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Seasonality of diet overlap among small pelagic fish in the waters southwest of the UK

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ABSTRACT: Small pelagic fish (SPF) play an important ecological role by facilitating energy transfer in marine ecosystems, from lower to higher trophic levels. The Celtic Seas ecoregion is home to several economically important SPF that spend some or all their life in these waters. In recent decades, major changes in the relative abundances of the 6 main SPF in the region (anchovy, herring, horse mackerel, mackerel, sardine, and sprat) have been observed. Changes in the region may impact SPF, and previous studies in neighbouring seas have highlighted possible diet overlap of these species; therefore, it is important to understand the changes in diet overlap and trophic relationships, particularly across different seasons. Consequently, we investigated the seasonal diet composition of these 6 SPF in the Celtic Seas ecoregion, identified diet overlap, and determined species selectivity towards prey size. Combining historical and new observations on fish stomach contents, diet-overlap indices were computed to quantify potential seasonal intra- and inter-specific overlap. Diet overlaps among species changed between seasons; in particular, sprat and anchovy changed significantly between spring and autumn, and mackerel between spring, summer, and winter. SPF species primarily consumed calanoid copepods, with herring and horse mackerel having more selective diets compared to mackerel, anchovy, and sardine. All species fed at similar trophic levels between seasons. To our knowledge, this study is the first to show seasonal variability in diet overlap among the six SPF in the Celtic Seas ecoregion. These results can improve the understanding of feeding dynamics for SPF in ecosystem model outputs.

KEY WORDS: Diet composition · Stomach contents · Feeding ecology · Interspecific competition · Seasonality · Celtic Seas ecoregion

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1 Introduction

Small pelagic fish (SPF) are important components of marine ecosystems. They are predominantly planktivorous and as such, link lower and higher trophic levels (TLs) (Cury et al. 2000). They support 25% of the world's total fish landings (in weight), primarily through anchovy, sardine, mackerel, and herring (FAO 2018). The state of their populations therefore plays a critical role, ecologically, economically, and socially. Thus, understanding the underlying mechanisms driving their stocks and population dynamics is vital. SPF are often short-lived with high recruitment, and so may be a useful indicator species for ecosystem changes, because of their important ecological links between plankton and higher TLs (Bakun 2006). Furthermore, SPF are affected by changes in environmental conditions (van der Lingen et al. 2006), both indirectly, through their planktonic prey, and directly, by interannual variability in recruitment (Lloret et al. 2004, Patti et al. 2020). In addition, biomass changes in SPF could be partially attributed to inter- and intra-specific interactions, e.g. food competition (Utne et al. 2012, Bachiller et al. 2021). The feeding behaviour of these species within the ecosystem influences the stability of marine food webs. Generalist (non-selective) feeders are able to readily switch between prey types depending on availability, and can help maintain stability by compensating for oscillations of specific food sources generated by environmental changes, thus supporting energy flows (Dunne et al. 2002, Beckerman et al. 2006, Rooney et al. 2006, Gravel et al. 2011). As SPF are prey for piscivorous fish (Trenkel et al. 2005), marine mammals, and seabirds (Kaschner et al. 2006), food webs with SPF that are generalist (non-selective) feeders are deemed to be more resilient to climatic variability (Beaudoin et al. 2001).

The Celtic Sea, Irish Sea, and English Channel, defined as the Celtic Seas ecoregion (ICES 2004), supports important commercial mixed fisheries targeting many different benthic, demersal, and pelagic stocks. The ecoregion is home to a diverse range of SPF species, including Atlantic herring *Clupea harengus*, Atlantic mackerel *Scomber scombrus*, sprat *Sprattus sprattus*, European anchovy *Engraulis encrasicolus*, European sardine *Sardina pilchardus*, and Atlantic horse mackerel *Trachurus trachurus*. Each of these species is planktivorous for at least part of their lifecycle, and therefore they likely have overlapping diets (Raab et al. 2012, Bachiller & Irigoien 2015). Sprat, sardine, and herring are found throughout the year in the Celtic Seas ecoregion, including during the spawning season (Wallace & Pleasants 1972, Bréchon et al. 2013). The larvae and juveniles utilise the relatively shallow waters as nursery grounds. Horse mackerel and mackerel larvae drift from the shelf edge (the main spawning ground) into the coastal waters after hatching (Jansen et al. 2015). Anchovies overwinter within the Celtic Sea region, possibly to escape the colder waters of the North Sea (Huret et al. 2020). Several of these planktivorous species have shown substantial changes in abundance in the region (e.g. Beare et al. 2004, ICES 2010, Shephard et al. 2014). For example, European anchovy in the area has increased since the mid-1990s (Beare et al. 2004), due to increased recruitment success (Petitgas et al. 2012, Huret et al. 2020). In contrast, some herring populations in the region have been in decline, causing fisheries closures (ICES 2020). The region is also an important spawning and nursery ground for migratory species, notably Atlantic mackerel, and Atlantic horse mackerel (Ellis et al. 2002, ICES 2007), which have also exhibited changes in their distribution in the region (van der Kooij et al. 2015). Sardine populations have been shown to fluctuate with climatic variability (Alheit & Hagen 1997), and a recent increase in autumn spawning activity of sardine in the English Channel has been observed (Coombs et al. 2010). Sprat stock and structure within the Celtic Seas ecoregion is generally unknown. However, since 2013, there has been ICES advice on sprat within the region due to new surveys providing an acoustic survey index (ICES 2022). In other regions, such as the Baltic Sea, there have been changes in sprat abundance over time (Eero et al. 2012), possibly attributable to many different factors (indirect and direct), including bottom-up processes, e.g. food availability and temperature. As such, it is acknowledged that the changes in SPF populations are partially climate driven (Alheit et al. 2009, Checkley et al. 2009).

Given the possible diet overlap between these planktivorous species, it is likely that the increase of any of these species will have an impact on the food availability for others and may particularly impact specialist feeders. Thus, understanding the dietary overlap between these co-occurring species is crucial, as it will help determine the trophic interactions within the community, and the distribution of other species within the ecosystem (Bachiller & Irigoien 2015, Bachiller et al. 2021), ultimately affecting fisheries yields. Better understanding of the dietary overlap between SPF is also important for improving fisheries advice. This is because many fish population dynamics models use diet data to understand trophodynamics and feeding ecology to underpin fisheries management, e.g. ATLANTIS (a spatially explicit end-to-end marine ecosystem model with dynamically integrated physics, ecology and socio-economic modules; Fulton et al. 2004, Audzijonyte et al. 2019), Ecopath with Ecosim (Pauly et al. 2000, Christensen et al. 2014), and OSMOSE (Object-oriented Simulator of Marine Ecosystems; Shin & Cury 2001). In addition, single species models and individual-based models including fish energy budget can provide spatial and temporal estimates of biomass of certain SPF (e.g. Boyd et al. 2018, 2020a). To our knowledge, there have only been a handful of diet studies in the Celtic Seas ecoregion (Hillgruber & Kloppmann 2001, Pinnegar et al. 2015, Denis et al. 2016, Lamb et al. 2019). Many of the diet studies focused on higher TLs (du Buit 1982, 1992, 1995, 1996, Pinnegar et al. 2002, Mahe et al. 2007, Lauria et al. 2012, Rault et al. 2017), and information on SPF is limited. SPF are important facilitators of energy in ecosystems, which respond strongly to bottom-up changes (Peck et al. 2021), such as plankton availability. The planktonic communities in the Celtic Seas ecoregion change seasonally (Johns 2006, Eloire et al. 2010); therefore, understanding overlapping resources between these SPF at the seasonal scale can help understand the ecological relevance of these species to the ecosystem.

The main aim of this paper is to adopt a multispecies approach to determine the diet composition of 6 main SPF across seasons and investigate their potential inter-specific competition in the Celtic Seas ecoregion. We hypothesise that the SPF species will have generalist feeding behaviours and similar diets within the Celtic Seas ecoregion. To investigate this, we used stomach content analyses from fish samples collected during a multidisciplinary fishery survey (Pelagic ecosystem survey in the western English Channel and Celtic Sea [PELTIC]) in October 2019 (Cefas 2019, Doray et al. 2021) to complement the historical stomach data archived in a database, DAPSTOM (an integrated Database Portal for fish STOMach Records) (Pinnegar 2014). The compiled dataset was used to (1) simultaneously determine the diets of 6 pelagic species at different life stages (i.e. larvae and non-larvae) across seasons to establish feeding strategies (i.e. generalist vs specialist); and (2) compute a species pairs diet overlap index (Pianka) to understand potential competition between species pairs. By addressing potential trophic interactions of key pelagic species, this study provides insights relevant to fisheries management multispecies assessment and food web modelling (e.g. Lauria et al. 2012, Bentorcha et al. 2017).

2 Methodology

2.1 Sampling area

The study area includes the western English Channel, Celtic Sea, and Irish Sea, collectively defined here as the Celtic Seas ecoregion (ICES 2004). The SPF community in this area are generally confined to shelf waters of < 200 m depth (Fig. 1). Two seasonal front systems develop during spring and determine the main oceanographic features in the area: the Celtic Sea Front (separating the Celtic Sea from the Irish Sea) and the Ushant Front, which develops from the coast of Brittany and extends to the western English Channel (dividing the Celtic Sea from the English Channel) (OSPAR 2000). These fronts generate spatial heterogeneity in oceanic conditions, including gradient of food distribution for SPF in this area.

