Diet of dominant demersal fish species in the Baltic Sea: Is flounder stealing benthic food from cod?

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Diet of dominant demersal fish species in the Baltic Sea: is flounder stealing benthic food from cod?

Running page title: Diet of Baltic cod and flounder

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Abstract

Knowledge about ecological interactions between species is of paramount importance in ecology and ecosystem-based fisheries management. To understand species interactions, studies of feeding habits are required. In the Baltic Sea, there is good knowledge of the diet of cod, but little is known about the diet of the second most abundant demersal fish, the flounder. In this study the diets of cod and flounder were for the first time investigated using stomach content data collected simultaneously in 2015-2017 over a large offshore area of the southern Baltic Sea. The diet of flounder was relatively constant between sizes and seasons and dominated by benthos with especially a high proportion in weight of the benthic isopod *Saduria entomon*. The diet of cod differed between seasons and showed an ontogenetic shift with a relative decrease of benthic prey and an increase of fish prey with size. Historic diet data of cod were used to explore cod diet changes over time, revealing a shift from a specialized to generalist feeding mode paralleled by a large relative decline in benthic prey and especially in *S. entomon*. Flounder populations have increased in the past two decades in the study area and therefore we hypothesized that flounder has deprived cod of important benthic resources through competition. This competition could be exacerbated by the low benthic prey productivity due to increased hypoxia, contributing to explain the current poor status of the Eastern Baltic cod. The results of this study point to the importance of including flounder in multispecies end ecosystem models.

1. Introduction

Investigating trophic relationships is central in ecology and ecosystem-based fisheries management (EBF). One of the pillars of an EBFM is the move from a single-species to multi-species fisheries management, in which knowledge about the interactions between species is of para-mount importance (Pikitch et al., 2004). To understand species interactions, studies of feeding habits, and how they vary in time and space, are required.

The Baltic Sea is one of the most extensively studied ecosystems of the world. In the literature, much effort has been done to explore and understand the competitive and predator-prey interactions in the offshore pelagic habitat between cod (*Gadus morhua*), sprat (*Sprattus sprattus*) and herring (*Clupea harengus*), mainly using stomach content analyses (Köster & Möllmann 2000, Neuenfeldt & Beyer 2003, Casini et al. 2004) and modelling (e.g. Tomczak et al. 2012). On the other hand, much less is known about the ecological interactions between fish in the offshore demersal habitat.

Cod and the flounder species complex (*Platichthys flesus* and *Platichthys solemdali*, hereafter simply referred to as flounder) are the dominant demersal fish species in the Baltic Sea (Orio et al. 2017). In this region, cod is the main target species for the fishery and the dominant demersal predator (Casini et al. 2008, Lindegren et al. 2009), while flounder is the most abundant and landed flatfish (Florin & Höglund 2008, Orio et al. 2017).

In the last three decades, the Eastern Baltic cod (hereafter simply referred to as Baltic cod) has experienced a massive drop in biomass and a contraction of its distribution to the southern areas (Orio et al. 2019). Furthermore, its mean body condition has decreased ~ 30% since the early 1990s (Casini et al. 2016). Several hypotheses, not mutually exclusive, have been proposed to explain the worsened state of the Baltic cod, such as increased hypoxia, shortage of benthic food, decreased availability of pelagic fish prey, increased parasite infestation and change in the fisheries selectivity (summarized in ICES 2017a). Flounder has also shown changes in the last four decades, including an overall increase in abundance (ICES 2017b, c, d) and in the extent of its distribution (Orio et al. 2019).

Long-term monitoring data indicate a negative relationship between the abundance and distribution of the Baltic cod and flounder (Orio et al., 2017, 2019). Furthermore, the decline in cod condition started during the increase in flounder stocks. These negative relationships could indicate intense inter-specific interactions between cod and flounder in the Baltic Sea (Orio et al. 2017, 2019). However, while it is known that large cod feed on flounder (ICES 2016), the knowledge about potential competition between these species is very limited. As a first step to understand the competition between cod and flounder for food resources, information on their diet is required.

Several studies have described the diet of the Baltic cod in the offshore areas of the central Baltic Sea (Dziaduch 2011, Pachur & Horbowy 2013, Huwer et al. 2014, Neuenfeldt et al. 2020). ICES (2016) showed a change in the diet of cod throughout its ontogeny, where the mesopelagic mysid *Mysis mixta* is the most important prey for cod under 20 cm and the benthic isopod *Saduria entomon* for cod until 30 cm. For larger cod, the pelagic fish sprat and herring and other fish increase subsequently in importance, although *S. entomon* still constitute an important share of the cod diet throughout its ontogeny. The largest cod, from around 50 cm, show also cannibalism. The diet composition of cod has also changed during the past decades, with a relative decrease of benthic food since the inflow stagnation period in the 1980s (Huwer et al. 2014, ICES 2016, ICES 2017e, Neuenfeldt et al. 2020).

For flounder, the available diet studies in the Baltic Sea focus mostly on juveniles (Pihl 1982, Aarnio et al. 1996, Zloch at al. 2005, Nissling et al. 2007, Florin & Lavados 2010) or are limited to small coastal areas. In these coastal studies, the diet of adult flounder consisted mostly of Bivalves, such as *Mytilus sp*. in the Muuga Bay in the Gulf of Finland (Järv et al. 2011) and *Limecola balthica* in the Gulf of Gdansk (Karlson et al. 2007). Moreover, Polychaeta and Crustacea, like Amphipoda and the isopod *S. entomon*, have been found in the stomachs of adult flounder caught in the Archipelago Sea in the northern Baltic and in the Lithuanian zone (Šiaulys et al. 2012, Borg et al. 2014).

These previous studies on cod and flounder diet have been performed in different areas, at different spatial scales and in different periods, and are therefore hardly comparable. Therefore, the diet similarities/differences between cod and flounder remain almost unknown at the population level in the Baltic Sea. For this purpose, simultaneously collected stomach samples from larger areas are required. In this study, we contribute to fill this knowledge gap using stomach data collected in 2015-2017 in the offshore areas of the Baltic Sea to improve the understanding of the potential interactions between cod and flounder in the central Baltic Sea. The aims of this study are 1) to characterise and compare for the first time the current diet of cod and flounder in the offshore Baltic Sea, 2) to relate our findings to the historical diet of cod using an existing stomach content database and 3) to discuss the results in view of the observed decline in cod condition.

