

**Drivers of trophic ecology in large predatory fishes:
Environmental and anthropogenic influences within a changing pelagic realm**

Elena Fernández Corredor

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Ph.D. thesis

**Drivers of trophic ecology in large
predatory fishes:**

**Environmental and anthropogenic
influences within a changing pelagic
realm**

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“Far and away the biggest threat to the ocean is ignorance. It’s a lack of understanding that what we put in, what we take out matters- not just to the ocean, but matters to us.”

– Sylvia Earle

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Summary

Top predators are key components of marine ecosystems. Despite their important ecological and socioeconomic roles, their populations have undergone substantial declines across their range. The cumulative impacts of climate change and overfishing are the main threats to top predators, particularly large pelagic species such as tunas, billfishes, and pelagic sharks, which are both sensitive to environmental change and heavily exploited by fisheries. Their broad-ranging movements, aggregated distributions, and migratory habits further complicate effective conservation and management, highlighting the urgent need to improve the understanding of these species, especially for sharks and billfishes, whose ecology and population dynamics remain less studied than those of tunas. In the concurrent context of global change, this Ph.D. thesis investigates how trophic interactions of large pelagic predatory fishes vary across time and space, their relationships to environmental and anthropogenic impacts, and how these patterns can inform ecosystem monitoring and management.

Chapter 1 combines diet analyses obtained through various techniques (i.e., stomach content and stable isotope analyses) to describe the swordfish (*Xiphias gladius*) trophic ecology and evaluate its temporal changes in the northwestern Mediterranean Sea. Swordfish exhibited a generalist and opportunistic diet, primarily based on squid, fish, and gelatinous species. By comparing the shifts in diet with the temporal trends in prey abundance, this chapter unravels the potential role of swordfish as ecosystem sentinels for the study area.

Chapter 2 uses stable isotopes to study the trophic ecology of swordfish on a larger spatial scale covering the western Mediterranean Sea and the adjacent Atlantic Ocean waters. It explores the relationships between dietary estimates and biological, environmental, and anthropogenic drivers using a statistical framework. This framework is then 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. Overall, the

swordfish diet varied in response to sea surface temperature, mixed layer depth, chlorophyll a concentration, and fishing pressure, showing different dietary changes under contrasting future global change scenarios. This chapter presents useful results to assess the diet of this predator and highlights how incorporating trophic interactions into projections can improve our understanding of future distributions.

Chapter 3 aims to unravel the complex ecological relationships between large pelagic predatory fish, including swordfish, blue shark (*Prionace glauca*), and shortfin mako shark (*Isurus oxyrinchus*), their prey, and the environment. It combines spatial distribution data with isotopic niche metrics and diet reconstructions to describe intra- and interspecific competition between these three sympatric predators. Then the role of competitor abundance, pelagic productivity, and fishing pressure in shaping competition metrics within and between species is investigated. The results of this chapter support the hypothesis that niche partitioning is reduced under a high resource availability scenario, and suggest that pelagic productivity and competitor abundance shape trophic niche partitioning among large pelagic predators, with high trophic overlap increasing the potential for shared impacts of prey declines.

Overall, this Ph.D. thesis advances our understanding of the trophic ecology of large pelagic predators, highlighting their ecological flexibility, responses to environmental variability, and potential as ecosystem indicators. This thesis emphasizes the value of interdisciplinary approaches that combine environmental and spatial analyses with methods for reconstructing diet and trophic niches within statistical models capable of identifying the drivers of diet and predicting patterns across space and time. Finally, these findings underscore the importance of integrating trophic ecology into conservation planning to anticipate and manage species' dietary responses to changing environmental conditions and human pressures, ensuring that predator energetic needs are met.

Keywords: large pelagic fish, top predators, swordfish, blue shark, mako shark, stable isotopes, diet, competition, fisheries, climate change

Resumen

Los depredadores superiores son componentes clave de los ecosistemas marinos. Sin embargo, sus poblaciones han sufrido reducciones sustanciales, afectando su importante función ecológica y socioeconómica. Los impactos acumulados del cambio climático y la sobrepesca constituyen las principales amenazas para los grandes depredadores pelágicos como los atunes, los peces espada y los tiburones, que son especialmente sensibles al cambio ambiental y están altamente explotados por la pesca. Sus hábitos migratorios y distribuciones agregadas dificultan la conservación y la gestión eficaces, resaltando la urgente necesidad de mejorar la comprensión de estas especies, especialmente de los tiburones y los peces espada, cuya ecología y dinámica poblacional siguen siendo menos estudiadas que las de los atunes. En el contexto actual de cambio global, esta tesis investiga cómo varían las interacciones tróficas de los grandes peces depredadores pelágicos a lo largo del tiempo y el espacio, su relación con los impactos ambientales y antropogénicos, y cómo estos patrones pueden orientar el seguimiento y la gestión de los ecosistemas.

El capítulo 1 combina el análisis de contenido estomacal con el análisis de isótopos estables para describir la ecología trófica del pez espada (*Xiphias gladius*) y evaluar sus cambios temporales en el Mediterráneo noroccidental. El pez espada mostró una dieta generalista y oportunista, basada en calamares, peces y organismos gelatinosos. Comparando cambios en la dieta y tendencias temporales en la abundancia de presas, este capítulo destaca el potencial del pez espada como centinela del ecosistema.

El capítulo 2 utiliza isótopos estables para estudiar la dieta del pez espada a una escala espacial mayor, abarcando el Mediterráneo occidental y las aguas atlánticas adyacentes. Explora las relaciones entre la dieta y los factores biológicos, ambientales y antropogénicos. Utilizando un marco estadístico, desarrolla predicciones espaciales del consumo actual de presas y, como ejercicio prospectivo, proyecta cambios en su consumo bajo diferentes escenarios futuros de cambio climático. La dieta del pez espada varió en

respuesta a la temperatura superficial, la profundidad de la capa de mezcla, la concentración de clorofila y la presión pesquera, mostrando diferentes alteraciones en escenarios futuros. Este capítulo presenta resultados útiles para evaluar la dieta de este depredador y destaca cómo incorporar interacciones tróficas en las proyecciones puede mejorar nuestra comprensión de las distribuciones futuras.

El capítulo 3 estudia las relaciones entre tres grandes depredadores pelágicos [pez espada, tintorera (*Prionace glauca*) y marrajo dientuso (*Isurus oxyrinchus*)], sus presas y el ambiente. Combinando datos de distribución espacial con métricas de nicho isotópico y reconstrucciones de dieta, describe la competencia intraespecífica e interespecífica entre los tres depredadores y evalúa los efectos de la abundancia de competidores, la productividad pelágica y la presión pesquera. Los resultados respaldan la hipótesis de que la partición de nichos se reduce en escenarios de alta disponibilidad de recursos y sugieren que la productividad pelágica y la abundancia de competidores son claves en la segregación de nichos tróficos entre grandes depredadores pelágicos.

Esta tesis doctoral profundiza en la comprensión de la ecología trófica de los grandes depredadores pelágicos, destacando su flexibilidad ecológica, sus respuestas a la variabilidad ambiental y su potencial como indicadores ecosistémicos. Esta tesis destaca el valor de los enfoques interdisciplinarios al combinar análisis ambientales y espaciales con métodos para reconstruir la dieta y los nichos tróficos dentro de modelos estadísticos capaces de identificar qué factores influyen en la dieta y de predecir patrones en el espacio y el tiempo. Finalmente, estos hallazgos subrayan la importancia de integrar la ecología trófica en la planificación de la conservación para anticipar y gestionar la redistribución de especies bajo el cambio global, asegurando satisfacer las necesidades energéticas de los depredadores.

Palabras clave: grandes peces pelágicos, depredadores apicales, pez espada, tintorera, marrajo dientuso, isótopos estables, dieta, competencia, pesquerías, cambio climático

Resum

Els depredadors superiors són components clau dels ecosistemes marins. Tanmateix, les seves poblacions han patit descensos substancials, afectant la seva important funció ecològica i socioeconòmica. Els impactes acumulats del canvi climàtic i la sobrepesca constitueixen les principals amenaces per als grans depredadors pelàgics com les tonyines, els peixos espasa i els taurons, que són especialment sensibles al canvi ambiental i estan altament explotats per la pesca. Els seus hàbits migratoris i distribucions agregades dificulten la conservació i la gestió eficaces, posant en relleu la necessitat urgent de millorar la comprensió d'aquestes espècies, especialment dels taurons i els peixos espasa, l'ecologia i la dinàmica poblacional dels quals continuen sent menys estudiades que les de les tonyines. En el context actual de canvi global, aquesta tesi investiga com varien les interaccions tròfiques dels grans peixos depredadors pelàgics al llarg del temps i l'espai, la seva relació amb els impactes ambientals i antropogènics, i com aquests patrons poden orientar el monitoratge i la gestió dels ecosistemes.

El capítol 1 combina l'anàlisi de contingut estomacal amb l'anàlisi d'isòtops estables per descriure l'ecologia tròfica del peix espasa (*Xiphias gladius*) i avaluar-ne els canvis temporals a la Mediterrània nord-occidental. El peix espasa va mostrar una dieta generalista i oportunista, basada en calamars, peixos i organismes gelatinosos. Comparant els canvis en la dieta amb les tendències temporals en l'abundància de preses, aquest capítol destaca el paper potencial del peix espasa com a sentinella de l'ecosistema.

El capítol 2 utilitza isòtops estables per estudiar la dieta del peix espasa a una escala espacial més gran, abastant la Mediterrània occidental i les aigües atlàntiques adjacents. Explora les relacions entre la dieta i els factors biològics, ambientals i antropogènics. Mitjançant un marc estadístic, desenvolupa prediccions espacials del consum de preses i, com a exercici prospectiu, projecta canvis en el seu consum sota diferents escenaris futurs de canvi climàtic. La dieta del peix espasa va variar en resposta a la temperatura superficial del mar, la profunditat de la capa de mescla, la concentració de

clorofil·la i la pressió pesquera, mostrant diferents alteracions en escenaris futurs. Aquest capítol presenta resultats útils per avaluar la dieta d'aquest depredador i destaca com la incorporació d'interaccions tròfiques en les projeccions pot millorar la nostra comprensió de les distribucions futures.

El capítol 3 estudia les relacions entre tres grans depredadors pelàgics [peix espasa, tintorera (*Prionace glauca*) i solraig (*Isurus oxyrinchus*)], les seves preses i el medi ambient. Combinant dades de distribució espacial amb mètriques de nínxol isotòpic i reconstruccions de dieta, descriu la competència intraespecífica i interespecífica entre els tres depredadors simpàtrics i avalua el paper de l'abundància de competidors, la productivitat pelàgica i la pressió pesquera. Els resultats donen suport a la hipòtesi que la partició de nínxols es redueix en un escenari d'alta disponibilitat de recursos, i suggereixen que la productivitat pelàgica i l'abundància de competidors són clau en la partició de nínxols tròfics entre grans depredadors pelàgics.

Aquesta tesi doctoral aprofundeix en la comprensió de l'ecologia tròfica dels grans depredadors pelàgics, destacant-ne la flexibilitat ecològica, les respostes a la variabilitat ambiental i el potencial com a indicadors ecosistèmics. Aquesta tesi destaca el valor dels enfocaments interdisciplinaris en combinar anàlisis ambientals i espacials amb mètodes per reconstruir la dieta i els nínxols tròfics dins de models estadístics capaços d'identificar els factors que influeixen en la dieta i de predir patrons en l'espai i el temps. Finalment, aquests resultats subratllen la importància d'integrar l'ecologia tròfica a la planificació de la conservació per anticipar i gestionar la redistribució d'espècies sota el canvi global, assegurant que se satisfacin les necessitats energètiques dels depredadors.

Paraules clau: grans peixos pelàgics, depredadors apicals, peix espasa, tintorera, solraig, isòtops estables, dieta, competència, pesqueries, canvi climàtic

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General introduction

Top predators are ecologically, economically, and culturally important ecosystem components of the Ocean. As upper trophic level consumers, many of them regulate food webs through direct predation and trophic cascades, influence prey diversity by limiting competitively dominant species, and provide carrion subsidies that sustain scavenger communities (Baum & Worm, 2009; Ferretti et al., 2010). Beyond their top-down control, marine top predators contribute to multiple **ecosystem functions**, including nutrient and carbon cycling, habitat modification, and even climate regulation (e.g., increasing net primary production by predating on herbivore populations; redistributing nutrients across ecosystems and enhancing productivity and carbon sequestration) (Estes et al., 2016; Sergio et al., 2008).

These species play a key role in sustaining marine ecosystem structure and function; however, their capacity to do so is increasingly constrained by severe population declines driven by overexploitation, habitat degradation, and climate-driven changes in ocean conditions. From the historical exploitation of whales and seals to the industrial-scale fishing of tuna, billfish, and sharks, top predators have long constituted valuable resources for human populations (Hobday et al., 2015). Because of their strong links to socioecological systems, population declines of these predators have major socioeconomic consequences, triggering the disruption of **ecosystem services** that underpin food security through fisheries (Hammerschlag et al., 2019). In fact, fishing represents the most extensive and direct way humans utilize top predators, particularly targeting the large predatory fishes that inhabit the **pelagic realm**.

The pelagic realm as a case study

The pelagic system, which is defined as the column of water between the ocean's surface and the seafloor, is a vast, large-scale, continuous habitat that

presents unique challenges and opportunities to both marine organisms and scientists. The pelagic ocean represents **Earth's largest biosphere**, occupying more than 90% by volume of the available living space on the planet (Haddock & Choy, 2024). Yet, it has been historically understudied, and at least 80% remains underexplored (Webb et al., 2010).

The lack of structural features/barriers, particularly in the vertical dimension, makes this complex environment difficult to delimit and different layers are defined according to biophysical characteristics, primarily depth and penetration of sunlight (Sutton, 2013). As we descend from the ocean surface, strong environmental gradients are found, including increasing pressure, decreasing temperature, and rapidly diminishing light (**Figure 1**). Temperature drops steeply below sunlit waters, and half of the light is lost near the surface, with 99% gone by between 100 and 200 m depth, depending on the amount of dissolved biological and inorganic material. At this point, light levels during daytime are not enough to support primary production, setting the lower boundary of the **euphotic zone**, also known as the **epipelagic layer**. The pelagic system is essential for global primary production, and photosynthesis in this layer accounts for c. 50% of the global carbon fixation (Field et al., 1998), supporting most of the oceanic zooplankton production and biomass (Sutton, 2013). Below this boundary, where light levels are enough for organisms to differentiate diel cycles but lower than what is required for photosynthesis, begins one of the largest, least understood habitats on earth: the **mesopelagic layer** (Martin et al., 2020; St. John et al., 2016). This layer, also known as the **twilight zone**, is connected to epipelagic processes such as upper thermal mixing and still comprises broad environmental ranges of temperature, light, and oxygen (I. S. Iglesias et al., 2023; Sutton, 2013). Oxygen levels decline with depth, and when respiration exceeds oxygen supply, an **oxygen minimum zone** (OMZ) is formed. Beneath this hypoxic zone, oxygen levels rise again due to the influx of oxygen-rich deep waters from polar regions. The lower limit of the OMZ

and the base of the permanent thermocline usually define the upper limit of the **bathypelagic layer**, going below 1000 m depth to 100 m from the seafloor. This biome is characterized by the absence of measurable light and its high stability regarding temperature and salinity (Sutton, 2013).

However, the exact boundaries between zones are **highly dynamic** across space and time and are modified by macro- and mesoscale dynamics, including boundary currents, eddies, regional upwelling systems and fronts that result in changes in the physical and chemical properties (Braun et al., 2022). The open ocean pelagic community is therefore dynamic and heterogeneous in space and time: pelagic organisms shift their range throughout the year and can migrate across these boundaries, which are likely human constructs (Haddock & Choy, 2024).

Up to 226 highly mobile fish species, including teleost and elasmobranchs, were identified in the pelagic ocean (Maguire et al., 2006). However, the average concentration of biota in the ocean is generally low, and pelagic ecosystems overall have low prey abundance, presenting a critical problem for ocean predators (Benoit-Bird, 2024). Instead, the pelagic system is filled with hot spots of activity that result in **patchily distributed, high-density aggregations of prey** that are key to the survival of pelagic consumers. One of the best examples are the complex, dense aggregations often formed by organisms that inhabit the mesopelagic depths —such as myctophid fishes, squids, crustaceans, and jellyfish—characterized by their strong acoustic backscatter, referred to as **deep scattering layers** (DSLs) (Braun et al., 2022). Part of these organisms ascend to and disperse at the epipelagic layer at night, performing what is known as the largest vertical migration on Earth: the **diel vertical migration** (Brierley, 2014), and provide a significant amount of the diet intake of commercially important pelagic fishes (Willis et al., 2025).

This highly dynamic and heterogeneous nature, together with its remoteness and vast scale, makes pelagic food webs **challenging to model** in space and time and to assess the impacts of human-induced stressors (Ortuño Crespo & Dunn, 2017). Therefore, compared to coastal and demersal ecosystems, there is much less knowledge of pelagic organisms and food webs (Coll et al., 2024). Our limited knowledge of the pelagic realm entails an increasing global concern/hot topic, as it may be especially vulnerable to global threats like climate change, deoxygenation, acidification, human activities such as overfishing, and other threats with unknown potential for feedback to the climate system (Haddock & Choy, 2024; Koslow et al., 2018; Ortuño Crespo & Dunn, 2017).

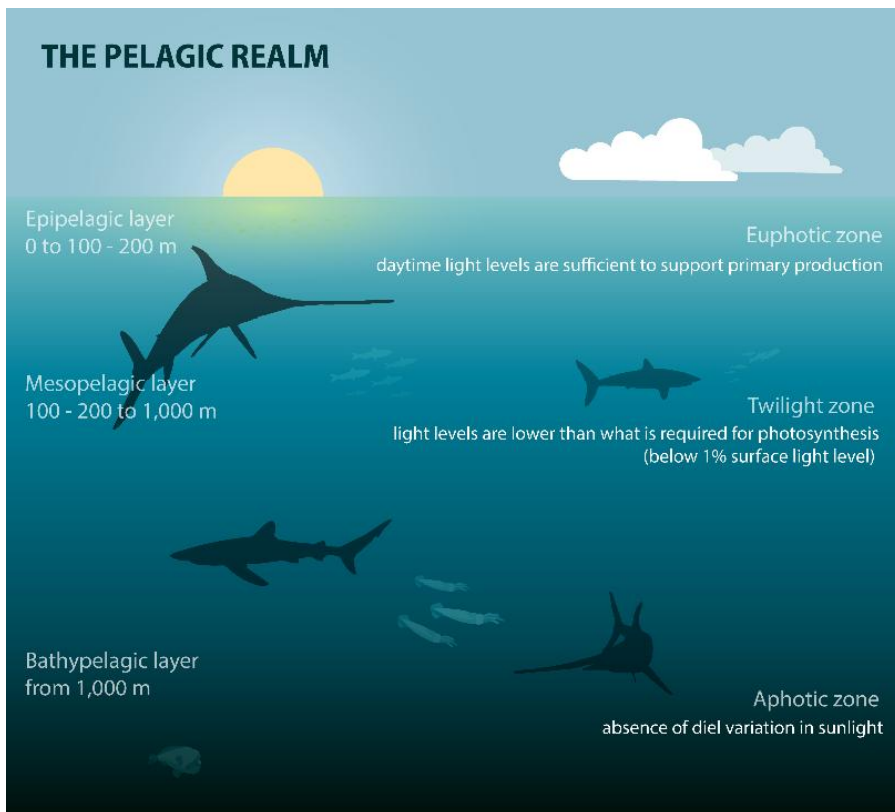


Figure 1. Vertical divisions of the pelagic realm adapted from Martin et al. (2020).

Large pelagic predatory fishes

Several pelagic fishes are among the largest megafaunal predators in the open ocean. Those large pelagic predatory fishes include **tunas**, **billfishes**, and **pelagic sharks**, which are characterized by their highly migratory behavior, their wide-range distribution, and their high exploitation by fisheries. As top predators, they play a crucial role in maintaining the balance and health of ecosystems (Ferretti et al., 2010; Giménez et al., 2022). Changes in their abundance or distribution can have widespread consequences along food webs (Fernández-Corredor et al., 2024), potentially impacting their prey, coexisting predators, and competitors (Baum & Worm, 2009; Dunne, 2009). Their migratory nature and use of large-scale ocean features make large pelagic highly migratory species particularly sensitive to environmental change (Crear et al., 2023). They exhibit clear responses to environmental variability and reflect anthropogenic impacts and pressures on the ecosystem, all in a timely and measurable way (Hazen et al., 2019), which are key characteristics of a **sentinel species**.

Ecosystem sentinel species: “conspicuous, easily accessible, and observable species” that respond to fluctuations within the ecosystem and can serve as indicators of potential shifts in ecosystem function that might otherwise go unnoticed (Hazen et al., 2019).

Therefore, large pelagic fishes offer an exciting lens through which we can interpret life in the open ocean and its responses to multiple drivers of global change (Willis, 2025). These wide-ranging species have been used as **ocean observer platforms** to collect oceanographic data in under-sampled regions (Pagniello et al., 2024; Wiernicki et al., 2025). Due to their regular diving behavior, large pelagic fishes have also been proposed as **reliable samplers** of the midwater communities they feed on (Duffy et al., 2017; Olson et al., 2014; Willis, 2025), which are globally understudied and where periodic sampling is not common (Martin et al., 2020; St. John et al., 2016).

Although marine ecological extinctions are rare, overexploitation has led to historical declines in large pelagic predators' abundance and biomass (Dulvy et al., 2021; Juan-Jordá et al., 2022), and many tuna, billfish, and oceanic shark species are included in the IUCN Red List as **species of conservation concern**. The wide-ranging and migratory nature of these species, together with their spatially aggregated distributions, complicates both their conservation and management, particularly in the high seas where governance is limited (Letessier et al., 2017). This highlights the urgent need to improve our ecological understanding, especially for sharks and billfishes, whose current status remains less documented than that of tunas.

The low encounter rates, together with the high economic costs of offshore exploration, hinder access to living specimens, restricting the in-situ research (Benoit-Bird, 2024). However, open ocean fisheries are highly monitored and information available is usually more detailed for top predators, although they have lower diversity than other taxonomic groups (Coll et al., 2010), thus providing a good opportunity to measure progress toward global biodiversity and sustainability targets (Juan-Jordá et al., 2022).

Cumulative impacts: climate change and fisheries

Human-induced alterations are having a greater impact on species and ecosystems compared to natural variability (Keck et al., 2025). Anthropogenic threats are diverse and usually overlap, resulting in cumulative impacts that have altered the dynamics of marine ecosystems globally (Halpern et al., 2015; IPCC-AR6, 2023). These threats come from multiple factors, rather than one individual stressor, with climate change and overfishing accounting for most cumulative impacts (**Figure 2**) (Halpern et al., 2025).

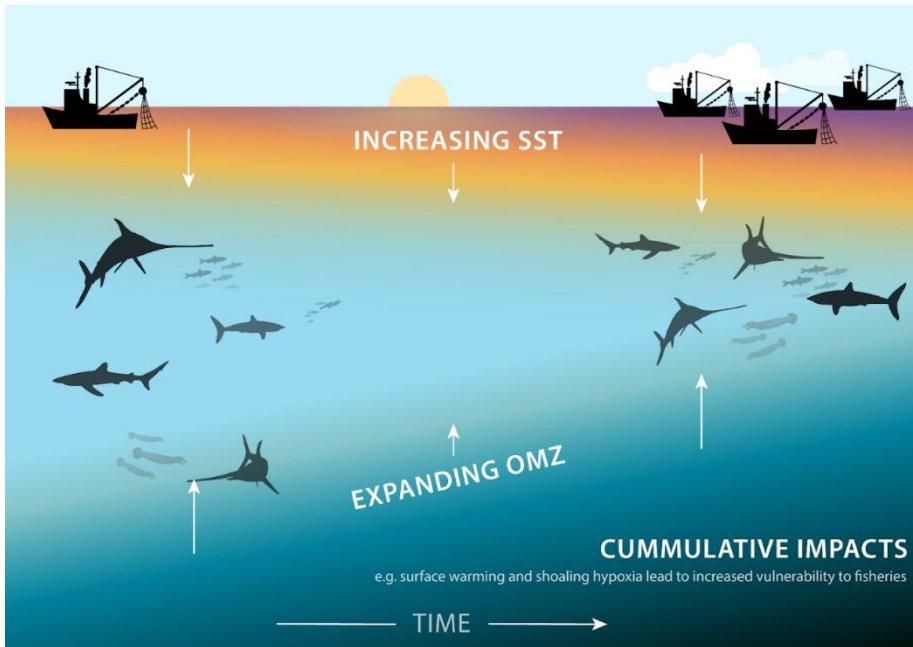


Figure 2 Schematic diagram of the compound effects of expanding oxygen minimum zones (OMZs) at depth and increasing sea surface temperatures (SST), which act together to further reduce vertically available pelagic predators and prey habitat volumes, concentrating their biomass and reducing refuge and escape from fishing pressures. Adapted from Waller et al. (2024).

Whether natural or human-induced, marine pelagic ecosystems are sensitive to **climatic change**, particularly through the influence of temperature on atmospheric circulation, ocean currents, and wind patterns. These alterations on water column mixing also influence pH, salinity, oxygen, and nutrient concentration, leading to changes in primary productivity, acidification, mixed layer depth (MLD), and deoxygenation of the waters (Beaugrand & Kirby, 2018), which translate into constraints in marine species distributions, consequently affecting their feeding habits (Kuhnert et al., 2012). Together with increasing sea surface temperature (SST), the shoaling of the MLD and the expanding oxygen minimum zones are one of the major climate change effects on pelagic predators, restricting the depth distribution of pelagic species into a narrower surface layer and compressing their foraging habitat (**Figure 2**) (Tickler et al.,

2023; Young et al., 2015). Altogether, climate change can alter the local ecological conditions of pelagic habitats and disrupt the distribution and abundance of marine species, leading to changes in community composition and ecosystem functioning known as **regime shifts** (Bindoff et al., 2019; Breitburg et al., 2018; Pecl et al., 2017). In pelagic systems, regime shifts are usually triggered by large-scale climatological processes and are more likely to occur in systems with reduced biodiversity or trophic levels and less resilience, mainly due to overfishing (Ortuño Crespo & Dunn, 2017).

In the open ocean, fisheries significantly improved with the technological advancements following the Industrial Revolution, which allowed an expansion in fishing capacity and spatial extent (Swartz et al., 2010). Those improvements allowed pelagic fleets to travel further and target highly mobile species, with medium and large pelagic fish species representing 80% of the catch, mainly coming from purse seiners and longliners (Ortuño Crespo & Dunn, 2017). However, alterations in oceanographic conditions and their effect on primary production and distribution of marine species also have consequences for **fisheries**, which are increasingly threatened by climate change, pollution, biodiversity loss, and unsustainable fishing practices (IPCC, 2022; Sharma et al., 2025).

The cumulative impacts of overfishing, bycatch, mismanagement, and illegal, unreported and unregulated (IUU) fishing are the main drivers of long-term diversity loss in open ocean predators (Pacoureau et al., 2021; Worm et al., 2005), and have consequences that go beyond the direct impact at the species level. These changes disrupt **top-down control** mechanisms, where predators regulate prey populations across multiple trophic levels (Baum & Worm, 2009). This phenomenon is known as "Fishing Down the Food Web", where the trophic level of catches declines due to the depletion of long-lived, slow-growing, and high-trophic-level species, reducing biodiversity and resilience in ocean systems (Pauly et al., 1998). On the other hand, the removal of prey species from

the system can transform the availability of food resources and can significantly alter competition between and within predators (Arlinghaus et al., 2021).

Altogether, unsustainable fisheries can lead to profound alterations in pelagic ecosystem integrity and the ecosystem services they provide, which can have consequences for food security (Sharma et al., 2025). Since open ocean species are highly migratory, pelagic fisheries often span multiple national jurisdictions, requiring international agreements for governance and management (Ortuño Crespo & Dunn, 2017).

To establish governance frameworks beyond the national jurisdictions, regional fisheries management organizations (**RFMOs**) were created through the mandate of the United Nations Fish Stocks Agreement (1995) and have the responsibility to adopt legally binding conservation and management measures, with five of them focused on highly-migratory species, mainly **tuna and tuna-like species** (TTLs; including billfishes, swordfish, bonitos, mackerels and tunas) (Ortuño Crespo et al., 2018). Although TTLs total catches constitute less than 5 percent of the total fish catches globally, they account for nearly 20 percent of the total world landed value (Maguire et al., 2006). Their high market value leads to high levels of exploitation by purse seiners and longliners; and TTLs are among the most closely monitored fishing targets (Nóbrega et al., 2025). These species are increasingly sustainably managed to ensure maximum yield (Juan-Jordá et al., 2022; Sharma et al., 2025). However, most fleets are multispecific, allowing parallel exploitation of species that would not be profitable to target due to their low biomass (Branch et al., 2013). In particular, the multispecific nature of **pelagic longline fleets**, which are among the most widespread fisheries in the open ocean (Kroodsma et al., 2018), results in the capture of non-targeted species as **bycatch**, as well as of undesirable sizes or age classes of targeted species that are **discarded** (Fernandez-Carvalho et al., 2015). Longline discards and bycatch are associated with high mortality rates and have been responsible for the collapse of several populations (O. Anderson

et al., 2011; Pacoureaux et al., 2021). This is the case of many large pelagic predators including **oceanic sharks**, whose populations have a high spatial overlap with longlines (Queiroz et al., 2019) and remain largely unregulated with poor monitoring and data reporting (Queiroz et al., 2016; Sharma et al., 2025) while their extinction risk continues to increase (Juan-Jordá et al., 2022; Pacoureaux et al., 2021).

Compared to the terrestrial ones, pelagic food webs are challenging to study due to their large spatial scales and the strong influence of physical factors. A good way to better describe pelagic food webs is to focus on the diets of their dominant predators (i.e., tunas, billfish, and sharks) (Haddock & Choy, 2024), which provides an opportunity to **quantitatively monitor marine ecosystems** by characterizing the diversity, distribution, and availability of prey species (Duffy et al., 2017; Hazen et al., 2019; Nicol et al., 2013). Understanding how climate change and fisheries shape the trophic ecology of key marine species is not only complex but foundational for evaluating their cumulative impact on the ecosystem's structure and functioning (Dambacher et al., 2010; Halpern et al., 2015). Rather than considering climate and fishing individually, this thesis applies integrative approaches that account for the interplay between these two major stressors to address the challenges that global change may pose to marine ecosystems, and to large pelagic fishes in particular (Coll et al., 2019; Gissi et al., 2021; Perry et al., 2010; Ramírez et al., 2022).

Objectives

The main objective of this thesis is to provide new insights into the trophic ecology of large pelagic predatory fish and to unravel the biological, environmental, and anthropogenic drivers that shape their trophic dynamics. To achieve the overall objective, the thesis pursues the following specific objectives:

- **Chapter 1:** to compare diet inferences performed with different techniques and evaluate the potential role of a large pelagic predator as an ecosystem sentinel in our study area.
- **Chapter 2:** to investigate the potential influence of environmental and human drivers on trophic ecology, identify spatial patterns, and apply a statistical framework for exploring and predicting the diet composition of a large pelagic predator both in time and space.
- **Chapter 3:** to identify the drivers of competition and unravel the complex relationships between large pelagic predatory fish, their prey, and the environment.

Methodological overview

This thesis addresses several aspects of the trophic ecology of three large pelagic predatory fishes: the swordfish (**Box 1**), the blue shark (**Box 2**), and the shortfin mako shark (**Box 3**), in the western Mediterranean Sea and the adjacent Atlantic waters (**Figure 3**). This section provides a detailed description of the studied species and the study area. Together with the sampling process, it presents an overview of the methodologies used both to describe trophic ecology and its relationships with the selected environmental, biological and anthropogenic drivers, leaving the specific details to be addressed individually in each chapter.

Study area

The study area of this thesis extends along the western Mediterranean Sea and the northeastern Atlantic Ocean, from the Gulf of Cádiz to the Canary Islands (**Figure 3**). The northeastern Atlantic and the Mediterranean Sea are important fishing grounds for pelagic longline fleets, with the Spanish fleet leading the total catches across these regions (Nóbrega et al., 2025). The study area covers two of the main fishing hotspots: off the Spanish coast and around the Balears archipelago in the Mediterranean; and the Madeira and Canarias Archipelagos in the Western African shelf. Several **Biologically Significant Marine Areas (EBSAs)** are recognized within this area: the North-western Mediterranean Pelagic Ecosystems, the Gulf of Cádiz, the West Iberian Canyons and Banks, and the Oceanic Islands and Seamounts of the Canary Region (CBD, 2025).

Both Mediterranean and Atlantic basins exhibit distinct physical and oceanographic properties (Longhurst, 1998) and different fisheries characteristics. These highly dynamic areas are undergoing continuous change, thus offering the opportunity to study the temporal (**Chapter 1**) and spatial variability of diet (**Chapters 2 and 3**) and competition (**Chapter 3**) of large pelagic

predators and to evaluate the environmental and human drivers underlying that variability.

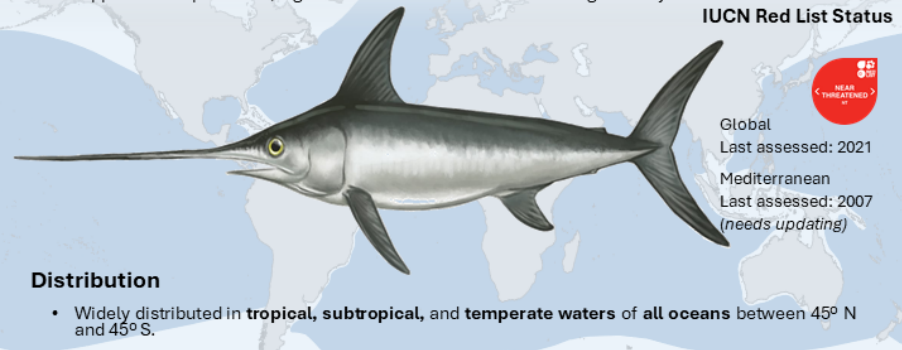
Box 1. The swordfish

Class Teleostei Order Carangiformes Family Xiphiidae

Xiphias gladius (Linnaeus, 1758)

Biology

- Long-lived and fast-growing: max. lengths over 3 m and weights over 500 kg.
- High metabolic rates and **partial endothermy** around their brain and eyes, enabling them to maintain warmer body temperatures in cold, deep waters.
- Asynchronous oocyte development. Multiple spawning in warm tropical and sub-tropical waters.
- Reproductive migration from the Atlantic to the Mediterranean Sea.
- One of the **fastest** predators in the ocean, reaching high speeds up to 80 km/h.
- Opportunistic predators, high use of the **sub-thermocline** through the day.



IUCN Red List Status



Global
Last assessed: 2021
Mediterranean
Last assessed: 2007
(needs updating)

Distribution

- Widely distributed in **tropical, subtropical, and temperate waters of all oceans** between 45° N and 45° S.
- Generally moves towards the equator by winter and returns to the temperate foraging grounds in spring and summer.
- Population structure:
 - **Three different Atlantic populations** (South, North and Mediterranean).
 - Each population has delineated reproduction areas, although information on stock mixing and boundaries is incomplete for the Mediterranean population.

Fisheries and Management

- Main fishing gears: **pelagic longlines**. Harpoon and gillnet fisheries operate in some regions. Also taken as bycatch in tuna fisheries.
- Listed under **Annex III** of the **Barcelona Convention**.
- Management bodies are RFMOs, with ICCAT responsible for Atlantic and Mediterranean stocks:
 - **North Atlantic Stock:**
 - Last assessment (2022) points to a stock status of **not overfished**, with **no overfishing**.
 - Management measures include total allowable catches (TACs) and minimum size limits.
 - **Mediterranean Stock:**
 - Over the last 50 years, stock biomass showed declining trends. The last assessment (2020) indicates that the stock is most likely **overfished** and current fishing mortality is just below unsustainable levels (**no overfishing**).
 - Management measures include TACs, driftnet ban, three-month fishery closure, gear specifications, minimum size regulations, list of authorized vessels, fishing capacity restrictions, and domestic observers onboard on longlines.

