Ecosystems
https://doi.org/10.1007/s10021-025-00990-9

ECOSYSTEMS

ORIGINAL ARTICLE

Identifying Bottlenecks to Energy Circulation in the Bay of Biscay Pelagic Food Web: Key Species Under the Spotlight

Beñat Iglesias,[1]* Maite Louzao,[1] Izaskun Preciado,[2] Maysa Ito,[3] Joan Giménez,[4] Lucía López-López,[2] Paula Méndez-Fernandez,[5] Tiphaine Chouvelon,[5,6] Paco Bustamante,[7] Jérôme Spitz,[5,8] Xavier Corrales,[9] Eider Andonegi,[9] Aitor Lekanda,[9] Javier Franco,[1] Guillermo Boyra,[1] María Santos Mocoroa,[1] and Marco Scotti[3,10]

[1]AZTI Marine Research, Basque Research and Technology Alliance (BRTA), Pasaia, Spain; [2]Instituto Español de Oceanografía (IEO-CSIC), Centro Oceanográfico de Santander, Santander, Spain; [3]GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel, Germany; [4]Instituto Español de Oceanografía (IEO-CSIC), Centro Oceanográfico de Málaga, Málaga, Spain; [5]Observatoire Pelagis, UAR 3462, CNRS-La Rochelle Université, La Rochelle, France; [6]Ifremer, Unité Contamination Chimique Des Écosystèmes Marins (CCEM), Centre Atlantique, Nantes, France; [7]Littoral Environnement et Sociétés (LIENSs), UMR 7266, CNRS-La Rochelle Université, La Rochelle, France; [8]Centre d'Etudes Biologiques de Chizé (CEBC), UMR 7372, CNRS-La Rochelle Université, Villiers-en-Bois, France; [9]AZTI Marine Research, Basque Research and Technology Alliance (BRTA), Sukarrieta, Spain; [10]Institute of Biosciences and Bioresources, National Research Council of Italy, Sesto Fiorentino, Italy

ABSTRACT

Understanding the functioning and resilience of marine ecosystems requires identifying the main energy flow pathways. Key trophic groups occupy strategic positions in the trophic interactions network, acting as hubs that control the energy distribution across the ecosystem. This study examines the Bay of Biscay's pelagic food web using stable isotope analysis with stomach content data, creating a network of 38 trophic groups and 125 interactions. Both annual-weighted and seasonal (spring and late summer) networks were constructed. The analysis of unweighted and weighted annual networks found that low-trophic level epipelagic fish (European anchovy, *Engraulis encrasicolus*; sardine, *Sardina pilchardus*; and sprat, *Sprattus sprattus*) is a key trophic group displaying higher scores in many centrality indices. These forage fish play a central role in facilitating energy transfer across trophic levels, thus representing a critical link between the planktonic food web and higher trophic level predators and fisheries. Overall, annual networks showed that phytoplankton-dominated grazing chains support a higher diversity of predators compared to chains originating from particulate organic matter (POM). The analysis of weighted networks accounting for seasonal varia-

---

Received 5 December 2024; accepted 24 June 2025

Supplementary Information: The online version contains supplementary material available at https://doi.org/10.1007/s10021-025-00990-9.

Author Contributions: BI, MSco, ML, IP, and MI conceptualized and designed the study. GB and MSan conducted the oceanographic surveys. PMF, TC, and PB provided stable isotope data. All authors contributed to the final manuscript.

**Corresponding author; e-mail:* b.iglesiascastillo@gmail.com

tions in trophic interactions revealed that, during late summer, predators occupy more vulnerable positions than in spring. Changes in feeding preferences cause blue whiting to shift from mostly depending on grazing chains during spring to occupying a position along POM-dominated chains in late summer. These findings highlight the need for fisheries management strategies to prioritize the conservation of key trophic groups supplying energy to predators while considering seasonal shifts in the structure of the energy flow network.

Key words: Centrality indices; Dominator tree; Ecosystem-based fisheries management; Stable isotope mixing models; Trophic networks.

HIGHLIGHTS

- Low-trophic level epipelagic fish are critical for energy transfer in the Bay of Biscay.
- Stable isotope analysis reveals seasonal dietary shifts and key energy pathways
- Seasonal changes in energy pathways underline the need for adaptive management strategies.

INTRODUCTION

Comprehending the dynamics and resilience of marine ecosystems relies on understanding how energy flows through them. Energy pathways link organisms across different trophic levels (Eddy and others 2021) and rely either on primary producers or detritus (Odum 1969). Primary producers, such as phytoplankton, convert solar energy into chemical energy through photosynthesis. An alternative energy source at the bottom of marine food webs comes from detritus (Simenstad 2016), which consists of particulate organic matter (POM). While some consumers are specialized, most marine organisms integrate these basal resources in different proportions, creating an intricate network with myriads of branches where energy flows from the basal resources up to the top predators (Irigoien and others 2009; Anderson and others 2017; Perkins and others 2022). The amount of energy transferred through either grazing or POM-dominated chains depends on several factors among which ocean productivity seems to have a predominant role (Sommer and others 2018). The main pathways transferring energy to higher trophic levels (for example, large fish, seabirds and marine mammals) are likely regulated by nutrient availability and environmental conditions, which tend to display characteristic seasonal variations.

The study of food webs maps out the relationships between producers, consumers, and their predators within the ecosystem (Pimm and others 1991). These interconnected networks provide a holistic view of species interactions, with nodes corresponding to species or functional groups and links representing predator–prey interactions (Borrett and others 2018). The topological analysis of a food web provides qualitative information that depends on the arrangement of binary trophic links (that is, unweighted, portraying presence or absence of interaction) between species or functional groups (Kadoya and others 2012). But providing estimates of the amount of matter and energy flowing though the network topology (that is, weighed networks, including the strength of interactions) complements the topological approach, being important to understand temporal changes in food web functioning (Scotti and others 2007; Kortsch and others 2021).

Network metrics based on network topology interaction strengths provide insights into community stability and mechanisms of trophic control within the food web (Table S1). These models can be investigated to determine the functional role of species and trophic groups within the network by using centrality indices, thereby identifying keystone species, energy bottlenecks and connectivity hubs (Table S1). The roles depend on the position occupied by a species/trophic group (that is, the nodes) in the network and are not uniform. Keystone species are identified as species or groups of species that exert a disproportionately large impact on ecosystem functioning relative to their abundance, and whose decline could cause cascading effects (Power and others 1996). Cascading effects refer to a chain reaction of changes that occur in an ecosystem when a keystone species is removed or declines. Identifying key species in trophic networks can help to define effective ecosystem management strategies and reduce the risk of ecosystem collapse (Bersier and others 2002; Estrada 2007; Jordán 2009).

The relevance of species in structuring the food web may vary throughout the year, as the role of seasonality in shaping food webs is a complex and multifaceted issue (White and Hastings 2020). As trophic interactions change across both space and time (Alpine and Cloern 1992; Kortsch and others 2019; Bass and Falkenberg 2024), it is challenging to understand the impact of seasonal variations on the structural properties of food webs. For instance, in temperate pelagic ecosystems, seasonal variations in the hydrodynamic conditions can induce changes in nutrients, primary production and primary consumers (Iglesias and others 2023). The Bay of Biscay (hereafter BoB) is a characteristic temperate marine ecosystem off the Atlantic coasts of France and Spain. In its offshore areas, a major phytoplankton bloom occurs in spring and a secondary one in autumn, closely followed by two annual peaks in zooplankton abundance and biomass (Valdés and others 2007; Bode and others 2011). Although these events can modify the functioning of the pelagic ecosystem, particularly affecting predator–prey interactions, these changes are not always consistent in the BoB (Iglesias and others 2023). Several studies have focused on seasonal variations in the trophic ecology of commercial fish and marine megafauna in the BoB (Meynier and others 2008; Bachiller and Irigoien 2015; Iglesias and others 2023), but none has described how annual succession can modify the main pathways of energy circulation and the identity of bottlenecks to energy circulation in the food web.

The lack of seasonal or temporal food web data could be attributed to the significant effort required for conventional methods, such as stomach content analysis (SCA) (McMeans and others 2015). SCA provides short-term information on ingested prey, so complementary analyses have been developed to discriminate feeding preferences. Stable isotope analysis (SIA) of carbon and nitrogen is a powerful tool for identifying the feeding habits and the assimilated prey species. Moreover, SIA is advantageous for repeated analyses as it provides a time-integrated dietary measure and enables the simultaneous characterization of the diets of several species. Thus, SIA has been frequently used to study seasonal variations in assimilated diets despite presenting fewer taxonomic resolution than SCA (Lloret-Lloret and others 2020) and it proved to be an effective tool to build quantitative food webs and assess potential seasonal shifts in their structure.

In this study, we examined the structure and functioning of the BoB pelagic food web by constructing a trophic network where the feeding preferences were quantified by integrating stomach content data and SIA through the application of Bayesian mixing models (Moore and Semmens 2008). Our goal was to quantify the overall role of species using centrality indices, focusing on nodes that control energy delivery along the trophic chain. Additionally, we aimed to identify the main energy pathways and structural dominance patterns, considering both overall and seasonal feeding preferences. We hypothesized that the dependence of fish and marine megafauna (for example, large predator fish, seabirds, marine mammals) on either phytoplankton- or POM-derived trophic chains would be related to their habitat preferences (for example, demersal, pelagic, and deep sea). Moreover, we expected that seasonal differences in the dominance of energy circulation patterns (that is, spring vs. autumn) would reflect changes in ecosystem productivity. Our analysis combines field data, principles of trophic ecology and food web modeling to identify species controlling energy circulation in marine food webs. Such a framework could be applied to prioritize species management with a holistic framework such as the ecosystem-based approach.