2. Materials and Methods

2.1. Sampling

The diet of flounder and cod was analysed using stomach contents. The stomach samples were collected in the south-western Baltic proper (Figure 1) by the Swedish SLU's Department of Aquatic Resources during the Baltic International Trawl Survey (BITS) in November (quarter 4) of 2015 and 2016 and in February (quarter 1) of 2016 and 2017 (Table 1). In total, 2877 stomachs (1061 flounder and 1816 cod) were sampled in 105 trawl hauls. The depth range of the trawl hauls was between 34 and 122 m (Fig. 2). The samples were collected following the BITS protocol (ICES 2017f). The average proportion (in number caught per hour of trawling) between the two species in the trawl hauls was 23% flounder and 77% cod. The stomach sampling was designed to collect flounder and cod stomachs from the same trawl hauls. Fish total length and weight were measured closely after hauling. Whenever possible, 1 flounder and 1 cod stomachs were collected for each 1-cm of fish length and trawl haul and the stomachs were extracted and frozen as fast as possible. Information about the haul (geographical coordinates and depth) was also recorded.

2.2. Stomach analysis

Signs of regurgitation were detected onboard by remains of prey in the mouth and everted swim bladder, and also by the stage of the gallbladder following the procedure in Huwer et al. (2014). The taxonomic identification of the prey in the stomachs (excluding those regurgitated, i.e. 72 cod stomachs) was performed by the National Marine Fisheries Research Institute in Gdynia, Poland. The prey organisms were identified to the species level or to the lowest taxonomic level possible. The number of each prey in the stomach was counted and the weight of the prey category was noted. Whenever possible, the individual length and weight of each prey item were also measured.

2.3 Data analysis

All analyses were performed with the software R version 3.6.1 (R Core Team, 2017), using the packages ggplot2, dplyr, tidyr, reshape2, ggrepel, cowplot, ggpubr, OpenStreetMap, mapdata and maps.

Abundant prey species in the stomachs and species that are mentioned in literature as important prey for either predators were kept separated in the diet analyses. The other prey were grouped in wider taxonomic groups. Prey that could not be identified down to a taxonomic group chosen were classified as unidentified, for example "unidentified Crustacea". Prey groups that occurred only rarely and made up less than 10% of the relative frequency in weight of the diet content (for any of the length classes considered, see below), were combined and shown as “other Invertebrates” (for both cod and flounder) “other Pisces” (for cod) and “Pisces” (for flounder). Both these groups can include unidentified taxa, like “unidentified Clupeidae”. Consult Supplementary Table S1 to see how the prey were grouped. This grouping procedure was chosen to keep rather low the number of taxa in the analyses and to focus on the prey represented the most in the stomachs of the two respective species. For example, the use of *C. harengus* as single prey species is meaningful for cod, but not for flounder, thus *C. harengus* was pooled in the higher taxa “Pisces” for flounder. It can be supposed that the taxa constituting less than 10% of the stomach content of the respective species have a lower impact on ecology and inter-specific competition, and therefore that the different groupings have a minor influence on the interpretation of the results. Notwithstanding this, the relative importance of all the rare prey groups (i.e. below 10% of the relative frequency in weight of the diet, and therefore not used in the main analyses) in the diet of cod and flounder are shown in the Supplementary Table S1.

Both predators were grouped in length classes (LCs) to analyse the potential ontogenetic changes in the diet. The LCs for cod were chosen according to the ontogenetic diet shift shown in literature (Huwer et al. 2014) and were the following: 6-20 cm, 21-30 cm, 31-40 cm, 41-50 cm and >50 cm. The LCs for flounder were chosen at first according to the literature of flounder diet (Järv et al. 2011) and size at maturity (i.e. 20 cm; ICES 2014a) and then a further split was applied to have a similar resolution to the one of cod. For flounder the LCs were 9-20 cm, 21-30 and >30 cm.

2.4 Diet analysis

To explore diet diversity of the predators, two diversity indices estimated for each LC separately using the lowest taxonomic level of the prey, the species richness and the Shannon index H (Magurran 1988). To explore the feeding strategy and niche width of the predators at the individual level we produced modified Costello plots (Amundsen et al. 1996). This method estimates prey importance and the inter- and intra-individual components of niche width with a graphical approach by standardizing the amount of food in each stomach (Amundsen et al. 1996). To produce the Costello plots, the frequency of occurrence of each prey taxon was plotted against its prey-specific abundance separately for each predator LC. The frequency of occurrence is the percentage of stomachs in which a specific prey occurs (Ni/Nt x 100%) where Ni is the number of stomachs with prey (i) in the stomach, and Nt is the total number of stomachs. Prey specific abundance in weight (Si/Sti x 100%) is the percentage of a specific prey in the stomachs in which this prey occurs where Si is the stomach content in weight composed by prey (i), and Sti is the total stomach content weight from those predators with prey (i) in their stomachs. To compare diet for each predator by LCs, the relative frequency in weight (Si/St x 100%) was calculated, where Si is the stomach content in weight composed by prey (*i*), and *St* is the total stomach content. The latter was calculated separately for each quarter.

2.5. Historical cod stomach content data

Historical cod stomach data collected by trawling from 1963 to 2013 were retrieved from the ICES website (http://www.ices.dk/marine-data/data-portals/Pages/Fish-stomach.aspx) (see also ICES 2016, Neuenfeldt et al. 2019). Only stomachs sampled in the same areas (i.e. the same ICES rectangles) of the new samples from 2015-2017 were selected to allow temporal comparability (Figure S1). In total 4816 historical cod stomach samples were used. The samples were grouped into two time periods, 1963-1974 (1611 stomachs, all in quarter 1) and 2006-2013 (1534 stomachs in quarter 1 and 1671 stomachs in quarter 4), that had enough data in the selected area. The historical cod stomach content data were analysed in the same way as the data 2015-2017, explained above. Also, the same taxonomic grouping as explained above for the samples collected in 2015-2017 was used for the historical cod diet. To the best of our knowledge, no historical stomach data from the same area are available for flounder that could allow a temporal comparison.

3. Results

3.1 Diet of flounder

In the diet of flounder, 19 different prey species were found in the period 2015-2017. The Shannon Index decreased with increasing length (Table 2). The percentage of empty stomach increased from 30% to 45% with increasing size in quarter 1, while in quarter 4 the percentage was around 25% across the LCs (Figure S2).

