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RESEARCH ARTICLE

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Environmental and human factors shape the trophic ecology of a widespread marine predator

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Abstract

1. Integrative approaches that investigate trophic ecology drivers provide knowledge to explore and predict changes in food-web dynamics under contrasting scenarios of global change. However, there are few studies that analyse the relationship between environmental factors and trophic interactions and that additionally consider other human stressors such as fisheries.
2. Here, we use Bayesian Stable isotope mixing models to study the trophic ecology of a widespread pelagic predatory fish, the swordfish (*Xiphias gladius*), in the western Mediterranean Sea and the adjacent Atlantic waters. We explore the relationships between dietary estimates and biological, environmental and anthropogenic drivers using generalized additive models (GAMs). GAMs are used to develop spatial predictions of present prey consumption and, as a prospective exercise, to project changes in prey consumption under different future climate change scenarios.
3. Overall, we found that swordfish diet varied as a response to changing environmental conditions, particularly to varying sea surface temperature (SST), mixed layer depth (MLD) and chlorophyll-*a* concentration (Chl); and to fishing pressure. Fish consumption was related to SST and MLD. Squid consumption was related to SST, with the greatest contributions observed in swordfish of intermediate lengths. Squid had a higher contribution to swordfish diet around the Canary Islands and the western Mediterranean Sea, while gelatinous organisms were more consumed around the Gulf of Cádiz. The consumption of gelatinous organisms was higher in smaller swordfish and in areas with lower productivity.
4. Our prospective exercise suggested different diet alterations under contrasting future global change scenarios. For the first time, we provide quantitative evidence of how large-scale, spatial–temporal patterns in fishing pressure and environmental conditions can shape the diet of swordfish. Our study presents useful results to assess the diet of this predator and highlight how incorporating

trophic interactions into projections can improve our understanding of future distributions.

KEYWORDS
diet, environment, fishing pressure, gelatinous organisms, global change, pelagic fish, squid, swordfish

1 | INTRODUCTION

The world is facing transformations at unprecedented rates, with both environmental variations and human activities producing changes in ecosystems' structure and functioning (Bindoff et al., 2019; Pecl et al., 2017). Those alterations have broad ecosystem consequences, such as variations in ocean productivity and consumers' biomass (Tittensor et al., 2021; Worm & Lotze, 2021), to which species are responding in several ways, including changes in abundance, phenology, behaviour, demography and distribution (Poloczanska et al., 2013).

In this context, developing ecosystem assessment tools that allow continuous monitoring is becoming increasingly important in ocean management (Braun et al., 2023; Link et al., 2023). Recent human-induced climate-driven environmental changes have altered the dynamics of marine ecosystems globally (IPCC-AR6, 2023). Concurrently, overfishing is altering exploited populations and consequently modifying trophic interactions among species (Maureaud et al., 2017; Pauly et al., 1998). Understanding how environmental factors and fisheries shape the trophic ecology of key marine species is a challenging task that constitutes the basis for evaluating their cumulative impact on the structure and functioning of marine ecosystems (Dambacher et al., 2010; Halpern et al., 2015). Rather than considering these two major stressors individually, integrative approaches that account for the interplay between climate and fishing should be considered for addressing the challenges that global change may pose over marine ecosystems (Coll et al., 2019; Gissi et al., 2021; Perry et al., 2010; Ramírez et al., 2022).

Few studies to date have considered the relationship between environmental factors and trophic interactions in marine ecosystems using statistical modelling, including as well the potential relationship with other human stressors such as fisheries (Bassoi et al., 2020; Duffy et al., 2017; Kuhnert et al., 2012; Nickels et al., 2023; Preti et al., 2023). Since future environmental changes can be now predicted at multiple scales (IPCC-AR6, 2023), integrative approaches that consider diet–environment relationships may also provide the necessary means for exploring and predicting changes in food-web dynamics under contrasting scenarios of climate change and human impacts. This can certainly contribute to the development of ecosystem assessment and monitoring tools which ensure that the energetic needs of predators are met by the management strategies (Braun et al., 2023; Carroll et al., 2024; Link et al., 2023).

Apex predators, such as large pelagic fishes, are clear examples of organisms impacted by both fishing and climate change (Juan-Jordá et al., 2022; Worm & Tittensor, 2011), with effects that can reach the food-web level (Baum & Worm, 2009; Fernández-Corredor et al., 2024). Despite their relatively low total biomass, they can be keystone species that play a pivotal role in shaping marine ecosystems by regulating prey populations and influencing trophic dynamics (Fortuna et al., 2024; Hazen et al., 2019). Understanding their trophic ecology can provide valuable insights into broad community-scale changes in the abundance, availability and diversity of mid-trophic communities (Kuhnert et al., 2012). Such information on large pelagic fishes is particularly important given that data on offshore pelagic prey are scarce (Olson et al., 2014). The difficulty and expense of collecting biological samples in the open ocean often result in trophic studies of top predators being spatially and/or temporally restricted (Duffy et al., 2017; Hazen et al., 2019; Ouled-Cheikh, Giménez, et al., 2022). Biochemical tracers such as stable isotopes are, nevertheless, being increasingly used since the isotopic composition of predators' tissues provides temporally integrated information on the assimilated fraction of the diet (Phillips, 2012; Young et al., 2015).

Investigating the trophic ecology of top predators provides a unique opportunity to unravel the relationship between environmental factors, predator–prey dynamics and the influence of human activities. Here, we investigated the diet of swordfish (*Xiphias gladius*), a large pelagic predatory fish with a generalist diet (Fernández-Corredor et al., 2023), in response to environmental patterns and fishing pressure. Although swordfish diet has previously shown temporal, spatial and size-related variation, the majority of observed dietary variation remained unexplained (Preti et al., 2023). Environmental conditions affect the diet both directly through changes in energetic costs (i.e. altering the energetic needs of predators and the energetic content of prey, Queiros et al., 2024) and by constraining predator and prey distribution, consequently affecting their feeding habits (e.g. sea surface temperature, SST; Kuhnert et al., 2012). The shoaling of the mixed layer depth (MLD) and the oxygen minimum zones are one of the major climate change effects altering the trophodynamics of marine predators by restricting the depth distribution of pelagic species into a narrower surface layer, compressing their foraging habitat and consequently affecting diet composition (Duffy et al., 2017; Kuhnert et al., 2012; Tickler et al., 2023; Young et al., 2015). Moreover, chlorophyll-*a* concentration (Chl), closely related to primary productivity, serves as an indicator of the resources available for prey and therefore of the prey availability, and has been shown to influence the diet of large pelagic predators (Druon et al., 2022; Duffy et al., 2017; Virgili et al., 2024).

