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Gadiform species display dietary shifts in the Celtic Sea

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Abstract :

Global changes, through their impacts on ecosystem trophic structures, are behind regime shifts and cascading effects, and could result in the reorganization of whole ecosystems. The Celtic Sea is a temperate sea at risk of the above because of the interplay between climate change and fisheries. This sea has only displayed slight changes in species diversity between the late 20th century and the present day. However, this apparent stability in species diversity could be hiding structural transformations, including the rearrangement of trophic relationships. Historical stomach content database offers the opportunity to investigate changes in ecosystem trophic structure. Based on such database, this study explored shifts in the feeding habits of gadiform species in the Celtic Sea in the 1980s, 1990s, and 2010s. To this end, it examined dietary generalism and composition for four top predator fish species. During the target period, generalists maintained their diets, while specialists adopted more generalist diets. There were also decreases in frequencies of occurrence of certain fishes within the diets of gadiform species. These recent changes in trophic structure organization have likely been caused by the influence of global changes on both top-down and bottom-up processes that occurred in the Celtic Sea.

Highlights

► From the 1980s–2010s, specialists top predators in the Celtic Sea switched to generalist diets. ► Fish occurrence decreased in the diets of top predators while crustaceans increased. ► Top-down and bottom-up processes might have caused this trophic structure re-organization.

Keywords : Stomach Contents, Specialist, Generalist, Global Change, Feeding strategies, North East Atlantic

1. Introduction

Marine ecosystems are dynamic and experience myriad anthropogenic pressures, whose increasing frequency and magnitude might foster ecosystemic structural reorganization (Harley et al., 2006, Bryndum-Buchholz et al., 2019). Among those variations, the trophic structure of ecosystems is shaped by interactions between predator and prey as well as between predators and their competitors, which are likely to be affected by global changes (Holland et al., 2020, Nagelkerken et al., 2020).

There is a rich history of research exploring ecosystem trophic structure, with the aim of understanding and characterizing the above interactions (Levinton, 1972, Woodin & Jackson, 1979). Stomach content analysis was the first tool developed to study species trophic ecology (Hyslop 1980, Hynes, 1950). It offers a detailed snapshot of an individual's diet in the few hours prior to sampling (Hyslop, 1980, Amundsen & Sanchez-Hernandez, 2019, de Carvalho et al., 2019). Thus, the existence of historical data on stomach contents offers a unique opportunity to investigate ecosystem-level trophic changes over intermediate to long term periods (Buckland et al., 2017, Garrison & Link, 2000).

The Celtic Sea is a temperate sea where demersal top predators (e.g. anglerfish, plaice, megrim, sole, cod, haddock, hake and whiting) occupy a central position in trophic functioning of the ecosystem (Moullec et al., 2017, Hernvann et al., 2020). Historically, fishing activities have resulted in regular data collection, including information on the stomach contents of commercial species; such has created an opportunity to precisely characterize the area's trophic change over time (Pinnegar, 2014). Despite ongoing resource exploitation and environmental fluctuations, the Celtic Sea has only experienced slight changes in species diversity from the end of the 20th century to the present (Mérillet et al., 2020, Hernvann et al., 2020). Such apparent taxonomic stability might hide insidious degrees of structural reorganization, especially in trophic relationships (Pinnegar et al., 2002).

This study examined whether some changes occurred in the diets of four top predator fish species in the Celtic Sea between three time periods running from the 1980s to the 2010s. Specifically, we looked at the detailed diet composition of four gadiform species: cod, *Gadus morhua*; haddock, *Melanogrammus aeglefinus*; whiting, *Merlangius merlangus*; and hake, *Merluccius merluccius*. Adults of these species are commercially important (Hernvann & Gascuel, 2020) and, as top predators, they are important regulators of trophic interactions within ecosystems (Moullec et al., 2017, Hernvann et al., 2020, Lynam et al., 2017, Baum & Worm, 2009). Since species degree of generalism could be interpreted as species trophic niche breadth, generalist species, having a broader trophic niche breadth than specialized ones, the degree of dietary generalism of these species was also investigated.

2. Materials and Methods

To analyze species' diets, two sources were used: a database containing historical information on fish stomach contents from the 1980s and 1990s (Pinnegar, 2014) and data from the EATME project for 2010s (Robert et al., 2022) that contains information from 2014 to 2016 (Table S1).

The data availability in the stomach content database was explored for the four species of interest from the oldest data available to the most recent ones, in the Celtic Sea (ICES rectangles VIIf, VIIg, VIIh and VIIj). Because of the large number of individuals represented in the database for those periods, focus was placed on the 1980s (1981, 1984, and 1985) and the 1990s (1991, 1992, and 1993). The data collection framework from these periods were documented in du Buit 1982, 1995, 1996, du Buit & Merlinat 1987 and Pinnegar 2003. The EATME project took place during the EVHOE campaign (*EValuation des ressources Halieutiques de l'Ouest de l'Europe*), which was part of the International Bottom Trawl Survey (Leaute et al., 2016, 2015, Duhamel et al., 2014). EVHOE samples were collected with a demersal trawl (Day et al., 2019).

Changes in fish morphometric characteristics and habitats during their life commonly result in size dependent diets (Karpouzi & Stergiou, 2003, Day et al., 2019). In the analysis, only individuals that have already completed their ontogenetic diet shift were considered, i.e. individuals exceeding 60 cm for cod, 23 cm for haddock, 22 cm for whiting, and 21 cm for hake (Day et al., 2019, Mahe et al., 2007).