The Costello plots for flounder (Figure 3) showed that *L. balthica* was the most important prey species in all LCs, with high frequency (around 50%) and prey specific abundance (above 50%). *Mytilus* sp. decreased in frequency, but was stable in prey specific abundance (around 50%), with increasing size. *S. entomon* increased in frequency with increasing size and was the most frequent prey in the stomachs of flounder > 20 cm. Amphipoda and other Invertebrates decreased along both axes with increasing size. Pisces occurred with high prey specific abundances but low frequencies.

Figure 4 shows the diet composition in weight of flounder by length-class and quarter. For LC 9-20 cm *L. balthica* was the dominant prey, for the other LCs *S. entomon* was, together with *L. balthica,* the most important prey. The proportions of Amphipoda and *Mytilus* sp. decreased with increasing size. The composition of Pisces and other invertebrates are shown in the Supplementary material (Figure S3). Overall these patterns were similar in the two quarters, but for LCs > 30 cm the relative frequency of *S. entomon* in the diet was higher (~ 70%) in quarter 1.

3.2 Diet of cod

In total, 37 different prey species were recorded in the diet of cod, 16 in the time period 1963-1974, 33 in the time period from 2006-2013 and 25 in the time period from 2015-2017. The Shannon

Index was the lowest in the time period 1963-1974 for all LCs except for the LC >50 cm. Moreover, the Shannon Index was overall higher for the intermediate LCs in all time periods (Table 2). The percentage of empty cod stomachs was around 20% across the LCs in quarter 1, while in quarter 4 the percentage increased from 10% to 30% with increasing size (Figure S4).

The Costello plots of cod (Figure 5) varied strongly between the time periods and the LCs. In the most recent period (2015-2017) most of the prey were located in the lower left part of the plots, picturing a generalist individual diet. Polychaeta, Cumacea, Mysida and other invertebrates decreased along both axes with increasing size. *S. entomon* increased in frequency up to 25% in the LC 21-30 cm and decreased afterwards in the larger LCs. *C. harengus* and *S. sprattus* increased first to high abundance values in the LC 21-30 cm and then increased in frequency with increasing size. Other Pisces increased in frequency with increasing cod size. Gadiformes, mainly cannibalism on other cod, occurred mostly with high abundance and low frequency in the cod > 30 cm. Similar patterns were also found in the time period 2006-2013, but most of the prey were located higher on the left part of the plots, picturing a relatively more specialized individual diet. In 2006-2013 the decrease of Polychaeta, Cumacea, Mysida and other invertebrates was slower along both axes with increasing cod size and *S. entomon* increased to a frequency of 40% for middle-sized cod. Other Pisces increased less in frequency and decreased in abundance with increasing size. In the time period 1964-1974 most of the prey were located in the upper left part of the plots, representing a highly specialized individual diet. Compared to the later periods, Polychaeta did not decrease with size and was the most important prey in all LCs. *C. harengus* and *S. sprattus* increased much less in frequency, but to high abundances, with cod size and the same occurred for Gadiformes and other Pisces.

Figure 6 shows the diet composition of cod in weight for each LC, quarter and time period (the composition of other Pisces and other invertebrates for each time period is shown in the Supplementary material, Figures S5-7). In the time period 2015-2017 the percentage of fish prey reached over 50% in the LC 21-30 cm in both quarters and increased to nearly 100% at LCs > 30 cm. The most important fish prey were *S. sprattus* and *C. harengus*. Another important prey was Mysida especially for smaller cod in quarter 4. In the time period 2006-2013 the percentage of fish prey reached over 50% in the LC 21-30 cm in quarter 1, and 50% already in the LC 6-20 cm in quarter 4. The percentage of fish prey reached nearly 100% in cod sizes > 40 cm in both quarters. The most important fish prey were *S. sprattus* and *C. harengus*. For smaller cod, other important prey were Polychaeta, Mysida and to some extent *S. entomon*. In the time period 1963-1974 the percentage of fish prey, mainly constituted by *S. sprattus*, exceeded 50% only for cod >50 cm. Polychaeta were overall the most important prey, but their relative importance decreased with cod size from ~50 % in the LC 6-20 cm to ~20% in the cod > 50 cm. Another important prey was *S. entomon* ranging between 20-35% in the cod LCs > 20 cm. A relatively large amount of the diet data from the time period 1963-1974 was collected in one ICES rectangle, and excluding this rectangle in diet analyses led to higher shares of *S. entomon* and lower shares of Polychaeta (Figure S8).

4. Discussion

Our study investigates and compare for the first time the diet of flounder and cod in the Baltic Sea using stomachs collected simultaneously in different seasons and over a large area of the offshore species distribution. The results of our study are in line with the general knowledge of the diet of Baltic cod presented in literature, while the diet of flounder in large areas of the offshore Baltic Sea has been so far elusive. Hereafter, the current diet of flounder and cod from the recent sampling effort (2015-2017) is discussed in relation to the changes in the diet of cod during the past decades from historical diet data.

4.1. Current diet of flounder and cod

Our results show that the diet of flounder is highly constant over the sizes and between quarters, picturing a predator with a small niche width (Järv et al. 2011), which can also be seen in the small number of prey organisms found in the stomach. The bivalve *L. balthica* and the isopod *S. entomon* were the most important prey species in our study, followed by Amphipoda and *Mytilus* sp.. A decrease in the proportion of small invertebrates (Amphipoda) was noticeable with increasing flounder size, while an increase in *S. entomon* occurred. The share of *S. entomon* in flounder stomachs was higher in quarter 1 and this could be explained by a higher availability of *S. entomon* in offshore areas in winter due to the movements of this species into deeper waters (Haahtela 1990). Studies from coastal areas have also shown *L. balthica* and *Mytilus* sp. as important prey species for flounder (Karlson et al. 2007, Järv et al. 2011), while Amphipoda and *S. entomon* occur only rarely in its diet in shallow areas (Šiaulys et al. 2012, Borg et al. 2014). To the best of our knowledge, the diet of flounder in offshore areas of the Baltic Sea have been rarely investigated. Zalachowski et al. (1975) showed that in the beginning of 1970s the diet of flounder in a restricted offshore area of the Gdańsk region consisted mainly of Polychaeta and Crustacea with a share of 15-20% of *S. entomon*. Our study, focusing on a larger offshore area and four decades later, confirmed the importance especially of *S. entomon* in flounder diet suggesting an enduring relevance of this food resource for flounder.