Together with dissolved oxygen, Chl is one of the dominant influencing factors in the distribution of the mesopelagic community, which is usually preyed upon by swordfish (Song et al., 2022). One of the most common fish prey for swordfish, the blue whiting (*Micromesistius poutassou*; Carmona-Antoñanzas et al., 2016; Hernández-García, 1995), is intensively fished and has declined in the most recent years in the Mediterranean (FAO, 2025; Mir-Arguimbau et al., 2022), which has also been reflected in the diet of swordfish (Fernández-Corredor et al., 2023). Hence, we expected that one of the anthropogenic factors influencing the diet of swordfish is probably intensive fishing, removing prey from the ecosystem and therefore altering prey availability and trophic dynamics (e.g. Arlinghaus et al., 2021).

In this study, we aimed to (1) identify spatial patterns in diet composition, (2) investigate the potential influence of environmental and human drivers on trophic ecology and (3) apply a statistical framework for exploring and predicting diet composition both in space and time. Specifically, we statistically modelled the diet of swordfish collected from a large-scale survey covering the western Mediterranean Sea and the adjacent Atlantic waters, from the Gulf of Cádiz to the Canary Islands. These cover important areas where swordfish diet was not studied (e.g. the Alboran Sea) or was poorly described (e.g. the Canary Islands).

Our primary interest lies in identifying general patterns and understanding how they relate to the selected drivers, which in turn allows us to perform projection exercises under different future scenarios. Based on previous dietary studies for similar species (e.g. tunas, Kuhnert et al., 2012), we expected variations in the diet of swordfish in response to spatial fluctuations along a gradient of environmental conditions and human impacts. We hypothesized a higher consumption of cephalopods in deeper and colder waters since their consumption has been previously linked to offshore feeding (e.g. Peristeraki et al., 2005; Young et al., 2006). We also expected a higher consumption of fishes by larger individuals (Fernández-Corredor et al., 2023) and a lower consumption in highly exploited areas where some of the fishes that were common prey for swordfish have declined (e.g. blue whiting; Mir-Arguimbau et al., 2022). Finally, we hypothesized that, in highly productive regions, the abundance of more energetic prey (i.e. fish and squid) may reduce consumption of gelatinous prey by generalist predators, such as swordfish. Understanding these differences in diet is particularly relevant given the overlap of intensive fishing with regions where climate change is expected to have significant impacts (Ouled-Cheikh, Coll, et al., 2022).

2 | METHODS

2.1 | Model species

Swordfish are apex predators found in the open waters of the Atlantic, Pacific and Indian Oceans and the Mediterranean Sea, between 45° N and 45° S (Palko et al., 1981). They are opportunistic predators with high trophic plasticity (Bello, 1991; Palko et al., 1981). They display diel vertical migrations and spend long periods within the mixed layer at nighttime with high daytime use of sub-thermocline (Abecassis et al., 2012), likely tracking the deep scattering layer (DSL) (Madigan et al., 2021) and feeding on a wide range of prey that range from fish to gelatinous organisms (Cardona et al., 2012; Fernández-Corredor et al., 2023). This feeding behaviour contributes to the demersal-pelagic coupling of the ecosystem (Navarro et al., 2017, 2020) and makes them good samplers of epipelagic and deep-water species (Bello, 1991; Romeo et al., 2011).

2.2 | Study area and data collection

Swordfish individuals ($n=253$) were collected between May 2017 and December 2018 by drifting longline fishing vessels working along the western Mediterranean Sea and the north-eastern Atlantic Ocean, from the Gulf of Cádiz to the Canary Islands (Figure 1). More information about technical characteristics and fishery strategies of longlines can be consulted in García-Barcelona et al. (2010, 2013). While connected by the Strait of Gibraltar, both basins exhibit distinct physical and oceanographic characteristics (Longhurst, 1998), thus offering the opportunity to study the spatial variability of the diet of swordfish along a gradient of environmental conditions and human activities.

All swordfish were measured on-board from the tip of the lower jaw to the posterior margin of the middle caudal rays (lower jaw fork length, LJFL). White muscle samples of each individual were collected on-board and frozen at −20°C until their analyses were conducted. Samples were collected under the SGBTM/BDM/AUTSPP/76 permit, with no ethics approval required.

2.3 | Stable isotope analyses and diet reconstruction

Muscle samples were dried at 60°C and ground to a fine powder. Prior to stable isotopic determinations, lipids were extracted with a chloroform/methanol (2:1) solution to correct the effect of high tissue lipid ratio on carbon ($\delta^{13}C$) values (Bodin et al., 2009). Analyses of $\delta^{13}C$ and nitrogen ($\delta^{15}N$) stable isotopes were performed at the Laboratory of Stable Isotopes (EBD-CSIC, Spain) as described in Fernández-Corredor et al. (2023).

We used Bayesian stable isotope mixing models (BSIMMs) to estimate the swordfish diet based on stable isotope values (i.e. $\delta^{15}N$ and $\delta^{13}C$). To spatially assess the dietary patterns, the models were run at the individual level. BSIMMs were computed using the *MixSIAR* R package v3.1.12 (Stock et al., 2018) and run with a generalist type prior, three Markov chain Monte Carlo chains of 300,000 draws and a burn-in of 200,000 draws. The convergence of models was checked using Gelman-Rubin and Geweke diagnostics (Stock et al., 2018; Stock & Semmens, 2016).

Model input data included $\delta^{15}N$ and $\delta^{13}C$ values of individual swordfish and their potential prey species. Potential prey were selected according to previous studies on swordfish diet from the western Mediterranean Sea (Biton-Porsmoguer et al., 2022;

