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ENSO effect on trophic interactions of three top predators in adjacent waters to Cabo San Lucas, Baja California Sur

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Abstract

Trophic competition among top predators is also influenced by environmental variability. However, the magnitude of the changes in contrasting events such as El Niño Southern Oscillation (ENSO) is poorly studied. The stomach contents of striped marlin (*Kajikia audax*), blue marlin (*Makaira nigricans*), and dolphinfish (*Coryphaena hippurus*) were analysed. We included the ENSO effect on the diet because we analysed organisms captured during 2010–2011 and 2014–2015, periods that, according to the Ocean Niño Index, were defined as the cold phase (CP) and warm phase (WP), respectively. Trophic diversity, feeding habits and strategy, trophic position (TP), trophic niche amplitude, and diet overlap were calculated. It was found that, despite a wide trophic spectrum, all three species were specialist predators in both phases. The most important prey species during both phases for striped marlin was *Dosidicus gigas*, while *Auxis* spp. was the most important prey of blue marlin. Dolphinfish fed mainly on *Oxyporhamphus micropterus* during the CP and *Pleuroncodes planipes* during the WP. Our results indicated that during both ENSO phases, all species maintained a trophic position similar to previous reports for the study area. However, for striped marlin, these differences were significant. Greater trophic competition was found during the CP (seven prey taxa shared) than in the WP (three prey taxa shared). These species often share the same environment, but their preference for feeding on different prey makes them occupy different trophic spaces, an aspect that allows their coexistence in time and space.

Research Article

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Introduction

Trophic interactions inferred from feeding habits can contribute to a better understanding of the effects of fishing and climate change on marine resources, although evidence of direct effects of climate change on the local abundance of marine species is limited (Sinclair *et al.*, 2002; Hobday and Evans, 2013). Currently, research has shown that climate change can impact ocean ecosystems through increased water temperature and a consequent decrease in primary productivity (Petrik *et al.*, 2020). Considering that these impacts are propagated throughout the trophic web, the diets of top predator species can be considered as a good indicator of changes in the ecosystem due to environmental variability.

Striped marlin (*Kajikia audax*), blue marlin (*Makaira nigricans*), and dolphinfish (*Coryphaena hippurus*) are amongst the most important species for the recreational fishery of Cabo San Lucas (CSL). Striped marlin is an oceanic species that periodically enters coastal waters and is distributed in tropical, subtropical, and temperate waters of the Pacific and Indian Oceans, usually in waters with a sea surface temperature (SST) of 20–25 °C. In the Eastern Pacific Ocean (EPO), its distribution is continuous from southern California (USA) to Chile, and its greatest abundance is recorded off the Mexican Pacific coast (Nakamura, 1985). Blue marlin is a cosmopolitan, highly migratory species distributed in the tropical and temperate waters of the Pacific and Indian Oceans, generally in waters with SSTs above 24 °C. It spends 90% of the time at depths where the water temperature is 1–2 °C less that SST (Nakamura, 1985; Su *et al.*, 2008). Dolphinfish is a highly migratory epipelagic species inhabiting tropical and subtropical waters worldwide, with its distribution limited by the 20 °C isotherm (Palko *et al.*, 1982; Moltó *et al.*, 2020). These species are all distributed in the Pacific Ocean, where the oceanographic event El Niño Southern Oscillation (ENSO) occurs.

The ENSO is an oceanographic event consisting of a warm phase (El Niño), characterized by abnormal warming of the EPO waters, and a cold phase (La Niña) characterized by unusual cooling of the Pacific and the American coast. These events have been found to cause changes in the migratory processes and relative abundance of large pelagic species, since changing environmental conditions, particularly SST, affect the life cycle of many species (Lluch-Belda *et al.*, 2005). It is now recognized that climate change is decreasing ecosystem productivity in most tropical and subtropical oceans, seas, and lakes, while increasing at high latitudes. Consequently, the presence of ENSO events are predicted to be more frequent and of higher intensity (e.g., Timmermann *et al.*, 1999; Hansen *et al.*, 2006). That is why studies that investigate the behaviour of trophic ecology and its competencies during the cold and

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warm phases of ENSO are of great importance in predicting species' behaviour in the presence of these events.

Materials and methods

Sampling for each ENSO phase

The specimens were collected for three consecutive days each month from 2010 to 2011 for the cold phase and from 2014 to 2015 for the warm phase from the landings of the sport fishing fleet that operated in CSL (Figure 1). The organisms were caught by rod and line with either live bait (*Mugil cephalus* or *Decapterus macrosoma*) or artificial bait (trolling) between 06:00 and 15:00.

Environmental information

The Oceanic Niño Index (ONI) is the official ENSO indicator at the National Oceanic and Atmospheric Administration (NOAA). It is based on SSTs in the Niño 3.4 region (5°N-5°S, 120°-170°W) in the east-central tropical Pacific Ocean (https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php). ONI values greater than or equal to 0.5 were considered indicative of an El Niño event; values lower than or equal to −0.5 indicated a La Niña event. According to SST anomalies in the study area and the ONI values, the ENSO phases were established as cold phase during 2010 and 2011 and a warm phase during 2014 and 2015. Considering that SST and chlorophyll-*a* (Chl-*a*) concentration are two variables closely related to the ENSO (López-Martínez *et al.*, 2023), both were used to relate them to prey diversity. SST and Chl-*a* concentration were inferred from monthly satellite image composites of the AVHRR (advanced very high-resolution radiometer) sensor with a resolution of 1.1 km, taking into account the area of operation of the sport fishing fleet.

Stomach analysis

The lower jaw fork length (LJFL ± 1 cm) for billfishes and curved fork length (FL cm) for the dolphinfish were recorded. A total of 351 stomachs during the cold phase and 448 stomachs during the warm phase were sampled. The stomachs were transported to the laboratory, where their contents were placed in a strainer and washed with water to remove excess gastric fluids and to separate the contents. Prey items were counted and weighed with a precision of ±0.01 g on an analytical balance. When bait was found in the stomach content (identified by its minimal digestion and the evident insertion point of the hook), it was discarded. Likewise, if bait was the only content in the stomach, it was considered empty.

Prey were identified at the lowest possible taxonomic level. For highly digested fish, the identification was based on the axial skeleton, mainly vertebrae, following the criteria of Clothier (1950), Monod (1968), Miller and Jorgensen (1973), Barrera-García (2008), Tercerie *et al.* (2022), and McEwan *et al.* (2022). Slightly digested fish were identified based on the keys by Allen and Robertson (1994) and Fischer *et al.* (1995). Hard structures of cephalopods and crustaceans were identified by consulting the keys of Wolff (1984), Brusca (1980), and Fischer *et al.* (1995). In the case of squid beaks, identification guides were