Conversely to flounder, the current diet of cod differed strongly with increasing cod size and also between the quarters. Small cod (6-20 cm) fed mainly on small benthic prey as shown by the high percentages of Polychaeta, Cumacea, Mysidae and *S. entomon* in their diet. Middle sized cod (21-40 cm) are in the transition from a benthos- to a more fish-specific diet and therefore had the widest niche width, which can be seen from the high Shannon Index. Cod >40 cm have completed the ontogenetic shift and predated nearly exclusively on fish, mainly on *S. sprattus* and *C. harengus*. The decrease in importance of benthic prey for cod > 20 cm can be due to several reasons such as lower availability of large benthic prey and/or a higher ability to predate on fish prey. The general ontogenetic switch from invertebrates to fish is in line with the literature on Eastern Baltic cod (Huwer et al. 2014, ICES 2016) and is confirmed also in the western Baltic Sea (Funk 2017). Similar diet switch can also be found in other gadoids, like whiting (*Merlangius merlangus*) in both the Baltic and North Sea (Hislop et al. 1991, Ross et al. 2016). The Costello plots suggest that the ontogenetic shift starts with some small individuals predating on a new prey (shown by high abundances and low frequencies of the new prey), before the whole population changes its diet (shown by increasing frequencies of the new prey). The switch between benthic to fish prey seems to be more gradual and occurred at a larger size in quarter 4; this could be due to the higher availability of pelagic fish for small cod in quarter 1 when pelagic fish new recruits start to be more distributed in the open waters, and/or due to a higher availability of Mysida in quarter 4 (Barz & Hirche, 2009). Cannibalism occurred mainly in quarter 1, which is in accordance with what found by Pachur & Horbowy (2013) in Polish waters, explainable with the different availability of young and small cod at the beginning of the year. In average, 20% of the cod stomachs were empty, conforming to the situation of the past 15 years presented in literature (ICES 2014b). The relative proportion of empty stomachs was increasing with cod size in quarter 4, up to 30% for the larger cod, as also found in Huwer et al. (2014) for the whole central Baltic Sea. The increasing proportion of empty stomachs with cod size can be explained by the switch from continuous invertebrate feeding to intermittent fish feeding, which requires probably more time to hunt and digest.

4.2. Temporal changes in cod diet

The ontogenetic shift in the diet of cod from benthic to fish prey with increasing size was visible in all three time periods investigated in this study. However, this shift was more gradual in the 1963-1974 and became successively more abrupt in the later time periods. In particular, in the time period 1963-1974, benthic prey, mainly represented by Polychaeta and *S. entomon*, still represented a large fraction of diet of the large cod. Conversely, in the time periods 2006-2013 and 2015-2017, fish started to dominate cod diet already at a size of >20 cm and the largest cod fed almost exclusively on fish especially in the latest period. The increased relative importance of fish prey in recent years can be potentially explained by the decline in benthos as consequence of the expansion of hypoxic and anoxic areas (Karlson et al. 2007, Villnäs et al. 2012) and/or increased flounder populations (see below).

Our results also show an ontogenetic shift in the relative importance of *S. sprattus* and C. *harengus* in the diet of cod, with a subsequent increase of the larger *C. harengus* with increasing cod size (see also Huwer et al. 2014, Pachur & Horbowy 2013). However, in the time period 1963-1974, *S. sprattus* was the dominant clupeid in the stomachs independently of cod size. On the contrary, in the time periods 2006-2013 and 2015-2017, *S. sprattus* dominated in the diet of small cod and *C. harengus* in the diet of large cod. This relative shift could be due to the parallel temporal decline in the mean size of herring (ICES 2018), which became therefore more suitable for the size-classes of cod analysed in our study. The relative higher proportion of *C. harengus* in cod diet in the latest two periods could also be due to a decline in the abundance of *S. sprattus* in the main area of cod distribution where the samples were collected (Casini et al. 2016) and an increase in the central Baltic *C. harengus* stock (ICES 2018).

The Costello plots revealed also differences in the feeding strategies of individual cod in the different time periods. In the time period 1963-1974, most of the prey are located in the upper left of the plots reflecting a population where different individuals are specialists on different prey. This specialisation is confirmed by the generally low Shannon Index in this period. On the other hand, in the time period 2015-2017 the prey are located at the lower left of the plots, reflecting a generalized feeding strategy, which could be described as "picking what is available". The time period 2006-2013 reflects an intermediate feeding strategy. In literature, it has been shown that the feeding strategy of fish can change due to changing environmental conditions (Hecht & van der Lingen 1991) and that a declining prey abundance leads to a generalisation of the diet (Horn, 1983). Therefore, the temporal changes from a specialized to a generalist feeding strategy found in our study for individual cod could be linked to the increase in hypoxic and anoxic areas in the Baltic that have caused a massive decrease in macrofaunal biomass on large extensions of the sea bottom (Conley et al. 2009, Villnäs et al. 2012). Another interpretation of these changes could also be a current spatial homogenization of the benthic assemblages, but due to the lack of historical data on the Baltic benthic fauna in the study region, it is not currently possible to test it.

4.3. Potential interspecific competition and implications for cod performance

Our results showed that the proportion of benthos in the diet of cod has decreased drastically over time and presently pelagic fish start to dominate cod diet already at a size of 20 cm, confirming previous investigations (ICES 2016). Currently, the share of benthic prey is extremely low in cod stomachs and is almost null in large cod. Benthic prey are essential for cod (ICES 2017f, Neuenfeldt et al. 2019) and the decline of benthos, especially of *S. entomon*, in the diet have been put forward in literature as explanation for the drop in cod condition and growth occurred in the past two decades (Casini et al. 2016, ICES 2017f, Neuenfeldt et al. 2020). Another important aspect of the diet change of cod over the time periods relates to the nutritional quality of different prey. For instance, the high content of essential fatty acids typical of benthic invertebrates cannot be easily compensated by the availability of other prey, even if the energy content of fish prey is higher (ICES 2017f), and it can represent an important limiting factor in the recent time period leading to lower nutritional condition with negative impact also on reproductive success (Mion et al. 2018).