MATERIALS AND METHODS

Study Area

The BoB, located in the NE Atlantic along the northern coast of Spain and the western coast of France, is characterized by a continental slope that extends up to 200 km in the bay's eastern part and narrows to less than 10 km in the southern area (Figure 1) (Borja and others 2019). The oceanic water circulation is weak and over the shelf it is controlled mainly by wind- and density-induced currents in the southern part, and by tides in the northern part (Ferrer and others 2009). Winter in the BoB features mixed conditions and light limitation, followed by a nutrient-limited spring bloom, stratified summer conditions with a deep chlorophyll maximum, and a second bloom in autumn (Longhurst 2007). The abundance and biomass of zooplankton reach their peak in spring and autumn, shortly after the phytoplankton blooms (Valdés and others 2007).

Data Sources for Stable Isotopes

The pelagic domain of the BoB was thoroughly characterized by analyzing the isotopic signature of a large number of pelagic taxa, including zooplankton, crustaceans, cephalopods, fish, and megafauna (tunas, seabirds, and marine mammals) (Table 1). Isotopic signatures had seasonal resolution (spring and late summer) for about one third of the taxa, while mean isotopic values were available for the rest of the community. Isotopic data sources and availability for each species and trophic group are summarized in Tables 1 and S2, respectively.

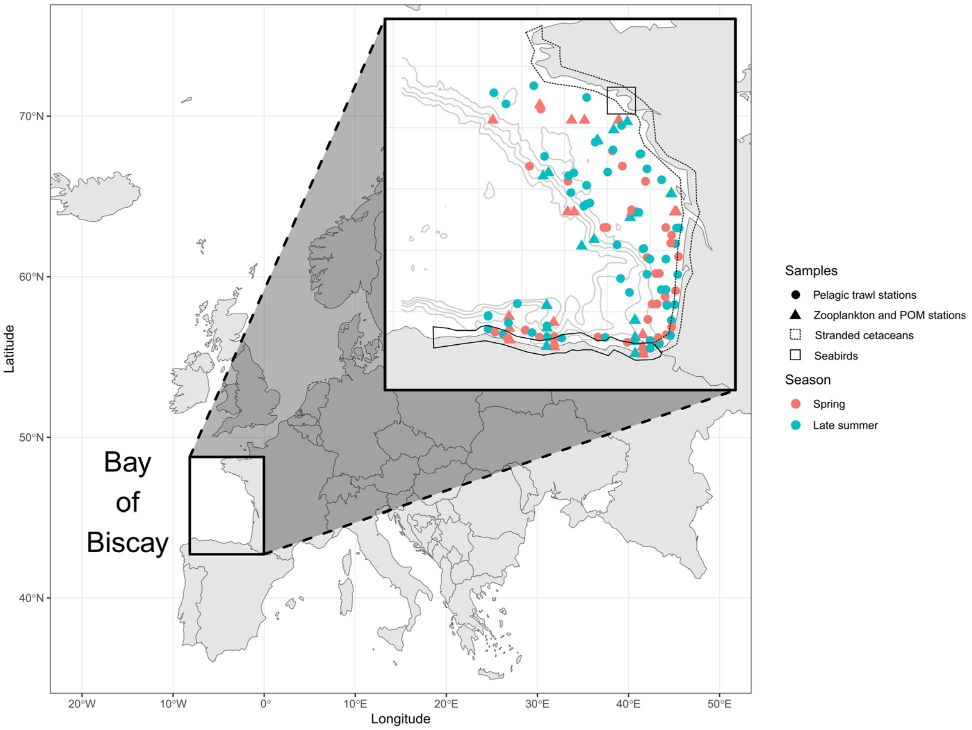

Figure 1. Geographic distribution of samples in the Bay of Biscay. Fish, the broadtail shortfin squid, the Norwegian krill, and the Henslow's swimming crab were collected at pelagic trawl stations. Pelagic trawling and the collection of zooplankton and POM samples were executed across different seasons. Cetacean samples were obtained from strandings and bycatch. Seabird samples were collected from strandings and living individuals.

The megafauna comprised 11 species, including seven cetaceans, two tuna species and two seabirds, with isotopic data collected throughout the year. The isotopic data for all these species were obtained from Iglesias and others (2024), except for northern gannets *Morus bassanus*, which were obtained from Gaspar and others (2022). Fish (excluding tunas) were represented by 16 species. Seasonal isotopic data were available for half of these species, and were obtained from Iglesias and others (2023); single-season isotopic data for two species were retrieved from the JUVENA surveys (late summer) of 2020 and 2021; mean isotopic values for the remaining species were extracted from Chouvelon and others (2012) and Iglesias and others (2024). Cephalopods included 10 species, with seasonal isotopic data available for the broadtail shortfin squid *Illex coindetii*, obtained from Iglesias and others (2023), and mean isotopic values for the other species (Iglesias and others 2024). Crustaceans comprised five species, with seasonal isotopic data available for three species (Iglesias and others 2023). Due to limited sample sizes for each season, data for hyperiids were combined. Mean isotopic values for the glass shrimp *Pasiphaea* spp. and the Atlantic mud shrimp *Solenocera membranacea* were obtained from Iglesias and others (2024) and the isotope database of IEO-CSIC research center, respectively. Zooplankton and gelatinous organisms encompassed five groups, with seasonal isotopic data obtained from Iglesias and others (2023). However, due to limited sample sizes for each season, data for crustacean larvae, mollusks, and cladocerans were combined.

Pelagic Food Web Construction

The first step of the food web assembly was defining the nodes that make up the trophic network and identifying the architecture of their feeding interactions. Characteristics of the species such as taxonomy, habitat and depth distribution were considered in this step (Table 1). Trophic levels for multi-species compartments were determined based on a cluster analysis of mean δ^{15}N values, as conducted in Iglesias and others (2024). Grouping ecologically similar species in this way reduces the number of sources per consumer, thereby enhancing model convergence and accuracy, since mixing-model performance decreases markedly as the number of prey sources increases (Phillips and others 2014). Megafauna (cetaceans, tunas, sea-

Table 1. List of Species and Their Classification Based on Taxonomy, Horizontal and Vertical Habitat, and Trophic Level

Species	Taxon	Habitat$_{H\text{-}V}$[a]	TL[b]	Acronym	Node	Data source[c]
Phytoplankton	Phytoplankton			PHYTO	1	–
Particulate organic matter	Detritus			POM	2	I
Copepoda spp. (Copepod)	Zooplankton			COPSPP	3	II
Crustacean larvae	Zooplankton			CRULAR	4	II
Mollusca spp. (Mollusk)	Zooplankton			MOLLUS	5	II
Podonidae spp. (Cladoceran)	Zooplankton			PODSPP	6	II
Detritus feeder decapod	Crustacean (Cr)	N-B		DECSPP	7	–
Solenocera membranacea (Atlantic mud shrimp)	Crustacean (Cr)	N-D		SOLMEM	8	III
Polybius henslowii (Henslow's swimming crab)	Crustacean (Cr)	N-E		POLHEN	9	II
Hyperiidea spp. (Hyperiid)	Crustacean (Cr)	O-E		CrOE	10	II
Meganyctiphanes norvegica (Norwegian krill)	Crustacean (Cr)	O-E		CrOE	10	II
Pasiphaea spp. (Glass shrimp)	Crustacean (Cr)	O-M		PASSPP	11	IV
Polychaeta spp.	Polychaete			POLYCH	12	–
Thaliacea spp. (Salp)	Gelatinous (G)	O-E		THASPP	13	II
Microchirus variegatus (Thickback sole)	Fish (F)	N-B		MICVAR	14	IV
Conger conger (European conger)	Fish (F)	N-D	HTL	FNDHTL	15	IV
Dicentrarchus labrax (European seabass)	Fish (F)	N-D	HTL	FNDHTL	15	IV
Merlangius merlangus (Whiting)	Fish (F)	N-D	HTL	FNDHTL	15	IV
Micromesistius poutassou (Blue whiting)	Fish (F)	N-D	LTL	FNDLTL	16	II
Argentina spp. (Argentine)	Fish (F)	N-D	MTL	FNDMTL	17	V
Boops boops (Bogue)	Fish (F)	N-D	MTL	FNDMTL	17	IV
Merluccius merluccius (Hake)	Fish (F)	N-D	MTL	FNDMTL	17	II
Trisopterus minutus (Poor cod)	Fish (F)	N-D	MTL	FNDMTL	17	I
Engraulis encrasicolus (European anchovy)	Fish (F)	N-E	LTL	FNELTL	18	II
Sardina pilchardus (European sardine)	Fish (F)	N-E	LTL	FNELTL	18	II
Sprattus sprattus (European sprat)	Fish (F)	N-E	LTL	FNELTL	18	II
Scomber colias (Atlantic chub mackerel)	Fish (F)	N-E	MTL	FNEMTL	19	II
Scomber scombrus (Atlantic mackerel)	Fish (F)	N-E	MTL	FNEMTL	19	II
Trachurus trachurus (Atlantic horse mackerel)	Fish (F)	N-E	MTL	FNEMTL	19	II
Scomberesox saurus (Atlantic saury)	Fish (F)	O-E		SCOSAU	20	IV
Lobianchia gemellarii (Cocco's lantern fish)	Fish (F)	O-M		FOM	21	IV
Maurolicus muelleri (Mueller's pearlside)	Fish (F)	O-M		FOM	21	I
Notoscopelus kroyeri (Lancet fish)	Fish (F)	O-M		FOM	21	IV
Eledone cirrhosa (Horned octopus)	Cephalopod (C)	N-B		ELECIR	22	IV
Ancistrocheirus lesueurii (Sharpear enope squid)	Cephalopod (C)	O-MB	HTL	COMBHTL	23	IV
Histioteuthis spp. (Cock-eyed squid)	Cephalopod (C)	O-MB	HTL	COMBHTL	23	IV
Todarodes sagittatus (European flying squid)	Cephalopod (C)	O-MB	HTL	COMBHTL	23	IV
Haliphron atlanticus (Seven-arm octopus)	Cephalopod (C)	O-MB	LTL	COMBLTL	24	IV
Teuthowenia megalops (Atlantic cranch squid)	Cephalopod (C)	O-MB	LTL	COMBLTL	24	IV
Galiteuthis armata (Armed cranch squid)	Cephalopod (C)	O-MB	MTL	COMBMTL	25	IV
Gonatus steenstrupi (Atlantic gonate squid)	Cephalopod (C)	O-MB	MTL	COMBMTL	25	IV
Illex coindetii (Broadtail shortfin squid)	Cephalopod (C)	N-D		ILLCOI	26	II
Loligo spp.	Cephalopod (C)	N-E		LOLSPP	27	IV
Balaenoptera physalus (Fin whale)	Cetacean			BALPHY	28	IV
Delphinus delphis (Common dolphin)	Cetacean			DELDEL	29	IV
Globicephala melas (Long-finned pilot whale)	Cetacean			GLOMEL	30	IV
Phocoena phocoena (Harbor porpoise)	Cetacean			PHOPHO	31	IV
Stenella coeruleoalba (Striped dolphin)	Cetacean			STECOE	32	IV
Tursiops truncatus (Bottlenose dolphin)	Cetacean			TURTRU	33	IV
Ziphius cavirostris (Cuvier's beaked whale)	Cetacean			ZIPCAV	34	IV
Morus bassanus (Northern gannet)	Seabird			MORBAS	35	VI