First, a study database was built that brought together information on prey identities over the focal decades. It included data on 195 taxa (96 from the 1980s, 78 from the 1990s, and 106 from the 2010s), which were grouped at three levels of taxonomic resolution to facilitate the analysis. The first and less detailed level included 7 groups: *Pisces*, *Crustacea*, *Mollusca*, *Cnidaria*, *Echinodermata*, *Polychaeta*, and *Other*. The second level was an intermediate taxonomic scale with 33 groups, mostly Family level. The third and most detailed level included 195 groups (Table S2). All the analyses were conducted at all three scales. However, because the analyses yielded similar results, not all results from all level of taxonomic resolution are presented below.

Since documentation on prey number estimation methodologies were not available for all periods and following Buckland et al. (2017) recommendations on stomach content data comparisons, only prey frequencies of occurrence were used. Prey frequencies of occurrence were defined as the prey occurrences, standardized by the total number of prey taxa present in each predator individual stomach (Equation 1-2), these values ranged from 0 to 100.

(1) $Fo_{j,i} = Oc_{j,i}/\sum_{j=1,m} Oc_j$

$Fo_{j,i}$ corresponded to the standardized prey occurrence by individual predator, i, stomach, the occurrence, $Oc_{j,i}$ is a binary value, either 0 or 1, that corresponded to the presence or the absence of the prey taxa j in the stomach of predator individual *i* for the selected predator species, divided by the sum of occurrence of each prey taxa, Oc_j, over the total number, *m*, of prey taxa.

$$(2)\ Foccu_j = \sum_{i\,=\,1,n} Fo_{j,i}/n \times 100$$

$Foccu_j$ corresponded to frequencies of occurrence of a given taxa, *j*, for the selected predator species, the sum of the standardized prey occurrences in individual predator *i*, $Fo_{j,i}$, over all predator individuals of this specific predator species, divided by the total number of individual predator, *n*, of this specific predators species, multiplied by 100. Results analysis were done at the predator species level based on $Foccu_j$ values.

Normalized Shannon’s index were calculated to estimate the niche breadth of each predator species (Shannon & Weaver 1949, Colwell & Futuyma, 1971). The normalized index range from 0, i.e. fully specialist predator, to 1, i.e. generalist predator that consumes all possible prey types equally. The index was calculated at the first and less detailed taxonomical level, as such generalist species were predators feeding on different taxonomical groups and not predators feeding on different species within the same taxonomical group. The index were estimated based on prey frequencies of occurrence (Equation 3).

$$(3)\ h_i = -(\ln N)^{-1} \Sigma_{j=\,1,N} Foccu_{i,j} \ln(Foccu_{i,j})$$

N was the total number of prey taxa groups and $Foccu_{i,j}$ is the frequency of occurrence of prey taxon *j* in the diet of predator species *i*.

3. Results

Overall, the diet of cod remained fairly consistent over time. Its primary prey were crustaceans (1980s: 54%; 1990s: 56%; and 2010s: 49%) that were mostly members of Anomura, Brachyura, and Caridea (Table S3). Ranking second were fish (1980s: 37%; 1990s: 36%; and 2010s: 26%), mainly gadiforms and perciforms; however, these two groups decreased slightly in frequency over the three focal decades. The dietary frequency of mollusks increased over time, from 2% in the 1980s to 5% in the 1990s to 19% in the 2010s. The dietary frequency of polychaetes decreased slightly over time, from 7% in the 1980s to 3% in the 1990s to 2% in the 2010s (Figure 1, Table S3). Overall, cod maintained the same degree of generalism in its diet (1980s: 0.411; 1990s: 0.438; and 2010s: 0.448).

The most generalist of the study species was haddock, even though its degree of generalism decreased over time from 0.731 in the 1980s to 0.671 in the 1990s to 0.560 in the 2010s. This species mainly ate echinoderms, crustaceans, polychaetes, and mollusks. The dietary frequency of echinoderms increased from 23% in the 1980s to 35% in the 1990s to 38% in the 2010s, while that of polychaetes decreased from 26% in the 1980s to 18% in the 1990s and 12% in the 2010s (Figure 1, Table S3).

Both whiting and hake displayed similar dietary patterns. The two species were highly specialized in the 1980s (0.128 and 0.038, respectively) but adopted a more generalist diet in the 1990s (0.356 and 0.288, respectively), a trend that continued into the 2010s (0.406 and 0.481, respectively). Specifically, both species initially specialized more on fish and then progressively shifted to primarily consuming a variety of crustaceans. For whiting, the dietary frequency of fish was 94% in the 1980s, 73% in the 1990s, and 12% in the 2010s. For hake, these figures were 99% in the 1980s, 78% in the 1990s, and 41% in the 2010s. In the 1980s, both predators largely fed on gadiform fish (48% for whiting and 55% for hake), dominated by *Trisopterus spp.* and blue whiting *(Micromesistius poutassou).* Sprat *(Sprattus sprattus)*, and horse mackerel (*Trachurus trachurus)* were also observed in their stomach contents (Table 1). In the 1980s, Scombridae was frequently represented in the diet of hake but was not reported from the diet of whiting (Table 1). For whiting, the dietary frequency of crustaceans was 5% in the 1980s, 22% in the 1990s, and 76% in the 2010s. For hake, these figures were less than 1% in the 1980s, 20% in the 1990s, and 52% in the 2010s. There was no clear pattern in the types of crustaceans consumed in the case of whiting. In hake, the dietary frequency of Crangonidae increased slightly over time: it was less than 1% in the 1980s and 1990s but had risen to 7% by the 2010s (Figure 1, Table S3, Table 1).

