Environmental variability shifts the trophic dynamics and ecological niche partitioning of billfishes using stable isotope analysis

Ching-Tsun Chang[1], Wei-Chuan Chiang[1], Yi-Jay Chang[2], Nan-Jay Su[3], Chi-Lu Sun[4]
[1]Eastern Fishery Research Center, Fisheries Research Institute
[2]Institute of Oceanography, National Taiwan University
[3]Department of Environmental Biology and Fisheries Science, National Taiwan Ocean University
[4]Institute of Fisheries Science, National Taiwan University
Email: ctchang@mail.tfrin.gov.tw, wcchiang@mail.tfrin.gov.tw

Abstract

Climate-driven environmental variability is rapidly restructuring marine ecosystems, yet how these apex predators adjust their trophic dynamics and habitat uses remain poorly understood. Here, we used long-term stable isotope data ($\delta^{15}N$ and $\delta^{13}C$; 2008 – 2024) to investigate trophic ecology and niche structure of five billfish species in thhe western Pacific under El Niño–Southern Oscillation (ENSO) variability and sea surface temperature anomalies (SSTA). Across all species, $\delta^{15}N$ increased with body size, indicating an ontogenetic increase in trophic position (TP). However, species exhibited distinct responses to environmental variability. Black marlin and swordfish showed habitat driven responses; striped marlin demonstrated trophic flexibility; and sailfish and blue marlin exhibited coupled shifts in both habitat and feeding. Isotopic niche analyses further revealed that niche width and interspecific overlap varied across ENSO phases, indicating dynamic resource partitioning and potential competition. These findings suggest that environmental variability influences the habitat use, trophic dynamics, and interspecific interactions of billfishes, with implications for future stock assessments.

Introduction

Large-scale environmental variability influences the distribution and migration of apex predators by altering physical oceanographic structures and resource availability (Gomes et al., 2024; Le Grix et al., 2022; Welch et al., 2023). Climate-driven processes such as ENSO can modify temperature, productivity, and water mass distribution, thereby reshaping marine food webs and predator–prey interactions. Recently, periods of unusually high sea surface temperatures (e.g., 2014–2016 and 2021–2023) have further intensified ocean variability (Hobday et al., 2018; Oliver et al., 2021). Understanding how apex predators respond to such variability is critical for predicting ecosystem dynamics under ongoing climate change.

Billfishes are highly migratory apex predators that play important roles in pelagic ecosystems and have been heavily exploited for centuries (Hinman, 1998; Collette et al. 2011; Punt et al. 2015). Their wide-ranging movements and high trophic positions make them sensitive to environmental variability. However, how different billfish species respond to climate variability remains poorly understood, particularly in terms of their habitat use and trophic dynamics.

Stable isotope analysis (SIA) has been widely used to investigate the trophic and migration ecology of marine predators across broad spatial and temporal scales (Pethybridge et al. 2018; Logan et al. 2020). Nitrogen isotopes ($^{15}N/^{14}N$, measured as $\delta^{15}N$) are used to estimate the trophic position (TP) of marine organisms, reflecting food chain-length and differences between oligotrophic and eutrophic environments (Post 2002; McCutchan et al. 2003, Vanderklift & Ponsard 2003). Furthermore, carbon isotopes ($^{13}C/^{12}C$, measured as $\delta^{13}C$) reflect the source of primary production and are commonly used to infer habitat use, distinguishing between coastal versus offshore or surface versus deeper foraging environments (Kelly 2000, McCutchan et al. 2003). Integrating $\delta^{13}C$ and $\delta^{15}N$ allows understanding of habitat use and trophic structure, providing insights into how predators adjust their ecological strategies under changing environmental conditions.

In this study, we investigated the trophic ecology and response strategy of multiple billfish species under the influence of climate-driven variability in the western Pacific Ocean. Specifically, we aim to (1) quantify the long-term (2008–2024) isotopic responses of five billfish species to environmental variabilities in the Western Pacific; (2) differentiate whether isotopic shifts are driven by habitat shifts (migration) or dietary shifts; (3) assess how environmental stress influence niche width and resource partitioning. By integrating isotopic patterns with environmental variability, this study provides new insights into the ecological strategies of billfish and their potential responses to future ocean change.

Methods

Sample collection

White muscle tissue from five billfish species was collected in waters of eastern Taiwan from 2008 to 2024. The basic information of billfish were recorded, including species, weight and eye-fork length (EFL). The samples were stored at -80°C until processing.

Stable isotope analysis

The white muscle tissues were rinsed with distilled water and freeze-dried at -50°C for 48 hr. Approximately 0.4-0.8 mg of powder were packed into ultra-clean tin capsules. $\delta^{13}C$ and $\delta^{15}N$ values were determined using an elemental analyzer and mass spectrometer. The isotope values were expressed in standard ‰ notation relative to Vienna Pee Dee belemnite (V-PDB) for carbon and atmospheric N_2 for nitrogen. Because lipids have lower $\delta^{13}C$ values relative to other animal tissues, and the variability in tissue lipid content can affect $\delta^{13}C$ values (Focken & Becker 1998), the $\delta^{13}C$ values of billfish (C:N > 3.5) were normalized using lipid normalization algorithms for muscle from Atlantic bluefin tuna *Thunnus thynnus* (Logan et al. 2008).

Baseline $\delta^{13}C$ and $\delta^{15}N$

A model of ocean biogeochemistry and isotopes (MOBI; Somes et al. 2017) was used to derive baseline phytoplankton $\delta^{13}C$ and $\delta^{15}N$ at the potential habitats of billfish based on the previous tagging results (Chiang et al. 2011; 2015; 2020). The parameters in the $\delta^{13}C$ isoscape model included specific growth rate of phytoplankton species, the concentration of [CO2]aq, Suess effect, mixed layer depth (MLD), sea surface temperature (SST), net primary production, and nitrate concentration. The parameters in the $\delta^{15}N$ isoscape model included nitrate concentration, net primary production, SST, and dissolved oxygen. The environmental variables were obtained from Copernicus Marine Service.

Trophic position and other index

The trophic position of billfish species was calculated by the following equation:

$$TP = \Delta^{15}N_{Billfish\ -\ Baseline}/TDF + TP_{baseline}$$

where $\Delta^{15}N_{Billfish - Baseline}$ represents the predictions for baseline phytoplankton $\delta^{15}N$ values were subtracted from the values of individuals billfish. TDF is the trophic discrimination factor (TDF) of 2.8 (Vanderklift & Ponsard 2003). The $TP_{baseline}$ was set at 1 as the TP of phytoplankton.