ICCAT (2025), NOAA (2025), Madigan et al. (2021)

Box 2. The blue shark

Class Elasmobranchii Order Carcharhiniformes Family Carcharhinidae

Prionace glauca (Linnaeus, 1758)

Biology

- Large pelagic shark reaching max. lengths over 4 m and weights up to 200 kg.
- **Ectothermic** with a large thermal tolerance.
- Placental viviparous. One of the most **productive** shark species with an average litter size of 35.
- Reproduction and breeding are mainly seasonal and occur in late spring or summer.
- Opportunistic predator, feeds mainly on relatively small prey, although its diet can include small sharks, marine mammals and sea birds.



IUCN Red List Status

Global

Last assessed: 2018

NEAR
THREATENED

Mediterranean

Last assessed: 2016

CRITICALLY
ENDANGERED

Distribution

- **Oceanic** and **epipelagic**, most abundant in offshore waters.
- One of the widest distributed sharks. Found in **tropical, subtropical** and **temperate waters worldwide** between 62°N and 54°S.
- Highly migratory, exhibits large-scale movements influenced by reproduction and prey distribution
- Population structure:
 - Genetic studies suggest a single, highly connected global population with **regional substructure**, managed as separate stocks (Atlantic, Pacific, Indian).
 - Mediterranean blue sharks may function as a **metapopulation** relying upon local demographic processes and connectivity dynamics due to the limited genetic exchange with the Atlantic population.

Fisheries and Management

- Most commonly caught pelagic shark: high distributional overlap with important fisheries.
- Mostly caught as target species or bycatch in the **pelagic longline fisheries**.
- Amongst the most abundant shark species in international trade for the meat and fins.
- Listed under **Appendix II** of the **Convention on Migratory Species** and **Annex III** of the **Barcelona Convention**.
- Listed under **Appendix II** of **CITES**, international trade requires an export permit and Non-Detriment Findings.
- Management bodies are RFMOs, with ICCAT responsible for Atlantic and Mediterranean stocks:
 - **North Atlantic Stock:**
 - Last assessment (2023) points to a stock status of **not overfished**, with **no overfishing** (probability of being overfished is 50%).
 - Management measures include total allowable catches (TACs) and mandatory retention of all parts of the shark onboard.
 - **Mediterranean Stock:**
 - Management measures include a 'zero-quota' for this stock.
 - Stock status is **not assessed** due to current data limitations.

Domingo et al. (2022a), ICCAT (2025), Pacoureau et al. (2021)

Box 3. The shortfin mako shark

Class Elasmobranchii Order Lamniformes Family Lamnidae

Isurus oxyrinchus (Rafinesque, 1810)

Biology

- Slow growth and max. lengths up to 4 m and weights up to 500 kg.
- **Endothermic**, maintains higher temperatures than that of the surrounding waters in musculature, brain, eyes and viscera.
- Aplacental viviparous, producing around 12 pups per litter, and up to 30. Embryos exhibit oophagy (feeding on unfertilized eggs).
- Mating occurs from summer to fall.
- Opportunistic and generalist predator. Prey include pelagic fishes, squid, and occasionally small sharks and marine mammals



IUCN Red List Status

- Global
Last assessed: 2018
Endangered
- Mediterranean
Last assessed: 2016
Critically Endangered

Distribution

- Highly migratory oceanic and epipelagic species.
- Distributed in the **upper zones** throughout **all oceans** in **tropical, subtropical** and **temperate** waters between 60°N and 50°S
- Tends to segregate temporally and spatially by size and/or sex, during feeding, mating-reproduction, gestation and birth processes.
- Population structure: little to no differentiation across large spatial scales, supporting **widespread gene flow** and genetic homogeneity.

Fisheries and Management

- High fishing pressure across its broad geographic range.
- Targeted and caught as bycatch in **pelagic longline fisheries** for tuna and swordfish.
- Second most by-caught shark species in global pelagic longline fisheries.
- Listed under **Appendix II** of the **Convention on Migratory Species** and **Annex II** of the **Barcelona Convention**.
- Listed under **Appendix II** of **CITES**, international trade requires an export permit and Non-Detriment Findings.
- Management bodies are RFMOs, with ICCAT responsible for the Atlantic stocks:
 - **North Atlantic Stock** (including the Mediterranean):
 - Last assessment (2019) points to an **overfished** state, currently experiencing **overfishing**
 - Management measures include **prohibition on retaining on board, transshipping and landing**, whole or in part, gear restrictions, observer programs, and improvements in catch data collection.

Domingo et al. (2022b), ICCAT (2025), NOAA (2022)

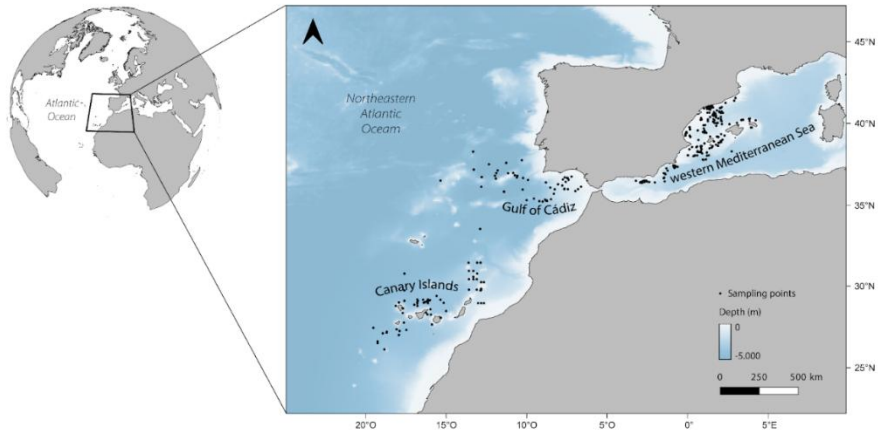


Figure 3 Study area including the western Mediterranean Sea and the northeastern Atlantic Ocean. Black dots represent sampling locations.

The northeastern Atlantic Ocean

The **northeastern Atlantic** holds a high biological diversity and is a vital nursery and migration zone for large pelagic fishes (Abascal et al., 2015; Nóbrega et al., 2023; Sharma et al., 2025). It includes one of the most productive ecosystems: the **Canary Current** upwelling system (Kämpf & Chapman, 2016). The intense upwelling generated by this current brings nutrient-rich waters to the surface, increasing primary production and marine life (P. Chang et al., 2023; Sambe et al., 2016). As a consequence, the high abundances of small pelagic fish that concentrate in this area attract both large predators and fisheries (Grecian et al., 2016), the northeastern Atlantic being the FAO Major Fishing Area with the highest average annual reported shark and rays landings between 1950 and 2021 (Sharma et al., 2025). Very diverse but poorly monitored fleets operate in the eastern central Atlantic, showing an increasing trend in landings, with half of the stocks unsustainably exploited (Sharma et al., 2025). However, this dynamic system is projected to experience changes in its intensity, timing, and spatial distribution, influencing nutrient cycling, species distributions, and the

productivity of the dependent fisheries (P. Chang et al., 2023; Ouled-Cheikh, 2025).

The Atlantic Ocean is connected to the Mediterranean by the Gulf of Cádiz and the Strait of Gibraltar, which acts as a key biological migration corridor. The **Gulf of Cádiz** is characterized by its wide continental shelf and warm waters in the summer (Prieto et al., 2009). Although highly oligotrophic in the middle zone, the area remains an important fishing ground, and longliners represent a small part of the fishing activity, mainly targeting swordfish and pelagic sharks (Torres Leal, 2013). In this transition area, Atlantic waters flow through the upper layer into the Mediterranean, while highly saline and dense Mediterranean water penetrates the Gulf of Cádiz through the inferior layer (Baringer & Price, 1997). This exchange of water constitutes the main source of water renewal for the Mediterranean Sea. The colder waters from the Atlantic create a quasi-permanent anticyclonic gyre that generates an oceanographic break 350 km to the east of the Strait of Gibraltar, known as the Almería-Oran jet (Millot, 1999). This feature limits the eastern border of the **Alboran Sea** and acts as the main oceanographic barrier between the Atlantic Ocean and the Mediterranean Sea.

The western Mediterranean Sea

The **Mediterranean Sea** is a semi-enclosed basin that presents strong environmental gradients: the higher evaporation in the east and the Atlantic influence in the west create a pronounced northwest–southeast gradient in salinity, temperature, and productivity. It is characterized by its narrow continental shelves and large areas of open ocean. Although it is generally considered oligotrophic, it presents enriched coastal areas due to changing wind conditions, temporal thermoclines, currents and river discharges (Estrada, 1996). This wide range of oceanographic conditions allows the co-occurrence of temperate and subtropical species, together with a high percentage of endemic

species, making the Mediterranean Sea a **biodiversity hotspot** (Coll et al., 2010).

However, intense and diversified human activities have historically driven biodiversity changes in the Mediterranean, mainly through overexploitation and habitat loss. Most fish stocks are exploited at unsustainable levels, and declining trends in landings have followed the historical peaks (Sharma et al., 2025). Besides, this area is seriously impacted by the effects of other climate and human-driven changes, such as global warming, coastal degradation, and pollution (Navarro et al., 2015; Salat et al., 2019), which are occurring at a faster rate than the global average (Coll et al., 2012; Salat et al., 2019; Tuel & Eltahir, 2020). These combined pressures have made the Mediterranean one of the most impacted seas globally (G.-U. Kim et al., 2019), which has been characterized as a sea ‘under siege’ (Coll et al., 2012; Micheli et al., 2013).

In particular, the **western Mediterranean** is considered the most diversified sub-basin (Coll et al., 2012) and stands out as a major megafauna hotspot, yet it is also the most anthropized, leading to a high co-occurrence of megafauna and fisheries (Lambert et al., 2025). In the **northwestern subregion**, the freshwater inputs from the Rhone and Ebro rivers, in combination with strong winds, make a relatively productive area due to upwelling (Bosc et al., 2004; Estrada, 1996). As a consequence, the northwestern is one of the most exploited fishing grounds of the Mediterranean Sea (Coll et al., 2012; Colloca et al., 2017; Fernandes et al., 2017), and an important area for pelagic fisheries that target small, medium, and large pelagic fishes (Nóbrega et al., 2025; Palomera et al., 2007; Pennino et al., 2020). Several commercial and non-commercial species, including pelagic (e.g., European sardine, *Sardina pilchardus*) and demersal ones (e.g., European hake, *Merluccius merluccius*), have declined in both abundance and biomass (FAO, 2022; Piroddi et al., 2017). This area is also essential for the conservation of marine predators (Coll et al., 2015), and was selected as a case study in **Chapter 1**.

Sampling

Swordfish ($n = 353$), blue shark ($n = 187$), and shortfin mako shark ($n = 31$) individuals were sampled between 2012 and 2020 on longline fishing vessels operating along the western Mediterranean Sea and the northeastern Atlantic Ocean, from the Gulf of Cádiz to the Canary Islands (**Figure 3**). The samples were collected by the Spanish Oceanographic Institute (IEO, CSIC) onboard observer program monitoring the Spanish surface longline fleet under the SGBTM/BDM/AUTSPP/76 permit, with no ethics approval required and planned according to ICCAT recommendations. This fleet primarily targets swordfish and albacore (*Thunnus alalunga*), operating at different times of the day and including drifting and stationary gear (García-Barcelona et al., 2010).

All individuals 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) for swordfish and from the tip of the snout to the fork of the tail (fork length, FL) for sharks. White muscle and stomach samples were collected on board and frozen at -20°C .

How to study the trophic ecology of pelagic predators

Direct observations of predation events are the most accurate and oldest approach to describe trophic interactions between predators and their prey (Majdi et al., 2018). However, predator–prey encounters are difficult to observe in the open ocean, requiring the use of different approaches to characterize prey consumption for marine predators (Schoombie et al., 2024). A diversity of methods is used to investigate the trophic ecology of free-ranging species, including visual observations like stomach content analysis (SCA), which provides short-term dietary snapshots of the ingested diet, and the analysis of biochemical tracers such as stable isotopes (SIA), which offer a time-integrated perspective on assimilated diet (Nielsen et al., 2018).

Stomach content analysis

Stomach content analysis, which involves the examination and identification of undigested or partially digested prey items found in the stomachs of consumers, has been a fundamental tool in trophic ecology, particularly in the marine ecosystem, where predation events are difficult to observe (Majdi et al., 2018). This method provides highly resolved, species-level dietary information and allows for the estimation of different metrics such as prey frequency in number (%N; percentage of individuals of prey *i* versus the overall number of prey), prey frequency of occurrence (%F; percentage of stomachs containing prey *i*), prey percentage of reconstructed weight (%W; percentage of the weight of prey *i* versus the overall weight of prey), or the Index of Relative Importance (IRI = (%N + %W) * %F; Hart et al., 2002). These metrics are used in **Chapter 1** to describe the diet of juvenile swordfish.

Although SCA provides a high-resolution taxonomic description of diet composition, it is a snapshot view in time, providing information about recently ingested prey. Besides, it can be biased due to differential digestion rates (Baker et al., 2014), particularly in species that retain hard structures such as cephalopod beaks or fish otoliths, as in the case of large pelagic predatory fish.

Stable isotopes analysis

Based on the premise that “*you are what you eat (plus a few permil)*” (DeNiro & Epstein, 1978), the isotopic composition of a consumer reflects the composition of its diet (Phillips, 2012). Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) are the traditional and most commonly used isotopes for studying trophic ecology (Nielsen et al., 2018). On the one hand, measuring $\delta^{13}\text{C}$ allows for differentiation between coastal and pelagic foraging: inshore

Stable isotopes: Specific forms of elements that have the same number of protons but different numbers of neutrons, giving them a different atomic mass (Fry, 2006). The isotopic compositions are reported in the conventional δ notation, expressing the ratio of the heavy to the light isotope, reported as the per mil (‰) deviation from an international standard.

sources tend to be $\delta^{13}\text{C}$ -enriched compared to offshore ones. On the other hand, differences in $\delta^{15}\text{N}$ can indicate feeding at different trophic levels and/or feeding in areas with different isotopic baselines (Cherel & Hobson, 2007; Newsome et al., 2007).

By analysing stable isotopes in tissue samples from a consumer and its prey, we can use mathematical **mixing models** to convert isotopic data into estimates of diet composition (Fry, 2006). This is particularly useful when quantifying the consumption of organisms, such as gelatinous species (e.g., salps, jellyfish), which are not typically detected in stomach contents analysis due to rapid degradation (Cardona et al., 2012).

These models require information on isotopic signatures from consumer and potential prey, as well as **diet-to-tissue discrimination factors** (DTDF), which are the difference between isotopic ratios of an animal and its diet. Due to a lack of experimental studies for our studied species, DTDFs in this thesis were calculated following the regression equations presented in Caut et al. (2009). Potential prey were included in the models according to stomach content analysis (i.e., prey species with >10%W) in **Chapter 1**, and according to literature in **Chapter 2** and **Chapter 3**.

Over the years, several tools have been used to develop mixing models, producing robust estimates on complex dietary systems (Parnell et al., 2010). In this thesis (**Chapters 1, 2 and 3**), we applied **Bayesian isotopic mixing models** (BSIMM) using the *MixSIAR* R package (Stock et al., 2018), which incorporates uncertainty in consumers, sources and diet-to-tissue discrimination factors, integrating multiple sources of error (i.e., process and residual error). In this thesis, the appropriate parameterization of the BSIMM 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). In addition, Bayesian mixing models allow for the incorporation of

supplementary information based on previous dietary knowledge (e.g., SCA), providing more realistic dietary estimates (e.g., Chiaradia et al., 2014; Giménez, Marçalo, et al., 2017). In **Chapter 1**, we used diet proportions estimated from the stomach contents to construct informative prior distributions, which allowed us to incorporate both sources of data into a single framework.

Stable isotope ratios are also used to provide both quantitative and qualitative insights into the ecological niche, visualized within a multivariate space with different isotope ratios as dimensions: the **isotopic niche** (Newsome et al., 2007). SIA is a pivotal tool for quantitatively studying niche dynamics and resource partitioning among sympatric species (e.g., Galindo et al., 2021; B. Iglesias et al., 2024; R. K. Logan, Vaudo, et al., 2023b; Marsaly et al., 2023) and has been extensively used for addressing complex ecological questions related to intra- and interspecific interactions. For example, the isotopic niche width can be used as a proxy for diet diversity, which likely shapes **intraspecific competition**; while the isotopic niche overlap between coexisting species can estimate the similarity of exploited resources, potentially reflecting **interspecific competition** when shared resources are limited (Pelage et al., 2022; Teichert et al., 2024). This approach is used to study competition between and within the three studied species in **Chapter 3**.

Ecological niche: A species' ecological niche is divided into the biotic and abiotic factors that influence its ability to persist in a given locality, and the impact of species on those factors (Chase, 2011).

Modeling the relationships with drivers

Beyond dietary assessment, the approaches used in this thesis enable evaluation of the environmental and anthropogenic drivers that shape predators' diets. Trophic relationships are shaped by a combination of **intrinsic** (species-specific) and **extrinsic** (environmental) factors (Walters et al., 2025). Internal factors include biological traits such as body size, age, dispersal capacity, and reproductive state, all of which influence what organisms can

capture and consume and how prey and predators interact. External factors involve prey availability, ecosystem productivity, oceanographic conditions, and fishing pressure, which can alter both the abundance of resources and the interactions among predators.

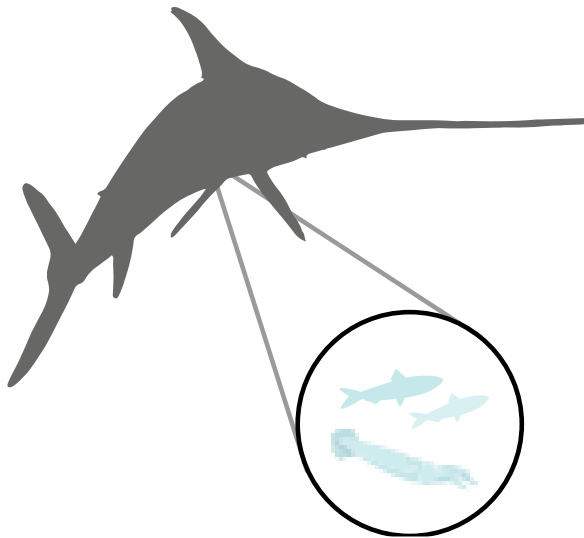
Statistical models are widely employed in ecology to explore the complex relationships between a response variable and the factors that drive its variation. One of the most frequently used and flexible frameworks applied to many problems in statistical ecology is Generalized Additive Models (GAMs) (Hastie & Tibshirani, 1986), which are generalized linear models with a linear predictor involving a sum of smooth functions of covariates (Wood, 2017). GAMs can flexibly model nonlinear relationships, providing a semi-parametric approach to uncover these patterns without assuming a strict linear form. GAMs support various types of response variables (e.g., proportions, individuals), making them suitable for testing a wide range of ecological questions. Smooth functions, commonly implemented using splines, can be specified as either parametric or non-parametric, allowing GAMs to flexibly capture a wide range of relationships. The use of penalized smooth functions helps prevent overfitting while still allowing for flexible modeling of complex relationships. Parameter estimation in GAMs is typically carried out using penalized maximum likelihood estimation methods (Wood, 2017). Once the model is fitted, GAMs can be used to draw inferences or make predictions about the response variable based on the values of the predictors.

In this thesis, this methodology was applied in **Chapter 2** to describe the relationship between the selected biological (predator length), environmental (temperature, dissolved oxygen, mixed layer depth, chlorophyll-a concentration), and anthropogenic (fishing pressure) drivers with prey consumption. The best-fitted models were then used to predict the spatial patterns of prey consumption and to project prey consumption under two different climate change scenarios.

GAMs were used in **Chapter 3** to standardize fisheries catch data (i.e., number of individuals per thousand hooks) and account for overdispersion (Hoyle et al., 2024). The best-fitted models were used to estimate the relative abundance of swordfish, blue shark, and shortfin mako in our study area. GAMs were also applied to evaluate the influence of biological (predator abundance), environmental (mixed layer depth, chlorophyll-a concentration, Ocean Productivity available to Fish), and anthropogenic (fishing pressure) drivers in the potential competition of the three large pelagic predators targeted in this thesis.

Chapter 1.

Assessing juvenile swordfish (*Xiphias gladius*) diet as an indicator for marine ecosystem changes in the Northwestern Mediterranean Sea



Reference:

Fernández-Corredor, E., Francotte, L., Martino, I., Fernández-Álvarez, F. Á., García-Barcelona, S., Macías, D., Coll, M., Ramírez, F., Navarro, J., & Giménez, J. (2023). Assessing juvenile swordfish (*Xiphias gladius*) diet as an indicator of marine ecosystem changes in the northwestern Mediterranean Sea. *Marine Environmental Research*, 192, 106190. <https://doi.org/10.1016/j.marenvres.2023.106190>

Abstract

To preserve marine biodiversity, we need reliable early warning indicators that inform changes in marine ecosystems. As reliable samplers of mid-trophic level communities, studying the trophodynamics of large pelagic fish can contribute to monitoring these changes. Here, we combined stomach content and stable isotope analyses to reconstruct the diet of juvenile swordfish (*Xiphias gladius*) in the north-western Mediterranean Sea, in a time-lapse of almost a decade (2012 and 2020). Overall, our study showed that swordfish fed on a wide range of fish and cephalopod species from both pelagic and demersal habitats. A dietary shift towards increasing consumption of cephalopods and decreasing consumption of Gadiformes had been observed between 2012 and 2020. Stable isotope approaches revealed that gelatinous organisms were also important prey, particularly for smaller-sized swordfish. We underline the importance of combining multiple and complementary approaches to better reconstruct the diet of generalist species. Our findings highlight the generalist and opportunistic diet of Mediterranean swordfish, which makes them good candidates for monitoring changes in the ecosystem.

INTRODUCTION

Within the current context of global environmental change, there is an urgent need for developing reliable, early warning indicators informing on changes in the structure and functioning of marine ecosystems (Pecl et al., 2017). In this context, the use of species as ‘sentinels’ of different processes in the marine environments they inhabit has gained interest in marine ecosystem monitoring and management (Siddig et al., 2016). Ecosystem sentinel species are defined as “conspicuous, easily accessible, and observable species” that respond to fluctuations within the ecosystem and can serve as indicators of potential shifts in ecosystem function that might otherwise go unnoticed (Hazen et al., 2019). Marine top predators integrate trophic processes and interactions along food webs and can be reliable sentinel species informing on ecosystem changes and cause-effect relationships in a realistic way (Moore et al., 2014). They play an important role in shaping marine food webs, exhibit clear responses to environmental variability, and reflect anthropogenic impacts and pressures on the ecosystem, all in a timely and measurable way (Hazen et al., 2019), which are key characteristics of a good sentinel species.

The diet of these marine sentinels provides an opportunity to quantitatively monitor marine ecosystems by characterizing the diversity, distribution, and availability of prey species (Duffy et al., 2017; Hazen et al., 2019; Nicol et al., 2013). Large pelagic fish such as tunas or seabirds such as penguins have been proposed as reliable samplers of the mid-trophic level communities (Carpenter-Kling et al., 2019; Olson et al., 2014), as they can collect data on offshore prey, which are usually scarce (Duffy et al., 2017). This is particularly relevant given that human and climate stressors are causing significant shifts in the composition of marine communities, and species with short life cycles and adaptability to temporal and spatial changes, such as cephalopods and

gelatinous organisms, may thrive in this changing environment (Doubleday & Connell, 2018; Hoving et al., 2013).

The swordfish (*Xiphias gladius*) is a paradigmatic example of an efficient sampler of pelagic and mesopelagic species (Bello, 1991; Markaida & Hochberg, 2005; Romeo et al., 2011). This widespread species performs vertical migrations (Canese et al., 2008), and contributes to the demersal-pelagic coupling of marine ecosystems (Navarro et al., 2017, 2020). It feeds on a wide range of prey from epipelagic and mesopelagic to benthopelagic and demersal species, showing high trophic plasticity (Abid et al., 2018; Carmona-Antoñanzas et al., 2016; Preti et al., 2023; Rosas-Luis et al., 2017). Despite being currently listed as “Near Threatened” in the Mediterranean Sea by the International Union for the Conservation of Nature (IUCN; (Collette et al., 2022), swordfish remain highly overfished (ICCAT, 2020) due to their high commercial interest (Damalas & Megalofonou, 2014; Palko et al., 1981), which also facilitates sample collection.

In the Mediterranean Sea, previous studies have reported information on the diet of swordfish (e.g., Biton-Porsmoguer et al., 2022; Navarro et al., 2017; Romeo et al., 2009). However, differences in the methodology across studies have resulted in contrasting conclusions regarding the relative importance of different prey in its diet; thus, hampering the proper evaluation of swordfish trophodynamics in response to varying environmental conditions. While studies based on stomach content analysis have identified fish and cephalopods as the main prey consumed (Biton-Porsmoguer et al., 2022; Carmona-Antoñanzas et al., 2016), the use of stable isotopes has highlighted the significance of gelatinous organisms as an important part of the assimilated diet of swordfish (Cardona et al., 2012). Both techniques have their own biases (Boecklen et al., 2011; Hyslop, 1980; Young et al., 2015). Stomach content analysis can provide a high-resolution taxonomic description of diet composition, yet it can be biased due to differential digestion rates (Hyslop, 1980). While biochemical tracers such as stable isotopes provide integrated information on the assimilated

fraction of the diet, they can be based on untested or unrealistic assumptions such as some parameter selection related to the paucity of experimental studies (Young et al., 2015). The combined use of both approaches has been proposed as a suitable means for providing more realistic dietary estimates (Chiaradia et al., 2016; Giménez, Marçalo, et al., 2017; Navarro et al., 2014); particularly when it comes to quantifying the consumption of organisms, such as gelatinous species, that are not usually detected in stomach contents analysis due to fast degradation (Cardona et al., 2012; Chiaradia et al., 2016). Moreover, few studies on swordfish have previously evaluated dietary changes across periods (e.g., Preti et al., 2023); thus, precluding inferences on food web dynamics and changes in the structure and functioning of marine ecosystems.

Here, we provide a diet reconstruction of swordfish inhabiting the highly impacted north-western Mediterranean Sea, based on the combination of stomach content analyses and stable isotope approaches. Specifically, we aimed to describe the trophodynamics of juvenile swordfish and to compare diet inferences performed with different techniques. We evaluate dietary shifts between two years separated by almost a decade and hypothesize likely responses to changes in the community. This is particularly important in our study area, where climate and human-driven changes (e.g., warming water temperatures) are occurring at a fast rate (Coll et al., 2012; Salat et al., 2019; Tuel & Eltahir, 2020) and several commercial and non-commercial species, including swordfish prey (e.g., European hake, *Merluccius merluccius*), have declined in both abundance and biomass (FAO, 2022; Piroddi et al., 2017). As a reliable sentinel species and a mesopelagic sampler, we expect that the swordfish diet would closely track the reported changes in prey availability and, hence, the structure and functioning of the marine community.

MATERIALS AND METHODS

Study area and sampling procedures

A total of 100 juvenile swordfish were caught by drifting longline fishing vessels operating in Tarragona (north-western Mediterranean Sea, Figure 1) between summer and autumn of two years separated by almost a decade (2012 and 2020). No anomalous environmental conditions for sea water potential temperature ($^{\circ}\text{C}$) and net primary productivity ($\text{mg}\cdot\text{m}^{-3}\cdot\text{day}^{-1}$) that could potentially impact individuals' diet or foraging behaviour were observed within our study area for the sampling years (see Supplementary Methods in Appendix A). Once on board, the lower jaw fork length (LJFL) was measured, then white muscle samples and the whole stomach were collected and frozen at -20°C until further analyses were conducted.

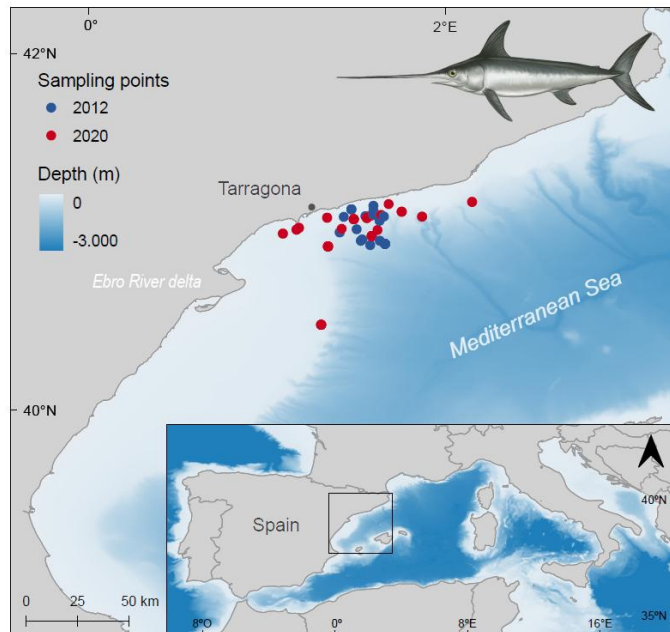


Figure 1. Sampling area in the north-western Mediterranean Sea. The geographic position of the studied area in the Mediterranean Basin is also indicated in the bottom right corner. Swordfish illustration by Alex Mascarell.

Lab analyses

The stomach contents were carefully separated by filtering using two different sieves (1 mm and 500 μm). Prey items retained in the sieves were identified to the lowest possible taxonomic level. Prey otoliths were stored dry and measured using stereomicroscopes and identified using the AFORO database (<http://aforo.cmima.csic.es>, Lombarte et al., 2006). The otolith length (OL) was used to infer individual length and weight using otolith length–fish length and fish length–fish weight published regressions (see Table A.1 from the Appendix). Round sardinella (*Sardinella aurita*) individuals with low digestion signs were excluded from the analysis as this species was used as bait by the longliners. Cephalopod beaks were preserved in 70% ethanol and identified using an in-house beak collection (AFOC, ICM-CSIC; Sánchez-Márquez et al., 2023). Lower Rostral Length (LRL) and Crest Length (CL) were measured to estimate the length and weight using published regressions (Table A.1; Clarke, 1986).

Muscle samples were dried at 60 °C and ground to a fine powder. Before analysis, lipids were extracted with a chloroform/methanol (2:1) solution to correct for the effect of high lipid ratio in the tissue on carbon ($\delta^{13}\text{C}$) levels (Bodin et al., 2009). Analyses of $\delta^{13}\text{C}$ and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios were carried out at the Laboratory of Stable Isotopes of the Estación Biológica de Doñana - CSIC (Sevilla, Spain). Samples were combusted at 1020 °C using a continuous flow isotope-ratio mass spectrometry system (Thermo Electron) using a Flash HT Plus elemental analyser interfaced with a Delta V Advantage mass spectrometer. Based on laboratory standards, the measurement error was ± 0.1 and ± 0.2 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. The standards used were EBD-23 (cow horn, internal standard), LIE-BB (whale baleen, internal standard), and LIE-PA (razorbill feathers, internal standard). These laboratory standards

were previously calibrated with international standards provided by the International Atomic Energy Agency (IAEA, Vienna).

Statistical analyses

Ontogenetic shifts in the diet of the swordfish have been previously reported (e.g., Romeo et al., 2009; Salman, 2004). Since 2012 individuals were larger than 75 cm, individuals from 2020 were split into two groups: small 2020 individuals (LJFL < 75 cm) and large 2020 individuals (LJFL > 75 cm), to compare only similar body sizes between 2012 and 2020.

We calculated five trophic metrics to characterize the diet of swordfish: i) the frequency in number (%N; percentage of individuals of prey *i* versus the overall number of prey), ii) the frequency of occurrence (%F; percentage of stomachs containing prey *i*), iii) the percentage of reconstructed weight (%W; percentage of the weight of prey *i* versus the overall weight of prey), iv) the Index of Relative Importance ($IRI = (\%N + \%W) * \%F$; Hart et al., 2002), and v) the Vacuity Index (%V; percentage of empty stomachs). We used a Costello diagram (Costello, 1990) modified by Amundsen et al. (1996) to evaluate the feeding behaviour of swordfish. The frequency of occurrence (%F) was plotted against the prey-specific importance of each prey taxon (%P_{*i*}), where the contribution by weight of prey *i* to the stomach content (W_i) was divided by the total stomach content weight (W_H) in those individuals that had consumed prey *i*. Overall, the distribution of prey types in the Amundsen diagram provides insights into the feeding strategy and niche width of the predator population. We assessed prey diversity in the diet composition with the Shannon diversity index (*H'*) calculated from prey abundance composition within the stomachs.

Differences in diet composition between the stomach contents of the three groups (2012, and large and small 2020 individuals) were tested using permutational multivariate analysis of variance (PERMANOVA) based on the Bray-Curtis distance matrix. PERMANOVA tests use an observed value of a

statistical test (pseudo-F ratio) compared to a recalculated statistic test generated from a random reordering (Permutation) of the data to obtain the p-values (M. J. Anderson, 2001). Data was square-rooted to reduce the impact of outliers prior to statistical testing. When the evidence of differences was strong (i.e., p value < 0.05), pairwise tests were performed. We used the R package *vegan* v2.6-2 to perform PERMANOVA tests (Oksanen et al., 2022).

Differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between the three groups were tested using 2-way PERMANOVA tests on the Euclidian distance matrix. To compare the degree of isotopic niche width and overlap between the three groups, corrected standard ellipses area (SEA_c , area containing 40% of the data) and Bayesian standard ellipses area (SEA_b) were calculated using the *SIBER* R package v2.1.6 (Jackson et al., 2011).

To estimate the proportional prey contribution to swordfish diet based on stable isotope values (i.e., $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$), Bayesian Stable Isotope Mixing Models (BSIMM) were computed using the *MixSIAR* R package v3.1.12 (Stock et al., 2018). The models were run with 3 Markov chain Monte Carlo (MCMC) analyses of 300,000 draws, and a burn-in of 200,000 draws. The convergence of the models was checked using both Gelman-Rubin and Geweke diagnostics (Stock et al., 2018; Stock & Semmens, 2016). BSIMM input data included $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of individual swordfish and potential prey species. Prey groups were selected according to stomach content analysis (i.e., prey species with >10%W) and previous studies in the western Mediterranean, including gelatinous species as important prey for swordfish (Cardona et al., 2012). Stable isotopic prey values were obtained from the literature (see Table A.2 from the Appendix) and grouped using a meta-analysis approach (*metafor* R package v3.4-0; Viechtbauer, 2010).

The diet-tissue discrimination factors (DTDF; $3.08 \pm 0.29\text{‰}$ for $\delta^{15}\text{N}$ and $1 \pm 0.14\text{‰}$ for $\delta^{13}\text{C}$) were estimated following Caut et al. (2009). The appropriate

parameterization of the BSIMM was validated through the simulation of mixing polygons, where all consumer data corrected for TDFs should fall within the bounds of the mixing space (Phillips et al., 2014; Smith et al., 2013). In addition, we used diet proportions estimated from the stomach contents from this study to construct informative prior distributions, which allowed us to incorporate both sources of data into a single framework. Models for each group (2012, large 2020, and small 2020) were run twice, first with uninformative Dirichlet priors (predator consumes all n prey in equal proportions, $1/n$, $\alpha = 1,1,1,1,1$), and second with informative priors, where the prey sources' relevance in the model was scaled by their weight in the stomach samples, which relates to its importance as an energy source (%W for each prey group scaled so that $\sum \alpha = 5$, the number of sources).

RESULTS

Stomach content analysis

A total of 1,442 individual prey, belonging to 64 species, 39 families, and 17 orders were identified in swordfish's stomachs (Table 1), with all stomachs containing at least one prey (0%V). Overall, teleosts were the most frequent (94%F) and diverse group of prey, with 45 species from the epipelagic (e.g., European anchovy, *Engraulis encrasicolus*), mesopelagic [e.g., elongate lanternfish (*Notoscopelus elongatus*)], bathypelagic [e.g., silvery lightfish (*Maurolicus muelleri*)], and demersal (e.g., European hake) habitats. Swordfish also fed frequently on cephalopods (80%F) from 16 different species, including mainly squid from the family Ommastrephidae [e.g., European flying squid (*Todarodes sagittatus*)], but also octopuses and bobtails [e.g., greater argonaut (*Argonauta argo*), and odd bobtail (*Heteroteuthis dispar*)]. Crustaceans were less frequent in swordfish's stomach contents (24%F). Only five shrimp species were found. Gelatinous organisms were the less frequent group, represented by

cnidarians from the order Siphonophorae (6%F), which were only found in swordfish from 2012.