2.2 Stomach Sampling

Stomach contents of 6 main pelagic species (Atlantic herring, Atlantic mackerel, sprat, European anchovy, European sardine, and Atlantic horse mackerel) were examined in this study. The stomach contents included a combination of historical data (DAPSTOM; Pinnegar 2014) and new samples collected onboard the PELTIC survey. These new samples were collected because the historical data for species such as anchovy were underrepresented within this region in certain seasons.

2.2.1 Historical Data

The DAPSTOM dataset is a stomach contents database designed and built by Pinnegar (2014), in response to a ‘data-rescue’ call from the EU Network of Excellence project EurOcean. The current database (version 5.3) spans from 1893 to 2016, sampled across all seasons. DAPSTOM was filtered for the 6 species of interest and samples taken from the Irish Sea, Celtic Sea, and English Channel. DAPSTOM contains both ‘pooled’ and individual fish stomach data (where ‘pooled’ data is a single record for multiple stomachs sampled, more commonly recorded in the earlier surveys). In some circumstances, the actual number of a particular prey item was not recorded; instead, the ‘frequency of occurrence’ of a particular prey item was collected (i.e. the number of stomachs containing a particular prey item). Therefore, all records are considered as the minimum number of prey items in the stomach, although it is possible that prey items and consumption could be underestimated (Pinnegar 2014). The number of stomach samples used from DAPSTOM is shown in Table 1.

2.2.2 PELTIC Stomach Sampling Survey

The PELTIC survey is an annual autumn survey conducted on board the RV ‘Cefas Endeavour’ and is designed and implemented by the Centre for Environment, Fisheries and Aquaculture Science (Cefas) since 2012 (ICES 2012). This survey aimed to address gaps in the knowledge about SPF and the surrounding ecosystem to understand the role these species play in the ecosystem, and to help inform sustainable management practices.

Stomach samples used in this study were collected during the survey in 2019 (30 September to 28 October) from the Celtic Sea and western English Channel. Anchovy, sardine, sprat, and horse mackerel were sampled from catches obtained by the 20 × 40 m herring mid-water trawl. The sampling strategy was opportunistic: at each station, a minimum of 3 individuals of the same species were analysed. The total numbers of stomachs sampled of each species are found in Table 1 (PELTIC values presented in parentheses). Prior to stomach extraction, each fish was measured (to the nearest 0.5 cm) and weighed (nearest 0.1 g). Stomach extraction and content analysis were carried out on board following recommended methods (Amundsen & Sánchez-Hernández 2019) and in line with methods used in DAPSTOM. Stomachs were preferably analysed immediately after extraction (or preserved in 90% ethanol for a maximum of 90 d) using a binocular microscope (Olympus SZX16 with the SZX2 base) and a magnification of 0.7−11.5 and ×10 optic lenses. The linear size of prey (mm), if fully intact, was taken. The minimum number of individuals within each prey group was recorded and they were identified to the highest taxonomic resolution.

The stomach contents from historical records from the Celtic Seas ecoregion were merged with those from the survey (Table 1). This data was split by meteorological seasons: spring (March−May), summer (June−August), autumn (September−November), and winter (December−February), to explore the possible effects of prey availability. As the life history of the species can influence size and prey (Wilson et al. 2018), the data was split based on fish length, into larvae (≤ 4 cm), and juveniles and adults, which together we call non-larval fish (> 4 cm). This threshold was chosen based on a natural split of around 4 cm of the available fish lengths in the dataset across the different species (Fig. S1). Spatial coverage of stomach samples is shown in Fig. 1. Due to the inconsistency in data availability, it was not possible to analyse the dataset by specific areas, i.e. Celtic Sea, Irish Sea, and western English Channel (see Fig. S2).

For consistency, the prey groupings were standardised based on those available from DAPSTOM and were dependent on the taxonomic resolution during identification. The numerical estimations (percentage contribution of each prey group) were calculated per SPF species by summing the minimum number of each prey group, dividing by the total number of prey, and then dividing by the total number of non-empty stomachs. Any prey group that contributed to < 3% of the overall stomach were removed for ease of interpretation and to identify the major prey groups, as rare or uncommon prey groups for species with small sample size may be overemphasised (Berg 1979). All further analyses used the calculated proportions. It was assumed that stomachs for all individuals are at 100% and of equal capacity, as DAPSTOM does not have a stomach fullness measure. All analyses and figures were generated in R (version 3.6.3; R Core Team 2020), and the diet composition network using R package ‘visNetwork’ (Almende et al. 2019).

2.3 Fractional trophic Levels

Fractional TL of a species represents the trophic position of the species based on weighted average contribution of prey from different TLs into its diet. Fractional TL for each pelagic species was calculated seasonally from the diet matrix representing the fractions of prey in the diet of the predator and the fractional TLs of the prey species using Eq. (1) (Cortés 1999):

$$TL_i = 1 + \left(\sum_{j=1}^{n} DC_{ij} \cdot TL_j \right) \qquad (1)$$

where TL is the trophic level of predator species *i*, TL_j is the fractional trophic level of prey group *j*, DC_{ij} represents the fraction of *j* in the diet of *i*, and *n* is the total number of prey species. For the calculation, prey groups require a trophic level, these were obtained from literature sources (Table S2).

2.4 Strategies of Feeding

To understand the feeding strategy (i.e., specialised or generalised) and prey importance by diet (Bacha & Amara, 2009) of the SPF species, prey composition was analysed. We followed the graphical method described in Costello (1990) with the modifications outlined by Amundsen et al. (1996) by using prey numbers (Scharf et al. 2000). The method compares the relative frequency of occurrence (i.e., the percentage of non-empty stomachs that a prey group occurred) with the frequency in numbers (percentage of abundance) as described in Bachiller et al. (2021).

To examine how relative prey size (linear length in mm) differs among fish species across seasons we generated relative frequency histograms of predator/prey size ratios (PPSRs) of prey consumption as described in Bachiller et al. (2013, 2021). The size of prey was taken from measurements on the PELTIC survey or DAPSTOM. For the prey groups where size information was not available, size ranges from literature were used (Supplementary material Table S3). A high PPSR value represents smaller prey items consumed, while lower PPSR values larger items ingested into the stomach (Scharf et al., 2000).

2.5 Diet Overlap

From the relative prey proportions generated from stomach data, three different overlap indices were computed for further analyses: Morisita, Schoener (also known as percentage overlap), and Pianka (Krebs 1999). Although the Morisita index (range 0–1, where 0 = no similarity and 1 = complete similarity) takes into consideration the abundances of the prey groups within the stomachs and is less dependent on sample size (Wolda 1981, Krebs 1999), it can overrepresent similarities, with values sometimes exceeding 1 (i.e. >100%) (Chao et al. 2006).. On the other hand, the Schoener percentage overlap (Schoener 1970) is often biased by sample size (Krebs 1999), and was not considered for our data, which included varying sample size for six species. We therefore focused only on the Pianka overlap index (Pianka, 1973), defined by Equation 2, for further analysis.

$$O_{jk} = \frac{\sum_{i}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i}^{n} p_{ij}^{2} \sum_{i}^{n} p_{ik}^{2}}} \tag{2}$$

where O_{jk} = Pianka's measure of niche overlap between species j and species k, p_{ij}=proportion of resource i of the total resources used by species j, p_{ik} = proportion of resource i of the total resources used by species k, and n = total number of resources states. Pianka overlap ranges from 0 (where there are no resources in common) to 1.0 (a complete overlap). The Pianka overlap was calculated using R Core Team (2020; version 3.6.3) and package 'spaa' (Zhang 2016). The Pianka index was bootstrapped with 1000 iterations to estimate a 95% confidence interval. To compare the spread of the bootstrap, a normalised metric was derived (hereafter termed normalised spread - NS) which was calculated by dividing the spread of the confidence intervals by the average of Pianka index calculated from the diet matrix and multiplied by 100. The lower the normalised spread, the greater the confidence in the range as the sample-to-sample variation is smaller. This provided a defined and normalised value to compare between different samples. The Pianka index was categorised into low (<0.4), medium (0.4-0.7), and high (>0.7) (Keast 1978, Novakowski et al. 2008). A Principal Component Analysis (PCA; Legendre & Legendre 1998) was applied to explore the differences and overlap in the species' diet. The PCA was undertaken in R (R Core Team 2020; version 3.6.3) using the 'factoextra' package (Kassambara & Mundt 2020).

2.6 Diversity Indices

Shannon diversity (H') of prey consumed and prey richness (S, defined as the total number of prey groups consumed) indices were calculated to understand whether there was a difference in diversity of prey groups between the stomachs of the SPF species. Shannon diversity index (H') is described in equation (3).

$$H' = -\sum_{i=1}^{S} p_i \ln p_i \qquad (3)$$

where p_i is the proportion of the prey group made up of species *i*. Prey richness (S) is the total number of prey groups consumed.

2.7 Statistical Analyses

An ANOVA was performed for diet overlap, H', and S between non-larval fish species to understand the differences between species and seasons. Only non-larval species (i.e. > 4 cm) were chosen due to data constraints with the larval species, with many of them only sampled during 1 season. The ANOVA was computed in R (R Core Team 2020; version 3.6.3).

3 Results

3.1 Diet composition and feeding strategies across seasons

The diet composition of the SPF in the study area changed across seasons, highlighted by the difference in abundances of prey groups (Fig. 2). Most of the species consumed calanoid copepods regardless of season. Values of S and H' for all non-larval species differed between seasons, with both indices statistically significant (ANOVA, $F = 7.0491$, $p = 0.0262$; ANOVA, $F = 18.48$, $p = 7.5 \times 10{-}12$, respectively).