Data analysis

Linear regressions were used to examine relationships between $\delta^{13}C$ and $\delta^{15}N$ values and body length across ENSO phases. To remove size-related effects, residuals from the regressions of $\delta^{13}C$ and $\delta^{15}N$ against body length were calculated and used for subsequent analyses. These size-corrected residuals were compared among ENSO phases independent of body size.

Isotopic niche width was quantified using the standard ellipse area corrected for small sample size (SEAb). SEAb was used as a measure of trophic flexibility, with larger ellipse areas indicating broader niche width. Niche overlap among species was calculated as the percentage of overlap between standard ellipses. Overlap was used to assess the degree of shared resource use and potential niche partitioning among species across ENSO phases.

Results and Discussions

Overall patterns

A total of 1478 individuals across five apex predator species were analyzed (Table 1). Black marlin had the largest average EFL (194 ± 39 cm), followed by blue marlin (182 ± 27), while swordfish had the smallest average length (123 ± 33). Across all samples, $\delta^{15}N$ ranged from 7.63‰ to 15.32‰, and $\delta^{13}C$ ranged from -21.66‰ to -15.35‰. Detailed information for each species, including sample size, weight, EFL, $\delta^{13}C$ and $\delta^{15}N$ values of each billfish species were listed in Table 1.

Among species, black marlin had highest average $\delta^{15}N$ values (12.58‰) but lowest average $\delta^{13}C$ values (-17.56‰). In contrast, the blue marlin had the lowest $\delta^{15}N$ values (11.24‰) and the highest $\delta^{13}C$ values (-16.97‰). Across all species, $\delta^{15}N$ for all species increased significantly with the EFL ($p < 0.05$, Fig. 1); while $\delta^{13}C$ values showed no correlation ($p > 0.05$, Fig. 2). The positive relationships of $\delta^{15}N$ and billfish size suggested the ontogenetic trophic shift is a core biological trait of all billfish species. Furthermore, the black marlin had the highest average TP (4.3), followed by sailfish (4.2), striped marlin (4.1) and swordfish (4.1), and the blue marlin had the lowest TP (3.8), consistent to previous study (Guillemin et al. 2022). Regardless of climate stress, the follow the fundamental rule that they eat higher on the food chain as they grow bigger.

Species-specific adaptive responses

Black marlin

Black marlin exhibited relatively stable $\delta^{15}N$ across ENSO phases and body sizes, indicating a consistent trophic position, while $\delta^{13}C$ varied among environmental conditions (Fig. 1-3). This pattern suggests that black marlin primarily respond to environmental variability through habitat shifts rather than dietary changes. Size-corrected $\delta^{13}C$ residuals showed modest separation among ENSO phases (Fig. 3), with El Niño individuals tending toward higher values (positive), and neutral individuals toward lower (more negative) values, implies greater use of coastal or productive waters. The decrease in $\Delta^{13}C$ relative to the baseline with increasing SSTA indicates a shift toward deeper or more offshore foraging habitats (Fig. 4-6). These findings are consistent with previous tagging and fishery studies showing changes in vertical and horizontal habitat use under warming conditions (Farchadi et al. 2018; Rohner et al. 2022).

Blue marlin

The $\delta^{15}N$ values showed a slight positive relationship with body length across all ENSO phases, with a steeper increase observed during El Nino (Fig. 1), indicating ontogenetic trophic shifts. However, size-corrected $\delta^{15}N$ residuals were generally lower during El Niño compared to neutral and La Niña periods, and trophic position (TP) also decreased under these conditions (Fig. 5), suggesting reduced trophic feeding in warmer environments. In contrast, $\delta^{13}C$ values showed a slight negative relationship with body size, and size-corrected $\delta^{13}C$ residuals were lower during El Niño and higher during La Niña (Figs. 2–3), indicating a shift toward more offshore or pelagic habitats during warm periods. The occurrence of individuals with particularly low $\delta^{13}C$ values during the extreme warming events of 2015–2016 further supports this interpretation. Centroid analysis confirmed these patterns, showing a consistent shift toward lower $\delta^{13}C$ and $\delta^{15}N$ values during El Niño relative to other ENSO phases (Fig. 4). Additionally, $\Delta^{13}C$ relative to the baseline increased with SSTA, while TP slightly decreased (Fig. 6), suggesting a decoupled response in which habitat shifts toward offshore environments are accompanied by feeding at lower trophic levels. This pattern implies that blue marlin may increasingly rely on mid-trophic pelagic prey, such as squid or forage fishes, under warming conditions. These findings are consistent with previous studies indicating broader spatial movements during non-La Niña periods (Carlisle et al. 2017), supporting the interpretation of environmentally driven habitat shifts.

Sailfish

The positive $\delta^{15}N$–length relationship during La Niña indicates increasing trophic position with size, whereas the negative relationship during El Niño suggests a shift toward lower trophic feeding at larger sizes (Fig. 1). However, size-corrected $\delta^{15}N$ residuals were generally higher during El Niño, indicating an overall increase TP or feeding on ^{15}N-enriched prey under these conditions (Fig. 3). This apparent discrepancy suggests that sailfish may experience shifts in both size-structured feeding and baseline or prey composition, resulting in complex trophic responses across environmental conditions. $\delta^{13}C$ patterns further indicated clear habitat shifts among ENSO phases (Fig. 2). Higher $\delta^{13}C$ residuals during El Niño and neutral periods (Fig. 3) suggest increased use of more enriched, likely productive or coastal-associated habitats, whereas lower $\delta^{13}C$ values during La Niña indicate greater reliance on more depleted, offshore or pelagic habitats. The presence of extremely low $\delta^{13}C$ values during La Niña (2008–2009) further supports episodic use of strongly pelagic or distinct water masses during these periods. Previous studies have shown that sailfish abundance is strongly associated with SST, while ENSO influences distribution indirectly through changes in thermocline depth, oxygen structure, and prey availability (Marrari et al., 2023). Our isotopic results further suggest that these environmental processes are accompanied by coupled shifts in both habitat use and trophic dynamics. Both $\Delta^{13}C_{\text{Sailfish – Baseline}}$ and TP increased with warming, indicating a shift toward more ^{13}C -enriched carbon sources and higher trophic feeding under elevated temperature conditions. Sailfish preferentially occupy warm, oxygenated waters and adjust their vertical and horizontal movements to maintain favorable thermal conditions while exploiting productive areas (Clyde-Brockway et al., 2025). These mechanisms provide a biological basis linking large-scale climate variability (e.g., ENSO and SSTA) to observed isotopic shifts, as changes in habitat accessibility and prey availability can alter both $\delta^{13}C$ (habitat use) and $\delta^{15}N$ (trophic dynamics). Our results indicate a coupled response in which sailfish adjust both habitat use and trophic position under environmental variability, likely by moving into more productive habitats and targeting higher trophic prey during warming periods.

