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### Permalink

<https://escholarship.org/uc/item/41h6k1v3>

### Journal

ICES Journal of Marine Science, 82(8)

### ISSN

1054-3139

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### Publication Date

2025-08-06

### DOI

10.1093/icesjms/fsaf139

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Peer reviewed

# Foraging ecology of swordfish in the California Current Large Marine Ecosystem during an ecosystem regime shift

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## Abstract

Marine heatwaves are periods of anomalously warm ocean temperatures that can substantially impact marine ecosystems. These events can lead to changes in trophic interactions, food webs, and ecosystem structure, even after they have subsided. In this study, we described changes in swordfish (*Xiphias gladius*) foraging ecology in the California Current Large Marine Ecosystem (CCLME) over a period of rapid oceanographic and ecosystem change. We used 17 years of data (2007–23) to examine how swordfish diet composition varied through time in the CCLME before, during, and after the severe marine heatwave of 2014–16. Stomachs were collected by fishery observers aboard commercial vessels using drift gillnet and deep-set buoy gear. Prey were identified to the lowest taxonomic level possible and diet composition was analysed using univariate and multivariate methods. Our results showed a shift in diets occurred from cephalopods to epipelagic teleosts in 2014–16. While jumbo squid (*Dosidicus gigas*) was the most important prey during the early years of the study, Pacific hake (*Merluccius productus*) and northern anchovy (*Engraulis mordax*) dominated the diets in more recent years. The diet shifted towards teleosts in 2014–16 coincided with warm sea surface temperature anomalies, stronger stratification and shallower isothermal layer depths, negative North Pacific Gyre Oscillation, and higher anchovy biomass in the study region. Overall, swordfish diets appeared to integrate prey availability, environmental forcing, and spatiotemporal patterns in the CCLME. Our results showed that swordfish are generalist and opportunistic predators that have many characteristics of useful ‘ecosystem sentinels’ such as conspicuousness, sensitivity to ecosystem processes, and timely response to ecosystem shifts. Our findings can inform ongoing ecosystem monitoring efforts in the CCLME, as well as the development of ecosystem models. We also provide a unique perspective on how marine heatwaves may impact trophic connections and marine ecosystems.

**Keywords:** swordfish; trophic ecology; marine heatwaves; California Current

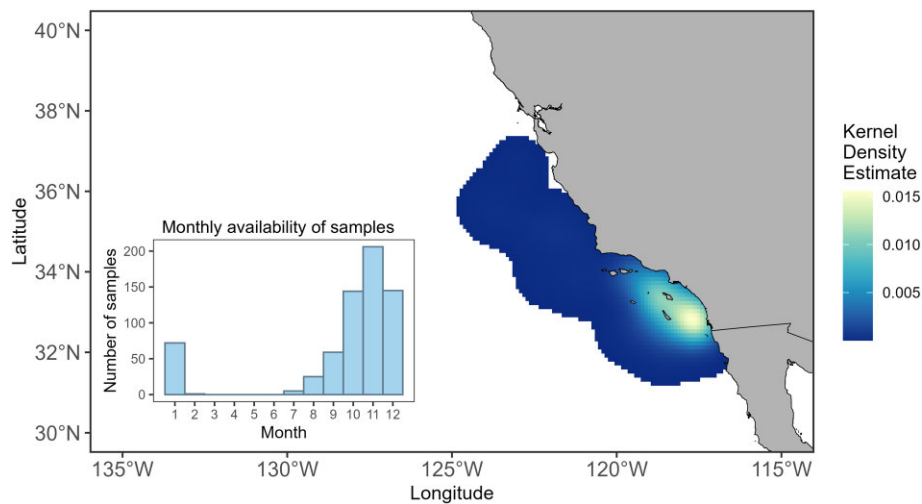
## Introduction

Marine heatwaves are periods of elevated sea surface temperatures (SSTs) lasting from days to months (Hobday et al. 2016). These periods of anomalously warm conditions can greatly impact marine ecosystems (Smale et al. 2019) with cascading impacts on predator–prey interactions, food webs, and ecosystem structure (Gomes et al. 2024a, Guibourd de Luzinais et al. 2024). In some instances, impacts from marine heatwaves can be relatively short-lived, with communities and ecosystems returning to preheatwave baselines once temperatures have cooled (Hunsicker et al. 2022). Conversely, community-level impacts from marine heatwaves can persist for months or years after the initial heatwave has subsided, resulting in a ‘regime shift’ to a different ecosystem state (Suryan et al. 2021, Smith et al. 2023).

The California Current Large Marine Ecosystem (CCLME) is a dynamic eastern boundary upwelling ecosystem characterized by high but variable biomass of forage resources (Chelton et al. 1982, Checkley and Barth 2009, Thompson et al. 2019, Gomes et al. 2024b). Due to its high productivity, the CCLME is a key foraging habitat for multiple top predators, includ-

ing bony fish, sharks, and mammals (Szoboszlai et al. 2015). Starting in 2014, the region was impacted by a series of marine heatwaves, leading to record warm temperatures and reduced primary productivity, as well as dramatic shifts in the distribution and biomass of a broad suite of species (Weber et al. 2021, Thompson et al. 2022, Free et al. 2023). As a result, the prey assemblages available to predators during and after this time period likely also changed. Time-series of top predator diet composition can integrate variability in prey availability and abundance across multiple trophic levels and depth habitats (Young et al. 2015, Hazen et al. 2019). They can thus potentially function as valuable indicators of ecosystem shifts in response to environmental drivers, such as marine heatwaves.

Swordfish (*Xiphias gladius*) are distributed circumglobally in tropical and temperate waters (Ward et al. 2000). The southern CCLME is an important foraging ground for swordfish, where individuals from various regions of the eastern and central north Pacific aggregate during summer and fall (Sepulveda et al. 2020). To date, there have been several studies of swordfish feeding habits in the southern CCLME (e.g. Fitch and Lavenberg 1971, Frey 1971, Mearns et al. 1981,



**Figure 1.** Collection area of swordfish used for diet analyses, 2007–2023. Specific locations are not shown to preserve confidentiality of commercial fishing locations: the contours show the kernel density estimate of all locations, with smoothing performed using a Gaussian kernel in the *spatstat* package (Baddeley et al. 2015). Inset: histogram showing month of capture for all swordfish used in diet analyses.

Markaida and Sosa-Nishizaki 1998, Markaida and Hochberg 2005, Preti et al. 2023). However, all of these studies included <10 years of observations, and none span strong ecological perturbations such as the 2014–16 marine heatwave. As a generalist predator (Preti et al. 2023), swordfish diets offer a potentially powerful tool to track ecosystem responses to the heatwave. They may be able to identify the presence of both short-lived changes to prey fields, and longer-lasting regime shifts between ecosystem states, with broader implications for fisheries and ecosystem-based management (e.g. Caputi et al. 2016, Karp et al. 2019).