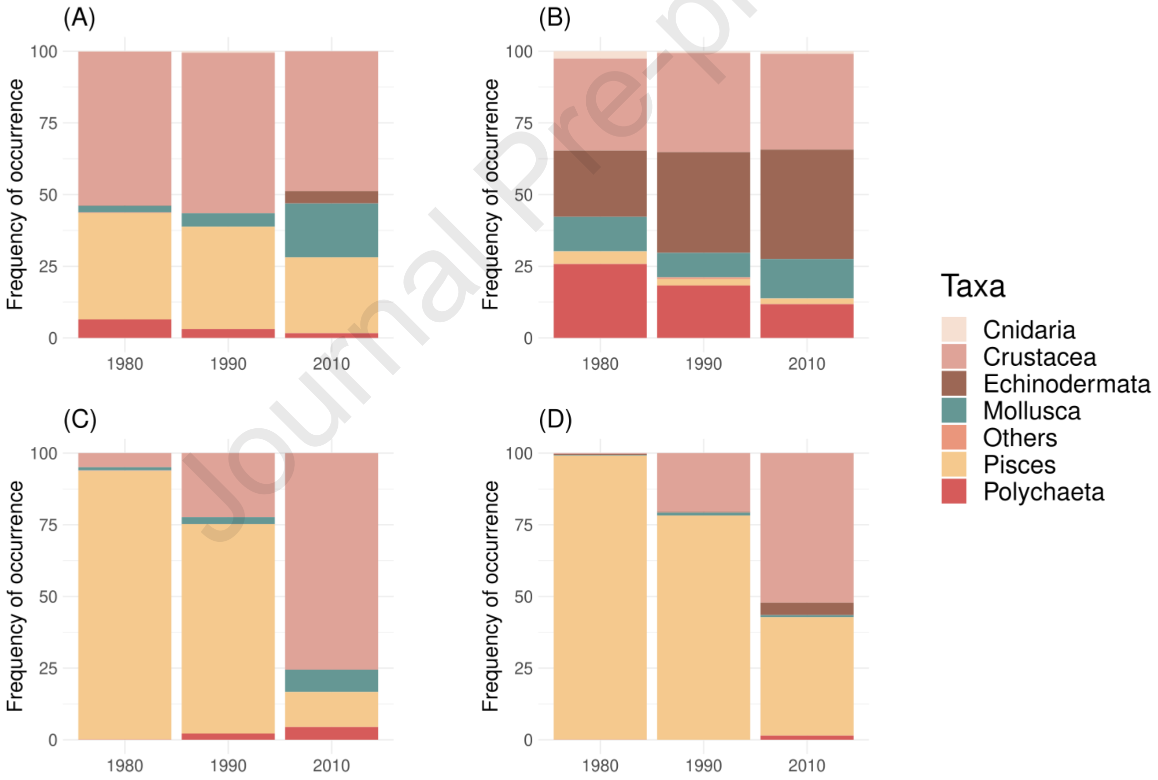

Figure 1 Frequencies of occurrence (%) over time of the different prey groups in the stomach contents of the four fish study species: (A) cod *(Gadus morhua)*, (B) haddock *(Melanogrammus aeglefinus*), (C) whiting *(Merlangius merlangus)*, and (D) hake *(Merluccius merluccius)*. The less detailed taxonomic level was used.

Table 1 Frequencies of occurrence (%) over time of different prey belonging to Pisces and Crustacea in the stomach contents of whiting *(Merlangius merlangus)* and hake (*Merluccius merluccius)*. The most detailed level of taxonomic resolution was used. Only frequencies of occurrence that exceeded 5% during the 1980s, 1990s, or 2010s are presented.

				Whiting			Hake		
Subgroup		**Species**	**Common name**	1980s	1990	2010	1980	1990	2010
Pisces	Gadiforms	*Trisopterus* spp.	-	39.8	17.2	2.2	21.2	13.7	3.6
	Actinopteri other	*Sprattus sprattus*	Sprat	29.3	9.5	0.0	7.6	0.3	0
	Gadiforms	*Micromessistius poutassou*	Blue whiting	6.8	0.2	0.0	29.9	8.7	0.0
	Osteichtys other	Osteichtys-teleostei	-	2.9	28.0	0.0	0.1	19.9	0.0
	Actinopteri other	Actinopteri	-	0.0	0.0	7.8	0.0	0.0	22.9
	Perciforms	*Trachurus trachurus*	Horse mackerel	5.0	0.6	2.2	13.3	3.3	6.5
		Scombridae	-	-	-	-	11.9	17.7	2.9
	Others	Other		9.7	17.6	0.0	15.1	14.6	5.3
	Total			**93.7**	**73.1**	**12.2**	**99.1**	**78.2**	**41.3**
Crustacea	Crustacea	Crustacea	-	0.0	8.3	0.0	-	-	-
	Eumalacostraca	Eumalacostraca	-	0.0	0.0	45.6	0.0	0.0	39.6
	Caridea	Crangonidae	-	1.4	2.1	10.0	0.2	0.6	6.5
	Amphipoda	Amphipoda	-	0.0	0.0	7.8	-	-	-
	Caridea	Pandalidae	-	-	-	-	0	12.3	0.7
	Others	Other		2.6	8.4	11.5	-	-	-
	Total			**4.9**	**22.3**	**75.6**	**0.3**	**20.5**	**52.2**

4. Discussion

In the Celtic Sea, the generalist species cod and haddock have maintained the same diet composition over decades. Conversely, over the same time period, the specialists whiting and hake have adopted more generalist diets. Cod diets characterized by crustaceans and fish preys displayed comparable shifts from specialist to generalist diets in the Baltic Sea between the 1960s and 2010s (Haase et al., 2020), while in the Barents Sea their diets stayed relatively stable between the 1930s and 2010s (Townhill et al., 2019). In an environment undergoing global changes, generalist species may be favored over specialist species, given potential differences in their adaptive capacities (van Denderen et al., 2018, Beger, 2021, Clavel et al., 2011, Olin et al., 2022). Because the Celtic Sea is experiencing global changes, these differences may have pushed specialists to become generalists, resulting in a species-level increase in generalism.

