2	M	29° 10'N	167° 39'W	5/28-9	Koshin Maru No. 7
CNPO	NP38Lc	9	7	2005	65.817	1168.963	1.611	53	U	31° 57'N	160° 49'W	LL1805-07-02-04	N/A
CNPO	NP39c	9	19	2005	68.830	1265.729	1.615	61	U	32° 15'N	160° 36'W	LL1825-17-02-04	N/A
CNPO	NP3Lc	9	10	2002	57.224	1043.238	4.015	73.5	M	28° 29.6'N	157° 29.6'W	LAJ-0013	N/A
CNPO	NP40Rc	9	18	2005	55.045	974.283	1.290	70	U	32° 00'N	159° 58'W	LL1825-16-01-02	N/A
CNPO	NP5Lc	9	10	2002	79.819	1062.090	2.511	64.6	M	28° 36.6'N	157° 06.1'W	LAJ-0014	N/A
CNPO	NP6Lc	2	21	2002	57.366	1121.033	2.003	76.6	M	30° 27.3'N	163° 26.5'W	CJV-0005	N/A
CNPO	NP7Lc	9	11	2002	69.208	1263.329	2.512	61.5	M	28° 56.3'N	157° 12.1'W	JDP-0007	N/A
CNPO	NP8Rc	9	14	2002	50.409	1204.692	1.900	60.3	M	28° 32.8'N	156° 57.8'W	JDP-0008	N/A
CNPO	NP9Lc	9	12	2002	58.578	1149.128	4.039	58.2	F	28° 37.9'N	157° 19.8'W	LAJ-0016	N/A
EEPO	E10Rc	U	U	2005	35.257	817.380	0.308	U	U	U	U	200607-10-04	N/A
EEPO	E11Rc	12	23	2005	37.333	1073.667	1.149	96.5	U	U	U	CS-106	N/A
EEPO	E13Rc	12	23	2005	59.524	1319.255	3.572	98	U	U	U	CS-107	N/A
EEPO	E15Lc	6	15-20	2005	42.366	826.349	0.388	81	U	00° 02'S	93° 15'W	200607-11-05#33	N/A
EEPO	E16Lc	12	29	2005	48.806	1270.711	1.500	96.5	U	U	U	(BE)114	N/A
EEPO	E17Lc	7	29	2005	51.607	897.678	0.590	87	U	U	U	200607-11-08#58	N/A
EEPO	E18Lc	U	U	2005	42.238	774.783	0.535	U	U	U	U	200607-10-02	N/A
EEPO	E19Rc	12	16	2005	53.205	1366.370	1.023	99.7	U	04° 40'N	83° 50'W	(BE)113	N/A
EEPO	E1Lc	12	1	2005	61.794	1150.376	2.289	99	U	U	U	(DT)101	N/A
EEPO	E22Pc	6	15-20	2005	54.710	694.392	0.392	96	U	00° 02'S	93° 15'W	2006-13-12#36	N/A
EEPO	E24Lc	7	28	2005	27.581	733.750	0.302	93	U	U	U	200607-11-04#61	N/A
EEPO	E2Rc	12	7-25	2005	53.003	1244.427	0.859	98.5	U	03° 03'N	84° 40'W	(EP)111	N/A
EEPO	E3Rc	12	15	2005	71.334	1206.235	1.639	99.5	U	03° 40'N	83° 50'W	(BE)112	N/A

NURSERY	LACIPMS ID	MONTH	DAY	YEAR	Mg:Ca	Sr:Ca	Ba:Ca	EFL (CM)	SEX	LAT	LONG	ORIGINAL SAMPLE ID	VESSEL
EEPO	E5Rc	6	15-20	2005	30.699	840.627	0.768	94	U	00° 02'S	93° 15'W	200607-13-13#28	N/A
EEPO	E6Lc	12	11	2005	34.418	985.382	0.685	91	U	U	U	(EJ)104	N/A
EEPO	E8Rc	12	11	2005	66.376	1117.863	1.676	99	U	U	U	(LMR)103	N/A
WNPO	WP10c	1	5	2004	47.481	1206.246	1.655	90.2	F	39° 01'N	151° 48'E	2/9--1	Shinei-maru No. 16
WNPO	WP11Rc	2	29	2004	46.806	1292.129	1.833	74.2	M	31° 30'N	157° 47'E	4/5--4	Shinei-maru No. 17
WNPO	WP12Lc	1	19	2004	37.131	1021.509	1.097	90.7	M	32° 14'N	149° 04'E	2/9--5	Shinei-maru No. 16
WNPO	WP13Rc	4	11	2004	58.192	1334.995	2.875	91.7	M	34° 16'N	163° 23'E	4/26--4	Shinei-maru
WNPO	WP14Rc	1	20	2004	34.293	1184.285	1.309	94.4	M	31° 8'N	143° 26'E	2/9--6	Shinei-maru No. 16
WNPO	WP15Lc	1	27	2004	38.125	1225.882	4.538	66.1	M	32° 4'N	144° 00'E	2/9--10	Shinei-maru No. 16
WNPO	WP16R	3	28	2004	50.871	896.931	0.493	87	F	27° 6'N	162° 10'E	4/26--1	Shinei-maru
WNPO	WP17Rc	3	1	2004	52.179	938.810	1.017	74.2	M	31° 17'N	157° 38'E	4/5--5	Shinei-maru No. 17
WNPO	WP18Lc	3	31	2004	55.904	1136.858	0.916	83.2	F	27° 31'N	162° 22'E	4/26--2	Shinei-maru
WNPO	WP19c	4	11	2004	52.932	1008.378	0.738	91.7	M	34° 16'N	163° 29'E	4/26--4	Shinei-maru
WNPO	WP1Lc	2	28	2004	47.057	1009.953	1.703	73.8	M	31° 03'N	157° 26'E	4/5--3	Shinei-maru No. 17
WNPO	WP20Lc	1	26	2004	62.876	982.881	0.833	72	M	32° 06'N	143° 34'E	2/9--9	Shinei-maru No. 16
WNPO	WP21Rc	1	17	2004	40.727	880.909	0.906	88.3	F	32° 19'N	143° 25'E	2/9--3	Shinei-maru No. 16
WNPO	WP3Rc	1	19	2004	30.361	889.405	1.220	74.2	F	32° 07'N	143° 25'E	2/9--4	Shinei-maru No. 16
WNPO	WP4Lc	2	27	2004	35.971	1150.075	3.505	70.2	M	31° 45'N	157° 23'E	4/5--2	Shinei-maru No. 17
WNPO	WP5Lc	2	19	2004	45.064	1221.019	1.920	75	F	31° 02'N	154° 54'E	3/15--4	Shinei-maru No. 16
WNPO	WP6Lc	2	15	2004	35.907	992.795	1.396	74.2	F	31° 02'N	154° 54'E	3/15--3	Shinei-maru No. 16
WNPO	WP7Lc	2	13	2004	34.405	1170.537	2.871	72.7	F	33° 21'N	154° 12'E	3/15--1	Shinei-maru No. 16
WNPO	WP8c	1	21	2004	39.555	1128.452	1.121	76.2	F	31° 23'N	143° 46'E	2/16--1	Shinei-maru No. 17
WNPO	WP9Lc	2	22	2004	53.616	1113.500	3.470	68.7	M	31° 10'N	155° 25'E	3/15--5	Shinei-maru No. 16

APPENDIX B: ADULT SWORDFISH RAW DATA

FISHING REGION	LACIPMS ID	MONTH	DAY	YEAR	Mg:Ca	Sr:Ca	Ba:Ca	EFL (CM)	LAT	LONG	ORIGINAL SAMPLE ID
HI	HI1S	11	19	2014	43.353	1259.115	0.600	200	U	U	LL5125-05-01-01
HI	HI10	3	8	2015	44.365	1193.141	2.368	118	30.5817	-155.3267	LL5225-13-01-08
HI	HI12	1	27	2015	31.809	1233.458	1.517	137	32.4000	-154.0417	LL5204-01-02-08
HI	HI13	12	5	2014	44.150	1308.717	0.676	110	23.9083	-157.3117	LL5150-02-05-10
HI	HI14	11	6	2014	40.612	1264.246	2.589	127	24.8550	-155.9933	LL5111-09-04-04
HI	HI16	10	29	2014	41.150	1440.419	0.794	120	20.0567	-153.3533	LL5105-06-02-10
HI	HI17	12	11	2014	34.397	1160.643	2.197	124	23.2833	-158.5300	LL5154-05-04-12
HI	HI18	2	19	2015	32.974	1171.395	1.988	172	32.9367	-148.6133	LL5215-03-02-01
HI	HI20	12	19	2014	44.392	1451.659	0.902	121	18.2117	-162.0917	LL5160-07-03-14
HI	HI21	2	19	2015	37.988	1128.390	0.726	144	32.9367	-148.6133	LL5215-03-02-15
HI	HI22	12	5	2014	32.633	1399.614	0.972	116	23.9083	-157.3117	LL5150-02-02-05
HI	HI24	1	28	2015	39.815	1311.405	0.569	165	32.2217	-154.1517	LL5204-02-01-14
HI	HI25	1	7	2014	42.977	1397.659	1.695	161	32.4000	-154.0417	LL5204-01-02-07
HI	HI26	12	13	2014	38.794	1165.530	1.527	110	23.4083	-158.5700	LL5150-09-04-07
HI	HI27	12	8	2014	38.517	1285.260	0.934	144	21.3950	-168.4400	LL5147-11-04-03
HI	HI4	10	22	2014	51.869	1250.807	1.195	114	26.6750	-151.4150	LL5099-07-03-10
HI	HI5	2	20	2015	44.615	1235.902	2.103	126	32.3383	-148.6150	LL5215-04-01-05
HI	HI6	3	5	2015	35.606	1280.128	3.423	153	29.9100	-152.7617	LL5225-11-01-01
HI	HI7	1	28	2015	41.911	1095.892	2.020	110	32.2217	-154.1517	LL5204-02-01-15
HI	HI8	12	16	2014	38.938	1092.471	0.781	127	23.6033	-155.8100	LL5152-09-02-11
HI	HI9	12	21	2014	69.968	917.519	0.355	170	18.2950	-161.7067	LL5160-08-03-07

FISHING REGION	LACIPMS ID	MONTH	DAY	YEAR	Mg:Ca	Sr:Ca	Ba:Ca	EFL (CM)	LAT	LONG	ORIGINAL SAMPLE ID
CA	C1S	9	28	2012	39.484	1170.173	2.441	197	32.6970	-117.5700	MLK0035S
CA	CA10	11	24	2013	43.792	1013.791	0.666	136	32.3380	-119.7550	JOV0097S
CA	CA11	9	30	2012	37.863	1384.464	1.209	168	32.6170	-118.3920	CXL0287S
CA	CA13	1	17	2014	41.974	1218.309	1.386	147	31.9070	-118.3020	HRC0040S
CA	CA16	11	24	2013	44.150	1308.717	0.676	140	32.3380	-119.7550	JOV0095S
CA	CA17	11	1	2013	40.424	1156.978	1.856	179	32.6480	-118.7450	TRJ0007S
CA	CA18	11	25	2013	38.123	1353.188	0.551	190.5	39.1030	-124.3830	CXL0406S
CA	CA19	11	24	2013	49.451	1602.910	2.088	148	32.3380	-119.7550	JOV0096S
CA	CA20B	11	24	2013	56.651	1197.784	1.223	159	32.3380	-119.7550	JOV0099S
CA	CA22	11	9	2013	35.078	1374.202	0.624	150	32.1880	-119.2550	JOV0089S
CA	CA23	10	24	2013	59.992	1342.681	1.507	158	33.0030	-120.8400	JSP0226S
CA	CA24	11	4	2013	44.221	1340.726	1.072	173.9	32.5330	-118.2300	CXL0390S
CA	CA25	11	24	2013	41.535	1322.645	1.479	160	32.3380	-119.7550	JOV0098S
CA	CA26	11	27	2013	34.299	1462.166	2.303	124	32.2300	-118.2480	HRC0027S
CA	CA27	11	20	2013	37.630	1202.426	0.569	191	39.7880	-125.4650	JSP0242S
CA	CA28	12	15	2012	39.708	1425.759	0.401	196	36.6880	-124.0650	MLK0058S
CA	CA29	10	24	2013	50.418	1457.279	0.852	192	33.0030	-120.8400	JSP0228S
CA	CA30	11	25	2013	38.230	1399.614	0.920	193.8	39.1030	-124.3830	CXL0408S
CA	CA31	12	14	2013	29.606	1656.910	0.416	194	35.6550	-124.3620	JOV0108S
CA	CA6	10	2	2012	35.768	1252.273	0.595	180	32.7120	-117.6150	CXL0289S
CA	CA8	11	1	2013	38.105	1257.893	1.007	169	32.7380	-118.5280	707-06
CA	CA9	1	16	2014	38.911	1390.084	1.668	187	32.8720	-118.3170	HRC0039S

FISHING REGION	LACIPMS ID	MONTH	DAY	YEAR	Mg:Ca	Sr:Ca	Ba:Ca	EFL (CM)	LAT	LONG	ORIGINAL SAMPLE ID
MX	M1S	3	20	2013	58.210	1630.765	1.412	180.0	24.9167	-112.9000	10
MX	MX10	11	12	2013	67.263	1359.297	1.235	123.3	26.4833	-114.0600	36
MX	MX11	11	8	2013	59.213	1517.877	0.437	151.3	26.6833	-114.1067	32
MX	MX12	12	10	2013	39.690	1360.518	1.161	152.2	24.9883	-113.6733	67
MX	MX13	10	26	2013	35.087	1601.443	3.066	141.0	23.4950	-111.8400	25
MX	MX15	12	10	2013	41.974	1218.309	1.386	151.3	24.9883	-113.6733	66
MX	MX16	11	21	2013	45.457	1180.680	4.942	132.6	24.7417	-112.9783	46
MX	MX19	12	8	2013	37.335	1016.968	1.310	152.2	24.7367	-113.2133	63
MX	MX20	11	22	2013	43.505	1447.750	2.893	142.0	24.8350	-113.1183	49
MX	MX21	12	18	2013	58.953	1231.748	1.351	149.4	25.5933	-114.9150	77
MX	MX22	12	16	2013	41.105	1365.894	0.716	153.2	25.1617	-113.0000	74
MX	MX23	11	24	2013	52.854	1336.572	1.157	144.8	24.7067	-112.9150	54
MX	MX24	11	28	2013	42.314	1257.893	1.463	152.2	25.9917	-113.5817	61
MX	MX26	11	21	2013	41.033	1559.905	1.786	188.7	24.7417	-112.9783	44
MX	MX27	11	25	2013	47.938	1639.561	2.031	171.9	26.4833	-114.0600	37
MX	MX28	11	25	2013	37.783	1178.236	0.917	164.4	25.2867	-113.4883	58
MX	MX29	11	25	2013	45.833	1552.574	3.180	184.9	25.2867	-113.4883	56
MX	MX30	12	15	2013	30.108	1259.603	1.327	190.5	25.2850	-113.6283	72
MX	MX6	10	20	2013	41.194	1106.399	1.805	153.2	23.3650	-111.7933	16
MX	MX8	10	24	2013	41.821	1143.783	1.632	149.4	23.3083	-111.6067	22
MX	MX9	12	7	2013	37.111	1134.498	1.043	153.2	24.6717	-113.1900	62