Cooperation between fisheries participants and biologists offers valuable opportunities to collect data on species that are otherwise difficult to sample (Baker et al. 2023). In this study, we leveraged swordfish collected by fisheries observers on commercial fishing vessels to describe changes in foraging ecology over a period of rapid oceanographic and ecosystem change. We used a relatively long time-series of 17 years of data to examine how swordfish diet composition varied through time in the southern CCLME before, during, and after the severe marine heatwave of 2014–16. We investigated the relationships between observed diet variability and a suite of predictors capturing environmental conditions, prey abundance, fishing method, and predator characteristics. We also identified key prey species driving dietary shifts, and examined the predictability of these prey in swordfish diets through time. Our results can inform ongoing ecosystem monitoring efforts in the CCLME, and the development of ecosystem models. They also provided a unique perspective on the impacts of marine heatwaves to marine ecosystems, and previewed the potential for altered trophic connections in a warming world.

## Materials and methods

### Sampling at sea

Our study builds on Preti et al. (2023), who described diets of 299 swordfish collected between 2007 and 2014. Detailed descriptions of swordfish stomach collections and processing are given in Preti et al. (2023), and summarized briefly here. Swordfish stomachs were collected by federal fishery

observers during the 2007–23 fishing seasons. Vessels operate within the U.S. Exclusive Economic Zone, primarily in the southern CCLME, with the majority of effort from mid-August through the end of January (Fig. 1). Because the annual fishing season spans two calendar years, samples from January and February were grouped with those from the previous year in our analyses.

Swordfish in the CCLME have historically been targeted by a nighttime large-mesh drift gillnet (DGN) fishery. As this fishery is scheduled to be phased out by the end of the 2027 fishing season, new gears are being developed and adopted, including deep-set buoy gear (DSBG) that targets swordfish at depth during the day (Sepulveda et al. 2014). The DGN fishes in the upper 100 m during the night, while the DSBG fishes below the thermocline (~300 m depth) during the day (Sepulveda et al. 2014). No special permits were required to collect the stomachs as they are considered to be commercial fisheries discards. Stomachs were extracted at sea, then bagged and frozen for transport to the laboratory. Capture date, location, and fish size were also recorded, but sex was not determined. Three swordfish captured outside of the core fishing grounds in the northern CCLME (north of 45°N) were excluded from our analyses. All the other stomachs were collected in the southern CCLME (Fig. 1).

### Processing in the laboratory

Prey items were separated, identified to the lowest possible taxonomic level using taxonomic keys (Wolff 1982, Lowry 2011), enumerated, measured and weighed. Prey condition ranged from fresh (head, body, skin, fins mostly intact) to hard parts only (otoliths, vertebrae, jaws). For hard parts, fish otoliths and upper and lower squid beaks were counted in pairs when possible, with the highest count representing the minimum number present. These numbers were added to the numbers of intact prey. The total weight of each prey taxon was estimated as the weight of the undigested and partially digested items found in the stomach. Genetic analyses were used to identify diet items that could not be identified visually. Tissue samples for DNA extraction were taken from the interior of the sample to minimize cross contamination with

other prey. DNA was extracted using a DNeasy blood and tissue kit (Qiagen) following the manufacturer's protocols. The 'Barcode' region of the mitochondrial cytochrome c oxidase I (COI) gene was amplified by polymerase chain reaction (PCR) following Ivanova et al. (2007) using their COI-3 primer set with M13 tails. No template negative controls were run for each PCR batch to monitor for potential DNA contamination of reagents. PCR products were sequenced using BigDye v 3.1 dye terminator chemistry (Life Technologies), using the sequencing primers M13F(-21) and M13R(-27) following manufacturers' protocols. Aligned and edited sequences were entered into the BOLD v4 (Ratnasingham and Hebert 2013) and matches >98% identity to a single taxon were considered to be the correct species assignment for the prey item.

### Data analysis

Size range was reported for prey in fresh and intermediate states of digestion, while prey identification, number and weight were based on all remains. Degree of prey digestion was estimated using a six-point scale following Preti et al. (2023). Mean and median prey size were measured for 328 specimens of 32 prey taxa in a fresh and intermediate state of digestion during the period 2007–14 (see Preti et al. 2023) and for 6212 specimens of 27 prey taxa in the same digestive states during the period 2015–23 (Supplementary Table S1). Prey size range was reported, and mean and median prey size by species were calculated for prey with at least two specimens available.

The importance of each prey type was summarized using three standard Relative Measures of Prey Quantities: % frequency of occurrence (%F); % composition by number (%N); and % composition by weight (%W) (Pinkas et al. 1970, Hyslop 1980, Pierce and Boyle 1991, Bowen 1996). Empty stomachs or those that contained only slurry and/or detritus were not considered when calculating percentages. We used the percentage Prey-Specific Index of Relative Importance (%PSIRI) (Brown et al. 2012), the geometric index of importance (GII), Assis (1996) and its percentage form %GII to rank prey taxon importance. PSIRI and GII are useful indices to rank prey importance since they factor in both numerical and weight-based importance to the diet. Some authors favour %PSIRI (Kvaavik et al. 2019, Young et al. 2021) others GII (Preti et al. 2012, Tripp-Valdez et al. 2015), although all such combined indices have drawbacks (Pierce and Boyle 1991, Preti et al. 2023).

We included several environmental variables as potential predictors of diet composition. We first considered broad indicators of the ecosystem state. The Oceanic Niño Index and North Pacific Gyre Oscillation (NPGO: Di Lorenzo et al. 2008) have been linked to ecosystem level variability in the CCLME, and were extracted at monthly resolution from the NOAA National Weather Service Climate Prediction Center and Brown University via the *rsoi* package (Albers 2023). We also extracted a monthly anomaly of SST from the 5 km NOAA Global Coral Bleaching Monitoring product (NOAA Coral Reef Watch 2019), within the polygon encompassing sample locations (Fig. 1), as a more local indicator of marine heatwaves than the two basin-scale indices. We extracted three predictors at the sampling dates and locations (longitude, latitude) of each swordfish: SST, isothermal layer depth (ILD), and surface chlorophyll. These variables capture ocean conditions near to the time and location a swordfish was

foraging, and were hypothesized to impact local prey availability. SST and ILD were sourced from a daily, 0.1° implementation of the Regional Ocean Modeling System for the CCLME region (Neveu et al. 2016) using a historical re-analysis (1980–2010) and a near real-time product (2011–20; oceanmodeling.ucsc.edu). Surface chlorophyll was sourced from the Copernicus-GlobColour level 4 multi-sensor interpolated daily 4 km gap-free product (<https://doi.org/10.48670/moi-00281>). This predictor was natural-log transformed to reduce strong right skewness, which can impact the results of multivariate analyses.