Non-larval sprat consistently consumed copepods in all seasons, particularly calanoid copepods (16– 72%; Fig. 2). S of prey groups in non-larval sprat across the seasons was low (between 2 and 3); spring had a maximum S equal to 3 and a higher value of H' (0.786) compared to autumn, which had the lowest H' (0.44; Fig. 3). The dominant prey group for non-larval sprat changed between seasons: calanoid copepods (72%) in spring, cyclopoid copepods (84%) in autumn, and teleost eggs (72%) in winter (Fig. 2). Non-larval sprat also consumed diatoms (16%) and copepod eggs (12%) in spring. The Costello diagram (Fig. 4) indicated that across all seasons, calanoid copepods was the dominant prey group for non-larval sprat, with > 45% occurrence. The low PPSR values indicated consumption of relatively large prey groups across all seasons (Fig. 5).

Sprat larvae had greater S in spring and autumn (4), mostly consuming phytoplankton in spring (67%) and winter (86%). However, sprat larvae in autumn ingested an almost equal split between calanoid copepods, diatoms, other phytoplankton, and tintinnids (26, 26, 26, and 23% respectively; Fig. 2), resulting in a higher value of H’ than in spring (1.38 and 1.00 respectively; Fig. 3). Sprat larvae diet in winter had a lower H’ (0.41) and S (2) compared to spring and autumn.

Calanoid copepods were consumed in all seasons by non-larval herring (18–95%) and were the dominant prey groups in summer and autumn (Fig. 2). In autumn and summer, herring almost exclusively consumed calanoid copepods (95% and 81% respectively), with a low S (2), and low H’ (0.18) in autumn Fig. 3). The highest value of H’ was in winter (1.34) alongside the highest S (4). There was no dominant prey group in winter (Fig. 2). During spring, over half of non-larval herring diet was dominated by teleost eggs (54%), with the rest consisting of calanoid copepods (32%) and euphasiids (7%; Fig. 2). In winter, herring prey group frequencies were <50% (Fig. 4), compared to summer and autumn, in which calanoid copepods were dominant in the diet.

Similarly, herring larvae had a varied diet in winter, consuming a wider range of prey groups (winter: S = 5; spring: S = 4; Fig. 3), and a higher H’ than in spring (winter: H’ = 1.51; spring: H’ = 1.23; Fig. 3). Calanoid copepods were present in spring and winter of herring larvae diet (Fig. 2), accounting for 51% of the ingested prey in spring, with the remaining 49% equally split between cirripedes, copepod eggs, and bivalves. No data for herring larvae in summer and autumn were available.

Sardines varied their diet across seasons (Fig. 2), although it was the only species which consistently consumed phytoplankton throughout the year. Throughout the seasons, S did not change (4); however, H’ was lowest in autumn (0.77) and highest in spring (1.31). In spring, they consumed mainly calanoid copepods (33%) and amphipods (33%), while in summer, they switched towards a greater phytoplankton based diet (50% diatoms, 5% other phytoplankton, 41% calanoid copepods, and 4% crustaceans). Sardine's diet in autumn was dominated by calanoid copepods (77%; Fig. 2). Many of the prey groups consumed had a frequency of abundance of < 50% and frequency of occurrence < 60%, with calanoid copepods most dominant in autumn and summer and no group dominant in spring (Fig. 4). Sardine consumed a wide range of prey sizes from relatively large to small, indicated by both low and high PPSR groups (Fig. 5). Sardine larvae were only sampled in the summer and only consumed copepod eggs; as such, H' and S were low (S = 1, H' = 0; Fig. 3). Anchovies had a varying diet across the seasons, although calanoid copepods (18−57%) and crustaceans (5−18%) were part of their diet in all seasons sampled (spring and autumn; Fig. 2). They had the same S values (5) in spring and autumn, and similar H' values for each season (spring: H' = 1.32; autumn: H' = 1.24; Fig. 3). In spring, anchovies consumed mostly shrimp (50%), with a mixture of amphipods (18%), copepods (18%), crustaceans (4%), and euphausiids (9%). In autumn, the diet of anchovies showed an increase in calanoid copepods to 57%, and an increase in crustaceans to 23%. Shrimp and calanoid copepods were the dominant prey groups in spring and autumn respectively, at > 50% in frequency and occurrence (Fig. 4). The size of prey consumed was relatively large in comparison to body length, with mainly low PPSR values in both seasons (Fig. 5). No anchovy larvae samples were available. The main constituent of horse mackerel diet across all seasons was calanoid copepods (e.g. 79% and 71% of diet in spring and autumn respectively; Fig. 2). This is also consistent with the Costello diagram (Fig. 4) in autumn where the frequency and occurrence were > 50%. The remaining diet in spring consisted of euphausiids (21%) and in autumn of a mixture of crustaceans (16%) and cyclopoid copepods (4%). Horse mackerel diet in autumn had a higher S, H’, and a cluster of low frequency and low occurrence prey groups than in spring (autumn: S = 4, H’ = 0.88; spring: S = 2, H’ = 0.51; Fig. 3). Overall, the PPSR low values demonstrated that horse mackerel consume relatively large prey groups (Fig. 5). Horse mackerel larvae had an S of 4 in summer,

consuming calanoid copepods (38%), cyclopoid copepods (22%), diatoms (24%), and Cladocera (16%), supported by a higher H’ value (summer: H’ = 1.33; autumn: H’ = 0.95; Fig. 3). In autumn, horse mackerel larvae had a lower S (3), as they did not consume phytoplankton (diatoms), but, like the non-larval horse mackerel, they consumed a higher amount of calanoid copepods (58%; Fig. 2).

Mackerel switched diet across seasons, with calanoid copepods as the consistent prey group, e.g. 53% of the diet in spring and 85% in summer (Fig. 2). Values of S and H’ were highest in spring (S = 7, H’ = 1.48), decreasing to an S of 4 in summer and winter. Winter had higher H’ compared to summer (winter: H’ = 1.14; summer: H’ = 0.58; Fig. 3). In winter, non-larval mackerel consumed less calanoid copepods (7%) and more non-diatom phytoplankton (52%) compared to the other seasons. The remaining composition consisted of appendicularians, which increased from 11% in spring to 29% in winter; no appendicularians were consumed in autumn (Fig. 2). In winter, there was no dominant prey group (Fig. 4). Mackerel consumed relatively large prey groups for their size, as demonstrated by low PPSR groups; however, alongside sardines, they were the only species to consume a high PPSR group (Fig. 5).

In summer, there was no dominant prey group for mackerel larvae. They consumed copepod eggs (38%), calanoid copepods (21%), copepod nauplii (20%), Cladocera (13%), and phytoplankton (9%; Fig. 2). This resulted in a high S (5) and H' (1.49) (Fig. 3). Mackerel larvae consumed relatively large prey groups for their size, demonstrated by low PPSR groups (Fig. 5).

In general, the majority of the prey groups had low frequency of occurrence (Fig. 4), but there was a wide spread of prey groups in the diet of all 6 species (Fig. 2). This observation suggests that all 6 SPF exhibit generalist feeding behaviours (Fig. 4). Notably, both the relative frequency and occurrence of calanoid copepods were high (> 70%) in the diet of herring in summer, in herring larvae in spring, horse mackerel in autumn, horse mackerel larvae in autumn and spring, and sprat in spring.

Regarding PPSR, many of the species (horse mackerel; horse mackerel larvae, mackerel larvae, herring larvae, and anchovy in all seasons) consumed large prey, representing > 50% of diet composition (indicated by low PPSR values). Non-larval sardine in autumn and mackerel in winter were the only predators to consume smaller sized prey groups compared to their body size (indicated by higher PPSR values; Fig. 5).

3.2 Trophic Levels

TLs for most SPF were variable across seasons, except for horse mackerel (3.27−3.28), which had minimal fluctuations (Table 2). Sprat larvae had the lowest TL of 2.16, of all species regardless of season, while anchovy had the highest overall TL of 3.51 in spring (Table 2). In autumn, horse mackerel larvae had their highest TL, while for herring it was in winter. However, 1-way ANOVA indicated there were no statistically significant differences in TLs across seasons and across species (ANOVA, F = 0.667, p = 0.587).

3.3 Diet Overlap

The PCA (Fig. 6) showed that non-larval mackerel differed from all other SPF in spring (Fig. 6a), as they consumed prey groups the other species did not (such as copepod nauplii, Chaetognatha, Appendicularia, and fish larvae). All other SPF were closely located in orthogonal space, and as such, consumed similar prey groups (Fig. 6a). In spring, high diet overlap was observed between all combinations of mackerel, herring larvae, horse mackerel, and sprat, with the highest overlap between horse mackerel and sprat (Pianka index = 0.932, NS = 107.3; Fig. 7, Table S4). Herring larvae had high overlap with mackerel (Pianka = 0.81), sprat (Pianka = 0.89), and horse mackerel (Pianka = 0.85; Fig. 7). In summer, there was only 1 cluster, formed by sardine larvae, mackerel larvae, and horse mackerel larvae (Fig. 6b), while sardine, mackerel, and herring were isolated in orthogonal space, in particular, herring driven by calanoid copepods, harpacticoid copepods, and mysids (Fig. 6b). Sardine larvae had only 1 high overlap, with mackerel larvae (Pianka = 0.76, NS = 43), while mackerel larvae diets had generally low overlaps (< 0.45) with the other SPF considered (Fig. 7). Herring and mackerel presented the highest diet overlap in summer (Pianka = 0.98, NS = 101.7). In autumn, horse mackerel larvae, sprat, anchovy, horse mackerel, and herring formed a cluster (Fig. 6c). Sardine and sprat larvae were isolated, driven by dinoflagellates/bivalves and phytoplankton/tintinnids respectively (Fig. 6c). Autumn was characterized by high diet overlap between anchovy and horse mackerel, and between herring and sardine (Pianka = 0.98, NS = 34.3; Pianka = 0.979, NS =

102.0, respectively; Fig. 7, Table S3). In general, anchovy had a high diet overlap with all other species except sprat and sprat larvae. Sprat only had low overlaps (< 0.4) in autumn. In winter, no clear clustering was observed (Fig. 6d); herring larvae and sprat diets were both driven by copepod Calanoida and teleost eggs. The only high diet overlap in winter was between sprat larvae and mackerel (Pianka index = 0.84, NS = 118.0). Overall, horse mackerel larvae had a high diet overlap with both herring and sardine in both summer and autumn, while the sprat–sprat larvae, herring–sprat larvae, and anchovy–sprat combinations had generally low diet overlaps throughout the seasons.