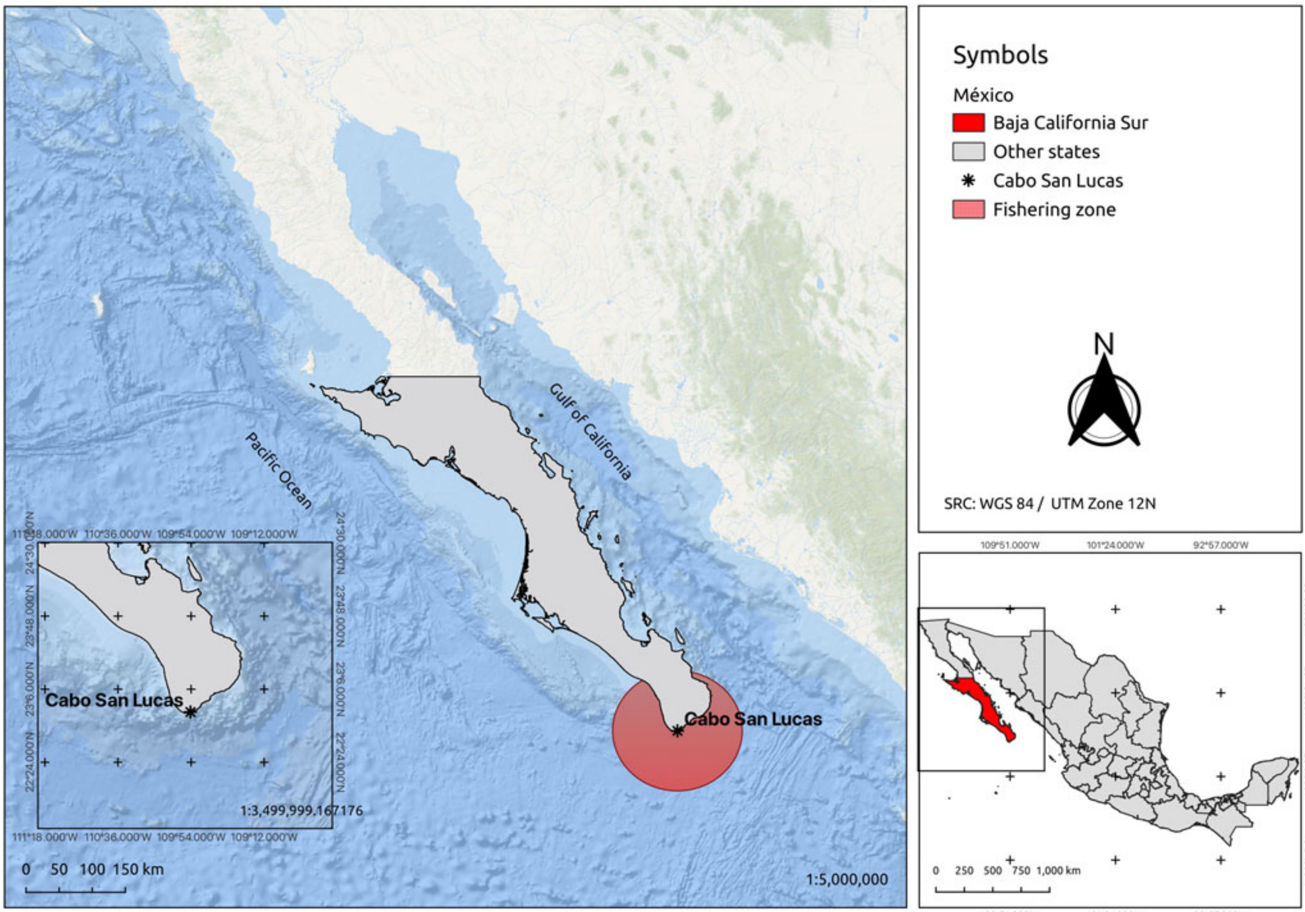

Figure 1. Study area: Cabo San Lucas (CSL), the one where the sport fishing fleet operates.

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used based on the studies by Clarke (1962, 1986), Wolff (1984), and Acuña-Perales *et al.* (2020).

The quantification of prey items was based on the number of eye pairs, heads, mouthparts (jaws), telsons, otolith pairs, or other anatomical structures that could serve as a reference for whole specimens (Ortega-García *et al.*, 2017).

Trophic analysis

Using the methodology of Hsieh *et al.* (2016), which is a modification to the one proposed by Chao *et al.* (2014), trophic diversity to infer sample sufficiency was determined from interpolation and extrapolation curves, which allowed us to identify the percentage of the diet calculated from the Hill numbers estimates with 95% confidence intervals.

The contribution of each food taxa to the diet was assessed using the prey-specific index of relative importance (%PSIRI) proposed by Brown *et al.* (2012) using the formula:

$$\%PSIRI_i = \frac{\%FO_i \cdot (\%PN_i + \%PW_i)}{2}$$

where $\%FO_i$ is the number of stomachs containing the prey i divided by the total number of stomachs ($\%FO_i = n_i/n$), $\%PN_i$ is the specific abundance per prey, and $\%PW_i$ is the weight of each prey.

The breadth of the diet (Bi) was estimated with the Levin's index (Krebs, 1989). This method allows inferences on the diet breadth by considering the proportion of each abundance of prey present and how they are distributed to the total. The values obtained from Levin's index range from 0 to 1, which derives if the predator is a specialist ($Bi \leq 0.6$) or a generalist ($Bi \geq 0.6$).

For the determination of the trophic position (TP_K), the equation proposed by Christensen and Pauly (1992) was applied:

$$TP_K = 1 + (\sum_{j=1}^{n} DC_{ij})(PT_j)$$

where DC_{ij} is the prey proportion (j) in the diet of predators (i), PT_j is the trophic position of the prey (j), and n is the total number of groups.

The trophic position of the prey at the species level was obtained from the FishBase database (https://www.fishbase.se/search.php). For those prey that could not be identified at the species level, the position values reported by Cortés (1999) were used.

The average trophic position was estimated for each species in both phases and compared them applying a Wilcoxon test considering the normality and homoscedasticity test results.

For the analysis of the trophic interactions between the three species during both phases, the prey they shared according to the % Frequency of occurrence and % Specific abundance of the prey were compared using the methodology proposed by Costello (1990) and modified by Amundsen *et al.* (1996).

A permutational analysis of variance (PERMANOVA) was used to assess the trophic overlap in the diets entered by the species. A non-metric multidimensional scaling ordination (nMDS) (Field *et al.*, 1982) was also applied to better visualize the overall pattern. A similarity of percentages analysis (SIMPER) was conducted to identify which prey taxa were important in discriminating between species (Clarke, 1993). The studies were performed using the package vegan in R statistical software.

The ONI value was used to define the months in which the cold and warm phases of ENSO were present. The relationship between SST and of Chl-*a* concentration in the feeding and their trophic competition was determined by applying canonical discriminant analysis (CDA) and a MANOVA statistical test.

Table 1. Summary of the total number of organisms per species (*N*), length range and stomachs with food and empty stomachs during the cold and warm phases of ENSO in the adjacent waters to Cabo San Lucas, Baja California Sur

	Kajikia audax	*Makaira nigricans*	*Coryphaena hippurus*
COLD PHASE			
Length range (cm)	144–232	168–282	58–146
N	228	54	69
N with food	164	31	49
% vacuity	64	23	20
WARM PHASE			
Length range (cm)	123–345	185–247	42–124
N	177	19	252
N with food	145	13	147
% vacuity	32	6	105

Results

During the cold phase, the average SST was 25.1 °C (±2.9 SD), and the average Chl-*a* concentration was 0.51 mg/m^3 (±0.4 SD). During the warm phase, the average SST was 26.6 °C (±2.7 SD), and the Chl-*a* concentration was 0.52 mg/m^3 (±0.1 SD). Total number of organisms sampled per species (N), length range (lower jaw fork length for billfish and fork length for dolphinfish), number and percentage of stomachs with food and empty stomachs are shown in Table 1.

Trophic diversity

From the interpolation and extrapolation curves, 26 prey families were identified in striped marlin trophic diversity during the cold phase (96.1% of their diet) and 28 prey families (98.7% of their diet) during the warm phase. For blue marlin, ten prey families were identified during the cold phase (88.4% of their diet) and three prey families (50% of their diet) during the warm phase. Finally, for dolphinfish, 19 prey families were identified during the cold phase (81% of their diet) and 25 prey families (94.9% of their diet) during the warm phase (Figure 2).

Stomach content analysis (SCA)

During the cold phase, the diet of striped marlin consisted of 37 prey taxa, which were identified and from three higher taxonomic groups: 27 fish taxa (%PSIRI = 53.5), nine cephalopod taxa (%PSIRI = 46.1) and one crustacean (%PSIRI = 0.4). For the warm phase, 45 prey taxa were identified, comprising 32 fish taxa (%PSIRI = 62.1), 11 cephalopod taxa (%PSIRI = 36.2), and two crustaceans (%PSIRI = 1.7). The most important prey species for striped marlin during both phases was *Dosidicus gigas* (%PSIRI CP = 30.4 and WP = 18.5%PSIRI). Other important prey taxa during the cold phase included the cephalopod *Argonauta* spp. (%PSIRI = 12.5), the fish *Caranx caballus* (%PSIRI = 19.3) and *Auxis* spp. (%PSIRI = 6.6) (Table 2). Important prey during the warm phase (Table 3) also included the fish *Lagocephalus lagocephalus* (%PSIRI = 15.5), *Balistes polylepis* (%PSIRI = 11.2), as well as the cephalopod *Argonauta* spp. (%PSIRI = 11.3).