Swordfish diet composition was also likely impacted by the available biomass of key prey species. While indices of abundance are not available for most swordfish prey, annual spawning stock biomass and recruitment are available for northern anchovy (*Engraulis mordax*) from Hinchliffe et al. (2025). As swordfish primarily consumed adult sized anchovy (see Supplementary Table S1), we included anchovy spawning stock biomass as a predictor. In addition, the Pacific hake (*Merluccius productus*) stock assessment (Grandin et al. 2024) provides estimates of hake total biomass, spawning stock biomass, recruitment, and biomass by age (<2 years and 2+ years). As hake in swordfish diets were primarily of immature size (Grandin et al. 2024, Supplementary Table S1), we included an index of age 0–1 biomass as a predictor of swordfish diet composition.

In addition to environmental and prey biomass predictors, we included several spatiotemporal predictors in multivariate models. These included latitude and month of capture, and water depth (extracted from the ETOPO1 dataset hosted at <https://coastwatch.pfeg.noaa.gov/erddap/griddap/etopo360>). We also included lunar illumination, extracted from the *lunar* package in R (Lazaridis 2022), as swordfish are known to adjust their vertical behaviour depending on moon phase (Dewar et al. 2011). Swordfish eye-to-fork length (EFL) (cm) was also included as a predictor. Some swordfish only had lower-jaw fork length ( $n = 176$ ) or cleithrum to fork length recorded ( $n = 20$ ). For these fish, we used published equations from Uchiyama et al. (1999) to convert these lengths to EFL. The shift from historical reliance on DGN to the recent incursion of DSBG to target swordfish may have implications for the selectivity of species found in our diet samples. To capture this effect, we included fishing method (DGN or DSBG) as a categorical variable in our analyses. Multicollinearity was assessed across all predictors before multivariate analyses were run. SST showed strong correlation with ILD ( $r = 0.72$ ), and was therefore removed from the suite of predictors.

Raw prey abundances were aggregated to family level before multivariate analysis to account for varying taxonomic resolution. Rare taxa found in <4 stomachs across the dataset, as well as taxa not identified to at least family, were removed. We first used Nonmetric Multidimensional Scaling (NMDS) ordination to visualize overall temporal variability in swordfish diet composition. NMDS was applied to Morisita–Horn dissimilarities (Horn 1966) on a matrix of prey proportional abundances in the *vegan* package (Oksanen et al. 2022). We then investigated the ability of our suite of environmental predictors to explain variability in diet composition using Distance-Based Redundancy Analysis (dbRDA), also in *vegan*. dbRDA is similar to Redundancy Analysis, but it allows non-Euclidean dissimilarity indices (McArdle and Anderson 2001).

**Table 1.** Number of stomach samples by fishing year and fishing method. 'All' = number of all stomachs; 'w/food' = number of stomachs with at least one prey item; '% w/food' = % of stomachs with at least one prey item.

| Year | All | DGN w/food | % DGN w/food | DSBG w/food | % DSBG w/food |
|------|-----|------------|--------------|-------------|---------------|
| 2007 | 48  | 47         | 97.9         | NA          | NA            |
| 2008 | 17  | 16         | 94.1         | NA          | NA            |
| 2009 | 38  | 37         | 97.4         | NA          | NA            |
| 2010 | 12  | 12         | 100          | NA          | NA            |
| 2011 | 56  | 54         | 96.4         | NA          | NA            |
| 2012 | 37  | 36         | 97.3         | NA          | NA            |
| 2013 | 57  | 56         | 98.2         | NA          | NA            |
| 2014 | 40  | 35         | 100          | 5           | 100           |
| 2015 | 24  | 17         | 100          | 6           | 85.7          |
| 2016 | 31  | 21         | 95.4         | 9           | 100           |
| 2017 | 54  | 16         | 94.1         | 25          | 67.6          |
| 2018 | 76  | 15         | 93.75        | 49          | 81.7          |
| 2019 | 37  | 14         | 93.3         | 15          | 68.2          |
| 2020 | 54  | 8          | 88.9         | 38          | 84.4          |
| 2021 | 58  | 22         | 100          | 34          | 94.4          |
| 2022 | 37  | 3          | 100          | 32          | 94.1          |
| 2023 | 36  | 13         | 100          | 23          | 100           |

Differences in diet composition among groups of predators were quantified using multivariate permutational analysis of variance (PERMANOVA; Anderson 2005) in *vegan*. Comparisons across two different groupings were undertaken using PERMANOVA: we first tested whether swordfish diets were different between DGN and DSBG within each year, for the years when both gears were commonly in use (2014–23). We also tested whether diets were different before and after the strong marine heatwave that began in 2014. To quantify the relative contribution of unequal variance to diet differences, pairwise tests for homogeneity of multivariate dispersion (PERMDISP) were also performed in *vegan*.

Lastly, we identified several key prey taxa that were important in driving shifts in swordfish diets through time. We used Generalized Additive Models (GAMs) in the *mgcv* package (Wood 2011, 2017) to examine (i) whether proportional abundance of these prey in swordfish diets was predictable using the same suite of predictors used in the dbrDA, and (ii) which type of predictors (environmental, prey abundance, spatiotemporal) were most influential for each key prey species. GAMs used a beta distribution with a logit link, and spurious predictors were penalized out of the GAMs using the double-penalty approach (Marra and Wood 2011). Partial response plots were visualized using the *gratia* package (Simpson 2024). All analyses were conducted in R version 4.4.0 (R Core Team 2024).

## Results

### Sample composition

A total of 712 swordfish stomachs were collected from observed trips in the CCLME: 443 from DGN gear and 269 from DSBG (Table 1). Samples were primarily collected in the southern CCLME, especially the Southern California Bight, with 91.1% collected south of Point Conception (Fig. 1). SST at the time of sample collection ranged from 12.8°C to 24.7°C (mean 17.8°C). Swordfish ranged in size from 74 to 257 cm EFL (Fig. 2). Following DeMartini et al. (2000), almost all the specimens in this study were larger than the median size at maturity for males (102 cm ± 2.5 cm EFL) and a majority were above the typical size at maturity for females (144 ± 2.8 cm EFL). Of the 712 swordfish stomachs examined, 658 con-

tained food remains belonging to 69 different prey taxa overall. Sixty-four of these prey taxa were identified to at least family. Forty families were identified overall, with a mean of 1.6 (range 1–8) higher-resolution taxa (i.e. identified to genus or species) per family. Sample coverage was relatively stable through time, but the relative proportion of samples from fish caught on DSBG increased (Table 1).