Striped marlin

The $\delta^{15}N$ values showed a positive relationship with body length, with similar slopes between El Niño and La Niña (Fig. 1). $\delta^{13}C$ values exhibited a slight negative relationship with length, with no clear difference among ENSO phases (Fig. 2). The size-corrected $\delta^{15}N/\delta^{13}C$ residuals between El Nino and La Nina were similar (Fig. 3). The centroid analysis showed substantial overlap between ENSO phases, with only minor shifts in $\delta^{15}N$ and $\delta^{13}C$ between El Niño and La Niña (Fig. 4). These results suggest that both habitat use ($\delta^{13}C$) and TP ($\delta^{15}N$) are relatively stable across broad climate regimes, indicating weak sensitivity to ENSO-driven environmental variability. The $\Delta^{13}C_{\text{Striped marlin – Baseline}}$ did not change and TP increased with increasing SSTA (Fig. 6). While previous studies show striped marlin can shift their spatial distribution in response to environmental variability (Lam et al. 2022), our isotopic results suggest relatively stable habitat use. Instead, shifts in TP ($\delta^{15}N$) were clearer, suggesting that striped marlin may adjust their diet within broadly similar habitats rather than undergoing large-scale habitat shifts.

Swordfish

Swordfish exhibited relatively stable $\delta^{15}N$ patterns across ENSO phases and along the SSTA gradient, indicating limited variation in trophic position. The consistent positive $\delta^{15}N$–length relationship and overlapping residuals among ENSO phases suggest that swordfish maintain a stable trophic role regardless of climate variability (Fig. 1, 3). In contrast, $\delta^{13}C$

showed clearer variability among ENSO phases, with lower values during El Niño and higher values during La Niña (Fig. 2, 3), indicating shifts in carbon sources or habitat use. The more negative $\delta^{13}C$ values observed during El Niño suggest increased reliance of offshore and/or mesopelagic prey, whereas enriched values during La Niña indicate relatively more productive or coastal-associated habitats. Notably, two individuals with particularly low $\delta^{13}C$ values (-4‰) were observed in El Nino (2019). The centroid analysis demonstrated a shift in $\delta^{13}C$ between phases, with lower $\delta^{13}C$ during El Nino compared to La Nina, while $\delta^{15}N$ values remained similar (Fig. 4). In addition, the $\Delta^{13}C_{\text{Swordfish – Baseline}}$ slightly decreased with increasing SSTA, while TP remained relatively stable (Fig. 6), further supporting a gradual shift toward more ^{13}C-depleted carbon sources under warming conditions. Previous studies have shown that swordfish diet composition can shift under warming conditions, with a change from cephalopods to epipelagic teleosts during 2014-2016 (Preti et al. 2025). Together, these results suggest that swordfish respond to environmental variability by adjusting prey composition and habitat use, while maintaining a relatively stable TP within the food web.

Isotopic niche of five billfish species

The analysis of isotopic niche width and overlap revealed that resource partitioning among billfish species is not static but varies across environmental conditions. The ellipse plots revealed distinct isotopic patterns among ENSO phases (Fig. 7, 8). During El Niño, isotopic niches of most species largely overlapped, with some separation along the $\delta^{15}N$ axis. Blue marlin occupied a broader range of $\delta^{13}C$ values and generally lower $\delta^{15}N$ compared to other species. In contrast, sailfish, black marlin, and striped marlin showed greater variation in $\delta^{15}N$ than in $\delta^{13}C$, with sailfish exhibiting the highest $\delta^{15}N$ values. During neutral conditions, separation between species was more apparent. Black marlin had higher $\delta^{15}N$ values and lower $\delta^{13}C$ values compared to blue marlin. Additionally, black marlin exhibited a broader $\delta^{13}C$ range during neutral periods than during El Nino. During La Niña, isotopic niches were more dispersed, with clearer separation along the $\delta^{13}C$ axis. Sailfish had lower and broader ranges $\delta^{13}C$ values, whereas other species occupied relatively high $\delta^{13}C$ positions. Pairwise niche overlap showed most of species had lower overlapped during El Nino than in La Nina (Fig. 9). Swordfish had greater overlap with other species (black marlin, blue marlin, and sailfish) during La Nina than during El Nino. Blue marlin and black marlin had highest overlap during neutral periods, followed by La Nina, and the lowest overlap during El Nino. Our results indicate that trophic interactions and competition among species are dynamic and environmentally mediated.

Conclusions

Billfish species exhibited diverse, species-specific responses to climate variability. Isotopic patterns revealed that some species primarily adjusted habitat use ($\delta^{13}C$; e.g., black marlin and swordfish), and others altered diets ($\delta^{15}N$/TP; e.g., striped marlin). Some showed coupled shifts in both habitat and trophic dynamics (e.g., sailfish, blue marlin). Sailfish showed both changes in habitat use and TP, indicating that they shift both where they feed and what they eat, whereas blue marlin exhibited decoupled responses, changing habitat while feeding at lower trophic levels. These response strategies suggest that environmental variability influences both spatial distribution and feeding behavior of billfishes, thereby affecting the availability and catchability of billfishes. As a result, changes in CPUE may not solely reflect population abundance, but also environmentally driven shifts in habitat use and trophic dynamics. This study highlights the importance of integrating ecological indicators, such as stable isotope data into stock assessments to improve the robustness of fisheries management under ongoing climate change.