Table 1. Importance of prey species identified in the stomach contents of juvenile swordfish (*Xiphias gladius*) captured in 2012 and 2020 in the north-western Mediterranean Sea. Prey importance is given as: %N (percentage of individual prey species identified), %F (percentage of stomachs with each prey category), %W (percentage of reconstructed prey weight), %IRI (Index of Relative Importance). Individuals from 2020 were split into two groups: small 2020 individuals (LJFL < 75 cm) and large 2020 individuals (LJFL > 75 cm) in order to compare only similar body sizes between 2012 and 2020. LJFL: Lower Jaw Fork Length.

	2012				2020							
	n = 41 ($\bar{x}$ = 92 cm)				LJFL > 75 cm ($\bar{x}$ = 90 cm), n = 16				LJFL < 75 cm ($\bar{x}$ = 66 cm), n = 42			
	N%	F%	W%	IRI%	N%	F%	W%	IRI%	N%	F%	W%	IRI%
ACTINOPTERYGII	94.47	100	82.86	95.83	78.14	87.50	53.91	79.15	41.58	85.71	49.01	38.04
Anguilliformes												
Congridae												
<i>Ariosoma balearicum</i>					0.40	6.25	-	-	0.14	2.38	-	-
<i>Conger conger</i>	0.03	2.38	0.27	0.01								
<i>Gnathophis mystax</i>					0.40	6.25	0.39	0.11	0.27	4.76	0.10	0.04
Atheriniformes												
Atherinidae												
<i>Atherina</i> sp.									0.14	2.38	0.02	0.01
Aulopiformes												
Aulopidae												
<i>Aulopus filamentosus</i>									0.14	2.38	1.06	0.07
Paralepididae												
<i>Arctozenus rissoi</i>	5.53	50.00	12.48	16.89	9.72	37.50	3.66	10.99	3.40	16.67	3.75	2.89
<i>Lestidiops jayakari</i>	7.32	66.67	18.78	32.64	45.75	37.50	27.68	60.38	15.90	40.48	11.37	26.77
<i>Paralepis speciosa</i>									0.41	7.14	-	-
Paralepidae unid.					0.40	6.25	-	-				
Evermannellidae												
<i>Evermannella balbo</i>	0.03	2.38	0.08	<0.01	0.40	6.25	0.31	0.10				
Carangiformes												
Carangidae												
<i>Trachurus mediterraneus</i>									0.14	2.38	0.90	0.06
Carangidae unid.									0.41	4.76	-	-
Clupeiformes												
Clupeidae												
<i>Alosa fallax</i>									0.14	2.38	1.88	0.12
<i>Sardina pilchardus</i>	0.10	7.14	0.59	0.09	0.81	6.25	2.08	0.40				
<i>Sardinella aurita</i>	0.54	21.43	9.69	4.11	1.62	12.50	8.45	2.76	0.68	7.14	9.40	1.75
Engraulidae												
<i>Engraulis encrasicolus</i>	0.47	26.19	1.48	0.96	2.83	12.50	2.99	1.59	0.82	4.76	1.46	0.26
Clupeiformes unid.	0.24	16.67	0.46	0.22								

Gadiformes												
Lotidae												
<i>Molva</i> sp.	0.07	2.38	<0.01	<0.01								
Gadidae												
<i>Micromesistius poutassou</i>	15.63	47.62	26.61	37.72					0.14	2.38	1.65	0.10
<i>Trisopterus capelanus</i>									0.27	4.76	0.40	0.08
<i>Gadiculus argenteus</i>	0.07	4.76	0.06	0.01					0.27	2.38	0.17	0.03
Merlucciidae												
<i>Merluccius merluccius</i>	0.24	9.52	3.09	0.59	0.40	6.25	0.50	0.12				
Macrouridae												
<i>Coelorinchus caelorinchus</i>	0.10	4.76	0.07	0.02								
Gadiforme unid.	0.58	4.76	-	-								
Mugiliformes												
Mugilidae												
<i>Mugil cephalus</i>									0.14	2.38	-	-
Myctophiformes												
Myctophidae												
<i>Benthoosema glaciale</i>	0.07	4.76	0.04	0.01	0.40	6.25	0.25	0.09	0.54	7.14	0.07	0.11
<i>Ceratoscopelus maderiensis</i>	0.88	33.33	0.61	0.93					5.43	19.05	0.73	2.85
<i>Diaphus holti</i>					2.43	6.25	0.45	0.39				
<i>Electrona risso</i>	0.03	2.38	<0.01	<0.01					0.27	4.76	0.03	0.03
<i>Hygophum benoitii</i>					0.40	6.25	0.13	0.07	0.14	2.38	<0.01	0.01
<i>Lampanyctus pusillus</i>	0.03	2.38	<0.01	<0.01	0.40	6.25	0.02	0.06	0.14	2.38	0.01	0.01
<i>Lobianchia</i> sp.					0.81	6.25	0.16	0.13	0.68	7.14	0.18	0.15
<i>Myctophum punctatum</i>	0.17	11.90	0.14	0.07	1.62	12.50	0.49	0.58	0.54	2.38	0.30	0.05
<i>Notoscopelus elongatus</i>	1.59	28.57	0.81	1.29	0.40	6.25	0.19	0.08	0.41	4.76	0.26	0.08
<i>Symbolophorus veranyi</i>	0.07	4.76	0.15	0.02	1.21	12.50	0.79	0.55	0.14	2.38	<0.01	0.01
Myctophidae unid.	0.07	4.76	-	-					0.41	4.76	-	-
Notacanthiformes												
Notacanthidae												
<i>Notacanthus bonaparte</i>	0.03	2.38	0.01	<0.01								
Ophiidiforme												
Ophiidiidae												
<i>Ophidion barbatum</i>									0.14	2.38	1.86	0.12
Ophidiformes unid.									0.14	2.38	-	-
Gobiiformes												
Gobiidae												
<i>Lesueurigobius</i> sp.	0.03	2.38	0.02	<0.01								
Gobiidae unid.					0.40	6.25	-	-				
Eupercaria incertae sedis												
Sparidae												
<i>Boops boops</i>									0.27	4.76	1.91	0.25
<i>Pagellus bogaraveo</i>									0.14	2.38	0.31	0.03
<i>Sparus aurata</i>	0.03	2.38	3.65	0.16								

<i>Spicara</i> sp.									0.41	4.76	3.90	0.50
Sparidae unid.					1.21	6.25	-	-	0.41	7.14	-	-
Scombriformes												
Centrolophidae unid.	0.07	4.76	-	-	0.40	6.25	-	-				
Trichiuridae												
<i>Lepidopus caudatus</i>	0.03	2.38	0.42	0.02					0.27	2.38	0.20	0.03
Scombridae												
<i>Scomber colias</i>					0.40	6.25	4.65	0.69	0.41	7.14	6.81	1.25
Perciformes												
Triglidae unid.	0.03	2.38	-	-					0.14	2.38	-	-
Stomiiformes												
Gonostomidae												
<i>Gonostoma</i> sp.	0.03	2.38	0.07	<0.01					0.41	7.14	0.17	0.10
Phosichthyidae												
<i>Vinciguerria</i> sp.	0.10	2.38	0.03	<0.01								
Sternoptychidae												
<i>Maurolicus muelleri</i>	0.03	2.38	<0.01	<0.01					0.95	11.90	0.10	0.30
Stomidae												
<i>Chauliodus sloani</i>	0.07	4.76	0.03	0.01								
<i>Stomias boa</i>	0.03	2.38	0.68	0.03	0.40	6.25	0.74	0.16				
Stomidae unid.					0.40	6.25	-	-				
Unidentified fish	60.09	64.29	-	-	4.45	25.00	-	-	5.84	47.62	-	-
CEPHALOPODA												
	4.34	76.19	16.73	4.06	19.84	62.50	46.09	20.85	57.20	85.71	50.99	61.96
Myopsida												
Loliginidae unid.									0.14	2.38	-	-
Octopoda												
Argonautidae												
<i>Argonauta argo</i>	0.20	9.52	0.17	0.07					4.08	35.71	2.70	5.87
Tremoctopodidae												
<i>Tremoctopus</i> sp.									0.14	2.38	0.34	0.03
Oegopsida												
Ancistrocheiridae												
<i>Ancistrocheirus</i>												
<i>lesueurii</i>					2.83	6.25	2.12	0.68	7.88	26.19	1.52	5.97
Cranchiidae												
<i>Galiteuthis armata</i>					1.21	6.25	4.09	0.73				
<i>Taonius pavo</i>					0.40	6.25	0.12	0.07	0.14	2.38	0.16	0.02
<i>Teuthowenia megalops</i>									0.14	2.38	0.08	0.01
<i>Cranchia scabra</i>									1.49	4.76	2.31	0.44
Enoploteuthidae												
<i>Abralia veranyi</i>									4.21	7.14	5.24	1.64
Enoploteuthidae unid.									2.17	4.76	-	-
Histioteuthidae												
<i>Histioteuthis reversa</i>					0.40	6.25	0.49	0.12	1.90	19.05	1.61	1.64
Ommastrephidae												
<i>Illex coindetii</i>	0.17	7.14	3.02	0.43	1.21	12.50	2.73	1.08	0.82	11.90	9.54	2.99

<i>Todarodes sagittatus</i>	0.51	16.67	8.99	2.97	7.69	18.75	34.78	17.14	17.80	45.24	21.26	42.86
<i>Todaropsis eblanae</i>	0.14	4.76	3.28	0.30					0.14	2.38	5.22	0.31
Ommastrephidae unid.					0.40	6.25	-	-				
Onychoteuthidae												
<i>Ancistroteuthis lichtensteinii</i>	0.03	2.38	0.33	0.02	1.62	6.25	0.74	0.32	0.82	2.38	0.52	0.08
Pyroteuthidae												
<i>Pyroteuthis margaritifera</i>					0.81	6.25	0.20	0.14				
Sepiolida												
Sepiolidae												
<i>Heteroteuthis dispar</i>	0.31	11.90	0.94	0.28	1.21	6.25	0.82	0.28	0.54	4.76	0.48	0.12
<i>Rondeletiola minor</i>	0.03	2.38	-	-								
Sepiolidae unid.	0.14	7.14	-	-	0.40	6.25	-	-	0.68	7.14	-	-
Unidentified cephalopod	2.81	42.86	-	-	1.62	12.50	-	-	14.13	40.48	-	-
CRUSTACEA												
	1.19	38.10	-	-	2.02	12.50	-	-	1.22	14.29	-	-
Euphausiacea												
Euphausiidae												
<i>Meganctiphanes norvegica</i>									0.14	2.38	-	-
Decapoda												
Pandalidae												
<i>Plesionika sp.</i>	0.03	2.38	-	-								
Pasiphaeidae												
<i>Pasiphaea sivado</i>	0.03	2.38	-	-	0.40	6.25	-	-	0.95	9.52	-	-
<i>Pasiphaea multidentata</i>	0.14	2.38	-	-								
Penaeidae												
<i>Parapenaeus longirostris</i>					0.40	6.25	-	-				
Sergestidae												
<i>Robustosergia robusta</i>					1.21	6.25	-	-				
Sergestidae unid.									0.14	2.38	-	-
Unidentified crustacea	0.98	30.95	-	-								
CNIDARIA												
Siphonophorae	0.41	14.29	<0.01	0.11								

For 2012 individuals, the most important prey in %N, %W, and %IRI were the fish of the order Gadiformes, with blue whiting (*Micromesistius poutassou*) representing 26.6% of the total prey weight (Table 1). In contrast, the diet of large 2020 individuals mainly included cephalopods (*T. sagittatus*, 34.8%W) and mesopelagic fish of the family Paralepididae, with barracudina (*Lestidiops jayakari*) and spotted barracudina (*Arctozenus risso*) representing together the

31% of the total prey weight (Table 1). Remains of Gadiformes consumption were only found in one stomach (*M. merluccius*, 0.5%W). For small 2020 swordfish, the most important prey in %N, %F, %W, and %IRI were the cephalopods from the family Ommastrephidae, with the European flying squid (21%W) as the main prey species (Table 1), followed by mesopelagic (barracudina and spotted barracudina, 15%) and pelagic fish (round sardinella, 9.4%).

The most frequent prey had low prey-specific abundance (e.g., barracudina and European flying squid), while some less frequent species, such as the Mediterranean horse mackerel (*Trachurus mediterraneus*) or the lesser flying squid (*Todaropsis eblanae*), had high prey-specific abundances (Figure 2). Species with high frequency and high prey-specific abundance were not found.

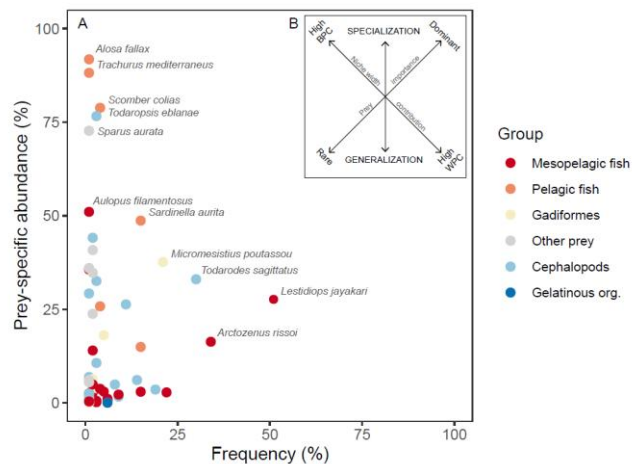


Figure 2. Prey-specific abundance plotted against the frequency of occurrence of prey species for juvenile swordfish from the north-western Mediterranean Sea. The explanatory axes used are those of Costello (1990) as modified from Amundsen *et al.* (1996). The two diagonal axes indicate the importance of prey (dominant vs. rare) and the contribution to the niche width (between-phenotype contribution (BPC) vs. within-phenotype contribution (WPC)); the vertical axis is used to define the feeding strategy (specialist vs. generalist).

PERMANOVA tests revealed differences in stomach contents between the three groups ($p < 0.001$, see Table A.3 from the Appendix). Pairwise analysis showed strong evidence for diet composition differences among individuals from 2012 and 2020 ($p\text{-value} < 0.001$), but not between small and large individuals from 2020 ($p\text{-value} = 0.09$). Regarding the diversity of prey species, small 2020 swordfish had the highest dietary diversity (Shannon-Index = 2.43). Large 2020 and 2012 individuals had less diverse diets, with Shannon-Index values of 1.83 and 1.34, respectively.

Stable isotopes analysis

Differences were found for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopes values between three swordfish groups (pseudo- $F = 51.18$, $p < 0.001$; Table 2). Regarding the isotopic niche, large 2020 individuals presented the smallest standard ellipses area (mean $\text{SEA}_b = 0.69$), followed by small 2020 individuals (mean $\text{SEA}_b = 0.83$) and individuals from 2012 ($\text{SEA}_b = 0.94$) (Figure 3, see Table A.4 from the Appendix). There was no overlap between the isotopic niche of small and large individuals from 2020, and large individuals from 2020 only overlapped with individuals from 2012 by less than 10% (Figure 3, Table A.4).

Table 2. Mean values and standard deviation (SD) of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopes for juvenile swordfish from 2012 (large individuals) and 2020 (small and large individuals). LJFL: lower jaw fork length (cm); n: number of samples.

Group	LJFL range (cm)	n	$\delta^{15}\text{N}$ (‰)		$\delta^{13}\text{C}$ (‰)	
			mean	SD	mean	SD
Large 2012	77 - 104	25	10.14	0.78	-18.55	0.46
Large 2020	76.6 - 100	17	11.3	0.61	-18.1	0.34
Small 2020	52 - 74	41	9.23	0.57	-17.77	0.46

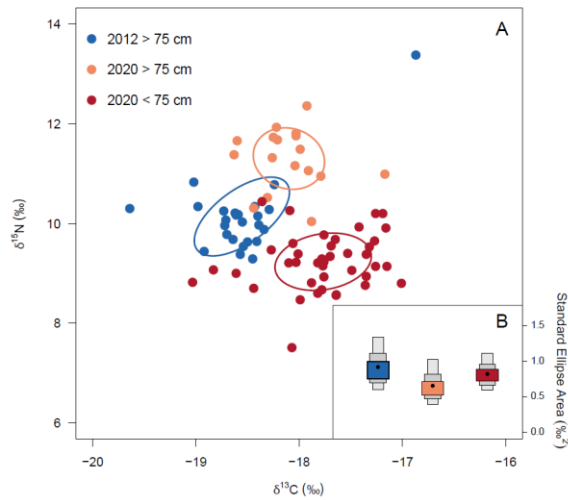


Figure 3. (A) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for juvenile swordfish by year and size with the corrected Standard Ellipses Area (SEAc). (B) Bayesian standard ellipses area (SEAb) for each group. Density plots represent the 95%, 75%, and 50% credibility intervals of SEAb.

All except one swordfish isotopic values were inside the 95% mixing region delimited by the mixing polygon of the five prey groups' isotopic values adjusted to DTDFs, thus pointing to a suitable isotopic scenario for the MixSIAR models fitted with those prey groups (Figure 4).

When comparing MixSIAR dietary reconstructions for large swordfish from 2012 and 2020, mesopelagic fish were found to be the most assimilated prey for both groups (Figure 5, Table A.5). Cephalopods and pelagic fish assimilation were found to be higher in 2020 than in 2012, using both informative and uninformative priors, which was in accordance with the stomach content results. When using uninformative priors, Gadiformes assimilation was higher in 2020 than in 2012, however, the inverse pattern was shown by the model with informative priors and the stomach contents. Gelatinous organisms' assimilation was also found to be higher in 2012 individuals using both informative and uninformative priors, which was aligned with the findings of the stomach contents.

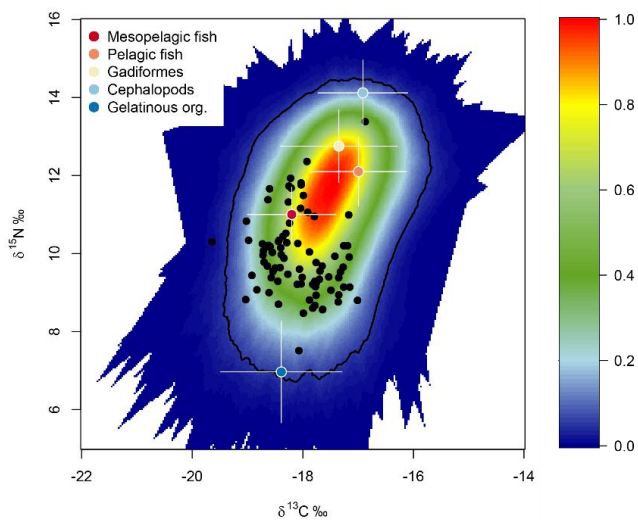


Figure 4. Mixing polygon including the juvenile swordfish isotopic values (black dots) and the potential prey sources (mean $\pm$ SD isotopic value: coloured dots and error bars). The colour background displays the probability that a consumer's isotopic signature is explained by the proposed mixing model. The probability contour is coloured at a 95% level.

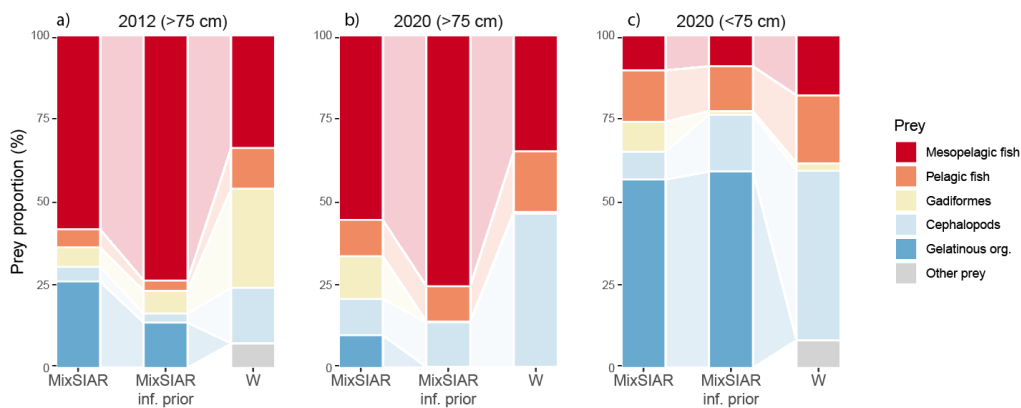


Figure 5. Relative proportions of prey groups in the diet of (a) 2012 juvenile swordfish, (b) large 2020 juvenile swordfish (LJFL > 75 cm), and (c) small 2020 juvenile swordfish (LJFL < 75 cm). Diet proportions were estimated from the MixSIAR models with uninformative (MixSIAR) and informative priors (MixSIAR inf. prior), and from stomach contents (%W; percentage of reconstructed weight).

Regarding the individuals from 2020 alone, both informed and uninformed models' results showed that large 2020 individuals had higher consumption of mesopelagic fish and similar consumption of pelagic fish and cephalopods than small ones (Figure 5, Table A.5), as seen in the stomach contents. The proportion of Gadiformes in the uninformed models was higher in large individuals, but higher for small individuals when informative priors were used. The assimilation of gelatinous organisms appeared to be higher for small 2020 individuals, representing nearly 50% of the diet.

DISCUSSION

Here, we combine two complementary sources of trophic information to estimate the diet of swordfish in the north-western Mediterranean Sea. The results indicate that swordfish predominantly feed on teleosts and cephalopods, but point to gelatinous plankton as an overlooked prey, particularly relevant in the diet of small-sized swordfish. Whether swordfish diets rely on cephalopods or fish is commonly discussed in diet studies based on stomach contents (e.g., Salman, 2004). However, prior research in the western Mediterranean Sea based on stable isotopes has pointed to gelatinous organisms as important swordfish prey (Cardona et al., 2012). Thus, the difference in estimates previously obtained highlights biases when trying to reconstruct the true diet consumed using only stomach contents, which is biased towards species that have hard structures (e.g., otoliths from fish); or BSIMM techniques, which examine assimilation and do not always reflect the ingested diet proportions (e.g., Chiaradia et al., 2014). Indeed, the proportion of cephalopods was higher in stomach contents than in the diet obtained through stable isotopes for the three groups considered in the present study, supporting that cephalopod beaks accumulate in the stomach and may be overrepresented in stomach content studies (Amundsen & Sánchez-Hernández, 2019). To overcome those biases, both methods are combined here by using the prey

proportions found in stomach contents to inform the mixing models, which is particularly helpful when prey sources have similar isotopic values (A. I. Guerrero & Rogers, 2020). This helped to distinguish between Gadiformes and mesopelagic fish, obtaining more accurate diet estimates. These estimates uncovered a dietary transition in swordfish from 2012 to 2020, which appears to align with documented alterations in the marine ecosystem's structure and subsequent variations in prey availability.

Feeding strategy

Our study provides insights into the feeding strategy and niche width of swordfish in the north-western Mediterranean Sea, confirming that this large pelagic fish fed on a wide range of prey. Overall, most prey had low prey-specific abundance and moderate to low occurrence in the diet, which is consistent with a generalist feeding strategy consuming a great variety of prey types. Yet, some species had low frequency but high prey-specific abundance, which could indicate specialized feeding strategies in the population targeting schools of medium pelagic fish (e.g., Mediterranean horse mackerel), or that feeding in coastal habitats is limited to some individuals [e.g., Gilthead seabream (*Sparus aurata*)]. Furthermore, we found that the most frequent prey showed intermediate prey-specific abundances, suggesting that juvenile swordfish have a broad niche width and can exploit a range of prey species with varying levels of abundance.

The diversity of prey consumed both in specific and habitat terms also suggests that swordfish have a flexible foraging strategy. This wide range of prey from different habitats, including demersal, epipelagic, mesopelagic, and bathypelagic, evidences the swordfish's vertical migratory behavior and supports the benthopelagic coupling role of this species. Orders Gadiformes, Aulopiformes, Clupeiformes, and Myctophiformes were the most frequent fish prey for swordfish, while squids from the order Oegopsida, particularly from the

family Ommastrephidae, were the most frequent cephalopod prey, which agrees with previous studies on this species (Carmona-Antoñanzas et al., 2016; J. M. Logan et al., 2021; Young et al., 2010). Although low in %W, fish from the family Myctophidae were consumed frequently in both years and size groups. Together with the high consumption of mesopelagic cephalopods, this suggests frequent foraging of swordfish in mesopelagic waters, supporting their potential role as mesopelagic samplers. In fact, the swordfish is well-known as an efficient “cephalopod collector” (Romeo et al., 2011) due to the high diversity of cephalopod prey found in their diet, including some species of difficult collection due to oceanic lifestyles (e.g., *Cranchia scabra*, *Taonius pavo*; Fernández-Álvarez et al., 2022).

On the other hand, based on %N from the stomach contents, and therefore omitting the gelatinous organisms' consumption, differences in prey composition between the small and large 2020 individuals were not clear, which supports swordfish as good ecosystem sentinels since they are supposed to eat what is abundant regarding their size. Yet, there was no overlap between the isotopic niche of small and large 2020 individuals, suggesting that although prey ingestion may be similar, assimilation may change with swordfish growth.

Fish and cephalopods dominated the stomach contents of small 2020 swordfish, but these had lower $\delta^{15}\text{N}$ values when compared with other fish and cephalopod consumers (Cardona et al., 2012), and gelatinous organisms appeared to be a major prey source for them, representing nearly half of the assimilated diet. Although they were only found in the stomachs of 2012 individuals, consumption of gelatinous organisms, primarily tunicates, has been reported in other regions (Preti et al., 2023), and other large pelagic fish species (Thiebot & McInnes, 2020). This high consumption may appear noteworthy, but the abundance of gelatinous zooplankton in the Mediterranean could be enough to provide sufficient sustenance for a large pelagic fish through casual consumption (Cardona et al., 2012). Other possible explanations for this

consumption include opportunism, practicing hunting techniques, aggregation of prey, and potential acquisition of bio-active components that could have benefits for homeostatic challenges (Thiebot and McInnes, 2020; and references therein). Further research using other methods such as video cameras or DNA metabarcoding techniques could provide insights into the identification of these organisms that are known to degrade fast (Fernández-Álvarez et al., 2018), and is needed to fully understand the reasons for this behavior.

Tracking changes in the marine community

The diet of generalist and opportunistic large predators, such as swordfish, closely tracks prey availability in their immediate environment (Palko et al., 1981). Therefore, the trophodynamics of swordfish can inform effectively on temporal changes in prey abundances. However, most of the previous swordfish diet studies were restricted temporally to a few years at most (e.g., Ceyhan and Akyol, 2017). Here, temporal variation in the diet of swordfish was observed. Gadiformes appeared as an important source of energy in 2012, while they seem to be absent in the diet of 2020 individuals. This dietary shift seems to reflect what is being observed in the community: over the last decade, highly fished gadiform species, such as blue whiting and hake, have experienced declining abundances and have remained at historically low levels in the most recent years in the northwestern Mediterranean (GFCM, 2022a; Mir-Arguimbau et al., 2022; Sion et al., 2019). Moreover, swordfish fed more on pelagic fish in 2020. Small pelagic fish such as European sardine (*Sardina pilchardus*) and anchovy are also suffering from high exploitation and their biomasses are showing declines in the north-western Mediterranean (GFCM, 2022b; Pennino et al., 2020). At the same time, the thermophilic round sardinella, which is the main pelagic species found in the stomach contents, is expanding its range due to ocean warming (Coll et al., 2019; Sabatés et al., 2006). This is aligned with the

increasing water temperatures observed in our study area (see Figure A.2), where its catch has increased in the last years (ICATMAR, 2023). On the other hand, changes in mesopelagic fish ingestion and assimilation between years were not observed. Despite that mesopelagic fish occupy a key position in the marine food web, biomass data in the Mediterranean Sea are scarce and they lack systematic monitoring campaigns (Clavel-Henry et al., 2020), therefore we could not evaluate if the swordfish diet is reflecting the mesopelagic community trends.

Our study area is one of the most exploited fishing grounds of the Mediterranean Sea (Coll et al., 2012; Colloca et al., 2017; Fernandes et al., 2017), and is seriously impacted by the effects of other climate and human-driven changes, such as water warming, coastal degradation, and pollution (Navarro et al., 2015; Salat et al., 2019). In this context of disturbance, cephalopods and gelatinous organisms, such as jellyfish and salps, are expected to benefit from the combination of changes in environmental conditions and reduced predators and competitors due to overfishing (Doubleday & Connell, 2018). Their rapid growth and strong life-history plasticity allow them to quickly adapt to changing environmental conditions and may trigger their success under the observed warming conditions (Brotz & Pauly, 2012; Hoving et al., 2013). Although jellyfish blooms have been recorded with increasing frequency and magnitude in many coastal areas, including the western Mediterranean Sea (Báez et al., 2022), gelatinous plankton densities were found to present strong long-term stability in this area (Feuilloley et al., 2022). Here, we found high proportions of gelatinous plankton in the diet of small 2020 individuals, suggesting their consumption may be related to swordfish size. The abundance or availability of these organisms may have fluctuated over time, but other factors such as changes in other prey availability may have influenced their consumption. Further research is needed to investigate the

long-term trends in the abundance and distribution of gelatinous plankton in the study area and their potential impacts on ecosystem dynamics.

On the other hand, Doubleday et al. (2016) suggest that the global depletion of fish stocks, together with the potential release of cephalopods from predation and competition pressure, could be driving the growth in cephalopod populations. Specifically, the north-western is one of the Mediterranean areas where the cephalopod community is best described, formed by a rather homogeneous mix of different species (Quetglas et al., 2019). Here, we found a small increase of cephalopods in large 2020 individuals, which seem to have switched to a more teuthophagus diet with regard to those from 2012. This increment may be tracking the putative increase in cephalopods' abundance in the ecosystem, even though the lack of long-term data on mesopelagic cephalopods, the main cephalopods consumed by swordfish, makes it difficult to test the hypothesis. Landings of commercial cephalopods in the study area have fluctuated over the last decade (ICATMAR, 2023), nevertheless, additional fishery-independent data, including non-commercial cephalopods, would be necessary to draw conclusions at the community level, particularly for pelagic species.

Further steps in ecosystem monitoring

Understanding the dietary preferences of swordfish is essential for developing effective management strategies and conservation efforts for this threatened species and the marine ecosystems they inhabit. We described the diet of swordfish in the northwestern Mediterranean Sea by combining two complementary sources of diet analysis, emphasizing the importance of combining different methods to obtain more accurate diet estimates, while partially addressing the limitations associated with each technique individually. We were able to estimate the consumption of gelatinous organisms and assess changes in the diet of these organisms as a plausible response to variations in

prey abundance. These findings should be corroborated through studies incorporating longer time series on diet and prey abundance. Overall, this is a common challenge when analyzing the diet of predatory species in marine ecosystems, where time series of diet information are mostly missing (e.g., Ouled-Cheikh et al., 2022).

In conclusion, our results highlight the role of swordfish as a good candidate to be an ecosystem sentinel in our study area. The lack of data on mesopelagic fish, mesopelagic cephalopods and gelatinous organisms presents a significant challenge for effective ecosystem-based management and conservation efforts, as these species play crucial roles in regulating ecosystem processes. These non-commercial species are frequently consumed by swordfish. Therefore, since swordfish are highly exploited all year long in the northwestern Mediterranean, continuous monitoring could be proposed, providing a long-term sampling of their prey, particularly relevant for the overlooked mesopelagic community. This would allow us to strengthen our understanding of how these organisms respond, in terms of their diet, to changes in the structure and functioning of the ecosystem. Consequently, we could establish the use of this species as valuable sentinels of the ecosystem in which they inhabit.

SUPPLEMENTARY MATERIALS

Supplementary Methods

Information on sea water potential temperature at the surface (SST, °C) and net primary production (NPP, mg·m⁻³·day⁻¹) was obtained for the study area (42°N to 39°N, 0°30'W to 3°30'E). This dataset was obtained from the Global Ocean Physics and Biogeochemistry Reanalyses (EU Copernicus Monitoring Environment Marine Service; <https://marine.copernicus.eu/>, accessed on August 2023). SST was downloaded as yearly mean composites at 0.0417° spatial resolution for the 1987–2021 time period (MEDSEA_MULTIYEAR_PHY_006_004, doi.org/10.25423/CMCC/MEDSEA_MULTIYEAR_PHY_006_004_E3R1). NPP was downloaded as yearly mean composites at 0.0417° spatial resolution for the 1999–2021 time period (MEDSEA_MULTIYEAR_BGC_006_008, doi.org/10.25423/cmcc/medsea_multiyear_bgc_006_008_medbfm3). Mean, maximum, and minimum SST and NPP in the study area are shown in Figures A.1 and A.2.

Supplementary Figures

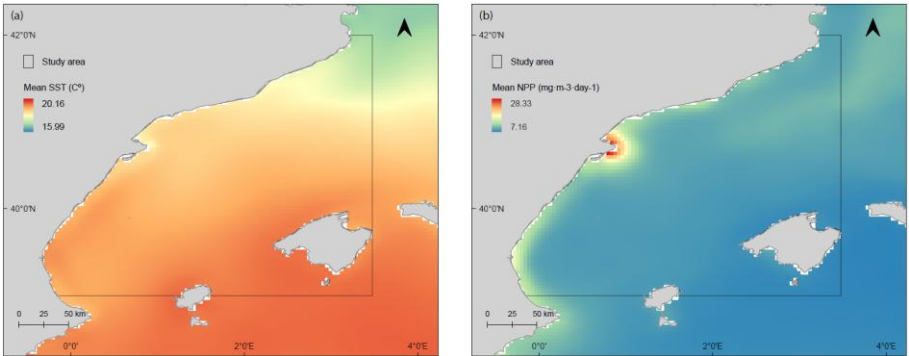


Figure A.1. Mean values of (a) sea water potential temperature (SST, from 1987 to 2020), and (b) net primary production (NPP, from 1987 to 2020) for the northwestern Mediterranean Sea.

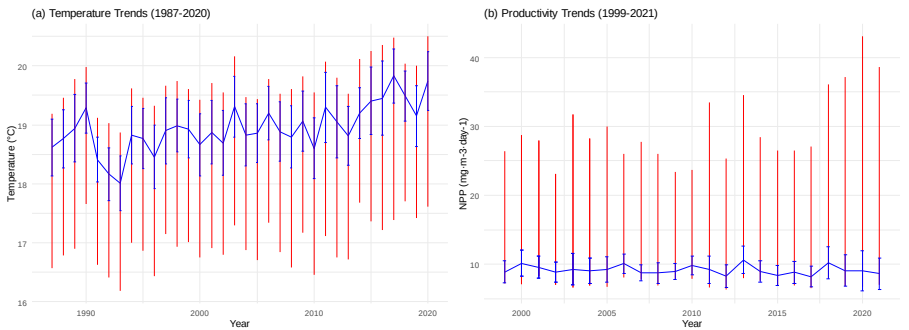


Figure A.2. Mean values $\pm$ standard deviation (in blue) and range (in red) values of (a) sea water potential temperature (SST), and (b) net primary production (NPP) from 1987 to 2020 in the northwestern Mediterranean Sea.

Supplementary Tables

Table A.1. Regression equations used to estimate fish and cephalopod weights: L, total length (mm); SL, standard length (mm); W, total weight (g); OL, Otolith length (mm); OW, otolith width (mm); CL, crest length (mm); LHL, lower hood length (mm); LRL, lower rostral length (mm).

