Assessing residency and movement dynamics of swordfish *Xiphias gladius* in the Eastern North Pacific Ocean using stable isotope analysis

Tatiana A. Acosta-Pachón[1,3,*], Sofía Ortega-García[1], Brittany Graham[2]

[1]Instituto Politécnico Nacional-CICIMAR, Departamento de Pesquerías y Biología Marina, La Paz,
Baja California Sur 23096, Mexico

[2]National Institute of Water and Atmospheric (NIWA) Research Ltd., Wellington 6021, New Zealand

[3]*Present address:* Universidad Autónoma de Baja California Sur, Departamento Académico de
Ciencias Marinas y Costeras, La Paz, Baja California Sur 23080, Mexico

ABSTRACT: Swordfish are migratory fish that inhabit tropical to temperate waters, but little is known about movement patterns or mixing between subpopulations of this species. This study examines carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios in growth rings of the anal fin spine and muscle tissue of swordfish from 3 different areas of the Eastern North Pacific Ocean (ENPO) — off Baja California Sur (Mexico) and California (USA), and in the North Pacific Subtropical Gyre (NPSG) — to assess swordfish movements between these areas. The analysis of $\delta^{13}C$ and $\delta^{15}N$ revealed no relationship between fish size and $\delta^{15}N$, suggesting a consistent consumption of prey items by this species over time. Differences between the anal fin spine and muscle were found, but interpreting these isotopic differences requires information on tissue-specific isotope turnover rates. The spatial pattern suggests that swordfish populations from these areas in the ENPO exhibit a relatively unexpected homing behavior at the temporal scale, according to anal spine and muscle turnover rates. Our findings support that swordfish may show site fidelity, which has important implications for their management and stock assessments.

KEY WORDS: Billfish · $\delta^{13}C$ · $\delta^{15}N$ · Muscle · Anal fin spine

1. INTRODUCTION

Swordfish *Xiphias gladius* are an economically and ecologically important species. From the ecological point of view, this species is a top-level predator that can impact food web dynamics (Kitchell et al. 2006). Swordfish are caught in the Eastern North Pacific Ocean (ENPO) using various fishing gear, including small- and large-scale longline fisheries, gillnet, harpoon, and, occasionally, recreational hook and line. Set longlines are the most common gear used to target this species; in 2012, longline swordfish catch in the ENPO was 20 000 t (IATTC 2014). Despite its importance in commercial fisheries, limited informa-

tion is available on the biology and ecology of this species (Young et al. 2003, Abascal et al. 2010, Dewar et al. 2011, Hinton & Maunder 2011, Evans et al. 2014).

The scarce information available about swordfish movements in the North Pacific has either been obtained from tagging studies or inferred from catch data. This information suggests that swordfish migrate to temperate or cold waters in summer for feeding and then return to warm waters in autumn for spawning and overwintering (Nakamura 1985). However, such movements have not been sufficiently documented yet. In some regions, spawning and foraging areas are in close proximity, reducing the migration scale (Evans et al. 2014). The horizontal

movements of swordfish in the North Pacific Ocean have been analyzed in previous studies (Carey & Robinson 1981, Abascal et al. 2010, Sepulveda et al. 2010, Dewar et al. 2011, Abecassis et al. 2012). However, little is known about their spatial extent, migration patterns, mixing rates, and whether fish return to same location in subsequent years, due to relatively small sample sizes and short tracking periods (less than 1 yr) (Abascal et al. 2010, Dewar et al. 2011). Previous studies have suggested the possibility of long-distance migrations; Dewar et al. (2011) reported a maximum distance of 2404 km in 60 d and 2528 km in 90 d.

Swordfish migration is complex and multidirectional (Palko et al. 1981), as their longitudinal movements do not seem to follow any particular pattern (Sedberry & Loefer 2001, Abecassis et al. 2012). Nevertheless, correlations have been found between oceanographic variables and the occurrence of swordfish; in particular, the presence, position, and strength of convergent and temperature fronts are key drivers of a high catch per unit effort (Podestá et al. 1993, Olson & Polovina 1999, Seki et al. 2002). Both conventional and satellite-tagging programs have reported a range of movement patterns away from tagging locations. Some tagged swordfish have been recovered near the point of release several years later (Beckett 1974), which would imply a homing behavior (Carey & Robinson 1981).

Kolody et al. (2008) explored alternative spatial assumptions related to homogeneous mixing vs. site fidelity with seasonal migration in swordfish collected in the Southwest Pacific. They concluded that the current assumption about migration has to be revisited within the context of a broader spatial scale. Tagging studies seemingly confirm that swordfish undergo directed seasonal migrations between temperate feeding areas and tropical spawning zones, but the level of fidelity to those sites is still unclear (Kolody et al. 2008). Moreover, the main prey items of swordfish should be identified to elucidate their feeding areas and obtain further information on migration patterns. Stomach content analyses have shown that swordfish feed primarily on squids such as *Dosidicus gigas*, teuthid cephalopods, and octopuses in waters off the Baja California Peninsula, Mexico (Markaida & Hochberg 2005). In California (USA), the most important prey include cephalopods (*D. gigas*) and fish of the orders Aulopiformes and Myctophiformes (Preti et al. 2015). In Baja California Sur (Mexico), the main prey items are cephalopods, including *D. gigas*, *Gonatus* spp., and *Argonauta* spp., followed by chub mackerel *Scomber*

japonicus (Trujillo-Olvera et al. 2018). According to Chancollon et al. (2006) and Young et al. (2006), the diet of swordfish changes with fish size; the diet of small swordfish may include a larger proportion of fish, while adults prefer to consume squids. However, Clarke et al. (1995) and Trujillo-Olvera et al. (2018) found no differences in the diet with respect to size or sex. Thus, further research is necessary to understand the feeding ecology of swordfish and the relationship of this species in the community.

Stable isotope analysis (SIA) is an alternative tool in ecology that is useful for understanding the feeding and migration patterns of organisms. It is a relatively cost-effective and rapid technique for studying long-distance migratory connectivity, as well as for tracking animals across a variety of taxa, which is useful for addressing questions at the population level (Hobson 1999, 2008, Carlisle et al. 2012, 2015, Trueman et al. 2012, Vander Zanden et al. 2015). Stable isotope composition of an organism depends on its trophic level, which is defined by diet, and on the isotopic signature at the base of the food web, which varies between regions (DeNiro & Epstein 1978, 1981, Graham et al. 2010), reflecting food web features at the local scale (Peterson & Fry 1987, Hobson 2008, Graham et al. 2010). Values of $\delta^{13}C$ ($^{13}C/^{12}C$) can be used to determine the source of primary production (e.g. inshore versus offshore), its contribution to food intake, and movements between different ecosystems (DeNiro & Epstein 1978, Peterson & Fry 1987, Fry et al. 1998). Values of $\delta^{15}N$ ($^{15}N/^{14}N$) are used not only as an indicator of the trophic position of a predator (DeNiro & Epstein 1981), but also to examine its movement patterns, since baseline nitrogen isotope values in the ocean show geographic variations (Graham et al. 2010) due to the different oceanic processes affecting them (Rau et al. 1982, Gruber & Sarmiento 1997, Altabet et al. 1999, Voss et al. 2001, Madigan et al. 2012a, Carlisle et al. 2015). For example, $\delta^{13}C$ values show a gradient between nearshore/benthic versus offshore/pelagic food webs, with $\delta^{13}C$ values increasing from offshore oligotrophic to nearshore productive ecosystems (Rau et al. 1982, France 1995). However, $\delta^{15}N$ values at the base of the food web are regulated by nutrient use, source (e.g. nitrate, ammonium, N_2) used by primary producers (Wada & Hattori 1976, Sigman et al. 1997, Altabet et al. 1999, Voss et al. 2001), and the differential influence of biological processes (e.g. denitrification, N_2 fixation, and isotopic fractionation) associated with nitrogen assimilation dynamics (Gruber & Sarmiento 1997, Montoya et al. 2002). In the eastern basin of the Pacific Ocean, these patterns generally