Table 1. continued

Species	Taxon	$\text{Habitat}_{\text{H-V}}$[a]	TL[b]	Acronym	Node	Data source[c]
Puffinus mauretanicus (Balearic shearwater)	Seabird			PUFMAU	36	IV
Thunnus alalunga (Albacore tuna)	Tuna			THUALA	37	IV
Thunnus thynnus (Atlantic bluefin tuna)	Tuna			THUTHY	38	IV

The node ID and the source of the isotopic data are reported. [a](H) Horizontal habitat. N: Neritic; O: Oceanic; (V) Vertical habitat. E: Epipelagic; M: Mesopelagic; MB: Meso-Bathypelagic; D: Demersal; B: Benthic. [b](TL) Trophic Level. L: Low; M: Mid; H: High. [c]Source of isotopic data. I: BIOMAN/JUVENA surveys (2020–2021); II: (Iglesias and others 2023); III: IEO-CSIC; IV: (Iglesias and others 2024); V: (Chouvelon and others 2012); VI: (Gaspar and others 2022).

birds) were treated as single-species nodes because they lack natural predators within this food web. Similarly, zooplankton taxa were treated as independent nodes to ensure sufficient sample sizes and prey availability, facilitating reliable dietary estimates for fish.

Using stable isotope analysis, we quantified dietary proportions for all groups for which individual and/or seasonal isotopic data were available (Table S2). We applied Bayesian isotopic mixing models (Moore and Semmens 2008) to distinguish the contributions of each prey identified in the literature. Potential predator–prey interactions were determined using published information on stomach content analysis conducted in the BoB or adjacent areas (Table S3). We only included in the analysis those predator–prey interactions that represent more than 5% of the weight of the diet (Iglesias and others 2024). This was possible for all species except the Balearic shearwater, the northern gannet, and the Norwegian krill, whose stomach contents have not been studied in the BoB. For these species we used the same potential prey identified in Meier and others (2017), Gaspar and others (2022) and Cabrol and others (2019), respectively. MixSIAR models (MixSIAR V3.1.12, Stock and Semmens 2016) were used for all megafauna, the broadtail shortfin squid (ILLCOI), the Norwegian krill (CrOE) and the Henslow's swimming crab (POLHEN), and fitted with predator-specific diet tissue discrimination factors (DTDF) (Table 2, Table S4). To assess the validity of the isotopic mixing model and to identify consumers whose isotopic composition may not be consistent with expected prey sources, a mixing polygon was constructed as described by Smith and others (2013). As recommended by Smith and others (2013), only individuals within the 95% mixing polygon region were used in the models. All models were run with Markov Chain Monte Carlo (MCMC) parameters set to ''long'' (number of chains = 3; chain length = 300,000; burn-in = 200,000; and thin = 100).

The EcoDiet model (Hernvann and others 2022) was used to analyze fish compartments for which individual isotopic and stomach content data were available (Table S4). Fish species were grouped into compartments according to their habitat and depth, as previously described. For compartments containing multiple species, they were also categorized by their trophic level. These compartments include low trophic level demersal fish (FNDLTL: blue whiting), mid-trophic level demersal fish (FNDMTL: hake), low trophic level epipelagic fish (FNELTL: European anchovy, sardine and sprat), mid-trophic level epipelagic fish (FNEMTL: Atlantic mackerel, chub mackerel and horse mackerel), and mesopelagic fish (FOM: Mueller's pearlside). EcoDiet integrates stomach content and stable isotope data to estimate dietary composition, providing more robust and holistic information of trophic interactions. The choice of this modeling approach was justified by the availability of both types of trophic data for the same fish individuals. For each group of fish, we identified the prey by selecting the species that make up more than 5% of the diet (Iglesias and others 2023). All models were run with the Markov Chain Monte Carlo (MCMC) parameters set to ''long'' (number of chains = 3; chain length = 300,000; burn-in = 200,000; and thin = 100). The dietary proportions derived from the models were used as the definitive representation for each fish category. Species without individual isotopic data are assumed to have the same dietary habits as the other ones in the same compartment.

A comprehensive literature review was undertaken to determine the dietary proportions of predators for which individual isotopic data were unavailable or for which isotopic data for some of their prey (16 nodes) were missing (Table S3, Table S4). In this latter case, the contribution of prey to consumers' diet was grouped according to the taxonomic classification and resolution adopted in this study. Only species representing more than 5% of the diet of each predator were selected

Table 2. Diet-tissue Discrimination Factors (DTDF) Used for Each Taxonomic Category

Predator	$\delta^{13}C$	$\delta^{15}N$	Source
Cetacean	1.01 ± 0.37 ‰	1.57 ± 0.52 ‰	Giménez and others 2016
Tuna	0.32 ± 0.09 ‰	1.46 ± 0.14 ‰	Varela and others 2012
Seabird	0.9 ± 0.5 ‰	1.7 ± 0.5 ‰	Ramos and others 2009
Broadtail shortfin squid	0.4 ± 1.3 ‰	3.4 ± 1.0 ‰	Post 2002
Norwegian krill	0.8 ± 0.3 ‰	2.0 ± 0.4 ‰	Cabrol and others 2019
Henslow's shimming crab	0.6 ± 0.7 ‰	1.6 ± 0.6 ‰	McCann and Jensen 2018

(Table S3). Trophic network visualization was implemented in the R statistical environment, version 4.2.0 (R Core Team 2022) with the *DiagrammeR* package (Iannone 2024).

Overall Trophic Network Properties

A comprehensive analysis of the structural properties characterizing the BoB pelagic food web was conducted using a wide variety of overall system metrics (Bersier and others 2002). All these structural properties depend only on the network topology. First, the numbers of nodes (n) and trophic links (l), the linkage density (LD = l/n), and the connectance ($C = l/n^2$) were summarized. These metrics inform about food web size and complexity. Then, we classified the nodes by calculating the fractions of top (that is, consumers that lack predators), intermediate (that is, consumers with both prey and predators), and basal groups (that is, nodes with predators only). Subsequently, we computed the prey vulnerability (V, average number of consumers per prey, that is, exposure to consumers) and generality (G, average number of prey per consumer), and determined the degree of omnivory (O), which is the proportion of consumers feeding at more than one trophic level. These metrics were computed using the *cheddar* package in R (Hudson and others 2022).

Network Centrality Indices and Dominator Tree

Centrality indices were quantified to identify key species regulating energy circulation in the BoB pelagic food web. We computed the degree centrality (D_{tot}), an index indicating the local importance of species based on their direct neighbors, irrespective of whether they are prey or predators. The degree centrality accounts for the total prey (in-degree, D_{in}) and predators (out-degree, D_{out}), that is, $D_{tot} = D_{in} + D_{out}$. Nodes with a high D_{tot} are hubs that locally interact with a high number of trophic groups (Rocchi and others 2017). Then, we determined the directed betweenness centrality (BC_i), which provides information on the number of shortest paths between all pairs of nodes that pass through the target node i. A high BC_i suggests a strong influence of the node in controlling the spread of indirect effects through the entire network (Freeman 1977). Lastly, we calculated the undirected closeness centrality (CL_i), which quantifies the length of shortest paths from a specific node to all the others (Rocchi and others 2017). High CL_i scores indicate nodes occupying barycentric positions in the entire network (Xing and others 2021). We weighted the calculations of both BC_i and CL_i using the contribution of prey to consumers' diets while for D_{tot} we considered only the network topology.

Furthermore, a dominator tree was constructed to elucidate structural dominance patterns in the pelagic food web of the BoB. The dominator tree is a topological structure that reveals the main linear pathways for energy delivery in the food web (Allesina and Bodini 2004). It connects nodes sequentially to their direct dominators, thus clarifying whether consumers are mainly dependent on grazing or POM-based chains for their food intake. Given that the method is based on directed, binary, and acyclic networks, it specifically captures the primary routes by which energy is transferred from basal resources upward, rather than quantifying the complete circulation of energy throughout the ecosystem. In this context, our interpretation of the dominator tree outputs focuses on highlighting potential points of control within the network rather than suggesting a comprehensive summary of energy circulation. Centrality indices and the dominator tree were computed and visualized using the *igraph* and *tidyverse* packages in R (Csardi and Nepusz 2006; Wickham and others 2019).

Seasonal Trophic Networks

Using seasonal stable isotope data, we constructed two trophic networks with interaction strengths representing dietary proportions during spring and late summer. We analyzed the variations in dietary proportions for half of the nodes that comprised the network. Specifically, for megafauna and the Mueller's pearlside, seasonal differences depend on variations in prey isotopic data (Iglesias and others 2023), as stable isotope samples of these consumers were not available for both seasons. Feeding preferences were quantified using the same criteria and methods as described in section ''Pelagic food web construction''. When seasonal isotopic data were unavailable for both prey and predators, the feeding preferences were quantified using literature data and remained the same across both seasons. In addition, we constructed different dominator trees for spring and late summer. Using seasonal dominator trees, we quantified the extent to which trophic groups act as dominators (that is, representing bottlenecks to energy circulation) and occupy vulnerable positions. Trophic-path vulnerability was calculated by counting the number of nodes separating each trophic group from the root. We then averaged the distance of all trophic groups from the root and obtained an overall trophic-path vulnerability of the food web.