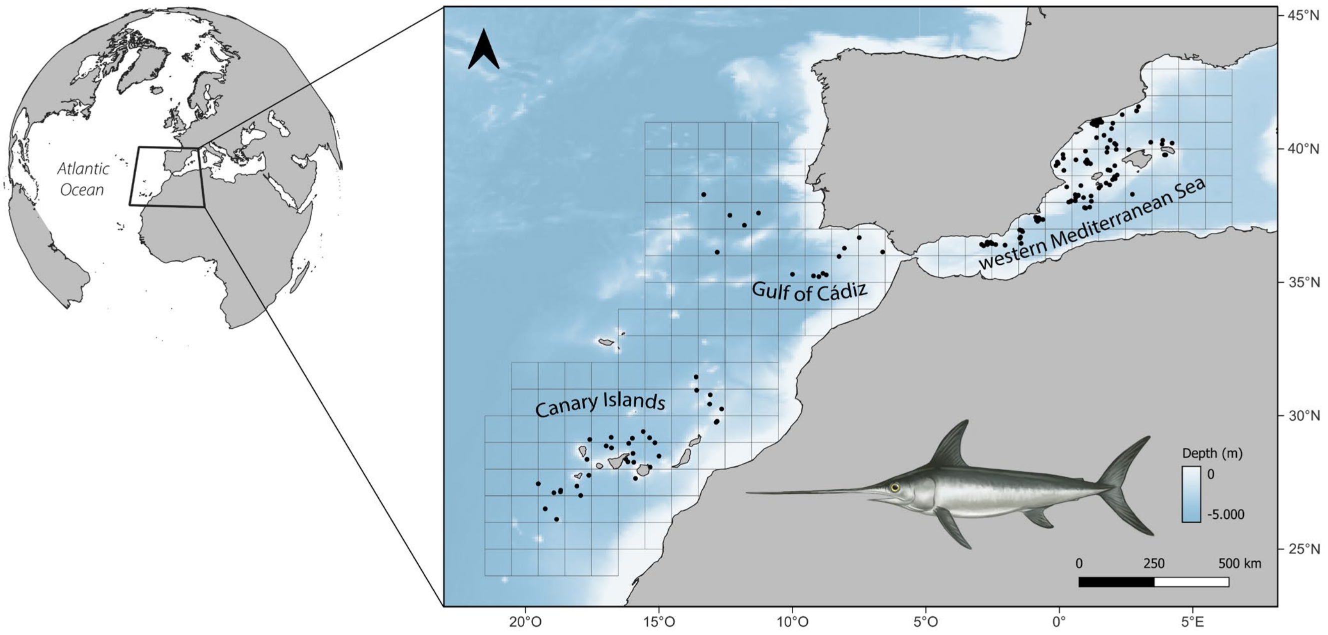

FIGURE 1 Study area including the western Mediterranean Sea and the north-eastern Atlantic Ocean. Black dots represent swordfish sampling locations. Grey lines delineate a spatial grid of 1°×1°. Swordfish illustration by Alex Mascarell.

TABLE 1 Biological, environmental and human factors used as explanatory variables and their respective units of measurement.

Variables		Units
LJFL	Swordfish lower jaw fork length	cm
Depth	Bathymetry (mean depth)	m
Chl	Chlorophyll concentration (mean at sea surface)	$\text{mg}\cdot\text{m}^{-3}$
MLD	Mixed layer depth (mean)	m
SDO	Dissolved oxygen concentration (mean at sea surface)	$\mu\text{mol}\cdot\text{m}^{-3}$
SST	Sea surface temperature (mean)	°C
Fishing effort	Cumulative fishing effort (sum)	$\text{h}\cdot\text{km}^{-2}$

Cardona et al., 2012; Carmona-Antoñanzas et al., 2016; Fernández-Corredor et al., 2023; Navarro et al., 2017), the Gulf of Cádiz (Abid et al., 2018; Hernández-García, 1995) and the Canary Islands (Hernández-García, 1995). To minimize the potential issue of environmental conditions affecting stable isotope baselines, we used region-specific prey values obtained from the literature (Table S1). When isotopic values from prey species were only found from a different region, site-specific isotopic values were corrected following Somes et al. (2010) (Supporting Information Methods). Prey items were grouped into five dietary end-points based on similar isotopic values and taxonomy: mesopelagic fishes; gadiforms, small and medium pelagic fishes; squid group I, squid group II and gelatinous organisms, using a meta-analysis approach (Table S1; Supporting Information Methods). Results of prey consumption obtained through BSIMMs were subsequently grouped into (1) fish (including mesopelagic fishes, gadiforms, small and medium pelagic fishes), (2) squid (including squid groups I and II) and (3) gelatinous organisms.

The diet-tissue discrimination factors (DTDF; 2.62±0.31‰ for δ^{15}N and 1.06±0.12‰ for δ^{13}C) were estimated following Caut et al. (2009). The appropriate parameterization of the BSIMMs was validated through the simulation of mixing polygons, where all consumer data corrected for DTDFs should fall within the bounds of the mixing space (Phillips et al., 2014; Smith et al., 2013).

2.4 | Diet modelling and prediction

We fitted generalized additive models (GAMs) to evaluate the relationships among prey consumption and explanatory variables, including biological, environmental and anthropogenic drivers (Table 1). Mean values of consumption obtained through BSIMMs for each individual and each group of prey were used as response variables. The response variables were proportions and took values from 0 to 1. Therefore, we employed Beta regression models, including linear and additive relations with the covariates and spatial variability. All models were proposed according to the following equation:

$$Y_{ijks} \sim \text{Beta}\left(\pi_{ijks}, \phi\right), \quad i = 1, \ldots, n,$$

$$\text{logit}\left(\pi_{ijks}\right) = \beta_0 + \sum_j \beta_{ij} X_{ij} + f_k\left(X_{ik}\right) + f_s\left(x_{is}, y_{is}\right),$$

where Y_{ijks} represents the proportion of prey Y (response variable) at the observation i with a total of n observations. Y_{ijks} follows a Beta probability distribution with parameters π_{ijks}, the mean of the proportion; and ϕ, the dispersion. The parameter of interest π_{ijks} is linked to the predictor by a logit link function; and the predictor contains a j number of fixed effects $\sum_j \beta_{ij} X_{ij}$; a k number of smooth functions $f_k(X_{ik})$ with thin plate regression splines; and a f_s tensor effect for the spatial variability $f_s(x_{is}, y_{is})$, where x_i and y_i correspond to the latitude and longitude of the observation i. Explanatory variables were fitted with a low spline complexity ($k = 5$) to reduce over-fitting. GAMs were built using the *mgcv* R package v1.9-1 (Wood, 2017).

Together with environmental and anthropogenic drivers, swordfish length was included as a covariate to account for ontogenetic diet shifts in our models (Table 1). Environmental variables were selected based on previous diet studies of pelagic predatory fish. Environmental layers integrating mean monthly values for the current period (2010–2020) were obtained from the Bio-ORACLE v3.0 database (www.bio-oracle.org; Assis et al., 2024), an environmental database for marine spatial analysis that combines satellite data with in situ measurements.

To detect which areas have been most exploited by fisheries, we used spatially explicit estimates of cumulative fishing effort obtained from Global Fishing Watch (Kroodsma et al., 2018; accessed in 2023 from https://developers.google.com/earth-engine/datasets). We summed daily fishing records from trawlers, purse seiners, gillnets and longliners to obtain spatially explicit totals covering the 2013–2017 period (Table 1). Environmental and fishing effort layers were cropped to encompass the study area and adjusted to a common resolution of 1°×1° grid cells (Figure S1) using the *raster* R package v3.6-14 (Hijmans, 2023). This spatial resolution was chosen to align with the movements of this vagile species while capturing the relevant spatial variability in diet composition and its relationships with the explanatory variables (Houssard et al., 2017, 2019; Vidal et al., 2023).