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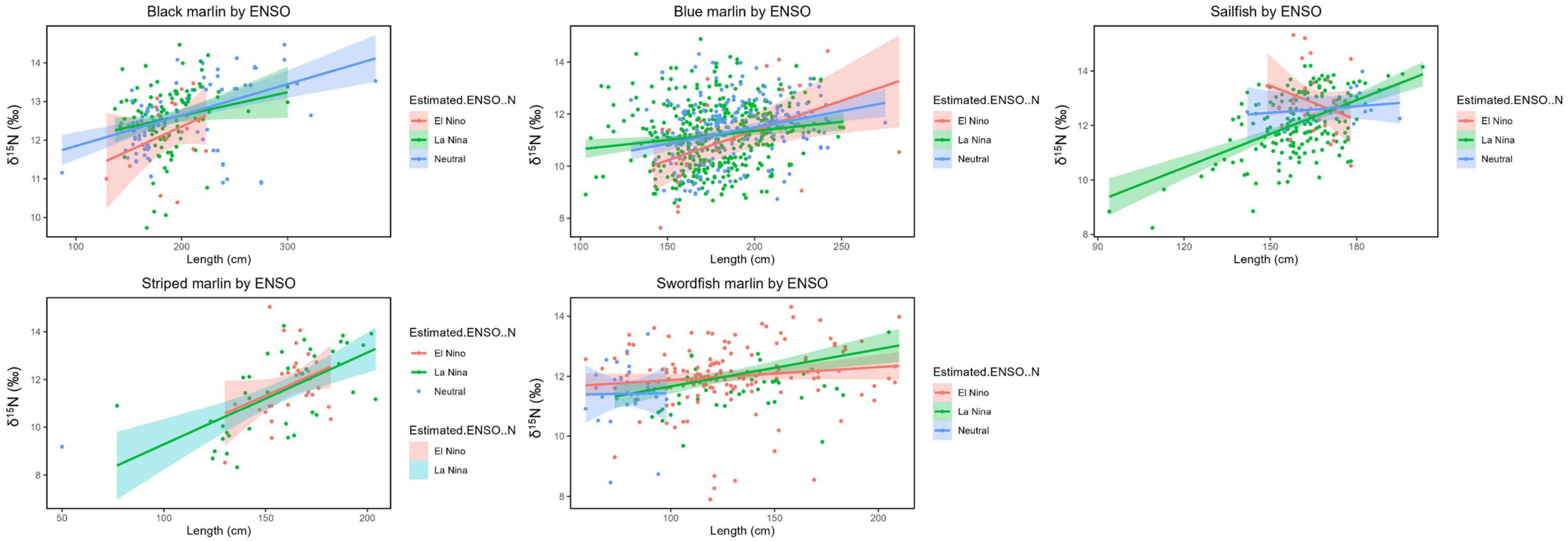
Table 1 Information for the sampling specimens, including samples size, weight, eye-fork-length (EFL), $\delta^{15}N$ and $\delta^{13}C$

Species	Number	Weight	EFL	$\delta^{15}N$	$\delta^{13}C$
Black marlin	238	6-564	87-383	9.73 ~ 14.47	-21.13 ~ -15.63
Blue marlin	656	9-245	103-283	7.63 ~ 14.88	-20.67 ~ -15.35
Sailfish	223	5-60	94-203	8.24 ~ 15.32	-21.66 ~ -15.95
Striped marlin	72	2-111	50-204	8.32 ~ 15.04	-18.39 ~ -15.93
Swordfish	289	3-139	59-210	7.9 ~ 14.31	-21.33 ~ -15.35

Table

Figures


Black marlin by ENSO

Blue marlin by ENSO

Sailfish by ENSO

Striped marlin by ENSO

Swordfish marlin by ENSO

Figure 1: Relationships of δ^{15}N and body length of five billfish species among ENSO phases (Red: El Nino, Green: La Nina, Blue: Neutral).

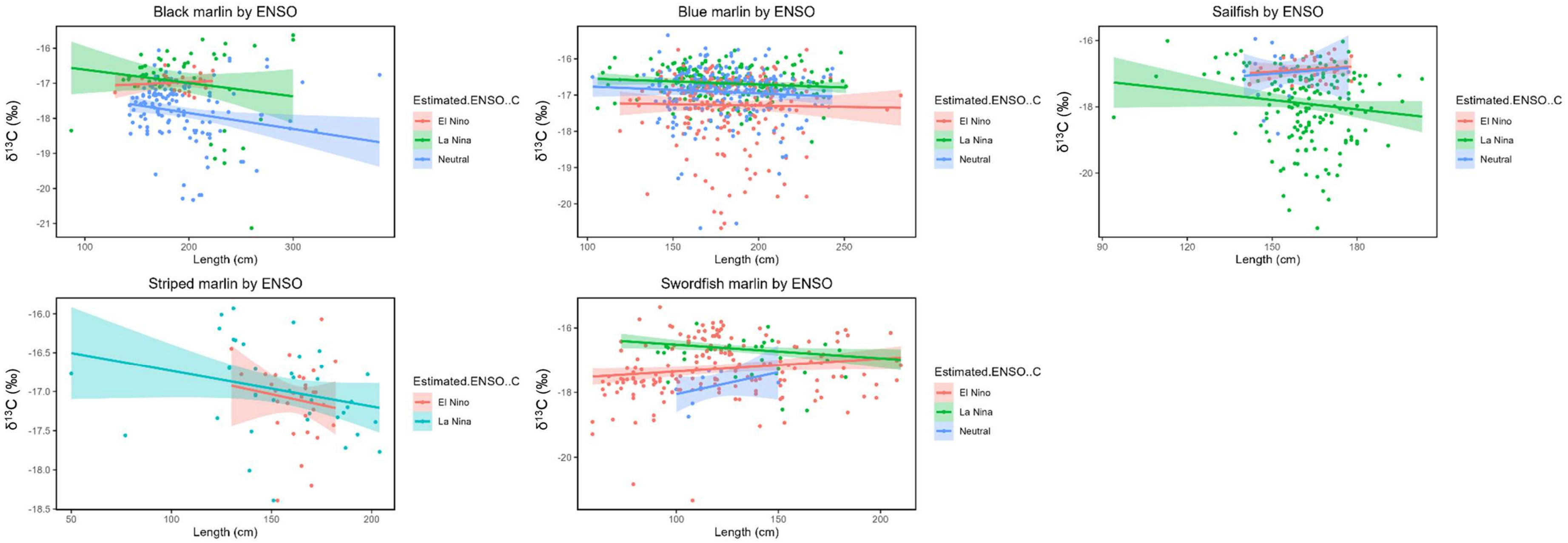


Figure 2: Relationships of δ^{13}C and body length of five billfish species among ENSO phases (Red: El Nino, Green: La Nina, Blue: Neutral).