To assess seasonal changes, several metrics were calculated based on dietary proportions and stable isotopes of distinct groups during spring and late summer. First, we compiled the dataset of the dietary preferences of fish and megafauna in both seasons. Second, we calculated the diet proportion-based or effective trophic level (TL_{diet}; Scotti and others 2006), the stable isotope-based trophic level (TL_{SIA}; Hussey and others 2014), and the Shannon–Wiener diversity index for the diet of trophic groups (H'; Scotti and others 2009). For each group, the stable isotope-based trophic level (TL_{SIA}) was calculated using the seasonal isotopic data from the filter-feeder *Thaliacea* spp. (THASPP) as the baseline and applying the following formula:

$$TL_{\mathrm{SIA}} = 2 + \frac{\log\left(\delta^{15}\mathrm{N}_{\mathrm{lim}} - \delta^{15}\mathrm{N}_{\mathrm{base}}\right) - \log\left(\delta^{15}\mathrm{N}_{\mathrm{lim}} - \delta^{15}\mathrm{N}_{\mathrm{sample}}\right)}{k}$$

where $\delta^{15}N_{sample}$ and $\delta^{15}N_{base}$ are the N isotopic signatures of each sample and the baseline (THASPP), 2 is the trophic level of the reference baseline, $\delta^{15}N_{lim}$ is the saturating isotope limit as trophic level increases, and k the rate at which $\delta^{15}N_{sample}$ approaches $\delta^{15}N_{lim}$. Values for $\delta^{15}N_{lim} = 21.926$ and $k = 0.137$ were provided by the meta-analysis of Hussey and others (2014).

Trophic levels and diversity in the diet were compared only for the trophic groups with individual isotopic data (that is, megafauna, the blue whiting, mid-trophic level demersal fish, low-trophic level epipelagic fish, mid-trophic level epipelagic fish, mesopelagic fish, the broadtail shortfin squid, and the Henslow's swimming crab). To investigate significant differences between seasons, a Wilcoxon test was performed. Seasonal trophic networks and dominator trees, and all the metrics were computed and visualized using the *cheddar*, *DiagrammeR*, *igraph*, *tidyverse*, and *vegan* packages in R (Csardi and Nepusz 2006; Wickham and others 2019; Hudson and others 2022; Oksanen and others 2022; Iannone 2024).

RESULTS

Overall Properties of the Pelagic Trophic Network

The constructed pelagic food web of the BoB is composed of 38 nodes and 125 trophic links, representing 53 distinct organisms and their interactions within the ecosystem (Figure 2). Link strengths were quantified by dietary proportions (Table S4). The nodes include a variety of pelagic groups, that is, fish (21.00%), cetaceans (18.42%), cephalopods (15.79%), crustaceans (13.16%), zooplankton (10.53%), seabirds and tunas (5.26%), and other components toward the bottom of the trophic chain such as polychaetes, gelatinous organisms, particulate organic matter (POM), and phytoplankton (2.63%). The network has a link density = 3.29 and connectance = 0.09. On average, there are 3.47 prey per consumer (G) and 4.63 consumers per prey (V), with a degree of omnivory = 0.71. Intermediate groups comprise the majority of the trophic network (65.79%), followed by top-level (28.95%) and basal groups (5.26%). Most trophic interactions occur between intermediate groups (48%), followed by top-intermediate pairs (40%). The proportion of links between intermediate and basal groups is 12%, while there are no direct links from bottom to top groups.

Centrality Indices and Dominator Tree—The Overall Network

Low-trophic level epipelagic fish (FNELTL) display the highest values in the degree, betweenness, and closeness centralities ($D_{tot} = 16$, $BC_i = 62$, $CL_i = 0.15$; Figure 3 and Table S5). Five species exhibit highest in-degree values (that is, striped dolphins, Balearic shearwaters, albacore tunas, Atlantic bluefin tunas, and thickback soles) while oceanic epipelagic crustaceans (that is, the Norwegian krill and hyperiids) have the highest out-degree (D_{out} = 12) (Table S5). Notably, 17 groups never occupy intermediate positions on the shortest pathways between any pair of nodes thus resulting in a betweenness equal to zero (that is, they are not bottlenecks for energy circulation).

The results of the dominator tree indicate that the pelagic food web is primarily controlled by phytoplankton (node 1), which dominates 25 nodes while POM (node 2) dominates 13 nodes (Figure 4). The phytoplankton-dominated branch controls six fish groups and eight megafauna, whereas the POM-dominated branch controls two fish groups and three megafauna. Copepods (node 3) are the most dominant zooplankton group, controlling 18 nodes while oceanic epipelagic crustaceans (node 10) are the most dominant crustacean group, controlling four nodes. Low-trophic level epipelagic fish (node 18) are the most dominant fish group, controlling six nodes. The longest phytoplankton-dominated chains consist of five nodes (average of 3.93 nodes), with six megafauna species at the top of the chains (that is, bottlenose dolphins, northern gannets, Atlantic bluefin tunas, harbor porpoises, long-finned pilot whales, and Cuvier's beaked whales). The longest POM-dominated chains consist of four nodes (average of 3.14 nodes), with broadtail shortfin squids and striped dolphins at the top of the chains. The average distance of fish to the root is 3.33 nodes in the phytoplankton-dominated chains while in the POM-dominated chains it is 3.00 nodes. The average distance of megafauna to the root is 4.75 nodes in the phytoplankton-dominated chains while in the POM-dominated chains it corresponds to 3.33 nodes.

Temporal Changes in Energy Circulation—The Seasonal Networks

We examined the strength of links between nodes during spring and late summer. Strengths were quantified by diet proportions, obtained for each season using stable isotopes (Table S4, Figure S1). Although the Wilcoxon tests did not show any significant differences ($p > 0.05$) for the average trophic level (TL_{diet}), the isotope-based trophic level (TL_{SIA}), and the diversity of trophic groups' diets

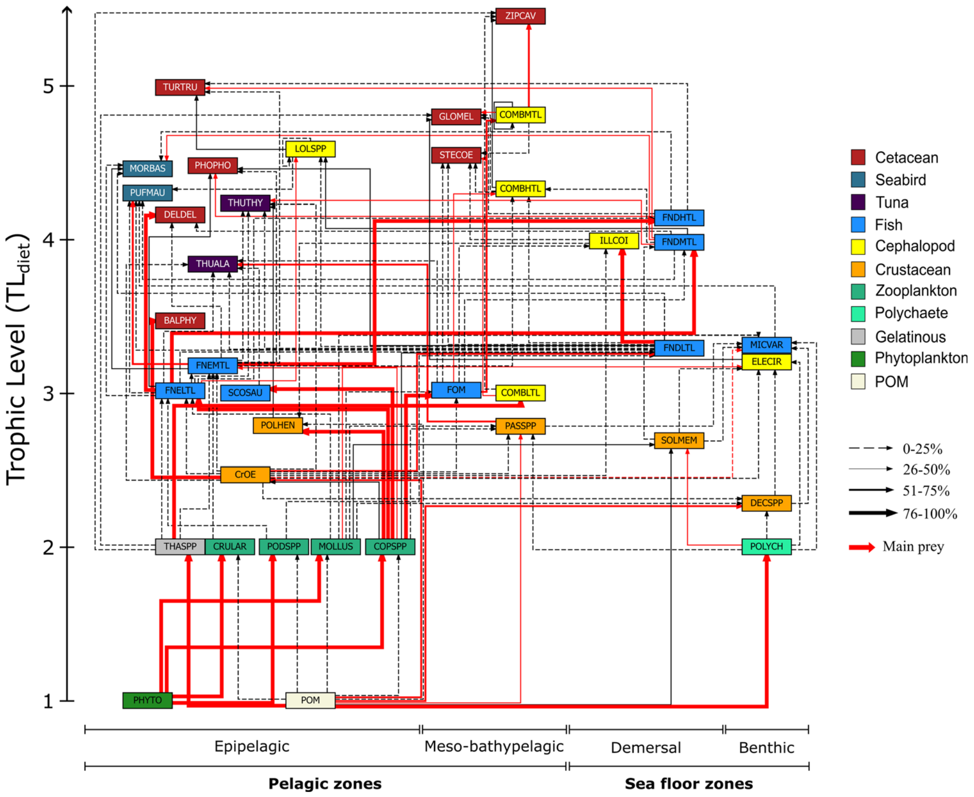

Figure 2. The pelagic food web of the Bay of Biscay. Nodes are arranged along the x-axis based on their oceanic depth habitat, and along the y-axis according to their effective trophic level (TL_{diet}). Node colors represent the ecological category. Each node (except for PHYTO and POM) has a red arrow pointing to it from its main prey. The width and type of the links represent the proportion of the diet. Definitions of acronyms are provided in Table 1.