There is a lack of data to explore the long-term change in the diet of flounder in the offshore areas analysed in our study, and therefore whether the diet of flounder has also changed is unknown, although there is some information (Zalachowski et al. 1975) suggesting that *S. entomon* has been an enduring important prey for flounder over time. Our study shows expecially that flounder > 20 cm currently feed extensively, between 30-70% in weight of its diet, on *S. entomon*. Furthermore, other benthic prey such as Amphipoda occurs in both predators, indicating a potential diet overlap and a potential competitive interaction between these two demersal predators, and especially between flounder and smaller cod. We hypothesize therefore that in recent periods, the increased abundance of the specialized benthos-feeder flounder could have outcompeted cod depriving it of important feeding resources. This could contribute to explain the decline in cod condition and growth (Casini et al. 2016, Orio et al. 2017) in agreement with the increase in flounder abundance in the Baltic Sea (Orio et al. 2017). In literature, it has also been suggested that the low abundance of cod in the southern Baltic Sea at the beginning of the 20th century was due to high competition for benthic prey between cod and flatfishes, and that the increase of cod abundance in the 1930s was facilitated by a decrease of intra-specific competition (Persson 1981). Competition between gadoids and flatfishes have also been shown for example in the Georges Bank (Link et al. 2015). In our study, considering the absolute weights of *S. entomon* found in the stomachs of the two species, and the relative size-specific abundance of the two species in the trawl hauls, and assuming similar digestion rates, we estimated that the flounder population was overall consuming three times as much the amount of *S. entomon* as the cod population for the quarters combined. This support the hypothesis that flounder could currently deprive cod of important benthic food resources. The difference in relative consumption between flounder and cod could be even higher at a larger spatial scale, since the proportion of flounder in the demersal fish community is higher when considering the whole central Baltic Sea where the two species currently co-occur (Orio et al. 2017). At the moment, there is no information on the absolute abundance of flounder in the Baltic Sea, since there is no stock assessment for this species (ICES 2018). Once these data will be available, deeper investigations, using species- and size-specific evacuation rates and performed also in other quarters of the year, should be done to estimate and compare the absolute consumption of the two species throughout the year.

In the Baltic Sea, the competition between cod and flounder for benthic prey could have been likely exacerbated by the increased extension of hypoxic and anoxic areas (Carstensen et al. 2014). The increased deoxygenation, besides having eliminated benthic macrofauna over vast areas and disrupted benthic food-webs (Villnäs et al. 2012), decreased also the suitable habitat for cod and flounder and led to a higher species overlap in the normoxic areas, where the feeding competition may increase (Orio et al. 2019). The area that was sampled in our study is dominated by muddy and sandy sediments where the most characterizing benthic species in biomass is *S. entomon* (Gogina et al. 2016). The currently different diet of cod and flounder, especially in relation to *S. entomon*, could be due to the strictly benthivore nature of flounder that might outcompete cod for this food resource when it becomes scarcer and to competitive exclusion leading to a shift in cod ecological niche. We hypothesize here that the combination of increased flounder abundance and hypoxia could have therefore led in recent years to a shortage of benthic prey, especially *S. entomon*, and explain the strong changes in the diet of cod over time with potential detrimental effects on the observed cod condition (Casini et al. 2016), individual growth (Svedäng & Hornborg 2014), maximum length (Orio et al. 2017) and reproductive success (Mion et al. 2018). Decline of benthos resources is expected to have a larger direct effect on small cod, which are most dependent on benthic prey and are not yet able to feed on pelagic fish, creating a growth bottleneck (Neuenfeldt et al. 2019). The low prey diversification and the diet similarities over the entire size range of flounder, could make flounder also prone to inter-specific competition and food limitation partially explaining the drop in growth (maximum size) when the flounder abundance increased in the central Baltic Sea after the early 1990s (Orio et al., 2017).

In our study we analysed the diet of flounder and cod pooling the data over a vast offshore region. Spatial differences in diet can however occur, due to hydrological and depth preferences of the prey, and therefore we could have missed potential differences in inter-specific interactions at a finer spatial scale. Moreover, the temporal comparison in cod diet, although minimized by comparing the same ICES rectangles, could have been biased by some differences in the sampling depths. However, since the data were all collected by trawling, the shallowest depths that likely different the most in terms of benthos composition across the bathymetry, were under-represented in all the periods. Finally, in our study we used different taxonomic groupings for the diet of flounder and cod, in order to put in evidence their main prey, and therefore we could have missed some information about the prey that are not heavily represented in the stomachs of the respective species.

4.4. Conclusions

In the offshore Baltic Sea, studies on trophic interactions among fish based on diet analyses, have been mainly addressed on the pelagic interplay between cod, sprat and herring and therefore multispecies stock assessment and management advice have been focused on these three species. Conversely, the interplay between fish dwelling in the benthic habitat are poorly known. The results of our study contribute to fill the knowledge gap on the feeding interactions between the two dominant demersal fish species of the Baltic Sea, cod and flounder, which can potentially contribute to explain some of the negative trends observed in cod condition and growth. Our results can provide basic ecological information to build new multispecies and food-web models, or to further improve the existing ones that incorporate competitive processes using diet information. These models are able to simulate stock's development under different climate/hydrological scenarios and fisheries pressure on the different interacting stocks, and our diet data can therefore represent an important support for the implementation of an ecosystem-based fisheries management in the Baltic Sea.

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Table 1: Numbers of analysed stomachs sampled in 2015-2017 by species and quarter.

	Quarter	Total
Flounder	1	618
	4	443
Cod	1	1025
	4	791

Table 2: Shannon Index for flounder and cod for each time period.