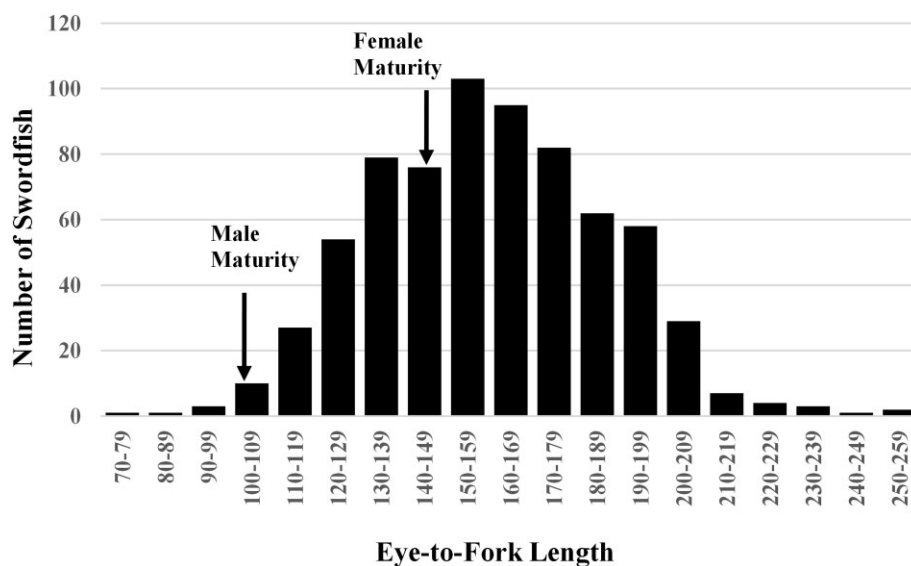
### Diet composition

Composition (%N) of swordfish diet from 2007 to 2023 highlighted the strong shift in diet through time (Fig. 3). Early years of the time series were dominated by cephalopods, particularly jumbo squid (*Dosidicus gigas*), while more recent years were dominated by finfish. Diets from 2011 and 2014 also had somewhat higher proportions of finfish: these were mostly hake and mesopelagic taxa such as Paralepididae.

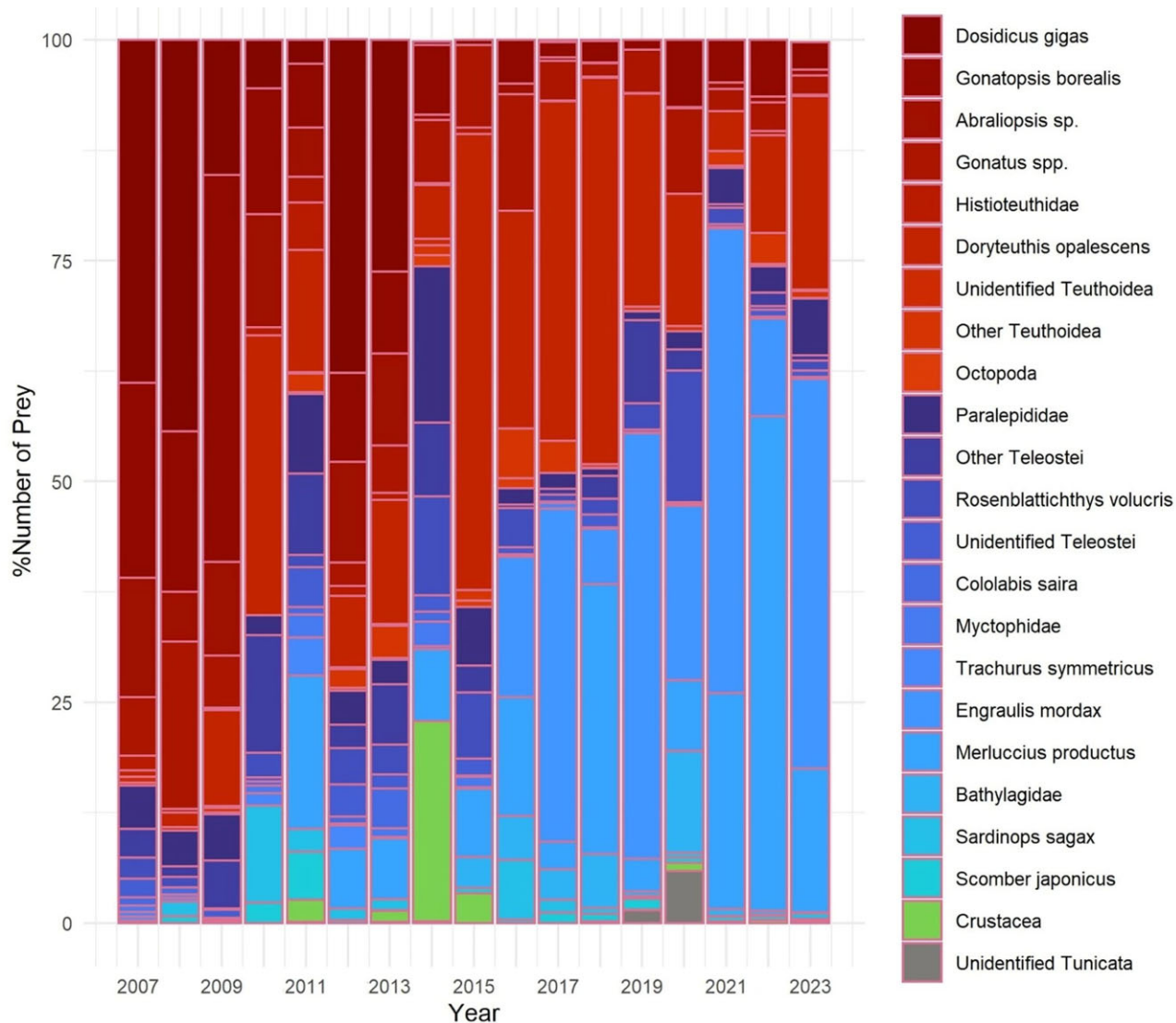
The NMDS results also showed a particularly strong shift in swordfish diet composition between 2014 and 2016, which was clearly visible in multivariate space (Fig. 4). Diets before 2015 were characterized by higher proportions of the squid families Ommastrephidae (mostly jumbo squid) and Euplotheutidae, and mesopelagic/bathypelagic fishes from the families Microstomatidae and Paralepididae. Swordfish diets after 2015 had a higher proportion of northern anchovy (Fig. 4).

Diet composition was significantly different between the two time-periods (2007–14 versus 2015–23). The PERMANOVA and PERMDISP tests indicated that both the centroids and dispersion of the two groups differed ( $P = .001$ ,  $P = .002$ , respectively). The annual median latitude of swordfish capture varied from ~32°N to 33.5°N without a strong temporal trend. However, the annual median water depth at swordfish capture was somewhat shallower in more recent years (Supplementary Fig. S1). We therefore re-ran the PERMANOVA and PERMDISP using a subset of available data where the collection location was in water shallower than 2000 m (87.3% of all samples available). Both tests remained highly significant on this reduced dataset (PERMANOVA  $P = .001$ , PERMDISP  $P = .002$ ).