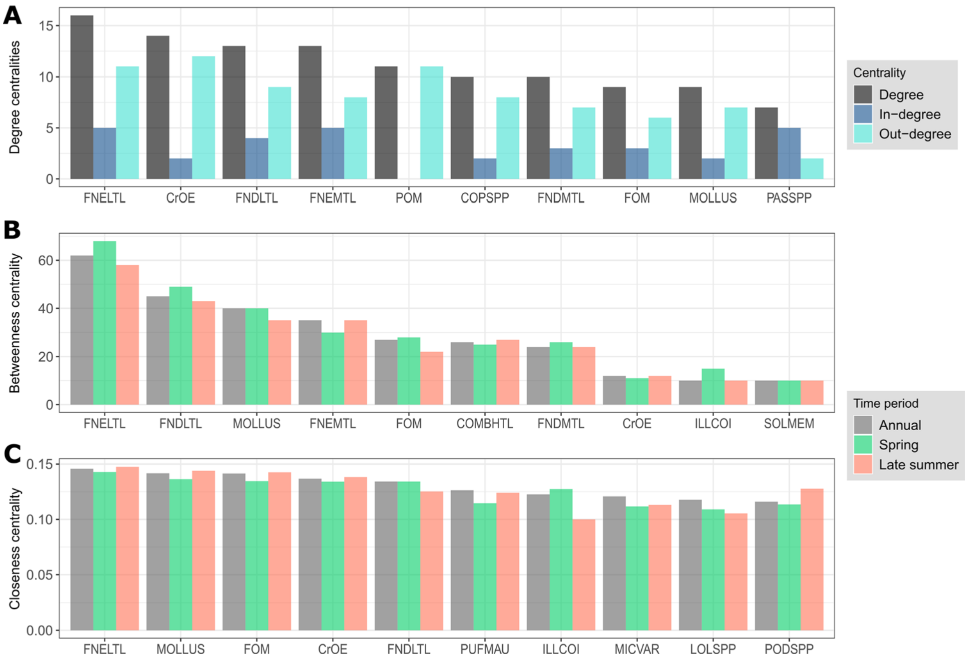

Figure 3. Network Centrality Indices: The top ten trophic groups with highest values are displayed. A: Degree centrality indices; B: Betweenness centrality; C: Closeness centrality. In plot A, colors represent total degree (dark gray, D_{tot}), in-degree (dark blue, D_{in}), and out-degree (light blue, D_{out}). In plots B and C, colors indicate the period of the year: Annual (light gray, BC_{an}, CL_{an}); spring (green, BC_{sp}, CL_{sp}); and late summer (red, BC_{ls}, CL_{ls}). Definitions of acronyms are provided in Table 1.

(H'), some trends were observed. The TL_{diet} computed for the entire network is higher in late summer (3.96 ± 0.80) compared to spring (3.90 ± 0.82). This pattern is confirmed by the TL_{SIA}: 3.35 ± 0.51 in late summer, and 3.29 ± 0.51 in spring (Figure S2). However, the H' is lower in late summer (0.99 ± 0.49) than in spring (1.03 ± 0.48) (Figure S2). Four species (that is, the harbor porpoise, the northern gannet, the blue whiting, and the broadtail shortfin squid) exhibit changes in their main prey (Table S4). In spring, harbor porpoises primarily feed on FNDHTL (35.7%) while in late summer they shift to FNELTL (46.7%). Northern gannets prefer FNEMTL (31.4%) in spring but switch to FNDMTL (30%) in late summer. The blue whiting shows a preference for copepods (45.7%) during spring and shifts to oceanic epipelagic crustaceans (CrOE, 73.2%) in late summer. Lastly, broadtail shortfin squids change their main prey from CrOE (56.8%) in spring to blue whiting (76.8%) in late summer (Table S4).

The late summer network shows a higher average trophic-path vulnerability (3.18) compared to the spring network (3.13). During late summer, the northern gannet (node 35) and broadtail shortfin squid (node 26) occupy more vulnerable positions than in spring as they are separated from the root by one additional node (Figure S3). The distance to the root for the northern gannet increases from four nodes in spring to five in late summer. In both seasons, the first two steps of the food chain remain the same, that is, phytoplankton (node 1) and copepods (node 3). However, in spring the sequence continues with mid-trophic level epipelagic fish (node 19) while in late summer it includes low-trophic level epipelagic fish (node 18) and mid-trophic level demersal fish (node 17). Similarly, the distance for broadtail shortfin squids (node 26) increases from three nodes in spring, dominated by POM (node 2) and oceanic epipelagic crustaceans (node 10), to four nodes in late summer, dominated by the same nodes but also by the blue whiting (node 16). In contrast, the harbor porpoise (node 31) is closer to the root and occupies a less vulnerable position in late summer than in spring. In spring, it is separated from the root by four nodes, being dominated by phytoplankton, copepods, mid-trophic level epipelagic fish, and high-trophic level demersal fish (node 15). In late summer, it is instead dominated by three nodes: phytoplankton, copepods, and low-trophic level epipelagic fish. Finally, a major shift occurs for the blue whiting (node 16); blue whiting is the only

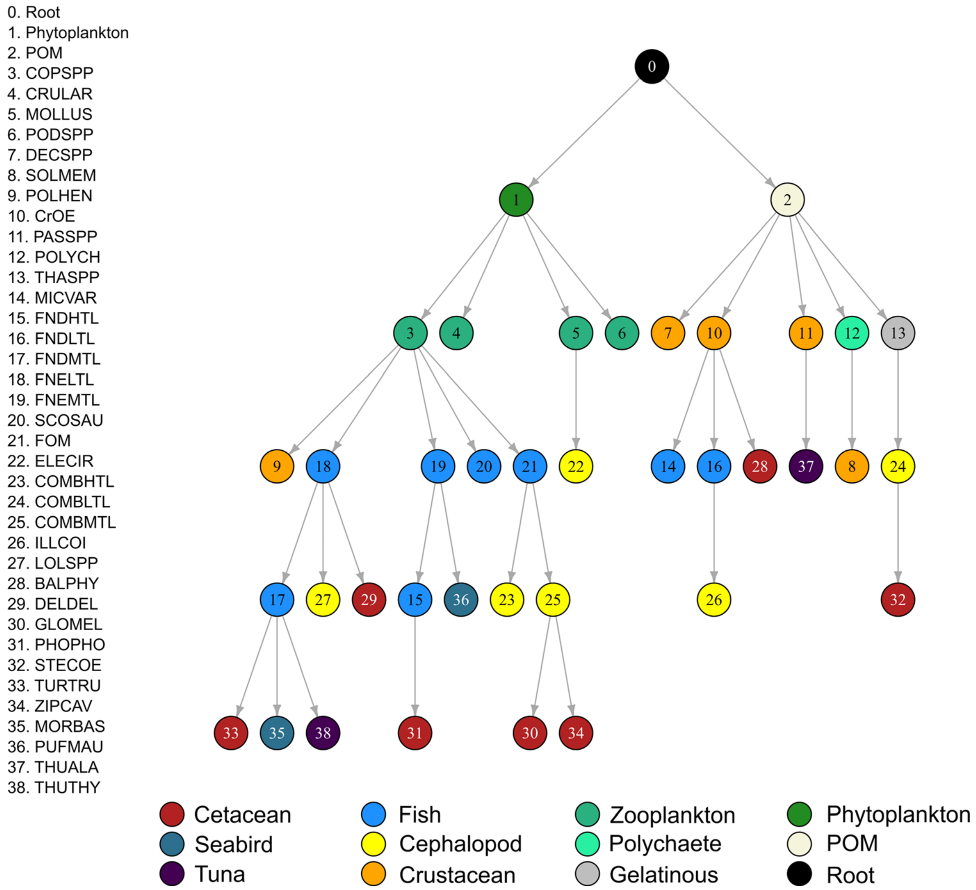

Figure 4. Dominator tree for the pelagic food web of the Bay of Biscay. The black node (ID = 0) represents the root. Nodes' colors indicate the ecological category and white labels denote megafauna. Definitions of acronyms are provided in Table 1.

trophic group that shifts from a position along the phytoplankton-dominated chain in spring to a POM-dominated chain in late summer.

DISCUSSION

Our study provides a comprehensive analysis of the BoB's pelagic food web by integrating stable isotope mixing models with stomach content data to construct weighted trophic networks. An average annual network, along with two seasonal versions describing feeding preferences in spring and late summer, was assembled using 38 nodes (species or trophic groups) corresponding to 53 distinct organisms. Our findings show the central role of low-trophic level epipelagic fish (that is, anchovy, sardine, and sprat) in connecting the planktonic food web to high-trophic level organisms. Higher trophic-path vulnerability has been associated with trophic groups that depend on POM, compared to those feeding along the phytoplankton-dominated grazing chain. Our results show that the trophic-path vulnerability increases from spring to late summer, with the blue whiting shifting from feeding along grazing chains in spring to POM domination in late summer. This study is innovative as it relies on stable isotope data from field samples to portray the feeding preferences of high-trophic level organisms (for example, cephalopods, fish, and marine mammals) in a weighted trophic network. Moreover, it uses seasonal isotopic data to identify bottlenecks to energy transfers in the pelagic food web during spring and late summer. This work illustrates a procedure that can help managers in prioritizing decisions on which trophic groups to protect during different seasons if the goal is to optimize both biodiversity conservation and ecosystem functioning.

Main Players in the Pelagic Trophic Network

Low-trophic level epipelagic fish (that is, anchovy, sardine, and sprat) have emerged as a key trophic group with the highest centrality scores. This group includes various near-surface species, also known as forage fish, which are fundamental to preserve energy circulation in marine ecosystems (Alder and others 2008; Scotti and others 2022). High values of degree and betweenness centralities indicate participation in numerous direct interactions with other species and the capability to serve as an intermediate link connecting different parts of the network. High closeness centrality illustrates the barycentric position occupied in the network, meaning that besides directly interacting as prey or predator with many species, the group transfers energy between different trophic levels, a typical feature displayed by forage fish (Pikitch and others 2014). In the BoB, forage fish account for a significant proportion of the total fluxes and are relevant for the benthic-pelagic coupling (Preciado and others 2008; Corrales and others 2022). The present study demonstrates that this group acts as a bottleneck to energy circulation, with a slightly stronger control of energy fluxes exerted during late summer (Figures 4 and S3).