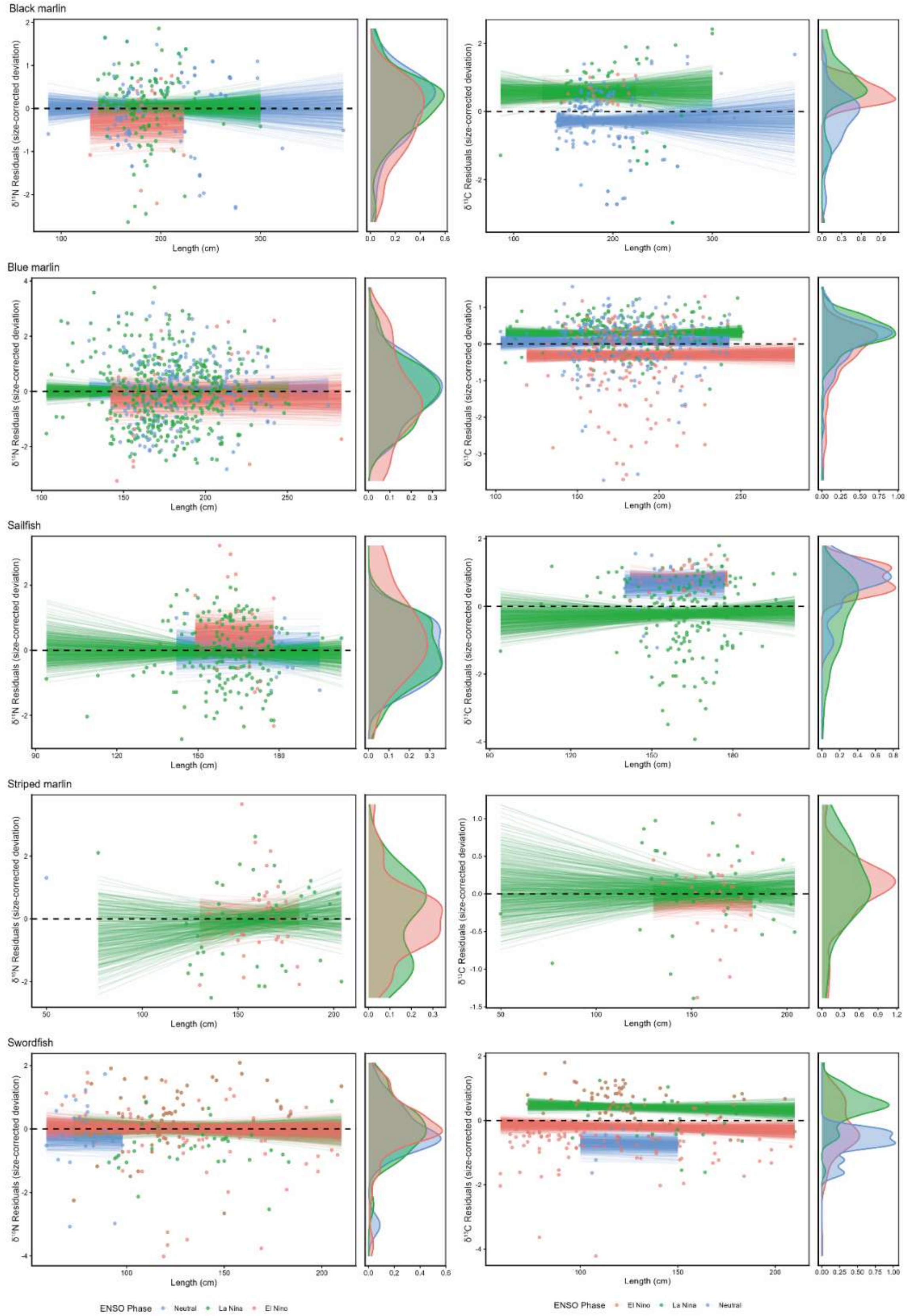


Figure 3: Size-corrected δ^{15}N (left) and δ^{13}C (right) residuals and the density plots of five billfish species among ENSO phases (Red: El Nino, Green: La Nina, Blue: Neutral).