Species	Estimated length (mm)	Reference	Estimated weight (g)	Reference
FISH				
<i>Alosa fallax</i>	$L = 44.24 \times OL^{1.65}$	AFORO	$W = 0.0147 \times L^{2.826}$	Torres et al. (2012)
<i>Arctozenus rissoi</i>	$L = 29.07 \times OL^{1.58}$	AFORO	$W = 1E-06 \times L^{3.0621}$	Battaglia et al. (2015)
<i>Atherina</i> sp. (<i>Atherina hepsetus</i>)	$L = 42.64 \times OL^{0.77}$	Giménez et al. (2016)	$W = 0.0055 \times L^{3.08}$	FishBase
<i>Aulopus</i> sp. (<i>Aulopus filamentosus</i>)	$L = 24.93 \times OL^{1.29}$	AFORO	$W = 0.0065 \times L^{3.099}$	Yapici et al. (2015)
<i>Benthoosema glaciale</i>	$SL = 38.211 \times OL - 0.6887$	Battaglia et al. (2015)	$W = 7E-06 \times SL^{3.229}$	Battaglia et al. (2015)
<i>Boops boops</i>	$L = 20.5 \times OL^{1.24}$	AFORO	$W = 0.0064 \times L^{3.1709}$	Falsone et al. (2022)
<i>Ceratoscopelus maderiensis</i>	$SL = 15.858 \times OL + 12.417$	Battaglia et al. (2010)	$W = 7.4E-06 \times SL^{3.144}$	Battaglia et al. (2010)
<i>Coelorinchus caelorinchus</i>	$L = 4.41 \times OL^{1.19}$	AFORO	$W = 0.1275 \times L^{3.023}$	Torres et al. (2012)
<i>Conger conger</i>	$L = 9.18 \times OL^{1.94}$	AFORO	$W = 0.00054 \times L^{3.225}$	Moutopoulos and Stergiou (2002)
<i>Diaphus holti</i>	$SL = 15.203 \times OL - 0.522$	Battaglia et al. (2010)	$W = 1.3E-05 \times SL^{3.102}$	Battaglia et al. (2010)
<i>Electrona risso</i>	$SL = 18.02 \times OL^{0.9}$	AFORO	$W = 1.7E-05 \times SL^{3.156}$	Battaglia et al. (2010)
<i>Engraulis encrasicolus</i>	$L = 44.6 \times OL^{0.96}$	AFORO	$W = 0.0036 \times L^{3.2233}$	Falsone et al. (2022)
<i>Evermannella balbo</i>	$L = 11.66 \times OL^{2.07}$	AFORO	$W = 0.00417 \times L^{3.12}$	FishBase. Bayesian estimates for subfamily
<i>Gadiculus argenteus</i>	$L = 17.59 \times OL^{0.98}$	AFORO	$W = 0.0562 \times L^{2.1066}$	Morey et al. (2003)
<i>Gnathophis mystax</i>	$L = 29.86 \times OL^{1.15}$	AFORO	$W = 0.0015 \times L^{2.919}$	Yapici et al. (2015)
<i>Gonostoma</i> sp. (<i>Gonostoma denudatum</i>)	$SL = 28.65 \times OL + 0.868$	Battaglia et al. (2010)	$W = 7.8E-5 \times L^{2.923}$	Battaglia et al. (2010)
<i>Hygophum benoitii</i>	$SL = 29.128 \times OL - 4.55$	Battaglia et al. (2010)	$W = 5.8E-6 \times SL^{3.306}$	Battaglia et al. (2010)

<i>Lampanyctus pusillus</i>	$L = 41.61 \times OL^{1.19}$	AFORO	$W = 0.004 \times SL^{3.232}/1000$	Olivar et al. (2013)
<i>Lepidopus caudatus</i>	$L = 91.91 \times OL^{1.26}$	AFORO	$W = 0.0003 \times L^{3.1417}$	Falsone et al. (2022)
<i>Lestidiops jayakari</i>	$L = 52.09 \times OL^{1.18}$	AFORO	$W = 0.0006 \times L^{3.439}$	Czudaj et al. (2022)
<i>Lesueurigobius</i> sp. (<i>Lesueurigobius friesii</i>)	$L = 22.86 \times OL^{1.01}$	Giménez et al. (2016)	$W = 0.0015 \times L^{3.847}$	Morey et al. (2003)
<i>Lobianchia dofleini</i>	$L = 16.14 \times OL^{1.03}$	AFORO	$W = 0.005 \times SL^{3.338}/1000$	Olivar et al. (2013)
<i>Maurolicus muelleri</i>	$SL = 24.768 \times OL - 2.493$	Battaglia et al. (2010)	$W = 1.6E-05 \times SL^{2.946}$	Battaglia et al. (2010)
<i>Merluccius merluccius</i>	$L = 18.46 \times OL^{1.07}$	Giménez et al. (2016)	$W = 0.0051 \times L^{3.1107}$	Falsone et al. (2022)
<i>Micromesistius poutassou</i>	$L = 16.69 \times OL^{1.08}$	AFORO	$W = 0.0038 \times L^{3.187}$	Mir-Arguimbau et al. (2020)
<i>Myctophum punctatum</i>	$SL = 22.842 \times OL - 2.739$	Battaglia et al. (2010)	$W = 1.4E-05 \times SL^{2.971}$	Battaglia et al. (2010)
<i>Notoscopelus elongatus</i>	$L = 16.828 \times OL^{6.7887}$	Battaglia et al. (2015)	$W = (0.004 \times SL^{3.248})/1000$	Olivar et al. (2013)
<i>Ophidion barbatum</i>	$L = 19.62 \times OL^{1.2}$	Giménez et al. (2016)	$W = 0.0036 \times L^{3.11}$	Edelist (2014)
<i>Pagellus bogaraveo</i>	$L = 21.82 \times OL^{1.14}$	AFORO	$W = 0.0103 \times L^{3.0573}$	Falsone et al. (2022)
<i>Sardina pilchardus</i>	$L = 55.75 \times OL^{0.95}$	Giménez et al. (2016)	$W = 0.0032 \times L^{3.306}$	Falsone et al. (2022)
<i>Sardinella aurita</i>	$L = 44.76 \times OL^{1.18}$	Giménez et al. (2016)	$W = 0.0065 \times L^{3.0251}$	Falsone et al. (2022)
<i>Scomber colias</i>	$L = 37.23 \times OL^{1.24}$	Giménez et al. (2016)	$W = 0.006 \times L^{3.1017}$	Falsone et al. (2022)
<i>Sparus aurata</i>	$L = 8.31 \times OL^{1.7}$	AFORO	$W = 0.021 \times L^{2.87}$	Crec'hriou et al. (2013)
<i>Spicara</i> sp.	$L = 32.82 \times OL^{0.97}$	Giménez et al. (2016)	$W = 0.0054 \times L^{3.2618}$	Valle et al. (2003)
<i>Stomias boa</i>	$L = 205.03 \times OL^{1.1}$	AFORO	$W = 7E-07 \times L^{3.1702}$	Battaglia et al. (2015)
<i>Symbolophorus veranyi</i>	$L = 17.12 \times OL^{1.18}$	AFORO	$W = (0.005 \times SL^{3.181})/1000$	Olivar et al. (2013)
<i>Trachurus mediterraneus</i>	$L = 24.05 \times OL^{1.16}$	AFORO	$W = 0.008 \times L^{2.98}$	Crec'hriou et al. (2013)
<i>Trisopterus capelanus</i>	$L = 12.38 \times OL^{1.2}$	AFORO	$W = 0.009 \times L^{3.06}$	Crec'hriou et al. (2013)

<i>Vinciguerria</i> sp. (<i>Vinciguerria attenuata</i>)	SL = 32.21 × OL + 0.91	AFORO	W = 1.4E-06 × L ^{3.587}	Battaglia et al. (2010)
CEPHALOPODS				
<i>Abralia veranyi</i>			ln W = 0.979 + 2.304 ln LRL	Romeo et al. (2012)
<i>Ancistrocheirus lesueurii</i>			ln W = -0.194 + 3.56 ln LRL	Clarke (1986)
<i>Ancistroteuthis lichtensteini</i>			log W = 0.196 + 2.424 log LRL	Šifner et al. (2018)
<i>Argonauta argo</i>			log W = -0.1110 + 0.1503 CL	Smale et al. (1993)
<i>Cranchia scabra</i>			ln W = 1.623 + 1.70 ln LRL	Clarke (1986)
<i>Galiteuthis armata</i>			ln W = 0.7 + 2.233 ln LRL	Romeo et al. (2012)
<i>Heteroteuthis dispar</i>			ln W = 1.033 + 2.527 ln LRL	Romeo et al. (2012)
<i>Histioteuthis reversa</i>			W = 2.827 LRL ^{3.302}	Würtz et al. (1992)
<i>Illex coindetii</i>			ln W = 0.897 + 2.64 ln LRL	Pedà et al. (2022)
<i>Pyroteuthis margaritifera</i>			ln W = 0.41 + 2.78 ln LHL	Lu and Ickeringill (2002)
<i>Taonius pavo</i>			ln W = 0.786 + 2.19 ln LRL	Clarke (1986)
<i>Teuthowenia megalops</i>			ln W = 0.9797 + 1.2345 ln LHL	A. Sánchez-Márquez (unpublished data)
<i>Todarodes sagittatus</i>			ln W = 0.783 + 2.83 ln LRL	Clarke (1986)
<i>Todaropsis eblanae</i>			ln W = 0.59 + 3.17 ln LRL	Clarke (1986)
<i>Tremoctopus</i> sp. (<i>Tremoctopus violaceus</i>)			log W = 0.5318 + 0.1951 CL	Smale et al. (1993)

Table A.2. Isotopic values from prey obtained through the meta-analysis.

Prey	Species	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		References
		Mean	SD	Mean	SD	
Gadiformes	<i>Micromesistius poutassou</i>	-18.30	0.95	9.64	0.62	Barría et al. (2015), Gómez-Campos et al. (2011), Lloret-Lloret et al. (2020), Mir-Arguimbau et al. (2020b), Navarro et al. (2009), Papiol et al. (2013, 2017)
Bathypelagic fish	<i>Arctozenus risso</i>	-19.15	0.69	7.89	0.39	Papiol et al. (2013)
Pelagic fish	<i>Sardinella aurita</i>	-17.94	0.76	8.99	0.56	Albo-Puigserver et al. (2019), Barría et al. (2015), Lloret-Lloret et al. (2020)
Cephalopods	<i>Todarodes sagittatus</i>	-17.86	0.70	11.01	0.53	(Cardona et al., 2015), Gómez-Campos et al. (2011)
Gelatinous organisms	<i>Cotylorhiza tuberculata</i> , <i>Pelagia noctiluca</i> , <i>Salpa</i> sp.	-19.34	0.99	3.86	1.00	Barría et al. (2015), Cardona et al. (2007, 2012, 2015), Fanelli et al. (2011, 2013), Mir-Arguimbau et al. (2020b)

Table A.3. Summary of PERMANOVA tests examining differences between swordfish groups: 2012, large 2020 (LJFL > 75 cm) and small 2020 individuals (LJFL < 75 cm).

Based on %N	Df	SumOfSqs	R2	F	Pr(>F)
Swordfish group	2	3.36	0.09	4.86	1.00E-04
Residual	96	33.18	0.91		
Total	98	36.54	1.00		

Pairwise tests	2012	Large 2020	Small 2020
2012	-		
Large 2020	1.00E-04	-	
Small 2020	1.00E-04	0.086	-

Table A.4. Mean Bayesian Standard Ellipses Area (SEA_B) and SEA_B overlap for 2012, large 2020 (LJFL > 75 cm) and small 2020 individuals (LJFL < 75 cm). The percentage of overlap of the isotopic area of groups is shown as the first column group versus the ones of the first row. 25% and 75% Bayesian credible intervals (CI) are given in parentheses.

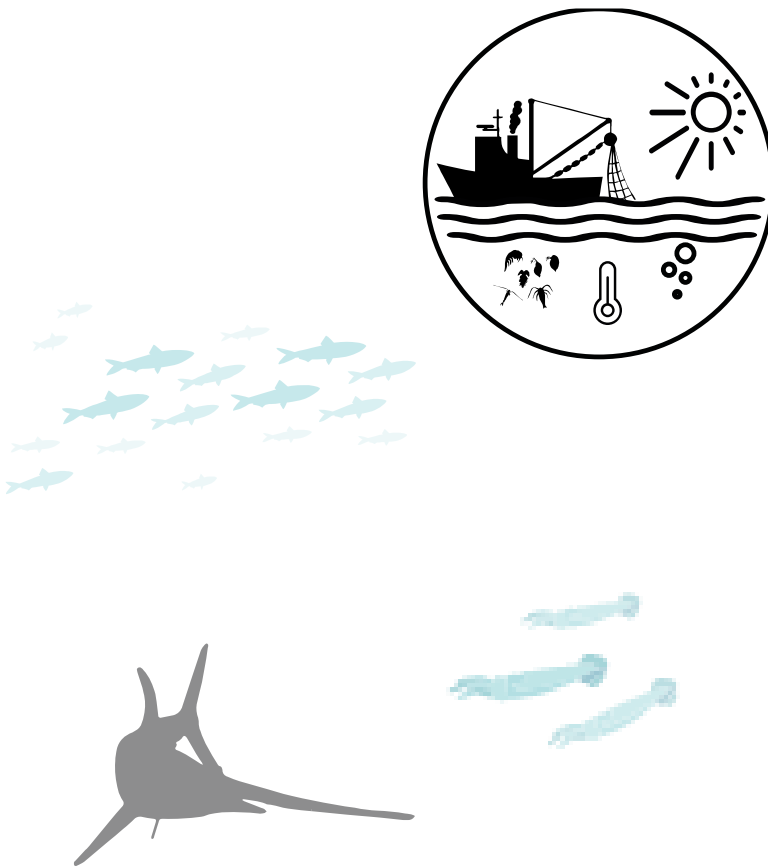
	SEA _B	SEA _B overlap		
	mean (CI)	2012	2020L	2020S
2012	0.94 (0.81, 1.06)	-	7.49 (0, 32)	0.14 (0, 0)
Large 2020	0.69 (0.57, 0.79)	9.89 (0, 45)	-	0 (0, 0)
Small 2020	0.83 (0.74, 0.91)	0.16 (0, 0)	0 (0, 0)	-

Table A.5. MixSIAR results summary and priors from stomach content analysis (SCA) used for all swordfish groups: 2012 (n = 41), large 2020 (LJFL > 75 cm, n = 16) and small 2020 individuals (LJFL < 75 cm, n = 42).

Prey	Swordfish groups					
	Large 2012		Large 2020		Small 2020	
	Mean	95% CI	Mean	95% CI	Mean	95% CI
w/ Uninformative priors						
Mesopelagic fish	0.583	(0.427, 0.738)	0.555	(0.368, 0.749)	0.106	(0.007, 0.306)
Pelagic fish	0.054	(0.003, 0.143)	0.109	(0.007, 0.267)	0.154	(0.013, 0.321)
Gadiformes	0.059	(0.004, 0.158)	0.129	(0.009, 0.302)	0.09	(0.005, 0.233)
Cephalopods	0.044	(0.003, 0.119)	0.109	(0.009, 0.247)	0.084	(0.007, 0.211)
Gelatinous org.	0.26	(0.161, 0.353)	0.098	(0.015, 0.198)	0.566	(0.488, 0.633)
w/ Informative priors						
Mesopelagic fish	0.62	(0.454, 0.804)	0.755	(0.609, 0.88)	0.093	(0.007, 0.254)
Pelagic fish	0.034	(0.001, 0.109)	0.106	(0.006, 0.267)	0.135	(0.015, 0.295)
Gadiformes	0.077	(0.012, 0.176)	0.002	(0, 0.008)	0.011	(0, 0.063)
Cephalopods	0.034	(0.002, 0.097)	0.134	(0.044, 0.238)	0.17	(0.058, 0.281)
Gelatinous org.	0.234	(0.113, 0.338)	0.003	(0, 0.005)	0.591	(0.519, 0.654)
SCA	%W		%W		%W	
Mesopelagic fish	33.917		34.866		18.079	
Pelagic fish	12.222		18.165		13.13	
Gadiformes	29.822		0.497		2.226	
Cephalopods	16.725		46.085		50.959	
Gelatinous org.	0.003		0		0	

Chapter 2.

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



Reference:

Fernández-Corredor, E., Fuster-Alonso, A., Ramírez, F., Giménez, J., García-Barcelona, S., Macías, D., Coll, M., & Navarro, J. (2025). Environmental and human factors shape the trophic ecology of a widespread marine predator. *Journal of Animal Ecology*, 94(9), 1784-1799. <https://doi.org/10.1111/1365-2656.70087>

Abstract

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 analyze the relationship between environmental factors and trophic interactions and that additionally consider other human stressors such as fisheries. 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. 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 positively related to increasing SST and MLD. In contrast, squid consumption was negatively 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. 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.

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, behavior, 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 the potential relationship with other human stressors such as fisheries (Basso et al., 2020; Duffy et al., 2017; Kuhnert et al.,

2012; Nickels et al., 2023; Preti et al., 2023). Since future environmental changes can now be 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, 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. 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 modeled 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 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).

METHODS

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 night-time 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. This feeding behavior 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).

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 northeastern 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.

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 ($\delta^{13}\text{C}$) values (Bodin et al., 2009). Analyses of $\delta^{13}\text{C}$ and nitrogen ($\delta^{15}\text{N}$) stable isotopes were performed at the Laboratory of Stable Isotopes (EBD-CSIC, Spain) as described in Fernández-Corredor et al. (2023).

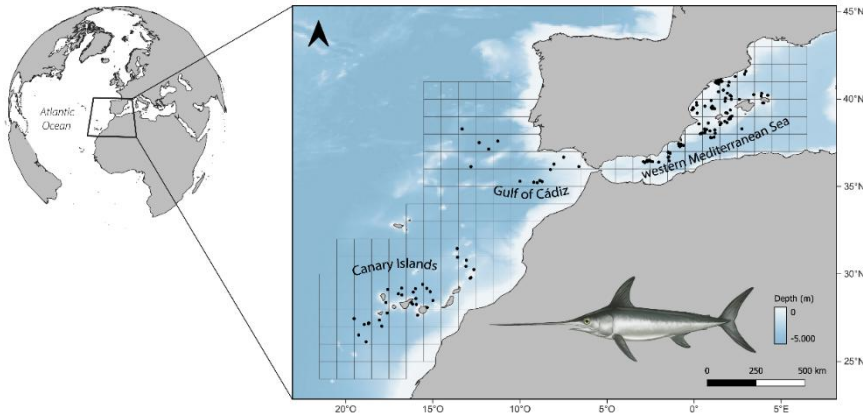


Figure 1. Study area including the western Mediterranean Sea and the northeastern Atlantic Ocean. Black dots represent swordfish sampling locations. Grey lines delineate a spatial grid of $1^\circ \times 1^\circ$. Swordfish illustration by Alex Mascarell.

We used Bayesian Stable Isotope Mixing Models (BSIMMs) to estimate the swordfish diet based on stable isotope values (i.e., $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$). 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 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ 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; 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) ([Supplementary 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, Supplementary 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 $\delta^{15}\text{N}$ and 1.06 ± 0.12 ‰ for $\delta^{13}\text{C}$) 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).

Diet modeling 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:

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

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

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 (Kroodsmas 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 $1^{\circ} \times 1^{\circ}$ 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).

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)	mg·m ⁻³
MLD	Mixed layer depth (mean)	m
SDO	Dissolved oxygen concentration (mean at sea surface)	μmol·m ⁻³
SST	Sea surface temperature (mean)	°C
Fishing effort	Cumulative fishing effort (sum)	h·km ⁻²

Explanatory variables were checked for potential Spearman correlation, and dissolved oxygen at surface and depth were excluded ($\text{corr} > 0.8$, 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 data for training. The specific metrics calculated for evaluating the predictive capacity of the 5 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).

RESULTS

Diet reconstruction

Isotopic values of swordfish muscle ranged from 8 to 14.4 ‰ for $\delta^{15}\text{N}$ and from -16.7 to -19.8 ‰ for $\delta^{13}\text{C}$ (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 (Figures 2 and 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%.

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 (Tables 2 and S5, 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

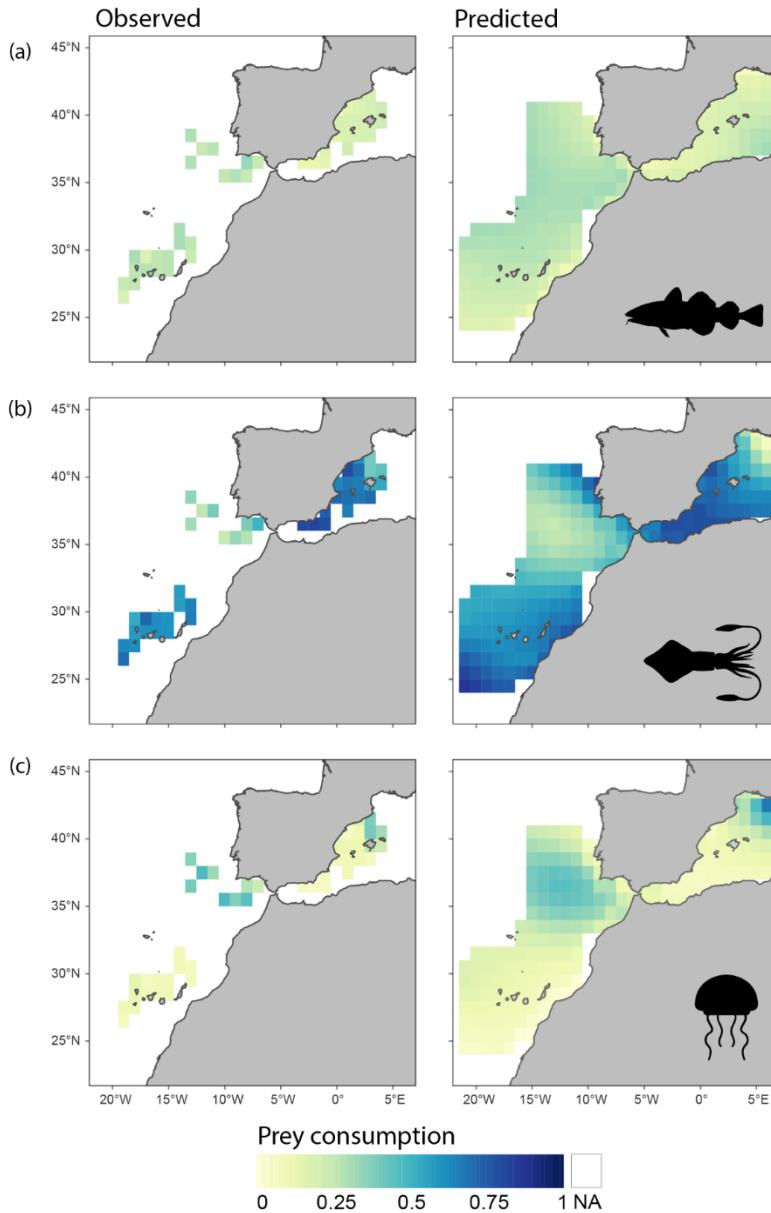


Figure 2. Spatial distribution of the contribution of fish (a), squid (b), and gelatinous organisms (c) to the diet of swordfish. The first column (Observed) shows the mean contribution of each prey based on BSIMMs. The second column (Predicted) shows the predicted consumption generated using GAMs for swordfish of 100 cm of lower jaw fork length.

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).

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	$\text{logit}(\pi_{si}) = \beta_0 + f_s(x_i, y_i) + f_{MLD}(MLD_i) + \beta_1 SST_i$	53.4
Squid	$\text{logit}(\pi_{si}) = \beta_0 + f_s(x_i, y_i) + f_{LJFLi}(LJFL_i) + f_{FEi}(FE_i) + \beta_1 SST_i$	71.7
Gelatinous org.	$\text{logit}(\pi_{si}) = \beta_0 + f_s(x_i, y_i) + f_{LJFLi}(LJFL_i) + f_{FEi}(FE_i) + \beta_1 Chl_i$	71.6

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 Cádiz and a slight decrease in the northwestern Mediterranean (Figure 4c).

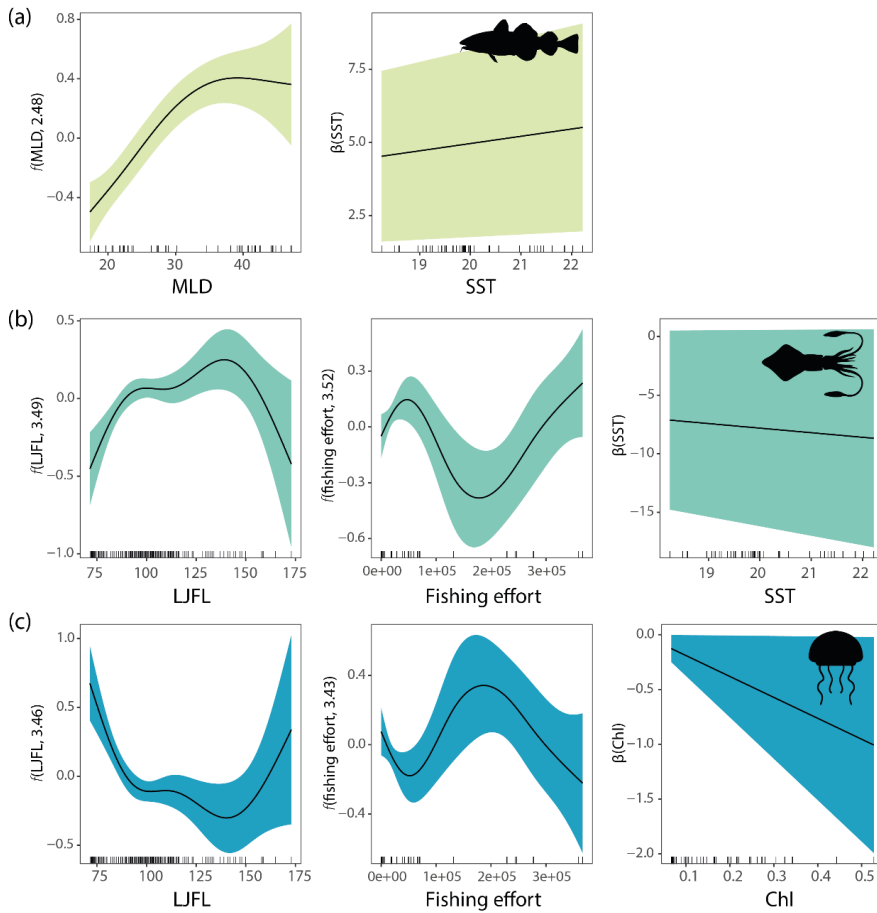


Figure 3. GAM partial effects of the explanatory variables for swordfish consumption of fish (a), squid (b), and gelatinous organisms (c). Shaded areas represent 95% confidence intervals around the main effects.

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 documents 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.

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. 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, and beyond the effect of this intrinsic factor, we found that

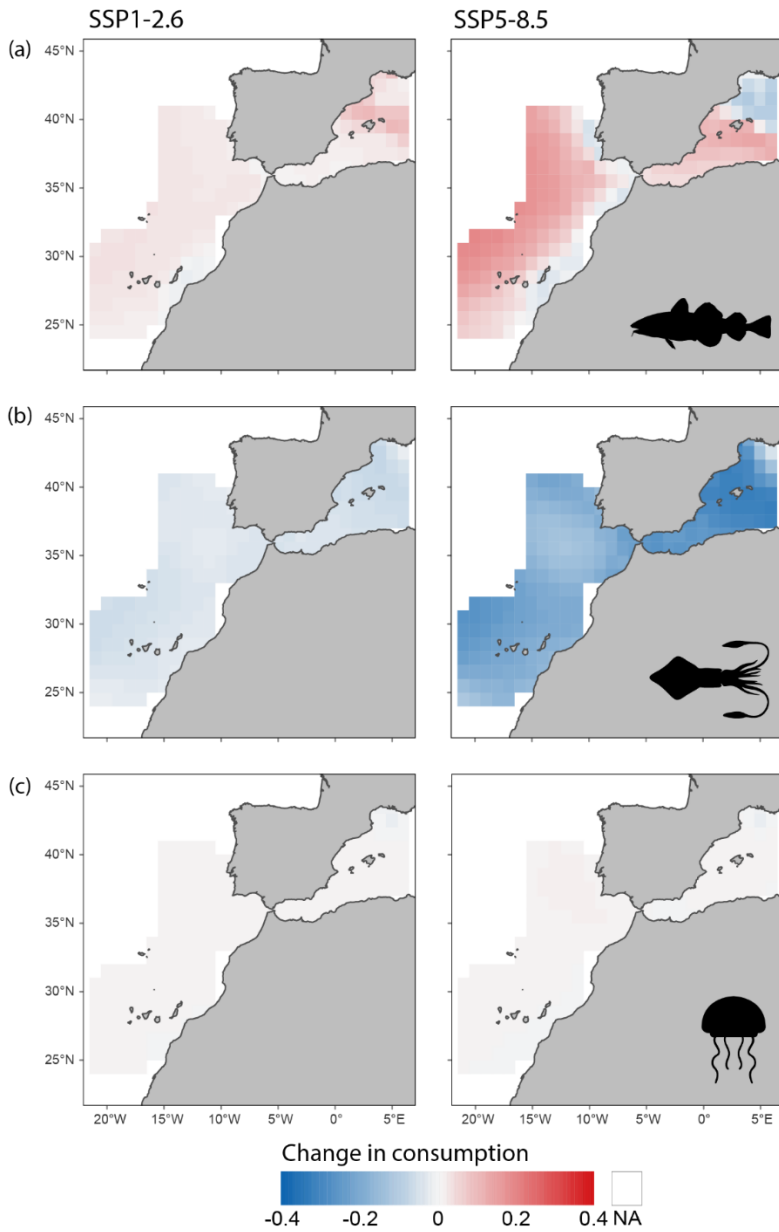


Figure 4. Projected change in the contribution of fish (a), squid (b), and gelatinous organisms (c) to the diet of swordfish (100 cm lower jaw fork length) between 2017-2018 and 2090-2100 based on SSP1-2.6 (first column) and SSP5-8.5 (second column). SSP, Shared Socioeconomic Pathway.

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 deep scattering layer. 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 (Díaz 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 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. On the other hand, 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.

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 world human population (Pecl et al., 2017).

Climate change may affect top predators directly through changes in their physiology, behavior, 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 northwestern 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). Nonetheless, Koslow et al. (2018) suggested that a winner-loser scenario is more likely than a single trend in mesopelagic fish abundance when midwater oxygen concentration decreases. On the other hand, 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 behaviorally 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 (R. K. Logan, Vaudo, et al., 2023a; 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 northwestern 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 (Alabía 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 (Alabía 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; E. 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.

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. On the other hand, 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 on a long-term time scale may be restricted by other biological interactions, such as prey abundance or recruitment, among others.

Despite these limitations, we aimed 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. On the other hand, 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 isotope 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, the swordfish diet will be affected as well, likely reflecting ecosystem alterations).

SUPPLEMENTARY MATERIALS

Supplementary methods: Meta-analysis development

BSIMM inputs included isotopic values of individual swordfish and their potential prey species. Potential prey were selected from previous studies on swordfish diet and grouped based on similar isotopic values and taxonomy: mesopelagic fishes; gadiforms, small and medium pelagic fishes; squid group I; squid group II; and gelatinous plankton. Isotopic values of prey were obtained from the literature (Table S2). When isotopic values from prey species were not found for the selected region (e.g., *Histioteuthis bonnellii* from the Gulf of Cádiz), isotopic values from the closest available area (e.g., northwestern Iberia) were corrected for $\delta^{15}\text{N}$ using Somes et al. (2010) as baseline.

The different studies included samples from different species, areas, and years. These arguments prevent direct comparisons among $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. Therefore, a meta-analysis was conducted to obtain the mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for each prey group and region.

In meta-analysis, statistical independence is one of the key assumptions when pooling effect sizes (i.e., $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values) (Higgins et al., 2009). This assumption was violated in our database because different studies are gathered and the same study can report several effect sizes for different species. To overcome this issue, we accounted for these dependencies through a Hierarchical Meta-Analysis Model (Harrer et al., 2021). To calculate the heterogeneity variance in all models, we used the Restricted Maximum Likelihood Estimator (REML; Viechtbauer, 2005) as it is the most robust method for continuous effect sizes (Langan et al., 2019). All models were fitted through the function “*rma.mv*” from the *metafor* R package v3.4-0 (Viechtbauer, 2010).

Supplementary figures

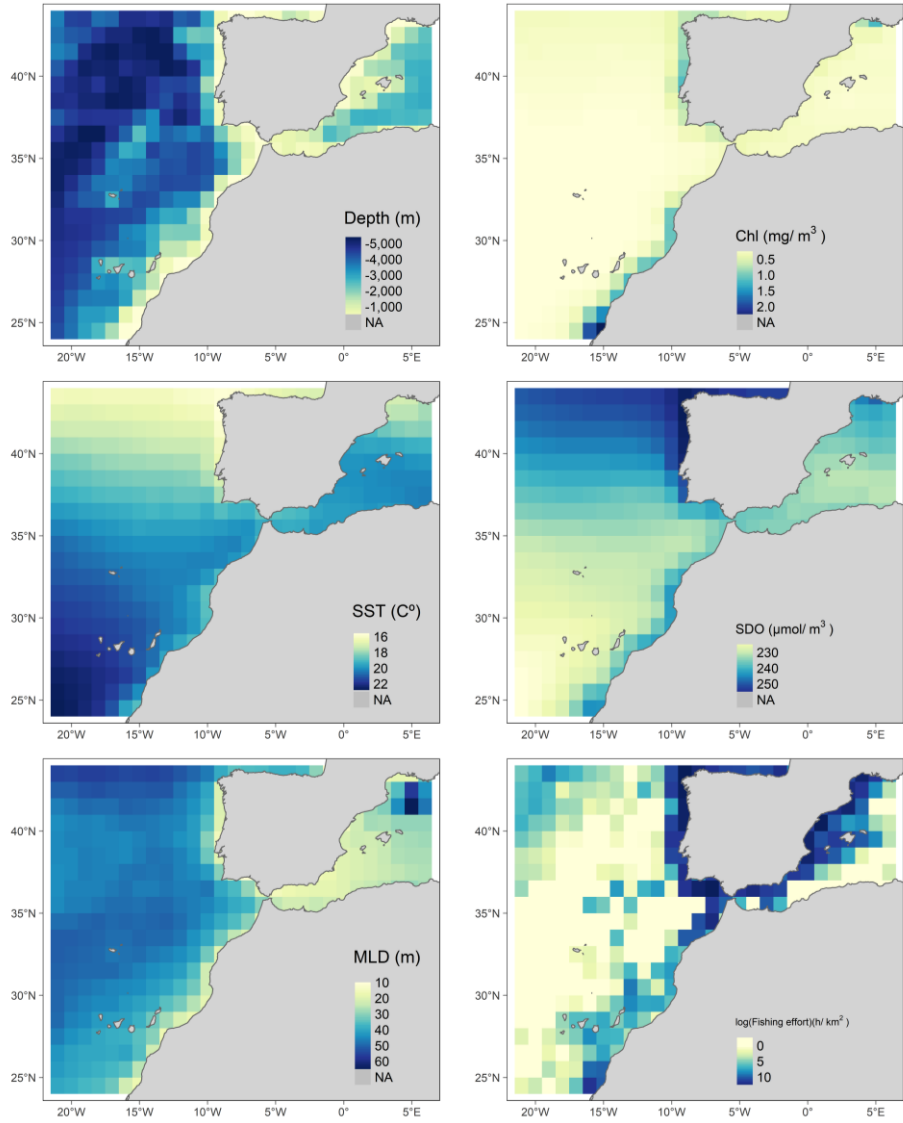


Figure S1. Average value per grid of environmental parameters incorporated into the models. Fishing effort is represented in logarithmic scale for visualization.

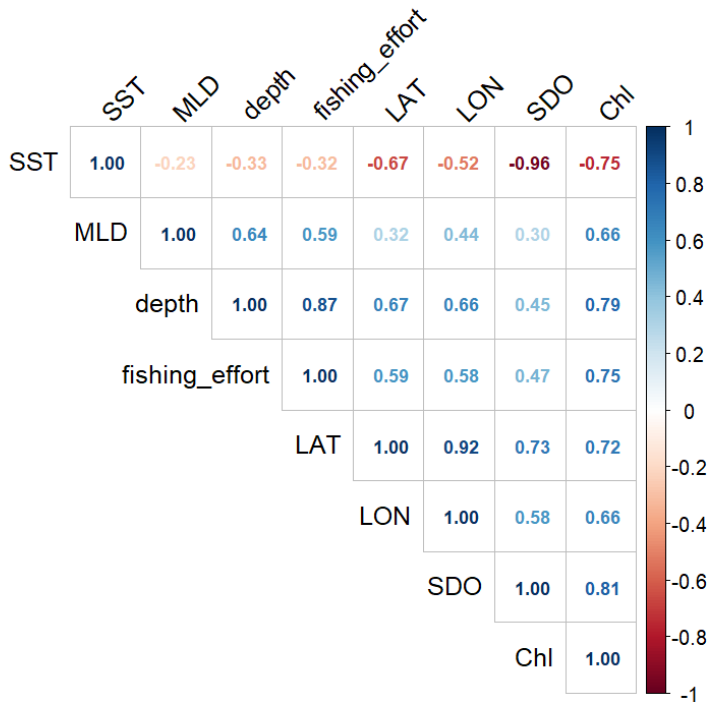


Figure S2. Spearman correlation between the environmental variables and fishing effort. SST: Sea surface temperature (mean); MLD: Mixed layer depth (mean); Depth: mean depth; fishing_effort: Cumulative fishing effort (sum); LAT: Latitude; LON: Longitude; SDO: Dissolved oxygen concentration (mean at sea surface); SBT: Sea bottom temperature (mean at mean depth); Chl: Chlorophyll concentration (mean at sea surface).

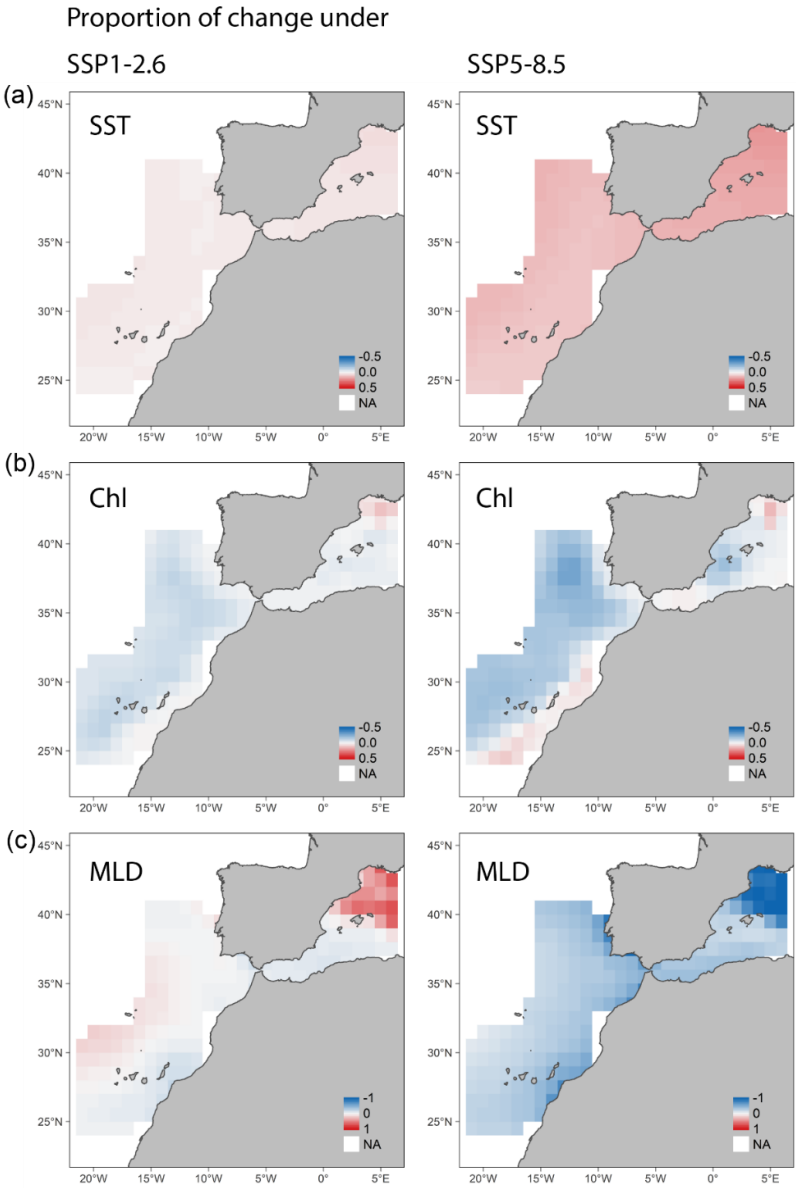


Figure S3. Proportion of change in SST (a), Chl (b) and MLD (c) between 2017-2018 and 2090-2100 under SSP1-2.6 and SSP5-8.5.

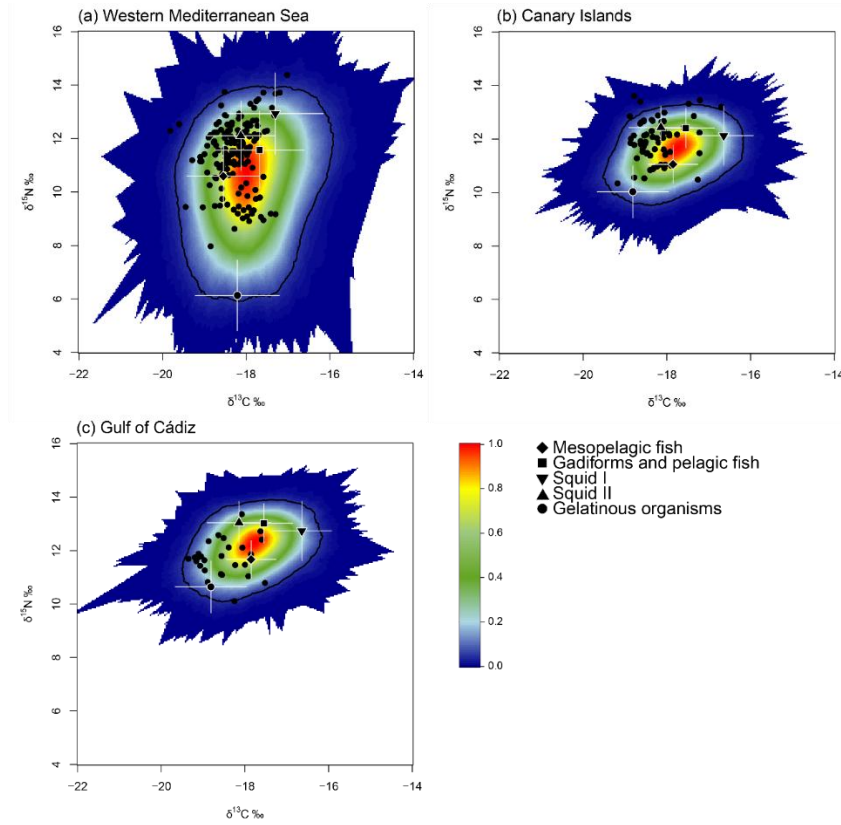


Figure S4. Mixing polygons including the swordfish isotopic values (black dots) and the potential prey sources (mean $\pm$ SD isotopic value: colored dots and error bars) for (a) the western Mediterranean Sea, (b) the Canary Islands, and (c) the South of Portugal/Gulf of Cádiz. The colored background displays the probability that a consumer's isotopic signature is explained by the proposed mixing model. The probability contour is colored at a 95% level.

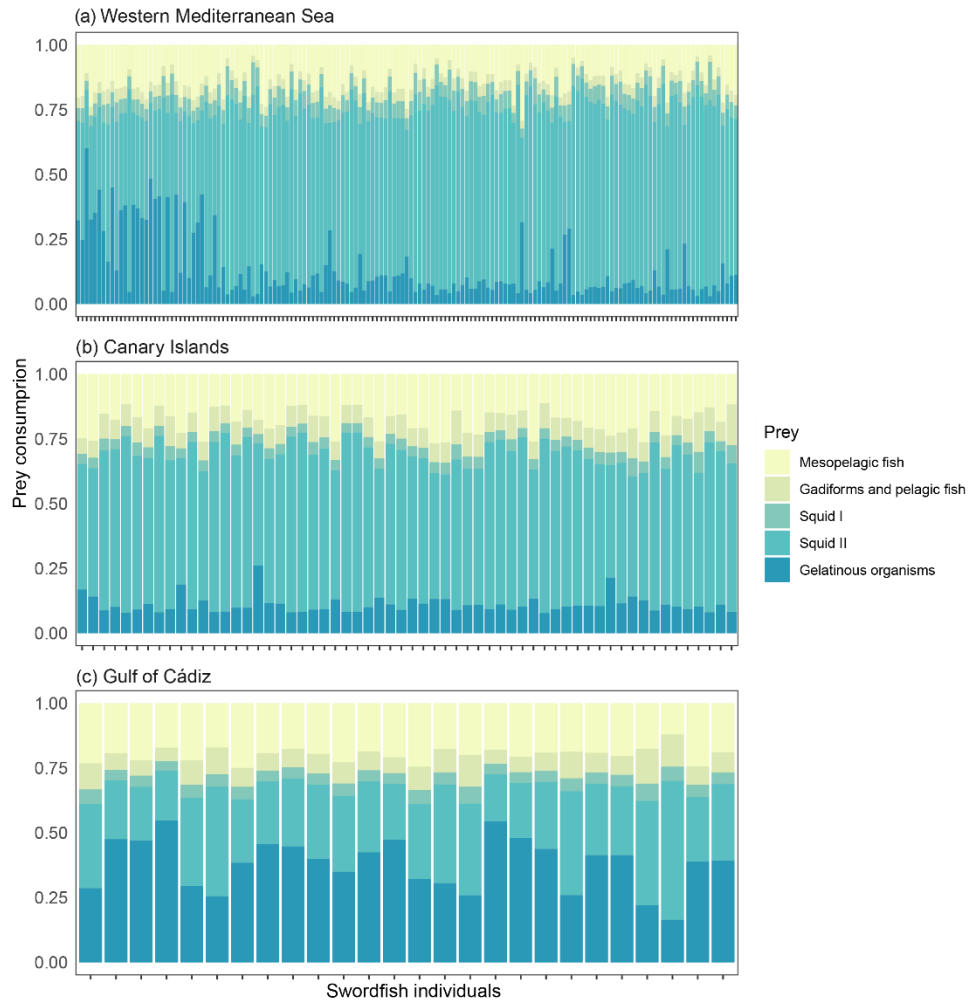


Figure S5. Relative consumption of prey groups in the diet of swordfish from (a) the western Mediterranean Sea, (b) the Canary Islands, and (c) the South of Portugal/Gulf of Cádiz obtained through Bayesian Stable Isotope Mixing Models (BSIMM). Swordfish individuals are ordered by increasing lower jaw fork length.

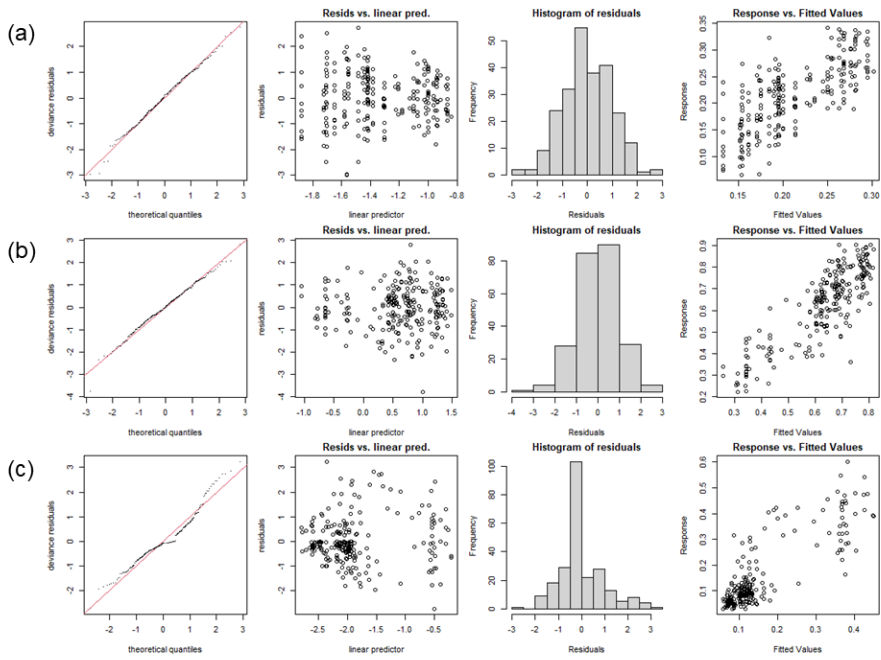


Figure S6. Diagnostic plots for the GAMs of consumption of fish (a), squid (b), and gelatinous organisms (c).

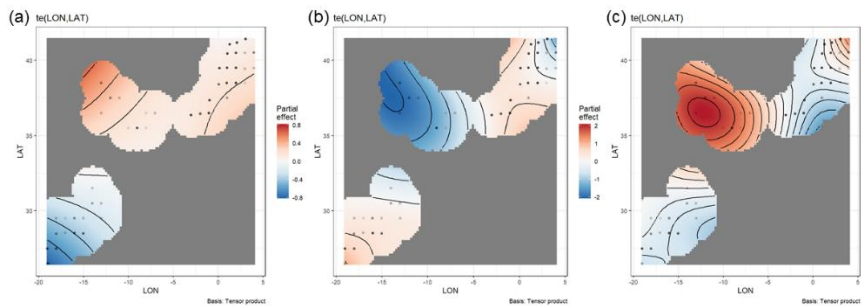


Figure S7. Tensor plots for the GAMs of consumption of fish (a), squid (b), and gelatinous organisms (c).

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

Prey	Species	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		References
		Mean	SD	Mean	SD	
Western Mediterranean Sea						
Mesopelagic fish	<i>Arctozenus risso</i> , <i>Ceratoscopelus maderensis</i> , <i>Electrona risso</i> , <i>Maurolicus muelleri</i> , <i>Myctophum punctatum</i> , <i>Notoscopelus elongatus</i>	-19.61	0.75	7.97	0.87	Cardona et al. (2007), Fanelli et al. (2011, 2013), Lloret-Lloret et al. (2020), Mir-Arguimbau et al. (2020), Papiol et al. (2013), Valls et al. (2014a, 2014b, 2017)
Gadiforms, small and medium pelagic fish	<i>Gadiculus argenteus</i> , <i>Merluccius merluccius</i> , <i>Micromesistius poutassou</i> , <i>Sardinella aurita</i> , <i>Sardina pilchardus</i> , <i>Trachurus trachurus</i>	-18.74	0.95	8.95	1.14	Albo-Puigserver et al. (2016, 2019), Bachiller et al. (2020, 2021), Barría et al. (2015), Cardona et al. (2012), Fanelli et al. (2013), Gómez-Campos et al. (2011), Lloret-Lloret et al. (2020), Mir-Arguimbau et al. (2020), Navarro et al. (2009), Papiol et al. (2013, 2017), Valls et al. (2014)
Squid I	<i>Todarodes sagittatus</i>	-18.36	1.03	10.31	1.21	Cardona et al. (2012, 2015), Gómez-Campos et al. (2011), Valls et al. (2014b, 2017)
Squid II	<i>Abralia veranyi</i> , <i>Ancistroteuthis lichtensteinii</i>	-19.19	0.70	9.48	0.99	Barría et al. (2015), Valls et al. (2014b, 2017)
Gelatinous organisms	<i>Cotylorhiza tuberculata</i> , <i>Pelagia noctiluca</i> , <i>Salpa</i> sp.	-19.27	0.89	3.51	1.02	Cardona et al. (2007, 2012, 2015), Fanelli et al. (2011, 2013), Mir-Arguimbau et al. (2020), Revelles et al. (2007), Tecchio et al. (2013), Tilves et al. (2018a, 2018b), Valls et al. (2014)

Canary Islands

Mesopelagic fish	<i>Diaphus brachycephalus</i> , <i>D. holti</i> , <i>D. rafinesquii</i> , <i>Chauliodus sloani</i> , <i>Maurolicus muelleri</i>	-18.91	0.48	8.43	0.40	Olivar et al. (2019), Sorell et al. (2017)
Gadiforms, small and medium pelagic fish	<i>Merluccius merluccius</i> , <i>Micromesistius poutassou</i> , <i>Sardina pilchardus</i> , <i>Scomber</i> sp., <i>S. colias</i> , <i>S. scombrus</i> , <i>Trachurus</i> sp., <i>T. picturatus</i> , <i>T. trachurus</i>	-18.61	0.58	9.79	0.67	Gimenez et al. (2017), Romero et al. (2021), Varela et al. (2013, 2018)
Squid I	<i>Illex coindetii</i> , <i>Todaropsis eblanae</i>	-17.70	0.59	9.50	0.80	Sorell et al. (2017), Varela et al. (2013, 2018)
Squid II	<i>Histioteuthis bonnellii</i>	-19.20	0.65	9.81	0.49	Mendez-Fernández et al. (2012)
Gelatinous organisms	Chaetognaths, Ctenophores, Hydromedusae, Scyphomedusae, Siphonophores, Tunicates	-19.87	1.95	7.41	0.42	Chi et al. (2021)

South of Portugal/Gulf of Cádiz

Mesopelagic fish	<i>Diaphus brachycephalus</i> , <i>D. holti</i> , <i>D. rafinesquii</i> , <i>Chauliodus sloani</i> , <i>Maurolicus muelleri</i>	-18.91	0.48	9.04	0.40	Olivar et al. (2019), Sorell et al. (2017)
Gadiforms, small and medium pelagic fish	<i>Merluccius merluccius</i> , <i>Micromesistius poutassou</i> , <i>Sardina pilchardus</i> , <i>Scomber</i> sp., <i>S. colias</i> , <i>S. scombrus</i> , <i>Trachurus</i> sp., <i>T. picturatus</i> , <i>T. trachurus</i>	-18.61	0.58	10.40	0.42	Gimenez et al. (2017), Romero et al. (2021), Varela et al. (2013, 2018)

Squid I	<i>Illex coindetii</i> , <i>Todaropsis</i> <i>eblanae</i>	-17.70	0.59	10.11	0.80	Sorell et al. (2017), Varela et al. (2013, 2018)
Squid II	<i>Histioteuthis</i> <i>bonnellii</i>	-19.20	0.65	10.42	0.49	Mendez-Fernández et al. (2012)
Gelatinous organisms	Chaetognaths, Ctenophores, Hydromedusae, Scyphomedusae, Siphonophores, Tunicates	-19.87	0.74	8.02	0.67	Chi et al. (2021)

Table S2. Mean values and standard deviation (SD) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes for swordfish from the western Mediterranean Sea, the Canary Islands, and the South of Portugal/Gulf of Cádiz. LJFL: lower jaw fork length (cm); n: number of samples.

Area	LJFL range (cm)	n	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)	
			mean	SD	mean	SD
Western Mediterranean Sea	71.5 - 173	159	-18.3	0.46	11.4	1.25
Canary Islands	78 - 159	66	-18.2	0.48	11.9	0.77
South of Portugal/Gulf of Cádiz	80 - 114	27	-18.5	0.55	11.7	0.68

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.

Area	Fish		Squid		Gelatinous prey	
	mean	range	mean	range	mean	range
Western Mediterranean	0.264	(0.19, 0.34)	0.626	(0.48, 0.73)	0.110	(0.08, 0.26)
Canary Islands	0.181	(0.07, 0.32)	0.686	(0.26, 0.9)	0.133	(0.03, 0.6)
South of Portugal/Gulf of Cádiz	0.280	(0.22, 0.33)	0.340	(0.22, 0.59)	0.379	(0.16, 0.55)

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).

Model	AIC	DE	RMSE	MAPE
Fish				
fish ~ te(LON, LAT) + s(MLD) + SST + s(fishing_effort)	-779.397	0.546	0.047	0.220
fish ~ te(LON, LAT) + s(LJFL) + s(MLD) + SST + s(fishing_effort)	-778.977	0.557	0.047	0.222
fish ~ te(LON, LAT) + s(MLD) + SST	-778.793	0.537	0.047	0.219
fish ~ te(LON, LAT) + s(LJFL) + s(MLD) + SST	-778.290	0.545	0.047	0.219
fish ~ te(LON, LAT) + s(MLD) + SST + s(fishing_effort) + Chl	-777.637	0.544	0.047	0.221
Squid				
squid ~ te(LON, LAT) + s(LJFL) + SST + s(fishing_effort)	-449.154	0.716	0.457	2.534
squid ~ te(LON, LAT) + s(LJFL) + s(Chl) + s(fishing_effort)	-448.966	0.716	0.457	2.536
squid ~ te(LON, LAT) + s(LJFL) + s(Chl) + SST + s(fishing_effort)	-448.829	0.718	0.457	2.536
squid ~ te(LON, LAT) + s(LJFL) + s(fishing_effort)	-448.784	0.714	0.456	2.532
squid ~ te(LON, LAT) + s(LJFL) + SST	-444.417	0.704	0.457	2.536
Gelatinous organisms				
gela ~ te(LON, LAT) + s(LJFL) + s(Chl) + s(fishing_effort)	-689.225	0.728	0.077	0.448
gela ~ te(LON, LAT) + s(LJFL) + s(Chl) + s(SST) + s(fishing_effort)	-688.594	0.730	0.078	0.447
gela ~ te(LON, LAT) + s(LJFL) + s(SST) + s(fishing_effort)	-686.558	0.727	0.078	0.442
gela ~ te(LON, LAT) + s(LJFL) + s(fishing_effort)	-684.765	0.721	0.078	0.447
gela ~ te(LON, LAT) + s(LJFL) + s(SST)	-683.605	0.716	0.078	0.447

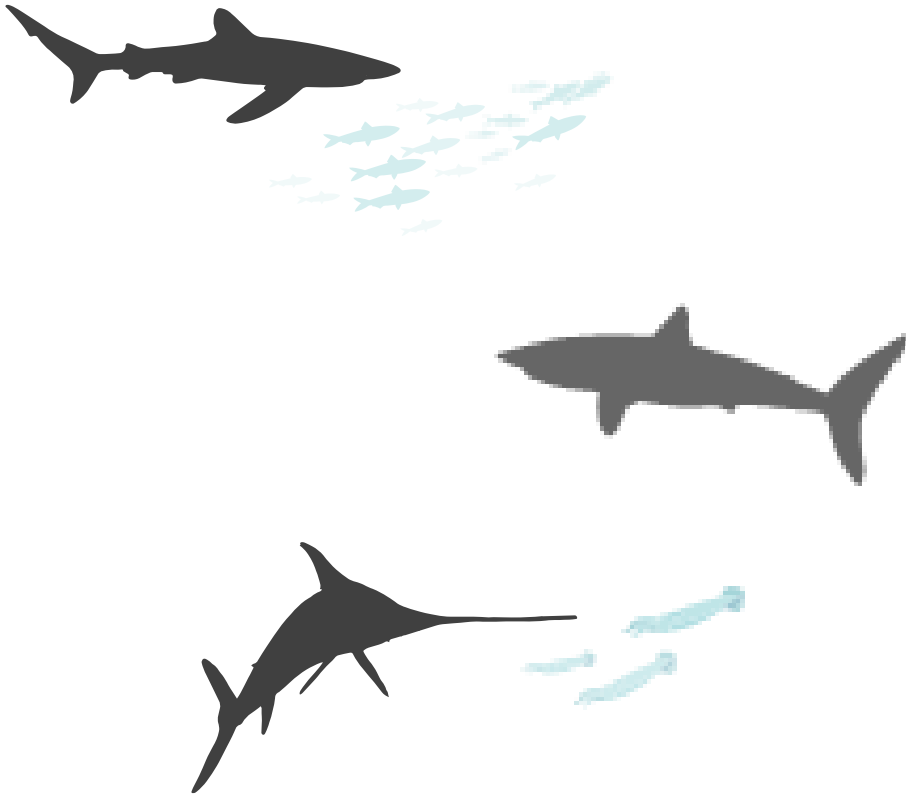
Table S5. Selected GAMs. SE: Standard Error, edf: Effective Degrees of Freedom, DE: deviance explained.

	Parametric coefficients			Smooth terms				
	Estimate	SE			edf		DE	
Fish								
(Intercept)	-6.29	1.63	***	te(LON,LAT)	4.94	***	53.4%	
SST	0.25	0.08	***	s(MLD)	2.48	***		
Squid								
(Intercept)	8.38	4.27	*	te(LON,LAT)	10.89	***	71.7%	
SST	-0.39	0.22	.	s(LJFL)	3.50	**		
				s(fishing effort)	3.52	*		
Gelatinous org.								
(Intercept)	-1.48	0.18	***	te(LON,LAT)	9.93	***	71.6%	
Chl	-1.91	0.95	*	s(LJFL)	3.46	***		
				s(fishing effort)	3.43	*		

Significant codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1

Chapter 3.

Pelagic productivity and abundance of competitors modulate trophic niche segregation between large predators



Reference:

Fernández-Corredor, E., Navarro, J., Fuster-Alonso, A., Giménez, J., García-Barcelona, S., Rueda, L., Macías, D., Coll, M., & Ramírez, F. (2025). Pelagic productivity and abundance of competitors modulate trophic niche segregation between large predators. *Proceedings of the Royal Society B: Biological Sciences*, 292(2057), 20251809. <https://doi.org/10.1098/rspb.2025.1809>

Abstract

In the open ocean, large pelagic predators often share similar food resources and feeding grounds, likely avoiding competition and coexisting through niche partitioning. Building on this hypothesis, we combined spatial distribution data with isotopic niche metrics and diet reconstructions based on N and C stable isotopes to describe intra- and interspecific competition between three sympatric predators: swordfish (*Xiphias gladius*), blue shark (*Prionace glauca*), and shortfin mako (*Isurus oxyrinchus*). We then evaluated the role of biological (competitor abundance), environmental (pelagic productivity), and anthropogenic (fishing pressure) drivers in shaping competition metrics within and between species. Shortfin makos had a high isotopic niche overlap with blue sharks (>80%), feeding on similar prey. In the Mediterranean, swordfish isotopic niche was narrower than, and highly overlapped with, that of blue sharks, although diet estimates suggest that swordfish rely more on fish while blue sharks rely more on squid. On average, the potential for intraspecific competition was highest for swordfish and lowest for shortfin makos. Our results suggest that pelagic productivity and competitor abundance are key drivers of intra- and interspecific trophic niche segregation between large pelagic predators, respectively. They support the hypothesis that niche partitioning is reduced under a high resource availability scenario.

KEYWORDS: swordfish, blue shark, shortfin mako, pelagic fish, isotopic niche, competition, stable isotopes, top predators, diet, species distribution

INTRODUCTION

Coexisting, ecologically similar individuals often compete for limited resources (Lizé et al., 2023; Roughgarden, 1976). However, competition, and ultimately competitive exclusion, can be mitigated through niche partitioning, a process by which individuals differentiate their use of resources (Schoener, 1974). This differentiation, involving fine-scale resource partitioning and spatial and/or temporal segregation, can occur within and between species (Giménez, Cañadas, et al., 2017) and serves as a key mechanism facilitating the coexistence of conspecifics and ecologically similar sympatric species (Chase & Leibold, 2003; Navarro et al., 2024). Among those limited resources that might be partitioned, food is particularly critical due to its significant effects on growth, development, and reproductive performance (e.g., Kowalczyk et al., 2014).

In both intra- and interspecific contexts, trophic niche width and overlap are determinants of competition dynamics (Bolnick et al., 2010; Costa-Pereira et al., 2018). The width of the trophic niche reflects the range of food resources exploited by individuals within species/populations and can vary with environmental heterogeneity and the presence of competitors (Lesser et al., 2020; Sexton et al., 2017). When resources become limited in the environment, the degree of competition and the amount of overlap can be directly related (Sale, 1974). High niche overlap between species can exacerbate competition and drive species towards specialization or broader generalist strategies over evolutionary time scales, depending on their relative abundance (Pianka, 1974).

In the open ocean, large pelagic predators often share similar food resources and feeding grounds and are examples of ecologically similar species likely to coexist in highly exploited marine regions and potentially exhibit niche partitioning (R. K. Logan, Vaudo, et al., 2023b). Many large pelagic species like pelagic sharks, tunas, and billfishes are heavily exploited by longline fleets, with

the Northeast Atlantic and the Mediterranean Sea being two of their primary fishing grounds, and the Spanish fleet leading the total catches across these regions (Nóbrega et al., 2025). The main target species of these fleets are swordfish (*Xiphias gladius*) and albacore tuna (*Thunnus alalunga*). However, ecologically similar species such as the blue shark (*Prionace glauca*) and shortfin mako (*Isurus oxyrinchus*) are also captured, with blue shark catches even exceeding those of swordfish (Nóbrega et al., 2025). While fisheries pose a significant threat to large pelagic species, they can also act as an additional competitor by removing prey and predators from the ecosystem, thereby altering food availability and trophic dynamics (Arlinghaus et al., 2021). Furthermore, blue and shortfin mako sharks may compete with swordfish for the same resources, as pelagic fishes and squid constitute the main prey for all three species (Biton-Porsmoguer et al., 2017; Fernández-Corredor et al., 2023). The abundance and availability of these prey species, which are also targeted by fisheries, are closely linked to oceanographic conditions such as marine productivity (Fernández-Corredor et al., 2021; Rodhouse et al., 2014) and play a key role in shaping and partitioning trophic niches (Lesser et al., 2020; MacArthur & Pianka, 1966).

Understanding the complexity of these competitive interactions remains a significant challenge since an appropriate proxy is required to study both intra- and interspecific competition. In this context, stable isotope analysis (SIA) has emerged as a pivotal tool for quantitatively studying niche dynamics and resource partitioning among sympatric species (e.g., Galindo et al., 2021; B. Iglesias et al., 2024; R. K. Logan, Vaudo, et al., 2023b; Marsaly et al., 2023). By integrating information on resource use and habitat through isotopic signatures (typically $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), this approach provides both quantitative and qualitative insights into the trophic niche, visualized within a multivariate space: the isotopic niche (Cherel & Hobson, 2007; Newsome et al., 2007). The isotopic niche width can be used as a proxy for diet diversity, which likely shapes

intraspecific competition. Simultaneously, isotopic niche overlap between coexisting species can be used to estimate the similarity of exploited resources, potentially reflecting interspecific competition when shared resources are limited (Pelage et al., 2022; Teichert et al., 2024). On the other hand, environmental variables such as those related to oceanographic conditions can influence the isotopic niche width and overlapped area between species (R. K. Logan, Vaudo, et al., 2023b; Pereira et al., 2023). In addition to assessing isotopic niche overlap between competitors, stable isotope mixing models can be used to evaluate the relative similarity in exploiting specific prey resources. These models provide a framework for estimating prey consumption based on the isotopic ratios of predators and their potential prey (Stock et al., 2018). This approach provides valuable proxies for evaluating the mechanisms underlying trophic competition and for predicting how shifts in ecosystem dynamics and fishing pressure may alter predator interactions and food web structure.

Most studies employing SIA have examined intra- and interspecific competition in isolation, with relatively few investigating both components simultaneously within ecological communities and across environmental gradients (e.g., Teichert et al., 2024). Here, we describe the isotopic niche and diet of swordfish, blue shark, and shortfin mako shark from the northeast Atlantic and the western Mediterranean Sea to unravel potential intra- and interspecific competition between these species in a heterogeneous seascape. By examining the isotopic niches of these species along a gradient of fishing pressure and environmental conditions, we aim to identify the drivers of competition and unravel the complex relationships between these top predators, their prey, and the environment. We hypothesize that niche partitioning occurs between species and among conspecifics, driven by the *per capita* availability of primary prey through competition. Specifically, we expect that (i) in areas of higher pelagic productivity, and therefore higher prey abundance, trophic niche partitioning may be reduced due to decreased competition; and (ii) an increase in the

abundance of potential competitors—including conspecifics, competing species, and fisheries—could diminish *per capita* food availability, intensifying competition, and enhancing trophic niche partitioning.

METHODS

Study species, area and data collection

We focused on three species of conservation concern: swordfish, blue shark, and shortfin mako shark. Swordfish and blue sharks are classified as Near Threatened by the International Union for Conservation of Nature (IUCN) at the global level, whereas shortfin makos are considered Endangered (Collette et al., 2022; Rigby, Barreto, Carlson, Fernando, Fordham, Francis, Herman, et al., 2019; Rigby, Barreto, Carlson, Fernando, Fordham, Francis, Jabado, et al., 2019). In the Mediterranean Sea, both shark species are classified as Critically Endangered (Sims et al., 2016; Walls & Soldo, 2016).

Swordfish (n = 253), blue shark (n = 187), and shortfin mako shark (n = 31) individuals were sampled between 2017 and 2019 by longline fishing vessels operating along the western Mediterranean Sea and the northeastern Atlantic Ocean (Figure 1). Both basins, connected by the Strait of Gibraltar, exhibit distinct oceanographic, ecological, and human impact characteristics (Longhurst, 1998; Narayanaswamy et al., 2013; Rousseau et al., 2024), thus offering the opportunity to study the niche segregation of those species along a gradient of environmental conditions and human activities.

Shark fork length (FL, in cm) and swordfish lower jaw fork length (LJFL, in cm) were measured on board. White muscle samples of each individual were collected and frozen at -20 °C until further analyses. Information related to technical characteristics and fishery strategies of longlines can be consulted in

García-Barcelona et al. (2013). Samples were collected under the SGBTM/BDM/AUTSPP/76 permit, with no ethics approval required.

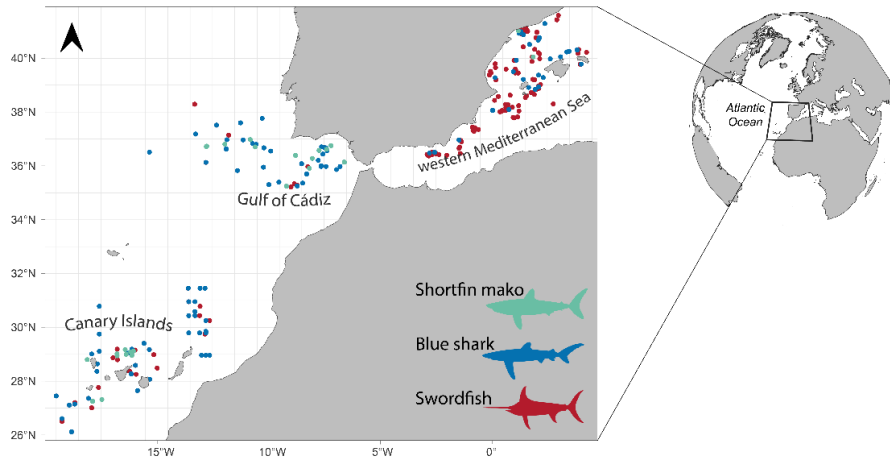


Figure 1. Study area and sampling locations along the western Mediterranean Sea and the northeastern Atlantic Ocean. Grey lines delineate a spatial grid of $1^{\circ} \times 1^{\circ}$.

Environmental drivers, fisheries, and abundance

Here, we evaluated the influence of surface chlorophyll-a concentrations (Chl) and the ‘Ocean Productivity available to Fish’ (OPFish) as proxies for prey availability (Vidal et al., 2023), whereas the mixed layer depth (MLD) was used as a proxy for mesopelagic and oxygen minimum zones (Y.-J. Chang et al., 2013; R. K. Logan, Vaudo, et al., 2023b). Chl and MLD monthly values for the 2015-2019 period were obtained from the EU-Copernicus Marine Environment Monitoring Service (<https://marine.copernicus.eu/>). The OPFish integrates the horizontal gradient of Chl, the range of Chl content, and the relative day length duration to refer to marine ecosystem feeding hotspots and use as a proxy of the potential fish production of pelagic species (Druon et al., 2021) and was obtained from Druon (2021).

Spatially explicit estimates of cumulative fishing effort were obtained from Global Fishing Watch (GFW, Kroodsma et al., 2018; accessed in 2024 from the Google Earth Engine: <https://developers.google.com/earth-engine/datasets>). We summed daily fishing records from commercial fisheries (trawlers, purse seiners, gillnets, and longliners) to obtain spatially explicit cumulative values covering the 2015–2019 period.

Table 1. List of explanatory variables used and their respective source and unit of measurement.

Variables		Source
Chl	Chlorophyll concentration ($\text{mg}\cdot\text{m}^{-3}$)	Copernicus
MLD	Ocean mixed layer thickness (m)	Copernicus
OPFish	Ocean Productivity available to Fish (% of daily favorable occurrence)	Druon (2021)
Fishing effort	Cumulative fishing effort (h/km^2)	Global Fishing Watch
Abundance	Individuals of each species caught per 1,000 hooks (nCPUE: ind/1000 hooks)	<i>this study</i>

Per capita food availability is also influenced by the abundance of potential competitors, including both conspecifics and individuals of ecologically similar species. As a proxy of the relative abundance of the three target species, data from 2,534 longline sets from the Spanish longline fleet targeting swordfish and albacore tuna along the study area between 2015 and 2019 were included in the analysis (IEO Observer Program). The catch per unit effort (nCPUE; number of individuals per thousand hooks) was standardized using Generalized Additive Models (GAMs) with a negative binomial error distribution to account for overdispersion in the catch data (Supplementary Methods: Relative abundance from standardized catch data). The number of hooks was included as an offset variable. Latitude and longitude were incorporated using a tensor product smooth function to capture spatial variability in catch rates. The longline type was included as a fixed factor, while year, month and boat were treated as

random effects to account for variability in sampling effort and fishing efficiency. Separate models were fitted for each species and basin (Mediterranean and Atlantic), resulting in five models (Table S1), with no model adjusted for shortfin mako in the Mediterranean Sea due to an excess of zero catch observations. These models were then used to predict the number of individuals caught per 1,000 hooks for each grid cell and longline type, providing spatially explicit estimates of species relative abundance across the study area (Table 1).