The numerous direct and indirect links from the low-trophic level epipelagic fish to other trophic groups highlight substantial influence of this group on energy circulation in the ecosystem. Common dolphins and mid-trophic level demersal fish such as mid-size hakes (20–50 cm) feed preferentially on low-trophic level epipelagic fish (Meynier and others 2008; Iglesias and others 2023). Several species of megafauna such as the bottlenose dolphin, the northern gannet, and the Atlantic bluefin tuna are indirectly affected because they have a feeding preference for mid-trophic level demersal fish, which links them to low-trophic level epipelagic fish although the latter do not constitute a significant part of megafauna species' diet. The fact that forage species represents more than half of the catches in the BoB is a source of concern (Corrales and others 2022). Changes in the biomass of low-trophic level epipelagic fish may result in cascading effects, potentially disrupting pathways ensuring stability and resilience to energy circulation in the ecosystem. Therefore, their significant reduction or removal may hinder the efficient transfer of energy between trophic levels. If there is a decline or collapse of a species due to fishing pressure (for example, anchovy), predators may have the capacity to change their trophic habits and search for other prey, as long as 'similar prey' (in size, shape and quality, for example, lipid content) are available. This was observed in the BoB when analyzing the relationship between blue whiting (prey) and hake (predator); in the absence of the blue whiting, hakes increased their consumption of all other available prey (Lopez-Lopez and others 2015). Additionally, the collapse of the blue whiting in 2008 in the BoB increased cannibalism rates among large hakes (Preciado and others 2015). If the species recovers (for example, due to reduced fishing pressure or better recruitment), the system has sufficient capacity for reorganization. However, if such changes persist and lead to species collapse, significant consequences for ecosystem functioning are anticipated (Blöcker and others 2023).

Dominance in the Pelagic Network

The analysis of the dominator tree reveals a hierarchical structure of dependencies in the energy flow network. Our results show that the phytoplankton exerts a significant control over a wide range of fish, marine mammals and seabirds. However, its dominance over a greater number of nodes compared to POM does not provide conclusive evidence that a larger proportion of energy flows through the grazing chain. The extent of this dominance is generally not altered by seasonality, with the exception of the blue whiting, which shifts from receiving most of its energy from grazing chains in spring to relying mostly on POM in late summer. This variation most likely reflects changes in the environmental and oceanographic conditions (for example, changes in primary production; Calbet 2001; Jennings and Mackinson 2003). In fact, this seasonal shift in dominant fluxes is expected in most predators within seasonal systems. Generally, many consumers rely on the fastest grazing chains during spring when pelagic production is high. Conversely, during periods of lower productivity, consumers benefit from the more complex and convoluted detritus-based pathways, which recycle surplus production and deliver energy to heterotrophs after systems' productivity peaks (that is, phytoplankton blooms; Rooney and others 2006; Mougi 2020; Giraldo and others 2024). While coupling is assumed to be the main function of predators, there is evidence of multichannel feeding at much lower trophic levels, indicating that the food web resilience associated with the coupling of trophic pathways is not exclusive from higher trophic levels (Blanchard and others 2011; Wolkovich and others 2014).

The longer chain length and greater average distances from the root in the phytoplankton-dominated branch suggest complex trophic dynamics (Hairston and Hairston 1997; D'Alelio and others 2016). These longer pathways might result in greater energy loss at each trophic level, potentially leading to less efficient energy transfer from phytoplankton to top predators (Degerman and others 2018). These conclusions, however, contradict previous evidence, which generally identify the plankton chains as the shortest and fastest, while detritus-based chains are longer and slower (Sommer and others 2018). Such contrasting results probably stem from the lower taxonomic and functional resolution used to represent microbial loop interactions in the planktonic food web. In our study, the lack of information on the smallest fractions of plankton, mostly related to the microbial loop and the detritus-based chains such as bacteria, heterotrophic nanoflagellates, ciliates and dinoflagellates leads to underestimate the length of POM-dominated chains (Blanchard and others 2011). The theoretical higher transfer efficiency of the shortest chains is often challenged by the seasonality of the production. Pulse production systems can be quite inefficient in channeling production toward the upper food web levels due to constrains of turnover times of consumers, with large part of the production lost through advection and/or sedimentation (Calbet 2001). This inefficiency highlights the importance of studying seasonal variations in the food web architecture as they may provide clues on its dynamical functioning. Our findings are suitable to quantify trophic-path vulnerabilities and dependencies among trophic groups for nekton and seabirds while they might overlook these aspects in the planktonic food web.

Seasonal Effects in the Pelagic Network

Seasonal variations in trophic level and diet diversity were not significant. The lack of statistically significant differences between the two seasons could be attributed to the sampling dates, May and September, which may have similar oceanographic conditions. However, the observed trends may still explain how environmental and oceanographic conditions shape the structure of the pelagic ecosystem. The slight increase in average trophic level during late summer suggests that species tend to feed higher along the trophic chain, a change potentially driven by differences in prey availability and predators' foraging behavior (Iglesias and others 2023). This shift could depend on seasonal fluctuations in primary productivity, which influence the biomass and distribution of prey. Shorter food chains in spring may be due to the high productivity pulses that occur during this season (Calbet 2001; Jennings and Mackinson 2003). Lower dietary diversity in late summer indicates a higher specialization during a period of lower primary productivity compared to spring. This finding contrasts with the optimal foraging theory, which predicts greater diet specialization when resources are abundant and a more generalized diet during food limitation (Stephens and Krebs 1986; Abreu and others 2019). Diet specialization in late summer may enhance foraging efficiency while increasing the vulnerability to fluctuations in prey biomass (Terraube and others 2011).

Seasonal shifts in feeding preferences may cause changes in diet specialization. In this study, harbor porpoises, northern gannets, blue whiting, and broadtail shortfin squids display diet differences between spring and late summer, potentially improving their adaptability to fluctuations in prey availability. For instance, the shift of the blue whiting toward consuming oceanic epipelagic crustaceans in late summer may compensate for the decline in copepods' biomass (Valdés and others 2007). These results underscore the importance of considering seasonal variations in trophic interactions, which can alter the resilience of predators with respect to energy delivery. Our seasonal analysis reveals a shift from phytoplankton-dominated trophic chains in the spring to an increased reliance on POM-dominated pathways in late summer. This pattern is broadly consistent with previous studies that have demonstrated the importance of switching among alternative energy pathways in marine food webs (Stibor and others 2004; D'Alelio and others 2019; McCormack and others 2020).

Describing seasonal changes in the main energy flow pathways and the resulting species' robustness may clarify how environmental conditions (for example, primary productivity) may alter ecosystem functions. Feeding preferences and network analysis can be applied to identify seasonal changes in the identity of key species dominating energy fluxes in the ecosystem. The primary goal of this analysis is to enhance conservation practices by identifying species that should be protected during different seasons, with the aim of maintaining energy delivery resilience. Considering seasonal differences in food chain structure, different management strategies might be implemented for protecting specific taxa, and ensuring a healthy flow structure in the ecosystem. These criteria establish species protection priorities based on their functional importance, and may complement existing procedures that focus on the conservation of charismatic or rare species (Jordán 2009; Scotti and Jordán 2015).

Limits to Characterizing Predators' Diets

Obtaining seasonal samples for megafauna such as marine mammals is challenging due to difficulties in the collection of material from living individuals, an aspect that forced us to rely mainly on strandings. Additionally, samples of some fish (for example, whiting, European seabass, and Atlantic saury) were difficult to obtain as they depend on oceanographic surveys, which usually target commercial species (for example, anchovy and sardine). The lack of seasonal isotopic data for some groups (for example, most cephalopod species and zooplankton groups) required making assumptions on their feeding preferences. Furthermore, our weighted networks inform about the relative importance of prey with respect to total predators' consumption, but the absence of details on the biomass of all nodes impaired the construction of mass-balanced networks and the quantification of carbon flowing through the different trophic links. Moreover, accurately determining the diet-to-tissue discrimination factor (DTDF) is crucial for modeling the assimilated diet from stable isotope data. It is known that DTDF may differ between species and tissues, and it varies in response to different environmental conditions such as temperature (Caut and others 2009; Ito and others 2019). As experimental DTDF values were not available for all species, for some we used values from the most closely related species. Although these values are the best available, results should be interpreted with caution, as the use of inappropriate DTDF can bias diet estimates (Bond and Diamond 2011). Furthermore, the resolution of Bayesian isotopic mixing models is limited by the number of sources that can be included (Phillips and others 2014), which requires lumping together the contribution of different but similar resources. This methodological constraint may limit the capability to model changes in the contribution of all potential dietary items, resulting in a lower ecosystem resolution.

CONCLUSIONS

Our study offers a robust framework for understanding seasonal changes in the structure of ecosystems in terms of energy transfer. It highlights the crucial role of low-trophic level epipelagic fish (that is, anchovy, sardine, and sprat) in maintaining the stability of energy flow from the planktonic food web to upper trophic level organisms in the BoB. The trophic chains are primarily dominated by phytoplankton. The relevance of the microbial loop (here considered as POM) increases in late summer and coincides with the decline of primary productivity. The present approach may have implications for ecosystem-based management as it identifies trophic groups that should be prioritized for protection depending on the seasons to avoid major energy-transfer disruptions within the ecosystem. The conservation of forage fish has been already shown to be strategic for setting into practice ecosystem-based management criteria (Scotti and others 2022; Kell and others 2024). In this work, we stress the importance of seasonal variations in trophic interactions when developing fisheries management plans. Adaptive management strategies that account for seasonal changes can mitigate the impacts of fluctuations in environmental and oceanographic conditions. These strategies may help to maintain a balance between different trophic levels, an essential condition to prevent cascading effects and ensure the health of the ecosystem.

ACKNOWLEDGEMENTS

We would like to thank the crew of the R/V 'Ángeles Alvariño', R/V 'Vizconde de Eza' and R/V 'Emma Bardán', as well as the AZTI and IEO-CSIC staff who took part in the BIOMAN and JUVENA surveys, allowing the collection of the samples used in this study. We also thank AZTI's scientific observers and others who contributed to the sample collection, including members of the French stranding scheme (RNE) for their continuous effort in collecting data on stranded cetaceans. The study was supported under the EPELECO project funded by the Spanish Government, and partially by the PETFISH project funded by the Basque Government and the BIOcean5D project (Horizon Europe grant agreement 10109915). BI was funded by a PhD fellowship from the Department of Economic Development, Sustainability and Environment of the Basque Government. ML was funded by a Ramón y Cajal contract (RYC-2012-09897) from the Spanish Government. The authors are grateful to Gaël Guillou for his assistance with stable isotope analyses. Thank you to Adrien Lambrechts, who made it possible to obtain the data on Balearic shearwaters. Thanks are also due to the CPER (Contrat de Projet Etat-Région) and the FEDER (Fonds Européen de Développement Régional) for funding the IRMS of LIENSs laboratory. Pelagis is funded by the French ministry in charge of the environment, the French Office for Biodiversity (Office Française de la Biodiversité—OFB), and by the "Communauté d'Agglomération de la Ville de

La Rochelle.'' PB is an honorary member of the IUF (Institut Universitaire de France). MSco acknowledges the German Federal Agency for Nature Conservation (Bundesamt für Naturschutz, BfN), which provided financial support with funds from the Federal Ministry of the Environment, Nature Conservation, and Nuclear Safety (BMU) under grant agreement FKZ: 3521532201. MI and MSco are grateful to the support from the EcoScope Project, funded by the European Commission's Horizon 2020 Research and Innovation Programme under grant agreement Nº 101000302. This is contribution number 1273 from AZTI, Marine Research, Basque Research and Technology Alliance (BRTA).