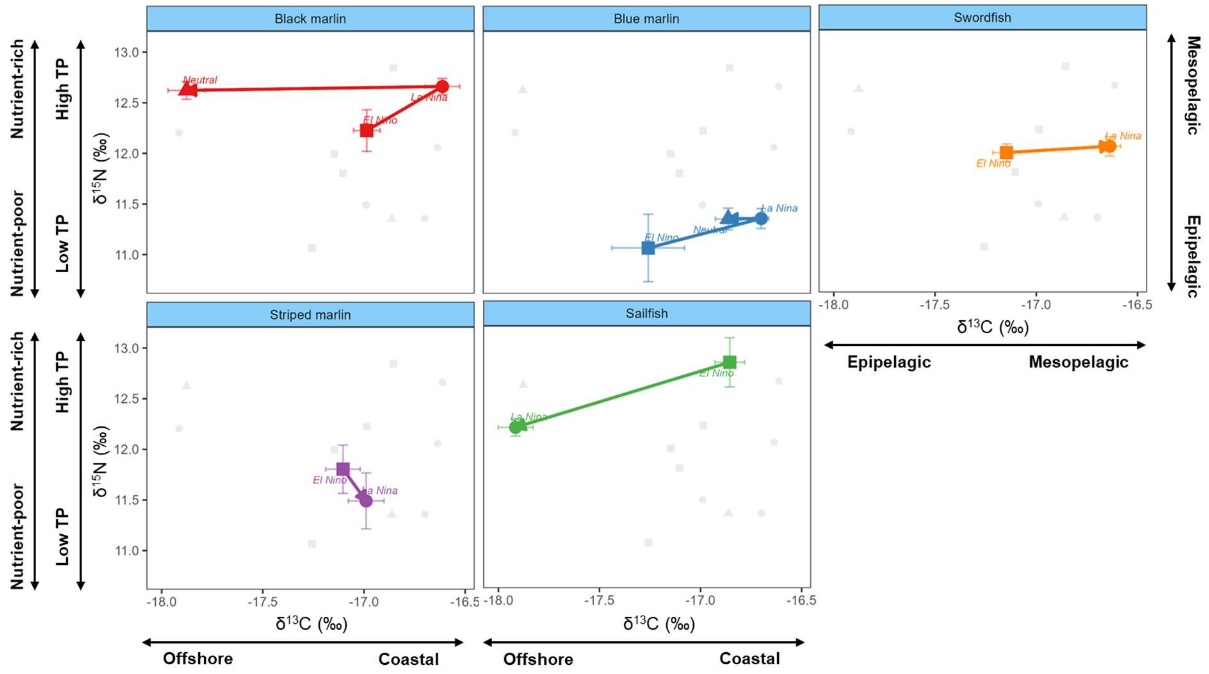


Figure 4: Centroid analysis in δ^{15}N and δ^{13}C of five billfish species. (Red: Black marlin; Blue: Blue marlin; Green: Sailfish, Purple: Striped marlin; Orange: Swordfish)

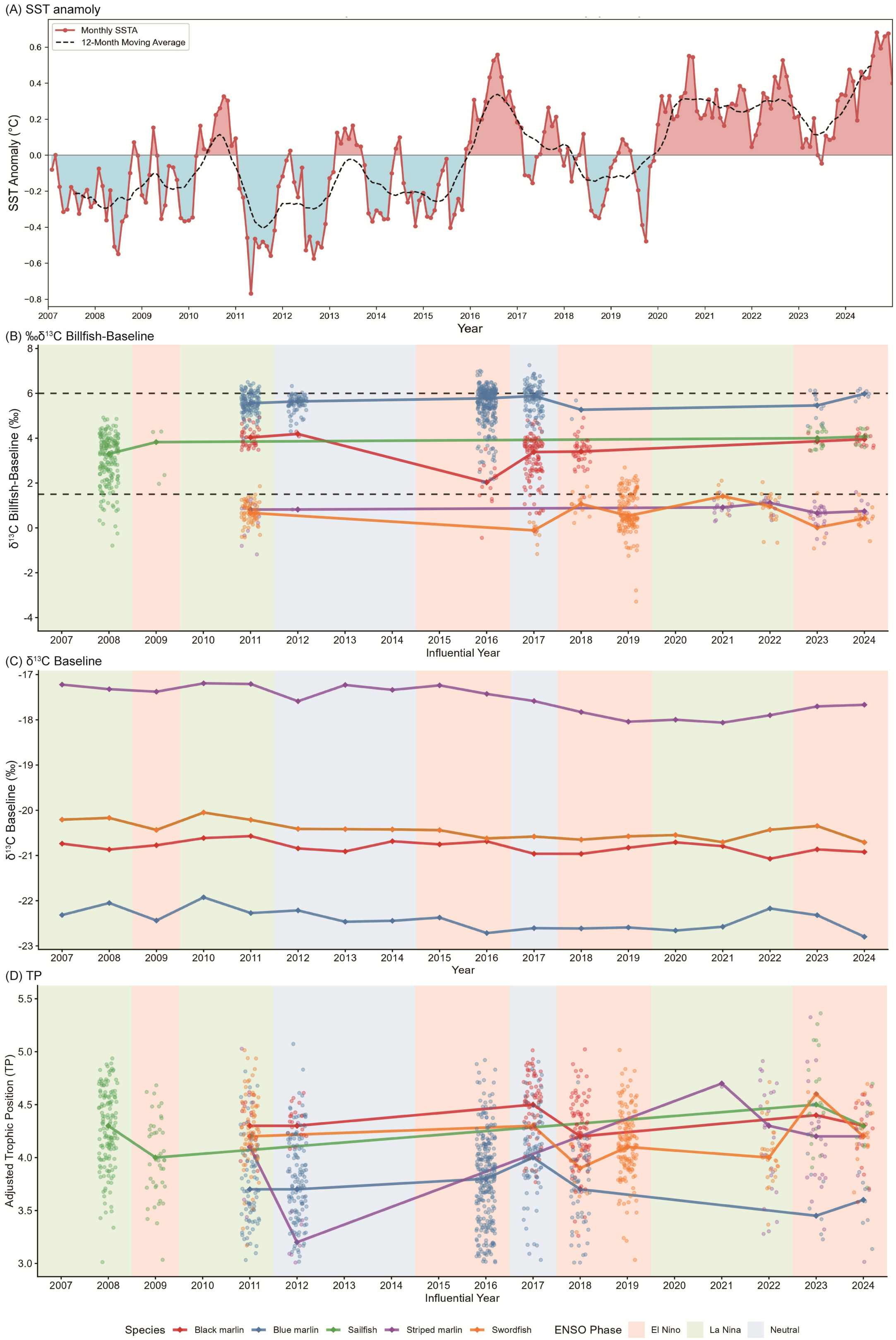


Figure 5: Long-term variations in (A) sea surface temperature anomaly, (B) $\delta^{13}C_{\text{Billfish-Baseline}}$, (C) $\delta^{13}C_{\text{Baseline}}$ of five billfish species, and (D) TP of five billfish species. (Red: Black marlin; Blue: Blue marlin; Green: Sailfish, Purple: Striped marlin; Orange: Swordfish)

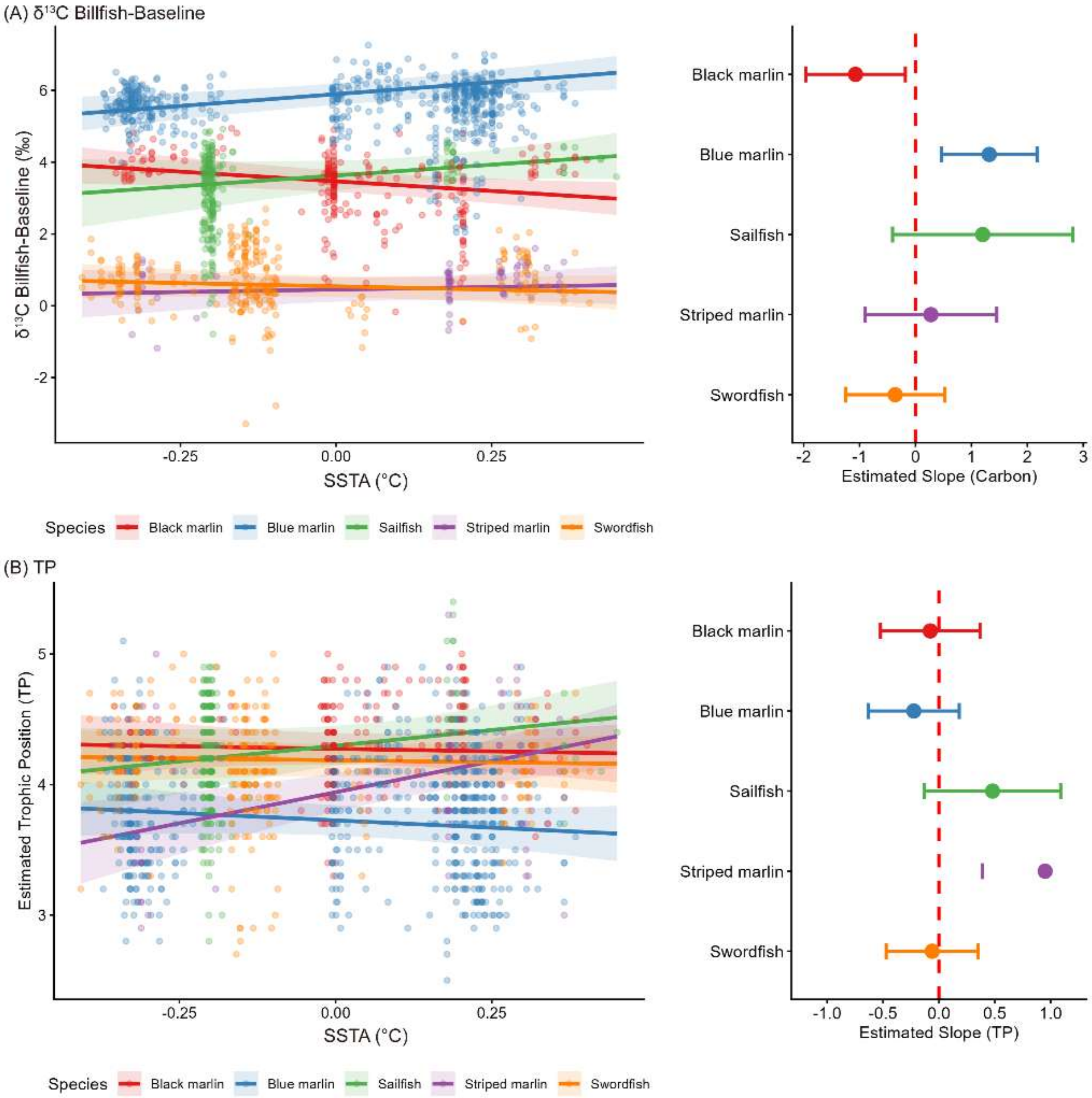


Figure 6: Relationships of (A) $\Delta^{13}C_{\text{Billfish-Baseline}}$ and sea surface anomaly (SSTA), (B) TP and SSTA of five billfish species (Red: Black marlin; Blue: Blue marlin; Green: Sailfish, Purple: Striped marlin; Orange: Swordfish)

