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NOTE

Pre-industrial ecology and foraging behavior of swordfish *Xiphias gladius* in the eastern North Pacific

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ABSTRACT: The historical ecology and foraging behavior of many apex marine predators are poorly known. This includes highly mobile pelagic species such as billfish (Xiphiidae and Istiophoridae), which have long held cultural significance for coastal peoples. In California's Santa Barbara Channel Region, Chumash people have hunted billfish for >2000 yr, providing a deep historical record of these species. We present bulk tissue $\delta^{13}C$ and $\delta^{15}N$ data for 15 Late Holocene archaeological swordfish *Xiphias gladius* and 1 striped marlin *Kajikia audax* previously identified to species through collagen fingerprinting. When compared to data sets of modern northeastern Pacific and archaeological Gulf of Maine swordfish, we identified significant overlap in the isotopic values of modern and archaeological swordfish from the Pacific, indicating that pre-industrial swordfish were reliant on food webs of the North Pacific Subtropical Gyre and the California Current System. We also identified differences in the isotopic composition of swordfish captured by island vs. mainland communities, with swordfish remains from mainland sites having lower and more variable $\delta^{13}C$ values, potentially indicating different source populations. The isotopic range of swordfish from California archaeological sites was much broader than those from the Gulf of Maine, suggesting a wider range of habitats used by Pacific swordfish. Our results provide important pre-industrial data for an apex marine predator.

KEY WORDS: Historical ecology · Archaeology · Stable isotope analysis · ZooMS · Billfish · Movement patterns

1. INTRODUCTION

Billfish (Xiphiidae and Istiophoridae), such as swordfish *Xiphias gladius*, are charismatic marine fish found in temperate, subtropical, and tropical waters worldwide (Palko et al. 1981). Swordfish are apex consumers in pelagic food webs, reaching over 500 kg and having few predators (Palko et al. 1981). Thought to be opportunistic feeders, they frequently consume schooling prey, including cephalopods, mesopelagic fishes, and crustaceans (Markaida & Sosa-Nishizaki 1998, Markaida & Hochberg 2005, Trujillo-Olvera et al. 2018). Swordfish are highly mobile, and individuals under-

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take significant vertical and horizontal migrations (Sepulveda et al. 2020). The mobile and pelagic lifestyle of swordfish makes detailed ecological studies difficult, and data on movement and dietary patterns of the species remain limited (Sepulveda et al. 2020).

Here, we present stable isotope data from Late Holocene archaeological swordfish and marlin *Kajikia audax* from the southern California Bight previously identified to species using collagen fingerprinting (Rick et al. 2019). Indigenous fisheries for billfish in the Americas are rare, confined primarily to California's Santa Barbara Channel (SBC) region, the Gulf of Maine, and north central Chile. The Maine and Chilean fisheries date primarily to the Middle or early Late Holocene, while the SBC billfish fishery occurred primarily after 2000–1500 yr ago (Davenport et al. 1993, Sanger 2009, Béarez et al. 2016). In the SBC, people hunted swordfish from boats using harpoons, and this fishery may be associated with the development of the *tomol*, or plank canoe (Arnold & Bernard 2005). Swordfish were a part of people's diet, ritual, and ceremonial systems and were thought to drive whales aground (Johnson 1990, Davenport et al. 1993).

2. MATERIALS AND METHODS

2.1. Archaeological billfish samples

We obtained 30 archaeological specimens from the SBC from museum collections and identified species via collagen fingerprinting (ZooMS; Rick et al. 2019). A total of 24 specimens yielded collagen fingerprints identifiable to species, consisting of 23 swordfish *Xiphias gladius* and a striped marlin *Kajikia audax*. We processed 23 of these specimens for bulk tissue stable carbon and nitrogen isotope ($\delta^{13}C$ and $\delta^{15}N$) analysis.