DATA AVAILABILITY

The data used for analyses and to create the figures of the manuscript are available from the electronic supplemental information provided with this manuscript.

REFERENCES

Abreu J, Staniland I, Rodrigues CF, Queirós JP, Pereira JM, Xavier JC. 2019. Squid in the diet of Antarctic fur seals: Potential links to oceanographic conditions and Antarctic krill abundance. Mar Ecol Prog Ser 628:211–221.

Alder J, Campbell B, Karpouzi V, Kaschner K, Pauly D. 2008. Forage fish: From ecosystems to markets. Annu Rev Environ Resour 33:153–166.

Allesina S, Bodini A. 2004. Who dominates whom in the ecosystem? Energy flow bottlenecks and cascading extinctions. J Theor Biol 230:351–358.

Alpine AE, Cloern JE. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnol Oceanogr 37:946–955.

Anderson TR, Pond DW, Mayor DJ. 2017. The role of microbes in the nutrition of detritivorous invertebrates: A stoichiometric analysis. Front Microbiol 7.

Bachiller E, Irigoien X. 2015. Trophodynamics and diet overlap of small pelagic fish species in the bay of biscay. Mar Ecol Prog Ser 534:179–198.

Bass A V., Falkenberg LJ. 2024. Seasonal effects and trophic pressure shape the responses of species interactions in a tropical seagrass meadow to marine heatwaves. Oikos:1–17.

Bersier L-F, Banašek-Richter C, Cattin M-F. 2002. Quantitative descriptors of food-web matrices. Ecology 83:2394–2407.

Blanchard JL, Law R, Castle MD, Jennings S. 2011. Coupled energy pathways and the resilience of size-structured food webs. Theor Ecol 4:289–300.

Blöcker AM, Sguotti C, Möllmann C. 2023. Discontinuous dynamics in North Sea cod Gadus morhua caused by ecosystem change. Mar Ecol Prog Ser 713:133–149. https://doi.org/10.3354/meps14342.

Bode A, Anadón R, Morán XAG, Nogueira E, Teira E, Varela M. 2011. Decadal variability in chlorophyll and primary production off NW Spain. Clim Res 48:293–305.

Bond AL, Diamond AW. 2011. Recent Bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors. Ecol Appl 21:1017–1023.

Borja A, Amouroux D, Anschutz P, Gómez-Gesteira M, Uyarra MC, Valdés L. 2019. Chapter 5: The Bay of Biscay. In: Sheppard C, editor. World Seas: An Environmental Evaluation Volume I: Europe, the Americas and West Africa. Second edi. London: Elsevier. pp 113–52.

Borrett SR, Sheble L, Moody J, Anway EC. 2018. Bibliometric review of ecological network analysis: 2010–2016. Ecol Modell 382:63–82.

Cabrol J, Trombetta T, Amaudrut S, Aulanier F, Sage R, Tremblay R, Nozais C, Starr M, Plourde S, Winkler G. 2019. Trophic niche partitioning of dominant North-Atlantic krill species, Meganyctiphanes norvegica, Thysanoessa inermis, and T. raschii. Limnol Oceanogr 64:165–181.

Calbet A. 2001. Mesozooplankton grazing effect on primary production: A global comparative analysis in marine ecosystems. Limnol Oceanogr 46:1824–1830.

Caut S, Angulo E, Courchamp F. 2009. Variation in discrimination factors (Δ15N and Δ13C): The effect of diet isotopic values and applications for diet reconstruction. J Appl Ecol 46:443–453.

Chouvelon T, Spitz J, Caurant F, Mèndez-Fernandez P, Chappuis A, Laugier F, Le Goff E, Bustamante P. 2012. Revisiting the use of δ15N in meso-scale studies of marine food webs by considering spatio-temporal variations in stable isotopic signatures - The case of an open ecosystem: The Bay of Biscay (North-East Atlantic). Prog Oceanogr 101:92–105. https://doi.org/10.1016/j.pocean.2012.01.004.

Corrales X, Preciado I, Gascuel D, Lopez de Gamiz-Zearra A, Hernvann PY, Mugerza E, Louzao M, Velasco F, Doray M, López-López L, Carrera P, Cotano U, Andonegi E. 2022. Structure and functioning of the Bay of Biscay ecosystem: A trophic modelling approach. Estuar Coast Shelf Sci 264.

Csardi G, Nepusz T. 2006. The igraph software package for complex network research. InterJournal Complex Sy:1695. https://igraph.org

D'Alelio D, Hay Mele B, Libralato S, Ribera d'Alcalà M, Jordán F. 2019. Rewiring and indirect effects underpin modularity reshuffling in a marine food web under environmental shifts. Ecol Evol 9:11631–11646.

D'Alelio D, Libralato S, Wyatt T, Ribera D'Alcalà M. 2016. Ecological-network models link diversity, structure and function in the plankton food-web. Sci Rep 6:1–13.

Degerman R, Lefébure R, Byström P, Båmstedt U, Larsson S, Andersson A. 2018. Food web interactions determine energy transfer efficiency and top consumer responses to inputs of dissolved organic carbon. Hydrobiologia 805:131–146.

Eddy TD, Bernhardt JR, Blanchard JL, Cheung WWL, Colléter M, du Pontavice H, Fulton EA, Gascuel D, Kearney KA, Petrik CM, Roy T, Rykaczewski RR, Selden R, Stock CA, Wabnitz CCC, Watson RA. 2021. Energy Flow Through Marine Ecosystems: Confronting Transfer Efficiency. Trends Ecol Evol 36:76–86. https://doi.org/10.1016/j.tree.2020.09.006.

Estrada E. 2007. Characterization of topological keystone species. Local, global and 'meso-scale' centralities in food webs. Ecol Complex 4:48–57.

Ferrer L, Fontán A, Mader J, Chust G, González M, Valencia V, Uriarte A, Collins MB. 2009. Low-salinity plumes in the oceanic region of the Basque Country. Cont Shelf Res 29:970–984.

Freeman LC. 1977. A Set of Measures of Centrality Based on Betweenness. Sociometry 40:35–41.

Gaspar C, Giménez J, Andonegi E, Astarloa A, Chouvelon T, Franco J, Goñi N, Corrales X, Spitz J, Bustamante P, Louzao M. 2022. Trophic ecology of northern gannets Morus bassanus highlights the extent of isotopic niche overlap with other apex predators within the Bay of Biscay. Mar Biol 169:1–14. https://doi.org/10.1007/s00227-022-04079-y.

Giménez J, Ramírez F, Almunia J, G. Forero M, de Stephanis R. 2016. From the pool to the sea: Applicable isotope turnover rates and diet to skin discrimination factors for bottlenose dolphins (Tursiops truncatus). J Exp Mar Bio Ecol 475:54–61. https://doi.org/10.1016/j.jembe.2015.11.001

Giraldo C, Cresson P, MacKenzie K, Fontaine V, Loots C, Delegrange A, Lefebvre S. 2024. Insights into planktonic food-web dynamics through the lens of size and season. Sci Rep 14:1–17. https://doi.org/10.1038/s41598-024-52256-4.

Hairston NGJ, Hairston NGS. 1997. Does food web complexity eliminate trophic-level dynamics? Am Nat 149:1001–1007.

Hernvann P-Y, Gascuel D, Kopp D, Robert M, Rivot E. 2022. EcoDiet: A hierarchical Bayesian model to combine stomach, biotracer, and literature data into diet matrix estimation. Ecol Appl 32.

Hudson L, Reuman D, Emerson R. 2022. Cheddar: analysis and visualisation of ecological communities. R package version 0.1–638.

Hussey NE, Macneil MA, Mcmeans BC, Olin JA, Dudley SFJ, Cliff G, Wintner SP, Fennessy ST, Fisk AT. 2014. Rescaling the trophic structure of marine food webs. Ecol Lett 17:239–250.

Iannone RO. 2024. DiagrammeR: Graph/Network Visualization. R package version 1.0.11. https://cran.r-project.org/package=DiagrammeR

Iglesias B, Giménez J, Preciado I, Méndez-Fernández P, Chouvelon T, Lambrechts A, Bustamante P, Fort J, Goñi N, Spitz J, Astarloa A, Louzao M. 2024. Trophic guilds and niche segregation among marine megafauna in the Bay of Biscay. Mar Environ Res 202. https://linkinghub.elsevier.com/retrieve/pii/S0141113624004124

Iglesias B, Louzao M, Bachiller E, López-López L, Santos M, Boyra G, Andonegi E, Cotano U, Preciado I. 2023. Influence of seasonal variability on the trophic structure of pelagic communities. Front Mar Sci 10:1185376.

Irigoien X, Fernandes JA, Grosjean P, Denis K, Albaina A, Santos M. 2009. Spring zooplankton distribution in the Bay of Biscay from 1998 to 2006 in relation with anchovy recruitment. J Plankton Res 31:1–17.

Ito M, Scotti M, Franz M, Barboza FR, Buchholz B, Zimmer M, Guy-Haim T, Wahl M. 2019. Effects of temperature on carbon circulation in macroalgal food webs are mediated by herbivores. Mar Biol 166:1–11. https://doi.org/10.1007/s00227-019-3596-z.

Jennings S, Mackinson S. 2003. Abundance–body mass relationships in size-structured food webs. Ecol Lett 6:971–974.