There was no statistically significant difference in diet overlap between seasons for all non-larval SPF species (ANOVA, F = 2.48, p = 0.082), indicating that collectively the average of diet overlaps of the predators between different seasons did not change. However, for a few given species, there were significant differences of overlap between seasons (Table 3): non-larval anchovy (ANOVA, F = 11.32, p = 0.012), sprat (ANOVA, F = 9.11, p = 0.019), and mackerel (ANOVA, F = 7.09, p = 0.027).

4 Discussion

4.1 Diet Composition and Overlap of Juveniles and Adults (Non-larvae)

This study found that the diet composition of SPF in the Celtic Seas ecoregion changed across seasons. Despite intra-annual variability in prey consumption by most species, calanoid copepods were the most prominent prey for all species, as well as some of the most abundant prey types, in agreement with other studies on similar species (e.g. Möllmann et al. 2004, Raab et al. 2012, Bachiller & Irigoien 2015). In fact, calanoid copepods are found throughout the year in the study area, with peaks in abundance in April and May, and a secondary peak between October and December, depending on specific calanoid species (Johns 2006, Kennington & Rowlands 2006). Calanoid species are most abundant around the Ushant Front area and south of Ireland (Johns 2006), where non-larval horse mackerel and mackerel were sampled, and west of the Isle of Man (Kennington & Rowlands 2006), where the majority of non-larval sprat and herring were sampled. These areas are associated with seasonal stratifications that could help result in elevated copepod abundances (Kennington & Rowlands 2006). This could explain the medium to high overlaps between these 2 species pairs, due to the peak in calanoid copepods in spring. Autumn was the season with the highest diet overlap between the SPF species (particularly the comparison anchovy– horse mackerel) possibly due to the consumption of similar prey groups and similar proportions. However, autumn is the ending of the planktonic growing season, with prey groups such as calanoid copepods lowest from December to March (Johns 2006). Winter had the smallest diversity of prey groups, likely because of the decrease in diversity in plankton in this season (Johns 2006, Giering et al. 2019). The majority of both horse mackerel and mackerel were sampled inbetween the 100 and 200 m isobaths towards the shelf edge (south of Ireland), where calanoid copepods are present and peak during spring (Johns 2006), which may explain the high overlap between these species.

Horse mackerel's diet was particularly selective towards calanoid copepods, possibly explaining the strong diet overlap between this species and the other SPF. Horse mackerel also preyed upon cyclopoid copepods in autumn, in coincidence with the peak in abundance of this species (Eloire et al. 2010). Observations from the Bay of Biscay and the Belgian part of the North Sea (Van Ginderdeuren et al. 2013, Bachiller & Irigoien 2015) indicated that horse mackerel can show an opportunistic active predation on larger prey items (e.g. euphausiids) when they are available. As such, the consumption of calanoid copepods in this study may indicate the absence of larger prey item in the planktonic community during feeding.

Similarly, this study found herring consumed a small range of prey groups of generally larger sizes, with calanoid copepods the most common, in addition to euphausiids and mysids, as also observed in the North Sea (Flinkman et al. 1998, Corten 2000, Casini et al. 2004). Celtic Sea herring are autumn-spawners, and it is thought that during the spawning period, feeding is limited (Hardy 1924, Muus & Nielsen 1999); therefore, even if herring consumed almost exclusively calanoid copepods in autumn, they are less likely to be competitors with other species during this season. Furthermore, herring can switch to smaller prey items if larger prey sizes are not available (Gibson & Ezzi 1992). In this study, herring did not have a dominant prey group during spring and winter but consumed a higher number of teleost eggs, likely as result of insufficient planktonic prey availability (Segers et al. 2007). Teleost eggs also contributed to sprat diet, which have been reported to prey on plaice eggs and cod eggs in the Irish Sea (Ellis & Nash 1997, Fox et al. 2012, Plirú et al. 2012) and in the Baltic Sea (Nissling 2004), respectively. Conversely, these species could actively select teleost eggs when available and as such, result in a lower proportion of calanoid copepods in the diet, due to opportunistic predation. This could be addressed with the addition of concurrent plankton biomass data; however, this is outside the scope of this study. Further studies would be required to understand the result in increased predation on fish eggs, as there are potential bottom-up effects on the recruitment of the species predated upon. Overall, herring and horse mackerel displayed more specialist feeding behaviours, and could be vulnerable to changes in the availability of a particular prey.

Mackerel showed a generalist feeding strategy with the largest values for species richness and Shannon diversity in spring, and diverse prey sizes consumed in winter, in agreement with several previous studies (e.g. Debes et al. 2012, Utne et al. 2012, Bachiller et al. 2016, Óskarsson et al. 2016, Kvaavik et al. 2019, references therein). This study has shown the importance of appendicularians in the diet of mackerel in the Celtic Seas ecoregion in spring and winter, which as such may be non-coincidental consumption, as reported in the Norwegian Sea (Prokopchuk & Sentyabov 2006, Langøy et al. 2012, Bachiller et al. 2016).

Sardine and mackerel were the main consumers of phytoplankton and were the only predators to consume smaller prey items (PPSR results), which is commonly reported for sardine (e.g. Garrido et al. 2008), particularly in nearshore habitats (Emmett et al. 2005). Sardine was the only species that consistently consumed phytoplankton throughout the year, but also consumed larger prey items such as crustaceans, decapods, and copepods, consistent with findings in the Bay of Biscay (Bachiller & Irigoien 2015). This demonstrates that this species can use both particulate and filter feeding (Garrido et al. 2007, Bachiller et al. 2020, 2021), although filter feeding is the main feeding mode (Garrido et al. 2008). Phytoplankton was also identified as part of sprat diet, although this has rarely been reported in non-larval sprat diet (this study, Falkenhaug & Dalpadado 2014), while other studies have observed the absence of phytoplankton within the diet (Casini et al. 2004, Bernreuther 2007, Dickmann et al. 2007, Voss et al. 2009, Raab et al. 2012). It is possible that phytoplankton were ingested, through a shift to filter feeding, to maximize energy intake and availability (Gibson & Ezzi 1992, Falkenhaug & Dalpadado 2014). Many SPF (e.g.

sardine and herring) can switch between filter (non-selective) and particulate (selective) feeding (e.g. van der Lingen et al. 2006, Garrido et al. 2007, Nikolioudakis et al. 2014), which allows the fish to appropriately exploit the planktonic food web (van der Lingen et al. 2009).

Anchovy consumed large prey groups compared to their body size, such as euphausiids in this study (PPSR results), in the North Sea (Raab et al. 2011) and in the Bay of Biscay (Bachiller & Irigoien 2015). This suggests that anchovy within the study area could use an opportunistic prey selection for larger prey items in spring. However, euphausiids have an initial peak in May and a main peak in October and are found primarily south of Ireland (Johns 2006). The spring samples are found in areas of high euphausiid abundance, compared to autumn samples located off the Cornish coast; therefore, prey availability could be a contributing factor to feeding strategy. Many of the dietary seasonal changes in this study are likely attributable to prey availability (Pinnegar et al. 2003), and will suit the SPF with generalist feeding behaviours (Dunne et al. 2002, Beckerman et al. 2006, Rooney et al. 2006, Gravel et al. 2011), such as mackerel and anchovy.

4.2 Diet Composition and Overlap of Larvae

Copepod eggs were a main component in sardine larvae diet, particularly in summer. During maturation, the larvae shift their diet from copepod eggs to copepodites and then adult copepods, concomitant with larvae size changes (Conway et al. 1994, Munuera-Fernández & González-Quirós 2006, Morote et al. 2010). In contrast with non-larval sprat, sprat larvae consumed largely phytoplankton, reflecting an ontogenetic shift in diet (Dickmann et al. 2007). As with sprat, herring showed an ontogenetic diet shift, as non-larval herring consumed prey groups larger than that of herring larvae, relative to their size (e.g. Wilson et al. 2018). The mackerel–herring larvae diet overlap observed in winter could be explained by phytoplankton consumption; however, herring larvae were mainly sampled nearshore in the Irish Sea, whereas mackerel were observed in Celtic Sea offshore waters. Therefore, this potential competition may not be such a concern.