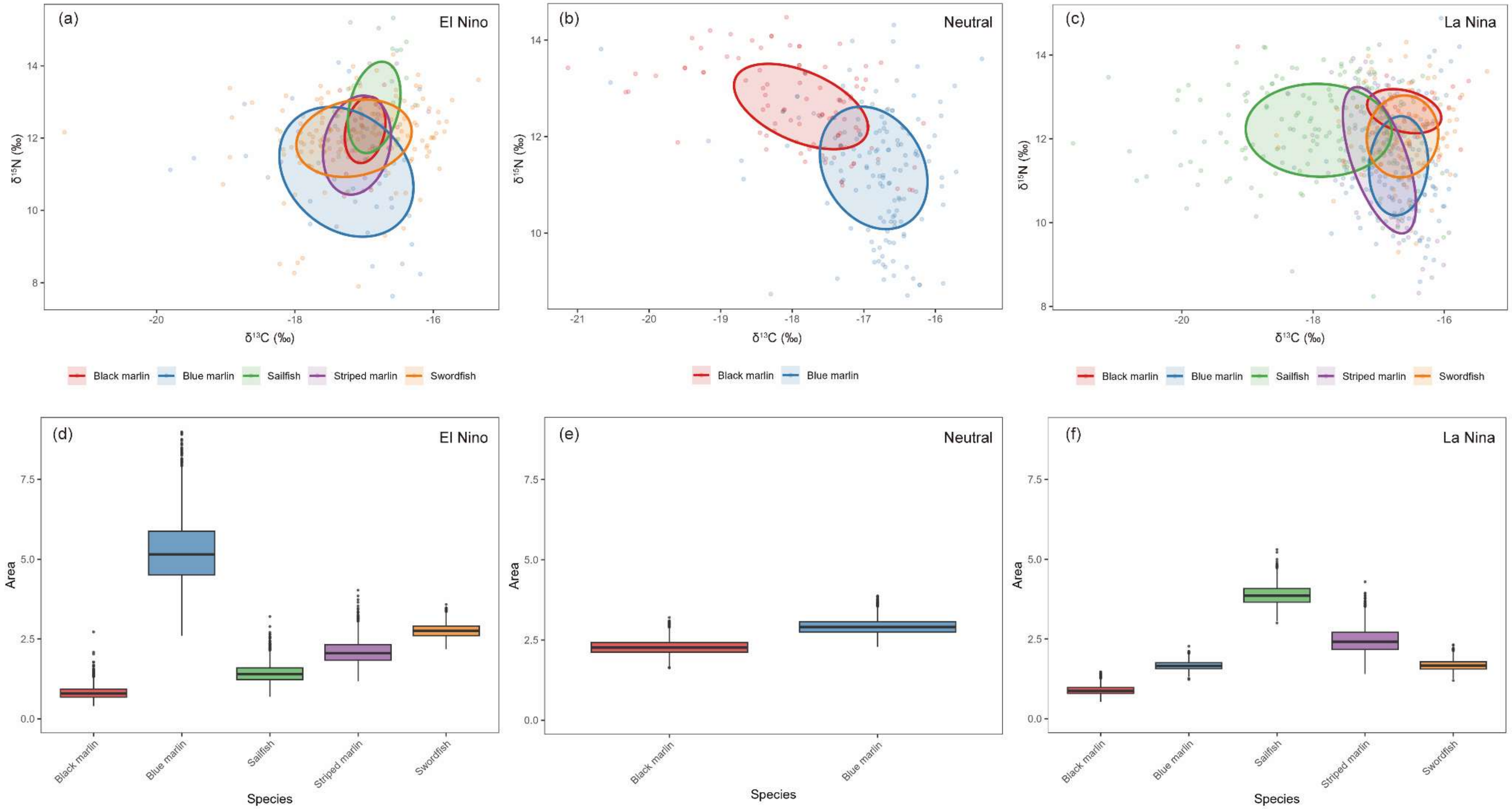


Figure 7: Isotopic niche width and and overlap of billfish species across ENSO phases. (a–c) Bivariate plots of δ^{13}C and δ^{15}N values showing isotopic niches of five billfish species during (a) El Niño, (b) neutral, and (c) La Niña conditions. Solid ellipses represent Bayesian standard ellipse areas (SEAb), indicating core isotopic niche space for each species. Points represent individual samples. (d–f) Isotopic niche width (SEAb) of each species under (d) El Niño, (e) neutral, and (f) La Niña conditions. Boxes indicate median and interquartile ranges, with whiskers representing variability.

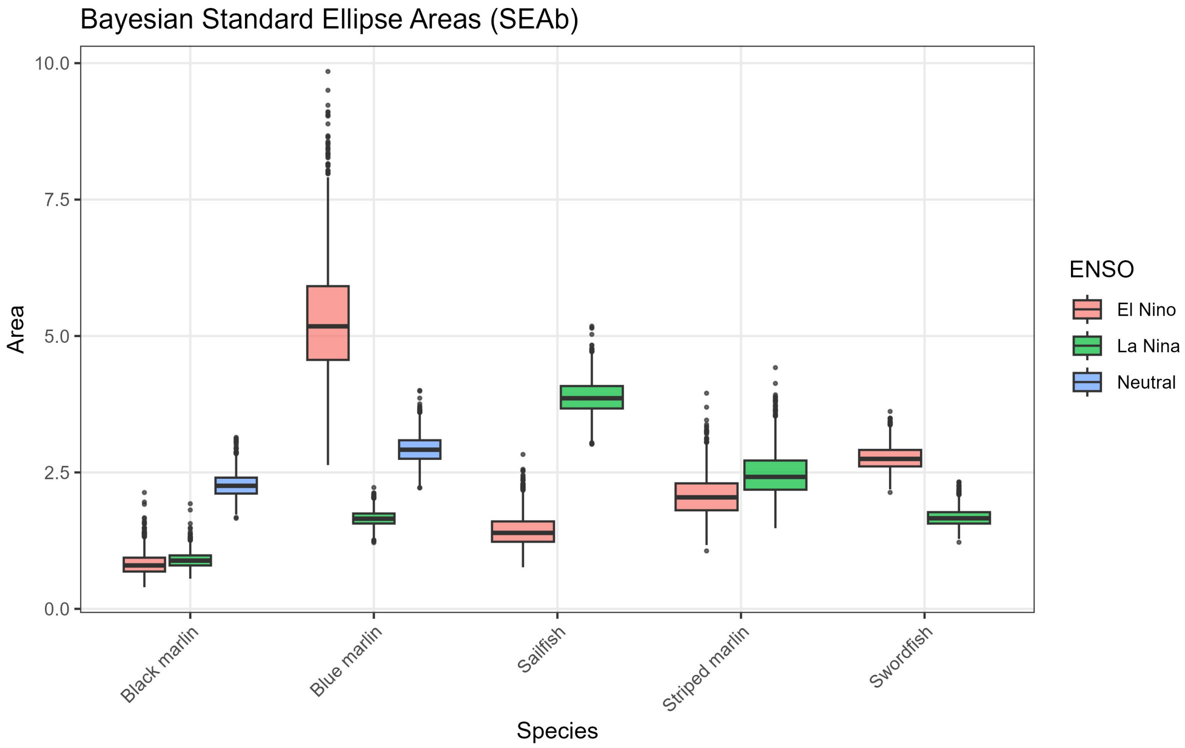


Figure 8:Comparison of SEAb across species and ENSO phases. Colors represent ENSO conditions (Red: El Niño, Green: La Niña, Blue: neutral).

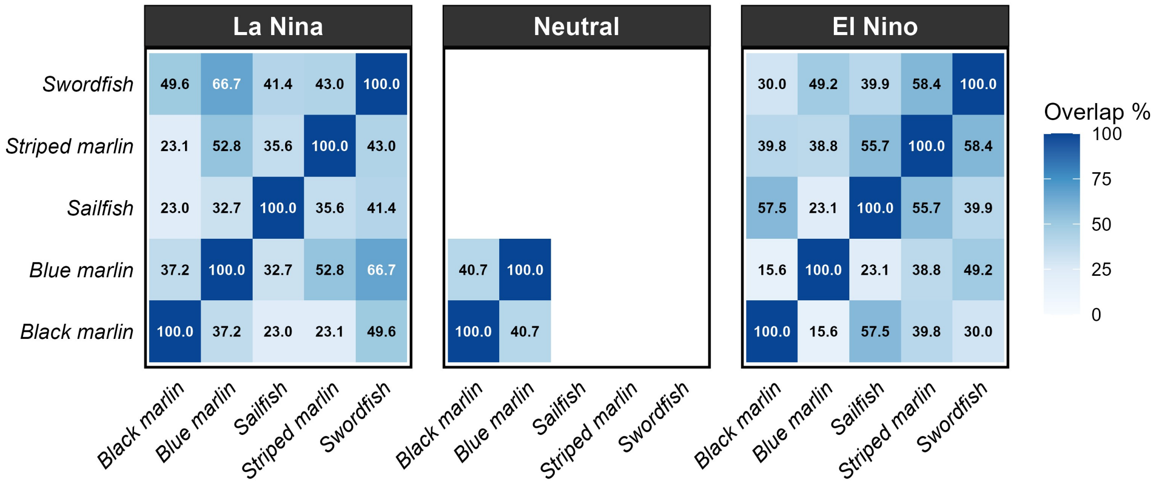


Figure 9: Pairwise niche overlap (%) among species based on SEAb under La Niña (left), neutral (center), and El Niño (right) conditions.