Jordán F. 2009. Keystone species and food webs. Philos Trans R Soc B Biol Sci 364:1733–1741.

Kadoya T, Osada Y, Takimoto G. 2012. Isoweb: A bayesian isotope mixing model for diet analysis of the whole food web. PLoS One 7.

Kell LT, Bentley JW, Feary D, Egan A, Nolan C. 2024. Developing management plans for sprat (Sprattus sprattus) in the Celtic Sea to advance the ecosystem approach to fisheries. Can J Fish Aquat Sci 81:1104–1121.

Kortsch S, Frelat R, Pecuchet L, Olivier P, Putnis I, Bonsdorff E, Ojaveer H, Jurgensone I, Strāke S, Rubene G, Krūze, Nordström MC. 2021. Disentangling temporal food web dynamics facilitates understanding of ecosystem functioning. J Anim Ecol 90:1205–1216.

Kortsch S, Primicerio R, Aschan M, Lind S, Dolgov AV, Planque B. 2019. Food-web structure varies along environmental gradients in a high-latitude marine ecosystem. Ecography (Cop) 42:295–308.

Lloret-Lloret E, Navarro J, Giménez J, López N, Albo-Puigserver M, Pennino MG, Coll M. 2020. The Seasonal Distribution of a Highly Commercial Fish Is Related to Ontogenetic Changes in Its Feeding Strategy. Front Mar Sci 7.

Longhurst AR. 2007. Ecological Geography of the Sea. 2nd Editio. Academic Press https://linkinghub.elsevier.com/retrieve/pii/B9780124555211X50001

López-López L, Bartolino V, Preciado I. 2015. Role of prey abundance and geographical variables in a demersal top predator's feeding habits (Merluccius merluccius). Mar Ecol Prog Ser 541:165–177.

McCann MJ, Jensen OP. 2018. Laboratory experiments to determine trophic enrichment factors of stables isotope and fatty acid biomarkers in the blue crab. Callinectes Sapidus. https://doi.org/10.7266/N76971K2.

McCormack SA, Melbourne-Thomas J, Trebilco R, Blanchard JL, Constable A. 2020. Alternative energy pathways in Southern Ocean food webs: Insights from a balanced model of Prydz Bay, Antarctica. Deep Res Part II Top Stud Oceanogr 174:104613. https://doi.org/10.1016/j.dsr2.2019.07.001.

McMeans BC, McCann KS, Humphries M, Rooney N, Fisk AT. 2015. Food Web Structure in Temporally-Forced Ecosystems. Trends Ecol Evol 30:662–672.

Meier RE, Votier SC, Wynn RB, Guilford T, McMinn Grivé M, Rodríguez A, Newton J, Maurice L, Chouvelon T, Dessier A, Trueman CN. 2017. Tracking, feather moult and stable isotopes reveal foraging behaviour of a critically endangered seabird during the non-breeding season. Divers Distrib 23:130–145.

Meynier L, Pusineri C, Spitz J, Santos MB, Pierce GJ, Ridoux V. 2008. Intraspecific dietary variation in the short-beaked common dolphin Delphinus delphis in the Bay of Biscay: Importance of fat fish. Mar Ecol Prog Ser 354:277–287.

Moore JW, Semmens BX. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. Ecol Lett 11:470–480.

Mougi A. 2020. Coupling of green and brown food webs and ecosystem stability. Ecol Evol 10:9192–9199. https://doi.org/10.1002/ece3.6586.

Odum EP. 1969. The strategy of ecosystem development. Science (80-) 164:262–70.

Oksanen J, Simpson GL, Blanchet FG. 2022. Vegan: Community Ecology Package. R package version 2.6–2. :295. https://github.com/vegandevs/vegan NeedsCompilation

Perkins DM, Hatton IA, Gauzens B, Barnes AD, Ott D, Rosenbaum B, Vinagre C, Brose U. 2022. Consistent predator-prey biomass scaling in complex food webs. Nat Commun 13.

Phillips DL, Inger R, Bearhop S, Jackson AL, Moore JW, Parnell AC, Semmens BX, Ward EJ. 2014. Best practices for use of stable isotope mixing models in food-web studies. Can J Zool 92:823–835.

Pikitch EK, Rountos KJ, Essington TE, Santora C, Pauly D, Watson R, Sumaila UR, Boersma PD, Boyd IL, Conover DO, Cury P, Heppell SS, Houde ED, Mangel M, Plagányi É, Sainsbury K, Steneck RS, Geers TM, Gownaris N, Munch SB. 2014. The global contribution of forage fish to marine fisheries and ecosystems. Fish Fish 15:43–64.

Pimm SL, Lawton JH, Cohen JE. 1991. Food web patterns and their consequences. Nature 350:669–674.

Post DM. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. Ecology 83:703–718.

Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT. 1996. Challenges in the Quest for Keystones. Bioscience 46:609–620.

Preciado I, Punzón A, Velasco F. 2015. Spatio-temporal variability in the cannibalistic behaviour of European hake Merluccius merluccius: The influence of recruit abundance and prey availability. J Fish Biol 86:1319–1334.

Preciado I, Velasco F, Olaso I. 2008. The role of pelagic fish as forage for the demersal fish community in the southern Bay of Biscay. J Mar Syst 72:407–417.

Ramos R, Ramírez F, Sanpera C, Jover L, Ruiz X. 2009. Feeding ecology of yellow-legged gulls Larus michahellis in the western Mediterranean: A comparative assessment using conventional and isotopic methods. Mar Ecol Prog Ser 377:289–297.

Rocchi M, Scotti M, Micheli F, Bodini A. 2017. Key species and impact of fishery through food web analysis: A case study from Baja California Sur, Mexico. J Mar Syst 165:92–102. https://doi.org/10.1016/j.jmarsys.2016.10.003.

Rooney N, McCann K, Gellner G, Moore JC. 2006. Structural asymmetry and the stability of diverse food webs. Nature 442:265–269.

Scotti M, Allesina S, Bondavalli C, Bodini A, Abarca-Arenas LG. 2006. Effective trophic positions in ecological acyclic networks. Ecol Modell 198:495–505.

Scotti M, Bondavalli C, Bodini A. 2009. Linking trophic positions and flow structure constraints in ecological networks: Energy transfer efficiency or topology effect? Ecol Modell 220:3070–3080.

Scotti M, Jordán F. 2015. The structural importance of less abundant species in Prince William Sound food web The structural importance of less abundant species in Prince William Sound food web. Isr J Ecol Evol 61:77–89. https://doi.org/10.1080/15659801.2015.1067972.

Scotti M, Opitz S, MacNeil L, Kreutle A, Pusch C, Froese R. 2022. Ecosystem-based fisheries management increases catch and carbon sequestration through recovery of exploited stocks: The western Baltic Sea case study. Front Mar Sci 9:1–23.

Scotti M, Podani J, Jordán F. 2007. Weighting, scale dependence and indirect effects in ecological networks: A comparative study. Ecol Complex 4:148–159.

Simenstad CA. 2016. Detritus Food Webs. In: Kennish MJ, editor. Encyclopedia of Estuaries. Encyclopedia of Earth Sciences Series. Dordrecht: Springer. pp 197–9. https://link.springer.com/https://doi.org/10.1007/978-94-017-8801-4_56

Smith JA, Mazumder D, Suthers IM, Taylor MD. 2013. To fit or not to fit: Evaluating stable isotope mixing models using simulated mixing polygons. Methods Ecol Evol 4:612–618.

Sommer U, Charalampous E, Scotti M, Moustaka-Gouni M. 2018. Big fish eat small fish: Implications for food chain length? Community Ecol 19:107–115.

Stephens DW, Krebs JR. 1986. Foraging theory. Princeton, New Jersey, USA: Princeton University Press.

Stibor H, Vadstein O, Diehl S, Gelzleichter A, Hansen T, Hantzsche F, Katechakis A, Lippert B, Løseth K, Peters C, Roederer W, Sandow M, Sundt-Hansen L, Olsen Y. 2004. Copepods act as a switch between alternative trophic cascades in marine pelagic food webs. Ecol Lett 7:321–328.

Stock BC, Semmens BX. 2016. MixSIAR GUI User Manual. https://github.com/brianstock/MixSIAR

Team RC. 2022. R: A language and environment for statistical computing. https://www.r-project.org/

Terraube J, Arroyo B, Madders M, Mougeot F. 2011. Diet specialisation and foraging efficiency under fluctuating vole abundance: A comparison between generalist and specialist avian predators. Oikos 120:234–244.

Valdés L, López-Urrutia A, Cabal J, Alvarez-Ossorio MT, Bode A, Miranda A, Cabanas M, Huskin I, Anadón R, Alvarez-Marqués F, Llope M, Rodríguez N. 2007. A decade of sampling in the Bay of Biscay: What are the zooplankton time series telling us? Prog Oceanogr 74:98–114.

Varela JL, de la Gándara F, Ortega A, Medina A. 2012. 13C and 15N analysis in muscle and liver of wild and reared young-of-the-year (YOY) Atlantic bluefin tuna. Aquaculture 354–355:17–21. https://doi.org/10.1016/j.aquaculture.2012.04.040.

White ER, Hastings A. 2020. Seasonality in ecology: Progress and prospects in theory. Ecol Complex 44.

Wickham H, Averick M, Bryan J, Chang W, McGowan L, François R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen T, Miller E, Bache S, Müller K, Ooms J, Robinson D, Seidel D, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H. 2019. Welcome to the Tidyverse. J Open Source Softw 4:1686.

Wolkovich EM, Allesina S, Cottingham KL, Moore JC, Sandin SA, De Mazancourt C. 2014. Linking the green and brown worlds: The prevalence and effect of multichannel feeding in food webs. Ecology 95:3376–3386.

Xing M, Wang Q, Li X, Li Y, Zhou X. 2021. Selection of keystone species based on stable carbon and nitrogen isotopes to construct a typical food web on the shore of Xingkai Lake, China. Ecol Indic 132. https://doi.org/10.1016/j.ecolind.2021.108263