In their life cycle, planktivorous SPF are consumers of organisms across the whole planktonic size spectra (e.g. phytoplankton, micro-, meso-, and macro- zooplankton), because with age and maturity, they can ingest prey of larger sizes (Bachiller et al. 2013). Often, when available, larger prey items are consumed, as they are more energetically valuable (Nikolioudakis et al. 2014). This study showed that larval species often consumed similar prey groups, such as copepod developmental stages in spring. Small copepods are particularly important to larval facultative filter-feeding species, such as sprat and herring, as low herring larval abundances have been associated with declines in copepods (Alvarez-Fernandez et al. 2015). The most critical phase of development for more specialist feeders such as herring are within the first few days, when they require sufficient suitable prey to successfully feed (Houde 2008). Therefore, recruitment success can be impacted by suitable planktonic prey availability, which in turn is influenced by other factors such as environmental conditions. In fact, small copepods have experienced changes within the region and adjacent seas. In the Celtic Sea region, smaller copepods have seen a decline over the last few decades, showing a negative correlation with sea surface temperature (Bedford et al. 2020), whilst in the adjacent North Sea, a decline in recruitment of commercially important fish stocks was linked to a decline in small copepod abundance (since the 1990s) and to declining primary production (Pitois & Fox 2006, Capuzzo et al. 2018).

4.3 Trophic Levels

Although the prey composition changed throughout the year, there was no statistically significant difference in TL between seasons of the SPF. A possibility is that the major contributor in the prey composition (calanoid copepods) was relatively abundant in the diet throughout the year, whereas the low frequency prey groups changed between seasons. Horse mackerel for example did not change dominant prey groups, explaining the similar TLs calculated for the seasons sampled. The averaged TLs identified in this study for SPF species such as mackerel and anchovy were different from levels presented in FishBase (Froese & Pauly 2009). This may be attributable to the different size ranges and life stage of the SPF species investigated. The data downloaded from FishBase was filtered for the region and to similar sizes; however, this was not always possible. For example, the relatively low TL calculated for mackerel, particularly in relation to those provided in FishBase (Froese & Pauly 2009), is likely due to the size of mackerel investigated in the study; most of the mackerel stomachs considered were obtained from smaller fish, while the TL calculated in FishBase contains a mixture of juvenile and adults (Froese & Pauly 2009). The waters southwest of the UK includes an important nursery area for mackerel, which may explain the prevalence of smaller mackerel found within this study. Fish are an important part of the diet of larger mackerel (Engelhard et al. 2013), and most of the larger mackerel tend to reside off the shelf area, outside the study area. The presence of phytoplankton in the stomachs of juvenile mackerel contributed to the reduction in this species' TL and is likely the result of available prey. In fact, mackerel could have consumed more phytoplankton in winter (52% of the diet) to meet their calorific requirements. Similarly, to mackerel, herring, horse mackerel, and sardine demonstrated lower TLs than in FishBase. In this study, sardine consumed phytoplankton, which was not present in the FishBase listed diet, and so explains the difference in TL. Horse mackerel in FishBase consumed finfish in the North Sea, which is a higher TL than the prey groups consumed by horse mackerel in this study. Interestingly, herring in FishBase demonstrated a higher TL than reported here; the consumption of bony fish (Ammodytidae) by herring reported in FishBase was the main difference between the TL calculations. Conversely, the reported TL in FishBase for anchovy was lower than in this study. This could be explained by the food items used for FishBase calculations containing more instances of phytoplankton, while the only instance of phytoplankton consumption in this study was 4% of diatoms in the autumn.

4.4 Potential impacts of environmental changes on SPF

SPF species pairings in this study does not always equate to competition, especially if there are enough food resources to achieve fish calorific intake and optimum fitness (Holt 1987), and spatial segregation. In contrast, top-down control by these planktivorous species (consuming large vs. small copepods) and feeding strategy (generalist vs. specialist) can affect the zooplankton community. Interactions may become apparent due to sea surface temperature changes in the Celtic Seas ecoregion, with a decadal mean of 0.66 ± 0.02°C (Lauria et al. 2012). This can change feeding conditions in the future and lead to shifting distribution scenarios (Pennino et al. 2020); in fact, European anchovy has increased its distribution in the study area (Beare et al. 2004), due to increased recruitment success of existing local northern stocks (Petitgas et al. 2012, Huret et al. 2020) and the ability of individuals to reach an overwintering size (Raab 2013). After spawning in the southern North Sea, adult and juvenile anchovy overwinter in the relatively warmer waters of the western English Channel (Huret et al. 2020). This will have indirect as well as direct effects on SPF, possibly forcing changes in growth and survival of SPF species through prey availability and distribution variability (e.g. Cushing 1990, Southward et al. 1995, Corten 2001). It is difficult to predict how these potential changes in prey availability and distribution will affect SPF, due to their variable seasonal diet and the ability to switch from specialist to generalist diets (e.g. herring in this study switching from specialist in autumn and summer, to generalists in winter and spring). The importance of SPF is clear, as the abundance of the SPF can drive the abundance of demersal species in the region through a bentho-pelagic trophic link (Eme et al. 2022).

4.5 Considerations on the methods and recommendations

The methodology adopted to collect, collate, and analyse fish stomach contents data may present some limitations, which should be considered when interpreting the results. The main caveat of this study is the lack of concurrent planktonic community data; as such, the feeding strategies of the species studied cannot be ascertained, as consumption may reflect prey availability. The Costello diagram provides insight into the dominant prey group, or groups, from which we can begin to explore the possibilities of feeding strategies. We would recommend the collection of concurrent zooplankton community data to confirm these feeding strategies across seasons. A general overview of the seasonally available prey can be determined from several detailed studies in the region (e.g. Eloire et al. 2010, Widdicombe et al. 2010, Reygondeau et al. 2015, Bedford et al. 2020, Pitois et al. 2021, Scott et al. 2021, Capuzzo et al. 2022). The historical samples (adopted in this study) span a wide timeframe where changes in the planktonic community and composition may have occurred (e.g. see Bedford et al. 2020). However, we still find similar prey groups from the earliest decades to the latest (see the DAPSTOM database; Pinnegar 2014), supporting the relevance of our results and conclusions.

To analyse stomach contents, a visual inspection was used to identify prey organisms. This method is likely to underrepresent more easily digestible prey such as phytoplankton (Sikora et al. 1972), and gelatinous organisms. Molecular techniques can be used to identify these (e.g. Lamb et al. 2019, Bachiller et al. 2020, references therein), but these methods return presence−absence of the prey type, rather than abundance and size. The use of abundance ratios in the diet can overemphasise the contribution of smaller prey groups in the stomach (van der Lingen et al. 2006, Pinnegar 2014). To counteract this bias, the abundances can be converted to biomasses using existing length−weight relationships. As many of the prey groups were of low taxonomic resolution, there were large variations in prey sizes, and so the biomass estimates were judged to be uncertain. Pinnegar (2014) stated that the limitation of pooled data can underestimate prey numbers, but can also mask individual variation of feeding (e.g. individual variation observed in the Bay of Biscay; Bachiller & Irigoien 2015). This variation could be due to gill raker size or feeding strategy by certain size fish species that can be even higher than differences in stomach contents of different species or different size ranges. The varying sample size may also have similar effects. Small sample sizes such as horse mackerel larvae in autumn and sardine in spring may overemphasise the importance of uncommon prey (Berg 1979). An increase in sample number would reduce this bias and will also improve the capability of accounting for any variability found in fish feeding behaviour, and as such, would provide a more reliable representation of overall diet (Winemiller 1990, Ferry & Cailliet 1996).

4.6 Conclusions

This study provides novel insights into the diet composition of SPF across different seasons in the Celtic Seas ecoregion, showing that dietary overlap between SPF vary between seasons, with the highest overlaps occurring in autumn. Despite seasonal variability in prey consumption of the lower frequency prey groups, calanoid copepods represented a key component of diet in all seasons and the main contributor to the diet of the six SPF.

The results of this study may be generalised to other temperate locations with similar populations of SPF. In the North Sea, for example, 6 forage fish species co-occur and (partially) compete for the same planktonic food sources (Dickey-Collas et al. 2013, Raab 2013). The results of this study may also provide important input to trophic models. These models often provide a platform to disentangle the complexities of food web functioning (trophic relationships), anthropogenic stressors, and the environment to predict how the ecosystem may respond to future scenarios (e.g. Boyd et al. 2020b). However, the accuracy of these models is dependent on ecosystem specific data (Essington 2007, Han et al. 2020), including specific TL and diet matrices. Many existing Ecopath with Ecosim models (Pauly et al. 2000, Christensen et al. 2014) take into consideration only the annual consumption patterns rather than seasonal. Therefore, including a seasonally varying diet matrix, such as the one derived in this study, may improve such models, allowing them to be used to evaluate ecosystems effects of fishing, and to explore management policy options amongst many other ecological questions at a seasonal scale.