Explanatory variables were checked for potential Spearman correlation, and surface dissolved oxygen and depth were excluded (corr >0.8, Figure S2). We aimed to select the simplest model that retained robust predictive performance while avoiding undue complexity and the risk of overfitting. To this end, explanatory variables were incorporated as linear fixed effects when their relationships with the response variable were deemed adequately represented by linear terms, without necessitating non-linear smoothing functions. We tested all combinations of drivers, ran the resulting GAMs and ranked the models according to the lowest Akaike information criterion (AIC). Deviance explained (DE) was used to assess the explanatory power. To assess the predictive capacity, model performance was evaluated across 25 repeated random splits of the data, each using 75% of the data for training. The specific metrics calculated for evaluating the predictive capacity of the five best-fitted models were root mean square error (RMSE) and mean absolute percentage error (MAPE). All statistical analyses were conducted using R v4.3.3 (R Core Team, 2024).

The best-fitted GAMs were then used to predict the spatial patterns of prey consumption (fish, squid and gelatinous organisms). Spatial predictions were restricted to cells not further than 2° from the sampled locations. We used 100 cm as the mean LJFL value for predictions. We assessed spatial autocorrelation using Moran's *I* test, which is a widely used method to detect spatial patterns in model residuals (Bivand & Wong, 2018).

Besides the spatial distributions, we were interested in evaluating changes in swordfish diet composition as a likely response to global change scenarios. Thus, fitted models were used to project changes in prey consumption considering two future projections of the environmental variables under different greenhouse gas concentration scenarios based on contrasting shared socioeconomic pathways (SSP1-2.6, low climate forcing; and SSP5-8.5, high climate forcing) forecasted to the 2090–2100 period (sourced from Bio-ORACLE v3.0).

3 | RESULTS

3.1 | Diet reconstruction

Isotopic values of swordfish muscle ranged from 8‰ to 14.4‰ for δ^{15}N and from −16.7‰ to −19.8 ‰ for δ^{13}C (Table S2). Individuals with isotopic values outside the 95% mixing region delimited by the mixing polygon of the five prey groups' isotopic values adjusted to DTDFs were deleted (11 out of 253 individuals), thus pointing to a suitable isotopic scenario for the BSIMMs fitted with those prey groups (Figure S4). BSIMMs dietary reconstructions showed spatial patterns for squid and gelatinous organisms' consumption (Figure 2; Figure S5). Squid showed a higher contribution to the diet of swordfish in the Atlantic waters around the Canary Islands (mean consumption = 63%, Table S3) and the western Mediterranean Sea (69%, Figure 2b), while gelatinous organisms were more consumed around the Gulf of Cádiz (38%, Figure 2c). In contrast, fish consumption was relatively homogeneous throughout the sampling area (Figure 2a), with relative contributions between 13% and 33%.

3.2 | Response to environmental and human drivers

The deviance explained by the selected models ranged from 53% to 72% (Table 2). Diagnostic plots suggested normality and homoscedasticity of the residuals for the three models, respectively (Figure S6). Results of Moran's *I* test indicate no spatial autocorrelation of the residuals for the three models ($p > 0.1$). For a list of the model subsets considered in the selection process, see Table S4.

GAMs revealed spatial and environmental influence in the consumption of the different prey (Figure 3). The spatial component $f_s(x_i, y_i)$ was included in all best-fitted models (Table 2; Table S5;

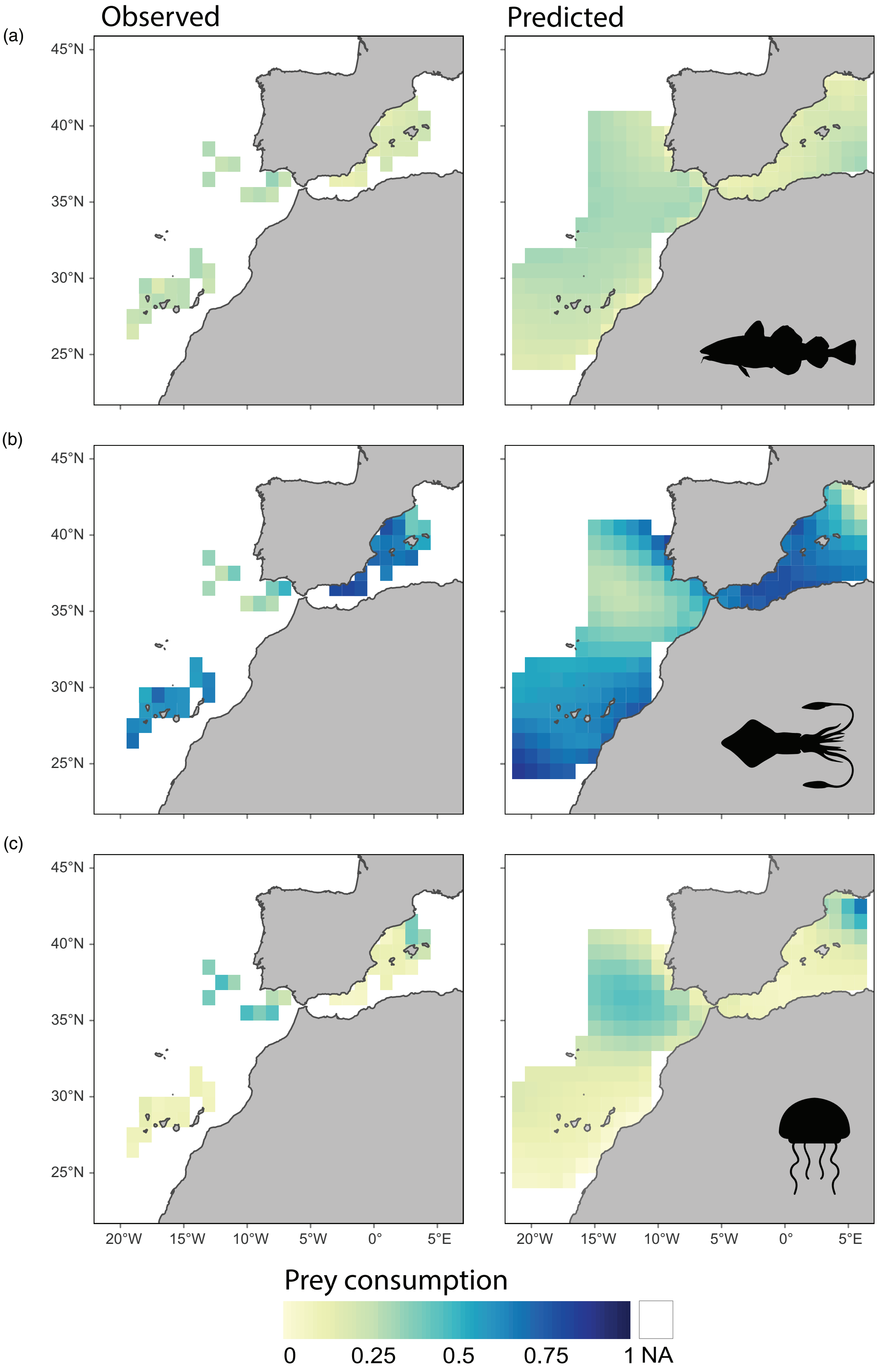

FIGURE 2 Spatial distribution of the contribution of fish (a), squid (b) and gelatinous organisms (c) to the diet of swordfish. The first column (observed) shows the mean contribution of each prey based on Bayesian stable isotope mixing models. The second column (predicted) shows the predicted consumption generated using generalized additive models for swordfish of 100 cm of lower jaw fork length.