result in offshore oligotrophic regions depleted of ^{15}N due to the predominance of N_2 fixation, while coastal regions are enriched from the upwelling of ^{15}N-enriched nitrate increasing baseline isotope values (Saino & Hattori 1987, Sigman et al. 1997, Altabet et al. 1999, Altabet 2001).

Recent SIA studies have shown the advantage of simultaneously analyzing $\delta^{13}C$ and $\delta^{15}N$ to better characterize overall patterns of niche variation (Layman et al. 2007, Semmens et al. 2009, Jackson et al. 2011). For instance, bi- or multivariate analyses (e.g. simultaneous analysis of $\delta^{13}C$ and $\delta^{15}N$ isotopic plots) help to identify potential correlations between variables, which are not possible with univariate analyses (Zar 1999).

The purpose of this study was to examine intraspecific and spatial differences in stable isotope composition of muscle and spine bone of swordfish in the Eastern North Pacific Ocean (ENPO). In particular, we aimed to (1) examine the relationship of $\delta^{13}C$ and $\delta^{15}N$ values in muscle and spine bone with fish size; (2) determine the relationship between $\delta^{13}C$ and $\delta^{15}N$ mean values in muscle and the last growth band in the anal spine bone, to provide a context for comparing the 2 tissues; and (3) compare $\delta^{13}C$ and $\delta^{15}N$ values from both tissues in swordfish caught in 3 different locations in the ENPO, considering that the tissues analyzed would reflect different timescales, namely years (muscle, based on tuna information) and ontogenetic reconstruction (spine bones).
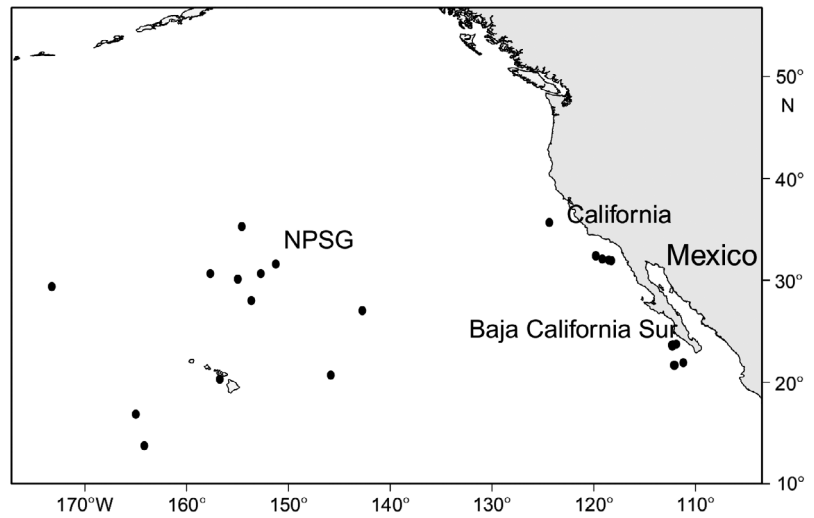

Fig. 1. Regions in the Pacific Ocean where swordfish *Xiphias gladius* aggregate and were caught for tissue sample collection between 2012 and 2014: Baja California Sur, Mexico; California, USA; and the North Pacific Subtropical Gyre (NPSG). Each dot represents one swordfish individual

Table 1. Number of samples, mean lower jaw fork length (LJFL, cm), mean values of $\delta^{15}N$ and $\delta^{13}C$, and C/N ratios (±SD) of swordfish *Xiphias gladius* from the 3 different areas (NPSG: North Pacific Subtropical Gyre; BCS: Baja California Sur), separated by tissue type

Area	Year	Samples	LJFL (cm)	$\delta^{15}N$	$\delta^{13}C$	C/N
Anal spine						
NPSG	2012	15	143.9	10.2 (±0.59)	−15.4 (±0.49)	3.76 (±0.43)
BCS	2013	15	168.0	14.7 (±1.13)	−14.8 (±0.96)	3.55 (±0.23)
California	2014	14	190.7	13.2 (±1.46)	−13.8 (±1.04)	3.31 (±0.30)
Muscle						
NPSG	2012	13	143.9	13.6 (±1.79)	−17.8 (±0.40)	3.46 (±0.62)
BCS	2013	14	168.0	16.6 (±1.23)	−18.2 (±1.63)	3.64 (±0.32)
California	2014	14	190.7	14.7 (±0.89)	−21.1 (±1.85)	8.13 (±2.82)

2. MATERIALS AND METHODS

2.1. Field collection

Samples of the second anal spine (A2) and muscle were obtained from 15 swordfish individuals from each of 3 regions (total n = 45): Baja California Sur (BCS), Mexico; the southern California Bight (CA), USA; and the North Pacific Subtropical Gyre (NPSG) (Fig. 1, Table 1). Fish were caught between 2012 and 2014 either during commercial longline or drift gill-

net operations or by research cruises (BCS). The geographic location and the lower jaw fork length (LJFL, cm) of each swordfish were recorded, except for the specimens caught off CA, for which eye fork length (EFL, cm) was measured. We used the LJFL–EFL conversion equation derived by Sun et al. (2002) to estimate LJFL for the fish from CA:

$$LJFL = 1.0647EFL + 7.7911 \ (df = 563 \text{ and } r^2 = 0.99) \quad (1)$$

The entire anal fin, including the condyle, was collected for analysis to ensure that A2 was obtained complete (Fig. 2). A2 is the source most commonly used for age determination in swordfish (Berkeley & Houde 1983, Tserpes & Tsimenides 1995, Ehrhardt et al. 1996, Cerna 2009). A complete growth ring comprises a wide opaque zone followed by a narrow
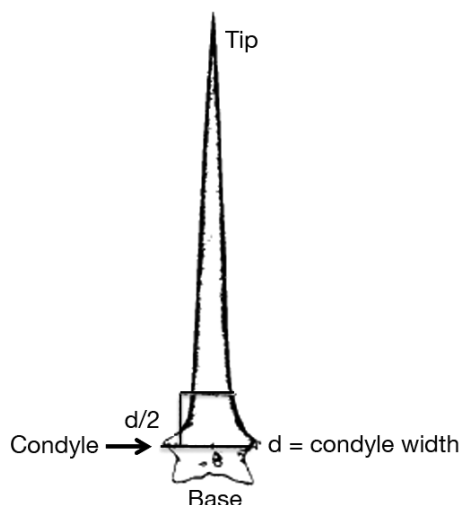
Fig. 2. Longitudinal view of the second anal fin spine of swordfish *Xiphias gladius* showing the tip, base, condyle, and length where a transversal section was obtained. A cut was made above the condyle base at one-half (d/2) of the condyle width. Fish specimens were caught in the Eastern North Pacific Ocean in 2012–2014

translucent zone. The cause of growth ring formation has not been fully established yet but involves factors such as the different stages of the swordfish lifecycle (spawning, migration, feeding), as well as environmental factors (Berkeley & Houde 1983, Tserpes & Tsimenides 1995, Ehrhardt et al. 1996, Sun et al. 2002, Chong & Aguayo 2009). In billfish spines, the outermost ring is the most recent one, and those at the core are the oldest; hence, the most recent growth band will hereafter be referred to as the last growth band.

Muscle samples of BCS and NPSG specimens were extracted from the dorsal side, whereas muscle samples of CA fish were obtained from the inner fin muscle.

2.2. SIA

Anal fin and muscle tissues were frozen at −20°C. A2 was removed and cleaned in the laboratory. The spine sections for isotopic analysis were obtained using the same protocol as for age determination, since previous studies have shown that this is the best structure for examining growth marks (Berkeley & Houde 1983, Tserpes & Tsimenides 1995, Ehrhardt et al. 1996, Cerna 2009). First, the maximum condyle width (CW) (±0.1 mm) was measured with a handheld caliper and the spine was then cut at ½ CW (Fig. 2). A ~5 mm cross section was cut and bone

powder was collected from systematic bands (~0.25 mm) using a micro-mill (New Wave Research) with drill bits of 0.6 mm (thick tip) coupled to an Olympus SZ61 stereomicroscope, following the protocol suggested by Acosta-Pachón et al. (2015) for analyzing stable carbon and nitrogen isotopes in spine bone powder. Lipids were not extracted from the spine because bone lipid concentrations in fish are low (Toppe et al. 2007, Garcia-Guixé et al. 2010).

Muscle samples were placed in vials and freeze-dried for 24 h at −45°C prior to analysis. Since samples were obtained from different body parts, lipids were removed as described by Kim & Koch (2012). Subsequently, 2.5 ml of petroleum ether (PE) were added to each sample, as PE is a non-polar solvent that extracts lipids more efficiently than other solvents while minimizing amino acid loss (Dobush et al. 1985, Kim & Koch 2012). The mixture was then sonicated for 15 min and centrifuged at $4032 \times g$ for 15 min at 10°C to separate the remaining tissue. The supernatant was removed and the tissue was washed in milli-Q water. Each cycle was repeated 4 times.

Isotope analyses of muscle and bone powder samples were carried out in 2 different laboratories. CA and NPSG samples were analyzed in the Stable Isotope Laboratory at the University of California at Davis (UCDavis) using a Carlo-Erba-Finnigan Delta Plus XL mass spectrometer interfaced with an NC 2500 elemental analyzer. BCS samples were analyzed in the Stable Isotope Laboratory at the Centro Interdisciplinario de Ciencias Marinas (CICIMAR), La Paz, BCS, Mexico, using an elemental combustion analyzer (model 4010 ECS, Costech Analytical Technologies) coupled to a Delta V Plus isotope ratio mass spectrometer (Thermo Fisher Scientific).

Control samples obtained from a single swordfish spine were included in all runs in both laboratories, in order to control for bias between laboratories. A single spine was cut, thoroughly pulverized with a handheld drill, and vortex-homogenized for 10 min. Control samples were analyzed every 10 to 11 actual samples in the analytical sequence to explore potential differences between laboratories. All stable isotope values were expressed in δ notation (‰), as $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$, where X is ^{13}C or ^{15}N, and R is the corresponding isotope ratio ($^{13}C/^{12}C$ or $^{15}N/^{14}N$). The standards used were Pee Dee Belemnite limestone for carbon-13 and atmospheric N_2 for nitrogen. Calibration standards were analyzed every 10 to 12 samples in each analytical sequence to detect and correct any instrument devi-

ation as required. The calibration standards in each laboratory were different: UCDavis used bovine liver ($\delta^{15}N$ = 7.72‰, $\delta^{13}C$ = −21.69‰), glutamic acid ($\delta^{15}N$ = 47.6‰, $\delta^{13}C$ = 37.62‰), and nylon 5 ($\delta^{15}N$ = −10.31‰, $\delta^{13}C$ = −27.72‰). The standard deviation (SD) of the calibration standards was <0.2‰ for $\delta^{13}C$ and <0.1‰ for $\delta^{15}N$ values. CICIMAR used marlin ($\delta^{15}N$ = 15.40‰, $\delta^{13}C$ = −15.90‰), alfalfa flour ($\delta^{15}N$ = 0.21‰, $\delta^{13}C$ = −27.52‰), bovine liver ($\delta^{15}N$ = 6.81‰, $\delta^{13}C$ = −17.85‰), and blood ($\delta^{15}N$ = 5.37‰, $\delta^{13}C$ = −17.13‰). The standard deviation (SD) of the calibration standards was <0.2‰ for $\delta^{13}C$ and $\delta^{15}N$ values.

2.3. Statistical analysis

Graphics were plotted and statistical tests were carried out using the R software (version R 3.3.3, 2017), with a 0.05 significance level.

Linear regressions were performed to examine (1) the relationship between LJFL (cm) and $\delta^{15}N$ and $\delta^{13}C$ values from A2 and muscle separately for the 3 locations, and (2) the relationship between $\delta^{15}N$ and $\delta^{13}C$ values recorded in muscle and the outermost ring of A2 of each specimen. A *t*-test was used to compare the isotopic values ($\delta^{15}N$ and $\delta^{13}C$) in muscle and in the last growth band. These analyses were carried out separately for the 3 locations where specimens were caught. ANOVA or a Kruskal-Wallis test was used, as appropriate, according to the results from prior tests of normality and homogeneity of variance, to test for differences in mean $\delta^{15}N$ and $\delta^{13}C$ values between locations. A Student's *t*-test was used to compare the stable isotope values obtained for control samples between laboratories.

2.4. Isotope niche metrics

Various metrics have been proposed to determine the isotopic niche based on average $\delta^{15}N$ and $\delta^{13}C$ for all species in a niche (Layman et al. 2007). In our case, such metrics were used to determine the potential isotopic overlap between sampling areas. The following metrics were computed: (1) total area (TA), i.e. the convex-hull area encompassing the most extreme points, which is a measure of the total amount of niche space occupied by each group. As this metric may be biased by differences in sample size (Jackson et al. 2012), Jackson et al. (2011) proposed an additional metric, i.e. (2) the standard ellipse area (SEA),

which measures the mean core population isotopic niche and is relatively unaffected by sample size; however, the SEA corrected for sample size (SEAc) avoids the bias that arises when sample sizes are very small (Jackson et al. 2012).