Time period	Flounder			Cod				
	LC9-20	LC21-30	LC>30	LC6-20	LC21-30	LC31-40	LC41-50	LC>50
1963-1974				1.18	1.51	1.58	1.49	1.7
2006-2013				1.72	2.08	2.19	2.17	1.97
2015-2017	2.04	2.02	1.38	1.84	2.14	2.11	1.55	1.27

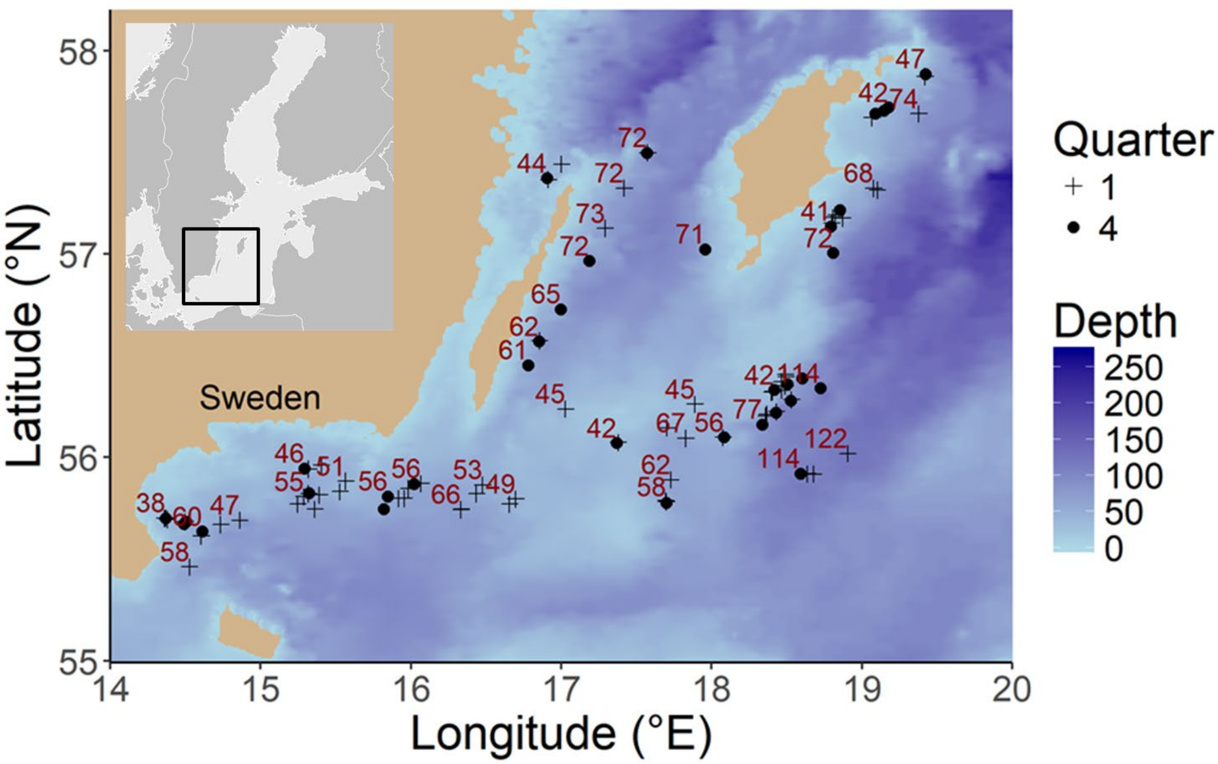

Figure 1: Location of the stomach sampling stations in 2015-2017. The map shows the bathymetry (blue shade) and the depth of the trawl hauls (red numbers) where stomachs were sampled. Crosses and dots represent the quarter 1 and 4, respectively.

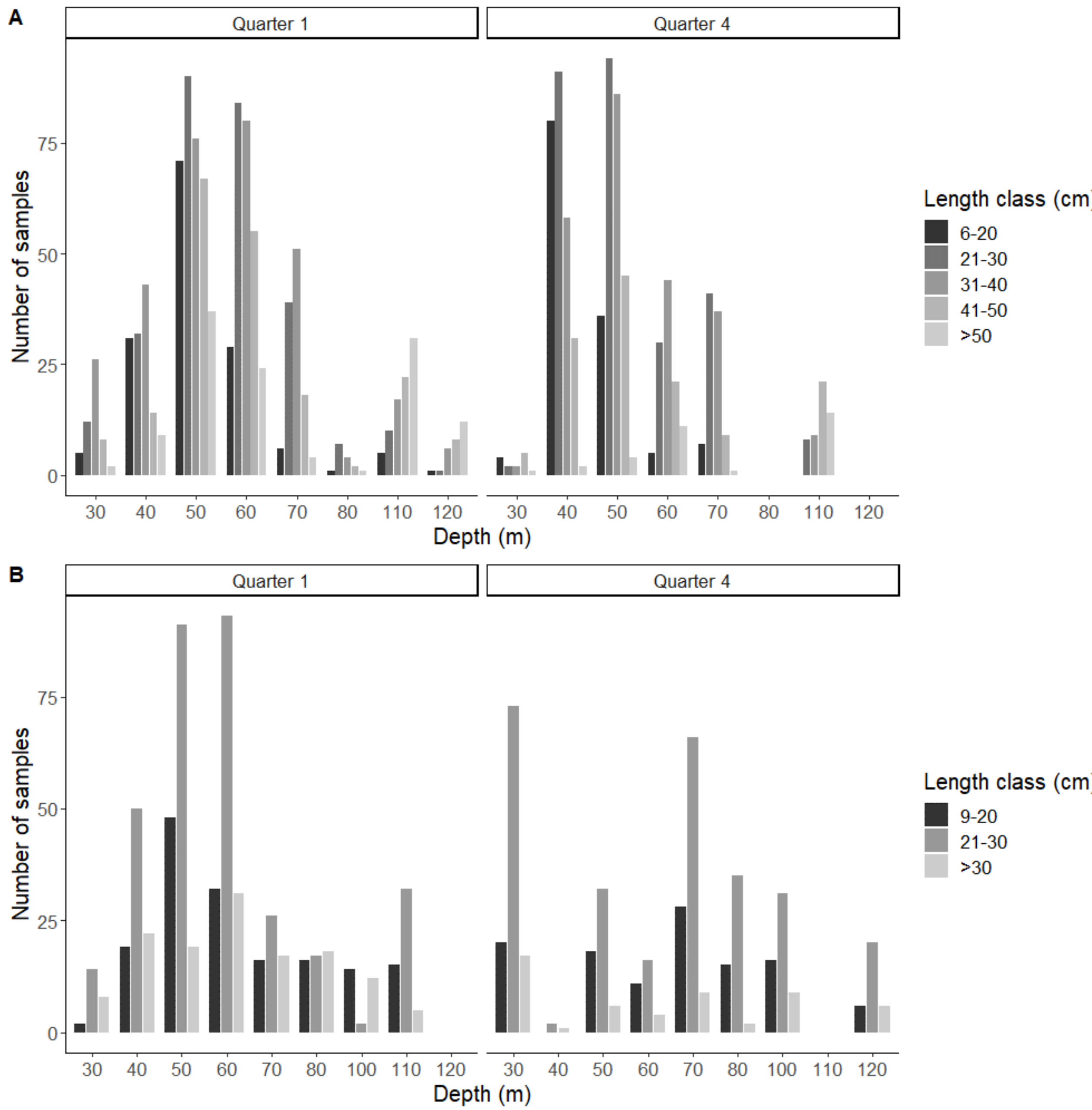

Figure 2: Depth distribution of the stomach samples (panel A for cod, panel B for flounder) collected in 2015-2017 shown as number of samples for every 10m, by length class and quarter.