TABLE 2 Summary of the selected GAM for each prey consumption showing the percentage of deviance explained (DE). Model summaries are shown in Table S5.

Prey	Models	%DE
Fish	$\mathrm{logit}(\pi_i) = \beta_0 + f_s(x_i, y_i) + f_{\mathrm{MLD}}(\mathrm{MLD}_i) + \beta_1 \mathrm{SST}_i$	53.4
Squid	$\mathrm{logit}(\pi_i) = \beta_0 + f_s(x_i, y_i) + f_{\mathrm{LJFL}_i}(\mathrm{LJFL}_i) + f_{\mathrm{FE}i}(\mathrm{FE}_i) + \beta_1 \mathrm{SST}_i$	71.7
Gelatinous org.	$\mathrm{logit}(\pi_i) = \beta_0 + f_s(x_i, y_i) + f_{\mathrm{LJFL}_i}(\mathrm{LJFL}_i) + f_{\mathrm{FE}i}(\mathrm{FE}_i) + \beta_1 \mathrm{Chl}_i$	71.6

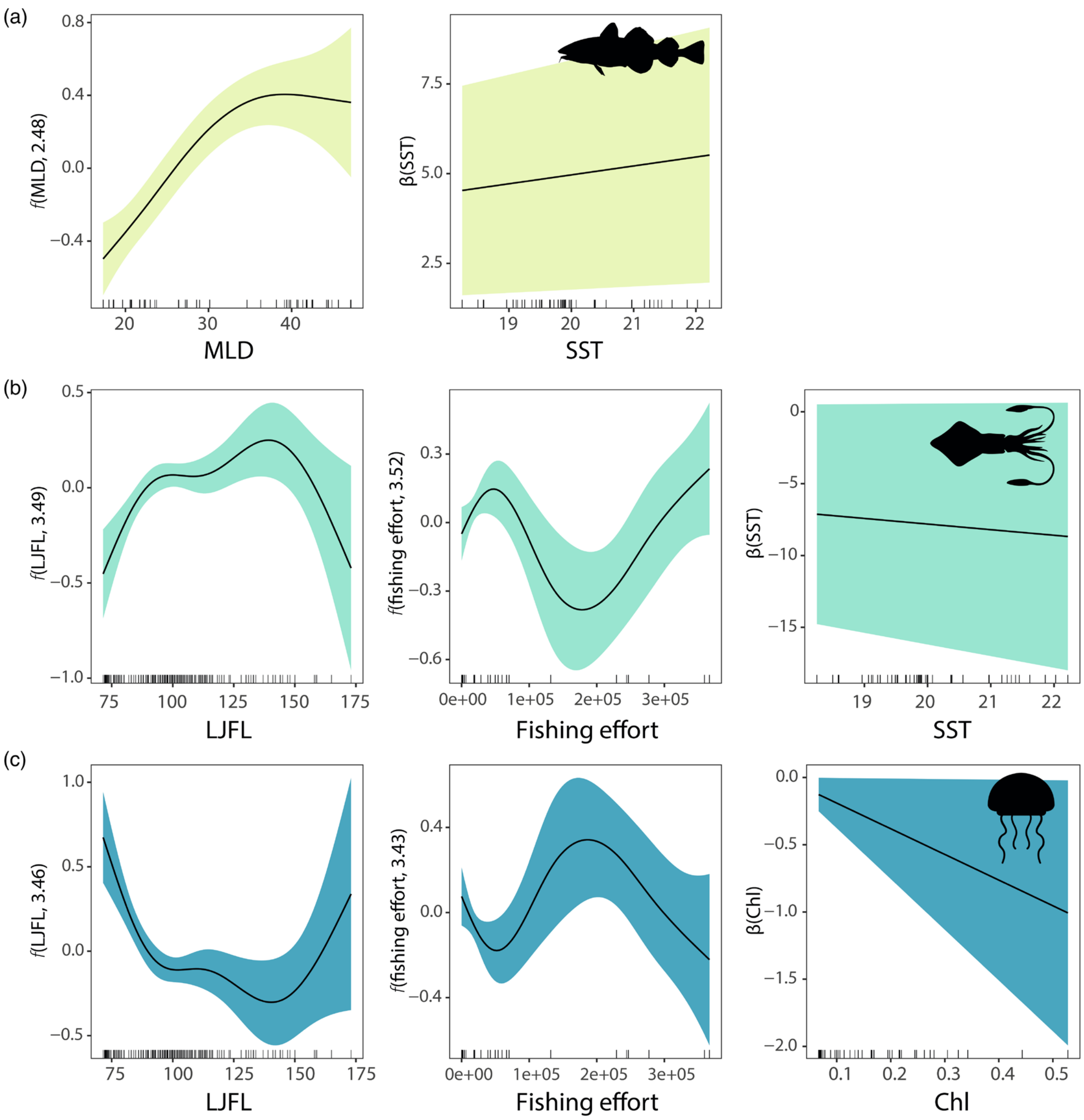

FIGURE 3 Generalized additive model partial effects of the explanatory variables for swordfish consumption of fish (a), squid (b) and gelatinous organisms (c). Shadowed areas represent 95% confidence intervals around the main effects. Chl, chlorophyll-*a* concentration; LJFL, lower jaw fork length; MLD, mixed layer depth; SST, sea surface temperature.

Figure S7). In addition to the spatial component, the best-fitted model for fish consumption contained effects of SST, fishing effort and MLD and explained 54.7% of the deviance. Fish consumption decreased at shallower MLD (Figure 3a). For squid consumption, the selected model explained 71.7% of the deviance and included effects of length, fishing effort and SST. Squid were more consumed by swordfish of intermediate lengths (Figure 3b). Although SST was retained in both fish and squid consumption models, the wide confidence intervals suggest these relationships should be interpreted with caution, as the influence of these variables may be weak. For gelatinous organisms' consumption, the selected model included effects of length, Chl and fishing effort, explaining 72% of the deviance. The consumption of gelatinous organisms was higher in areas with lower Chl and by smaller swordfish (Figure 3c).