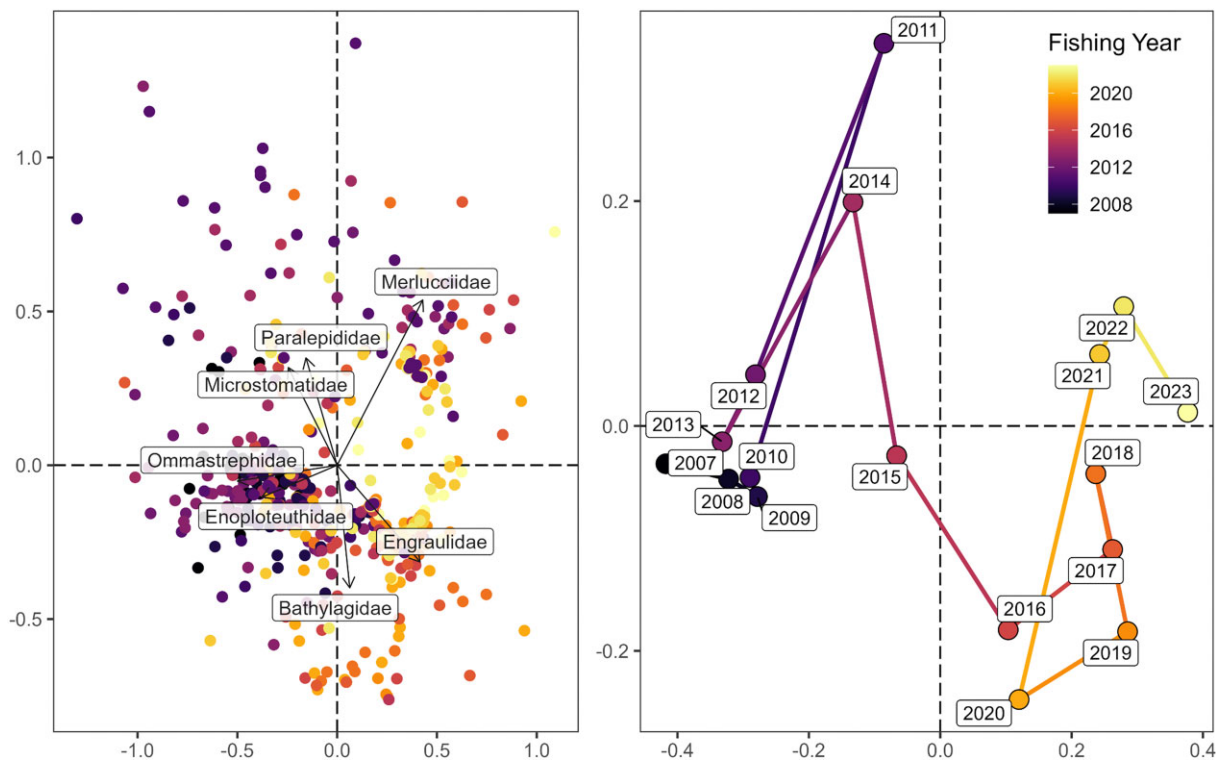
Comparison of PSIRI and GII between the two time periods (2007–14 and 2015–23) highlighted several changes in key prey. During 2007–14, jumbo squid (%PSIRI = 36.05; %GII = 43.39) was the most important prey item by weight



**Figure 2.** Length-frequency distribution of swordfish sampled in the diet study ( $n = 697$ ). Arrows indicate median sizes at maturity for males and females (DeMartini et al. 2000). EFL was measured in cm. Length was not recorded for 15 individuals of the 712 swordfish sampled.



**Figure 3.** Composition (%M) by year for swordfish diet components. Some prey taxa were combined by family, infraclass, or order for clarity. Red = Teuthoidea; Blue—Green = Teleostei; Yellow = Crustacea; Grey = Tunicata.



**Figure 4.** Left: NMDS ordination of swordfish diets from 2007 to 2023. Vectors show important prey families, defined as those with vector magnitudes > 0.35. Right: trajectory of swordfish diet composition through time, shown using annual means of scores along NMDS axes 1 and 2.

and number (Table S2). The boreopacific gonate squid (*Gonatopsis borealis*) (%PSIRI = 12.20; %GII = 28.72) was the second most important prey, and the most important by frequency of occurrence. Other important squid prey included *Abraliopsis* sp. (%PSIRI = 4.26; %GII = 15.93), *Gonatus* spp. (%PSIRI = 2.87; %GII = 14.67), and market squid (*Doryteuthis opalescens*) (%PSIRI = 5.27; %GII = 13.59). Pacific hake (%PSIRI = 10.92; %GII = 13.10) was the highest ranked teleost prey species, ranked third by %PSIRI and sixth by %GII. From 2015 to 2023, Pacific hake (%PSIRI = 28.94; %GII = 34.39) was the most important prey item by weight, %PSIRI and %GII (Table S3). Northern anchovy (%PSIRI = 20.86; %GII = 29.10) was the second most important prey according to %PSIRI, % GII, and the most important by number. Market squid (%PSIRI = 17.34; %GII = 28.97) ranked third in importance based on the %PSIRI and %GII and was the most important by frequency of occurrence. Other important squid prey included the boreopacific gonate squid (%PSIRI = 4.14; %GII = 16.93), *Gonatus* spp. (%PSIRI = 2.84; %GII = 16.56). The PSIRI tracked the GII closely for some prey but not for all. One species of elasmobranch, the cookiecutter shark (*Isistius brasiliensis*) was also observed for the first time in the CCLME as part of the swordfish diet during 2015–23 (Supplementary Fig. S2).

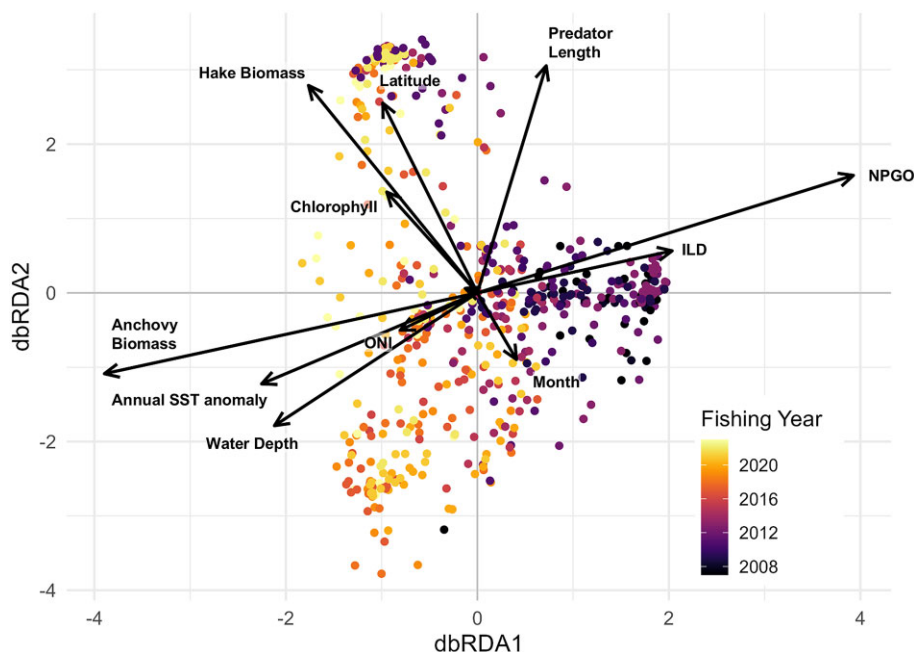
The dbRDA incorporating environmental covariates explained 23.4% of the total variability in swordfish diets (Fig. 5). dbRDA axis one captured 59.8% of the explained variability, while dbRDA axis 2 captured an additional 15.5%. Axis 1 captured much of the trend through time, with positive loadings along this axis associated with earlier years of the time-series, a positive NPGO, and deeper ILD. In contrast, negative loadings along this axis were associated with higher anchovy biomass, and higher area-averaged SST anomalies.