The billfish samples came from 6 archaeological sites on San Miguel and Santa Cruz islands and the mainland (Fig. 1). Several additional samples came from unknown sites in the same region. Long-distance trade is not a factor in our data set; given the time and geographical distance between Chile, the Gulf of Maine, and California, our samples most likely represent animals obtained from coastal California waters (Rick et al. 2019). All specimens are from villages or shell middens, where evidence indicates people employed maritime hunting and fishing strategies. None of the California specimens have been directly radiocarbon-dated, but associated

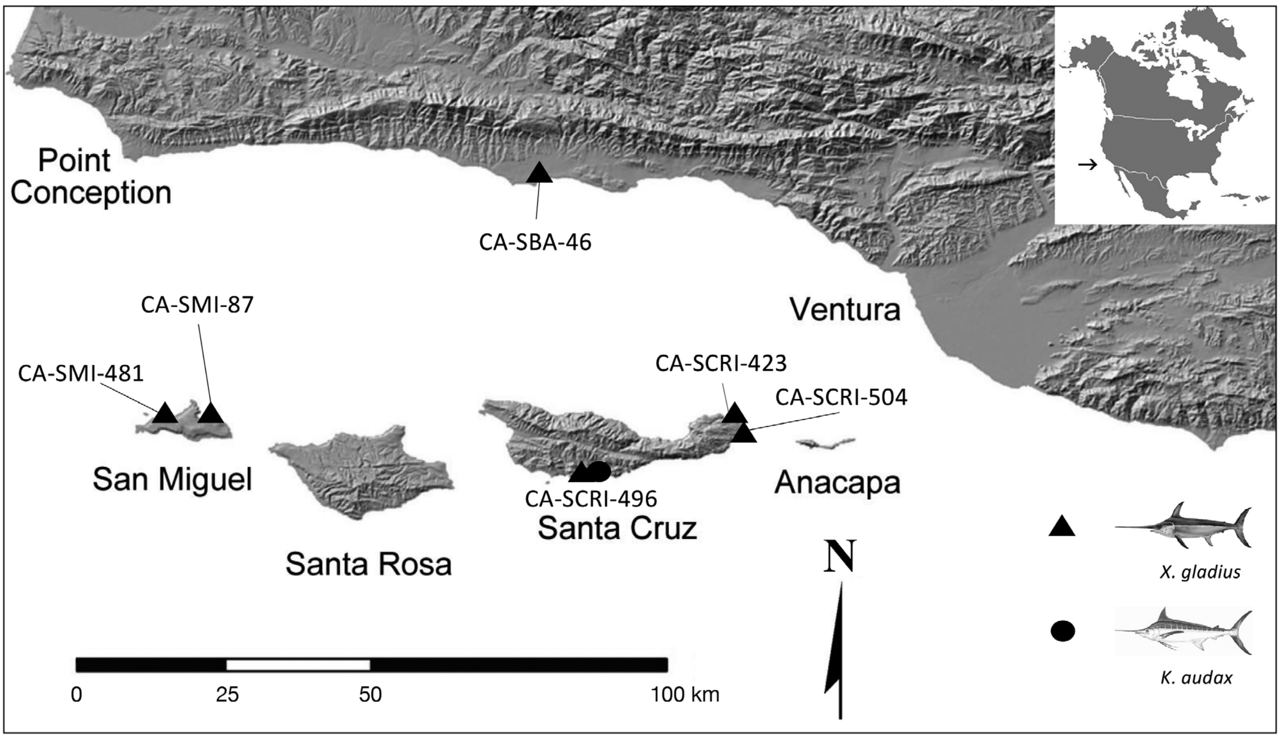

Fig. 1. Study region, showing the Northern California Channel Islands and broader location indicated in inset. Symbols represent archaeological sites from which the data presented in this paper originated. Triangles: sites of reliable isotope values from swordfish *Xiphias gladius* remains; circles: the same for striped marlin *Kajikia audax*

dates or time-sensitive artifacts define their age (Table S1 in Supplement 1, www.int-res.com/articles/suppl/m711p129_supp/; for all supplements). The mainland specimens from CA-SBA-46 likely date from prior to the 19th century. The Santa Cruz Island samples are from sites dated to the past 1500 yr, but no later than the 19th century. The San Miguel Island specimens came from CA-SMI-481, dated to ~1200 cal BP, and a single specimen from CA-SMI-87 (one of the oldest from the SBC) dates to 3000–2500 cal BP (Rick 2007). Collectively, these billfish remains provide a broad geographic and temporal cross-section of the Late Holocene SBC.

2.2. Isotopic methods

Collagen was extracted by demineralizing chunks of bone in 0.5 M HCl at room temperature. After demineralization, the samples were neutralized and then treated with 0.1 M NaOH at room temperature for successive 20 min treatments until no color change in the solution was apparent. The samples were again neutralized and refluxed in 0.01 M HCl at 75°C for 36 h to solubilize the collagen and then freeze-dried. The isotopic and elemental compositions of the collagen were determined using a Nu Horizon isotope ratio mass spectrometer coupled to a EuroVector 3300 elemental analyzer. The $\delta^{13}C$ and $\delta^{15}N$ values were calibrated relative to Vienna PDB standard and AIR using USGS40 and USGS66.

2.3. Isotopic corrections and statistical analyses

To make our archaeological billfish data comparable with published works (i.e. Acosta-Pachón et al. 2020), we corrected for isotope effects due to temporal baseline shifts (Clark et al. 2021) and sample preparation differences (Wilson & Szpak 2022) (Text S1 in Supplement 1). We conducted all isotopic corrections and analyses in Program R v.4.1.2 (R Development Core Team 2021; Supplement 3) with RStudio interface (v.2022.07.1-554). We compared our archaeological data to modern swordfish samples collected in the North Pacific Subtropical Gyre and California Current System (Acosta-Pachón et al. 2020). In that work, the authors presented $\delta^{13}C$ and $\delta^{15}N$ data from whole bone (anal spine) samples of 15 individuals (see Fig. 2). However, their raw data set is not publicly available, and therefore we used WebPlot Digitizer (Rohatgi 2021) to extract bulk tissue isotope values from Acosta-Pachón et al. (2020, their Fig. 6), and we generated 95% standard ellipse areas from these data using the R package 'SIBER' (Jackson et al. 2011).

3. RESULTS

Of the 23 specimens processed, 4 did not yield enough material for analysis following collagen extraction, and 3 others had atomic C:N ratios outside of the acceptable range for bone collagen (2.9–3.6; DeNiro 1985). Consequently, 16 archaeological billfish samples yielded reliable bulk tissue $\delta^{13}C$ and $\delta^{15}N$ values (Table S1).

Bulk tissue $\delta^{13}C$ and $\delta^{15}N$ values of archaeological billfish varied widely — with unadjusted values ranging from −16.4 to −10.6‰ ($\delta^{13}C$) and +6.5 to +14.2‰ ($\delta^{15}N$) (Table S1, Figs. 2 & 3). Swordfish remains from mainland sites had 2.6‰ lower average $\delta^{13}C$ values than those recovered from island sites (W = 46.5, $p < 0.01$) and a wider range of $\delta^{13}C$ values (mainland range: 4.7‰; island range: 2.7‰). The $\delta^{15}N$ values did not differ among regions (W = 35, p = 0.24).

4. DISCUSSION

In the Americas, archaeological evidence for billfish fisheries come from southern California, Maine, and north central Chile (Davenport et al. 1993, Sanger 2009, Béarez et al. 2016). In all cases, billfish hold ceremonial significance, and their remains are often modified into artifacts, including swords, bone bipoints, and cups (Rick et al. 2019). Bulk tissue isotope data from Late Holocene California billfish thus reflect the connections among Indigenous communities and marine ecosystems, providing insights into the historical relationship among people and pelagic food webs and important pre-industrial data on the ecology of an apex marine predator.

Our data demonstrate that billfish obtained by coastal California communities in the past foraged in a range of northeastern Pacific habitats. With 3 exceptions, the $\delta^{13}C$ and $\delta^{15}N$ values of archaeological California billfish fell within the observed isotopic range of modern swordfish sampled from the North Pacific Subtropical Gyre and California Current System (i.e. coastal California and Baja California Sur; Fig. 2). Variation in seasonal migration patterns exists among modern California swordfish with summer foraging grounds in the Southern California

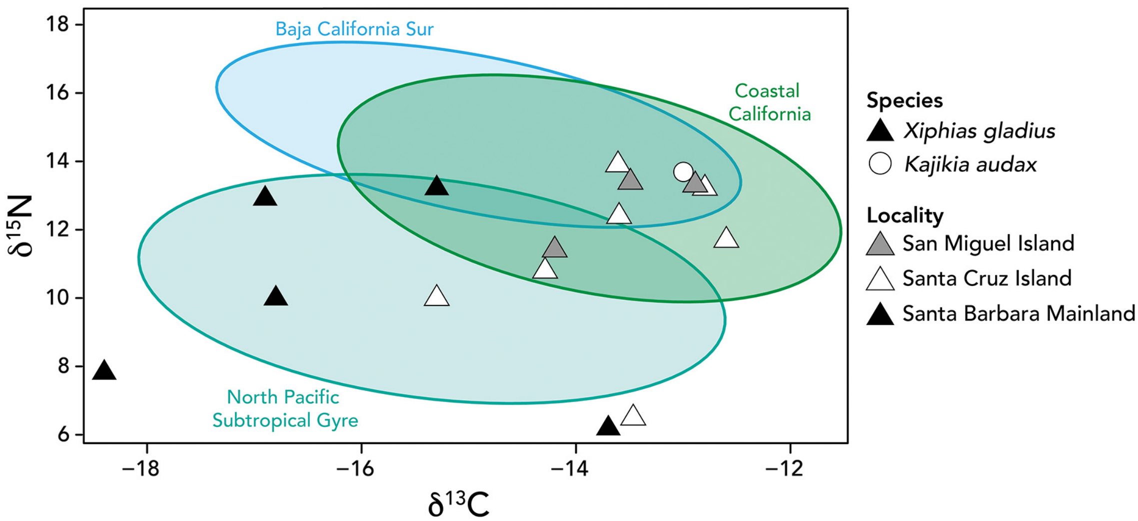

Fig. 2. Archaeological and modern billfish isotope data from the North Pacific. Triangles: archaeological swordfish *Xiphias gladius*; circle: the single striped marlin *Kajikia audax* specimen. Species IDs come from Rick et al. (2019). Symbol colors represent the geographic region the specimen was recovered from (Table S1, Fig. 1). Archaeological billfish data have been corrected for tissue- and temporal-specific isotope effects (Text S1 & Table S1). Colored ellipses: modern Pacific swordfish data obtained from Fig. 6 of Acosta-Pachón et al. (2020) via WebPlot Digitizer, as raw data were not provided. Shown are 95% standard ellipse areas (via SIBER; Jackson et al. 2011) of modern swordfish collected from the North Pacific Subtropical Gyre (teal), Coastal California (green), and Baja California Sur (light blue)

Bight (Acosta-Pachón et al. 2020, Sepulveda et al. 2020). In winter, Sepulveda et al. (2020) found that most of these swordfish migrated south but remained within the California Current System or Gulf of California. However, some 20% of swordfish tagged in the Southern California Bight ventured west near the Hawaiian Islands (i.e. North Pacific Subtropical Gyre). Our isotopic data from archaeological California swordfish complement these findings, documenting similar variability in migration and foraging patch use in pre-industrial swordfish populations.

Differences in the $\delta^{13}C$ values of swordfish recovered from island vs. mainland archaeological samples may reflect different fishing locations used by Indigenous peoples and territorial circumscription in fishing grounds (Rick et al. 2005). Billfish from island sites had higher $\delta^{13}C$ values by an average of 2.6‰, a narrower range of $\delta^{13}C$ values (2.7‰), and most individuals plotted within the isotopic niche of modern California Current System swordfish (Fig. 2). In contrast, billfish specimens from the mainland had lower and more variable $\delta^{13}C$ values (4.7‰), matching isotopic data from modern swordfish captured within the subtropical gyre (Fig. 2). People from the mainland presumably hunted billfish in the SBC (Fig. 1), potentially resulting in more frequent capture of animals migrating from distant western foraging grounds in summer. Island communities may have captured animals from the SBC or from waters south of the Channel Islands, including the large submarine canyons southwest of Santa Rosa and east of Anacapa (De Leo & Ross 2019). This south side of the northern Channel Islands was an area of high swordfish landings in the late 20th century (Bedford & Hagerman 1983). However, Chumash peoples likely obtained swordfish through a combination of cere-

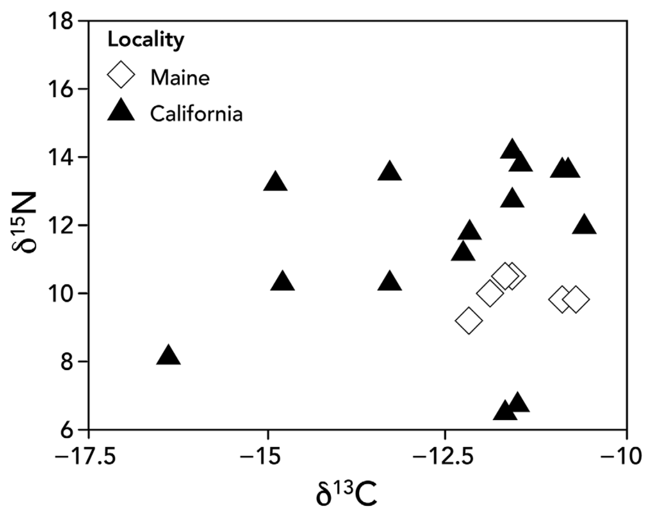

Fig. 3. Bulk tissue isotope data for California and Maine archaeological *Xiphias gladius*. Triangles: archaeological swordfish sampled in this study; diamonds: isotope values of Maine swordfish from ca. 4000 ^{14}C yr ago (Newsom et al. 2022). Data were measured via EA-IRMS; no adjustments for temporal isotope effects have been made. See Tables S1 & S2 in Supplement 1 for raw data as well as corrected data for California billfish specimens

monial hunting, opportunistic encounters, and exchange among communities (Davenport et al. 1993, Noah 2005).

We note a few significant isotopic outliers among sampled archaeological billfish from California (Table S1, Fig. 2). Two specimens (USNM 26 380b, 26 325; see Table S1) exhibited surprisingly low $\delta^{15}N$ values (<7‰), given the apex marine predator role of swordfish. One possible explanation for this is ontogenetic shifts in diet and differential foraging among juvenile and adult swordfish (Ménard et al. 2007, Dorado et al. 2012). The billfish bones we sampled were all modified by people or fragmentary, making animal size estimations difficult. However, 26380b and 26325 are comparable in size to other sampled elements (e.g. specimen 26380a), and we thus suspect ontogenetic isotopic variation is not at play. Instead, these low $\delta^{15}N$ values may reflect foraging by swordfish in oligotrophic waters dominated by nitrogen-fixing primary producers (Graham 2007, Dorado et al. 2012, Morrison 2013, Horii et al. 2018). Future work employing amino acid $\delta^{15}N$ and $\delta^{13}C$ analysis could help evaluate these patterns and provide additional evidence of billfish foraging grounds and historical residency patterns (Graham 2007, Vokhshoori et al. 2019).

Our findings also demonstrate the broad ecological niche of swordfish in the northeastern Pacific relative to other regions in the Americas (Fig. 3). In Maine, bulk tissue $\delta^{13}C$ and $\delta^{15}N$ values of billfish remains from archaeological sites show a much narrower range of isotopic values (Morrison 2013, Newsom et al. 2022). Isotopic values spanned <3‰ for both $\delta^{13}C$ and $\delta^{15}N$ in Maine swordfish samples dated to ca. 4000 ^{14}C yr, ago (Newsom et al. 2022) (Fig. 3). Maine swordfish $\delta^{15}N$ values were fairly low (~+8.5 to +10.5‰), suggesting historical foraging grounds in the oligotrophic Sargasso Sea. To our knowledge, isotopic data are not presently available for archaeological billfish from South America, though geochemical analyses are ongoing (Biton-Porsmoguer et al. 2022). Our findings and previous work highlight the value of zooarchaeological collections for modern ecological research and provide important historical data on billfish ecology and movement.

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