3.3 | Predictions and projections

Predicted prey consumption showed a complex spatial pattern (Figure 2). Fish consumption was similar across the study area, representing around 30% of the swordfish diet (Figure 2a). Squid were predicted as important prey items, particularly in the western Mediterranean and the southern part of the study area (Figure 2b). The predicted consumption of gelatinous prey was higher around the Gulf of Cádiz and adjacent offshore waters, and the Gulf of Lions (Figure 2c).

Future projections of the diet of swordfish showed a similar trend for squid consumption, with decreasing contributions under both low (SSP1-2.6) and high (SSP5-8.5) forcing scenarios, and a stronger decrease in the latter (Figure 4b). On the contrary, the proportion of fish in the diet showed different spatial patterns under both forcing scenarios. Under SSP1-2.6, fish consumption was projected to increase across the study area, while it was projected to decrease in the northern part of the western Mediterranean and the Atlantic nearshore areas under SSP5-8.5 (Figure 4a). The projected variation in Chl, the main environmental driver for gelatinous prey consumption (Figure 3c, Table 2), was similar under both scenarios (Figure S3). Therefore, similar patterns were found for gelatinous prey consumption projections under both scenarios, with a slight increase in gelatinous prey consumption around the Gulf of Cadiz and a slight decrease in the north-western Mediterranean (Figure 4c).

4 | DISCUSSION

The growth and survival of predators hinge on their relationship with prey, serving as a crucial factor in forecasting distribution and abundance patterns, particularly for widespread and highly mobile species such as swordfish. Despite the available data that document the role of environmental variability and fishing pressure in shaping the structure and functioning of marine ecosystems (and hence food availability; Gissi et al., 2021), there is still a gap of knowledge on how these two fundamental drivers of global ecological change may impact the trophic ecology of large pelagic fish; this being essential knowledge to ensure effective management and conservation of these commercially valuable species. Here, we provide, for the first time, quantitative evidence on how large-scale, spatial patterns in fishing pressure and environmental conditions can shape the diet of swordfish. Overall, we found that the swordfish diet was strongly linked to geographic location and responded to changing environmental conditions, particularly associated with key oceanographic factors such as SST, MLD and Chl, as well as to human stressors such as fishing pressure.

4.1 | Key drivers of swordfish diet composition

Previous research has provided conflicting evidence regarding size/age-related differences in the diet of swordfish, with studies showing no preference for prey regarding swordfish size (e.g. Abid et al., 2018), while others reported ontogenetic shifts (e.g. Fernández-Corredor et al., 2023; Peristeraki et al., 2005). These incongruences might be driven by local to regional processes and features likely affecting marine food webs and food availability, and point to the importance of large-scale studies, such as ours, for effectively assessing the trophic ecology of highly mobile pelagic species. Our results suggested that the diet of swordfish shifts towards a higher consumption of squid and a lower consumption of gelatinous prey in larger individuals. Nevertheless, beyond the effect of this intrinsic factor, we found that extrinsic factors such as environmental conditions and fishing pressure played a significant role as drivers of the swordfish diet.

Overall, we observed spatial patterns in prey consumption, and geographical location (latitude and longitude) was selected as a predictive variable for all prey groups. This suggested that different dynamic and regional-scale features and processes may be shaping prey availability, and hence swordfish diet. Regarding fish, we observed a relatively homogeneous consumption throughout the sampling area. Besides temperature, fish abundance is closely linked to MLD, especially relevant for mesopelagic fishes (Gallo et al., 2020; Koslow et al., 2018; Song et al., 2022). Although swordfish exploit both demersal and pelagic habitats, the most frequent prey are usually mesopelagic species like paralepidid fishes that associate with the DSL (Fernández-Corredor et al., 2023; Jones, 2018). This relationship was also found in the diet of other species that also spend long periods under the thermocline, like the bigeye tuna (*Thunnus obesus*), where paralepidid fishes became more prevalent as MLD increased (Duffy et al., 2017). Swordfish showed more squid consumption around the Canary Islands and the Mediterranean Sea, as previously reported in regional studies from both areas (Biton-Porsmoguer et al., 2022; Hernández-García, 1995). Our results also showed that swordfish from the South of Portugal and the Gulf of Cádiz had higher consumptions of gelatinous prey. This contrasts with the mainly piscivorous diet previously reported for swordfish from the Gulf of Cádiz (Abid et al., 2018; Hernández-García, 1995). However, these studies are based on stomach contents, where gelatinous species are not easily detected due to fast degradation (Fernández-Corredor et al., 2023). Besides these general patterns, the proportion of gelatinous prey in swordfish diet was related to chlorophyll, suggesting that swordfish may rely on gelatinous prey in less productive waters where preferred prey as fish and squid may be less abundant (Diaz Briz et al., 2018).

Regarding the effect of fishing activity, our models revealed an opposite and non-linear effect on squid and gelatinous consumption. Fisheries tend to concentrate their fishing effort in the most productive areas (Tremblay-Boyer et al., 2011). Areas with low fishing effort likely indicate low availability of common target species for both fisheries and swordfish. In such regions, swordfish may be compelled to rely on secondary prey, such as gelatinous organisms. Conversely, an increase in fishing effort may suggest greater availability of preferred prey, such as squid, leading to a higher contribution of this prey to the swordfish diet. However, squid consumption seems to

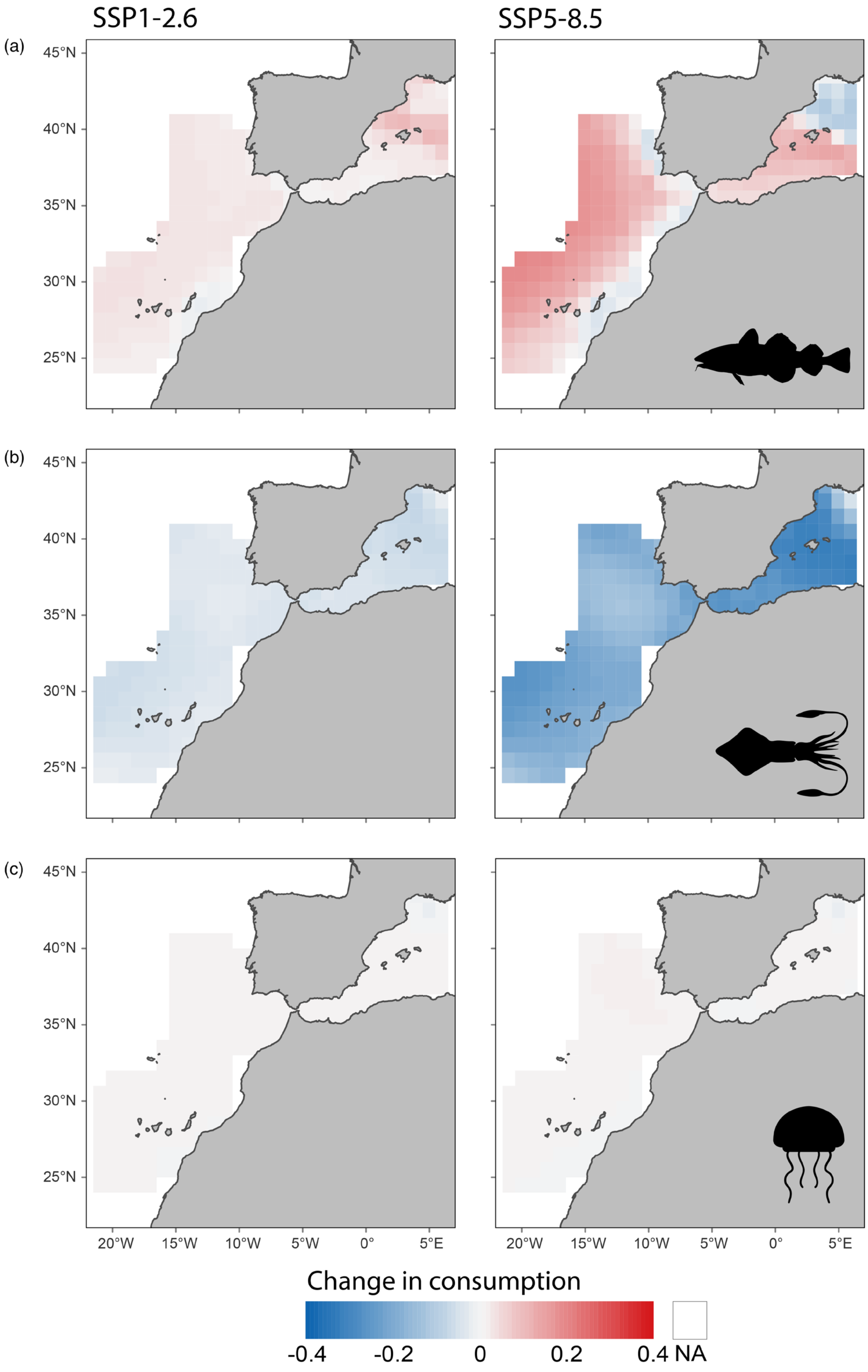

FIGURE 4 Projected change in the contribution of fish (a), squid (b) and gelatinous organisms (c) to the diet of swordfish (100 cm lower jaw fork length) between 2017–2018 and 2090–2100 based on SSP1-2.6 (first column) and SSP5-8.5 (second column). SSP, shared socioeconomic pathway.

drop at intermediate levels of fishing effort, although the interpretation of this pattern is complicated by the fact that fishing effort is heavily concentrated in specific areas, leaving few intermediate values for analysis. Squid prevailed as the preferred prey type in areas of high fishing effort. These findings suggest a potential influence of fishing effort on the trophic dynamics of swordfish, showing higher squid consumption in regions that are heavily impacted by industrial fisheries, where fishery-driven declines in fish biomasses are typically observed (Coll et al., 2013; Veloy et al., 2022). Monitoring the diet of swordfish provides valuable and integrative information on how global change affects the distribution and abundance of prey species and can be an early warning system for broader ecological shifts.

4.2 | Diet changes under global change scenarios

Besides contributing to our understanding of the spatial patterns of swordfish diet and of the environmental and human features driving prey consumption, we also explored how the diet of species inhabiting highly threatened marine ecosystems may change in response to climate impacts and fishing pressure. This holds particular importance within the current context of global ecological change, where pressure on marine ecosystems will likely exacerbate with the progress of climate change and the potential rising exploitation of marine resources to meet the growing food demands of an increasing human population (Pecl et al., 2017).

Climate change may affect top predators directly through changes in their physiology, behaviour and survival; or indirectly through impact on their prey. Consequences of climate change include rising temperatures, deoxygenation of waters and the decrease of primary production (IPCC-AR6, 2023). Our prospective exercise revealed that fish consumption would increase under the low climate forcing scenario as a result of rising water temperatures and a deeper MLD in the north-western Mediterranean. However, this projected rise contrasts with the decline in primary production expected globally as a consequence of increasing temperatures (Bopp et al., 2013), which may certainly affect negatively fish biomass. Global ecosystem models projected a general decline in demersal and pelagic fish in response to climate-change scenarios and the additional fishing impacts, but projected an increase in small bathypelagic fish and cephalopods (Coll et al., 2020). An increase in mesopelagic fish biomass was detected in the Mediterranean from 2005 onwards by Clavel-Henry et al. (2020), and a future increase in mesopelagic biomass is projected by Proud et al. (2017). Nonetheless, Koslow et al. (2018) suggested that a winner–loser scenario is more likely than a single trend in mesopelagic fish abundance when mid-water oxygen concentration decreases. Mesopelagic fishes are generally less energy-dense than small and medium pelagic fish, lowering their potential to meet swordfish energy requirements (López-Pérez et al., 2023).

With the reduction of dissolved oxygen concentration, the DSL is predicted to become shallower (Netburn & Koslow, 2015; Proud et al., 2017). Swordfish may behaviourally adapt and benefit from the creation of shallower hypoxic boundary layers because of their higher tolerance to low oxygen concentrations compared to other pelagic predators (Logan et al., 2023; Madigan et al., 2021). Nevertheless, their horizontal and vertical distribution is limited by hypoxia and temperature, and their suitable habitat is reduced when the oxygen minimum zone is shallower, probably because of the influence in the distribution of prey (Abecassis et al., 2012; Sepulveda et al., 2018; Tracey et al., 2023). Under a high climate forcing scenario, the MLD is projected to become particularly shallow in the north-western Mediterranean (Figure S3), where both fish and squid consumption are projected to decrease (Figure 4). While swordfish may exhibit resilience to the direct effects of environmental changes (e.g. they can tolerate low oxygen levels), the indirect impacts mediated by shifts in preferred prey availability could either exclude swordfish from this region or significantly alter their distribution. These findings highlight the critical role of trophic interactions in projecting future species distributions.

Our projections also suggested a reduction in squid consumption under the low forcing scenario. These results align with a reduction of suitable habitat for squid and a poleward shift in response to ocean warming, which could translate into less availability of squid resources and bottom-up impacts on their predators (Alabia et al., 2016; Coll et al., 2013), but contrast with the global increase of cephalopods projected by ecosystem models that also consider the impacts of fisheries in their scenarios (Coll et al., 2020). Cephalopods are expected to quickly adapt and respond faster to global change than other species due to their short life spans and strong life-history plasticity (André et al., 2010; Hoving et al., 2013), but their high sensitivity to inter- and intra-annual variability in environmental conditions hampers long-term predictions on their abundance (Alabia et al., 2016; Veloy et al., 2024), ultimately shaping consumption by swordfish. Similarly, the abundance of gelatinous organisms such as salps and jellyfish is largely driven by ocean dynamics and climate variability, and they are expected to thrive under anthropogenic alterations like overfishing, eutrophication and hypoxia that diminish their predators and competitors (Doubleday & Connell, 2018; Guerrero et al., 2018).

The trophic ecology of swordfish will also be shaped by the evolution of fisheries and their regulations, which are not considered in our projections. If prey communities shift to lower quality species or if prey size structure is reduced due to environmental changes or fishing pressure, these shifts could have consequences for top predators that have high energetic demands (Duffy et al., 2017). The availability and type of prey, together with the environmental conditions, can alter the allocation of energy reserves, affecting the quality of the swordfish products (Lazo-Andrade et al., 2021). A shift in swordfish diet to lower energetic prey items could contribute to reduced body condition (Johnson et al., 2015), affecting growth and reproduction (Hatzonikolakis et al., 2021). Such effects may be exacerbated if swordfish energy requirements are increased by warming waters (Queiros et al., 2024). Under both scenarios (SSP1-2.6 and SSP5-8.5), swordfish are projected to decrease in biomass and size regarding the fishing scenarios tested (Erauskin-Extramiana et al., 2023). Changes in swordfish abundance, condition and distribution due to prey variability can have significant economic implications, as swordfish support valuable commercial fisheries worldwide (Nóbrega et al., 2025). In this context, fisheries regulations need to consider which are the areas particularly impacted by diet alterations and the resulting effects for swordfish, allowing the dynamic management of these highly threatened and exploited populations.

4.3 | Model assumptions and further applications

Beyond diet, there are other sources of isotopic variability, including intrinsic traits (e.g. metabolic differences, Martino et al., 2019) and environmental effects such as temperature-driven fractionation (Bloomfield et al., 2011). Moreover, we used a temporally averaged summary of environmental variables. While this approach helps capture broad-scale spatial trends, it does not account for potential seasonal variability in environmental conditions or prey availability. Future studies could leverage this framework to disentangle finer temporal dynamics. Cumulative fishing effort was concentrated in shallow areas (Figure S1) and may partially reflect depth-related gradients in the models. Nonetheless, we were able to identify broad patterns in swordfish prey consumption and their main drivers. Regarding the projections, our outcomes on the future diet of swordfish should be taken as a prospective exercise, since they are only based on changing environmental conditions. Given the substantial changes anticipated in the future for certain parameters, future predictions must inevitably rely on extrapolation exercises, which are particularly uncertain—especially when effects may not follow a linear pattern. Additionally, it is essential to periodically reassess the relationships between environmental conditions and the diet of these organisms as these conditions evolve beyond the currently observed ranges, in order to better understand and predict the responses of these organisms. The spatially explicit future projections on swordfish diet should be revisited and updated by incorporating spatially explicit projections on those additional diet drivers (e.g. fishing pressure). Moreover, our ability to project swordfish diet in a long-term timescale may be restricted by other biological interactions such as prey abundance or recruitment, among others.

Despite these limitations, our aim was to identify broad patterns in prey consumption rather than provide a detailed description of swordfish diet; model swordfish dietary responses to environmental and anthropogenic drivers; and offer new insights to understand the potential effects of global environmental change. Enhancing the integration of trophic ecology in ecosystem studies can strengthen our ability to plan for and manage the redistribution of species under global change ensuring that the energetic needs of predators are met and identifying hotspots of predation interactions (Bas et al., 2025; Carroll et al., 2024). Continued large-scale monitoring of their feeding ecology is essential for ensuring sustainable management and the long-term viability of swordfish stocks. Relying on stable isotopes analysis to monitor the diet of these predators provides an easier way of obtaining samples and reduces time-consuming lab procedures, reducing the time between science outputs and their translation into policies. Our study provides key information needed to move towards adaptive management of this commercially important resource (Erauskin-Extramiana et al., 2023), not only in the long term (where uncertainty is greater) but also in the short and medium term (e.g. if a particular year is unusually warm, swordfish diet will be affected as well, likely reflecting ecosystem alterations).

AUTHOR CONTRIBUTIONS

Elena Fernández-Corredor: Conceptualization, methodology, formal analysis, investigation, data curation, writing—original draft, visualization. Alba Fuster-Alonso: Methodology, formal analysis, writing—review & editing. Francisco Ramírez: Conceptualization, methodology, formal analysis, writing—review & editing, supervision, funding acquisition, project administration. Joan Giménez: Conceptualization, methodology, formal analysis, writing—review & editing, supervision, project administration. Salvador García-Barcelona: Resources, writing—review & editing. David Macías: Resources, writing—review & editing. Marta Coll: Funding acquisition, writing—review & editing. Joan Navarro: Conceptualization, methodology, writing—review & editing, supervision, funding acquisition, project administration.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study and the code used are openly available in Zenodo https://doi.org/10.5281/zenodo.15528189 (Fernández-Corredor et al., 2025) and GitHub (https://github.com/ElenaFCorr/Swordfish-diet-drivers-and-predictions).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supplementary methods. Meta-analysis development.

Figure S1. Average value per grid of environmental parameters incorporated into the models.

Figure S2. Spearman correlation between the environmental variables.

Figure S3. Proportion of change in SST (a), Chl (b) and MLD (c) between 2017–2018 and 2090–2100 under SSP1-2.6 and SSP5-8.5.

Figure S4. Mixing polygons including the swordfish isotopic values (black dots) and the potential prey sources (mean ± SD isotopic value: colored dots and error bars) for (a) the western Mediterranean Sea, (b) the Canary Islands, and (c) the South of Portugal/Gulf of Cádiz.

Figure S5. Relative consumption of prey groups in the diet of swordfish from (a) the western Mediterranean Sea, (b) the Canary Islands, and (c) the South of Portugal/Gulf of Cádiz obtained through Bayesian stable isotope mixing models (BSIMM).

Figure S6. Diagnostic plots for the GAMs of consumption of fish (a), squid (b), and gelatinous organisms (c).

Figure S7. Tensor plots for the GAMs of consumption of fish (a), squid (b), and gelatinous organisms (c).

Table S1. Isotopic values for prey groups obtained through the meta-analysis.

Table S2. Mean values and standard deviation (SD) of $\delta^{13}C$ and $\delta^{15}N$ isotopes for swordfish from the western Mediterranean Sea, the Canary Islands, and the South of Portugal/Gulf of Cádiz.

Table S3. Mean values and range (min, max) of prey consumption for swordfish from the western Mediterranean Sea, Canary Islands and the South of Portugal/Gulf of Cádiz obtained through Bayesian stable isotope mixing models.

Table S4. Summary of the 5 best-fitted GAMs for each prey consumption showing the percentage of deviance explained (DE), the Akaike information criterion (AIC), root mean square error (RMSE) and mean absolute percentage error (MAPE).

Table S5. Selected GAMs.

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