The diet of blue marlin during the cold phase included 20 prey taxa, which were from two higher taxonomic groups: 17 fish taxa

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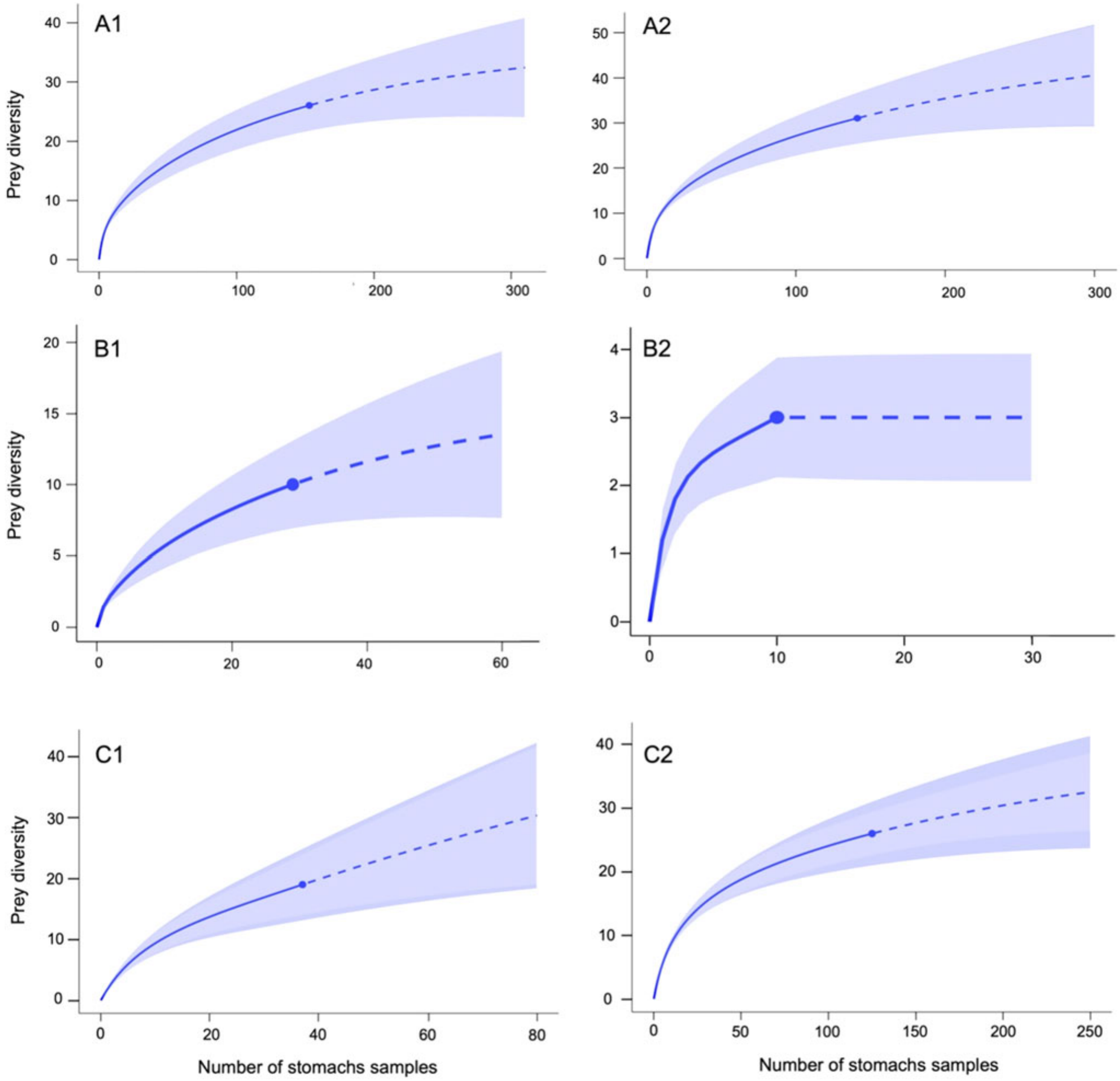

Figure 2. Interpolation and extrapolation curves to determine trophic diversity and represented diet percentage of striped marlin *Kajikia audax* (A), blue marlin *Makaira nigricans* (B) and dolphinfish *Coryphaena hippurus* (C) during cold (1) and warm (2) phase of ENSO in adjacent waters to Cabo San Lucas, Baja California Sur.

(%PSIRI = 82.7) and three cephalopod taxa (%PSIRI = 17.3). During the warm phase, the diet consisted of five prey taxa which were all fish (%PSIRI = 100). The most important prey species during both phases was the fish *Auxis* spp. (%PSIRI CP = 46.3 and %PSIRI WP = 50). Other important prey during the cold phase was the cephalopod *Dosidicus gigas* (%PSIRI = 14.8), and the fish *Katsuwonus pelamis* (%PSIRI = 8.5) and *Caranx caballus* (%PSIRI = 4.4) (Table 2). During the warm phase, the fish *Selar crumenophthalmus* (%PSIRI = 20.4), *Ablennes hians* (%PSIRI = 10), *Trachurus symmetricus* (%PSIRI = 10), and *Auxis thazard* (%PSIRI = 9.6) were also important (Table 3).

During the cold phase, the diet of dolphinfish was represented by 28 prey taxa, which were from three higher taxonomic groups: 21 fish taxa (%PSIRI = 70.5), four cephalopod taxa (%PSIRI = 21.9) and three crustaceans (%PSIRI = 7.6). For the warm phase, 36 prey taxa and three higher taxonomic groups were identified: 29 fish taxa (%PSIRI = 72.9), four cephalopod taxa (%PSIRI = 9.9), and three crustaceans (%PSIRI = 17.2). The most important prey species during the cold phase were the fish *Oxyporhamphus micropterus* (%PSIRI = 20.1), *Exocoetus volitans* (%PSIRI = 7.7) and *Auxis* spp. (%PSIRI = 5.7), and the cephalopods *Dosidicus gigas* (%PSIRI = 12.8) and *Argonauta* spp. (%PSIRI = 7.1; Table 2). During the warm phase, the most important prey species were red crab *Pleuroncodes planipes* (%PSIRI = 15.6) and the oceanic pufferfish *Lagocephalus lagocephalus* (%PSIRI = 14.6), followed by *Balistes polylepis* (%PSIRI = 9.2), *Selar crumenophthalmus* (% PSIRI = 9.2) and *Hemiramphus saltator* (%PSIRI = 5.6; Table 3).

MANOVA results show statistically significant differences between environmental and prey variabilities on which the three species fed during the cold phase ($F_{(3,85)} = 5.17$, $p < 0.0001$) and the warm phase ($F_{(3,86)} = 9.08$, $p < 0.0001$).

Based on the niche breadth values, striped marlin (*Bi* = 0.14 in both cold and warm phase), blue marlin (*Bi* = 0.22 cold phase and 0.38 warm phase), and dolphinfish (*Bi* = 0.19 cold phase and 0.09 warm phase) were characterized as being specialist predators during both phases of the ENSO.