Predator diets depend on feeding strategies. The latter may be opportunistic versus selective, and they can be discerned by looking at the correspondence between a predator’s realized trophic niche and the relative abundance of its prey in the local environment. Opportunist species consume prey in accordance with their local abundance, while selective species consume certain prey more than others in accordance with energetic trade-offs, which are determined by both prey abundance and nutritional quality (Scharf et al., 2000, Spitz et al., 2018).

In the Celtic Sea, cod, whiting and hake appear to be opportunistic foragers, given the spatial distribution of blue whiting, *Micromesistius poutassou* and pouting, *Trisopterus* spp. (Trenkel et al., 2005) and their representation in the predators' stomach contents. Opportunist relations between those predators and their preys would suggest that their diet composition have varied according to prey availability (Alonso et al., 2019). In the 1980s, whiting and hake consumed almost exclusively fish (> 90%). Then, in the 1990s, the compositions of their diets shifted to include a mixture of fish (~75%) and crustaceans (~20%). Finally, in the 2010s, their diets were more than half made up of crustaceans. In adjacent European waters (e.g., the Baltic Sea from 2011 to 2013 and the North Sea in 1981), whiting stomach contents studies evidenced a mainly piscivorous diet, dominated by gobies and clupeids (Hislop et al., 1991, Ross et al., 2016). Fish prey species might have become less available in the Celtic Sea, leading to the observed dietary shifts. The cause could have been changes in prey distribution or abundance as a result of environmental variation or overfishing (Calado et al., 2020, Hernández-Mendoza et al., 2022). Notably, the fish prey species of whiting and hake have commercial value in the Celtic Sea and have thus been affected directly by fishing. For instance, blue whiting *(M. poutassou*) abundance index decreased by more than 90%, from $8x10^{12}$ tonnes (standard deviation [SD]: $1x10^{12}$ tonnes) in 1997 to $5x10^{11}$ tonnes (SD: $4x10^{11}$ tonnes) in 2016 (Ifremer, 2023), possibly due to increased landings in the southern part of the Northeast Atlantic, including the Celtic Sea, during the same period (ICES, 2022). Moreover, worldwide, climate change has been proven to result in marine species to move into deeper waters and toward the poles (Poloczanska et al., 2013, 2016). These shifts could also have impacted prey abundances and distributions and led to an increase in the abundance of certain competitors, resulting in decreased prey availability for local predators (Perry et al., 2005, Dulvy et al., 2008). Fish and invertebrate prey (e.g., polychaetes and echinoderms) distribution shifts have already been evidenced in European waters and are likely to continue in the future (Schickele et al., 2021, Hiddink et al., 2015, Weinert et al., 2016).

In the case of predators feeding selectively, temporal variation in diet composition could also have been caused by changes in prey nutritional quality (Rijnsdorp et al., 2009, Heneghan et al., 2023). It is thought that feeding strategies are driven by energetic trade-offs, where predators prefer prey that yield more energy per unit handling time (Scharf et al., 2000). Smaller pelagic fish tend to contain higher levels of lipids than do larger pelagic fish, and pelagic fish have higher lipid contents, on average, than do demersal or benthic species, which could explain a selective behavior toward these species (Van Pelt et al., 1997, Pinnegar et al., 2003, Spitz et al., 2010). It has been hypothesized that whiting, hake and other congeners display selective foraging behavior in which they target specific prey (Belleggia et al., 2019, Shaw et al., 2008). Certain lipid-rich prey (e.g., blue whiting) may be consumed more frequently than would be expected based on their temporal availability alone (Pinnegar et al., 2003, Mahe et al., 2007). If certain prey declined in quality but still required the same foraging time investment, it could reduce their attractiveness to predators

(Schrimpf et al., 2012) and led the predator to show less selective feeding strategies toward them. In the Bay of Biscay, the weight at age and biomass of small pelagic fish (e.g. sardine, *Sardina pilchardus*, anchovy, *Engraulis encrasicolus* and horse mackerel, *Trachurus trachurus*) decreased since the 2000s (Doray et al., 2018, Boëns et al., 2021). Similar variations in small pelagic fish sizes and abundances could have occurred in the Celtic Sea, reducing predator selective behavior toward them. Dietary shifts comparable to those observed in this study have already been documented in top predator diets for different regions of the Atlantic ocean, such as cod in the Baltic Sea (Neuenfeldt et al., 2020) or seabirds in islands from from the tropical South Atlantic (Reynolds et al., 2019) and could imply that short-term ecosystem restructuring has taken place.