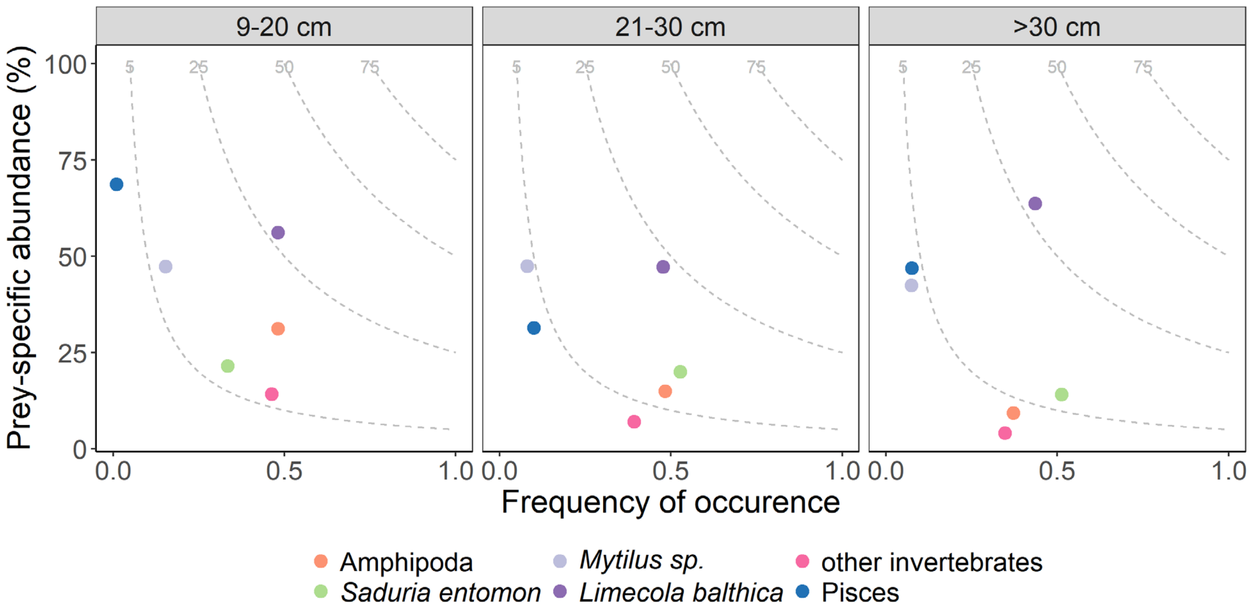

Figure 3: Costello plots of flounder caught in the time period 2015-2017 by length class. Prey-specific abundance (%) is plotted against the frequency of occurrence in the stomach content. Any combination of prey-specific abundance and frequency of occurrence equals a certain prey abundance (Amundsen et al. 1996); different values of prey abundance are represented by isopleths (dashed curves) on the graph (i.e. 5, 25, 50 and 75%). Prey taxa are identified by colour.

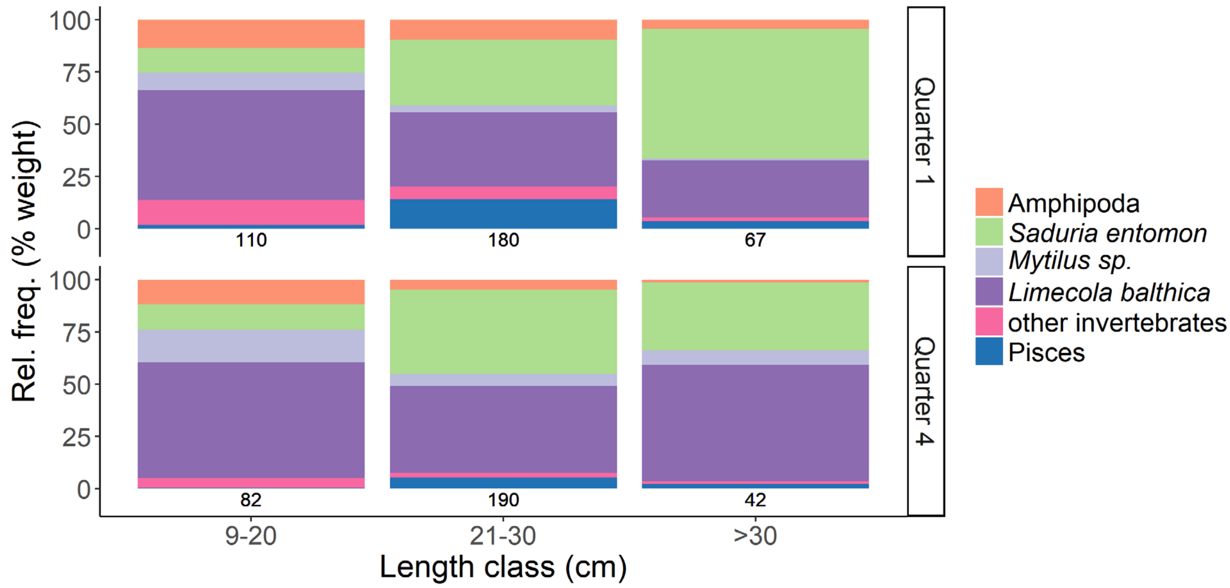

Figure 4: Diet composition of flounder as relative frequency in weight in the time period 2015-2017 by quarter and length class. The numbers under the bars show the number of samples in each length class.