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1046 # Figures

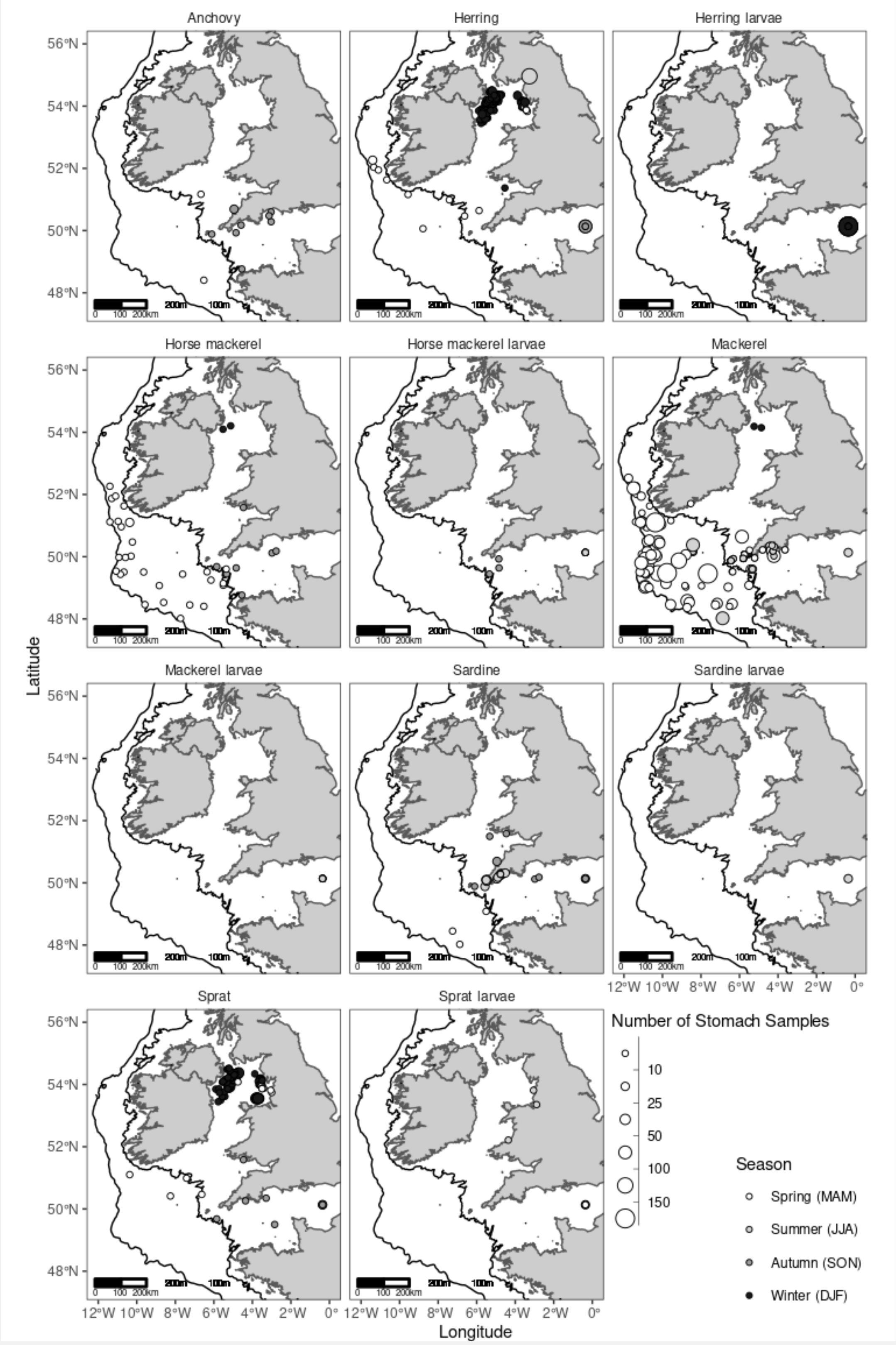

Figure 1: Spatial distribution and number of non-empty stomach samples from DAPSTOM and the PELTIC survey within the Celtic Seas ecoregion for 6 pelagic species (anchovy, herring, horse mackerel, mackerel, sardine, and sprat); larvae defined as < 4 cm. Thick black lines: simplified 100 and 200 m isobaths.

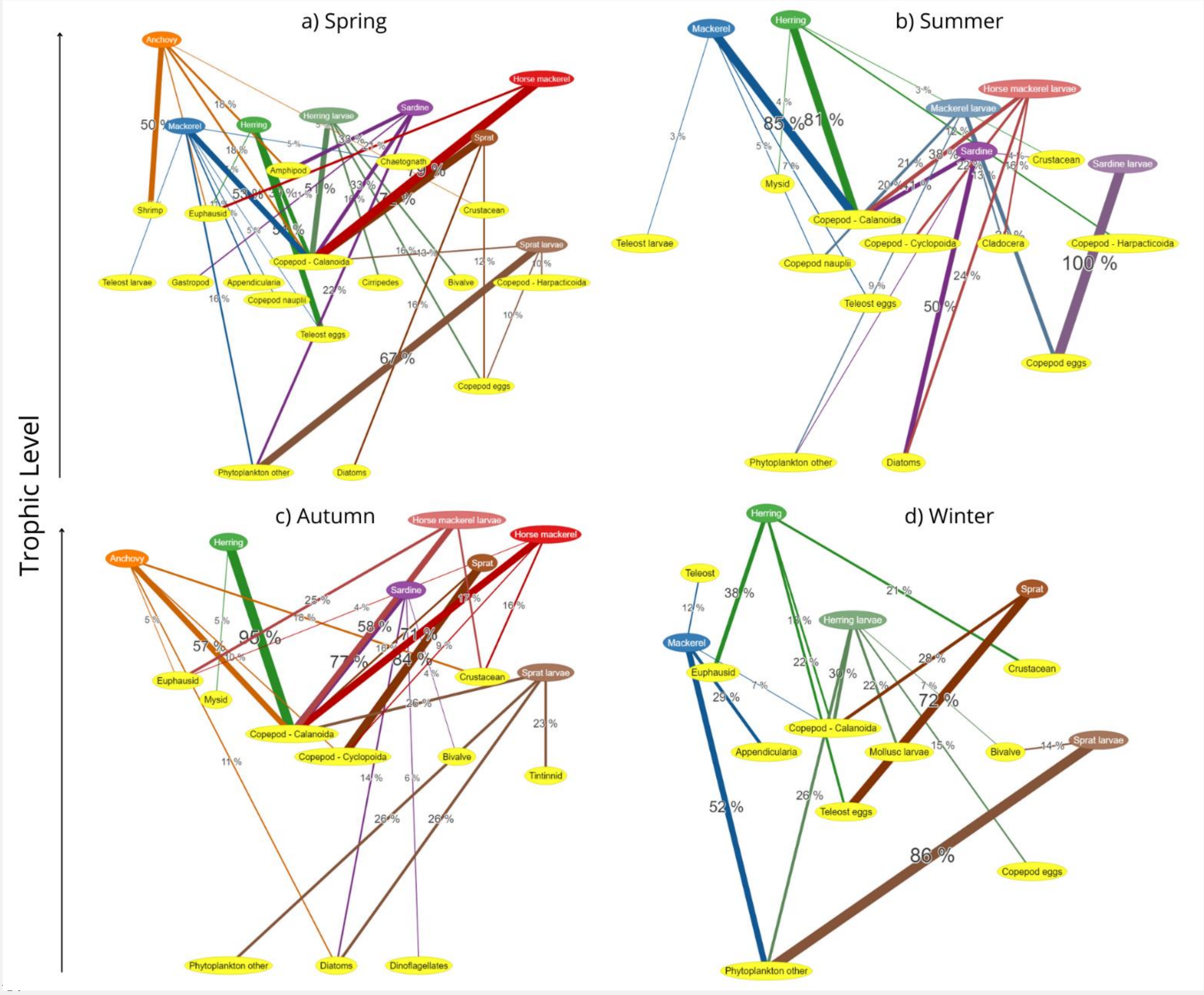

Figure 2: Average proportions of prey groups consumed by 6 pelagic species (anchovy, herring, horse mackerel, mackerel, sardine, and sprat) and overlapping prey types across seasons (a: spring, MAM; b: summer, JJA; c: autumn, SON; d: winter, DJF) in the Celtic Sea, Irish Sea, and English Channel. Yellow nodes: prey groups; non-yellow nodes: predators. Predator species arranged by trophic levels of the species (y-axis) and calculated from the diet composition shown in the network using Eq. (1). Percentage contribution of prey type to a species diet indicated by thickness and numerical value of each edge. Non-larval species are > 4 cm, unless defined as larvae, which are ≤ 4 cm.