Despite efforts to standardize the data and carry out temporal comparisons, these results should be interpreted with caution. On the one side, bias could emerged from the use of stomach content method itself. This method tend to overestimate the contribution of slowly digested taxonomical groups in species diets (Amundsen & Sanchez-Hernandez, 2019). Stomach content analysis also offered a snapshot of predator diet composition limited in time (e.g. days or weeks), as such it is sensitive to occasional spatio-temporal variations in prey availability and predator displacements (Buckland et al., 2017). On the other side, sample sizes and seasonal coverage differed over time. Seasonal variations in prey distributions and life-stages are likely to impact species diets (Holt et al., 2019, Eriksen et al., 2021). These concerns could have influenced the patterns observed, and the results presented here would benefit from complementary work to confirm whether these patterns persist in the near future. Seasonal variations observed in this study were marginal in comparison to inter-period variations, however collecting data all year around would strengthen our conclusions. That said, this study’s findings are valuable in better understanding past trophic variation in the Celtic Sea. Such important changes in top predators feeding habits could be the result of top-down and bottom-up processes currently in action in the Celtic Sea. Top-down forces could include a reduction in the abundance of fish occupying intermediate trophic levels, as a result of fishery exploitation (Moullec et al., 2017, Hernvann et al., 2020, Daskalov et al., 2007). In the Celtic Sea, biomass for species at higher trophic levels has been in decline since the second half of the 20th century, which has resulted in a progressive decrease in the mean trophic level of landings (e.g., a phenomenon known as “fishing down the food web”) (Pinnegar et al. 2002, Pauly et al., 1998). Since the end of the 20th century fishery management policy, mainly through the implementation of fishing quotas, have caused a decrease of the fishing mortality exerted on top predators. On the contrary, the fishing mortality of their fish prey has progressively increased, reducing their availability to predators. Top-down forces could also stem from increased competition between top predators. Additionally, climate change might have resulted in the arrival or increase in top predators coming from southern waters, who might be competing for the same resources (Lancaster et al., 2017). In contrast, bottom-up forces could have recently arisen from environmental changes (e.g. climate change, pesticide regulations) in temperate waters (Galloway & Winder, 2015, De Senerpont Domis et al., 2014). The results could have been shifts in phyto- and zooplankton abundances, sizes, and lipid contents. Such variations are likely to affect the abundance, size, and nutritional quality of primary consumers, such as small pelagic fish (Menu et al., 2023, Queiros et al., 2019, Frederiksen et al., 2006, Litzow et al., 2006). Bottom-up control could also have influenced the trophic structure of the Celtic Sea by directly boosting the occurrence of certain prey, such as crustaceans, echinoderms, or mollusks (Henderson et al., 2011, Hiddink et al., 2015, Weinart et al., 2016). As such, trophic ecology offers the opportunity to track both bottom-up and top-down processes alteration. Trophic ecology is also a valuable tool for investigating how global changes can affect ecosystem structure and function. Finally, diet shifts could cause a modification of the basic elements (e.g. protein and lipids) and energy inputs provided to the top predators, as crustaceans species contains on average almost 4 times less lipids than sprats and horse mackerel (Spitz et al., 2010). These modifications are likely to lead to energy allocation strategies modifications (Martin et al., 2017) and result in alterations of the growth and reproductive functions of the species (Alonso-Fernandez et al., 2012, Lloret et al., 2008).

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Data availability

Robert Marianne, Pawlowski Lionel, Kopp Dorothée (2022). **TrophicCS: Spatialized trophic data of the Celtic Sea continental shelf food web**. *Ecology*, 103(8), e3708 (2 pages). Publisher's official version: https://doi.org/10.1002/ecy.3708.

Pinnegar, J.K. (2014). DAPSTOM - An Integrated Database & Portal for Fish Stomach Records. Version 4.7. Centre for Environment, Fisheries & Aquaculture Science, Lowestoft, UK. February 2014, 39 pages.

References

Alonso, R. B., Romero, M. A., Reinaldo, M. O., Bustelo, P. E., Medina, A. I., & Gonzalez, R. (2019). The opportunistic sense : The diet of Argentine hake *Merluccius hubbsi* reflects changes in prey availability. *Regional Studies in Marine Science*, *27*, 100540.

Alonso-Fernandez, A., & Saborido-Rey, F. (2012). Relationship between energy allocation and reproductive strategy in *Trisopterus luscus*. *Journal of Experimental Marine Biology and Ecology*, *416*, 8-16.

Amundsen, P.-A., & Sánchez-Hernández, J. (2019). Feeding studies take guts–critical review and recommendations of methods for stomach contents analysis in fish. *Journal of Fish Biology*, *95*(6), 1364-1373.

Baum, J. K., & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology*, *78*(4), 699-714.

Beger, M. (2021). Accepting the loss of habitat specialists in a changing world. *Nature Ecology & Evolution*, *5*(5), 556-557.

Belleggia, M., Alves, N. M., Leyton, M. M., Álvarez-Colombo, G., Temperoni, B., Giberto, D., & Bremec, C. (2019). Are hakes truly opportunistic feeders? A case of prey selection by the Argentine hake *Merluccius hubbsi* off southwestern Atlantic. *Fisheries Research*, *214*, 166-174.

Boëns, A., Grellier, P., Lebigre, C., & Petitgas, P. (2021). Determinants of growth and selective mortality in anchovy and sardine in the Bay of Biscay. *Fisheries Research*, *239*, 105947.

Bryndum-Buchholz, A., Tittensor, D. P., Blanchard, J. L., Cheung, W. W., Coll, M., Galbraith, E. D., Jennings, S., Maury, O., & Lotze, H. K. (2019). Twenty-first-century climate change impacts on marine animal biomass and ecosystem structure across ocean basins. *Global Change Biology*, *25*(2), 459-472.

Buckland, A., Baker, R., Loneragan, N., & Sheaves, M. (2017). Standardising fish stomach content analysis : The importance of prey condition. *Fisheries Research*, *196*, 126-140.

Calado, J. G., Paiva, V. H., Ramos, J. A., Velando, A., & Munilla, I. (2020). Anthropogenic food resources, sardine decline and environmental conditions have triggered a dietary shift of an opportunistic seabird over the last 30 years on the northwest coast of Spain. *Regional Environmental Change*, *20*, 1-13.

Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species : Toward a global functional homogenization? *Frontiers in Ecology and the Environment*, *9*(4), 222-228.