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Table 2. Summary of the diet composition of striped marlin *Kajikia audax*, blue marlin *Makaira nigricans* and dolphinfish *Coryphaena hippurus* during cold phase of ENSO in adjacent waters to Cabo San Lucas, Baja California Sur, expressed by percentages frequency of occurrence (%FO), percent prey-specific number (%PN), percent number (%*N*), percent prey-specific weight (%PW), percent weight (%W) and prey-specific index of relative importance (% PSIRI)

COLD PHASE																		
	Kajikia audax						*Makaira nigricans*						*Coryphaena hippurus*					
Prey species	% FO	%PN	%N	%PW	%W	% PSIRI	% FO	%PN	%N	%PW	%W	% PSIRI	% FO	%PN	%N	%W	%PW	% PSIRI
FISH																		
Family Albulidae	0.7	100	0.1	100	0.02	0.7	—	—	—	—	—	—	—	—	—	—	—	—
Family Balistidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Balistes polylepis	1.3	62.5	1.1	52.8	0.01	0.8	7.1	25	2.6	29.2	2.1	1.9	2.6	100	0.3	100	13.4	2.6
Family Belonidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Platybelone argulus	—	—	—	—	—	—	3.6	25	1.3	25	1.2	0.9	—	—	—	—	—	—
Tylosurus pacificus	—	—	—	—	—	—	—	—	—	—	—	—	2.6	100	0.08	100	1.4	2.6
Tylosurus spp.	1.3	55.6	0.3	51.2	0.1	0.7	—	—	—	—	—	—	—	—	—	—	—	—
Family Carangidae indet.	1.3	41.7	0.9	37.5	0.4	0.5	—	—	—	—	—	—	2.6	100	0.08	100	2	2.6
Caranx caballus	17	67	6.4	71.4	8.4	11.8	10.7	37.5	5.2	44.4	4.7	4.4	5.1	74	10.5	78.5	6.7	3.9
Caranx spp.	—	—	—	—	—	—	3.6	25	1.3	33.3	0.9	1	—	—	—	—	—	—
Decapterus macrosoma	10.5	41.5	4.7	59.9	11.4	5.3	—	—	—	—	—	—	—	—	—	—	—	—
Decapterus muroadsi	2	19.9	0.7	38.9	1	0.6	3.6	12.5	1.3	33.3	2	0.8	—	—	—	—	—	—
Selar crumenophthalmus	2	56.7	0.4	61.1	1.4	1.2	—	—	—	—	—	—	2.6	2.4	0.4	25.9	3.4	0.4
Selene peruviana	3.3	39.1	3.4	28.7	9.4	1.1	—	—	—	—	—	—	2.6	100	0.08	100	0.04	2.6
Family Chaetodontidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chaetodon humeralis	—	—	—	—	—	—	—	—	—	—	—	—	2.6	100	0.08	100	0.02	2.6
Family Clupeidae	0.7	45.5	0.7	33.3	0.4	0.3	3.6	100	1.3	100	1.1	3.6	—	—	—	—	—	—
Family Coryphaenidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Coryphaena equiselis	0.7	100	0.1	100	7.5	0.7	—	—	—	—	—	—	—	—	—	—	—	—
Coryphaena hippurus	—	—	—	—	—	—	3.6	100	1.3	100	2.1	3.6	—	—	—	—	—	—

(*Continued*)

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Table 2. *(Continued.)*

COLD PHASE	*Kajikia audax*						*Makaira nigricans*						*Coryphaena hippurus*					
Prey species	% FO	%PN	%N	%PW	%W	% PSIRI	% FO	%PN	%N	%PW	%W	% PSIRI	% FO	%PN	%N	%W	%PW	% PSIRI
Coryphaena spp.	—	—	—	—	—	—	3.6	25	1.3	33.3	2	1	2.6	48.8	8.4	9.8	1.3	0.8
Family Dorosomatidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ophistonema libertate	—	—	—	—	—	—	—	—	—	—	—	—	2.6	100	8.4	100	3.9	2.6
Family Dussumieriidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Etrumeus acuminatus	9.2	55.2	4.8	49.5	4.8	4.8	3.6	75	7.8	33.3	2	1.9	2.6	100	0.8	100	2.6	2.6
Family Echeneidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Remora remora	—	—	—	—	—	—	—	—	—	—	—	—	2.6	94.3	8.4	74.7	10	2.2
Family Engraulidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Engraulis mordax	—	—	—	—	—	—	—	—	—	—	—	—	2.6	33.3	0.08	6.8	0.2	0.5
Family Exocoetidae indet.	—	—	—	—	—	—	—	—	—	—	—	—	2.6	25	0.4	24.5	1.4	0.6
Cheilopogon papilio	—	—	—	—	—	—	—	—	—	—	—	—	2.6	100	0.08	100	1.5	2.6
Exocoetus volitans	1.3	83.3	0.4	75	0.04	1	—	—	—	—	—	—	7.7	100	13	100	8.4	7.7
Family Fistulariidae indet.	0.7	50	0.1	4	0.01	0.2	—	—	—	—	—	—	—	—	—	—	—	—
Fistularia corneta	6.5	66.2	3.4	61.3	2.5	4.2	—	—	—	—	—	—	—	—	—	—	—	—
Family Hemiramphidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hemiramphus saltator	1.3	66.7	0.3	75	0.7	0.9	3.6	33.3	1.3	50	0.8	1.5	2.6	100	0.4	100	0.3	2.6
Oxyporhamphus micropterus	1.3	50	0.4	50	0.3	0.7	—	—	—	—	—	—	28.2	68.2	33.2	74	15.5	20.1
Family Mugilidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mugil cephalus	3.9	67.2	1.1	65.2	3.5	2.6	—	—	—	—	—	—	—	—	—	—	—	—
Family Myctophidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Benthosema panamense	0.7	100	0.1	100	0.01	0.7	—	—	—	—	—	—	—	—	—	—	—	—
Family Phosichthyidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

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Vinciguerria lucetia	0.7	60	0.4	95.9	0.05	0.5	—	—	—	—	—	—	—	—	—	—	—	—
Family Scombridae indet.	—	—	—	—	—	—	3.6	25	1.3	25	1.2	0.9	—	—	—	—	—	—
Acanthocybium solandri	—	—	—	—	—	—	3.6	25	1.3	25	1.2	0.9	—	—	—	—	—	—
Auxis spp.	11.1	62.9	4.9	55.3	4.8	6.6	57.1	80.7	37.7	81.2	39.3	46.3	7.7	72.2	0.7	76.9	2.4	5.7
Euthynnus linneatus	0.7	33.3	0.1	98.6	10.2	0.4	3.6	25	1.3	33.3	2	1	—	—	—	—	—	—
Katsuwonus pelamis	4.6	71.4	1.8	75.6	8.2	3.4	10.7	77.8	5.2	80.3	24.9	8.5	—	—	—	—	—	—
Scomber japonicus	4.6	51.4	1.8	83.2	2.3	3.1	3.6	50	1.3	50	1.5	1.8	2.6	33.3	0.3	64.5	7.4	1.3
Thunnus albacares	—	—	—	—	—	—	7.1	35	3.9	41.7	2	2.7	—	—	—	—	—	—
Family Soleidae	0.7	20	0.6	4.4	0.01	0.1	—	—	—	—	—	—	—	—	—	—	—	—
Family Sphyraenidae	1.3	50	0.3	69.5	4.8	0.8	—	—	—	—	—	—	—	—	—	—	—	—
Family Syngnathidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hippocampus ingens	—	—	—	—	—	—	—	—	—	—	—	—	1.6	50	0.08	95.2	0.2	1.9
Family Tetraodontidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sphoeroides annulatus	—	—	—	—	—	—	—	—	—	—	—	—	2.6	100	0.08	100	0.2	2.6
Sphoeroides lobatus	0.7	16.7	0.1	17.3	0.01	0.1	—	—	—	—	—	—	—	—	—	—	—	—
CEPHALOPODS																		
Family Amphitretidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Japetella diaphana	2.6	29.2	1.8	19.7	0.4	0.6	—	—	—	—	—	—	—	—	—	—	—	—
Family Ancistrocheiridae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ancistrocheirus lesueurii	2.6	49.3	1.3	44.2	0.8	1.2	—	—	—	—	—	—	7.7	31.7	1.3	5.1	0.1	1.4
Family Argonautidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Argonauta spp.	23.5	57.6	22.5	48.7	4.7	12.5	—	—	—	—	—	—	10.3	70.9	1	67.7	1.2	7.1
Family Enteroctopodidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Enteroctopus dofleini	—	—	—	—	—	—	3.6	50	2.6	33.3	2	1.5	—	—	—	—	—	—
Family Mastigoteuthidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mastigoteuthis spp.	0.7	50	1	12.9	0.03	0.2	—	—	—	—	—	—	—	—	—	—	—	—

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Table 2. (*Continued.*)