Axis 2 highlighted a secondary influence of swordfish length, latitude of capture, and age 0–1 hake biomass on diet composition (Fig. 5).

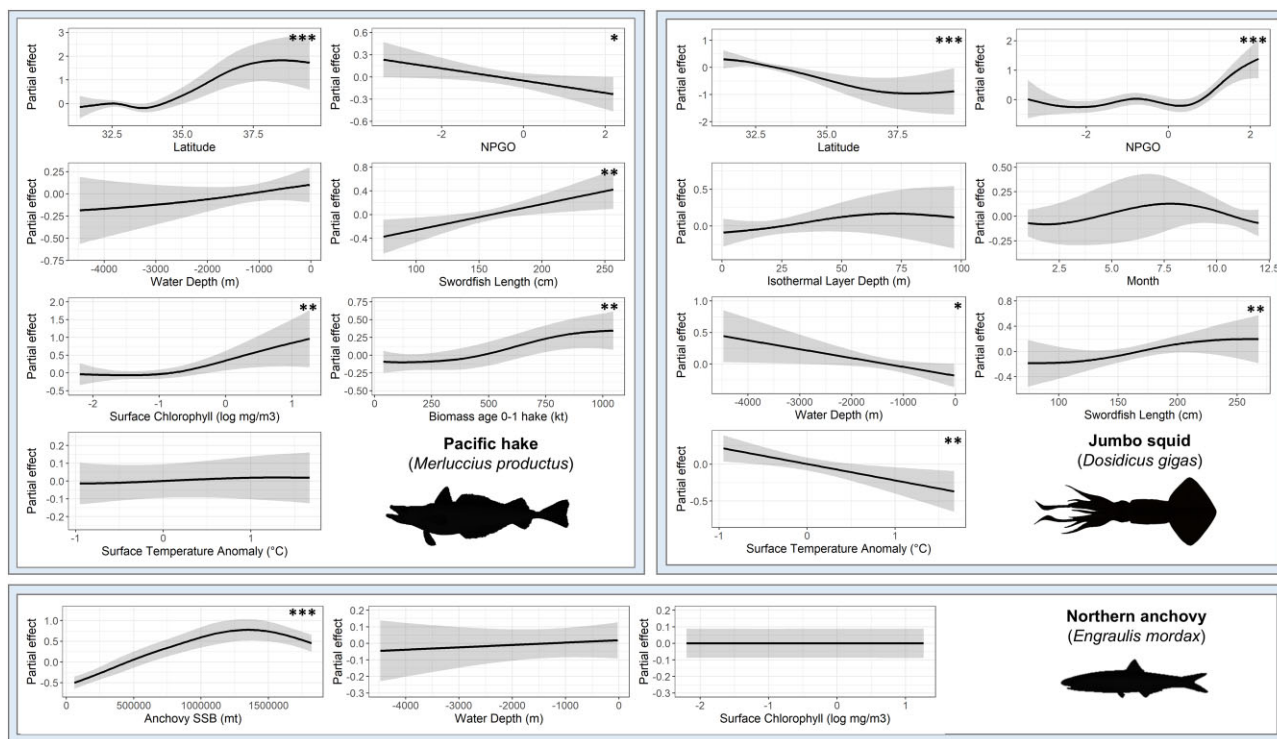
Based on the results of the NMDS and observed changes to dominant prey, we constructed GAMs for three key prey species: northern anchovy, Pacific hake, and jumbo squid. The GAM predicting the proportion of anchovy in individual swordfish guts explained 21.2% of the total deviance. Four predictors were retained in the model: anchovy spawning stock biomass, water depth, surface chlorophyll, and fishing method (DGN versus DSBG). Of these, anchovy biomass was by far the strongest predictor, explaining 19.5% of the total deviance on its own. The predicted proportion of anchovy in swordfish diets increased with increasing anchovy biomass before leveling off at ~1.3 million metric tons (Fig. 6). The proportion of anchovy in diets was higher for swordfish caught using DGN gear versus DSBG.

The GAM predicting the proportion of hake in swordfish diets explained 23.7% of the total variability. The proportion of hake in swordfish diets was positively related to biomass of age 0–1 hake, latitude of capture, water depth, swordfish length, and surface chlorophyll, and negatively related to the NPGO (Fig. 6). Fishing method was weakly significant to the jumbo squid GAM ( $P = .02$ ), with swordfish caught on DSBG having a higher proportion of hake in their guts.

The GAM predicting the proportion of jumbo squid in swordfish diets explained 31.6% of the total variability. Seven variables were retained in the final model. In contrast to hake, jumbo squid were more prevalent in diets at more southerly latitudes, in deeper waters, and when the NPGO was positive. Jumbo squid proportional abundance was also positively related with ILD and swordfish length, and negatively related with surface temperature anomaly (Fig. 6). In contrast to an-



**Figure 5.** Distance-based redundancy ordination plot of swordfish diets from 2007 to 2023 with respect to a suite of environmental, prey abundance, and spatiotemporal predictors.



**Figure 6.** Partial response plots for GAMs predicting the proportion of northern anchovy, Pacific hake, and jumbo squid in swordfish diets from 2007 to 2023. Only predictors not penalized out of each model are shown. Smooths that were estimated to be significantly different from a flat function are indicated ( $P < .05$  (\*),  $P < .01$  (\*\*), and  $P < .001$  (\*\*\*)).

chovy and hake, fishing method was not a significant predictor of jumbo squid in diets.

A global PERMANOVA showed that diets were significantly different ( $P = .001$ ) between swordfish caught on DGN versus DSBG (Supplementary Fig. S3). Pairwise PERMANOVA highlighted that swordfish diets were different

across gears in years 2018, 2020, 2021, and 2023, but not during 2016, 2017, and 2019. Given this result, we re-ran the PERMANOVA comparing the two time-periods (2007–14 and 2015–23) using only samples collected from swordfish caught on DGN gear, to remove any confounding influence of gear on the temporal trends observed. The difference between

the two time periods remained strong and significant using this reduced dataset ( $P = .001$ ).

## Discussion

### Temporal shift in swordfish diet composition

This study described the diets of swordfish in the CCLME during a period of 17 years (2007–23). An important feature of our study was the overlap of diet sampling with distinct oceanographic and biological regimes: the historical expansion of jumbo squid (Field et al. 2007), the rapid increase in anchovy biomass (Hinchliffe et al. 2025), and record marine heatwaves (Gentemann et al. 2017, Free et al. 2023).