Colwell, R. K., & Futuyma, D. J. (1971). On the measurement of niche breadth and overlap. *Ecology*, *52*(4), 567-576.

Daskalov, G. M., Grishin, A. N., Rodionov, S., & Mihneva, V. (2007). Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proceedings of the National Academy of Sciences*, *104*(25), 10518-10523.

Day, L., Kopp, D., Robert, M., & Le Bris, H. (2019). Trophic ecology of large gadiforms in the food web of a continental shelf ecosystem. *Progress in Oceanography*, *175*, 105-114.

De Senerpont Domis, L. N., Van de Waal, D. B., Helmsing, N. R., Van Donk, E., & Mooij, W. M. (2014). Community stoichiometry in a changing world : Combined effects of warming and eutrophication on phytoplankton dynamics. *Ecology*, *95*(6), 1485-1495.

de Carvalho, D. R., de Castro, D. M. P., Callisto, M., Chaves, A. J. de M., Moreira, M. Z., & Pompeu, P. S. (2019). Stable isotopes and stomach content analyses indicate omnivorous habits and opportunistic feeding behavior of an invasive fish. *Aquatic Ecology*, *53*(3), 365-381.

Doray, M., Petitgas, P., Huret, M., Duhamel, E., Romagnan, J. B., Authier, M., Dupuy, C., & Spitz, J. (2018). Monitoring small pelagic fish in the Bay of Biscay ecosystem, using indicators from an integrated survey. *Progress in Oceanography*, *166*, 168-188.

Du Buit, M. H. (1982). Essai d'évaluation de la prédation de quelques téléostéens en Mer Celtique. *ICES Journal of Marine Science*, *40*(1), 37-46.

Du Buit, M. H. (1995). Food and feeding of cod (*Gadus morhua* L.) in the Celtic Sea. *Fisheries Research*, *22*(3-4), 227-241.

Du Buit, M. H. (1996). Diet of hake (*Merluccius merluccius*) in the Celtic Sea. *Fisheries research*, *28*(4), 381-394.

Du Buit, M. H., & Merlina, F. (1985). Alimentation du merlan *Merlangius merlangus* L. en Mer Celtique. *Revue des Travaux de l'Institut des Pêches maritimes*, *49*(1-2), 5-12.

Duhamel, E., Salaun, M., & Pawlowski, L. (2014). *EVHOE 2014 cruise, RV Thalassa*.

Dulvy, N. K., Rogers, S. I., Jennings, S., Stelzenmüller, V., Dye, S. R., & Skjoldal, H. R. (2008). Climate change and deepening of the North Sea fish assemblage : A biotic indicator of warming seas. *Journal of Applied Ecology*, *45*(4), 1029-1039.

Eriksen, E., Skjoldal, H. R., Dolgov, A. V., Strand, E., Keulder-Stenevik, F., Prokopchuk, I. P., ... & Benzik, A. N. (2021). Diet and trophic structure of fishes in the Barents Sea: Seasonal and spatial variations. *Progress in Oceanography*, *197*, 102663.

Frederiksen, M., Edwards, M., Richardson, A. J., Halliday, N. C., & Wanless, S. (2006). From plankton to top predators : Bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology*, *75*(6), 1259-1268.

Galloway, A. W., & Winder, M. (2015). Partitioning the relative importance of phylogeny and environmental conditions on phytoplankton fatty acids. *PLoS One*, *10*(6), e0130053.

Garrison, L. P., & Link, J. S. (2000). Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. *Marine Ecology Progress Series*, *202*, 231-240.

Haase, K., Orio, A., Pawlak, J., Pachur, M., & Casini, M. (2020). Diet of dominant demersal fish species in the Baltic Sea: is flounder stealing benthic food from cod?. *Marine Ecology Progress Series*, *645*, 159-170.

Harley, C. D., Randall Hughes, A., Hultgren, K. M., Miner, B. G., Sorte, C. J., Thornber, C. S., Rodriguez, L. F., Tomanek, L., & Williams, S. L. (2006). The impacts of climate change in coastal marine systems. *Ecology Letters*, *9*(2), 228-241.

Henderson, P. A., Seaby, R. M. H., & Somes, J. R. (2011). Community level response to climate change : The long-term study of the fish and crustacean community of the Bristol Channel. *Journal of Experimental Marine Biology and Ecology*, *400*(1-2), 78-89.

Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. *Nature Climate Change*, *13*(5), 470-477.

Hernández-Mendoza, L. C., Escalera-Vázquez, L., & Arceo-Carranza, D. (2022). Estuarine fish feeding changes as indicator to mangrove restoration success in seasonal karstic wetlands. *Frontiers in Forests and Global Change*, *4*, 743232.

Hernvann, P.-Y., & Gascuel, D. (2020). Exploring the impacts of fishing and environment on the Celtic Sea ecosystem since 1950. *Fisheries Research*, *225*, 105472.

Hernvann, P.-Y., Gascuel, D., Grüss, A., Druon, J.-N., Kopp, D., Perez, I., Piroddi, C., & Robert, M. (2020). The Celtic Sea through time and space : Ecosystem modeling to unravel fishing and climate change impacts on food-web structure and dynamics. *Frontiers in Marine Science*, *7*, 578717.

Hiddink, J. G., Burrows, M. T., & García Molinos, J. (2015). Temperature tracking by North Sea benthic invertebrates in response to climate change. *Global Change Biology*, *21*(1), 117-129.

Hislop, J. R. G., Robb, A. P., Bell, M. A., & Armstrong, D. W. (1991). The diet and food consumption of whiting (*Merlangius merlangus*) in the North Sea. *ICES Journal of Marine Science*, *48*(2), 139-156.