COLD PHASE																		
	Kajikia audax						*Makaira nigricans*						*Coryphaena hippurus*					
Prey species	% FO	%PN	%N	%PW	%W	% PSIRI	% FO	%PN	%N	%PW	%W	% PSIRI	% FO	%PN	%N	%W	%PW	% PSIRI
Family Ommastrephidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dosidicus gigas	43.1	70.9	31	69.9	10.7	30.4	21.4	75.3	18.2	62.7	6.9	14.8	23.1	56.9	10.7	53.7	15.7	12.8
Sthenoteuthis oualaniensis	0.7	16.7	0.1	25	0.4	0.1	3.6	20	2.6	33.3	0.02	1	—	—	—	—	—	—
Family Onychoteuthidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Onychoteuthis banksii	1.3	26.7	0.3	33.3	0.1	0.4	—	—	—	—	—	—	—	—	—	—	—	—
Family Pholidoteuthidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pholidoteuthis massyae	2.6	22.1	1.3	24.3	0.6	0.6	—	—	—	—	—	—	2.6	20	0.4	27.8	0.2	0.6
Family Vampyroteuthidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Vampyroteuthis infernalis	0.7	33.3	0.7	8.3	0.01	0.1	—	—	—	—	—	—	—	—	—	—	—	—
CRUSTACEANS																		
Family Hemisquillidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hemisquilla californiensis	—	—	—	—	—	—	—	—	—	—	—	—	1.6	50	0.08	50	0.2	1.3
Family Munididae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pleuroncodes planipes	—	—	—	—	—	—	—	—	—	—	—	—	10.3	34.2	0.7	37.3	0.4	3.7
Family Squillidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Squilla biformis	0.7	50	0.1	85	0.03	0.4	—	—	—	—	—	—	—	—	—	—	—	—
Orden Stomatopoda	—	—	—	—	—	—	—	—	—	—	—	—	2.6	100	0.08	100	0.1	2.6

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Table 3. Summary of the diet composition of striped marlin *Kajikia audax*, blue marlin *Makaira nigricans* and dolphinfish *Coryphaena hippurus* during warm phase of ENSO in adjacent waters to Cabo San Lucas, Baja California Sur, expressed by percentages frequency of occurrence (%FO), percent prey-specific number (%PN), percent number (%N), percent prey-specific weight (%PW), percent weight (%W) and prey-specific index of relative importance (% PSIRI)

WARM PHASE																		
	Kajikia audax						*Makaira nigricans*						*Coryphaena hippurus*					
Prey species	% FO	%PN	%N	%PW	%W	% PSIRI	% FO	%PN	%N	%PW	%W	% PSIRI	% FO	%PN	%N	%W	%PW	% PSIRI
FISH																		
Family Acanthuridae	2.1	51.1	0.5	70.1	0.1	1.3	—	—	—	—	—	—	0.8	100	0.1	100	0.08	0.8
Family Argentinidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Argentina sialis	0.7	11.1	0.1	1.5	0.01	0.04	—	—	—	—	—	—	1.6	62.5	0.3	51	0.2	0.9
Family Balistidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Balistes polylepis	22	56.2	11.7	45.6	7.5	11.2	—	—	—	—	—	—	13.6	72.4	2.8	62.2	2.5	9.2
Familia Belonidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ablennes hians	—	—	—	—	—	—	10	100	5.3	100	40.4	10	4	48.3	0.3	39.1	0.9	1.8
Family Carangidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Caranx caballus	9.2	41.5	2.1	52.7	8	4.3	—	—	—	—	—	—	4.8	54.7	0.3	76.7	6.5	3.2
Caranx caninus	—	—	—	—	—	—	—	—	—	—	—	—	0.8	100	0.1	100	0.9	0.8
Decapterus macarellus	3.6	43.9	0.9	67.5	4.2	2	—	—	—	—	—	—	2.4	42.5	0.2	67	2.2	1.3
Decapterus macrosoma	3.6	68.1	0.7	78.8	1.3	2.6	—	—	—	—	—	—	1.6	70	0.2	71.8	0.6	1.1
Naucrates ductor	2.1	44.9	0.5	66.8	1	1.2	—	—	—	—	—	—	0.8	100	0.1	100	0.8	0.8
Selar crumenophthalmus	14.9	39.6	2.6	66.4	12.8	7.9	30	72.2	21.1	63.5	8.7	20.4	15.2	51.9	1.1	68.8	18	9.2
Selene peruviana	4.3	36	1.6	29	2	1.4	—	—	—	—	—	—	—	—	—	—	—	—
Trachinotus stilbe	0.7	33.3	0.1	59	0.4	0.3	—	—	—	—	—	—	—	—	—	—	—	—
Trachurus symmetricus	—	—	—	—	—	—	10	100	5.3	100	10.9	10	—	—	—	—	—	—
Family Chaetodontidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chaetodon humeralis	1.4	45	0.5	26.4	0.2	0.5	—	—	—	—	—	—	0.8	16.7	0.1	1.7	0.04	0.1
Forcipiger flavissimus	1.4	21.9	0.3	6.2	0.1	0.2	—	—	—	—	—	—	—	—	—	—	—	—
Johnrandallia nigrirostris	0.7	33.3	0.1	17.6	0.03	0.2	—	—	—	—	—	—	—	—	—	—	—	—
Family Coryphaenidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

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Table 3. (*Continued.*)

WARM PHASE																		
	Kajikia audax						*Makaira nigricans*						*Coryphaena hippurus*					
Prey species	% FO	%PN	%N	%PW	%W	% PSIRI	% FO	%PN	%N	%PW	%W	% PSIRI	% FO	%PN	%N	%W	%PW	% PSIRI
Coryphaena hippurus	0.7	50	0.1	90.3	3.6	0.5	—	—	—	—	—	—	0.8	100	0.1	100	1.5	0.8
Family Diodontidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Diodon holocanthus	2.1	16.1	0.3	9.5	0.08	0.3	—	—	—	—	—	—	8	70	0.8	68.4	3.2	5.5
Family Dorosomatidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lile stolifera	—	—	—	—	—	—	—	—	—	—	—	—	3.2	86.7	0.7	95	1.5	2.9
Family Dussumieriidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Etrumeus acuminatus	0.7	14.3	0.1	0.5	0.03	0.1	—	—	—	—	—	—	0.8	100	0.1	100	0.5	0.8
Family Echeneidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Remora albescens	—	—	—	—	—	—	—	—	—	—	—	—	0.8	100	0.1	100	0.8	0.8
Family Exocoetidae indet.	—	—	—	—	—	—	—	—	—	—	—	—	1.6	66.7	0.1	88.2	0.8	1.2
Exocoetus volitans	0.7	33.3	0.1	20.3	0.1	0.2	—	—	—	—	—	—	4	46.6	0.3	44.3	2.6	1.8
Cypselurus callopterus	1.6	75	0.1	69.6	2.3	1.2	—	—	—	—	—	—	—	—	—	—	—	—
Family Fistulariidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Fistularia corneta	4.3	32.5	1.2	41.7	1.5	1.6	—	—	—	—	—	—	—	—	—	—	—	—
Family Gempylidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gempylus serpens	1.4	4.1	0.2	24.5	0.5	0.2	—	—	—	—	—	—	—	—	—	—	—	—
Family Hemiramphidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hemiramphus saltator	2.1	53	0.3	94.9	0.9	1.6	—	—	—	—	—	—	7.2	69	0.6	86.2	5.1	5.6
Family Monacanthidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Aluterus scriptus	1.4	18.6	0.2	37.1	1.1	0.4	—	—	—	—	—	—	—	—	—	—	—	—
Family Mugilidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mugil curema	—	—	—	—	—	—	—	—	—	—	—	—	0.8	100	0.1	100	0.5	0.8
Family Mullidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pseudupeneus grandisquamis	—	—	—	—	—	—	—	—	—	—	—	—	0.8	50	0.1	15.1	0.4	0.3
Family Myctophidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