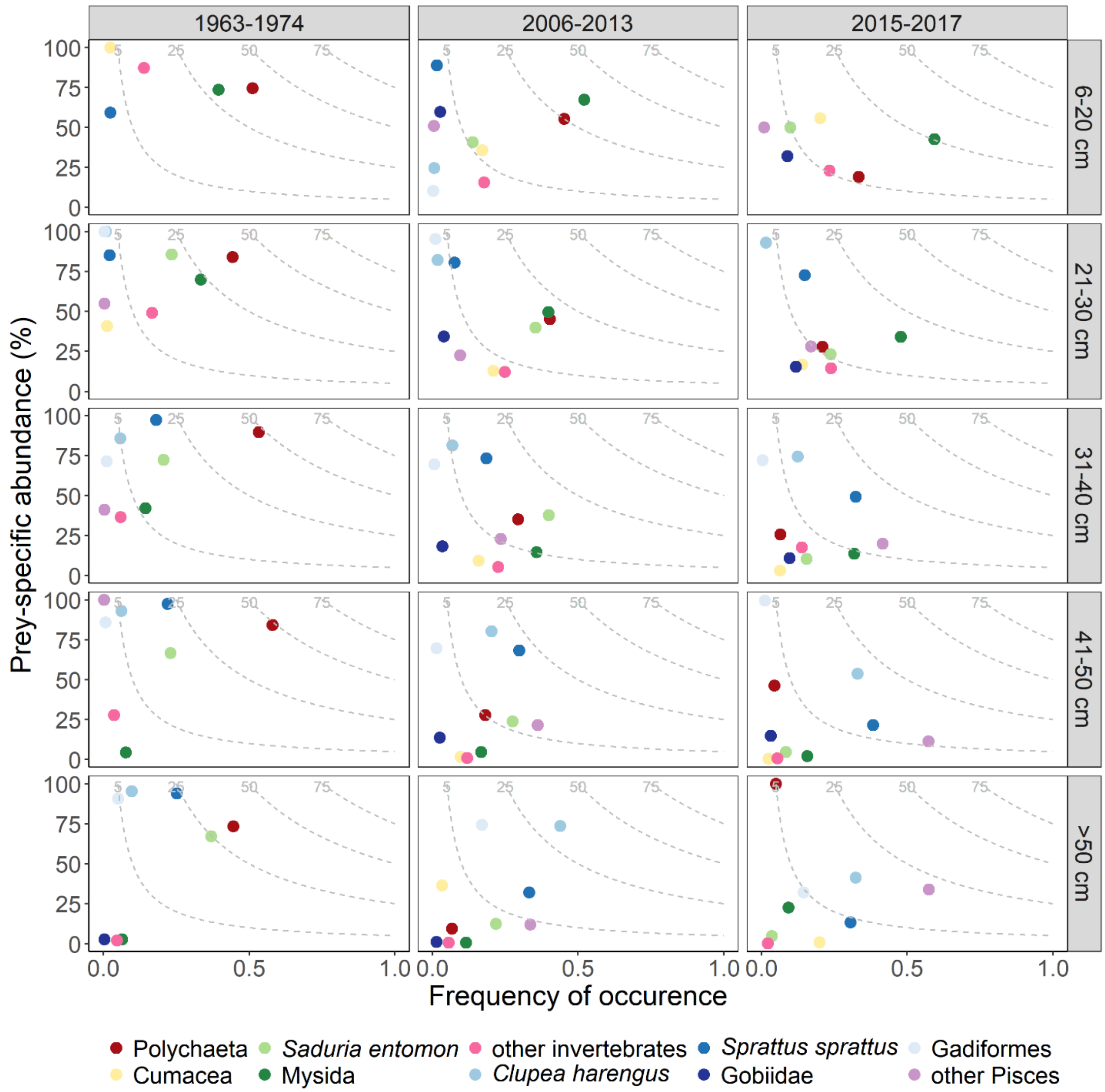

Figure 5: Costello plots of cod by length class and time period. Prey-specific abundance (%) is plotted against the frequency of occurrence in the stomach content. Any combination *of prey-specific abundance and frequency of occurrence equals a certain prey abundance* (Amundsen et al. 1996); *different values of prey abundance* are *represented by isopleths (*dashed curves) *on the graph (*i.e. 5, 25, 50 and 75%). *Prey taxa are identified by colour.*

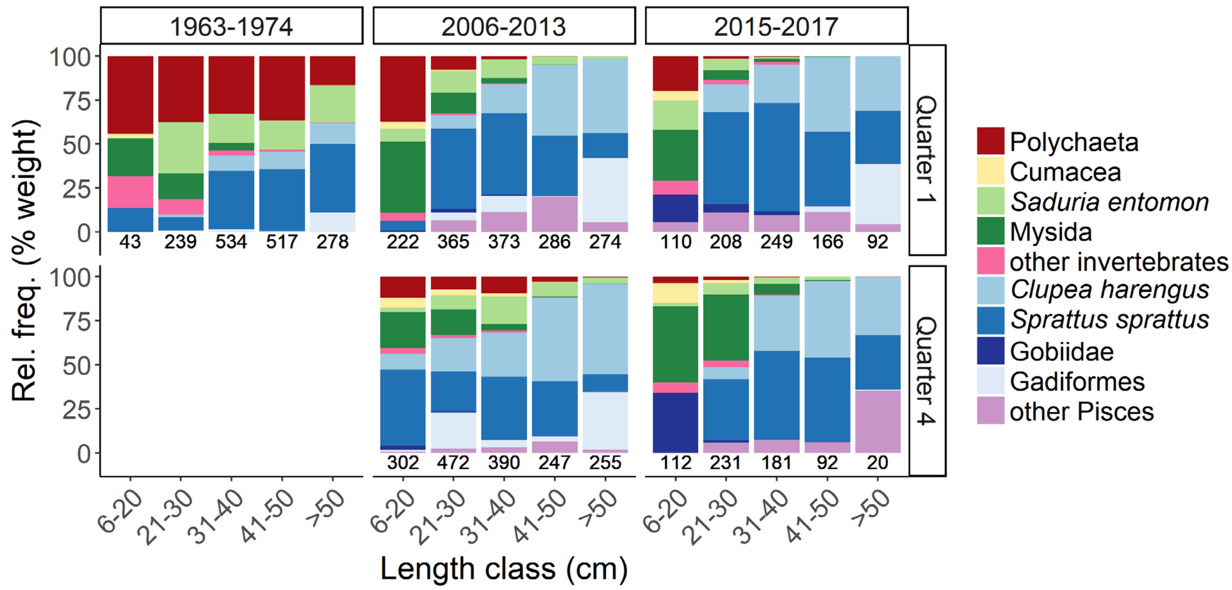

Figure 6: Diet composition of cod as relative frequency in weight by quarter and length class. The numbers under the bars show the number of samples in each length class.