Holland, M. M., Smith, J. A., Everett, J. D., Vergés, A., & Suthers, I. M. (2020). Latitudinal patterns in trophic structure of temperate reef-associated fishes and predicted consequences of climate change. *Fish and Fisheries*, *21*(6), 1092-1108.

Holt, R. E., Bogstad, B., Durant, J. M., Dolgov, A. V., & Ottersen, G. (2019). Barents Sea cod (*Gadus morhua*) diet composition: long-term interannual, seasonal, and ontogenetic patterns. *ICES Journal of Marine Science*, *76*(6), 1641-1652.

Hynes, H. B. N. (1950). The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. *Journal of Animal Ecology*, 36-58.

Hyslop, E. J. (1980). Stomach contents analysis—A review of methods and their application. *Journal of Fish Biology*, *17*(4), 411-429.

ICES. (2022). *Blue whiting (Micromesistius poutassou) in subareas 1–9, 12, and 14 (Northeast Atlantic and adjacent waters). ICES Advice : Recurrent Advice*.

Ifremer. (2023). *Indices de populations et de communautés issus des campagnes de surveillance halieutique de l'Ifremer*.

Karpouzi, V. S., & Stergiou, K. I. (2003). The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. *Journal of fish biology, 62*(6), 1353-1365.

Lancaster, L. T., Morrison, G., & Fitt, R. N. (2017). Life history trade-offs, the intensity of competition, and coexistence in novel and evolving communities under climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1712), 20160046.

Leaute, J. P., Pawlowski, L., & Garren, F. (2016). *EVHOE 2016 cruise, RV Thalassa*.

Leaute, J. P., Pawlowski, L., & Salaun, M. (2015). *EVHOE 2015 cruise, RV Thalassa*.

Levinton, J. (1972). Stability and trophic structure in deposit-feeding and suspension-feeding communities. *The American Naturalist*, *106*(950), 472-486.

Litzow, M. A., Bailey, K. M., Prahl, F. G., & Heintz, R. (2006). Climate regime shifts and reorganization of fish communities : The essential fatty acid limitation hypothesis. *Marine Ecology Progress Series, 315*, 1-11.

Lloret, J., Demestre, M., & Sanchez-Pardo, J. (2008). Lipid (energy) reserves of European hake (*Merluccius merluccius*) in the north-western Mediterranean. *Vie et Milieu/Life & Environment*, 75-85.

Lynam, C. P., Llope, M., Möllmann, C., Helaouët, P., Bayliss-Brown, G. A., & Stenseth, N. C. (2017). Interaction between top-down and bottom-up control in marine food webs. *Proceedings of the National Academy of Sciences*, *114*(8), 1952-1957.

Mahe, K., Amara, R., Bryckaert, T., Kacher, M., & Brylinski, J.-M. (2007). Ontogenetic and spatial variation in the diet of hake (*Merluccius merluccius*) in the Bay of Biscay and the Celtic Sea. *ICES Journal of Marine Science, 64*(6), 1210-1219.

Martin, B. T., Heintz, R., Danner, E. M., & Nisbet, R. M. (2017). Integrating lipid storage into general representations of fish energetics. *Journal of Animal Ecology*, *86*(4), 812-825.

Menu, C., Pecquerie, L., Bacher, C., Doray, M., Hattab, T., van Der Kooij, J., & Huret, M. (2023). Testing the bottom-up hypothesis for the decline in size of anchovy and sardine across European waters through a bioenergetic modeling approach. *Progress in Oceanography, 210*, 102943.

Mérillet, L., Kopp, D., Robert, M., Mouchet, M., & Pavoine, S. (2020). Environment outweighs the effects of fishing in regulating demersal community structure in an exploited marine ecosystem. *Global Change Biology*, *26*(4), 2106-2119.

Moullec, F., Gascuel, D., Bentorcha, K., Guénette, S., & Robert, M. (2017). Trophic models : What do we learn about Celtic Sea and Bay of Biscay ecosystems? *Journal of Marine Systems*, *172*, 104-117.

Nagelkerken, I., Goldenberg, S. U., Ferreira, C. M., Ullah, H., & Connell, S. D. (2020). Trophic pyramids reorganize when food web architecture fails to adjust to ocean change. *Science*, *369*(6505), 829-832.

Neuenfeldt, S., Bartolino, V., Orio, A., Andersen, K. H., Andersen, N. G., Niiranen, S., Bergström, U., Ustups, D., Kulatska, N., & Casini, M. (2020). Feeding and growth of Atlantic cod (*Gadus morhua* L.) in the eastern Baltic Sea under environmental change. *ICES Journal of Marine Science*, *77*(2), 624-632.

Olin, A. B., Olsson, J., Eklöf, J. S., Eriksson, B. K., Kaljuste, O., Briekmane, L., & Bergström, U. (2022). Increases of opportunistic species in response to ecosystem change : The case of the Baltic Sea three-spined stickleback. *ICES Journal of Marine Science*, *79*(5), 1419-1434.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., & Torres Jr, F. (1998). Fishing down marine food webs. *Science*, *279*(5352), 860-863.

Perry, A. L., Low, P. J., Ellis, J. R., & Reynolds, J. D. (2005). Climate change and distribution shifts in marine fishes. *Science*, *308*(5730), 1912-1915.

Pinnegar, J. K., Jennings, S., O'brien, C. M., & Polunin, N. V. C. (2002). Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. *Journal of Applied Ecology*, 377-390.

Pinnegar, J. K., & Platts, M. (2014). DAPSTOM-an integrated database & portal for fish stomach records. *Centre for Environment FAS, Lowestoft, UK.(ed)*.