White muscle tissue in large pelagic fishes reflects dietary intake over several months. To focus on broad-scale patterns of potential competition and reduce the influence of short-term variability, we standardized environmental variables (MLD, Chl, and OPFish), fishing effort, and relative abundances over a common temporal window (2015–2019). All layers were cropped to encompass the study area and adjusted to a common resolution of $1^\circ \times 1^\circ$ 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 these vagile species while capturing the relevant spatial variability in competition and its relationships with the explanatory variables (Fernández-Corredor et al., 2025; Houssard et al., 2017, 2019; Vidal et al., 2023).

Stable isotope analyses

Prior to stable isotopic analysis, lipids were extracted with a chloroform/methanol (2:1) solution to correct for the differences in lipid content in the tissue on $\delta^{13}\text{C}$ values (Bligh & Dyer, 1959). For shark samples, the urea content was extracted by placing the samples immerse in deionized water in a sonication machine to remove the supernatant of urea, following Kim and Koch (S. L. Kim & Koch, 2012). Samples were then dried at 60°C and ground to a fine powder. Analyses of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were performed at the Laboratory of Stable Isotopes (LIE-EBD, Spain) as described in Fernández-Corredor et al. (2023).

Interspecific differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were tested using two-way PERMANOVA tests on the Euclidean distance matrix including the species and the area (western Mediterranean, South of Portugal/Gulf of Cádiz, Canary Islands) as factors.

Isotopic niche partitioning

The isotopic niche was estimated using Kernel Utilization Density estimators (KUDs, Eckrich et al., 2020) using the *rKIN* R package v1.0.2 (Albeke, 2023). Niche width and niche overlap between species were reported using the 2D KUD of niche size at the 95% confidence level, which provides a good representation of irregularly distributed data (Eckrich et al., 2020). The potential for interspecific competition was estimated through the isotopic niche similarity between the species by calculating the distance to the competitor's centroid (CCD) within the isotopic niche space (see Box 1)(Layman et al., 2007; Teichert et al., 2024). The CCD measures the dietary niche similarity of a species with its potential competitors in the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ space and is defined as:

$$CCD_i = \frac{1}{N} \sum_{k=1}^N d(C_i, C_k),$$

where $d(C_i, C_k)$ is the Euclidean distance between C_i (the centroid of the species i) and C_k (the centroid of competitor k), N is the total number of potential competitors, and CCD_i is the mean of Euclidean distances between the centroid of the species i and those of their competitors.

The intraspecific competition was estimated using the Intraspecific Trophic Pressure index (ITP; modified from Pelage et al. (2022), calculated as:

$$ITP_{ij} = \log(nCPUE_{ij} + 1) / KUD_{ij},$$

where $nCPUE_{ij}$ is the standardized catch per unit effort (individuals of species j /1000 hooks) for the grid cell i and KUD_{ij} is the KUD of niche size at the 95% confidence level for the species j for the grid cell i . Abundant species with a narrow dietary niche show high ITP values, suggesting they exert strong trophic pressure on a limited set of resources; while less abundant species with a broad dietary niche show lower ITP values, reflecting their use of diverse resources (Andrades et al., 2021).

The distance to the competitor's centroid and the potential level of intraspecific competition were calculated based on the KUD at the grid cell level. We assessed the normality of the distribution of CCD and ITP values using the Shapiro-Wilk test. When normally distributed, we conducted a one-way ANOVA to evaluate differences between groups, and post-hoc pairwise comparisons were performed using the Tukey Honestly Significant Difference (HSD) test. For metrics that did not meet the normality assumption, we employed the Kruskal-Wallis test or Permutational Analysis of Variance (PERMANOVA). Pairwise comparisons were conducted using the pairwise Wilcoxon rank-sum test.

Competition metrics and relationship with drivers

To evaluate the effect of the environmental drivers and fishing pressure on inter- and intraspecific competition for each species, isotopic data were pooled over a $1^\circ \times 1^\circ$ grid and niche metrics were calculated for each cell. Models for Intraspecific Trophic Pressure index (ITP) and distance to the competitor's centroid (CCD) were fitted using GAMs with a Gamma distribution including linear and additive relations with the drivers (Table 1, Supplementary Methods). Latitude and longitude were incorporated using a tensor product smooth function to capture spatial variability in isotopic values. All predictor variables were checked for potential Spearman correlation, and Chl was excluded (corr >0.8, Figure S2). The Akaike Information Criterion (AIC) and the Deviance

Explained (DE) were used for model selection. For each competition metric, the model with higher DE and lower AIC was chosen to evaluate the effects of explanatory variables. GAMs were built using the *mgcv* R package v1.9-1 (Wood, 2017).

Food resource partitioning

We ran species-specific Bayesian Stable Isotope Mixing Models (BSIMMs) based on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values to estimate the relative contribution of the potential prey items in the diet of the three species. 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). The diet-tissue discrimination factors (DTDF) were estimated following Caut et al. (2009) (shortfin mako DTDF: 1.08 ± 0.25 for $\delta^{13}\text{C}$ and 2.4 ± 0.22 for $\delta^{15}\text{N}$; blue shark DTDF: 0.92 ± 0.23 for $\delta^{13}\text{C}$ and 2.39 ± 0.3 for $\delta^{15}\text{N}$; swordfish DTDF: 1.13 ± 0.18 for $\delta^{13}\text{C}$ and 2.62 ± 0.31 for $\delta^{15}\text{N}$; Table S2). 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). Prey groups were selected according to the available literature to represent the main potential prey in the diet of the three species in the Atlantic and Mediterranean, and included fishes, squids, gelatinous organisms, and large pelagic species (Biton-Porsmoguer et al., 2017; Fernández-Corredor et al., 2023; Garibaldi & Orsi Relini, 2000). Isotopic values of prey species were obtained from the literature and pooled into five groups (Phillips et al., 2005) using a meta-analysis approach based on similar isotopic values and taxonomy (Table S3, Figure S3, Supplementary Methods). To minimize potential confounding effects with stable isotope

baselines, we used region-specific prey values (Fernández-Corredor et al., 2025).

All statistical analyses were conducted using R v4.3.3 (R Core Team, 2024).

RESULTS

Spatial distribution of the abundance

The western Mediterranean showed the lowest densities for the three species (Figure 2). Swordfish nCPUE was higher in the Atlantic, particularly in the waters south of the Canary Islands, than in the Mediterranean, where more individuals were caught in the northern part. Blue sharks were more abundant in the Gulf of Cádiz and the southern waters of Portugal (Figure 2C). Shortfin mako was the least frequent species, with no model adjusted for the Mediterranean Sea due to a high number of zero catch observations. Shortfin makos had a higher nCPUE in the Gulf of Cádiz and the waters south of the Canary Islands (Figure 2B).

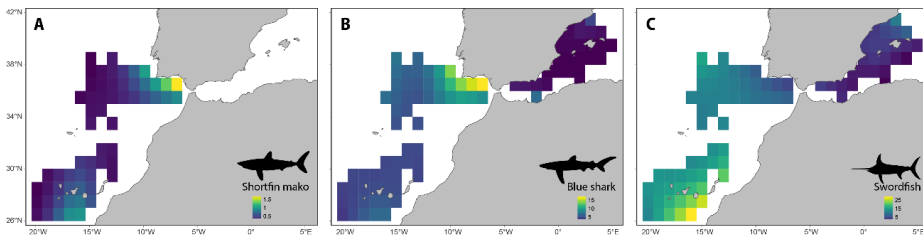


Figure 2. Spatial prediction of the abundance (nCPUE, individuals·1000⁻¹ hooks) for shortfin mako (A), blue shark (B), and swordfish (C) between 2015 and 2019. Data are predicted within a 1° × 1° grid.

Isotopic niche and competition metrics

The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values differed between species, showing differences between regions (Table 2). Overall, swordfish showed lower $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values than blue and mako sharks (PERMANOVA $p < 0.01$; Table S4). Regarding the isotopic niche width, blue sharks showed the largest KUD in the Canary Islands

(KUD area = 10.18‰^2), followed by swordfish (7.5‰^2) and shortfin makos (7.13‰^2) (Figure 3D). In the South of Portugal/Gulf of Cádiz, blue sharks showed the largest KUD area (10.83‰^2), followed by shortfin mako (8.8‰^2) and swordfish (7.42‰^2). The largest isotopic niche for both swordfish (KUD area = 10.47‰^2) and blue shark (23.06‰^2) was found in the western Mediterranean. Shortfin mako's KUD area in the western Mediterranean was not calculated due to low sample size ($n = 2$).

Table 2. Mean values and standard deviation (SD) of length (FL: Fork length, for sharks; LJFL: lower jaw fork length, for swordfish), $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for mako, blue shark, and swordfish. n: number of samples.

Species	Area	n	FL/LJFL (cm)		$\delta^{13}\text{C}\text{‰}$		$\delta^{15}\text{N}\text{‰}$	
			mean	range	mean	SD	mean	SD
Shortfin mako	Canary Is.	10	108.4	67-156	-17.87	0.66	11.91	0.70
	Portugal/Cádiz	19	130.2	72-189	-17.78	0.71	12.56	0.70
	Western Med.	2	123.8	88-160	-16.69	0.55	13.08	1.05
Blue shark	Canary Is.	50	159.0	93-237	-17.67	0.97	12.65	0.64
	Portugal/Cádiz	92	148.4	82-234	-17.72	0.99	12.87	0.64
	Western Med.	45	118.8	43-218	-17.49	0.96	11.29	1.32
Swordfish	Canary Is.	66	104.3	78-159	-18.25	0.48	11.94	0.77
	Portugal/Cádiz	27	103.4	80-114	-18.52	0.55	11.72	0.68
	Western Med.	160	100.1	72-173	-18.26	0.46	11.41	1.24

Canary Is.: Canary Islands; *Portugal/Cádiz:* South of Portugal/Gulf of Cádiz;

Western Med.: Western Mediterranean

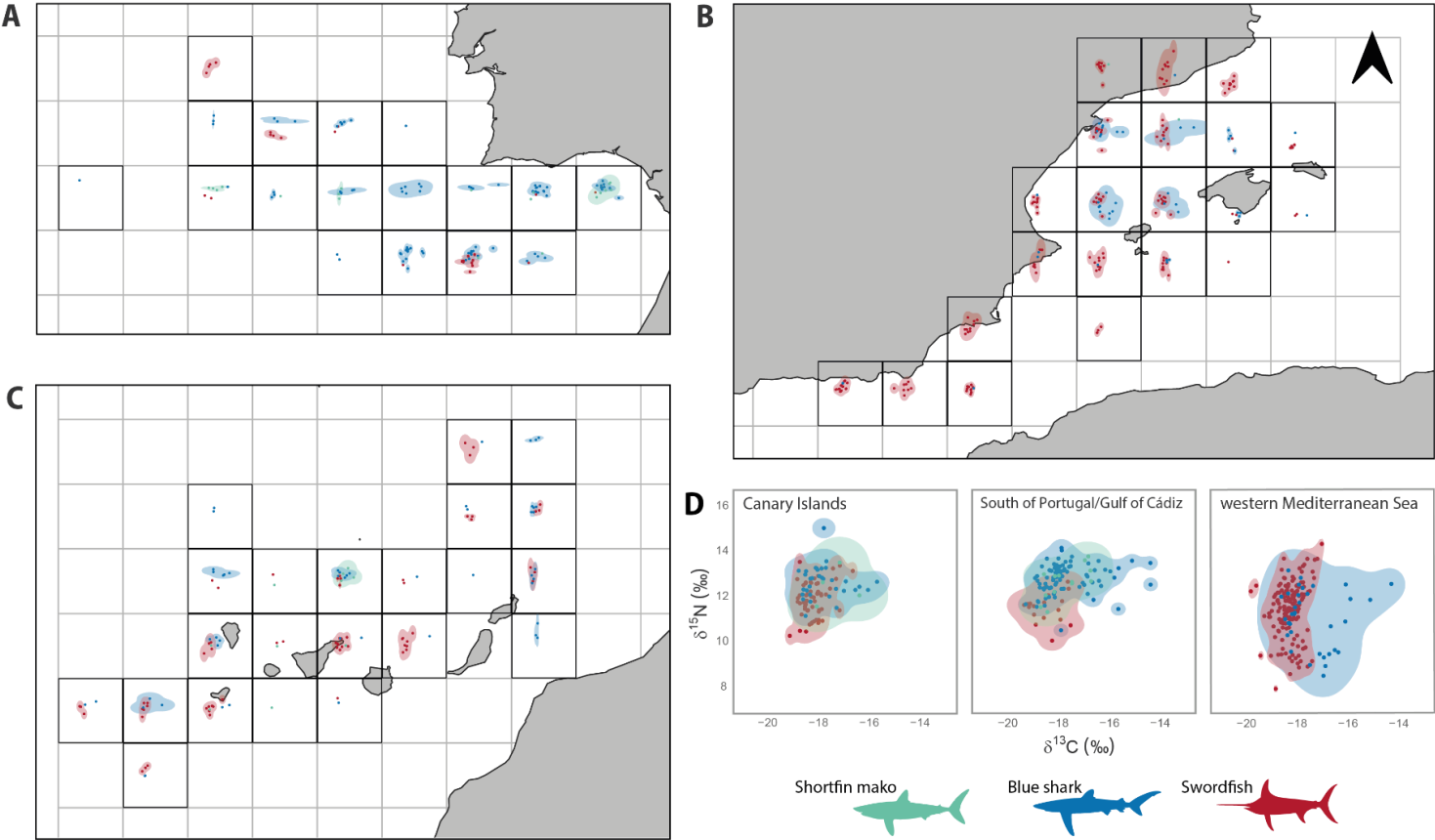
Regional differences were observed in the isotopic overlap between the three species (see Figure 3D and Table S5). The pairwise overlaps between species showed a higher isotopic overlap between mako and blue sharks than with swordfish. The percentage of overlap for swordfish isotopic niche was similar

with both shortfin mako and blue shark, with a high overlap with blue sharks in the Mediterranean Sea (92%), while this overlap only represented 42% of the blue shark isotopic niche.

Distances to the competitor's centroid were shorter in the western Mediterranean ($CCD = 1.13 \pm 0.52$ for blue sharks, and 1.17 ± 0.58 for swordfish) than in the South of Portugal/Gulf of Cádiz and the Canary Islands (ANOVA, $p < 0.05$). CCD for shortfin mako was higher in the Mediterranean (1.78 ± 0.83). The best-fitted model for CCD included the abundance of the three species and the spatial component, explaining 84.3% of the deviance (Table S6). Diagnostic plots suggested normality and homoscedasticity of the residuals (Figure S4). The distance to the potential competitor's centroid within the isotopic niche space increased with the abundance of the three species and decrease when intermediate abundances were reached (Figure 4A).

On average, the potential level of intraspecific competition was higher in the swordfish ($ITP = 0.75 \pm 0.76$) than in the blue shark (0.52 ± 0.65), with both species showing higher values than shortfin makos (0.08 ± 0.05 ; Kruskal Wallis $p < 0.01$, pairwise Wilcoxon test $p < 0.05$). The best-fitted model for potential intraspecific competition included pelagic productivity, the species, and the spatial component, explaining 52.7% of the deviance (Table S6). Diagnostic plots suggested normality and homoscedasticity of the residuals (Figure S4). Potential intraspecific competition intensity decreased as intermediate values of pelagic productivity were reached (Figure 4B).

Figure 3. Isotopic niche for shortfin mako, blue shark, and swordfish based on 95% kernel utilization densities. Isotopic niche is represented for each $1^\circ \times 1^\circ$ grid cell in the South of Portugal/Gulf of Cádiz (A), the western Mediterranean Sea (B), and the Canary Islands (C); and summarized by area (D). The axes for each grid cell in A, B, and C are the same as those in panel D. (next page)



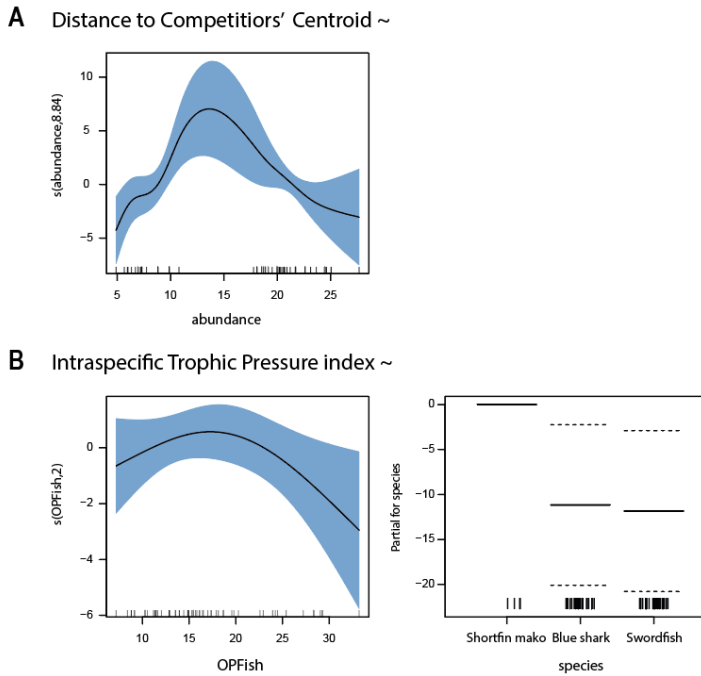


Figure 4. GAM partial effects of the explanatory variables for (A) the distance to the competitor's centroid within the isotopic niche space (CCD) and (B) the potential intraspecific competition estimated with the Intraspecific Trophic Pressure (ITP) index: the panel on the left shows the partial effect of OPFish (smooth term) on ITP across all species, while the panel on the right shows the partial effect of species (fixed term) on ITP. Shadowed areas represent 95% confidence intervals around the main effects.

Food resource partitioning

In the Canary Islands, squid 2 (cock-eyed squids) were the most consumed prey for the swordfish and blue shark. Together with fish 1 (mesopelagic fishes), they contributed to almost 50% of the diet of the shortfin mako. Dietary estimates suggested a low contribution of gelatinous prey to swordfish diet except in the south of Portugal/Gulf of Cádiz, representing almost 50% of the contribution to the diet (Figure 5) and followed by squid 2 (cock-eyed squids). Blue sharks showed a similar diet for both the south of Portugal/Gulf of Cádiz and the Canary Islands, with squid 2 being the main prey (around 40% of their diet), followed by large pelagics. All prey groups showed similar contributions to the diet of

shortfin mako in the Gulf of Cádiz, pointing to a generalist diet. Both sharks had higher fish contribution to their diet than swordfish in the Gulf of Cádiz and the Canary Islands. In the western Mediterranean, the swordfish diet was mainly based on fish 1 (mesopelagic fishes) and squid 2 (midwater and angel squid), while the estimated diet for blue sharks had a higher contribution of squid 1 (ommatrephids) and fish 2 (gadiforms and pelagic fish). Blue sharks showed the lowest assimilation of fish 1 (mesopelagic fishes) in both the Mediterranean and Atlantic Ocean. Gelman-Rubin and Geweke diagnostics suggested a satisfactory fit for the 8 models (Table S7).

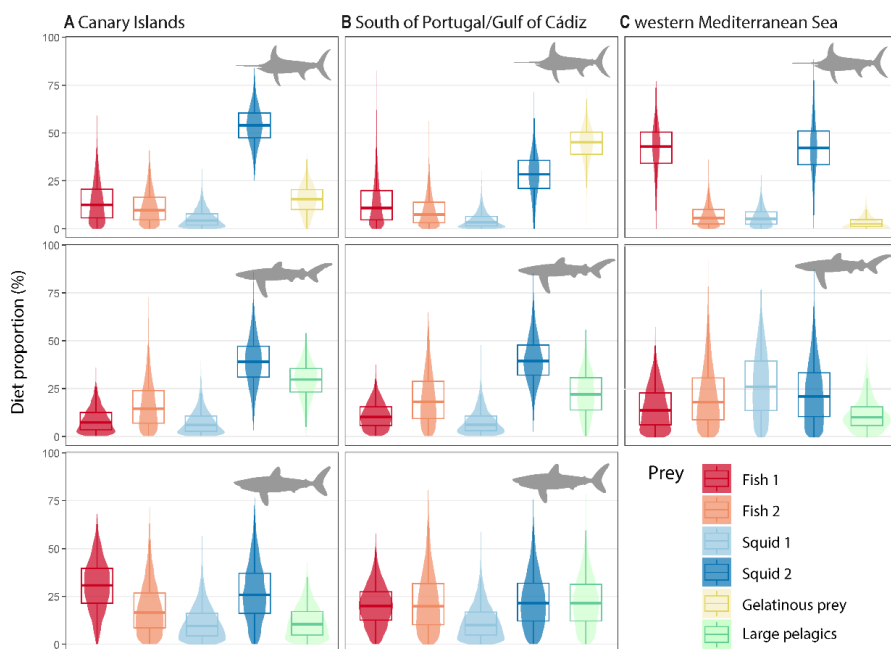


Figure 5. Relative contribution of prey to the diet of swordfish (top row), blue sharks (middle row), and shortfin makos (bottom row) from (a) the Canary Islands, (b) the South of Portugal/Gulf of Cádiz, and (c) the western Mediterranean Sea obtained through Bayesian Stable Isotope Mixing Models (BSIMMs). The composition of each prey group is available in Table S3.

DISCUSSION

Understanding the mechanisms that shape the trophic niche and facilitate the coexistence of ecologically similar species is a complex challenge, particularly in the open ocean, where direct observations and samples are difficult to obtain. Adopting an integrated approach, considering external drivers such as environmental variables and fishing pressures, can offer valuable insights into the processes that regulate competition between conspecifics and ecologically similar species. In this study, we combined spatial distribution data, isotopic niche metrics, and dietary reconstructions to describe spatial patterns of intra- and interspecific potential competition. This approach allowed us to understand how external drivers influence niche partitioning both between and within three ecologically similar sympatric large predatory fishes. Our results suggest that the pelagic productivity and the abundance of potential competitors are key drivers of intra- and interspecific trophic niche segregation between large sympatric pelagic predators.

Isotopic niche and food resource partitioning

The isotopic values and ranges observed between the three species suggest similar trophic ecologies (Rosas-Luis et al., 2017) with some degree of niche partitioning. Both shortfin mako and blue shark showed higher $\delta^{13}\text{C}$ values than swordfish, suggesting higher use of nearshore productive regions. In the Atlantic, swordfish showed lower $\delta^{15}\text{N}$ values than shortfin mako and blue sharks, which could be explained by swordfish feeding on smaller prey with lower trophic levels than sharks (Z. Li et al., 2024). This pattern is also highlighted in our diet estimates, with swordfish having higher consumptions of gelatinous organisms and mesopelagic fish. Shortfin mako sharks previously showed higher $\delta^{15}\text{N}$ values and higher trophic positions than blue sharks in the Pacific (Besnard et al., 2021; Maya Meneses et al., 2016). However, in the Atlantic, blue

sharks showed the highest $\delta^{15}\text{N}$ values of the three species, which could be explained by their scavenger behavior, occasionally feeding on marine mammal carcasses (Klarian et al., 2018; Z. Li et al., 2024). Higher $\delta^{15}\text{N}$ values for swordfish compared to blue sharks in the western Mediterranean can result from a higher exploitation of deeper waters (Eduardo et al., 2023), as inferred by a higher consumption of mesopelagic fishes in this area.

The three studied species are known to feed on multiple prey types and exploit diverse trophic resources and habitats, consequently occupying a broad niche space (Y. Li et al., 2016; Rosas-Luis et al., 2017). The opportunistic behavior of blue sharks is also reflected by their consistently wider isotopic niche along the studied area, indicative of a more generalist diet than swordfish and shortfin mako sharks. However, previous studies in the Pacific found a wider isotopic niche for shortfin mako, consuming a wider variety of prey than blue sharks, which were feeding mainly in the most abundant crustacean and squid species in the studied area, pointing to a more specialized diet (Maya Meneses et al., 2016). A wider isotopic niche can result from trophic plasticity and adaptation to environmental heterogeneity, as well as from limited *per capita* prey availability (Stephens & Krebs, 1986). In the Mediterranean, swordfish and blue sharks' isotopic niches were wider, suggesting more dietary variability in prey size/type in this area. Although the abundance of the three potential competitors is lower than in the Atlantic, *per capita* prey availability is likely limited. The western Mediterranean is a highly exploited area (Coll et al., 2012; Colloca et al., 2017) where fisheries are removing prey and can act as competitors themselves (Arlinghaus et al., 2021). This scarcity may lead to heightened interspecific competition, expanding trophic and isotopic niche breadths (Morin, 2009). In more productive areas such as the Eastern Tropical Pacific, no overlap was found between swordfish and blue shark or shortfin mako (Y. Li et al., 2016; Rosas-Luis et al., 2017). A lack of overlap was also reported for the three species in the northeast central Pacific (Y. Li et al., 2016); however, blue shark and

shortfin mako showed highly overlapping isotopic niches in the Ecuadorian Pacific area (Rosas-Luis et al., 2017). Here, we found that shortfin mako sharks had a high isotopic niche overlap with blue sharks (over 80%), with similar prey consumption obtained from the mixing models, suggesting the potential for competition for resources.

Although the studied species feed mainly on squid and pelagic fishes (Biton-Porsmoguer et al., 2017; Fernández-Corredor et al., 2023; Politi, 1997), regional variations in prey contribution proportions can lead to the observed isotopic differences. Regarding fish prey, swordfish showed higher consumption of mesopelagic fishes in the Mediterranean, while blue sharks seem to prefer pelagic fishes. We found a high overlap between swordfish isotopic niche and blue sharks in the western Mediterranean (more than 90%), suggesting that swordfish may share more food resources with blue sharks than in the Atlantic. However, the diet estimates suggested that these two species rely on different prey groups, with swordfish showing higher consumption of mesopelagic fish and midwater and angel squids, while blue sharks showed higher proportions of pelagic fishes and ommastrephids. Previous studies showed indications of trophic niche partitioning between the two shark species on the northeastern Atlantic, with fish being the main prey for shortfin makos, and blue sharks' diet being dominated by cephalopods (Biton-Porsmoguer et al., 2017). This example of food partitioning among coexisting species often reduces niche overlap and helps reduce interspecific competition (Vollrath et al., 2021).

Competition metrics and drivers

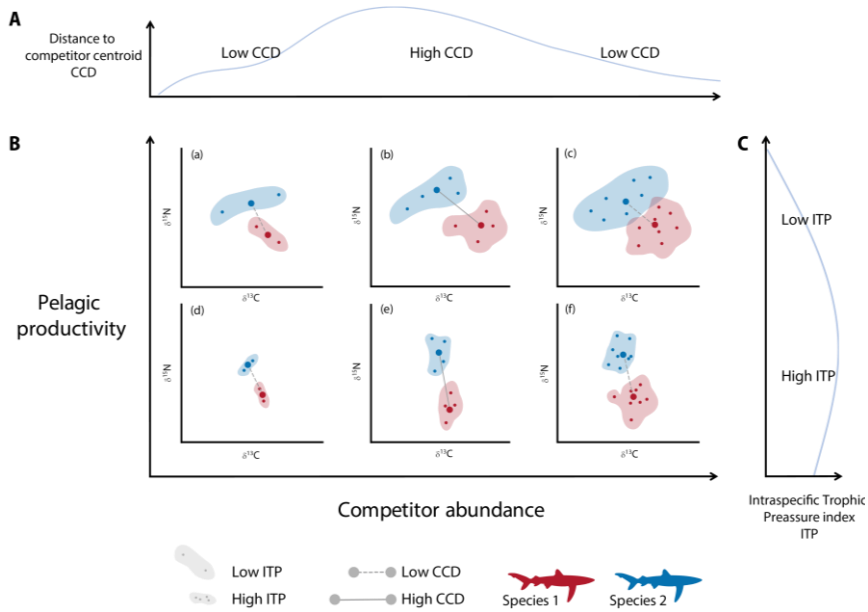
When the abundance of competitors is low, competition for resources is expected to be at its lowest, enabling an extensive niche overlap (Pianka, 1974). Under these conditions, generalist species such as those in this study are expected to feed on whatever is abundant, resulting in similar isotopic values and low isotopic distance between them. Accordingly, our results suggest that

isotopic differences between swordfish and sharks were minimal (i.e., low CCD; Figure 4A and Box 1A) in areas of low potential competitor abundances. As the abundance of competitors increased, the isotopic distance between species increased (i.e., high CCD), suggesting a possible change in trophic behavior through the diversification of prey items. This behavior can be interpreted as an example of food partitioning where species use different resources to avoid competition, which results in a higher isotopic distance (Lesser et al., 2020). However, as potential competitor abundance increased, the isotopic distance decreased, suggesting that in the areas with the highest abundance of competitors, the resource partitioning decreased. This could be explained by competitors aggregating in areas where food resources are abundant, leading to isotopic similarities due to similar prey consumption (Box 1).

In the open ocean, the distribution and the availability of pelagic resources over time and space are key factors shaping top predators' feeding behavior (Z. Li et al., 2024). Our results point to pelagic productivity as the main driver shaping the intraspecific competition and support the hypothesis of niche partitioning between conspecifics being reduced (i.e., low ITP) under a high resource availability scenario (Box 1C). Additionally, we anticipated that an increase in the abundance of competitors would enhance trophic niche segregation by reducing *per capita* food availability. However, we did not find a relationship between intraspecific trophic pressure and fishing effort, and found the highest isotopic distances in areas of intermediate predator abundance, although the limited number of intermediate values increased uncertainty in the observed peak (Figure 4A).

The different scenarios illustrating how isotopic niche dynamics are influenced by pelagic productivity and competitor abundance according to our results (see Box 1B) suggest that at both productivity scenarios, our indicators exhibit similar variations for both competitor abundance extremes (i.e., low ITP and low CCD

Box 1. Conceptual framework based on the modeled relationships between competitor abundance and isotopic distance to competitor centroid (CCD), and pelagic productivity and the Intraspecific Trophic Pressure index (ITP).



This figure illustrates the relationship between the different drivers and the different metrics used in this study to evaluate isotopic niche metrics as a proxy of intra- and interspecific competition. The blue lines represent the output from the GAMs showing (A) how the distance between centroids (y-axis) changes with competitor abundance (x-axis), and (C) how the intraspecific trophic pressure (x-axis) changes with pelagic productivity (y-axis). Panel B presents a matrix summarizing the interaction between pelagic productivity and competitor abundance, highlighting their effects on ITP and CCD. Each point in (B) represents individual isotopic values for species 1 (red) and species 2 (blue), bigger points denote the centroid for each species isotopic niche, represented by the shadowed area, and the grey lines represent the distance between the centroids.

Box 1. (continued)

The matrix is divided into six quadrants, representing various combinations of competitor abundance and pelagic productivity:

- a) *High pelagic productivity, Low competitor abundance*: Both ITP and CCD were low, reflecting a scenario where abundant resources minimize competition and niche segregation is not necessary.
- b) *High pelagic productivity, Intermediate competitor abundance*: Low ITP and high CCD characterize this scenario. Resource availability allows species to diversify their niches, increasing isotopic distance among species and maintaining the intraspecific pressure low.
- c) *High pelagic productivity, High competitor abundance*: Under conditions of high resource availability and competitor abundance, intraspecific competition may become more prevalent than interspecific competition. In such cases, species may maintain broader isotopic niches (low ITP) to reduce overlap with conspecifics, even if it results in greater isotopic overlap with other species (low CCD).
- d) *Low pelagic productivity, Low competitor abundance*: With fewer competitors and low productivity, competition persists due to resource scarcity, with limited isotopic niche separation (low CCD) and high competition among conspecifics (high ITP).
- e) *Low pelagic productivity, Intermediate competitor abundance*: The moderate abundance of competitors may encourage niche diversification, increasing isotopic distance between species (high CCD) while maintaining intraspecific competition pressure. This could be driven by density-dependent processes, where the most direct competitor is another individual with identical ecological requirements (high ITP).
- f) *Low pelagic productivity, High competitor abundance*: Limited resources likely intensify competition, reducing isotopic differentiation among conspecifics and competitors due to feeding on the same prey. This scenario results in high ITP and low CCD.

were found for the high pelagic productivity scenario at the lowest and highest competitor abundances). This limitation indicates that using only these two metrics may not be sufficient to comprehensively understand niche dynamics. It is likely that additional factors and mechanisms, such as behavioral plasticity, prey switching, or fine-scale habitat use, are influencing niche partitioning in ways not captured by isotopic metrics alone. Thus, our inferences should be viewed as conservative, and future studies should consider integrating

complementary approaches, such as tagging studies (e.g., Houssard et al., 2017), to gain a more holistic perspective on competitive interactions and resource use.

Limitations and broader implications

We examined trophic niche and food resource partitioning between ecologically similar species and conspecifics using isotopic niches and diet reconstructions through mixing models. White muscle isotopes reflect diet over several months, offering an integrated summary of trophic interactions but limiting fine-scale resolution. Moreover, while using temporally averaged pelagic productivity values helped capture broad-scale influence on competition, it does not account for potential seasonal variability. Nevertheless, the inclusion of pelagic productivity and potential competitor abundance significantly improved model performance over the null models, indicating their relevance in shaping ITP and CCD values, respectively. Our findings indicate that *per capita* food availability, likely driven by pelagic productivity and potential competitor abundance, plays a relevant role in shaping niche partitioning. However, we acknowledge that niche partitioning extends beyond the trophic dimension, encompassing other ecological and behavioural factors, including fine-scale temporal and spatial segregations (e.g., seasonal and diel variability in diving behavior; R. K. Logan, Vaudo, et al., 2023b). Despite overlapping horizontal habitats, both shark species undertake vertical movements up to 300 m during the day, returning to the surface at night, whereas swordfish display more pronounced vertical movements, spending daylight hours below the mixing layer and surfacing at night, as inferred by their high consumption of mesopelagic prey (Andrzejaczek et al., 2022; J. M. Logan et al., 2021; Madigan et al., 2021; Santos et al., 2021). Future research could leverage this framework to integrate these other dimensions, providing a more comprehensive understanding of niche

partitioning between ecologically similar species and disentangling finer temporal dynamics.

Our modeling approaches predict that blue sharks were particularly abundant in the Gulf of Cádiz and the southern waters of Portugal, thus aligning with findings from previous electronic tagging studies (Coelho et al., 2018; Queiroz et al., 2012). Model predictions also reveal higher abundances of shortfin mako sharks in the Gulf of Cádiz and the southern waters of the Canary Islands, as described in Santos et al. (2021). Our predictions for swordfish are consistent with previous research on this species and suggest higher abundances around the Canary Islands (Schirripa et al., 2021). We also provide the first assessments of swordfish distribution for the western Mediterranean Sea, despite the high commercial value of this species and the declining trends of this stock in the Mediterranean over the last 50 years (ICCAT, 2023). The reduced populations of the three species in the Mediterranean Sea, with shortfin makos nearly absent in the western part, make them more vulnerable to stochastic ecological stressors (Chase & Leibold, 2003) and highlight their vulnerability in the Mediterranean region. In this context, we could not estimate the diet of shortfin mako sharks in the Mediterranean due to insufficient samples. For the Canary Islands, while 10 samples for shortfin mako were available, larger sample sizes would provide more robust diet inferences.

Understanding how resource use and niche partitioning have shifted in response to historical variability can provide insights into how predators will respond to future environmental changes (Portner et al., 2025). According to our results, if global change, including fishing and climatic pressures, leads to declining prey abundance, interspecific competition will likely increase and may impact less opportunistic species more severely (Weideli et al., 2023). Further prey reductions may increase intraspecific pressure, driving shifts in feeding behavior and expanding niches, potentially causing greater overlap and

interspecific competition. Those may explain the low numbers of shortfin mako and blue sharks in the Mediterranean, where competitive pressures together with the slower intrinsic rates of population growth of sharks may favor swordfish (Dulvy et al., 2024). On the other hand, changes in prey abundance, particularly of squid, the main prey for the three species, are expected to be spatially heterogeneous (Veloy et al., 2024). In areas of high trophic overlap of predators, prey changes will potentially impact all species, while in regions where the overlap is lower, segregation could allow ecologically redundant species, less affected by the changes, to compensate for the ecological roles of more impacted species, potentially buffering ecosystem-level effects.