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Benthosema panamense	2.1	48.9	2.1	8.4	0.07	0.6	—	—	—	—	—	—	1.6	100	0.1	100	0.04	1.6
Myctophum aurolaternatum	5	55.5	4.7	28.9	0.6	2.1	—	—	—	—	—	—	—	—	—	—	—	—
Family Ostraciidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ostracion meleagris	—	—	—	—	—	—	—	—	—	—	—	—	0.8	100	0.1	100	0.6	0.8
Family Priacanthidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Heteropriacanthus cruentatus	1.4	35	0.6	15.9	0.2	0.4	—	—	—	—	—	—	—	—	—	—	—	—
Family Scombridae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Auxis spp.	5.7	31.1	2.5	53	5.4	2.4	50	100	57.9	100	36.5	50	3.2	63.6	0.3	73.4	5.6	2.2
Euthynnus lineatus	—	—	—	—	—	—	—	—	—	—	—	—	0.8	100	0.1	100	2.6	0.8
Auxis thazard	1.4	22.2	0.2	99.3	7.6	0.9	20	41.7	10.5	54.8	3.5	9.6	0.8	50	0.1	84.9	2.5	0.5
Scomber japonicus	2.8	47.9	0.5	63.2	1.5	1.6	—	—	—	—	—	—	—	—	—	—	—	—
Family Syngnathidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hippocampus ingens	0.7	100	0.1	100	0.02	0.7	—	—	—	—	—	—	—	—	—	—	—	—
Family Tetraodontidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lagocephalus lagocephalus	26.2	53.8	12.8	64.4	25.2	15.5	—	—	—	—	—	—	20.9	69.6	2.1	70.6	16.4	14.6
Family Trachipteridae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Trachipterus spp.	0.7	50	0.1	36.8	0.02	0.3	—	—	—	—	—	—	—	—	—	—	—	—
Family Phosichthyidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Vinciguerria lucetia	0.7	25	0.1	53.5	0.01	0.3	—	—	—	—	—	—	—	—	—	—	—	—
Family Zanclidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Zanclus cornutus	0.7	16.7	0.1	82.5	0.1	0.4	—	—	—	—	—	—	1.6	51.4	0.1	54.3	0.3	0.8
CEPHALOPODS																		
Family Amphitretidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Japetella diaphana	7.8	20	1.6	21.5	0.04	1.6	—	—	—	—	—	—	—	—	—	—	—	—
Family Ancistrocheiridae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ancistrocheirus lesueurii	4.3	30.9	1.5	36.1	0.03	1.4	—	—	—	—	—	—	2.4	77.8	0.2	68.2	0.3	1.8
Vitreledonella richardi	1.4	30.6	0.2	17	0.01	0.3	—	—	—	—	—	—	—	—	—	—	—	—
Family Argonautidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Argonauta spp.	32.6	47.6	19.5	21.9	1.1	11.3	—	—	—	—	—	—	6.4	63.2	0.9	55.7	0.3	3.8

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Table 3. (*Continued.*)

WARM PHASE																		
	Kajikia audax						*Makaira nigricans*						*Coryphaena hippurus*					
Prey species	% FO	%PN	%N	%PW	%W	% PSIRI	% FO	%PN	%N	%PW	%W	% PSIRI	% FO	%PN	%N	%W	%PW	% PSIRI
Family Gonatidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gonatus berryi	0.7	33.3	0.1	64.3	1.5	0.4	—	—	—	—	—	—	—	—	—	—	—	—
Gonatus spp.	0.7	3.7	0.1	1.5	0.01	0.02	—	—	—	—	—	—	0.8	100	0.1	100	0.01	0.8
Family Mastigoteuthidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mastigoteuthis dentata	7.8	35.5	3.4	29.3	0.3	2.5	—	—	—	—	—	—	—	—	—	—	—	—
Family Ommastrephidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dosidicus gigas	34.8	54.2	24.6	52.4	10.9	18.5	—	—	—	—	—	—	4.8	72.5	0.8	72.9	2.2	3.5
Sthenoteuthis oualaniensis	0.7	27.3	0.3	0.3	0.01	0.1	—	—	—	—	—	—	—	—	—	—	—	—
Family Pholidoteuthidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pholidoteuthis massyae	0.7	16.7	0.1	4.4	0.01	0.1	—	—	—	—	—	—	—	—	—	—	—	—
Family Tysanoteuthidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Thysanoteuthis rhombus	0.7	6.3	0.1	1	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—	—
CRUSTACEANS																		
Family Munididae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pleuroncodes planipes	0.7	9.1	0.1	4.9	0.02	0.1	—	—	—	—	—	—	19.2	90.9	87	72.1	18	15.6
Family Penaeidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Penaeus californiensis	0.7	100	0.1	100	0.08	0.7	—	—	—	—	—	—	—	—	—	—	—	—
Family Portunidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Arenaeus mexicanus	0.8	100	0.1	100	0.01	0.8	—	—	—	—	—	—	—	—	—	—	—	—
Euphylax dovii	—	—	—	—	—	—	—	—	—	—	—	—	1.6	100	0.1	100	0.04	1.6

The average trophic position, standard error and median values are shown in Table 4. Wilcoxon test indicate no significant differences in trophic position during both phases, neither blue marlin ($p = 0.4929$) nor dolphinfish ($p = 0.05994$), but significant differences were found in striped marlin ($p = 0.0021$).

Trophic competition

During the cold phase, striped marlin, blue marlin, and dolphinfish shared seven prey taxa, including *Auxis* spp., *B. polylepis*, *C. caballus, Etrumeus acuminatus, H. saltator*, *Scomber japonicus*, and *D. gigas*. During the warm phase, they only shared three prey: the fish *Auxis* spp., *A. thazard*, and *S. crumenophthalmus* (Figure 3).

Trophic overlap

The PERMANOVA showed that there was no statistically significant trophic overlap in diet between the three species during either the cold phase ($F_{(3221)} = 10.77$, $p = 0.001$) or the warm phase ($F_{(3264)} = 4.96$, $p = 0.001$), due to the preference of these species to feed on different prey and the low number of prey they shared in their diets. The nMDS showed a stress of 0.06 during the cold phase and 0.01 during the warm phase of ENSO (Figure 4). According to the SIMPER analysis, the prey taxa that contributed most to the similarity between the diets of the three species were from the families Echeneidae, Engraulidae, Enteroctopodidae, Exocoetidae, Hemiramphidae, Hemisquillidae, Munididae, Scombridae, and Syngnathidae (cold phase) and the families Belonidae, Scombridae, Mullidae, Munididae, Trachipteridae, Phosichthyidae, Pholidotheuthidae, Tysanoteuthidae, and Ommastrephidae (warm phase).

Trophic competitions and environmental variability

The first two axes of the CDA accounted for 100% of the variance between groups during the cold and warm ENSO phases (cold phase: 93.1% and 6.9% for axes 1 and 2, respectively; warm phase: 98.5% and 1.5% for axes 1 and 2, respectively). For the warm phase, only one canonical axis was plotted because the number of blue marlin data was very small and insufficient to construct the confidence ellipse around canonical mean (Figure 5). During the cold phase, significant statistically differences ($p < 0.001$) were observed in predator trophic interactions between the three species, which were associates with Chl-*a* concentration on canonical axis 1 and with SST on canonical axis 2 (Table S1). During the warm phase, significant statistical differences ($p < 0.001$) were observed in the interactions of blue marlin with striped marlin and dolphinfish, which were related to their feeding pattern (PSIRI) on canonical axis 1 and with SST on canonical axis 2. The results indicate that changes in

Table 4. Mean trophic position, standard error, median and sample size for each phase

	Cold phase				Warm phase			
	Mean	Standard error	Median	n	Mean	Standard error	Median	n
Striped marlin	4.88	0.39	5.1	164	4.77	0.39	4.8	145
Blue marlin	5.09	0.92	5.3	31	4.94	1.31	5	13
Dolphinfish	4.52	0.60	4.3	47	4.65	0.39	4.8	147

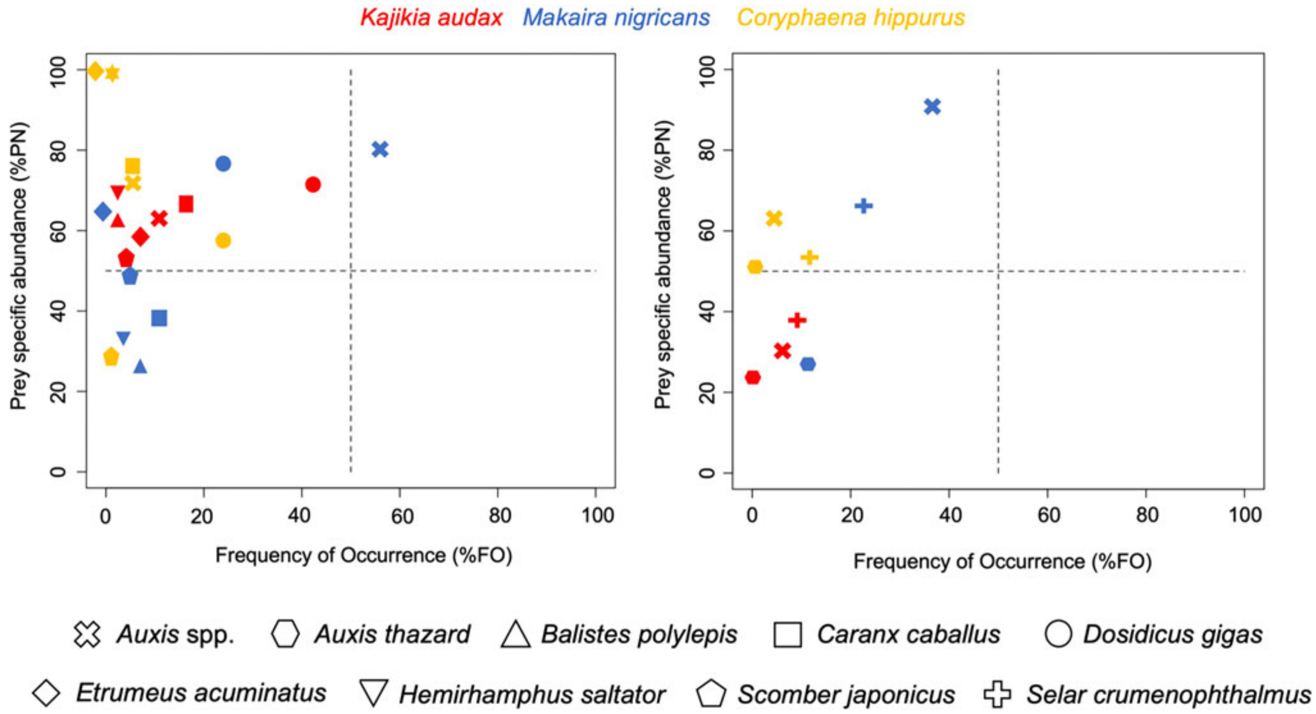

Figure 3. Trophic interactions among prey shared by striped marlin (*Kajikia audax*), blue marlin (*Makaira nigricans*) and dolphinfish (*Coryphaena hippurus*) during the (A) cold phase and (B) warm phase of ENSO.

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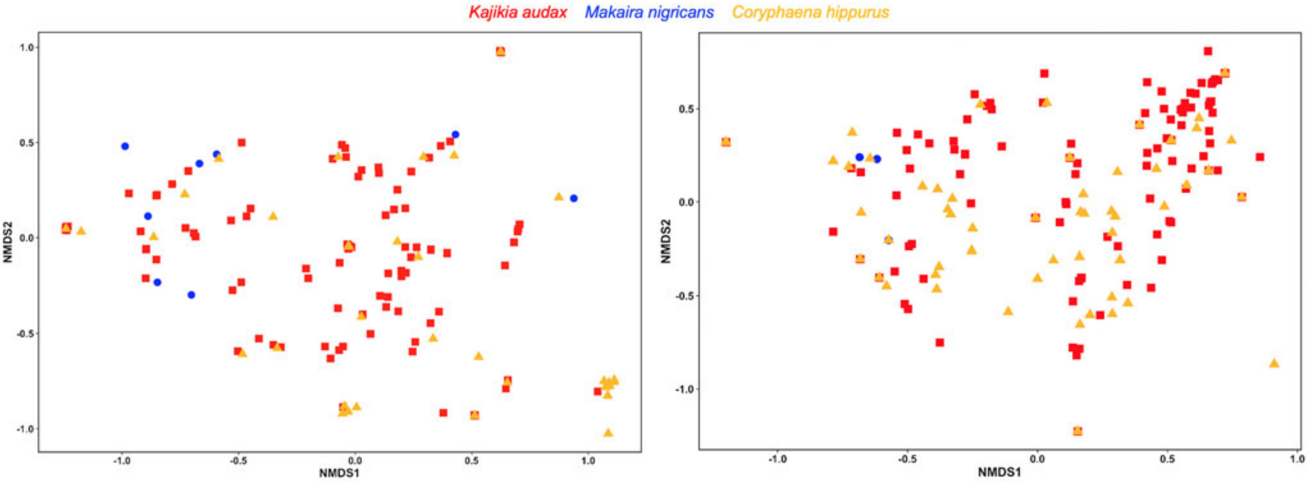

Figure 4. Non-metric multidimensional scaling (nMDS) to represent trophic overlap in the cold phase (A) and the warm phase (B) of ENSO.

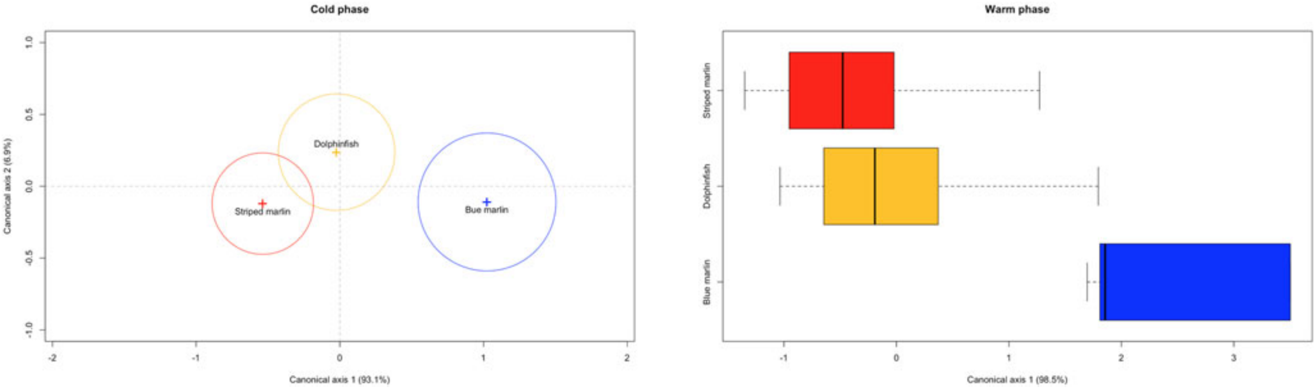

Figure 5. Canonical discriminant analysis (CDA) showing the relationship between trophic variability and environmental variability in the cold and the warm phase of ENSO.

environmental variability (SST and Chl-*a*) affect the presence of prey species and their interactions.

Discussion

Previous research indicates that among billfish species, the sport fishing fleet in CSL primarily captures striped marlin, with a rate of 0.6 fish per trip (Ortega-García *et al.*, 2003), followed by blue marlin at 0.06 fish per trip (Ortega-García *et al.*, 2006). Outside of billfish, dolphinfish are the most frequently caught species in the CSL area, averaging 1.33 fish per trip (Zúñiga-Flores *et al.*, 2008). The present study similarly observed a higher presence of striped marlin and dolphinfish compared to blue marlin. This might suggest these species have a greater tolerance to changes in SST and greater adaptability to changes in the environment compared to other large pelagic species (Shimose *et al.*, 2010). The low number of samples obtained for blue marlin might be related to the marked seasonality in their abundance (Ortega-García *et al.*, 2006). However, the stomach samples in this study allowed us to identify trophic diversity and at least 85% of the diet of these three predators.

In both phases of the ENSO, most of the stomachs presented some food, which agrees with what was reported by Ortega-García *et al.* (2017), who describe that these organisms feed at dawn, coinciding with the time in which this fishery is carried out. Therefore, it is possible to find some prey in different states of digestion in the stomach since this is a continuous process (Abitia-Cárdenas *et al.*, 1998).

Fish dominated the diet of striped marlin in both phases; however, at species level, jumbo squid *Dosidicus gigas* was the main prey in both periods. The abundance of jumbo squid in the diet of striped marlin suggests that this squid is relatively constant in the study area over time and that their contribution to the diet of this species varies according to their availability (Abitia-Cárdenas, 1992; Abitia-Cárdenas *et al.*, 1998, 2002; Shimose *et al.*, 2010; Torres-Rojas *et al.*, 2013 and Ortega-García *et al.*, 2017). Similarities were observed with previous studies, as striped marlin continued to feed over the same species through time.

Jumbo squid is an epipelagic species that occurs in areas where upwelling, convergence, or frontal events are common, such as the waters adjacent to Cabo San Lucas, where these predators are found. It can withstand a wide range of SST (16–30 °C), but prefers waters where SST ranges from 17 to 25 °C (Ehrhardt *et al.*, 1982; Ortega-García *et al.*, 2017). The change in the abundance of jumbo squid during both phases could be because it is a species that presents tropical and subtropical affinity (Fischer *et al.*, 1995), which performs extensive seasonal migrations concerning temperature changes, so during the warm phase due to the lower primary productivity present in the study area its abundance decreased (Nevárez-Martínez *et al.*, 2000, Chávez *et al.*, 2002; González-Máynez *et al.*, 2013).

The most common prey species for blue marlin throughout the years of study was *Auxis* spp. Tunas from this genus are mostly

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tropical species and their peak abundance in the study areas occurs in the boreal summer, when blue marlin is also more abundant. Further, *Auxis* spp. form large schools, which can facilitate its capture for the blue marlin and, consequently, is part of this species' trophic spectrum during both ENSO phases (Abitia-Cárdenas, 1992; Abitia-Cárdenas *et al*., 1999).

Oxyporhamphus micropterus was the main prey of dolphinfish during the cold phase. It is distributed between 1 and 6 m deep in the pelagic zone (Fischer *et al*., 1995), where dolphinfish is also distributed. During the cold phase, the sea temperature (25.1 °C) may have limited the vertical distribution of the dolphinfish due to the isotherm limiting their distribution (Palko *et al*., 1982), therefore relying more on available prey close to the surface. Although this species had been reported in the diet of dolphinfish in the study area, its contribution to the dolphinfish diet was usually less than 5% (Aguilar-Palomino *et al*., 1998 and Tripp-Valdez *et al*., 2010), while it accounted for 20%PSIRI in our dataset.

During the warm phase, the red crab *Pleuroncodes planipes* was the main prey of dolphinfish. Its presence in the study area could reflect its high tolerance to changes in water temperature, being a highly abundant species throughout the year in the waters adjacent to the Baja California peninsula (Salinas-Zavala *et al*., 2010). It reaches its southernmost distribution during the spring and summer seasons off the coast of Cabo San Lucas; however, in warmer waters, it tends to have more dense aggregations, which facilitates its consumption by its predators (Stevenson, 1970; Aurioles-Gamboa and Pérez-Flores, 1997 and De Anda-Montañez *et al*., 2016). In addition, it has been reported that *P. planipes* is frequent and abundant in areas of coastal upwelling forced by winds since they are productive areas and can feed on phytoplankton and zooplankton transported by the California current (Vallarta-Zárate *et al*., 2023).

De Anda-Montañez *et al*. (2016) described that, under El Niño environmental conditions in 2004, the abundance of red crab was lower, and that their distribution was restricted to greater depths, thus being more susceptible to capture during the night. In contrast, under La Niña environmental conditions recorded at the end of 2005 and the first three months of 2006, its abundance was greater, and it had a broader distribution. This means that its distribution and abundance are associated with the oceanographic patterns of the area, which coincides with the results obtained in this study, showing a greater contribution to the trophic spectrum of dolphinfish during the warm phase. Recently, Vallarta-Zarate *et al*. (2023) described the distribution and abundance of *P. planipes* on the western coast of Baja California. The authors reported that the most favourable conditions for red crab distribution and abundance occurred at temperatures greater than 16 °C.

Taxa such as *Caranx caballus*, *Auxis* spp., *Lagocephalus lagocephalus, Balistes polylepis,* and *Selar crumenophthalmus* form large schools (Fischer *et al*., 1995), thus attracting higher predators. Therefore, they form part of the trophic spectrum of the three species analysed and reduce competition. Furthermore, it has been reported by authors such as Ortega-García *et al.* (2017) that these species have a wide range of tolerance to SST (23.4–30.6 °C), so it was possible to find them during both ENSO phases.

The seasonal fluctuations in the trophic positions of this predator reveal how climatic variations influence dietary preferences. During fish and squid dominance periods, the increased consumption of these prey with higher trophic positions also increases the trophic position of the predators. On the other hand, when crustaceans or fish with lower trophic positions are abundant, the predators could also exhibit lower trophic positions. Our results indicate that during both phases of ENSO, blue marlin and dolphinfish maintained a trophic position similar to that reported in other studies in the study area (Olson and Watters, 2003; Torres-Rojas *et al*., 2013; Torres- Rojas *et al*., 2014). For striped marlin, significant differences were found, possibly attributable to a broader tropic spectrum observed during both phases and the greater number of samples. With prey with high and low trophic position, a large variation in the observed values was generated. As an example of this, this predator feeds on the fish *Mugil cephalus*, which has a low trophic position (TP = 2.5) because it is an omnivorous species, while taxa such as *Auxis* spp which is also important prey taxa for striped marlin has a higher trophic position value (TP = 4.4) (Whitfield *et al*., 2012; Froese and Pauly, 2023). Currently, there is no evidence that these differences have ecological relevance beyond statistical significance; more research is required to understand the ecological effect of a decline in trophic positions on energy flows in pelagic food webs.

Very few studies include the analysis of trophic competition between these three species. Most only include trophic competition between billfishes or between dolphinfishes and other large pelagic predators (Abitia-Cárdenas, 1992; Rudershausen *et al*., 2010; Torres-Rojas *et al*., 2013; Loor-Andrade *et al*., 2017). In this study, seven prey taxa represented their trophic competition during the cold phase, and three during the warm phase. These results coincide with those reported by Richert *et al.* (2015) for the Gulf of California, who mentions that some of the prey shared by these predators are *D. gigas, B. polylepsis, Auxis* spp., and *S. japonicus*, which were all reported in this study, as well as the fish *E. acuminatus, H. saltator,* and *C. caballus*. Trophic competition was greater during the cold phase than during the warm phase, which could indicate that SST and food availability seem to influence the abundance and distribution of the species and their prey; however, the low number of prey shared during the warm phase could be biased by the low number of stomachs analysed for blue marlin, so these results should be taken with caution.

Nakamura (1985) and Ruíz-Pérez *et al.* (2016) reported that although the large pelagic ichthyofauna usually share the same environment, they share the resources through differences in the feeding area, time of ingestion or the species that they predate, thus reducing competition. Hence, the division of habitats is important to understand the interactions of these species and to study their ecological differences.

Alterations in biological interactions can lead to changes in community structure and ecosystem functioning, as these changes occur throughout the food web (Hobday and Evans, 2013). Therefore, examining the responses of individual species to individual forcing factors, while essential, provides an incomplete story and highlights the need for more comprehensive, multi-species analyses at the ecosystem level (Doney *et al*., 2012).

Information on changes in feeding habits due to climatic conditions could be useful for fisheries' management of these species, their prey, and other predators with which they share space and resources. This is because many nations depend on fisheries for food security and public revenue (Sinclair *et al*., 2002), and research is needed to relate variations in the availability and abundance of prey and predator to changes in environmental variables such as SST and Chl-*a*.

Our results revealed that the three species studied play a very important role in the area and can be good indicators of the changes in the structure of the pelagic ecosystem's food web. The information on the variation in feeding habits due to climatic conditions could be useful for the fisheries management of these species and their prey, as well as other predators with which they share space and resources. It is necessary to carry out research that relates variations in the availability and abundance of prey and predators to changes in environmental variables such as SST

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and Chl-*a* concentration that helps us predict possible feeding changes or behaviours in the face of global warming.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S002531542400064X.

Data. The data that support the findings of this study are available from the corresponding author, upon reasonable request.

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Author contributions. AHA analysed the data, interpreted the findings, and wrote the article. SOG designed the study, collected fish samples, interpreted the findings, and wrote the article. ATV designed the study, interpreted the findings, and wrote the article. UJC interpreted the findings and wrote the article, RME interpreted the findings and reviewed the article, and SABH interpreted the findings and reviewed the article.

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Competing interests. The authors declare no conflict of interest.

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