Swordfish fed on a broad range of cephalopods and teleosts. During their diurnal vertical migrations, swordfish can move between epipelagic and mesopelagic habitats (Carey 1981, Braun et al. 2023). They can forage during both day and night, and frequently follow diel movements of the deep scattering layer (Stillwell and Kohler 1985, Dewar et al. 2011). Swordfish vertical distribution can be influenced by different factors, both abiotic (thermocline depth, dissolved oxygen, SST) and biotic (prey distribution and abundance, body physiology) (Sepulveda et al. 2010). They can show variable movement patterns during the day but are usually found in the upper mixed layer at night (Sepulveda et al. 2010). This flexibility in habitat use may allow swordfish to target a highly diverse range of prey that occupy distinct habitats (e.g. epipelagic, mesopelagic), and to switch between prey taxa depending on their availability. Swordfish are extremely tolerant of different temperatures and oxygen concentrations (Dewar et al. 2011, Abecassis et al. 2012). Environmental correlates of diets thus likely relate to ecosystem forcing and overall prey availability, and not physiological limits of swordfish.

Swordfish diets changed markedly throughout our study period. During earlier years (2007–14) swordfish fed heavily on cephalopods, particularly jumbo squid. In more recent years (2015–23), Pacific hake and northern anchovy became more prevalent in diets, and were the most important prey items overall. For example, from 2007 to 2014 only four anchovies were found from three swordfish stomachs, while in 2015–23, 3695 anchovies were recorded from 164 stomachs. Epipelagic teleosts in general became more numerous and frequent in diets, while contributions of jumbo squid, Enoploteuthidae squids, and mesopelagic/bathypelagic fishes from Microstomatidae and Paralepididae decreased. This represents a change in not only diet composition, but also the traits of major prey. Previous studies have noted the tendency of swordfish to forage on offshore cephalopods, and have grouped them in trophic guilds with other pelagic top predators such as shortfin mako (*Isurus oxyrinchus*), blue shark (*Prionace glauca*), Pacific bluefin tuna (*Thunnus orientalis*), and California sea lion (*Zalophus californianus*) (e.g. Bizzarro et al. 2023, Portner et al. 2025). Our results suggested that these guilds may be more flexible and dynamic through time than shorter time-series are able to show.

The marked change in swordfish diet composition between 2014 and 2016 coincided with a record marine heatwave, during which CCLME SSTs were up to 6°C above normal (Gentemann et al. 2017, Free et al. 2023). Since 2016, the CCLME has remained generally warmer than the long-term mean, with additional marine heatwaves recorded during some part of most years since 2019 (Thompson et al. 2024). Although heat-

wave conditions have not been present continuously, the shift in swordfish diet composition remained remarkably consistent. This result suggests a persistent ‘regime shift’ in trophic relationships, similar to that reported by Suryan et al. (2021) after the marine heatwave in Gulf of Alaska. The precise mechanisms driving this persistence are not clear, but may relate to ongoing shifts in availability of key prey. For example, anchovy biomass increased during the 2014–16 marine heatwave, and has remained at high levels since that time (Hinchliffe et al. 2025). Swordfish diet composition thus likely reflects persistent changes to mid-level forage communities, although the relative contributions from bottom-up versus top-down forcing on these communities are not known.

Our selected environmental predictors were able to explain a moderate amount of the variability in diet composition. The diet shift towards teleosts in 2014–16 coincided with warm SST anomalies, stronger stratification and shallower ILLDs, negative NPGO, and higher biomass of anchovy and small hake in the study region (Zaba and Rudnick 2016, Thompson et al. 2024, Hinchliffe et al. 2025). Spatially fixed predictors such as latitude and water depth were of secondary importance. The predominance of different key prey was driven by different processes. The proportion of northern anchovy in diets was primarily associated with their overall biomass: a higher abundance of anchovy in the system resulted in more anchovy in swordfish diets. During the 2014–16 heatwave, biomass of potential mesopelagic prey moved deeper in the water column (Iglesias et al. 2024). This may have made them less accessible to swordfish at the same time that epipelagic prey such as anchovy were becoming more available.

The proportion of Pacific hake in diets was associated with the estimated biomass of age 0–1 hake. In contrast, annual recruitment and total hake biomass from the stock assessment were not strongly correlated with hake prevalence in diets (results not shown). This is consistent with the size of hake that swordfish consumed, and suggests that strong recruitment events lead to high availability of hake of a suitable size for swordfish consumption ~1 year later (see Grandin et al. 2024). The location of swordfish in the system was also influential, with hake more common in diets of swordfish captured further north. Hake prevalence was also positively associated with chlorophyll concentration and swordfish size.

The high prevalence of jumbo squid in diets during earlier years coincides with the historical northward range expansion of this species in the CCLME that began after the 1997–1998 El Niño. This may be related to a shoaling hypoxic layer increasing availability of mesopelagic prey (Stewart et al. 2014). In our analyses, the proportion of jumbo squid in swordfish diets was most strongly associated with the NPGO, and jumbo squid were also more predominant in swordfish captured further south. The NPGO is correlated with salinity, nutrients, chlorophyll, and hypoxic depth in the southern California Bight, potentially via regional and basin-scale variations in wind-driven upwelling and horizontal advection (DiLorenzo et al. 2008, Stewart et al. 2014). Swordfish diets thus appeared to integrate overall prey availability, environmental forcing, and spatiotemporal patterns in the CCLME.

### Diet data for ecosystem monitoring

Predator diets can be powerful ecosystem monitoring tools, and have been used previously as ecosystem indicators in the eastern North Pacific. For example, Cunningham et al.

(2018) showed how rhinoceros auklet (*Cerorhinca monocerata*) chick diets responded to variation in forage fish availability: they fed more on capelin in cold years, and more on sand lance during warm years. Ainley et al. (1996) note that Cassin's auklet (*Ptychoramphus aleuticus*) diets integrate patterns in the prevalence of prey species both temporal and spatially, and provide important information on overall food web structure. California sea lion diets similarly show high inter-annual and decadal variability in response to abundance of key prey (Melin et al. 2012, Lowry et al. 2022). These pinnipeds shifted from an anchovy-based diet in the 1980s to feeding more on market squid in the 1990s and 2000s. Elegant tern (*Thalasseus elegans*) diets have been used as an ecosystem indicator of variation in the prey community in the southern California coastal prey assemblage (Horn and Whitcombe 2015). These birds have been described as 'sentinels of change' as their flexibility in diets allows them to feed on the most available prey. Trophic indicators not based on gut contents can also be useful for tracking ecosystem states. For example, humpback whale (*Megaptera novaeangliae*) diets inferred from stable isotope analyses can capture major oceanographic and ecological shifts in the CCLME (Fleming et al. 2016). This study showed that schooling fish were most important in humpback whale diets when the NPGO was negative, SSTs were warmer, when seasonal upwelling was delayed, and when anchovy and sardine population abundances were higher. In some cases, monitoring diets can provide information on population health or population dynamics. For example, Becker et al. (2007) showed that marbled murrelet (*Brachyramphus marmoratus*) reproductive success was positively linked to availability of rockfish and krill prey. Similarly, reproductive success in both California sea lion and Brandt's cormorant (*Urile penicillatus*) was positively linked to the availability of anchovy prey (Fennie et al. 2023).