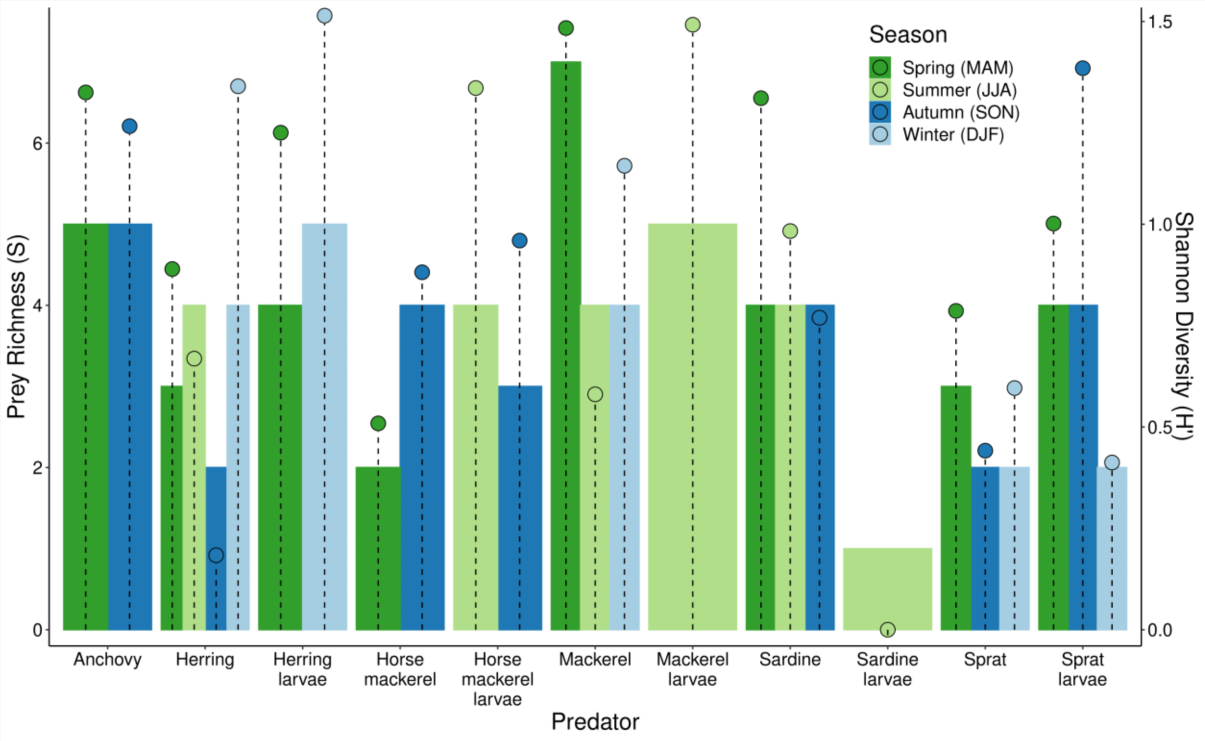

Figure 3: Prey richness (S; data bars; left-hand axis) and Shannon diversity index of prey (H ’; data points; right-hand axis) for 6 pelagic species (anchovy, herring, horse mackerel, mackerel, sardine, and sprat) in the Celtic Seas ecoregion. Non-larvae are > 4 cm, unless defined as larvae, which are ≤ 4 cm.

Figure 4: Costello diagram for 6 pelagic species (anchovy, herring, horse mackerel, mackerel, sardine, and sprat) in the Celtic Seas ecoregion. Non-larvae are >4 cm, unless defined as larvae, which are ≤4 cm. Amphi: Amphipods; Append.: appendicularians; Calan.: calanoid copepods; Chaeto.: Chae to gnatha; Clado.: Cladocera; Cop. eggs: copepod eggs; Crust.: crustaceans; Cyclo.: cyclopoid copepods; Dino.: dinoflagellates; Euphau.: euphausiids; Fish larv.: fish larvae; Gastro.: gastropods; Harpact.: harpacticoid copepods; Moll.: mollusc; Phyto. Other: phytoplankton other (non-diatoms or dinoflagellates); Tintin.: tintinnids.

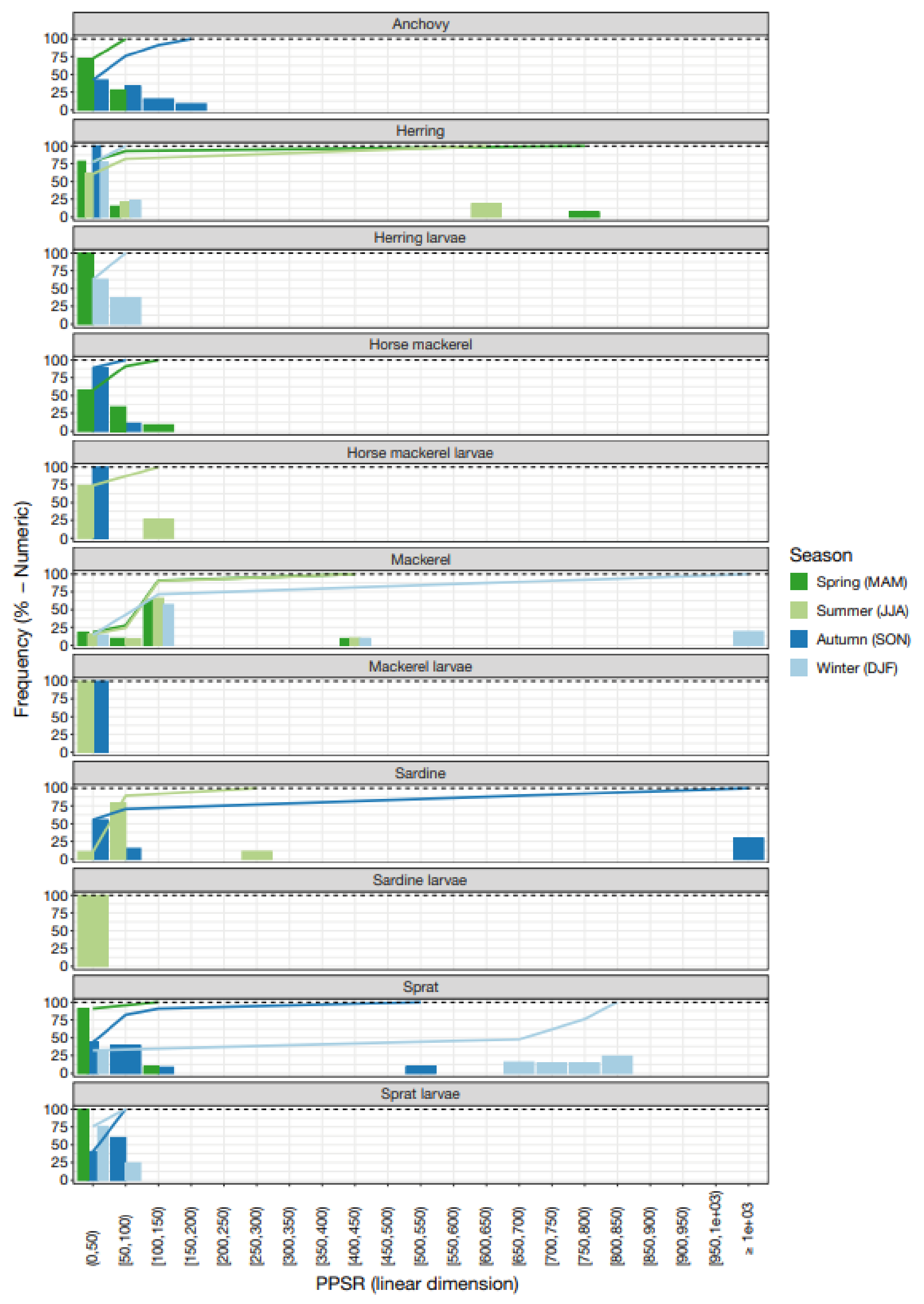

Figure 5: Seasonal variability of prey size using predator:prey size ratio (PPSR; total length predator:total length prey) for 6 pelagic species (anchovy, herring, horse mackerel, mackerel, sardine, and sprat) in the Celtic Seas ecoregion. Non-larval species are >4 cm, unless defined as larvae, which are ≤4 cm. Data lines: cumulative frequency of the predator:prey size ratio groups; dashed lines: 100% frequency.