In conclusion, our study highlights the interplay between resource use, competition, and oceanic productivity between large pelagic fishes in the Mediterranean and the northeast Atlantic. These pressures may intensify intra- and interspecific competition, potentially favoring species with adaptive advantages such as opportunistic feeding or rapid reproductive rates. Understanding these interactions becomes crucial for predicting population trends and developing effective conservation strategies that address both direct and indirect consequences of alterations in food availability.

SUPPLEMENTARY MATERIALS

Supplementary methods: Meta-analysis development

BSIMM inputs included isotopic values of shortfin mako, blue shark and swordfish, and their potential prey species. Potential prey were grouped based on similar isotopic values and taxonomy following Phillips et al. (2005): mesopelagic fishes; gadiforms, small and medium pelagic fishes; squid group I; squid group II; and gelatinous plankton. Isotopic values of prey were obtained from the literature (Table S2). When isotopic values from prey species were not found for the selected region (e.g., *Histioteuthis bonnellii* from the Gulf of Cádiz), isotopic values from the closest available area (e.g., northwestern Iberia) were corrected for $\delta^{15}\text{N}$ using Somes et al. (2010) as baseline.

The different studies included samples from different species, areas, and years. These arguments prevent direct comparisons among $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. Therefore, a meta-analysis was conducted to obtain the mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for each prey group and region.

In meta-analysis, statistical independence is one of the key assumptions when pooling effect sizes (i.e., $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values) (Higgins et al., 2009). This assumption was violated in our database because different studies are gathered and the same study can report several effect sizes for different species. To overcome this issue, we accounted for these dependencies through a Hierarchical Meta-Analysis Model (Harrer et al., 2021). To calculate the heterogeneity variance in all models, we used the Restricted Maximum Likelihood Estimator (REML; Viechtbauer, 2005) as it is the most robust method for continuous effect sizes (Langan et al., 2019). All models were fitted through the function “*rma.mv*” from the *metafor* R package v3.4-0 (Viechtbauer, 2010).

Supplementary methods: Relative abundance from standardized catch data

We fitted Generalized Additive Models to estimate the relative abundance of the three studied species using the catch per unit effort (nCPUE) from a total of 2,534 longline sets from the Spanish longline fleet targeting swordfish and albacore tuna along the study area between 2015 and 2019 (IEO Observer Program). Models were fitted with a negative binomial error distribution to account for dispersion in the catch data including linear and additive relations with the covariates, and spatial variability, according to the following equation:

$$Y_{ijks} \sim \text{Gamma}(\mu_{ijks}, \phi), \quad i = 1, \dots, n,$$

$$\log(\mu_{ijks}) = \sum_j \beta_j X_{ij} + f_k(X_{ik}) + f_s(x_i, y_i),$$

where Y_{ijks} represents the niche metric at the i observation with a total of n observations. Y_{ijks} follows a Gamma probability distribution with parameters μ_{ijks} , the number of individuals caught; and ϕ , the dispersion. The parameter of interest μ_{ijks} is linked to the predictor by a log link function; and the predictor contains a j number of fixed effects $\sum_j \beta_j X_{ij}$; a k number of smooth functions $f_{ik}(X_{ik})$; and a f_s tensor effect for the spatial variability $f_s(x_i, y_i)$ where x_i and y_i correspond to the latitude and longitude of the observation i . The number of hooks was included as an offset variable. The longline type was included as a fixed factor, while year, month and boat were treated as random effects to account for variability in sampling effort and fishing efficiency.

$$n_{\text{individuals}} \sim \text{te}(\text{LON}, \text{LAT}) + \text{longline} + s(\text{boat}, \text{bs} = \text{re}) + s(\text{year}, \text{month}, \text{bs} = \text{re}) \\ + \text{offset}(\log(n_{\text{hooks}}))$$

Separate models were fitted for each species and basin (Mediterranean and Atlantic), resulting in five models (Table S1), with no model adjusted for mako sharks in the Mediterranean Sea due to an excess of zero catch observations. These models were then used to predict the number of individuals caught per

1,000 hooks for each grid cell and longline configuration, providing a spatially explicit estimate of species relative abundance across the study area.

Supplementary methods: Competition metrics and relationship with drivers

We fitted Generalized Additive Models to evaluate the influence of environmental and anthropogenic drivers in the isotopic niche of large pelagic predators. Models for Intraspecific Trophic Pressure index (ITP) and distance to the competitor's centroid (CCD) were fitted with a Gaussian distribution including linear and additive relations with the covariates, and spatial variability, according to the following equation:

$$Y_{ijks} \sim \text{Gamma}(\mu_{ijks}, \phi), \quad i = 1, \dots, n,$$

$$\log(\mu_{ijks}) = \sum_j \beta_j X_{ij} + f_k(X_{ik}) + f_s(x_i, y_i),$$

where Y_{ijks} represents the niche metric at the i observation with a total of n observations. Y_{ijks} follows a Gamma probability distribution with parameters μ_{ijks} , the mean of the proportion; and ϕ , the dispersion. The parameter of interest μ_{ijks} is linked to the predictor by a log link function; and the predictor contains a j number of fixed effects $\sum_j \beta_j X_{ij}$; a k number of smooth functions $f_k(X_{ik})$; and a f_s tensor effect for the spatial variability $f_s(x_i, y_i)$.

All predictor variables were checked for potential Spearman correlation, and Chl was excluded ($\text{corr} > 0.8$, Figure S2).

We aimed to select the simplest model that maintained strong performance, avoiding unnecessary complexity or overfitting. For that, 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 of the 5 best-fitted models.

Supplementary figures

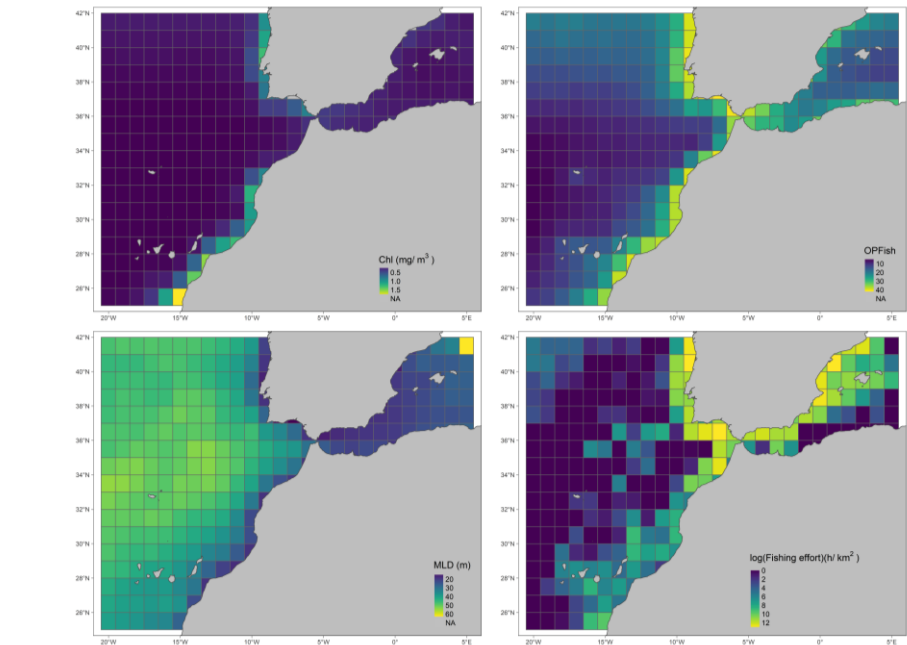


Figure S1. Average value per grid cell of the potential environmental drivers obtained from Copernicus and cumulative fishing effort calculated from Global Fishing Watch for the 2015-2019 period. Fishing effort is represented in a logarithmic scale for visualization.

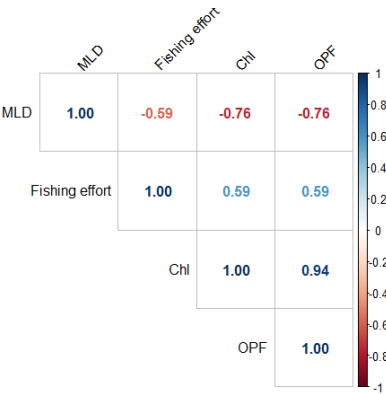


Figure S2. Spearman correlation between the environmental variables and fishing effort. MLD: Mixed layer depth (mean); Fishing effort: Cumulative fishing effort (sum); Chl: Chlorophyll concentration (mean at sea surface); OPF: Ocean Productivity available to Fish (mean).

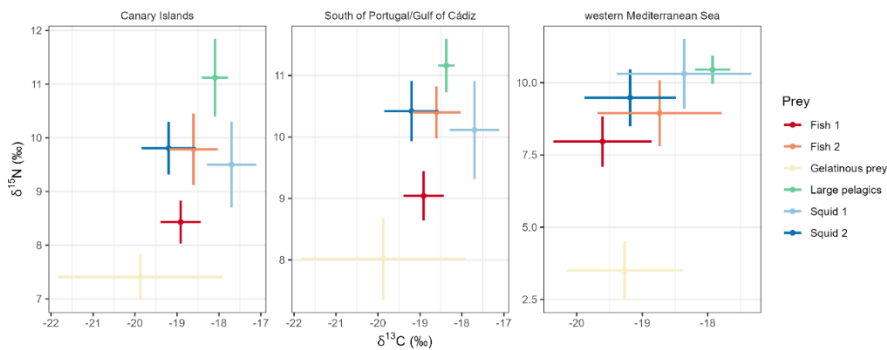


Figure S3. Isotopic values (mean $\pm$ SD) for the groups of potential prey sources described in Table S3.

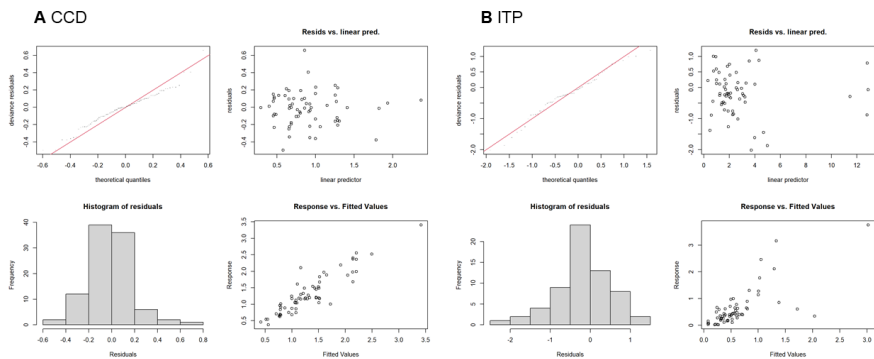


Figure S4. Diagnostic plots for the GAMs for (A) the distance to competitor centroids (CCD) and (B) Intraspecific Trophic Pressure (ITP) index.

Supplementary tables

Table S1. Summary of the selected GAM for each prey consumption, showing the percentage of deviance explained (DE).

Species	Basin	%DE
Shortfin mako	Atlantic	43.8
Blue shark	Atlantic	52.4
	Mediterranean	61.5
Swordfish	Atlantic	55.2
	Mediterranean	49.2

Table S2. Diet-tissue discrimination factors (DTDF) for shortfin mako, blue shark, and swordfish $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, estimated following Caut et al. (2009).

	DTDF	
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Shortfin mako	1.08 ± 0.25	2.4 ± 0.22
Blue shark	0.92 ± 0.23	2.39 ± 0.3
Swordfish	1.13 ± 0.18	2.62 ± 0.31

Table S3. Isotopic values for the different prey groups obtained from bibliography and pooled through meta-analysis.

Prey	Species	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		References
		Mean	SD	Mean	SD	
Western Mediterranean Sea						
Fish 1 (mesopelagic fishes)	<i>Arctozenus risso</i> , <i>Ceratoscopelus maderensis</i> , <i>Electrona risso</i> , <i>Maurolicus muelleri</i> , <i>Myctophum punctatum</i> , <i>Notoscopelus elongatus</i>	-19.61	0.75	7.97	0.87	Cardona et al. (2007), Fanelli et al. (2011, 2013), Lloret-Lloret et al. (2020), Mir-Arguimbau et al. (2020), Papiol et al. (2013), Valls et al. (2014a, 2014b, 2017)
Fish 2 (gadiforms and pelagic fish)	<i>Gadiculus argenteus</i> , <i>Merluccius merluccius</i> , <i>Micromesistius poutassou</i> , <i>Sardinella aurita</i> , <i>Sardina pilchardus</i> , <i>Trachurus trachurus</i>	-18.74	0.95	8.95	1.14	Albo-Puigserver et al. (2016, 2019), Bachiller et al. (2020, 2021), Barriá et al. (2015), Cardona et al. (2012), Fanelli et al. (2013), Gómez-Campos et al. (2011), Lloret-Lloret et al. (2020), Mir-Arguimbau et al. (2020), Navarro et al. (2009), Papiol et al. (2013, 2017), Valls et al. (2014b)

Chapter 3

Squid 1 (ommastrephids)	<i>Todarodes sagittatus</i>	-18.36	1.03	10.31	1.21	Cardona et al. (2012, 2015), Gómez-Campos et al. (2011), Valls et al. (2014b, 2017)
Squid 2 (midwater and angel squid)	<i>Abralia veranyi</i> , <i>Ancistroteuthis lichtensteinii</i>	-19.19	0.70	9.48	0.99	Barría et al. (2015), Valls et al. (2014b, 2017)
Gelatinous prey	<i>Cotylorhiza tuberculata</i> , <i>Pelagia noctiluca</i> , <i>Salpa</i> sp.	-19.27	0.89	3.51	1.02	Cardona et al. (2007, 2012, 2015), Fanelli et al. (2011, 2013), Mir-Arguimbau et al. (2020), Revelles et al. (2007), Tecchio et al. (2013), Tilves et al. (2018a, 2018b), Valls et al. (2014b)
Large pelagics	<i>Thunnus alalunga</i> , <i>Thunnus thynnus</i> , <i>Stenella coeruleoalba</i>	-17.93	0.27	10.45	0.49	Cardona et al. (2012), López-Berenguer et al. (2020), Medina et al. (2015), Revelles et al. (2007), Varela et al. (2012, 2018b, 2019)
South of Portugal/Gulf of Cádiz						
Fish 1 (mesopelagic fishes)	<i>Diaphus brachycephalus</i> , <i>D. holti</i> , <i>D. rafinesquii</i> , <i>Chauliodus sloani</i> , <i>Maurolicus muelleri</i>	-18.91	0.48	9.04	0.4	Olivar et al. (2019), Sorell et al. (2017)
Fish 2 (gadiforms and pelagic fish)	<i>Merluccius merluccius</i> , <i>Micromesistius poutassou</i> , <i>Sardina pilchardus</i> , <i>Scomber</i> sp., <i>S. colias</i> , <i>S. scombrus</i> , <i>Trachurus</i> sp., <i>T. picturatus</i> , <i>T. trachurus</i>	-18.61	0.58	10.4	0.42	Giménez et al. (2017), Romero et al. (2021), Varela et al. (2013, 2018)
Squid 1 (ommastrephids)	<i>Illex coindetii</i> , <i>Todaropsis eblanae</i>	-17.70	0.59	10.11	0.8	Sorell et al. (2017), Varela et al. (2013, 2018a)
Squid 2 (cock- eyed squids)	<i>Histioteuthis bonnellii</i>	-19.20	0.65	10.42	0.49	Mendez-Fernández et al. (2012)
Gelatinous prey	Chaetognaths, Ctenophores, Hydromedusae, Scyphomedusae, Siphonophores, Tunicates	-19.87	1.95	8.02	0.67	Chi et al. (2021)

Large pelagics	<i>Xiphias gladius</i> , <i>Thunnus alalunga</i> , <i>Thunnus thynnus</i> , <i>Stenella</i> <i>coeruleoalba</i>	-18.37	0.20	11.16	0.44	Fernández-Corredor et al. (2023), Pintado-Herrera et al. (2024), Prieto-Amador et al. (2022), Varela et al. (2018a, 2023)
Canary Islands						
Fish 1 (mesopelagic fishes)	<i>Diaphus</i> <i>brachycephalus</i> , <i>D.</i> <i>holti</i> , <i>D. rafinesquii</i> , <i>Chauliodus sloani</i> , <i>Maurolicus muelleri</i>	-18.91	0.48	8.43	0.4	Olivar et al. (2019), Sorell et al. (2017)
Fish 2 (gadiforms and pelagic fish)	<i>Merluccius</i> <i>merluccius</i> , <i>Micromesistius</i> <i>poutassou</i> , <i>Sardina</i> <i>pilchardus</i> , <i>Scomber</i> sp., <i>S. colias</i> , <i>S.</i> <i>scombrus</i> , <i>Trachurus</i> sp., <i>T. picturatus</i> , <i>T.</i> <i>trachurus</i>	-18.61	0.58	9.79	0.67	Giménez et al. (2017), Romero et al. (2021), Varela et al. (2013, 2018)
Squid 1 (ommastrephids)	<i>Illex coindetii</i> , <i>Todaropsis eblanae</i>	-17.70	0.59	9.5	0.8	Sorell et al. (2017), Varela et al. (2013, 2018a)
Squid 2 (cock- eyed squids)	<i>Histioteuthis</i> <i>bonnellii</i>	-19.20	0.65	9.81	0.49	Mendez-Fernández et al. (2012)
Gelatinous prey	Chaetognaths, Ctenophores, Hydromedusae, Scyphomedusae, Siphonophores, Tunicates	-19.87	0.74	7.41	0.42	Chi et al. (2021)
Large pelagics	<i>Xiphias gladius</i> , <i>Thunnus thynnus</i> , <i>Delphinus delphis</i> , <i>Stenella</i> <i>coeruleoalba</i> , <i>Stenella frontalis</i>	-18.09	0.31	11.12	0.72	Bode et al. (2022), Fernández-Corredor et al. (2023), Varela et al. (2022)

Table S4. Summary of PERMANOVA test examining differences in isotopic composition ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) between areas (western Mediterranean Sea, South of Portugal/Gulf of Cádiz, and the Canary Islands), species (mako, blue shark, and swordfish), and their interaction.

	Df	SumOfSqs	R2	F	Pr(>F)
Area	2	133.25	0.14	44.58	1.00E-04
Species	2	64.57	0.07	21.60	1.00E-04
Area × Species	4	32.76	0.04	5.48	2.00E-04
Residual	463	691.96	0.75		
Total	471	922.55	1.00		

Pairwise tests	Df	SumOfSqs	R2	F	p
<i>Species</i>					
Shortfin mako vs Blue shark	1	0.35	0.01	0.18	0.836
Shortfin mako vs Swordfish	1	25.75	0.06	18.10	0.001
Blue shark vs Swordfish	1	120.51	0.14	69.47	0.001
<i>Area</i>					
western Med. vs Portugal/Cádiz	1	122.57	0.16	66.23	0.001
western Med. vs Canary Is.	1	53.53	0.08	30.45	0.001
Portugal/Cádiz vs Canary Is.	1	10.30	0.03	7.52	0.001

Table S5. Isotopic niche estimates based on 95% kernel utilization densities (KUD) for swordfish, shortfin mako, and blue shark captured in the Canary Islands, the South of Portugal, and the western Mediterranean Sea. The percentage of overlap of the isotopic area of groups is shown as the first column group versus the ones of the first row.

		Isotopic niche area (95% KUD)	Isotopic niche overlap (%)		
			Shortfin mako	Blue shark	Swordfish
Canary Islands					
	Shortfin mako	7.13	-	82.9	70.9
	Blue shark	10.18	58.1	-	54.5
	Swordfish	7.50	67.3	74	-
South of Portugal/Gulf of Cádiz					
	Shortfin mako	8.80	-	80.2	57.8
	Blue shark	10.83	65.1	-	39.5
	Swordfish	7.42	68.6	57.6	-
Western Mediterranean					
	Blue shark	23.06		-	41.8
	Swordfish	10.47		92.1	-

Table S6. Selected GAMs for the distance to competitor centroids (CCD) and Intraspecific Trophic Pressure (ITP) index. SE: Standard Error, edf: Effective Degrees of Freedom, DE: deviance explained.

Parametric coefficients				Smooth terms			
	Estimate	SE			edf		DE
CCD							
(Intercept)	0.912	0.024	***	te(LON,LAT)	22.486	***	82.6%
				s(all spp. abundance)	8.837	***	
ITP							
Shortfin mako	13.606	4.465	**	te(LON,LAT)	8.378	**	52.6%
Blue shark	-11.17	4.466	*	s(opf)	2	.	
Swordfish	-11.84	4.467	*				

Significant codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1

Table S7. Mixing model diagnostics

		Gelman-Rubin Diagnostic	Geweke Diagnostic
Western Mediterranean Sea	Blue shark	Out of 39 variables: 0 > 1.01 0 > 1.05 0 > 1.1	Variables outside +/-1.96 in each chain (out of 39): Chain 1 Chain 2 Chain 3 1 0 2
	Swordfish	Out of 164 variables: 0 > 1.01 0 > 1.05 0 > 1.1	Variables outside +/-1.96 in each chain (out of 164): Chain 1 Chain 2 Chain 3 0 35 6
South of Portugal/Gulf of Cádiz	Shortfin mako	Out of 25 variables: 0 > 1.01 0 > 1.05 0 > 1.1	Variables outside +/-1.96 in each chain (out of 25): Chain 1 Chain 2 Chain 3 1 1 2
	Blue shark	Out of 83 variables: 0 > 1.01 0 > 1.05 0 > 1.1	Variables outside +/-1.96 in each chain (out of 83): Chain 1 Chain 2 Chain 3 1 3 8
	Swordfish	Out of 71 variables: 0 > 1.01 0 > 1.05 0 > 1.1	Variables outside +/-1.96 in each chain (out of 71): Chain 1 Chain 2 Chain 3 0 0 1
Canary Islands	Shortfin mako	Out of 21 variables: 0 > 1.01 0 > 1.05 0 > 1.1	Variables outside +/-1.96 in each chain (out of 21): Chain 1 Chain 2 Chain 3 4 0 1
	Blue shark	Out of 48 variables: 0 > 1.01 0 > 1.05 0 > 1.1	Variables outside +/-1.96 in each chain (out of 48): Chain 1 Chain 2 Chain 3 1 1 4
	Swordfish	Out of 34 variables: 0 > 1.01 0 > 1.05 0 > 1.1	Variables outside +/-1.96 in each chain (out of 34): Chain 1 Chain 2 Chain 3 0 0 2

General discussion

The central aim of this thesis was to generate new knowledge on the trophic ecology of large pelagic predatory fishes. Given that trophic interactions play a fundamental role in shaping ecosystem dynamics and functioning, accurately estimating the trophic ecology of predators is essential for advancing our understanding of natural systems (Nielsen et al., 2018). This thesis went beyond estimating trophic ecology by also evaluating its variability, particularly spatial variability, and examining how different biological, environmental, and anthropogenic factors interact to shape the trophic and competition dynamics of large pelagic fish. The studies addressed not only *what* predators eat, but also *how* and *why* their diets vary.

This discussion integrates the results obtained throughout the chapters of the thesis and frames them within the context of five overarching research questions:

1. Why should we study the trophic ecology of large pelagic fishes?
2. How can we best investigate their trophic ecology?
3. What are these predators feeding on?
4. How is global change affecting it?
5. How can we translate this into conservation and management?

Large pelagic fishes as sentinel species

To address the question of *why* it is important to study the trophic ecology of large pelagic fishes, this section explores their role as sentinel species, highlighting how their feeding ecology can provide critical insights into ecosystem dynamics and the impacts of environmental change.

As introduced earlier in this thesis, the difficulties inherent in observing the highly dynamic ocean at relevant timescales, along with the associated

technological constraints, limit the understanding of the scale and impact of environmental variation in the open ocean (see [The pelagic realm as a case study](#)).

While traditional observing systems (e.g., ship- and shore-based sampling, satellite-borne sensors) can monitor a wide range of environmental and physical properties, these measures are often constrained to single trophic levels or spatial scales (e.g., measurements derived from satellite data limited to the ocean surface). Therefore, understanding the impact of environmental and human stressors on the open ocean and the ecosystem response, which includes alterations in ecosystem function, distribution and abundance shifts of prey, cascading effects, and changes in food-web dynamics, requires new approaches.

In that sense, the use of “sentinel” species appears to provide information about unobserved components of the ecosystem (Hazen et al., 2019, 2024). Here, we focus on elucidating sentinels (i.e., when there are unmeasured or unstudied components of an ecosystem about which the sentinel provides information) (Hazen et al., 2019). These **ecosystem sentinels** are being increasingly used to improve our comprehension of human impacts and ecosystem changes that are otherwise difficult to directly observe or measure, particularly in data-sparse and highly variable regions such as the open ocean (e.g., Beltran et al., 2025). However, selecting the appropriate species can be challenging and includes criteria such as visibility, ease of sampling, and having a clear and measurable response to ecosystem perturbations (Clark-Wolf et al., 2024; Hazen et al., 2024).

One of the measurable attributes of sentinel species is their trophic ecology, offering direct insights into trophic position and ecosystem trophodynamics (Hazen et al., 2019). Top predators are good candidates as they are usually long-lived, large-bodied species that can be more sensitive and indicative of change

at multiple trophic levels, offering insights into prey species in areas and at scales that are otherwise difficult (when not impossible) to measure (Clark-Wolf et al., 2024).

Many marine top predators have been proposed as ecosystem sentinels (e.g., elephant seals, penguins; Beltran et al., 2025; Schoombie et al., 2024). In particular, large pelagic predatory fishes (i.e., tunas, billfishes, and oceanic sharks) are strong candidates for assessment of oceanic ecosystems due to several reasons (Juan-Jordá et al., 2022):

- 1) They are among the largest and most functionally unique megafaunal predators in pelagic ecosystems, playing a critical role in regulating the structure, function, and stability of oceanic ecosystems (Coll et al., 2024; Fernández-Corredor et al., 2024).
- 2) These highly mobile species often forage in extensive areas across ocean basins, integrating broad-scale prey abundance (Hazen et al., 2024) and providing a valuable indicator of prey populations in important but poorly understood ecosystems such as the open ocean (Beltran et al., 2025; Lorrain et al., 2020).
- 3) They display varying levels of resilience to overfishing and span a broad spectrum of fisheries categories, ranging from economically valuable target species to ecologically significant bycatch (Sharma et al., 2025).
- 4) They are consistently monitored and assessed by the five tuna RFMOs, which have generated time series data on biomass and fishing mortality rates for approximately 60% of their populations (Juan-Jordá et al., 2022).

Focusing on the three studied species —swordfish, blue sharks, and shortfin makos— they were all described as deep-diving, generalist predators (see [Trophic ecology overview for large pelagic predators](#)), and changes in their diet can be indicative of changes at the community level (Hazen et al., 2019).

However, we focus on swordfish as a potential sentinel species. Using commercial species guarantees a relatively easy access to samples and their continuous availability, allowing for large-scale monitoring. Although blue and shortfin mako sharks are commercially fished in the Atlantic, their capture in the Mediterranean is not allowed as direct catch. Therefore, together with the low abundances of both species reported in **Chapter 3**, swordfish was the most suitable candidate to act as a sentinel species in our study area.

As shown in **Chapter 1**, changes in time in the swordfish diet seemed to align with variations in prey availability documented from fisheries data. Their frequent foraging in mesopelagic waters, for which the lack of data presents a significant challenge, provides an opportunity for long-term monitoring of the overlooked mesopelagic community. Furthermore, we showed in **Chapter 2** that 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. Consequently, this supports the use of swordfish as valuable sentinels of the pelagic realm. Swordfish have also been proposed as a promising ecosystem sentinel species in the North Pacific, where long-term data on their trophic ecology were analyzed by Preti et al. (2025), finding that they largely track prey availability in their environment.

Monitoring ecosystem sentinels can also guide conservation efforts. Besides diet, variations in the demography of these sentinel species can also inform us on how fluctuations in lower trophic levels are traveling up the food web. Nevertheless, ecosystem sentinels are not only useful for monitoring the environment but also for informing management of potential ecosystem responses (e.g., diet projections for swordfish under different climate change scenarios, **Chapter 2**). By using sentinel species that are trophically linked and measured on shorter timescales, managers can more effectively detect and track shifts in ecosystem dynamics (Clark-Wolf et al., 2024). For example,

population declines in marine predators have typically presaged fisheries collapses (Velarde et al., 2019). However, sentinels are rarely used as actual scientific or management tools (Clark-Wolf et al., 2024) (see [Applications to conservation and management](#)).

Methodological considerations

In the marine environment, animal behavior, such as feeding and competitive interactions, is challenging to capture and quantify (Nielsen et al., 2018; Schoombie et al., 2024). Therefore, *how can we best investigate their trophic ecology?* We will need to use different combinations of complementary methods while we continue developing advanced dietary assessments. The low encounter rates, logistical difficulties, and the subsequent expense of collecting biological samples in the pelagic environment often result in a lack of empirical studies for large pelagic predators and their trophic ecology has traditionally been studied via SCA and, more recently, via chemical analyses (e.g., SIA, DNA metabarcoding). Biologging and biotelemetry also offer complementary tools to traditional methods for studying predator–prey interactions and feeding behaviour (Queiroz et al., 2017). For example, animal-borne video cameras have been employed to identify prey, capture events, and foraging behaviors in different marine predators, including large pelagic fishes (R. K. Logan, Luongo, et al., 2023; Schoombie et al., 2024). However, these recordings are typically limited to a few hours, and the quality of the data is influenced by ambient light conditions and water clarity. Consequently, additional methods are required to describe the trophic ecology of large pelagic diving predators.

Strengths and limitations of the different diet methodologies

Although it provides highly resolved, species-level dietary information (Hyslop, 1980), reconstructing the true diet of a species using only stomach contents can be biased towards species that have hard structures with slow digestion rates

(e.g., otoliths from fish or beaks from cephalopods; Amundsen & Sánchez-Hernández, 2019). This is supported by results obtained in **Chapter 1**, which showed a higher proportion of cephalopods and only two occurrences of gelatinous prey in stomach contents than in the diet obtained through BSIMMs. On the other hand, SIMM techniques infer prey assimilation, which do not always reflect the ingested diet proportions (e.g., Chiaradia et al., 2014), require prior knowledge of potential prey items, and are limited in their ability to assess the full diversity and specificity of a consumer's diet.

To overcome those biases, **Chapter 1** combined both SCA and SIA by using the prey proportions found in stomach contents to inform the mixing models, which was particularly helpful for distinguishing between fish sources that had similar isotopic values, obtaining a more accurate diet description for juvenile swordfish. However, to reliably use prior information in mixing models, an accurate stomach content analysis is required; otherwise, incomplete dietary data may bias the resulting diet estimates. This approach, however, demands a substantial number of stomach samples, which was not feasible for the analyses presented in Chapters 2 and 3. In **Chapter 2**, mixing models were applied at a fine spatial scale, which would require an individual SCA for each grid cell. In **Chapter 3**, diet was estimated for three species across three distinct regions, implying the need for nine separate SCA studies. Moreover, while SIA can be a non-lethal method, SCA normally requires dead individuals, which is not desired for the targeted species, particularly the blue shark and the shortfin mako, for which capture is prohibited in the Mediterranean. As a result, a literature review was conducted in both chapters to identify the potential prey sources for the mixing models.

Novelty and improvement provided by our framework

Rather than providing a detailed description of the diet of large pelagic predators, this thesis aimed to understand how temporal (**Chapter 1**) and

spatial (**Chapter 2**) variability in diet and competition (**Chapter 3**) might be driven by the selected biological (predator length, competitor abundance), environmental (temperature, dissolved oxygen, MLD, productivity), and anthropogenic (fishing pressure) drivers. To achieve that, we estimated both diet and competition metrics at a small-scale resolution. The resulting diet and competition metrics values were then used as response variables in the GAMs to unravel their relationship with the selected drivers. This approach allowed us to apply a statistical framework for exploring diet composition both in space and time (**Chapter 2**) and understand how the external drivers influence niche partitioning both between and within the three studied species (**Chapter 3**).

Continuous monitoring of the trophic ecology of large pelagic predators is essential for sustainable management and the long-term viability of their populations. However, trophic studies of pelagic predators are often spatially and/or temporally restricted (Duffy et al., 2017; Hazen et al., 2019; Ouled-Cheikh, Giménez, et al., 2022), leaving a gap in knowledge on the potential impacts of environmental variability and fishing pressure. This gap is addressed in **Chapter 2** by examining the relationship between fishing, environment, and prey consumption with a statistical approach (i.e., GAMs) that allowed us to explore and predict how diet can change in space (using a large-scale survey covering the western Mediterranean Sea and the adjacent Atlantic waters) and time (testing different future scenarios of global change). GAMs offer a powerful, flexible, and interpretable framework for analyzing the non-linear relationships often found in trophic ecology. Their ease of use, fast computation, and ability to visualize complex ecological patterns make them an ideal choice for ecologists studying predator-prey interactions and food web dynamics. Using the swordfish as a case study, we show that GAMs provide a useful framework for identifying the most influential drivers in prey consumption and assessing changes in the diet of these species. We estimated the diet based on stable isotopes analysis (i.e., BSIMMs), which offered an efficient approach to

assessing trophic dynamics, as it facilitates sample collection and storage and streamlines laboratory procedures (i.e., tissue samples are easier to obtain and smaller in size than stomachs, and SIA are less time-consuming than SCA). Altogether, our framework helps shorten the gap between scientific findings and their integration into policy, providing a first step towards adaptive management.

A similar framework is used in **Chapter 3** to understand which drivers are influencing competition in large pelagic predators. Most studies utilizing SIA have focused on either intra- or interspecific competition, with relatively few addressing both components concurrently within ecological communities or across environmental gradients (e.g., Teichert et al., 2024). Here, we calculate different isotopic niche metrics (i.e., the distance to the competitor's centroid and the Intraspecific Trophic Pressure index) and use them as response variables in GAMs to unravel the relationship of different drivers of food availability (i.e., fishing pressure, environmental conditions, abundance of competitors) with the potential intra- and interspecific competition between swordfish, blue shark, and shortfin mako shark. The resulting outputs allowed us to show a conceptual framework that illustrates the relationship between potential interspecific competition (estimated through isotopic distance to competitor centroid) and competitor abundance, and between potential intraspecific competition (estimated through the Intraspecific Trophic Pressure index) and pelagic productivity.

Trophic ecology overview for large pelagic predators

A comprehensive understanding of the diets of large marine predators is crucial for elucidating their ecological roles and for identifying the specific challenges they may encounter due to shifts in the availability and accessibility of their preferred prey. Thus, one of the central questions in the fields of ecology and ecosystem management is “*What does this predator feed on?*” (Nielsen et al.,

2018). The three studied species are known to feed on multiple prey types and exploit diverse trophic resources and habitats (Y. Li et al., 2016; Rosas-Luis et al., 2017). They reach deeper foraging depths than other predators, with maximum dive depths during the day (Portner et al., 2025). This thesis describes the trophic ecology of swordfish (**Chapters 1, 2, and 3**), blue sharks (**Chapter 3**), and shortfin makos (**Chapter 3**) across the study area using isotopic mixing models. In addition, mixing models for swordfish were combined with stomach content analysis for the first time to study their diet in the northwestern Mediterranean (**Chapter 1**). Here, we present an overview of the main findings for each species' diet.

Swordfish

Overall, **swordfish** showed a generalist and flexible feeding strategy and can exploit a wide range of prey species. These include prey from demersal, epipelagic, mesopelagic, and bathypelagic habitats, which evidences the swordfish's vertical migratory behavior and supports the benthopelagic coupling role of this species.

Previous studies have reported information on the diet of swordfish in our study area, with several studies for the western Mediterranean Sea (Biton-Porsmoguer et al., 2022; Cardona et al., 2012; Carmona-Antoñanzas et al., 2016; Fernández-Corredor et al., 2023; Navarro et al., 2017), and only two for the Atlantic part (Abid et al., 2018; Hernández-García, 1995). Here, we found that swordfish predominantly feed on squid, mainly midwater and angel squid in the Mediterranean and cock-eyed squids in the Atlantic, and fish, with higher proportions of mesopelagic fish in the Mediterranean. However, as shown by Cardona et al. (2012), our analyses point to gelatinous plankton as an overlooked prey, particularly relevant in the diet of small juveniles (**Chapter 1**) and around the Gulf of Cádiz (**Chapters 2 and 3**).

Whether swordfish diets rely on cephalopods or fish is commonly discussed (e.g., Salman, 2004). In the Atlantic, while Hernández-García (1995) reported a diet based on cephalopods in the Canary Islands and a mainly piscivorous diet in the Gulf of Cádiz, more recent studies show similar fish and cephalopod consumption in the latter (Abid et al., 2018). A similar pattern is observed in the western Mediterranean, where some studies have pointed to fish as the main prey (e.g., Carmona-Antoñanzas et al., 2016), while more recent ones have shown a diet based on cephalopods (e.g., Biton-Porsmoguer et al., 2022). This shift was also supported by the results in **Chapter 1**, where an increase in cephalopods and a decrease in gadiforms were observed in the swordfish diet from 2012 to 2020. This study, highlighting their flexible and generalist behavior, is one of the few that have evaluated dietary changes in swordfish over time (e.g., Preti et al., 2023).

As swordfish grew in length, their diet shifted toward eating less gelatinous prey and more squid. This pattern was also observed in swordfish from the Pacific Ocean (Young et al., 2006), while other studies found no preference for prey regarding size (e.g., Abid et al., 2018). These differences may be due to local or regional factors that affect marine food webs and prey availability. This highlights the importance of large-scale studies, like the one in this thesis, to better understand the feeding habits of large pelagic predators.

Blue shark and shortfin mako

The trophic ecology of blue and shortfin mako sharks is estimated in **Chapter 3** of this thesis. The **blue shark** diet was based mainly on squid, with cock-eyed squids being the main prey in the Gulf of Cádiz and South of Portugal and ommastrephids in the western Mediterranean. Regarding fish, the main contribution came from small and medium pelagic fish and gadiforms, with a low contribution of mesopelagic fish, slightly higher in the Mediterranean. These results align with previous studies pointing at cephalopods as the main prey,

both from studies based on stomach contents in the northeastern Atlantic (Biton-Porsmoguer et al., 2017; Henderson et al., 2005; Mendonça, 2009; Pusineri et al., 2008) and in the central Mediterranean (Garibaldi & Orsi Relini, 2000; Politi, 1997), and BSIMMs in the northwestern Mediterranean (Nuez et al., 2024). Although their diet seems to be specialized in cephalopods, the wide range of prey items identified in these studies (including invertebrates, small sharks, marine mammals and seabirds) suggests an opportunistic feeding behaviour for the blue shark (Ceyhan et al., 2020; Domingo et al., 2022a; García-Barcelona et al., 2010; Mendonça, 2009). This behavior is also reflected by their wide isotopic niche along the studied area, which can result from trophic plasticity and adaptation to environmental heterogeneity.

The **shortfin mako** is an opportunist and generalist predator (Domingo et al., 2022b), as pointed out by the wide isotopic niche found in **Chapter 3**, and BSIMMs showing similar contributions of the different prey groups. Previous studies in the northeast Atlantic between the Azores Archipelago and the Iberian Peninsula showed a piscivorous diet, with pelagic fish being the main prey for shortfin makos (Biton-Porsmoguer et al., 2017; Maia et al., 2006). In the Mediterranean, the diet of this species is not yet described in detail, indicating a knowledge gap that was not possible to cover in this thesis due to the small sample size of Mediterranean shortfin makos. There is only one report from the central Mediterranean documenting predation events on odontocetes by large shortfin makos (Storai et al., 2001). At early life stages, shortfin makos' diet estimates showed a high contribution of small pelagic fishes, largely derived from coastal-pelagic habitats (Gambardella et al., 2025). Predation on marine mammals was also described in the Atlantic by Biton-Porsmoguer et al. (2015).

Understanding the impacts of global change on large pelagic fish ecology

Understanding the effects of global change on marine ecosystems is one of the grand challenges in marine ecology (Borja, 2014). It holds particular importance within the current context, 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 world human population (Pecl et al., 2017).

Rapid global change can disrupt patterns and relationships established under current or past conditions, as populations face increasing exposure to variation in environmental conditions (Hobday et al., 2015). These novel conditions will affect the distribution and biological processes of pelagic top predator species, and their capacity to adapt will depend on different characteristics such as physiological limits (e.g., thermal and oxygen requirements), habitat use (e.g., movement, migration), and flexibility in resource use (Portner et al., 2025).

Focusing on the question “*How is global change affecting trophic ecology?*”, this thesis has advanced the understanding of how the diet of large pelagic fishes can be shaped by two fundamental drivers of global ecological change in marine ecosystems: climate-driven environmental variability and fishing pressures.

Understanding the impacts of climate change

Consequences of climate change include rising ocean temperatures and alterations in oxygen levels and primary production (IPCC-AR6, 2023). Marine species are responding to climate change in several ways, including changes in their physiology, behavior, and survival, with redistribution being one of the most ecologically significant responses (Pinsky et al., 2020). Many large pelagic fish preferred habitats are related to high primary productivity and the presence of strong thermal gradients, such as fronts and thermoclines (Erauskin-Extramiana

et al., 2019; Pinti et al., 2025; Queiroz et al., 2019), and their distributions are projected to change under different climate change scenarios (Birkmanis et al., 2020; Erauskin-Extramiana et al., 2020; Hazen et al., 2013). However, many of these species have high phenotypic plasticity and adaptive capabilities that can mitigate the effects of climate change (Hazen et al., 2013). For example, warming may result in loss of suitable thermal habitat for albacore (*Thunnus alalunga*) in the tropics and a reduction in total suitable habitat, but an increased access to higher latitudes (Muhling et al., 2025). Nevertheless, the influence of environmental variability can still affect these predators by constraining their prey distribution (Bas et al., 2025; Carroll et al., 2024; Hazen et al., 2013), consequently affecting their feeding habits. The vulnerability of prey species to the oceanographic alterations related to climate change will define those prey redistributions, potentially leading to a spatial match–mismatch between predators and prey. For example, small and medium pelagic fish populations are strongly dependent on the environment (Palomera et al., 2007), and have experienced a reduction in optimal habitat availability over the past decades (Ouled-Cheikh, Coll, et al., 2022). Most large pelagic fish feeding grounds occupy epipelagic and mesopelagic depths, which are experiencing different rates of environmental change (Brito-Morales et al., 2020) but are closely linked by the vertical movement of predators and prey (Haddock & Choy, 2024). However, the impacts of climate change on trophic connections across depths and on the structure of pelagic food webs remain poorly understood.

The effects of different environmental variables on the diet of a top pelagic predator were analyzed in **Chapter 2**, particularly in response to key oceanographic factors such as SST, MLD, and chlorophyll-*a* concentration (Chl). On the one hand, a warmer ocean leads to a reduction in productivity (Annasawmy et al., 2024), which may result in different prey availability and a diet switch in generalist pelagic predators. Here, we found that the proportion of fish and squid in the swordfish diet in our study area was related to SST, which

was also found to be related to squid consumption in the Pacific (Preti et al., 2023). Changes in the diet of tunas were also detected with increasing SST in the Pacific, including more crustaceans and less fish and squid in their diets (Kuhnert et al., 2012; Nickels et al., 2023). Alterations in SST can also affect the thermocline depth, which can alter prey accessibility (e.g., higher tuna trophic position estimates were found at greater thermocline depths (Houssard et al., 2017)).

On the other hand, the increase in water temperatures leads to a reduction in dissolved oxygen, affecting the MLD and restricting the depth distribution of pelagic species into a narrower surface layer, altering pelagic food webs and even biogeochemical cycles (**Figure 2**) (Netburn & Koslow, 2015; Waller et al., 2024). Alterations in the MLD and OMZs can compress the foraging habitat of large pelagic fishes and also contribute to the prediction of their diet (Kuhnert et al., 2012). Duffy et al. (2017) found more mesopelagic fish in the diet of bigeye tunas with the deepening of the mixing layer. This relationship was also found for swordfish, showing a higher fish contribution to their diet with increasing MLD (**Chapter 2**). However, the upper hypoxic boundary is projected to shoal under climate change scenarios, widening the DSL and altering the distribution of mesopelagic animals (Netburn & Koslow, 2015).

This combination of warm surface temperatures and shoaling of the OMZ is likely to affect pelagic predators, particularly species with high oxygen demands, such as lamnid sharks (e.g., the shortfin mako (Byrne et al., 2024; Nasby-Lucas et al., 2019; Waller et al., 2024)). Their trophic and competition interactions are also altered, reducing predation pressure and resource competition in species that are capable of tolerating mild hypoxia. For example, blue sharks reduced their feeding depths in response to decreasing dissolved oxygen in depth (Le Croizier et al., 2022; Vedor et al., 2021), while other species, like thresher sharks (*Alopias* spp.), have developed a high ability to exploit these hypoxic mesopelagic environments around OMZs (Wootton et al., 2015).

Although sharks may withstand moderate hypoxia for short periods, other pelagic predators with higher tolerance to low oxygen concentrations, like swordfish, may behaviorally adapt and benefit from the creation of shallower hypoxic boundary layers (R. K. Logan, Vaudo, et al., 2023a; Madigan et al., 2021).

The distribution of pelagic organisms will also be influenced by Chl concentration, altering the DSL depth (Song et al., 2022). Chl serves as an indicator of the resources available for prey and therefore of the prey availability (Virgili et al., 2024). The distribution and availability of these pelagic resources across space and time are key factors influencing the feeding behavior of top predators (Z. Li et al., 2024), and have been shown to influence the diet of large pelagic predators such as blue sharks (Druon et al., 2022; Vidal et al., 2023), albacore tunas (Duffy et al., 2017; Nickels et al., 2023), and swordfish (**Chapter 2**).

Pelagic productivity, and hence food availability, plays a central role in shaping intraspecific competition in pelagic predators: under conditions of high resource availability, niche partitioning among conspecifics is reduced (**Chapter 3**). Conversely, when productivity declines and resources become scarce, intraspecific pressure increases, driving shifts in feeding behavior and niche expansion, which can potentially lead to greater overlap and heightened interspecific competition. Such competition between species is likely to intensify under low-productivity scenarios and may disproportionately affect less opportunistic species (Weideli et al., 2023). Furthermore, if prey abundance declines due to weakened upwelling or more frequent deoxygenation events, even generalist species could struggle to maintain the energy reserves required for reproduction and migration.

The trophic ecology of pelagic predators can be directly affected by environmental variability through changes in energetic costs, which alter both predator energy requirements and the energetic content of available prey

(Queiros et al., 2024). The physiological stress caused by warming increases oxygen demands in ectothermic fish, resulting in more energy consumed by essential processes and less available for growth and reproduction (Clark et al., 2013), which may be less impactful in endothermic sharks (Dell’Apa et al., 2023). In this context, cephalopods and gelatinous organisms are expected to benefit from the combination of changes in environmental conditions and reduced predators (Doubleday & Connell, 2018), with their rapid growth rates and high life-history plasticity enabling rapid adaptation (Brotz & Pauly, 2012; Hoving et al., 2013). A dietary shift towards increased consumption of pelagic fish such as the thermophilic round sardinella, together with cephalopods and gelatinous organisms, was observed in swordfish in **Chapter 1**. These shifts suggest that the expanding range of species that show rapid, plastic responses to changing environmental conditions is already being reflected in predator diets, and underscore their potential role as sentinel species.

If prey communities shift to less-energy-dense 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). Incorporating energetic requirements into habitat models is therefore essential to anticipate the interplay between migration behavior, physiological constraints, and prey availability in shaping predator responses to climate change (Bas et al., 2025; Muhling et al., 2025), emphasizing the importance of trophic ecology studies.

Climate-driven shifts in habitat suitability are expected to alter predator–prey overlaps, with consequences for trophic interactions and ecosystem structure. Differences in the rate and direction of habitat shifts between predators and their prey can lead to spatial or temporal mismatches, reducing prey availability and potentially limiting the capacity of predators to meet energetic demands (Bas et al., 2025; Carroll et al., 2024; Pinsky et al., 2020). Such mismatches are particularly relevant in the current global change scenario, and are projected to

become more frequent (Carroll et al., 2024; Visser & Gienapp, 2019). Where suitable, high-quality prey are scarce, shifts toward lower-quality species could contribute to reduced body condition (Johnson et al., 2015), affecting growth and reproduction (Hatzonikolakis et al., 2021). This reduction in predator fitness may be exacerbated if their energy requirements are increased by warming waters (Queiros et al., 2024), unless compensated by behavioral plasticity, increased foraging effort, or adaptive responses.

When predators change their diet due to reduced overlap with historically important prey species, they can indirectly affect other predators by increasing competition within the same trophic guild (Bas et al., 2025; Carroll et al., 2024). Generalist pelagic predators, as our studied species, may adapt and benefit from an increase in squid abundance since they constitute a good portion of their diet. At the same time, changes in prey abundance—particularly squid—are expected to be spatially heterogeneous (Veloy et al., 2024), and the potential increase in the abundance of competitors targeting those prey can drive interspecific trophic niche segregation (**Chapter 3**).

Understanding the impacts of fisheries

Fishing pressure alters the trophic ecology of pelagic predators both indirectly, by removing prey from the ecosystem and altering trophic dynamics (e.g., Giménez et al., 2021; McCauley et al., 2010), and directly, through targeted harvest and bycatch, modifying potential competitor abundance.

Important commercial fisheries are heterogeneously distributed along the study area (Coll et al., 2012; Colloca et al., 2017; Fernandes et al., 2017; Morales et al., 2005; Palomera et al., 2007; Sharma et al., 2025), with low fishing effort areas likely indicating low availability of common target species for both fisheries and large pelagic predators. Common fish prey species for large pelagic predators are heavily exploited, with pronounced biomass declines in the Mediterranean, particularly in the western basin, where overfishing is most acute (FAO, 2025;

GFCM, 2022b, 2022a; Mir-Arguimbau et al., 2022; Pennino et al., 2020; Sharma et al., 2025). These reductions are reflected in their diets (**Chapter 1**), while other important prey, such as squid, are also subject to increasing fishing pressure (Hidalgo & Browman, 2019; Seto et al., 2023; Veloy et al., 2024). Given its large biomass, the mesopelagic community is under increasing interest for commercial exploitation (Grimaldo et al., 2020). However, these potential expansion of mesopelagic fisheries raises additional concerns, as these resources support a range of pelagic predators, including sharks, tunas, and billfishes (I. S. Iglesias et al., 2023; Willis, 2025).

Beyond prey depletion, direct fishing has historically influenced the distribution, habitat use, and foraging behavior of large pelagic species (Andrews et al., 2023). Although there is an overall decline in longline fishing effort in the Atlantic, catches of pelagic sharks remain concerning, with blue shark and shortfin mako being the top bycatch species (Nóbrega et al., 2025). Longline fleets exhibit predictable environmental preferences, with higher fishing intensity occurring above OMZs, where dissolved oxygen gradients may cause predator aggregation and habitat compression, increasing fishing-induced mortality (Ortuño Crespo et al., 2018; Vedor et al., 2021). Pelagic sharks are highly susceptible to longlines, and warming, low-oxygen waters may further elevate their post-release mortality (Dell'Apa et al., 2023).

Climate change compounds these pressures. Environmental changes influence the distribution of pelagic predators, and fisheries are responding (Báez et al., 2025; Farchadi et al., 2024). Nevertheless, while high trophic level species may be more sensitive to climate change than to fishing when maintained near maximum sustainable yield, different global change scenarios indicate an overall decline in stock productivity for many commercial large pelagic fishes, including tunas and swordfish, with decreases in biomass and size (Erauskin-Extramiana et al., 2023). Such changes in their abundance, condition and distribution can have significant economic implications, as they support

valuable commercial fisheries worldwide (Erauskin-Extramiana et al., 2023; Nóbrega et al., 2023, 2025; Sharma et al., 2025). The availability and type of prey, together with the environmental conditions, can alter the allocation of energy reserves, affecting the quality of their products (Lazo-Andrade et al., 2021) and the fisheries that rely on them.

In this context, fisheries management should consider both direct effects of climate change on large pelagic species and indirect effects through impacts on their trophic ecology and energy requirements, allowing viable populations of these highly threatened and exploited species under present and future global change scenarios.

Applications to conservation and management

Addressing the question of *“How can we translate this into conservation and management?”* requires examining how insights from trophic ecology can be applied to reconcile fisheries exploitation with the conservation of large pelagic predators. Coupling conservation measures with fisheries management is essential to reach international goals (e.g., Global Biodiversity Framework Target 3: Conserve 30% of Land, Waters and Seas) and support halting the loss of marine biodiversity, which has been particularly severe for large marine predators (Sequeira et al., 2025). However, conflicts of interest arise between fisheries and conservation, and negotiating those conflicts is one of the key issues for ecosystem managers.

Crucial fishing grounds, particularly in our study area, need region-specific management strategies. These strategies need to focus on pelagic sharks since these species remain undermanaged (Juan-Jordá et al., 2022) and target critical nations, such as Spain and Portugal, addressing their significant contributions to blue shark and shortfin mako catches (Nóbrega et al., 2025). In the western Mediterranean, the low abundances of pelagic sharks found in **Chapter 3**,

especially for shortfin makos, raise concerns. This area is considered an **EBSA** due to its importance as a reproduction and feeding area for large pelagic species (CBD, 2025). The northwestern part, recognized as an **Important Shark and Ray Area (ISRA)** by the IUCN (Jabado et al., 2023; Rohner et al., 2025), is highlighted as a major mating and nursery area for blue sharks (Poisson et al., 2024), and appears as an important area for swordfish in our models, suggesting urgent management to prevent fisheries exploiting swordfish from interfering with blue sharks' reproduction.

In the Atlantic, on the one hand, the Gulf of Cádiz, also designated as an EBSA, appears as an important area for both shark species, underscoring its potential as an important area to target conservation efforts. The Strait of Gibraltar is recognized as an ISRA for pelagic sharks' movement (Jabado et al., 2023). On the other hand, the higher abundance of both swordfish and pelagic sharks around the Canary Current emphasizes the importance of this area for fisheries management efforts. The Canary Islands are also recognized as an EBSA due to their importance for migratory species (CBD, 2025).

The protection of these species can enhance the conservation of the pelagic food webs they rely on, acting as **umbrella species** (Giménez et al., 2022; Roberge & Angelstam, 2004) and raising awareness about the importance of protecting not just the species themselves, but also their prey, ensuring long-term survival. Although fisheries management has traditionally ignored predators and prey of target species and other ecosystem components and interactions, an ecosystem-based approach that maintains long-term socioeconomic benefits without compromising the ecosystem is needed (Pikitch et al., 2004).

Ecosystem-based fishery management (EBFM): fishery management that reverses the order of management priorities to start with the ecosystem rather than the target species.

Estimating fish populations is essential for sustainable fishing, and **ecosystem-based fishery management (EBFM)** further demands an understanding of the

oceanographic and biological factors influencing the exploited species. EBFM takes into account that trophic interactions play an important role in marine ecosystem dynamics and spatial predator-prey dynamics need to be taken into account. Therefore, diet descriptions are crucial to identify key prey, critical habitats and design conservation and management strategies for large pelagic species.

Although large pelagic species spend much time in the high seas, Sequeira et al. (2025) suggested that an initial focus on enhancing protection within jurisdictions could provide the fastest benefits for large predators' conservation. One of the most common conservation measures is Marine Protected Areas (MPAs), although these are often designed to protect habitats rather than threatened mobile marine megafauna (Sequeira et al., 2025). While the very large MPAs approach emerges as a strategy towards achieving 30% ocean protection by 2030 (Trevail et al., 2025), MPAs along our study area are rather small (Rohner et al., 2025) and need to increase effective protection efforts to achieve conservation targets (Aminian-Biquet et al., 2024; Castro-Cadenas et al., 2025).

Following an ecosystem-based approach to target spatial planning, spatial reserves need to be designed to ensure the energetic needs of predators are covered and identify predation hotspots (Bas et al., 2025; Carroll et al., 2024). Mobile MPAs that shift with oceanographic features that have established and predictable relationships with the target species have been proposed (Gilmour et al., 2022; Maxwell et al., 2015), and a similar approach could be used to take into account prey distribution. However, protection by a no-take reserve does not usually reduce fishing effort but results in the redistribution of the effort (Hilborn, 2018), and this kind of spatial closure should come together with direct measures for reducing direct mortality from fisheries.

Currently focused on mitigating the effects of fishing on incidental catches (e.g., gear modification, safe handling and release practices, prohibition of retention of some species) (Juan-Jordá et al., 2022), conservation and management measures for pelagic sharks should integrate trophic ecology information (e.g., adjust fishing practices according to diet to reduce bycatch risk). Seasonal and adaptive spatial management could mitigate fisheries impacts on non-target species (Crespo et al., 2024). For example, the identification of feeding hotspots provides an effective approach to select candidate areas for spatial closures in the highly dynamic pelagic environment (Requena et al., 2020).

Large pelagic fishes are important consumers of prey targeted by fisheries. Besides reducing direct mortality in threatened large pelagic species, sustainable fishing practices must account for the needs of these predators and prioritize maintaining crucial prey stock to maintain the balance and stability of the entire ecosystem. Managing resource competition between fisheries and marine top predators has so far been difficult due to a lack of knowledge regarding the amount and distribution of prey required by top predators (Hentati-Sundberg et al., 2021). While traditional stock assessments focus on keeping targeted populations above certain biomass levels that sustain fisheries, adjusting these limits downward may be required to ensure enough fish remain to support predator populations (B. Iglesias, 2024), especially where predators and fisheries overlap. In the case of commercial large pelagic species, their role as highly valuable target species further underscores the importance of meeting their energy requirements, which is not only critical for maintaining healthy populations but is also directly relevant to the sustainability of fisheries that depend on them. Furthermore, reductions in body size if energy demands are not met can diminish the market value of catches and thereby reduce fisheries revenue (Erauskin-Extramiana et al., 2023).

Altogether, including bioenergetics in fisheries management can provide spatially explicit conservation targets for top predators and inform ecosystem-

based management measures, improving our ability to manage the trade-off between fisheries and conservation (Hentati-Sundberg et al., 2021).

To avoid the spatiotemporal misalignment between current management measures and the distribution of species, the spatiotemporal distribution of both prey and predators needs to be integrated when planning and managing their redistribution under different future scenarios of climate change (Carroll et al., 2024; Dell'Apa et al., 2023). One way to approach this is by projecting predator diets under future conditions (e.g., **Chapter 2**). Diet projections can inform planning not only in the long term, where uncertainty is greater, but also in the short and medium term. Evidence of such mismatches arises in the NW Mediterranean: while this area emerged as an important region for swordfish distribution in **Chapter 3**, no suitable prey for swordfish was projected in this area under one of the scenarios in **Chapter 2**. A complementary framework includes assessing future spatial overlap between prey and predators' distribution to identify potential areas of match or mismatch (e.g., Bas et al., 2025).

When assessing predators' prey requirements, it is essential to consider species-specific traits and adopt a multi-species perspective that accounts for competition dynamics (Hentati-Sundberg et al., 2021). **Marine Ecosystem Models (MEMs)** provide a useful framework for this purpose, as they mathematically represent trophic interactions and incorporate all food-web components (Christensen et al., 2024; Coll et al., 2008). These models are employed to predict how marine species and thus ecosystems respond to environmental and anthropogenic pressures and allow for testing the effects of alternative management efforts under potential scenarios of climate change (e.g., Coll et al., 2020, 2024). Reliable diet information is therefore critical to ensure accurate representation of large pelagic species within MEMs.

Future research directions

The results presented in each chapter not only prompted new research questions but also highlighted critical gaps in current knowledge.

Trophically mediated direct and indirect effects are central to ecosystem dynamics, underscoring the need to consider species interactions and community structure when assessing the impacts of global change (Beauchesne et al., 2025). The inherent complexity of pelagic systems, coupled with their high sensitivity to environmental variability and human impacts, highlights the need for continued research and the development of more refined models to strengthen EBFM approaches (B. Iglesias, 2024). To further advance on ecosystem-based management, accurate dietary information on large pelagic fishes within the study area is required, which in turn highlights the need for stomach content analysis studies. Although the diet of swordfish has been widely described in the study area, there is a gap in knowledge for pelagic sharks in the western Mediterranean. Obtaining such data can be challenging for endangered or low-abundance species (e.g., blue shark and shortfin mako in the western Mediterranean; **Chapter 3**) for which lethal sampling is not desired. In these cases, alternative emerging techniques such as the identification of genetic sequences of diet items in stomachs, guts, or faeces through DNA metabarcoding can provide high taxonomic resolution of prey (e.g., Canals et al., 2024; Olin et al., 2023). Although this method can be quantitative, DNA extraction through cloacal swabs offers a non-lethal, minimally invasive approach for obtaining dietary estimates of large pelagic species, even from individuals with empty or evaginated stomachs (e.g., Olin et al., 2023). This method is also able to detect highly degraded, rare or soft items such as gelatinous plankton. Gelatinous organisms, primarily tunicates, are found in the diet of different large pelagic predators, including marine mammals, seabirds, swordfish and several species of tunas (Thiebot & McInnes, 2020). However, the

reasons for these trophic relationships are still unclear. While being low-energy prey, possible explanations include obtaining nutritional benefits such as minerals and amino acids, opportunism, practicing hunting techniques, aggregation of prey, and potential benefits for homeostatic challenges or maintenance of body temperature (Thiebot & McInnes, 2020). We encourage further research to fully understand the reasons for this behavior widely extended among large pelagic fishes.

Only through effective long-term population and community monitoring can we adequately assess how marine ecosystems operate and respond to environmental and anthropogenic drivers. Nevertheless, sampling the open ocean presents additional difficulties. Prey species are rarely monitored through long-term programs, and dedicated oceanographic surveys targeting pelagic communities are costly and resource-intensive. Fisheries, however, provide a valuable opportunity for continuous sampling that can help bridge these gaps (e.g., Pardo et al., 2025). Large marine predators play a central role in this context: ongoing monitoring of these species offers valuable opportunities to anticipate otherwise hidden changes within the dynamic ocean environment and adapt management strategies accordingly (Hazen et al., 2019). Open ocean fisheries targeting tunas and swordfish are highly monitored, and the use of these species as ecosystem sentinels can yield critical insights into their prey. The use of large pelagic fishes as biological samplers offers an indirect but effective way to gather information on underexplored components of the pelagic realm, particularly relevant for the overlooked mesopelagic community. Long-term monitoring programs focused on such species can enhance our capacity to detect and Such data would significantly improve our knowledge of the pelagic realm and enable the construction of more realistic and reliable ecosystem models that allow, at the same time, for a better ecosystem-based management of the fisheries.

Conclusions

The main conclusions derived from this Ph.D. thesis are:

1. Swordfish are generalist predators with a flexible foraging strategy along the water column, evidencing the benthopelagic coupling role of this species. Swordfish predominantly feed on teleosts and cephalopods, but we point to gelatinous plankton as an overlooked prey, particularly relevant for small juveniles.
2. The lack of long-term data on mesopelagic fish, mesopelagic cephalopods, and gelatinous organisms represents a significant challenge for effective ecosystem-based management and conservation efforts, as these species play crucial roles in regulating ecosystem processes. These non-commercial species are frequently consumed by swordfish. Therefore, since swordfish are highly exploited all year long in the northwestern Mediterranean, continuous monitoring could be proposed, providing a long-term sampling of their prey, particularly relevant for the overlooked mesopelagic community. Consequently, we could establish the use of this species as valuable sentinels of the ecosystem they inhabit. This would allow us to strengthen our understanding of how these organisms respond, in terms of their diet, to changes in the structure and functioning of the ecosystem.
3. Using the prey proportions found in stomach contents to inform the mixing models is particularly helpful when prey sources have similar isotopic values, and helps obtain more accurate estimates of the assimilated diet.
4. The swordfish diet was strongly linked to geographic location and responded to changing environmental conditions, particularly associated with key oceanographic factors such as sea surface temperature, mixed layer depth (MLD), and chlorophyll-a concentration, as well as to human stressors such as fishing pressure.
5. Our prospective exercise revealed that fish consumption in swordfish was projected to increase under the low climate forcing scenario as a result of

rising water temperatures and a deeper MLD in the northwestern Mediterranean. Under a high climate forcing scenario, the MLD is projected to become particularly shallow in the northwestern Mediterranean, and both fish and squid consumption are projected to decrease. 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, highlighting the critical role of trophic interactions in projecting future species distributions.

6. Enhancing the integration of trophic ecology in conservation can strengthen our ability to predict and plan for the redistribution of species under global change, ensuring that the energetic needs of predators are met: Fisheries management should consider which areas are particularly impacted by diet alterations, allowing the dynamic management of highly threatened and exploited populations.
7. The lower relative abundance of the three species in the western Mediterranean Sea, with shortfin makos nearly absent, highlights their high vulnerability in the Mediterranean region.
8. *Per capita* food availability, likely driven by pelagic productivity and potential competitor abundance, plays a significant role in shaping niche partitioning between large pelagic fish.
9. In areas of high trophic overlap of predators, prey changes may impact all species, while in regions where the overlap is lower, segregation could allow ecologically redundant species, less affected by the changes, to compensate for the ecological roles of more impacted species, potentially buffering ecosystem-level effects.

Conclusiones

Las principales conclusiones derivadas de esta tesis doctoral son:

1. El pez espada es un depredador generalista con una estrategia de alimentación flexible a lo largo de la columna de agua, respaldando la función de acoplamiento bentopelágico de esta especie. El pez espada se alimenta principalmente de teleósteos y cefalópodos, destacando al plancton gelatinoso como una presa olvidada, particularmente relevante en la dieta de los juveniles pequeños.
2. La falta de datos a largo plazo sobre peces y cefalópodos mesopelágicos y organismos gelatinosos representa un desafío para la gestión y conservación eficaz de los ecosistemas. Estas especies no comerciales, que desempeñan un papel crucial en la regulación de los procesos ecosistémicos, son frecuentemente consumidas por el pez espada. Por lo tanto, dado que el pez espada es altamente explotado durante todo el año en el Mediterráneo noroccidental, se propone un monitoreo continuo de su dieta, que proporcionaría un muestreo a largo plazo de sus presas, particularmente relevante para la comunidad mesopelágica. En consecuencia, podemos establecer el uso de esta especie como valiosa centinela del ecosistema en el que habita. Esto permitiría fortalecer nuestra comprensión de cómo estos organismos responden, en términos de dieta, a los cambios ecosistémicos.
3. Utilizar las proporciones de presas encontradas en los contenidos estomacales para informar los modelos de mezcla es especialmente útil cuando las fuentes de presas tienen valores isotópicos similares y ayuda a obtener estimaciones más precisas de la dieta asimilada.
4. La dieta del pez espada estuvo estrechamente vinculada a la distribución geográfica y respondió a variaciones ambientales asociadas con factores oceanográficos clave como la temperatura superficial, la profundidad de la capa de mezcla (MLD) y la clorofila, así como a factores de estrés humano como la presión pesquera.
5. Nuestro ejercicio prospectivo reveló que el consumo de peces en el pez espada aumentaría en el escenario de forzamiento climático bajo debido

a un aumento de la temperatura del agua y a una capa de mezcla más profunda en el Mediterráneo noroccidental. En un escenario de forzamiento climático alto, la MLD se vuelve más superficial en el Mediterráneo noroccidental y se proyecta que el consumo de peces y calamares disminuya. Si bien el pez espada puede mostrar resiliencia a los efectos directos de los cambios ambientales (p.e., puede tolerar bajos niveles de oxígeno disuelto), los impactos indirectos mediados por los cambios en la disponibilidad de las presas preferidas podrían excluir al pez espada de esta región o alterar significativamente su distribución, lo que resalta el papel crucial de incluir las interacciones tróficas en la proyección de la distribución futura de las especies.

6. Mejorar la integración de la ecología trófica en la conservación puede fortalecer nuestra capacidad para planificar y gestionar la redistribución de especies en el contexto del cambio global, garantizando así la satisfacción de las necesidades energéticas de los depredadores. La gestión pesquera debería considerar qué zonas se ven especialmente afectadas por las alteraciones de la dieta, lo que permite una gestión dinámica de poblaciones altamente amenazadas y explotadas.
7. La menor abundancia relativa de las tres especies en el Mediterráneo occidental, con la casi ausencia del marrajo dientuso, pone de relieve su alta vulnerabilidad en la región mediterránea.
8. La disponibilidad de alimento per cápita, condicionada por la productividad pelágica y la abundancia de competidores potenciales, desempeña un papel relevante en la configuración de la distribución de nichos entre los grandes peces pelágicos.
9. En zonas con alta superposición trófica de depredadores, los cambios en las presas pueden afectar a todas las especies, mientras que en regiones donde la superposición es menor, la segregación podría permitir que las especies ecológicamente redundantes, menos afectadas por los cambios, compensen las funciones ecológicas de las especies más afectadas, amortiguando potencialmente los efectos a nivel de ecosistema.

Conclusions

Les conclusions principals derivades d'aquesta tesi doctoral són:

1. El peix espasa és un depredador generalista amb una estratègia d'alimentació flexible al llarg de la columna d'aigua, recolzant la funció d'acoblament bentopel·làgic d'aquesta espècie. El peix espasa s'alimenta predominantment de teleòstis i cefalòpodes, destacant el plàncton gelatinós com una presa oblidada, particularment rellevant en la dieta dels joves petits.
2. La manca de dades a llarg termini sobre peixos i cefalòpodes mesopel·làgics i organismes gelatinosos representa un desafiament per a la gestió i conservació eficaç dels ecosistemes. Aquestes espècies no comercials, que tenen un paper crucial en la regulació dels processos ecosistèmics, són freqüentment consumides pel peix espasa. Per tant, atès que el peix espasa és altament explotat durant tot l'any a la Mediterrània nord-occidental, es proposa un monitoratge continu de la seva dieta, que proporcionaria un mostreig a llarg termini de les seves preses, particularment rellevant per a la comunitat mesopel·làgica. Això permetria enfortir la nostra comprensió de com responen aquests organismes, en termes de dieta, als canvis en l'estructura i el funcionament de l'ecosistema. En conseqüència, podem establir l'ús d'aquesta espècie com a valuosa sentinella de l'ecosistema on habita.
3. Utilitzar les proporcions de preses trobades en els continguts estomacals per informar els models de mescla és especialment útil quan les fonts de preses tenen valors isotòpics similars i ajuda a obtenir estimacions més precises de la dieta assimilada.
4. La dieta del peix espasa va estar estretament vinculada a la distribució geogràfica i va respondre a variacions ambientals associades amb factors oceanogràfics clau com la temperatura superficial, la profunditat de la capa de mescla (MLD) i la clorofil·la, així com factors d'estrès humà com la pressió pesquera.

5. El nostre exercici prospectiu va revelar que el consum de peixos al peix espasa augmentaria a l'escenari de forçament climàtic baix com a resultat de l'augment de la temperatura de l'aigua i d'una capa de mescla més profunda a la Mediterrània nord-occidental. En un escenari de forçament climàtic alt, la MLD es torna particularment superficial a la Mediterrània nord-occidental i es projecta que el consum de peixos i calamars disminueixi. Si bé el peix espasa pot mostrar resiliència als efectes directes dels canvis ambientals (per exemple, pot tolerar baixos nivells d'oxigen dissolt), els impactes indirectes per canvis en la disponibilitat de les preses preferides podrien excloure el peix espasa d'aquesta regió o alterar-ne significativament la distribució, la qual cosa ressalta el paper crucial d'incloure les interaccions.
6. Millorar la integració de l'ecologia tròfica a la conservació pot enfortir la nostra capacitat per planificar i gestionar la redistribució d'espècies en el context del canvi global, garantint així la satisfacció de les necessitats energètiques dels depredadors. La gestió pesquera hauria de considerar quines zones es veuen especialment afectades per les alteracions de la dieta, cosa que permet una gestió dinàmica de poblacions altament amenaçades i explotades.
7. La menor abundància relativa de les tres espècies a la Mediterrània occidental, amb la gairebé absència del solraig, posa en relleu la seva alta vulnerabilitat a la regió mediterrània.
8. La disponibilitat d'aliment per càpita, probablement condicionada per la productivitat pelàgica i l'abundància de potencials competidors, té un paper rellevant en la configuració de la distribució de nínxols entre els grans peixos pelàgics.
9. En zones amb alta superposició tròfica de depredadors, els canvis a les preses poden afectar totes les espècies, mentre que en regions on la superposició és menor, la segregació podria permetre que les espècies ecològicament redundants, menys afectades pels canvis, compensin les funcions ecològiques de les espècies més afectades, esmorteint potencialment els efectes a nivell.

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