Our results showed that swordfish are a generalist and opportunistic predator that largely track prey availability in their environment (Palko et al. 1981, Preti et al. 2023). They thus have many characteristics of useful 'ecosystem sentinels' such as conspicuousness (i.e. large body size, observability), sensitivity to ecosystem processes, and timeliness in response to ecosystem shifts (Hazen et al. 2019). Our analyses showed how an ecosystem shift corresponding with the 2014–2016 marine heatwave was clearly apparent in swordfish diets, and how this shift persisted through time. Swordfish diet composition thus had high potential value as an index of ecosystem state, particularly as a relatively long time series already existed. Simple indices of prey prevalence in swordfish diets are already reported in annual publications such as the California Current Ecosystem Status Report (Leising et al. 2024) and the State of the California Current Ecosystem Report (Thompson et al. 2024). In addition, swordfish diet data are contributing to diet matrices informing several ecosystem models in the CCLME, such as EcoTran (Gomes et al. 2024b) and Atlantis (Liu et al. 2025). As ecological conditions and trophic connections can change rapidly, ecosystem models need up-to-date diet information to remain current. Diets of swordfish in combination with those of other top pelagic predators have also provided valuable insights into niche partitioning and resource use through time in the CCLME (e.g. Portner et al. 2025). Potential future applications could include the development of abundance indices or distribution models for key prey (e.g. Gaichas et al. 2023, Gunther et al. 2024), as well as

supporting overall progress towards Ecosystem Based Fishery Management.

### Study strengths and limitations

The main strength of the current study was the long time series of data available. Collecting diet data across shifts in environmental conditions and prey availability is likely necessary to show the full breadth of a predator's potential diet (Portner et al. 2025). We were also able to clearly show shifts in diet composition, which were not evident from shorter time series published previously (Preti et al. 2023). In addition, swordfish stomachs were collected through partnerships with commercial fisheries, which allowed the processing of many more samples than would be possible from fishery-independent surveys. While land-based sampling can be used to study the diets of central place foragers such as birds or California sea lions, tracking pelagic fish diets generally requires capturing and processing each animal, which is more difficult and labour-intensive. Working with the fishing industry thus offers a unique opportunity to track resource use of an apex predator that would be otherwise difficult to sample.

A disadvantage of relying on fishery-dependent samples is that fishing gears and spatiotemporal coverage can change over time. The DGN fishery in the CCLME is currently being phased out, and other gears are being developed, such as DSBG. We found that the effect of fishing gear on swordfish diet composition was weak and inconsistent, but significant in some years. There is currently no fishery-independent survey for large pelagic predators along the US West Coast, and so it is likely that future monitoring of swordfish diets will continue to rely on fishery-dependent collections. However, if these time-series are to be continued as an ecosystem monitoring tool, any bias from fishing gear used needs to be better quantified. Another limitation is that the swordfish fishery does not operate year-round, and so diet samples were primarily from summer, fall, and winter, with no coverage during spring. The area fished was also relatively small, focusing on the southern CCLME. As swordfish are flexible predators, our results may potentially miss the presence or importance of some prey that are most important during spring, or in the northern CCLME.

Lastly, many of the prey items in swordfish stomachs were highly digested. Although swordfish do not have the endothermic capabilities of some other large pelagic fishes (e.g. the bluefin tunas), they may be able to behaviourally thermoregulate by moving between cold waters below the thermocline and warmer surface layers (Stoeckl et al. 2018), allowing efficient digestion of prey. This can present a challenge for prey identification and taxonomic resolution. Previous studies (e.g. Gorni et al. 2012) have used methods such as Bayesian inference to quantify some of the uncertainty inherent in gut contents analysis, and these strategies could be explored further in the future.

### Conclusions

The data for our study provided a unique opportunity to analyse swordfish diet variation over a period of rapid environmental change. Our results confirmed the role of swordfish as generalist predators, exploiting a broad variety of prey. Swordfish diets changed markedly, with a strong shift in diet composition around 2014–2016, during the time of a se-

vere marine heatwave, from mainly cephalopods, particularly jumbo squid, during earlier years (2007–14) to finfish prey, especially anchovy, in more recent years (2015–23). An overall increase in anchovy biomass and changes to broad-scale forcing (e.g. the NPGO) appeared to be primary drivers of this shift. Overall, our findings suggest that swordfish diets integrate a broad array of ecosystem changes, and are a promising ecosystem sentinel species in the CCLME.

## Acknowledgements

This work would not have been possible without the assistance and samples provided by the NMFS Southwest Region Fishery Observer Program and the participating DGN and DSBG fishermen. We thank numerous assistant volunteers who helped process the stomach samples. Mark Lowry, Eric Hochberg, Bill Watson, John Hyde and Kelsey James helped identify some prey specimens. Lauren Martin identified the cookiecutter shark prey through DNA analysis. Chugey Sepulveda, Scott Aalbers, Craig Heberer and Michael Wang provided swordfish stomach samples. Elan Portner contributed to R code used in multivariate analyses. Annie Yau, Brad Erisman, Alex Curtis, Travis Richards, Heidi Dewar, Stephanie Flores provided useful comments on the draft. Debra Losey assisted with library research.

## Author contributions

Antonella Preti (Conceptualization [equal], Data curation [lead], Formal analysis [lead], Investigation [lead], Methodology [lead], Project administration [equal], Resources [lead], Writing – original draft [equal], Writing – review & editing [equal]), Barbara A. Muhling (Conceptualization [equal], Formal analysis [lead], Writing – original draft [lead], Writing – review & editing [equal]), Gerard T. DiNardo (Project administration [equal], Writing – review & editing [equal]), Graham J. Pierce (Supervision [equal], Writing – review & editing [equal]), Kady Lyons (Writing – original draft [equal], Writing – review & editing [equal]), and Stephen M. Stohs (Project administration [equal], Writing – original draft [equal], Writing – review & editing [equal])

## Supplementary data

**Supplementary material** is available at the *ICESJMS Journal* is available at *ICES Journal of Marine Science* online.

**Conflict of interest:** None declared.

## Funding

This work was partially supported by the NOAA Fisheries Cooperative Research Program, and the NOAA California Current Integrated Ecosystem Assessment program.

## Data availability

The data underlying this article are not shared publicly due to the metadata containing confidential fishing location data. Such data cannot be made public, under the Magnuson–Stevens Fishery Conservation and Management Reauthorization Act of 2006, section 402 (b), 16 U.S.C. 1881a. However, diet composition data without location or date information

attached can be shared upon reasonable request to the corresponding author.

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Handling Editor: Lucia Lopez-Lopez