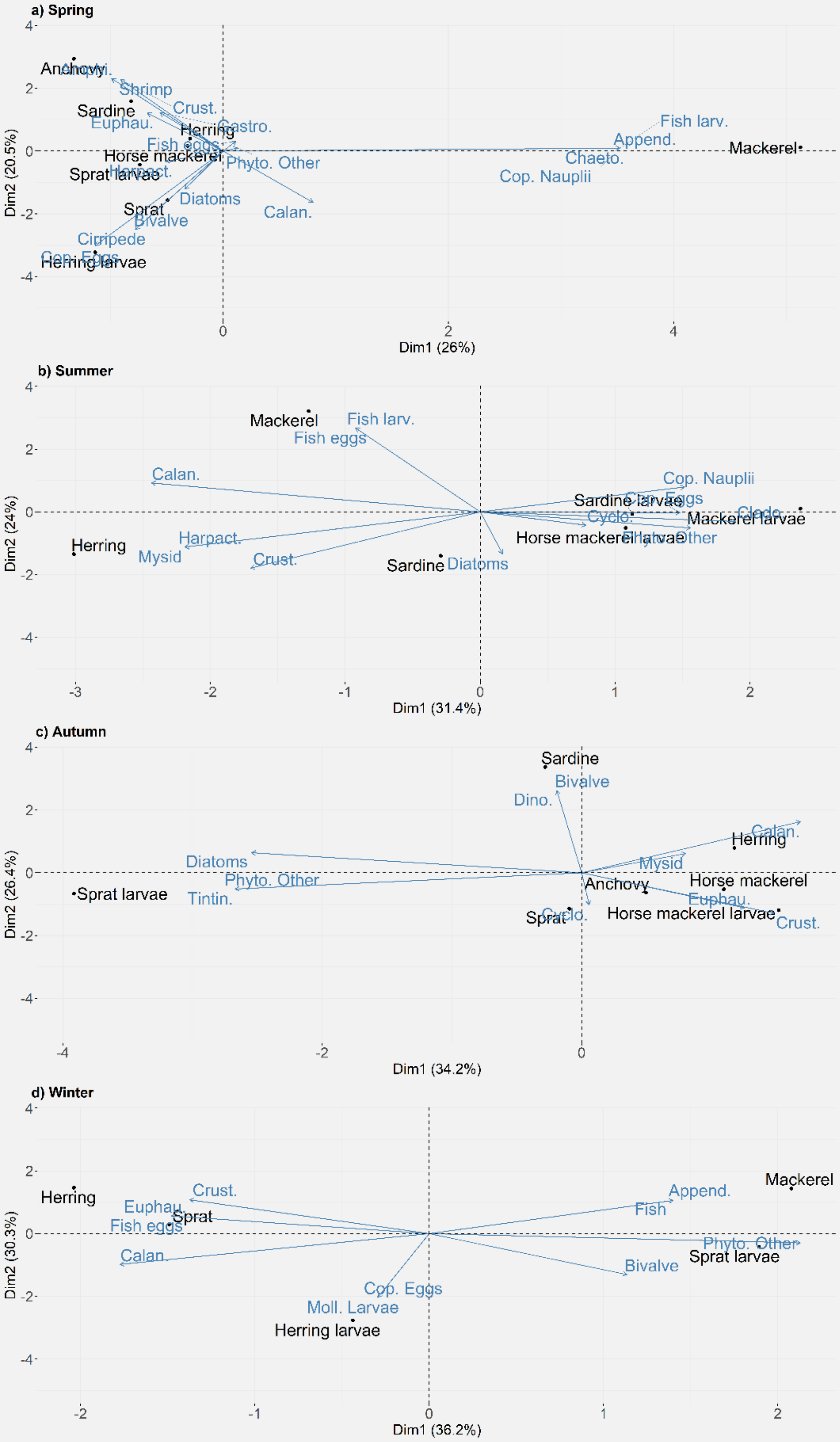

Figure 6: Principal component analysis (PCA) of diet composition for 6 pelagic species (anchovy, herring, horse mackerel, mackerel, sardine, and sprat) for 2 PCA components (Dim1 vs. Dim2) for each meteorological season (a: spring, MAM; b: summer, JJA; c: autumn, SON; d: winter, DJF) in the Celtic Seas ecoregion. Black text: pelagic species; blue text: prey species (variables); blue arrows: direction of the variables as projected into 2D space. Predators are >4 cm, unless defined as larvae, which are ≤4 cm. Prey abbreviations as in Fig. 4.

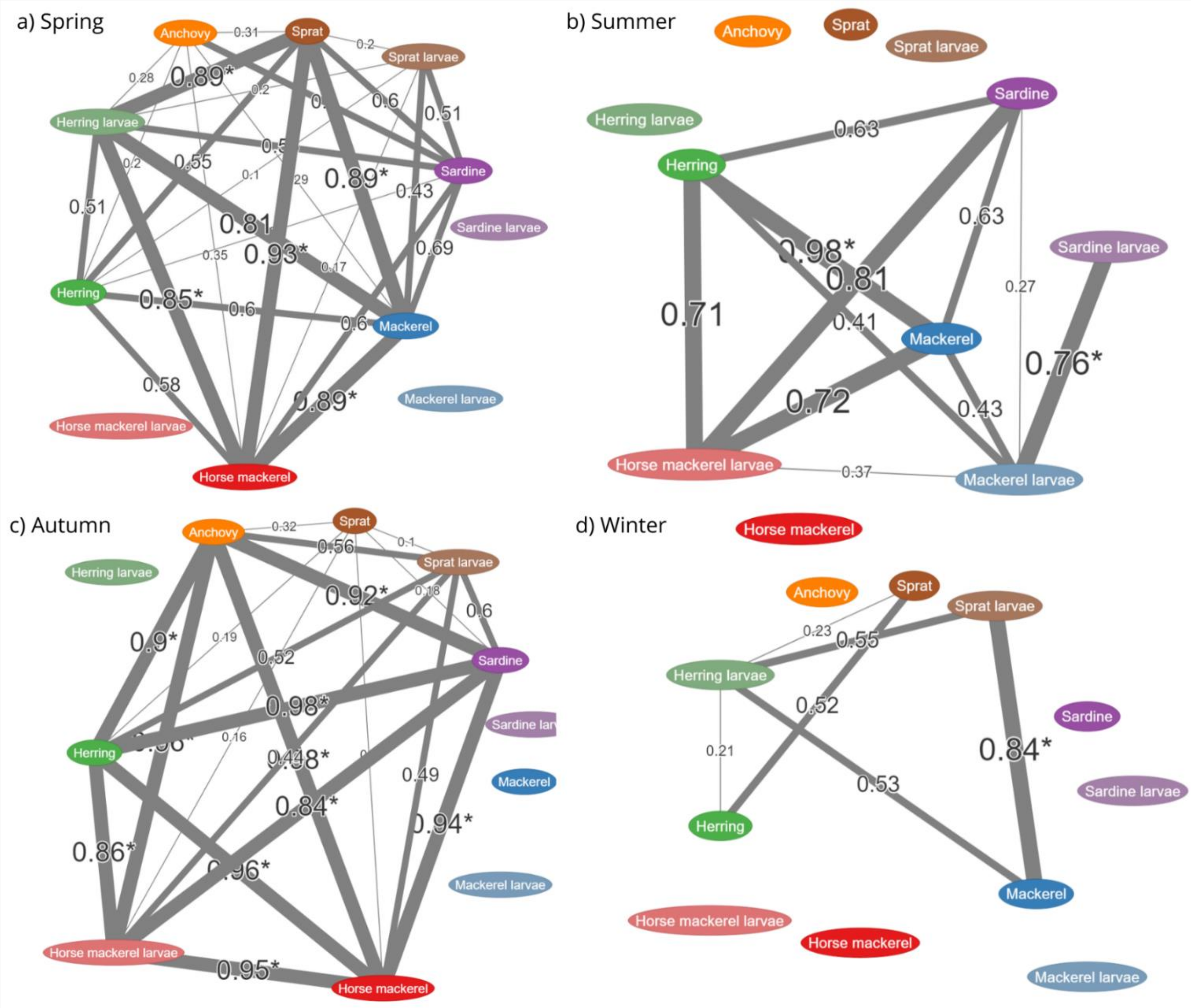

Figure 7: Pairwise dietary overlap (Pianka's index) network of 6 pelagic species (anchovy, herring, horse mackerel, mackerel, sardine, and sprat) across seasons (a: spring, MAM; b: summer, JJA; c: autumn, SON; d: winter, DJF) in the Celtic Seas ecoregion using Eq. (2). Pianka overlap ranges from 0 (where there are no resources in common) to 1.0 (a complete overlap). *Low normalised spread (normalised spread was calculated by dividing the spread of the confidence intervals by the average of the Pianka index multiplied by 100); these values are in Table S5. Predators are > 4 cm, unless defined as larvae, which are ≤ 4 cm. Thickness of lines represent Pianka index value.

6.1 Tables

Table 1: Number of stomach samples per season used in the analysis, in the Celtic Sea, Irish Sea, and western English Chan nel. Numbers not in parentheses: the combined non-empty stomach samples from the PELTIC Survey and DAPSTOM; numbers in parentheses: non-empty stomach samples from PELTIC only. Stomachs with no season assigned and the number of empty stomachs (from a combination of seasons) were not used in further analysis. (–) No data available for the species and season. Individuals classed as larvae were ≤ 4 cm in length, all other individuals were > 4 cm. *Due to low sample numbers these samples are removed from further analyses. Numbers of empty stomachs by season are in Table S1

	Season					
Species	Spring (MAM)	Summer (JJA)	Autumn (SON)	Winter (DJF)	Unknown Season	Empty Stomachs
Anchovy	13	-	38 (38)	-	-	9
Herring	97	154	66 (0)	360	-	904
Herring larvae	85	-	1* (0)	2968	26	1459
Horse mackerel	98	-	22 (19)	2*	9	385
Horse mackerel larvae	-	6	7 (4)	-	40	18
Mackerel	1949	259	-	15	-	806
Mackerel larvae	-	27	3 (0)	-	85	75
Sardine	7	106	65 (41)	-	-	37
Sardine larvae	-	24	3 (0)	-	15	345
Sprat	61	1*	79 (25)	487	-	559
Sprat larvae	70	2*	11 (0)	77	-	197

Table 2: Trophic levels calculated for each of the 6 species across seasons using Eq. (1). 'Average' (this study) and Fishbase (from Froese & Pauly 2009) values are mean ± SE. (−) No available data.

	Season					
Species	Spring (MAM)	Summer (JJA)	Autumn (SON)	Winter (DJF)	Average	FishBase
Herring	3.01	3.22	3.23	3.30	3.19 (±0.06)	3.4 (±0.1 se)
Herring larvae	-	3.06	-	2.76	2.91 (±0.15)	-
Anchovy	3.51		3.14	-	3.32 (±0.18)	3.2 (±0.36 se)
Sardine	3.11	2.65	2.97	-	2.88 (±0.17)	3.1 (±0.1 se)
Sardine larvae	-	2.50	-	-	2.50 (±)	-
Mackerel	3.01	3.18		2.65	2.94 (±0.16)	3.6 (±0.2 se)
Mackerel larvae	-	2.78	-	-	2.78	-
Sprat	2.94	-	3.12	2.92	2.99 (±0.06)	3.0 (±0.07se)
Sprat larvae	2.32	-	2.54	2.16	2.34 (±0.11)	-
Horse mackerel	3.28	-	3.27	-	3.27 (±0.00)	3.5 (±0.0 se)
Horse mackerel larvae	-	2.88	3.35	-	3.11(±0.23)	-

Table 3: ANOVA of Pianka index of all and individual species and the seasons that were compared. *Significant (p ≤ 0.05)

Species	F value	P value	Seasons
All	2.48	0.0823	Spring/Summer/Autumn/Winter
Anchovy	11.32	0.012*	Spring/Autumn
Herring	1.24	0.349	Spring/Summer/Autumn/Winter
Mackerel	7.10	0.0262*	Spring/Summer/Winter
Horse mackerel	0.41	0.541	Spring/Autumn
Sardine	0.86	0.460	Spring/Summer/Autumn
Sprat	9.12	0.0194*	Spring/Autumn