2.5. Isotope mixing model

The relative contributions of potential main prey species in different ecoregions (source) — which reflect the different areas that swordfish may be using as feeding grounds (consumer) — were estimated using the Bayesian isotope mixing model SIAR. The mixing model estimates the proportional contribution of various sources to a mixture. This model was fitted via a Markov chain Monte Carlo (MCMC) method that simulates plausible values of dietary source proportions consistent with the data. The Bayesian approach allowed including variations in the parameters, such as different numbers of consumers, sources, and trophic enrichment factors (Parnell et al. 2010). The model was run with 500 000 iterations (discarding the first 50 000 iterations). Mixing models were run for spine and muscle samples using isotopic information available for prey items. Trophic enrichment factors between sources and consumers were assumed to be 2.1 ± 0.4‰ (mean ± SD) for $\delta^{15}N$ (yellowfin tuna *Thunnus albacares*; Graham 2008) and 1 ± 1.0‰ for $\delta^{13}C$ (Post 2002). The main prey of swordfish were selected based on previous reports of stomach content analyses (Markaida & Hochberg 2005, Preti et al. 2015, Trujillo-Olvera et al. 2018).

3. RESULTS

3.1. SIA

SIAs were conducted on 41 muscle samples and 457 systematic ring spine samples from A2 of swordfish from 3 locations (Table 1). The LJFL of swordfish ranged from 80–183 cm in swordfish from NPSG, 143–213 cm in swordfish from BCS, and 156–239 cm in fish from CA (Table 1). Values of $\delta^{15}N$ in A2 ranged from 7.2–13.2‰ in NPSG, 10.9–16.6‰ in BCS, and 7.9–16.7‰ in CA. However, $\delta^{15}N$ values in muscle ranged from 9.9–15.8‰ in NPSG, 14.6–18.1‰ in BCS, and 13.3–16.5‰ in CA. $\delta^{13}C$ values in A2 ranged between −22.7 and −13.0‰ in NPSG; between −18.7 and −12.8‰ in BCS; and between −16.3 and −12.3‰ in CA. The corresponding values in muscle ranged between −18.4 and −16.9‰ in

NPSG; between −23.0 and −16.1‰ in BCS; and between −22.9 and −16.5‰ in CA. The mean isotopic values for each area and tissue are shown in Table 1.

3.2. Relationship of length and $\delta^{15}N$ and $\delta^{13}C$

The relationship between LJFL (cm) and $\delta^{15}N$ was examined separately for the 3 locations (Fig. 3). We found significant positive relationships only in muscle samples from BCS (n = 13, p < 0.001, r^2 = 0.63; Fig. 3D), anal fin spine samples from CA (n = 148, p < 0.001, r^2 = 0.061; Fig. 3G), and muscle samples from CA (n = 13, p < 0.05, r^2 = −0.027; Fig. 3H).

For $\delta^{13}C$ values, significant relationships were found only in anal fin spine samples (Fig. 4) from NPSG (n = 145, p < 0.05, r^2 = 0.021; Fig. 4E) and CA (n = 148, p < 0.001, r^2 = 0.398; Fig. 4G).

3.3. Differences between tissues

Muscle (15.1‰) was significantly enriched in ^{15}N compared to bone powder (12.7‰) ($t_{(0.05(2)13)}$ = 5.48, df = 13, p < 0.001). The opposite was found for ^{13}C; bone powder (−15.3‰) was significantly enriched relative to muscle (−18.9‰) ($t_{(0.05(2)13)}$ = −9.18, df = 13, p < 0.001).

A significant positive relationship was found between $\delta^{15}N$ values measured in the last growth band vs. muscle (n = 40, p < 0.001, r^2 = 0.591; Fig. 5), but no significant relationship was found for $\delta^{13}C$ values between muscle and last growth band (n = 40, p > 0.05, r^2 = 0.006). Based on these results, the following equation was derived to estimate $\delta^{15}N$ values in muscle ($\delta^{15}N_m$) from those measured in the last growth band of the anal fin spine ($\delta^{15}N_{as}$):
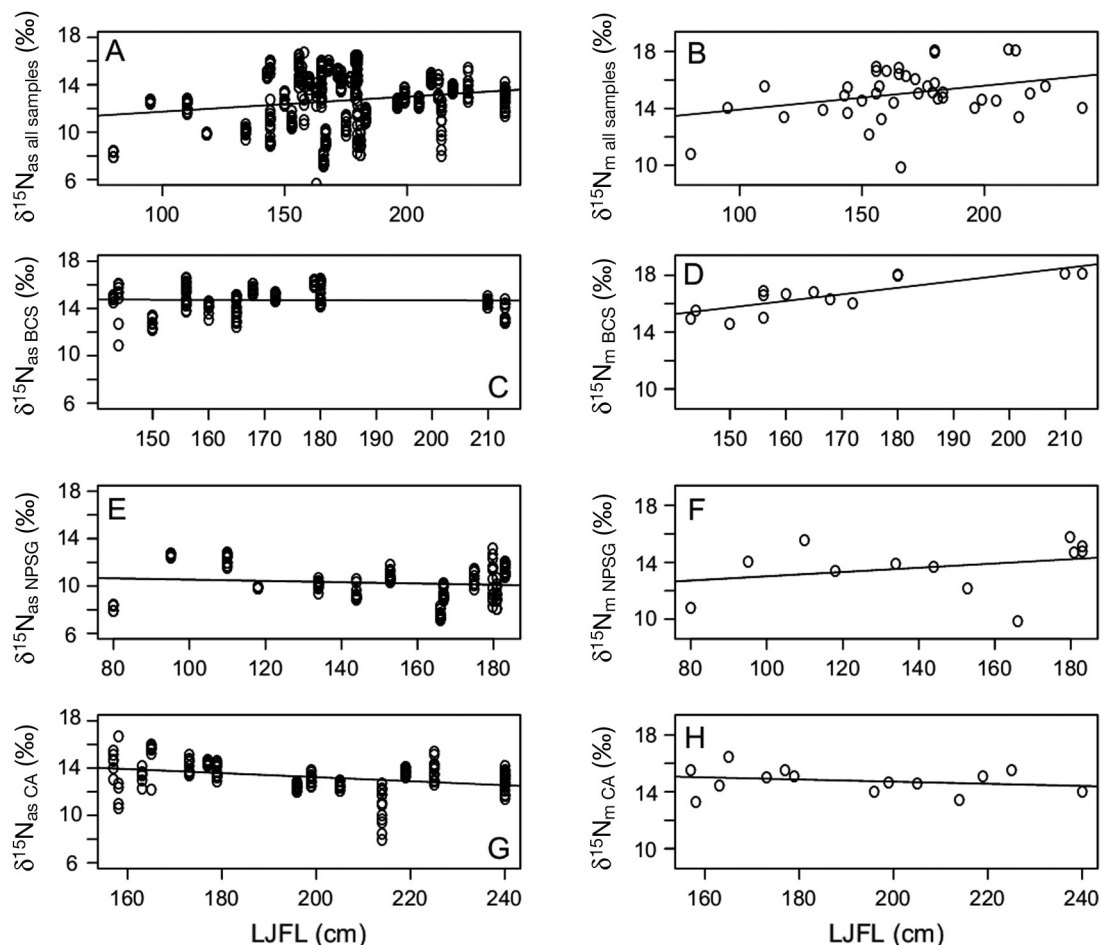
$$\delta^{15}N_m = 5.75 + 0.56(\delta^{15}N_{as}) \tag{2}$$

Fig. 3. Relationship between lower jaw fork length (LJFL, cm) and $\delta^{15}N$ (‰) values in *Xiphias gladius* in (A) all spine samples; (B) all muscle samples; (C) anal spine samples from Baja California Sur (BCS), Mexico; (D) muscle samples from BCS; (E) anal spine samples from the North Pacific Subtropical Gyre (NPSG); (F) muscle samples from the NPSG; (G) anal spine samples from California (CA), USA; and (H) muscle samples from CA

Table 1 shows the overall average (± SD) C/N ratio for muscle and systematic samples from the anal fin spine for each area. The highest value was found in swordfish muscle from CA (8.1 ± 2.8). C/N ratios in muscle and A2 spine of fish from the other 2 areas showed little variation between them and were lower than 3.8 in all cases.

3.4. Comparison of isotopic values between locations

Significant differences were found among areas in A2 spine in $\delta^{15}N$ ($\chi^2 = 313.8$, p < 0.01) and $\delta^{13}C$ ($\chi^2 = 115.7$, p < 0.01), and also in $\delta^{15}N$ ($F_{2,38} = 16.7$, p < 0.001) and $\delta^{13}C$ (Kruskal Wallis $\chi^2 = 13.7$, p < 0.01) when muscle values for BCS, CA, and NPSG were compared. Post hoc tests (Tukey's HSD for $\delta^{15}N$ and Mann Whitney-Wilcoxon for $\delta^{13}C$) were performed to determine which areas were different. For nitrogen, significant differences were found between CA and BCS and between NPSG and BCS, but not between CA and NPSG. For carbon, differences were found between CA and BCS and between CA and NPSG, but not between BCS and NPSG. All test values are shown in Table 2.

3.5. Comparison between laboratories

A total of 22 bone powder control samples from swordfish spine were analyzed at UCDavis, yielding average values of 10.5 ± 0.1‰ for $\delta^{15}N$ and −14.3 ± 0.1‰ for $\delta^{13}C$. On the other hand, the 25 control samples analyzed at CICIMAR yielded 10.8 ± 0.1‰ for $\delta^{15}N$ and −14.1 ± 0.2‰ for $\delta^{13}C$. No significant differences between laboratories were found for either variable: $\delta^{15}N$ ($t = -7.75$, p > 0.05) and $\delta^{13}C$ ($t = -2.79$, p > 0.05).
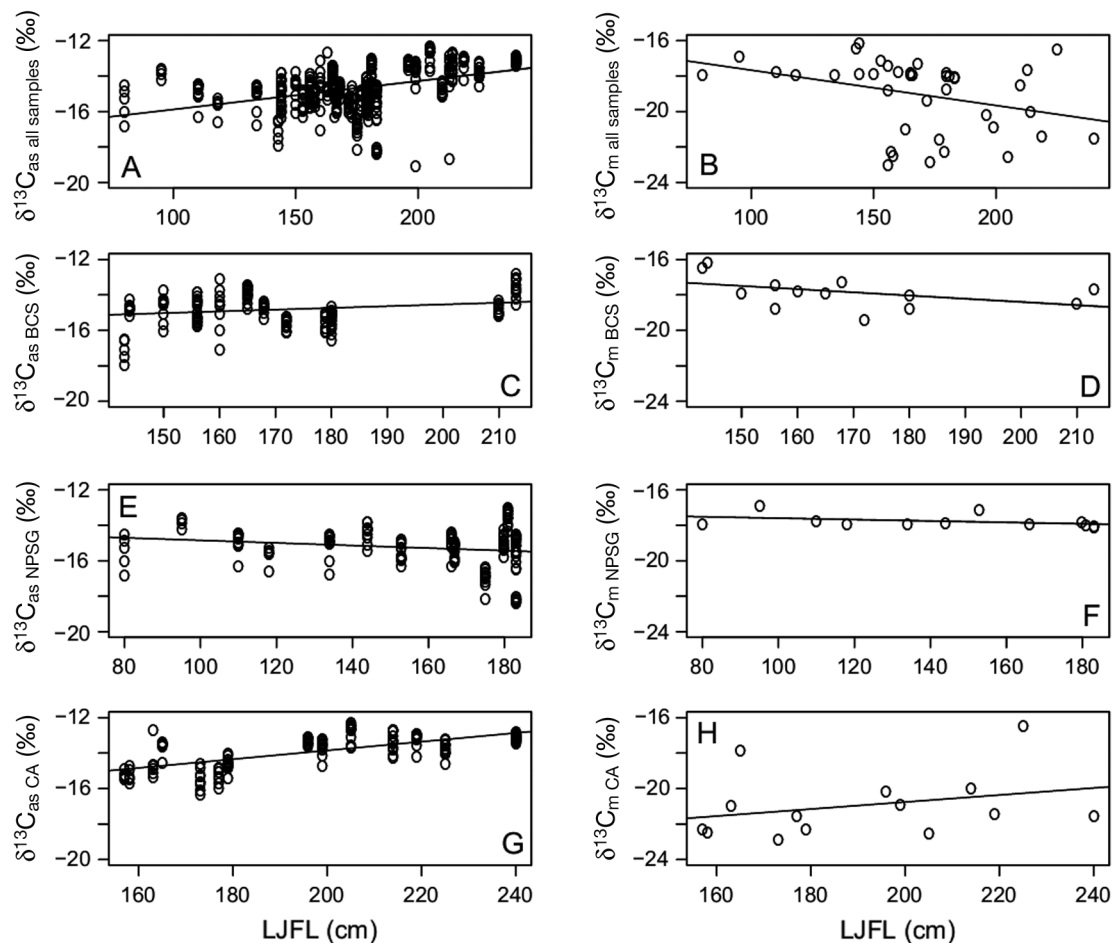
Fig. 4. Relationship between lower jaw fork length (LJFL, cm) and $\delta^{13}C$ (‰) values in *Xiphias gladius* in (A) all spine samples; (B) all muscle samples; (C) anal spine samples from Baja California Sur (BCS), Mexico; (D) muscle samples from BCS; (E) anal spine samples from the North Pacific Subtropical Gyre (NPSG); (F) muscle samples from the NPSG; (G) anal spine samples from California (CA), USA; and (H) muscle samples from CA
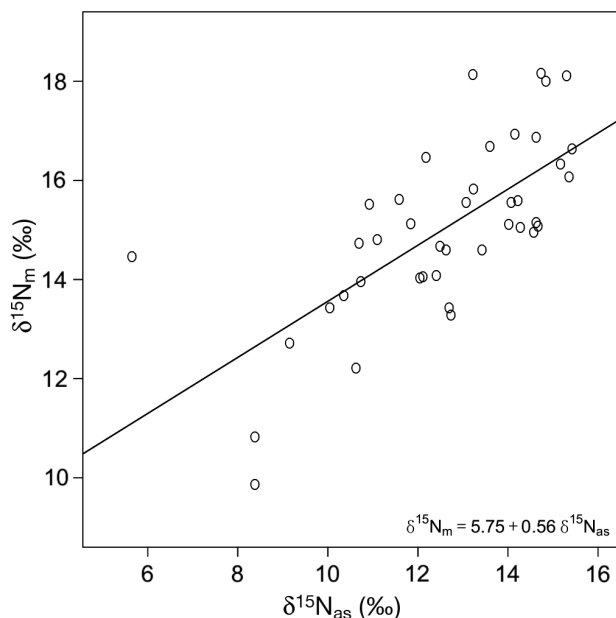
Fig. 5. Relationship between $\delta^{15}N$ values recorded in muscle ($\delta^{15}N_m$) and anal spine ($\delta^{15}N_{as}$) of *Xiphias gladius*. Specimens were caught in the Eastern North Pacific Ocean in 2012–2014

Table 2. Results (p-values) from Tukey's HD and Wilcoxon tests comparing $\delta^{15}N$ and $\delta^{13}C$ values of swordfish *Xiphias gladius* anal spine and muscle samples collected in Baja California Sur (BCS), California, and the North Pacific Subtropical Gyre (NPSG)

| Area | $\delta^{15}N$ | | $\delta^{13}C$ | |
	BCS	California	BCS	California
Anal spine				
California	<0.001	–	<0.001	–
NPSG	<0.001	<0.001	<0.001	<0.001
Muscle				
California	<0.001	–	<0.001	–
NPSG	<0.001	>0.05	>0.05	<0.001

3.6. Isotope niche metrics

Isotopic niche metrics measured in muscle samples showed the highest values for BCS; however, the highest values measured in spine bone samples were obtained for the NPSG (Table 3). Percentages of total overlap area estimated from spine samples with the convex-hull metric were higher than those obtained with the SEA metric. The percent overlap obtained with SEA was low in general, with no overlap for 2 combinations of areas when spine bone samples were analyzed (Table 4, Fig. 6). Similarly, the percent overlap in muscle samples estimated with SEA showed no overlap between the 3 areas. However,

with the convex-hull metric, low overlap values were found between CA and BCS and between BCS and NPSG, but no overlap was evident between CA and NPSG for muscle samples (Table 4, Fig. 7).

3.7. Isotope mixing model

Various prey species, mainly squids, for which $\delta^{15}N$ and $\delta^{13}C$ isotopic values were available (Table 5), were used to construct the mixing model and establish the relative contribution of different ecoregions. We decided to include an additional area that might also be related to swordfish movements, the Subarctic Gyre. The highest values of prey were found in BCS for both isotopes; the lowest were found in the NPSG for $\delta^{15}N$ and in the Subarctic Gyre for $\delta^{13}C$ (Table 5).

Analysis of spine samples from BCS and the NPSG showed that the sources that most contributed to the mixing were the areas where fish were caught. By contrast, for spines from CA, the NPSG

Table 3. Isotopic niche metrics for swordfish in caught in Baja California Sur (BCS), North Pacific Subtropical Gyre (NPSG), and California, pooled according to the tissue sampled. TA: total area (convex-hull area); SEA: standard ellipse area; SEAc: corrected standard ellipse area

Area	TA	SEA	SEAc
Muscle			
BCS	13.43	6.12	6.63
NPSG	5.14	2.26	2.46
California	7.52	3.33	3.61
Anal spine			
BCS	14.46	2.94	2.94
NPSG	21.05	4.57	4.59
California	21.47	3.68	3.71

Table 4. Total percentage of overlap in total area (convex-hull area) and in standard ellipse area (SEA) among swordfish collected in Baja California Sur (BCS), North Pacific Subtropical Gyre (NPSG), and California in anal spine and muscle

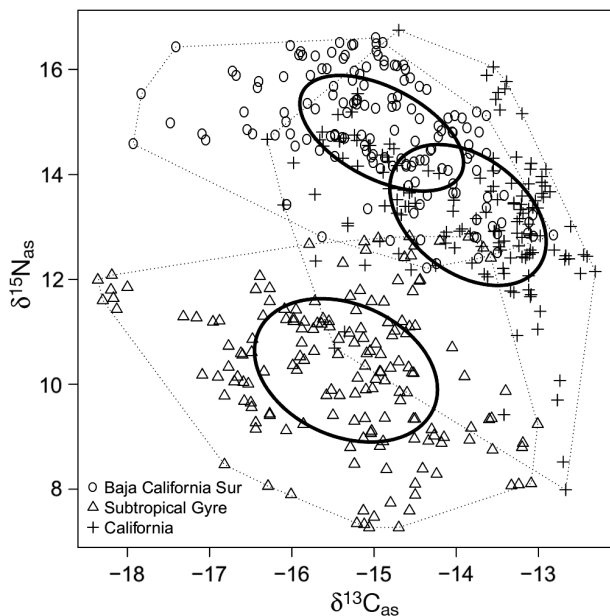| Area | Convex-hull area | | SEA | |
	BCS	California	BCS	California
Anal spine				
California	9.17	–	0.62	–
NPSG	0.67	7.37	2.68×10^{-16}	4.16×10^{-17}
Muscle				
California	0.54	–	5.20×10^{-18}	–
NPSG	0.59	0	0.04	0

Fig. 6. Total isotopic niche area (dotted line) and standard ellipse area (SEA, solid line) in anal spine (as) samples from swordfish caught in different areas: Baja California Sur, Mexico; North Pacific Subtropical Gyre; and California, USA
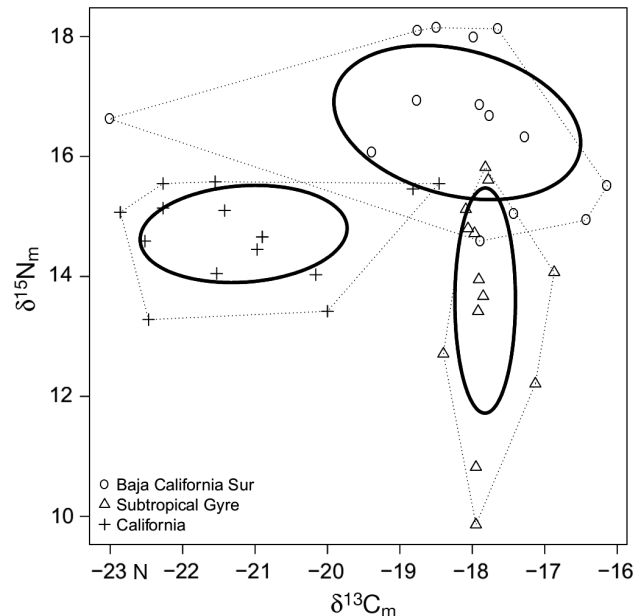

Fig. 7. Total isotopic niche area (dotted line) and standard ellipse area (SEA, solid line) in muscle (m) samples from swordfish caught in different areas: Baja California Sur, Mexico; North Pacific Subtropical Gyre; and California, USA

was the area with the greatest contribution (Table 6).

The analysis of muscle samples yielded similar results. For swordfish caught in BCS and the NPSG, the greatest contribution came from sources located in the same areas, but for swordfish from CA, the greatest contribution came from the Subarctic Gyre (Table 6).

4. DISCUSSION

This study used stable isotope ratios in muscle and spine bone of swordfish from the ENPO to examine intraspecific and spatial differences by comparing $\delta^{15}N$ and $\delta^{13}C$ values in both tissues in specimens from 3 different locations.

Table 5. Isotopic values of prey species of swordfish from the literature used to estimate mean $\delta^{15}N$ and $\delta^{13}C$ ecoregion values used in the SIAR mixing model to assess proportional contribution of different regions

Area	Prey group	Lowest taxonomic ID	$\delta^{15}N$ ($\pm$SD)	$\delta^{13}C$ ($\pm$SD)	Reference
Baja California Sur	Humboldt squid	*Dosidicus gigas*	14.7 ($\pm$2.7)	−17.2 ($\pm$1.0)	Torres-Rojas et al. (2013)
	Squid	*Argonauta* spp.	16.1 ($\pm$1.8)	−17.9 ($\pm$0.5)	Torres-Rojas et al. (2013)
Mean values			15.4 ($\pm$0.98)	−17.5 ($\pm$0.49)	This study
North Pacific Subtropical Gyre	Neon flying squid	*Ommastrephes bartramii*	9.6 ($\pm$4.2)	−20.5 ($\pm$0.6)	Parry (2003, 2008)
	Ommastrephid squid	Ommastrephidae	6.2 ($\pm$0.6)	−18.8 ($\pm$0.1)	Graham et al. (2007), Graham (2008)
	Purpleback flying squid	*Sthenoteuthis oualaniensis*	7.8 ($\pm$0.6)	−18.3 ($\pm$0.6)	Parry (2003), D. J. McCauley (unpubl.)
Mean values			7.9 ($\pm$1.7)	−19.2 ($\pm$1.1)	This study
California	Gonatid squid	*Gonatopsis* spp.	13.3 ($\pm$0.3)	−18.8 ($\pm$0.2)	D. J. Madigan (unpubl.)
	Humboldt squid	*Dosidicus gigas*	15.0 ($\pm$0.3)	−17.2 ($\pm$0.2)	Madigan et al. (2012b), D. J. Madigan (unpubl.)
Mean values			14.1 ($\pm$1.2)	−18.0 ($\pm$1.1)	This study
Subarctic Gyre	Gonatid squid	Gonatidae	14.0 ($\pm$1.3)	−21.7 ($\pm$0.5)	D. J. Madigan (unpubl.)
	Neon flying squid	*Ommastrephes bartramii*	11.7 ($\pm$1.3)	−18.4 ($\pm$0.7)	Gould et al. (1997)
Mean values			12.8 ($\pm$1.6)	−20.0 ($\pm$2.3)	This study

Table 6. Relative estimate of mean contribution of different ecoregions (sources) to the mixing models for swordfish collected in different areas, according to spine and muscle isotopic values. Also shown are confidence intervals (CI, lower and higher at 95%) and mode. **Bold** value: highest mean contribution for each group

Source	Contribution			
	— 95% CI —		Mode	Mean
ANAL SPINES				
Swordfish of Baja California Sur				
Baja California Sur	0.335	0.661	0.610	**0.533**
North Pacific Subtropical Gyre	0.282	0.371	0.023	0.330
California	0.000	0.356	0.023	0.125
Subarctic Gyre	0.000	0.029	0.002	0.010
Swordfish of North Pacific Subtropical Gyre				
Baja California Sur	0.000	0.061	0.031	0.030
North Pacific Subtropical Gyre	0.899	0.960	0.927	**0.930**
California	0.000	0.066	0.009	0.029
Subarctic Gyre	0.000	0.026	0.001	0.009
Swordfish of California				
Baja California Sur	0.011	0.462	0.403	0.323
North Pacific Subtropical Gyre	0.475	0.574	0.537	**0.528**
California	0.000	0.372	0.025	0.133
Subarctic Gyre	0.000	0.041	0.002	0.014
MUSCLE				
Swordfish of Baja California Sur				
Baja California Sur	0.074	0.614	0.364	**0.457**
North Pacific Subtropical Gyre	0.000	0.105	0.008	0.037
California	0.000	0.507	0.277	0.242
Subarctic Gyre	0.080	0.613	0.378	0.261
Swordfish of North Pacific Subtropical Gyre				
Baja California Sur	0.002	0.329	0.177	0.167
North Pacific Subtropical Gyre	0.196	0.472	0.345	**0.334**
California	0.008	0.389	0.215	0.209
Subarctic Gyre	0.099	0.463	0.286	0.287
Swordfish of California				
Baja California Sur	0.019	0.423	0.264	0.240
North Pacific Subtropical Gyre	0.145	0.339	0.250	0.243
California	0.005	0.455	0.271	0.242
Subarctic Gyre	0.037	0.467	0.284	**0.272**

No significant relationship was found between $\delta^{15}N$ and swordfish size, suggesting that trophic level does not change with increasing body size in this species. Body size plays a crucial role in predator–prey interactions; prey size and trophic level generally increase as body size increases (Jennings et al. 2002, Estrada et al. 2006, Ménard et al. 2007, Revill et al. 2009), but this paradigm does not hold in all cases. For example, although a general pattern for $\delta^{15}N$ has been observed in white sharks *Carcharodon carcharias* related to a major dietary change as their diet shifts from primarily fish to marine mammals, not all individuals follow this pattern, and some do not show marked changes in isotopic values or a higher trophic position with body

size (Kerr et al. 2006, Carlisle et al. 2012, Kim et al. 2012).

Furthermore, feeding strategies may vary among individuals (Kim et al. 2012); not all individuals behave in the same manner, and items at low trophic levels remain as major components in the diet of adult predators (Estrada et al. 2006, Kerr et al. 2006). An example is the striped marlin *Kajikia audax*, in which isotopic values do not change with size, probably because either the prey items consumed in different life stages are isotopically equivalent or the dietary shift is not sufficiently marked to affect the isotopic values (Torres-Rojas et al. 2013, Acosta-Pachón et al. 2015).

Some feeding studies on swordfish using stomach contents (Young et al. 2006) and SIA (Young et al. 2006, Ménard et al. 2007, Revill et al. 2009) have demonstrated a dietary shift from fish to squids with increasing body size. Other studies, however, have concluded that differences in prey composition might be linked to other factors, such as sampling area (Clarke et al. 1995, Hernández-García 1995, Chancollon et al. 2006, Castillo et al. 2007), regardless of predator size (Stillwell & Kohler 1985, Ibáñez et al. 2004). A recent feeding study on swordfish in the subtropical northeastern Pacific found similar diets between sexes and across maturity groups (fish size from 98–300 cm LJFL), demonstrating that all swordfish analyzed occupy the same trophic level (Trujillo-Olvera et al. 2018).

Thus, swordfish, as generalist top predators (Revill et al. 2009), likely feed on a wide range of prey size, including small-sized species and other taxa (Young et al. 2006) and large organisms. Moreover, behavioral and physiological differences between individuals could lead to different feeding strategies that may affect isotopic values. Last, a major shift in feeding habits might occur during the first year of life, when the growth rate of swordfish is higher, reaching an average LJFL of 88.6 cm (males) and 90.4 cm (females) (Sun et al. 2002); however, Acosta-Pachon & Ortega-Garcia (2019) found no change in trophic level through time for swordfish in age groups 1 to 9.

To our knowledge, the biochemical composition of bone or muscle tissue in swordfish has not yet been determined; nonetheless, it is clear that differences

between these 2 types of tissue should exist. For example, in Atlantic bluefin tuna *Thunnus thynnus*, different tissues showed differences in isotopic values: $\delta^{15}N$ values were 2–3‰ more depleted in scales than in muscle, but $\delta^{13}C$ values in scales were more enriched (by 3–4‰) than in bone and muscle (Estrada et al. 2005). This difference might be due to the amino acid composition of tissue as regards glycine: it is dominant in scales, accounting for 40% (by weight) of total amino acid content, while it only contributes 5% to total amino acid content in muscle tissue (Winters 1971). Moreover, both organic content and relative abundance of amino acids might affect $\delta^{15}N$ values in different tissues (Pinnegar & Polunin 1999, Estrada et al. 2005, MacNeil et al. 2006). Sampling different tissues in a top marine predator may provide insights into the movements of highly mobile predators at various temporal scales (Tieszen et al. 1983). Unfortunately, the isotopic turnover rate, i.e. the time for 50% of the original element to be replaced, which represents the half-life, in muscle and anal bone spine of swordfish has not been determined yet. As the fin spine is an accretionary tissue, it is metabolically less active than muscle (Tieszen et al. 1983). The turnover rate in muscle of some tuna species has been estimated at about 5 to 6 mo (Graham 2008) and 2–3 yr (Madigan et al. 2012a); moreover, the isotopic turnover rate varies between isotopes ($\delta^{15}N = 721$ d; $\delta^{13}C = 1103$ d) (Madigan et al. 2012a). Differences in the turnover rate between tissues are mainly given by differences in the relative contribution of metabolism to growth (Buchheister & Latour 2010), fish size, and physiology (Fry & Arnold 1982, Hesslein et al. 1993, Trueman et al. 2005).

When isotopic values in different tissues (muscle and spine) were compared, the highest and most significant correlation was found in $\delta^{15}N$ values. Similar results have been found in other species: in the Pacific bluefin tuna *T. orientalis*, between white muscle and liver (Madigan et al. 2012a); and in striped marlin, between muscle and bone spine (Acosta-Pachón et al. 2015). It is likely that the turnover dynamics of ^{15}N are more predictable than those of ^{13}C (Madigan et al. 2012a). Of note, the muscle tissue samples from CA were taken from fin skeletal muscle and had a higher C/N ratio than samples of bone fin spine and dorsal muscle from BCS and the NPSG (Table 1). This may have led to a higher variability in $\delta^{13}C$ values, as higher lipid content in tissues results in lower $\delta^{13}C$ values (Post et al. 2007, Logan et al. 2008). Differences in biochemical composition might exist between muscle tissues from different body parts. The C/N ratio has been used as a proxy for lipid content (Post et al. 2007, Logan et al. 2008). Swordfish likely use skeletal muscle as a major reservoir for lipid storage, as shown in other fish species (Pinnegar & Polunin 1999), which would be reflected in the C/N ratio. On the other hand, when C/N values from spine samples were analyzed, we found that the average C/N value for this tissue is ~3.5. Thus, it is probable that lipid content in this tissue is consistently low, below 5% (C:N < 3.5) (Post et al. 2007). The scarce information available on the biochemical composition of swordfish tissues restrains the validity of this conclusion; however, it should be taken into account for future studies.

The isotopic values of animals can be used as 'natural tracers' to track their movements through the various ecosystems that they have inhabited for an extended period of time (Fry 1981, Peterson & Fry 1987, Michener & Schell 1994). The isotopic composition of the tissues of an individual is determined by the area where it feeds; therefore, those values could be used for elucidating migration routes and breeding grounds, as well as for mapping of species dispersal (Cherel et al. 2008, Graham et al. 2010). Our results revealed a significant difference in tissues (Table 2), and such isotopic variations, especially in $\delta^{15}N$, could be related primarily to differences in feeding grounds. This can be corroborated with the slight or no overlap between the isotopic values from each region, with which the metrics (TA and SEA) were calculated for the 2 tissues (Table 4), i.e. spine (Fig. 6) and muscle (Fig. 7).

As expected, the highest values were found in BCS and the lowest in the NPSG; these differences in the isotopic values of prey are due to different oceanographic processes. Nitrogen uptake and conversion into nitrate can be produced by either (1) upwelling nutrients provided in the euphotic zone with $\delta^{15}N$ values of 4.8 ± 0.2‰ (Sigman et al. 1997) or (2) N_2 fixation by planktonic diazotrophs in oligotrophic waters, with $\delta^{15}N$ values typically around −2 to −1‰ (Montoya et al. 2002). Hence, trophic webs based on N_2 fixation in oligotrophic waters have lower isotopic values than those in more productive waters where phytoplankton use upwelling nitrogen (Altabet 2001, McClelland & Montoya 2002). Baseline $\delta^{15}N$ values decrease with latitude in the ENPO (Altabet et al. 1999, Voss et al. 2001, Vokhshoori & McCarthy 2014). This pattern was also observed in swordfish samples, as $\delta^{15}N$ values recorded in BCS were higher than those observed in the other 2 areas.

Furthermore, isotopic values recorded in muscle (months or years) and anal fin spine (ontogenetic

reconstruction) might suggest that the site where this apex predator was caught could also be its feeding area, thus implying site fidelity, as established in previous studies (Carey & Robinson 1981, Alvarado Bremer et al. 2006, Ménard et al. 2007). This hypothesis applies to swordfish caught in BCS and the NPSG; however, for the CA samples, it is possible that swordfish do not feed in this area, but instead in the NPSG, as evidenced by muscle samples (Table 6). The feeding grounds of CA swordfish are not at all clear. If swordfish from CA use another feeding area, this likely occurs over a timescale shorter than the tissue turnover rates. More advanced analytical methods or analyses of other tissues providing a better temporal resolution are necessary to investigate this possibility further.

Differences in δ^{13}C values between the 3 areas were also found in muscle and anal fin spine tissues. Values of δ^{13}C are also correlated with latitude (Rau et al. 1982, Goericke & Fry 1994, Schell et al. 1998), increasing at low latitudes (Goericke & Fry 1994). Additionally, δ^{13}C values are lower in offshore regions, where nutrients are more limited and phytoplankton growth rates are lower than in productive upwelling regions (France 1995, Burton & Koch 1999). The NPSG has the lowest mean value, reflecting an oligotrophic open ocean habitat where productivity is seemingly lower than in coastal areas that are more productive (Berger 1989). This finding is consistent with previous studies that evaluated isotopic differences in top predators from coastal and offshore habitats (Carlisle et al. 2012, 2015).

The results from this study support the idea that there is little or no increase in isotopic values in relation to swordfish size, but caution must be taken when comparing muscle from different parts of the body, as this may bias the interpretation of results. Further investigation on the isotopic turnover rate in different tissues of apex predator species, in particular swordfish, is necessary. The results reported here show that the stable isotope composition of swordfish tissues can be used as a natural tracer to differentiate the 3 different areas in the ENPO: BCS, CA, and the NPSG, as confirmed through different approaches. This study also confirmed that δ^{15}N baseline values could propagate through several trophic levels and even up to top predators such as swordfish. Knowledge about habitat use and movement patterns of species such as swordfish is crucial for effective management and to estimate the probability of local depletion in certain areas, in relation to differences in fishery schemes.

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