Pinnegar, J. K., Trenkel, V. M., Tidd, A. N., Dawson, W. A., & Du Buit, M. H. (2003). Does diet in Celtic Sea fishes reflect prey availability? *Journal of Fish Biology*, *63*, 197-212.

Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K., Bruno, J. F., Buckley, L. B., & Burrows, M. T. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, *3*(10), 919-925.

Poloczanska, E. S., Burrows, M. T., Brown, C. J., García Molinos, J., Halpern, B. S., Hoegh-Guldberg, O., Kappel, C. V., Moore, P. J., Richardson, A. J., & Schoeman, D. S. (2016). Responses of marine organisms to climate change across oceans. *Frontiers in Marine Science*, 62.

Queiros, Q., Fromentin, J.-M., Gasset, E., Dutto, G., Huiban, C., Metral, L., Leclerc, L., Schull, Q., McKenzie, D. J., & Saraux, C. (2019). Food in the sea : Size also matters for pelagic fish. *Frontiers in Marine Science*, *6*, 385.

Reynolds, S. J., Hughes, B. J., Wearn, C. P., Dickey, R. C., Brown, J., Weber, N. L., Weber, S. B., Paiva, V. H., & Ramos, J. A. (2019). Long-term dietary shift and population decline of a pelagic seabird—A health check on the tropical Atlantic? *Global Change Biology*, *25*(4), 1383-1394.

Rijnsdorp, A. D., Peck, M. A., Engelhard, G. H., Möllmann, C., & Pinnegar, J. K. (2009). Resolving the effect of climate change on fish populations. *ICES Journal of Marine Science*, *66*(7), 1570-1583.

Ross, S. D., Gislason, H., Andersen, N. G., Lewy, P., & Nielsen, J. R. (2016). The diet of whiting *Merlangius merlangus* in the western Baltic Sea. *Journal of Fish Biology*, *88*(5), 1965-1988.

Scharf, F. S., Juanes, F., & Rountree, R. A. (2000). Predator size-prey size relationships of marine fish predators : Interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Marine Ecology Progress Series*, *208*, 229-248.

Schickele, A., Goberville, E., Leroy, B., Beaugrand, G., Hattab, T., Francour, P., & Raybaud, V. (2021). European small pelagic fish distribution under global change scenarios. *Fish and Fisheries*, *22*(1), 212-225.

Schrimpf, M. B., Parrish, J. K., & Pearson, S. F. (2012). Trade-offs in prey quality and quantity revealed through the behavioral compensation of breeding seabirds. *Marine Ecology Progress Series*, *460*, 247-259.

Shannon, C. E., & Weaver, W. (1949). *The mathematical theory of communication, by CE Shannon (and recent contributions to the mathematical theory of communication), W. Weaver*. University of Illinois Press.

Shaw, M., Diekmann, R., Van DerKooij, J., Milligan, S., Bromley, P., & Righton, D. (2008). Assessment of the diets of cod *Gadus morhua* and whiting *Merlangius merlangus* juveniles in a frontal region close to the Norwegian Trench : Co-existence or competition? *Journal of Fish Biology*, *73*(7), 1612-1634.

Spitz, J., Mourocq, E., Schoen, V., & Ridoux, V. (2010). Proximate composition and energy content of forage species from the Bay of Biscay : High-or low-quality food? *ICES Journal of Marine Science*, *67*(5), 909-915.

Spitz, J., Ridoux, V., Trites, A. W., Laran, S., & Authier, M. (2018). Prey consumption by cetaceans reveals the importance of energy-rich food webs in the Bay of Biscay. *Progress in Oceanography*, *166*, 148-158.

Townhill, B. L., Holt, R. E., Bogstad, B., Durant, J. M., Pinnegar, J. K., Dolgov, A. V., ... & Ottersen, G. (2021). Diets of the Barents Sea cod (*Gadus morhua*) from the 1930s to 2018. *Earth System Science Data*, *13*(3), 1361-1370.

Trenkel, V. M., Pinnegar, J. K., Dawson, W. A., Du Buit, M. H., & Tidd, A. N. (2005). Spatial and temporal structure of predator–prey relationships in the Celtic Sea fish community. *Marine Ecology Progress Series*, *299*, 257-268.

Van Pelt, T. I., Piatt, J. F., Lance, B. K., & Roby, D. D. (1997). Proximate composition and energy density of some North Pacific forage fishes. *Comparative Biochemistry and Physiology Part A: Physiology*, *118*(4), 1393-1398.

van Denderen, P. D., Lindegren, M., MacKenzie, B. R., Watson, R. A., & Andersen, K. H. (2018). Global patterns in marine predatory fish. *Nature Ecology & Evolution*, *2*(1), 65-70.

Weinert, M., Mathis, M., Kröncke, I., Neumann, H., Pohlmann, T., & Reiss, H. (2016). Modelling climate change effects on benthos : Distributional shifts in the North Sea from 2001 to 2099. *Estuarine, Coastal and Shelf Science*, *175*, 157-168.

Woodin, S. A., & Jackson, J. B. C. (1979). Interphyletic competition among marine benthos. *American Zoologist*, *19*(4), 1029-1043.

Highlights

- From the 1980s to 2010s, specialists top predators in the Celtic Sea switched to generalist diets
- Fish occurrence decreased in the diets of top predators while crustaceans increased
- Top-down and bottom-up processes might have caused this trophic structure re-organization

Author statement

Morgane Amelot : conceptualization, methodology, data analysis and writing, **Marianne Robert** : funding acquisition, conceptualization, supervision, validation, **Maud Mouchet** : funding acquisition, conceptualization, supervision, validation, **Dorothée Kopp** : funding acquisition, conceptualization, supervision, validation.

Declaration of interests

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

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: