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Diet overlap between Cod (*Gadus morhua*) and European Flounder (*Platichthys flesus*) in the central Baltic Sea

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Master´s thesis • 30 hec
Lysekil 2018

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Credits:	30 hec
Level:	Second cycle, A2E
Course title:	Independent project in Biology
Course code:	EX0565

Place of publication:	Lysekil
Year of publication:	2018
Online publication:	https://stud.epsilon.slu.se

Keywords:	diet overlap, diet, cod, Gadus morhua, flounder, Platichthys flesus, Baltic Sea

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Abstract

The Baltic Sea is a frontrunner in ecosystem analysis and assessment, which have been used also in multispecies fisheries management advice. In the Baltic Sea, the multispecies assessment and management advice have been focused on the pelagic interactions between cod (*Gadus morhua*), sprat (*Sprattus sprattus*) and herring (*Clupea harengus*), by virtue of their well-known ecology. However, the fish interactions occurring in the benthic habitat are largely unknown. This study investigates, for the first time, the feeding interactions between the most important demersal fish species, cod and flounder (Platichthys flesus), in three areas of the eastern Baltic Sea. In this study I use stomach data from 2015 and 2016, collected in the ICES subdivisions 25 – 28 by the Swedish University of Agricultural Sciences, Department of Aquatic Resources. The diet of cod differs between the areas but, overall, shows an ontogenetic shift with a decrease of benthic prey and an increase of fish preys with size. In the coastal area the amount of benthic prey is always > 50% irrespective of predator size, while in the offshore areas the amount of fish prey increase > 50% with increasing cod size. Conversely, the diet of flounder is relatively constant between sizes and areas. Cluster analyses revealed similarity between the diet of flounder and small-medium size cod in the offshore areas. A significant diet overlap was found between cod < 30 cm and flounder > 20 cm in the offshore area in SD 25, which is mainly driven by similar benthic prey, especially *Saduria entomon*, in the diet of both predators. These results point to a food competition between cod and flounder, likely augmented by recent increased abundance of Baltic flounder stocks. This competition could decrease the availability of benthic prey for cod, which, in turn, can lead to low condition factor, a reduction of cod growth and ultimately accentuate the negative effects of hypoxia on cod. Because of all of these reasons, cod and flounder competition could be another factor explaining the current bad status of the Eastern Baltic Cod stock.

Keywords: diet overlap, diet, cod, *Gadus morhua*, flounder, *Platichthys flesus*, Baltic Sea

Popular Summary

Ecosystem-based fisheries management (EBFM) is a holistic approach for fisheries management, which aims at sustaining a healthy nature and satisfying societal and human needs for food and economic benefits. For an EBFM it is important to manage different species at the same time. This requires knowledge about how these species interact. One of the most important interactions, is the one for food. In the Baltic Sea, there is a good knowledge about the feeding habits of the species that occur in the open water (pelagic zone), i.e. sprat, herring and cod. The feeding interactions that happens between species occurring near to the bottom (demersal) are largely unknown. This study investigates the feeding habits of cod and flounder, the most important demersal fish species in the central and eastern Baltic Sea, and the potential similarities and dissimilarities in their diet.

The diet of cod changes with size (ontogenetic shift). The proportion of small invertebrate preys (crustaceans, worms etc.) decreases, while the proportion of fish preys increases. Closer to the coast in shallower waters, the proportions of invertebrates are higher than more offshore in deeper waters where fish preys are more important. The diet of flounder consists of less species and does not change that much with size and between different areas. The diet of flounder consists mainly of Bivalves and Saduria (a crustacean). The diet was similar between small-medium size cod (< 30 cm) and flounder especially in the Bornholm basin due to high proportions of invertebrates in their diets in this area.

These results point to a food competition between cod and flounder in the central Baltic Sea, which can decrease the availability of invertebrates and can therefore explain the current bad state of cod in the central and eastern Baltic Sea. This study contributes to fill the knowledge gap on fish interactions in the demersal habitat and constitute an important step towards the implementation of an EBFM.

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1 Introduction

Ecosystem-based fisheries management (EBFM) is a holistic approach for fisheries management, which aims at sustaining a healthy ecosystem and satisfying societal and human needs for food and economic benefits (Zhou et al., 2010). 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 paramount importance (Pikitch et al., 2004). To understand species interactions, studies of feeding habits, and how they vary in space, are required since they drive the spatial distribution and coexistence of fish populations (Schoener, 1974; Ross, 1986).

The Baltic Sea is a frontrunner in ecosystem analysis and assessment, which have been used also in management advice. This is due to the low complexity of the Baltic ecosystem, characterised by a small amount of species and a relatively distinct water body. However, some important gaps in the understanding of ecosystem functioning still exist. In the Baltic Sea, the multispecies assessment and management advice have been focused on the pelagic interactions between cod (Gadus morhua), sprat (Sprattus sprattus) and herring (Clupea harengus), by virtue of their well-known ecology. Conversely, the fish interactions occurring in the benthic habitat are largely unknown.

Cod is the dominant demersal predator in the Baltic Sea (Florin et al., 2013), is the most important commercial species over all European waters and the main target species in the Baltic Sea (Casini et al., 2008; Lindegren et al., 2009). Cod in the Baltic is managed as two separated stocks: the Western Baltic Cod Stock (WBC) in ICES subdivisions (SDs Figure 1) 22-24 and the Eastern Baltic Cod Stock (EBC) in SDs 25-32 (ICES, 2015a). Cod is, especially in the eastern Baltic Sea, on the limits of its geographical distribution and therefore more vulnerable to disturbances (Nissling, Kryvi and Vallin, 1994). In the last decades the EBC experienced several changes in distribution, abundance and fishing mortality. Furthermore, the mean condition of cod decreased since the early 1990´s (ICES, 2014; Casini et al., 2016) in particular for large fish in the deep basins. In the recent years, up to 20% of cod has shown low body condition (Fulton condition k < 0.8) (ICES, 2015a). There are also indications that the cod growth rate has declined during the past two decades (Svedäng and Hornborg, 2014) even though growth estimations are currently affected by very uncertain age determination (Hüssy et al., 2016). Several hypotheses, which could also be linked to each other, have been proposed to explain the bad state of the EBC: 1) increasing hypoxia, 2) decreasing availability of fish prey, 3) shortage of benthic food, 4) increasing infections of parasites and 5) change in selectivity of fisheries (ICES, 2015a).

Flounder (Platichthys flesus) in the eastern Baltic Sea is another important demersal predator (Florin et al., 2013), is the most landed flatfish in the Baltic Sea (Florin and Höglund, 2008; Orio et al., 2017b) and is managed as four different stocks (SDs 22-23, 24-25, 26+28 and 27+29-32). Two of the three flounder stocks in the eastern Baltic Sea (SDs 24-25 and SDs 27+29-32 stocks) show an overall increase in abundance in the last 5 years (ICES, 2017b, 2017a, 2017c). However, at the same time, a decrease in maximum length was detected by Orio et al. (2017b) for the flounder stocks in SDs 24-25 and SDs 26+28.

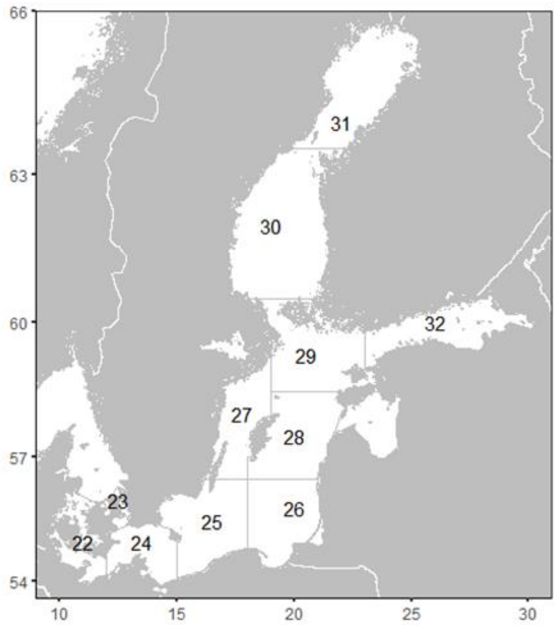

Figure 1: Subdivisions. The map shows the Baltic Sea and the *ICES Subdivisions*

Both cod and flounder are key species for the ecosystem (Orio et al., 2017b), but the knowledge about the ecological interactions between the two species is very limited. Long-term data indicate a negative relationship between the population dynamics of the EBC and flounder stocks. For example, in the eastern Baltic Sea the flounder stock in SD 26+28 decreased during the cod outburst in the late 1970`s and only recovered when the EBC collapsed (Orio et al., 2017b). Also, the decline in cod condition started during the increase in flounder stocks. These negative relationships between the two species could indicate intense ecological interactions, such as cod predation on flounder and competition for benthic prey (Orio et al., 2017b). To understand the competition between cod and flounder for food resources, information on their diet is required.

Several studies have described the diet of cod in the eastern (Dziaduch, 2011; Pachur and Horbowy, 2013; Huwer et al., 2014) and in the western Baltic Sea (Funk, 2017). Funk (2017) shows that shallow waters are important feeding grounds for cod in the western Baltic Sea and are responsible for the supply of benthic prey, especially the major prey species, the common shore crab (Carcinus maenas). Fish prey, mainly sprat and herring, becomes more important in the diet of bigger cod and in deeper waters. The diet studies targeting the EBC are more focused on the deeper areas. ICES (2015b) show a change in the diet of cod throughout its ontogeny, where Mysis mixta is the most important prey for cod under 20 cm and Saduria entomon for cod until 30 cm. For larger cod, sprat increase in importance until 50 cm and afterwards herring becomes the dominant prey. The largest cod show also cannibalism. The diet of cod has also changed, with a decrease of benthic food, since the inflow stagnation period in the 1980`s. While big cod can compensate this shortage of benthic food with an increase of fish in their diet, small cod undergo a decrease in consumption rates, which may lead to growth limitation and an increase of starvation-related mortality (ICES, 2018).

For flounder, the available diet studies in the Baltic Sea focus mostly on juveniles (Pihl, 1982; Weatherley, 1989; Aarnio, Bonsdorff and Rosenback, 1996; Nissling, Jacobsson and Hallberg, 2007; Florin and Lavados, 2010) or are limited to small coastal areas like the Muuga Bay in the Gulf of Finland (Järv et al., 2011) or a small part of the Gulf of Gdansk (Karlson et al., 2007). In these very coastal areas, the diet of adult flounder consists mostly of Bivalves. In the Muuga Bay the diet can include up to 90 % of Mytilus sp. (Järv et al., 2011), while in the Gulf of Gdansk the diet can include up to 50% of Limecola balthica (Karlson et al., 2007). Next to the Bivalves, Polychaeta and Crustacea, like Amphipoda and Saduria entomon, have been found in the stomachs of adult flounder caught in an archipelago in the northern Baltic and in the Lithuanian zone (Šiaulys et al., 2012; Borg, Westerbom and Lehtonen, 2014).

Due to the local scale and scattered locations of the previos studies on flounder diet in the Baltic, the feeding overlap of cod and flounder remains almost unknown at the population level. For this purpose, simultaneously collected stomach samples from large areas are required. In this study, I use stomach data from 2015 and 2016, collected by the Swedish University of Agricultural Sciences, Department of Aquatic Resources, to improve an understanding of the interactions between the most important demersal fish, cod and flounder, in the eastern Baltic Sea. The aims of this study are 1) to characterise the diet of both cod and flounder, 2) to investigate for potential similarities in their diet and 3) to quantify the diet overlap between these two species.

2 Materials and Methods

2.1 Stomach data

The diet of cod and flounder was analysed using stomach contents. The stomach samples were collected from the ICES subdivisions 25, 26, 27 and 28 in the central Baltic Sea (Figure 2) in 2015 and 2016. In total 2246 stomachs (1436 cod and 810 flounder) were sampled.

The majority of the samples were collected during the Baltic International Trawl Survey (BITS) in the fourth quarter (Q4) of 2015 and in quarter 1 and 4 of 2016 (Table 1). The depth range of the trawl hauls was between 34 m and 122 m. The samples were taken following the BITS protocol (ICES, 2017d). After the catch was sorted into species, length, wet weight, sex, maturity stage, liver weight and gutted weight were measured and documented. If possible, 5 cod and flounder stomachs were collected for each cm per SD. The stomachs were frozen as fast as possible. Also, information about the haul, for example, the exact location, date, depth etc. were collected.

A smaller part of the samples (Table 1) were collected during the BONUS project INSPIRE (www.bonus-inspire.org) gillnet Survey in quarter 2 of 2015 in SD 25. The depth range of the gillnet survey was between 8 and 77 m. The fish were caught with an Extended Nordic coastal multi-mesh Gillnet, the net is 1.8 m deep and 45 m long with 5 m long panels of different mesh sizes stringed together. The mesh sizes are: 10, 12, 15, 19, 24, 30, 38, 48 and 60 mm knot to knot. One 5 m and one 50 m extra panel with the mesh sizes 6.25 and 75 mm, respectively, were added to increase the catchability of small and large fish (Orio *et al.*, 2017a). The net was set out at dusk and lifted at dawn the next day following the standard procedure for gillnet monitoring (Bergström *et al.*, 2012). The fish was sorted and processed as for the BITS Survey and the stomachs were stored in ice until the ship reached the harbor and the stomach samples could be frozen. Also, the haul information was collected.

Alongside with the gillnet samples of the INSPIRE project, stomachs were also collected during commercial gillnet fisheries trips (Table 1) in quarter 4 of 2015 in SD 25. The depth range was between 1.5 and 19 m. The samples were collected in the same way described for the INSPIRE project.

Table 1: Numbers of analysed predator stomachs per Survey, Quarter and Year. In brackets are the numbers of fish with regurgitated stomach.

Species	Survey	Q2 2015	Q4 2015	Q1 2016	Q4 2016
COD	BITS	-	383 (14)	413 (11)	414 (6)
COD	INSPIRE	42 (0)	-	-	-
COD	commercial	-	135	-	-
FLE	BITS	-	188 (0)	253 (0)	254 (0)
FLE	INSPIRE	6 (0)	-	-	-
FLE	commercial	-	57 (0)	-	-

The sampling was designed in order to collect cod and flounder stomachs from the same positions at the same time. To see the exact locations of each haul, see Figure 2.

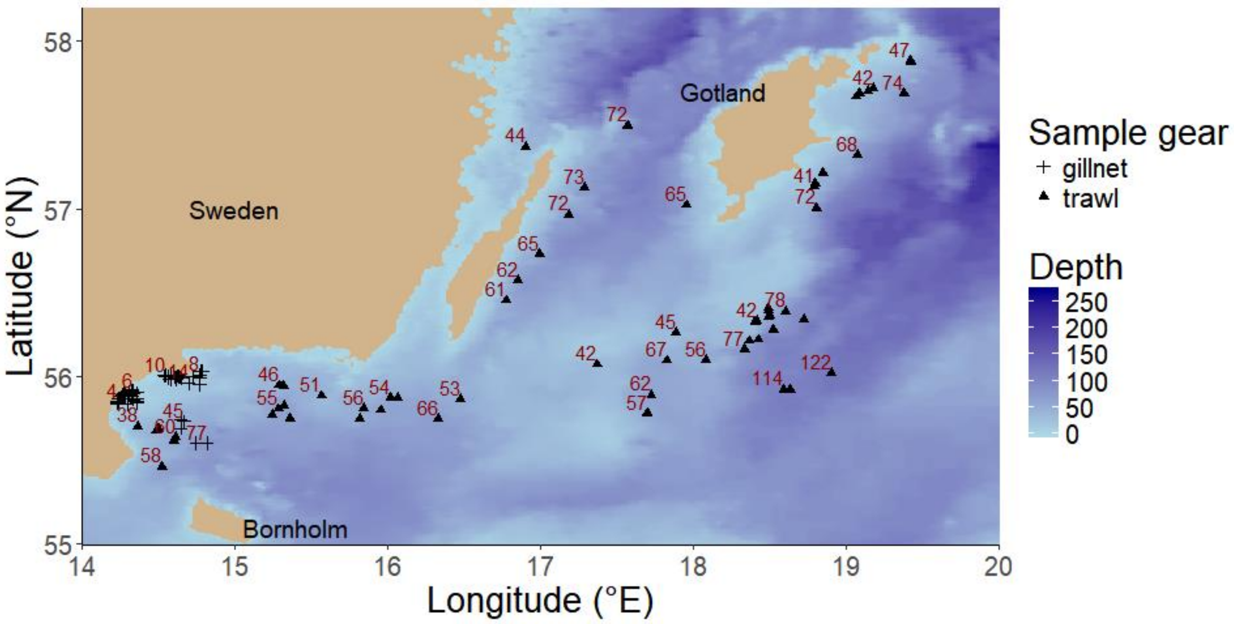

Figure 2: Sampling locations. The map shows the bathymetry (blue shade) and the depth of each haul (white numbers).

2.2 Stomach analysis

Signs of regurgitation were detected onboard by remains of prey in the mouth and everted swim bladder, but also due to stage of the gallbladder. Gallbladder stages are shown in Table 2. When the fish was associated with gallbladder stage 1 or 2 (indicating feeding state) and have an empty stomach, the fish was marked as regurgitated. All fish that show signs of regurgitation were excluded from the data analysis (Table 2).

Table 2: Explanation of the gallbladder stages and their meaning for the stomach state

Stage	Gallbladder	Bile color	Hind gut	State
1	Shrunken, empty or with small amount of bile	Pale	Contains large amounts of bile and digested food material	Feeding
2	Elongate	Pale green to light emerald green	Contains some bile and digested food particles	Feeding
3	Elongate	Dark green	Empty or contains some food particles	Empty
4	Round	Dark blue	Empty	Empty

The frozen stomachs (excluding those regurgitated) were sent to the Sea Fisheries Institute of Gdynia, Poland. There, the stomachs were unfrozen and the contents were analysed. 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. When possible, the length of each prey item was measured and then the prey item was weighed individually.

Each stomach was categorized according to its fullness (1 = full, 0 = empty). Full stomachs were also categorized according to their content (1 = only skeletal remains, 0 = others).

Each prey was also categorized into three digestion stages: 0 = undigested or only minimal signs of digestion; 1 = partly digested and 2 = greatly digested, only hard parts like scales or shells left.

2.3 Data analysis

All analyses were performed with the statistic software R (R Core Team, 2017), including the following packages: ggplot2 (Wickham, Chang and RStudio, 2009), dplyr (Wickham *et al.*, 2017), tidyr (Wickham, 2017), reshape2 (Wickham, 2007), ggrepel (Slowikowski, 2017), cowplot (Wilke, 2017), ggpubr (Kassambara, 2017), OpenStreetMap (Fellows, 2016), mapdata (Becker, Wilks and Brownrigg, 2016) and maps (Becker *et al.*, 2017).

In order to compare the diet of cod and flounder between coastal and offshore areas, the samples were grouped into two depth strata, 0-30 m and >30 m. The strata were chosen to separate also the sample gears (gillnet and trawl), except for the gillnet stations at 50 and 70 m (Figure 3). The offshore samples were divided in SD 25 and SDs 26-28. The decision to pool the SDs 26-28 together was based on the similar hydrographic conditions, especially salinity and oxygen, of the locations where the samples were collected (samples bordering the western Gotland basin and west of the island of Gotland). Three areas were therefore used: SD 25 coastal (gillnet samples), SD 25 offshore (gillnet and trawl samples) and SDs 26-28 (trawl samples). No obvious differences were noted between stomach contents sampled in Q4 2015 and Q4 2016 (BITS survey), and therefore these data were pooled together.

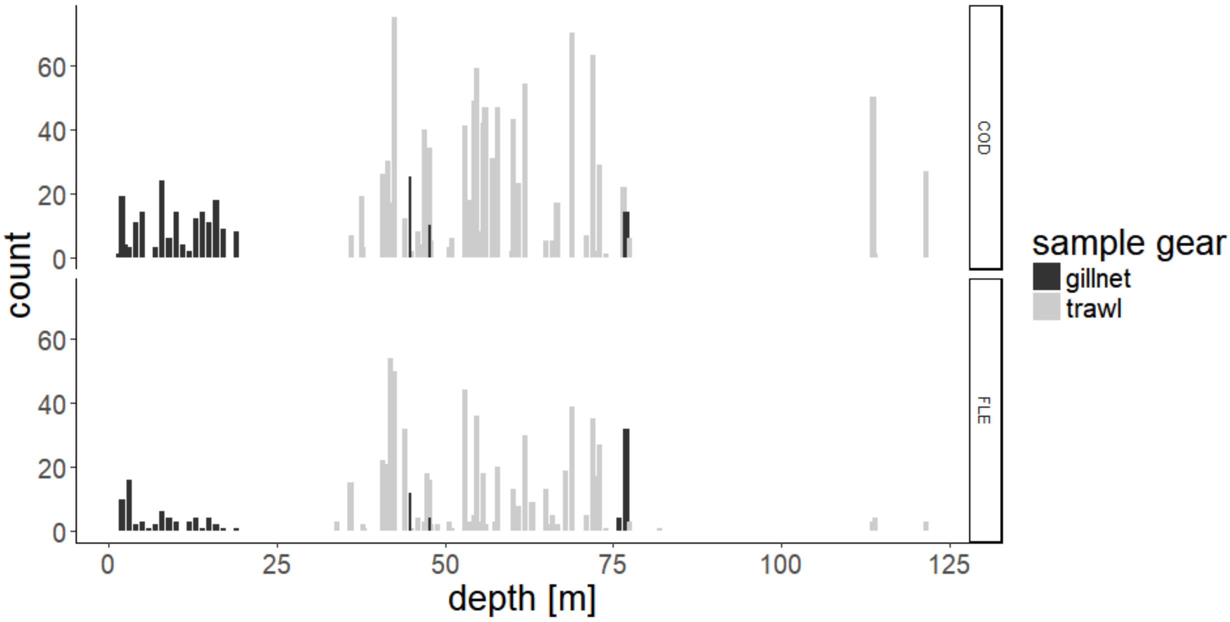

Figure 3: Depth distribution of the stomach samples. Gillnet samples from INSPIRE and Commercial samples are shown in black, trawl samples from BITS are shown in grey.

Both predators were grouped in length classes (Lcs) to find out the changes in the diet with increasing size and to be able to evaluate the diet overlap between cod and flounder according to the predator size. The Lcs for cod were chosen according to the ontogenetic diet shift shown in literature (Huwer *et al.*, 2014). For flounder the same Lcs were chosen. Due to a small amount of anaylsed fish under 10 cm and over 30 cm (for flounder) or 50 cm (for cod), Lcs with a bigger size range were constructed. Pre-analysis showed no relevant diet differences within this bigger Lcs. Cod under the size of settlement in the eastern Baltic Sea (6 cm) (Hüssy *et al.*, 2016), were excluded from the data analysis. For cod the Lcs are the following: 6-20 cm, 21-30 cm, 31-40 cm, 41-50 cm and >50 cm. For flounder the Lcs are the following: 8-20 cm, 21-30 and >30 cm.

2.4 Diet analysis

Abundant prey species in the stomachs and species that are mentioned in literature as important prey for one predator were kept separated in the diet analyses. For example *Sprattus sprattus, Saduria entomon* or *Mytilus sp.* The other preys were grouped in wider taxonomic groups. Fish preys were pooled at the family level, except for Gadidea, Lotidea, Pleuronectidea, Scophthalmidae. These families were pooled together at the order level Gadiformes and Pleuronectiformes, to have only occasional appearing families Lotidea and Scophthalmidae within the groups. Most of the Crustacean were grouped according to their order, for example Amphipoda and Cumacea, to pool the different families together. Exceptions are Cirripedia and Copepoda, both grouped at class level. Also grouped at class levels are Polychaeta, Priapulida and Gastropoda. Prey that could not be identified down to the taxonomic group chosen are classified as unidentified, for example "unidentified Crustacea". Consult Table 3 to see how every single prey has been grouped.
The relative frequency in number and weight was calculated for each prey group per area, quarter and Lcs with the following formula:

$$rel.freq_n[i] = (numberofprey[i, j, q, lc, a] \times 100) \div totalnumberofprey[j, q, lc, a]$$

$$rel.freq_w[i] = (weightofprey[i, j, q, lc, a] \times 100) \div totalweightofprey[j, q, lc, a]$$

were *i* is the prey, *j* is the predator, *q* is the quarter, *lc* the predator Lc and *a* the area.

To illustrate and compare the mean diet of each predator between the areas, quarters and different sizes, prey groups, which occur only rarely, are shown as “other invertebrates” and “other Pisces” (Table A 1).

2.5 Diet overlap

To find out the similarities and overlap between the diet of cod and flounder for each Lc and quarter, the relative frequencies in numbers for each prey group were used. The analyses were done for each area separately. Only mean stomach contents based on 5 or more analysed predators are considered. Hierarchical cluster analysis

was performed for each sampled area, to identify groups of objects with similar diets. The diet overlap, expressed with the Morisita index, was estimated over all the combinations of length-classes and quarters, separately for each area.
A distance matrix was calculated with the vegan R package (Oksanen *et al.*, 2018) based on the Bray-Curtis dissimilarity index (B) (Bray and Curtis, 1957).

$$B = \frac{\sum|X[i] - Y[i]|}{\sum(X[i] + Y[i])}$$

X[i] and Y[i] are the proportions of the prey item i from predator X and Y respectively. I chose the Bray-Curtis index, because it is known to outperform most other similarity measures when two objects have no prey in common (Clarke, Somerfield and Chapman, 2006). Additionally, the index has a minimum (0) and a maximum (1) value, which are only achieved when the objects are totally identical (0) or totally dissimilar (1). Furthermore, the Bray-Curtis index does not measure a lower dissimilarity if two objects do not contain a certain species. Clarke, Somerfield and Chapman (2006) wrote, that "species can be absent for many different reasons in different samples, and it is biologically unwise to infer that two samples are similar because neither contains a particular species". After calculating the distance matrix, the cluster tendency was visually checked with a principal component analysis (PCA) (Kassambara, 2015) which suggested that there were meaningful clusters one the basies of differences in the diet in each sampled area. Hierarchical cluster analysis do not give the number of clusters automaticlly, therefore the next step was to calculate the optimal number of clusters. The optimal number of clusters was determined by calculating 24 different indices with the NbClust package (Charrad *et al.*, 2014) in R. Following the majority rule (Clarke, Somerfield and Chapman, 2006) the optimal number of cluster was the number, which was given from most of the indices. The hierarchical cluster analysis was performed with the R base function *hclust* and visualized with the factoextra R package (Kassambara, 2017). Different methods to link the objects in clusters, for example “complete linkage” or “ward.D2”, were checked. I chose the “complete linkage” method to create the dendrogram, because it creates compact clusters and occurs most frequently among all tested linking methods with the highest cophenetic correlation between the dendrogram and the distance matrix. The cophenetic correlation measures, how much the created dendrogram reflects the initial distance matrix (Kassambara, 2015).

A modified Morisita index (M) was used, which is specially constructed to calculate the diet overlap and is described as (Horn, 1966):

$$M = \frac{2 * \sum X[i] * Y[i]}{(\lambda[X] + \lambda[Y]) * (\sum X[i] * \sum Y[i])}$$

$$\lambda[X] = \frac{\sum X[i] * (X[i] - 1)}{\sum X[i] * \sum X[i] - 1};$$

$$\lambda[Y] = \frac{\sum Y[i] * (Y[i] - 1)}{\sum Y[i] * \sum Y[i] - 1}$$

where X[i] and Y[i] are the proportions of the prey item i from predator X and Y respectively. λ is the Simpson Index of diversity. Krebs (1999) recommends using the Morisita index to calculate the diet overlap over other indices, because it minimizes bias. The Morisita index varies between 0 and 1, a value of 0 means a totally different stomach content and a value of 1 an identical stomach content. The overlap is suggested to be ecologically significant when the value is greater or equal to 0.6 (Zaret and Rand, 1971).

3 Results

3.1 Digestion stage

In all areas the digestion stage 1, which indicates partial digestion of the prey, is the most common digestion stage with up to 80% records. Digestion stage 2 appears more frequently in cod caught in the offshore areas and in flounder caught in the coastal area. Stage 0 occurs rarely (Figure 4).

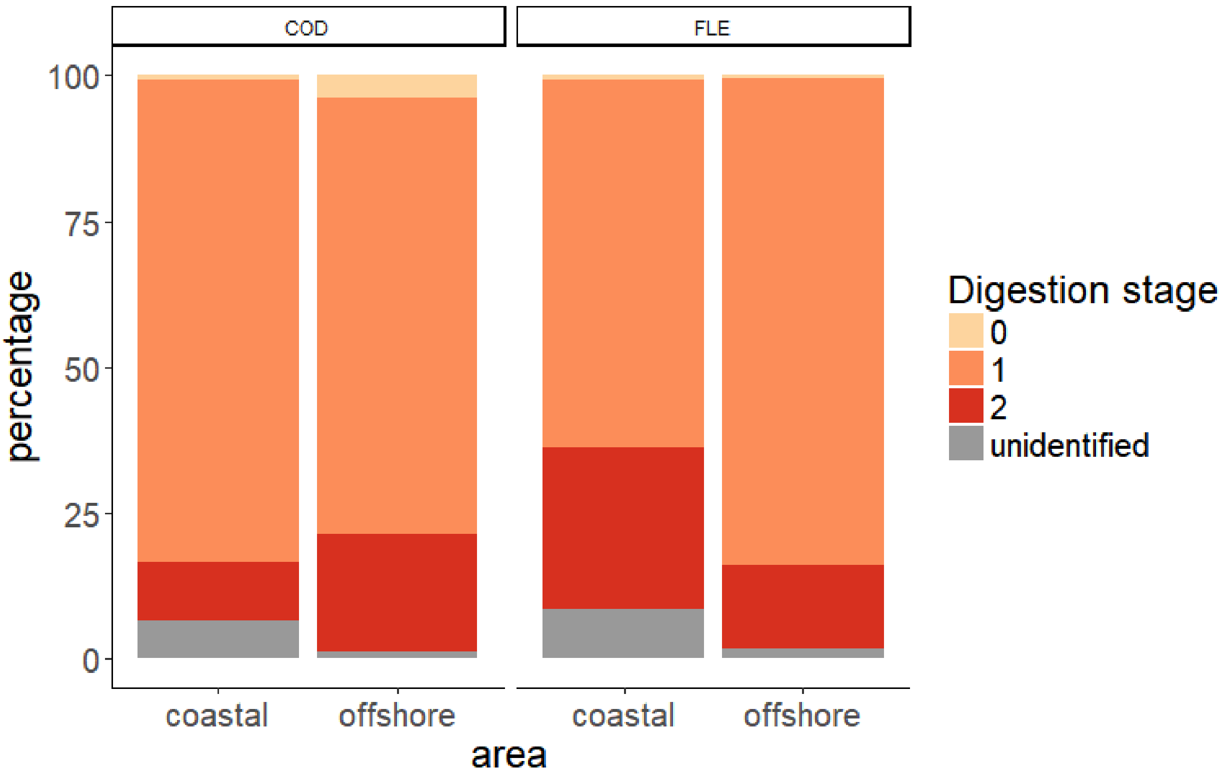

Figure 4: Percentages of each digestion stage separately for each predator and area.

3.2 Length distribution

The length distribution of the sampled cod (Figure 5) shows in general, a relative equal length range for the Q1 and Q4 in both offshore areas. In Q1, the length ranges from 13 to 77 cm in SD 25 and between 7 and 67 cm in SDs 26-28. In Q4 the length ranges between 6 and 77 cm in SD 25 and between 8 and 65 cm in SDs 26-28. The length range for SD 25 in coastal areas is somewhat narrower than in offshore area in the same SD.

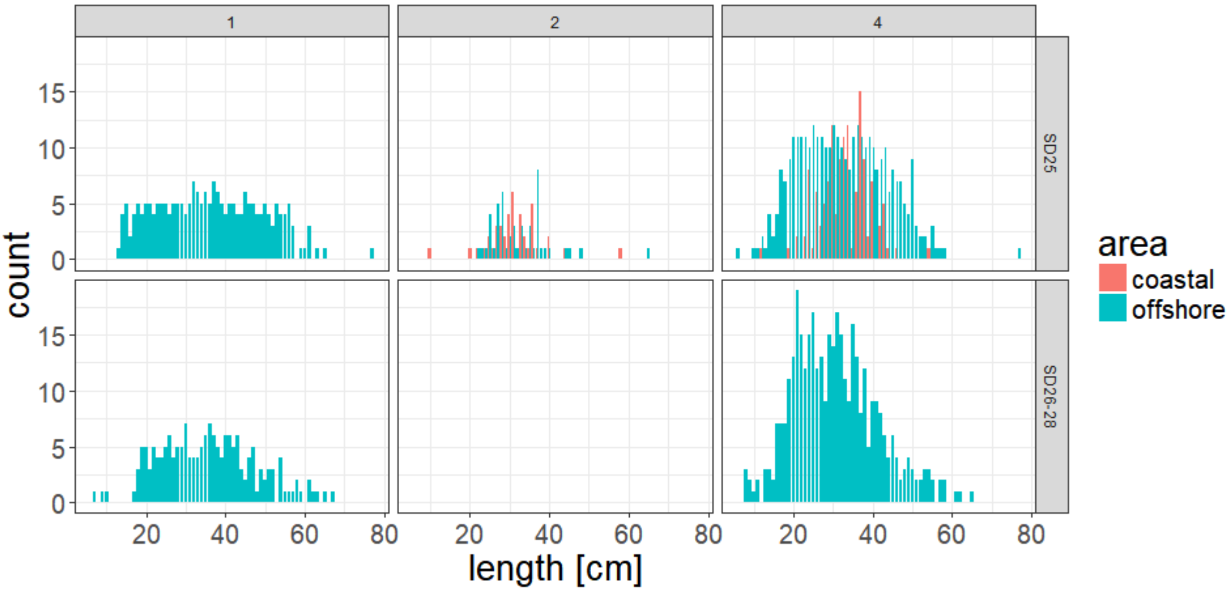

Figure 5: Length distribution of sampled cod for each quarter and area.

The length distribution of flounder (Figure 6) shows also, a relatively equal length range between Q1 and Q4. In Q1, the length ranges from 14 to 47 cm in SD 25 and between 13 and 37 cm in SDs 26-28. In Q4 the length ranges between 15 and 40 cm in SD 25 and between 9 und 35 cm in SDs 26-28. The length range for SD 25 in coastal areas is somewhat shifted toward smaller sizes than in the offshore area in the same SD.

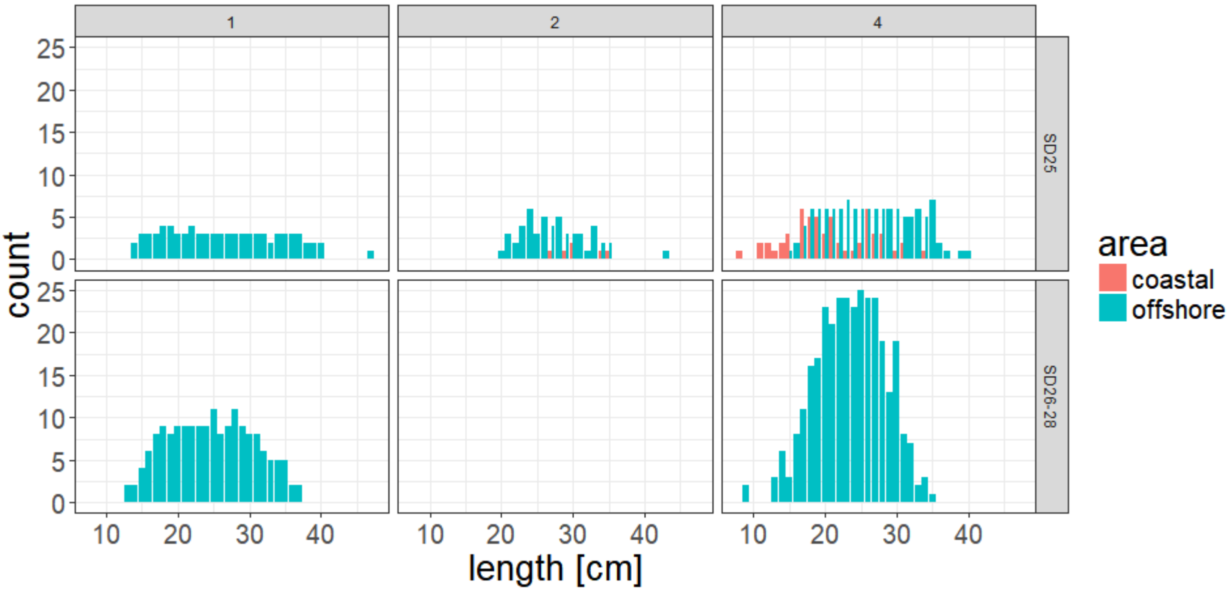

Figure 6: Length distribution of sampled flounder for each quarter and area.

3.3 Maturity status

Figure 7 shows histograms of the maturity stages in the three quarters analysed for each predator. The majority of analysed fish are in pre-spawning, corresponding to maturity stages 1 to 4. Some fish are in post-spawning, corresponding to stages 7-9, in Q4 and a very small amount of fish in Q1. Only in Q1 there are a few cod and some male flounder in spawning preparation (stage 5) and around 200 Flounders (mostly males) in spawning (stage 6).

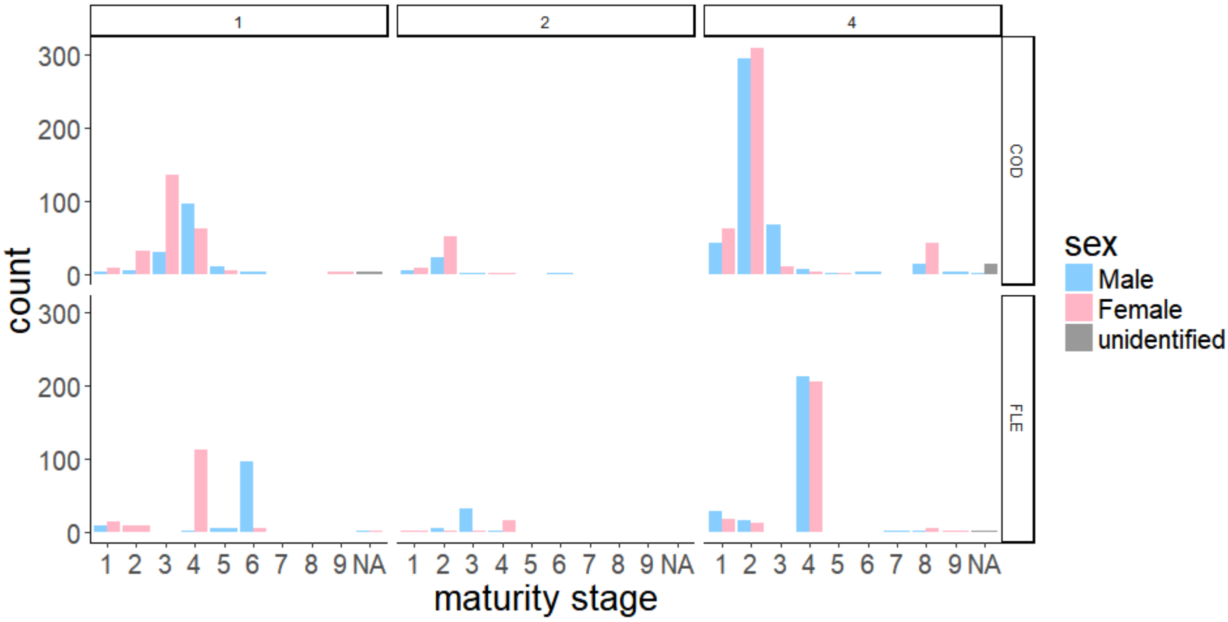

Figure 7: Maturity stage per quarter, predator and sex.

3.4 Empty stomachs

The percentage of empty stomachs of cod seems to differ between areas, quarters and length classes (Lcs) (Figure 8). In coastal waters (Figure 8 A), the percentage of empty stomachs lies around 13% for Lcs with more than 10 analysed cod, except for the Lc 31-40 cm in Q2, where no empty stomachs occur. In offshore water (Figure 8 B) the percentage of empty stomachs lies around 25% in SD 25 and is stable over the Lcs. In SDs 26-28, the percentage varies with the Lcs. In Q1, the percentage of empty stomach decreases until the Lc 31-40 cm from 60% to 20% and then increases again to 45%. In Q4, the percentage of empty stomachs increases from 20% to 75% with increasing Lcs.

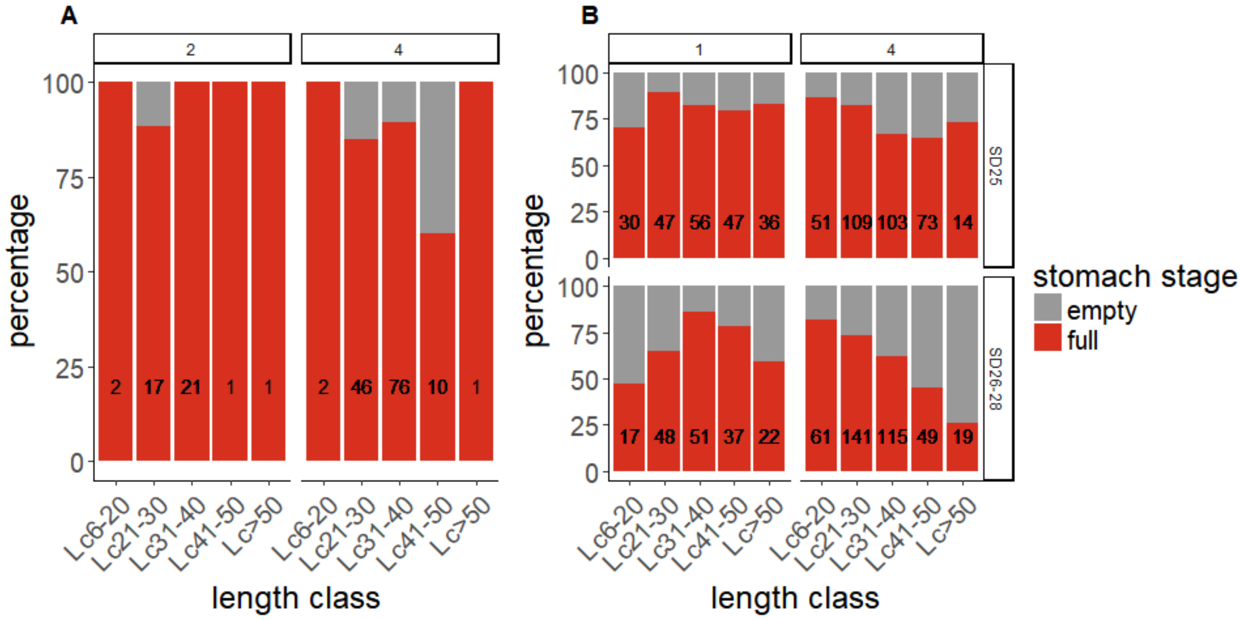

Figure 8: Percentage of empty stomachs of cod caught in the coastal (panel A) and in offshore areas (panel B) for each quarter. Black numbers in the bars show the number of samples.

The percentage of empty stomachs of flounder seems to differ between coastal and offshore areas and Lcs (Figure 9). In the coastal area (Figure 9 A), the percentage of empty stomachs lies around 10% for Lc 8-20 cm in Q4. For larger fish, the percentage of empty stomachs increases to 30%. In the offshore areas (Figure 9 B) the percentage of empty stomachs lies also around 30% for flounder below 30 cm in Q1 in SD 25 and doubles for the larger Lc. In Q4 in the same SD, the percentage of empty stomachs increases from 12% to 28% with increasing Lcs. In SDs 26-28 in Q1, the percentage of empty stomachs is similar between the Lcs with values around 50%. In Q4, the percentage of empty stomachs lies around 40% for flounder smaller than 30 cm and decreases to 10% for the larger Lc.

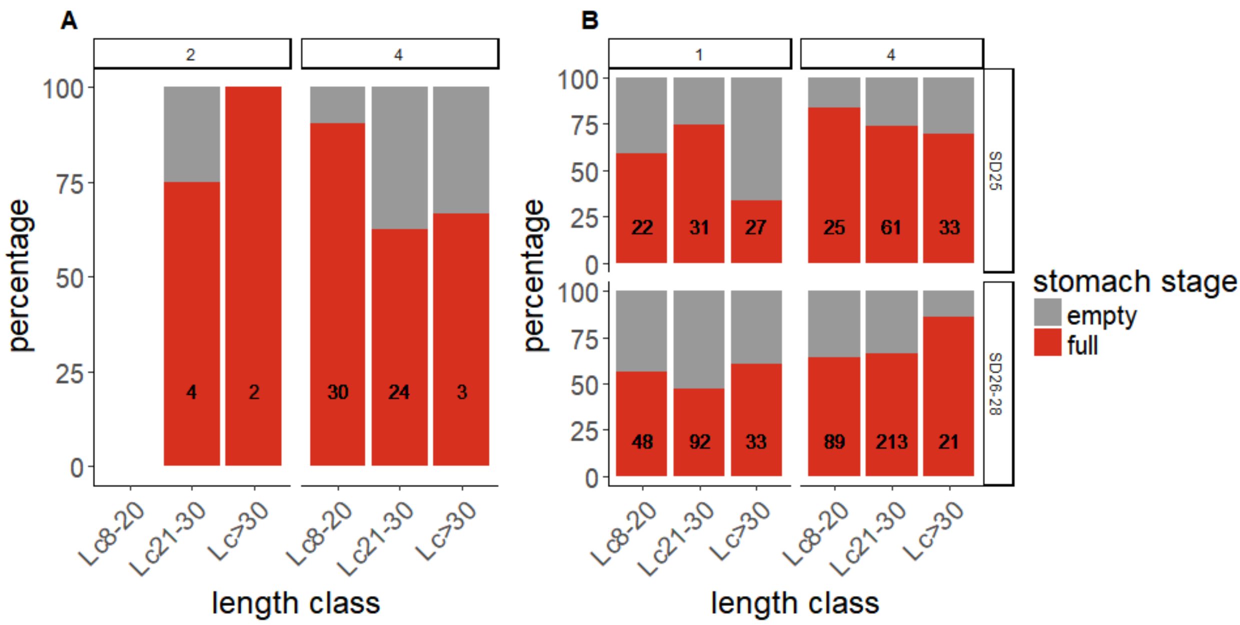

Figure 9: Percentage of empty stomachs of flounder caught in the coastal (panel A) and in offshore areas (panel B) each quarter. Black numbers in the bars show the number of samples.

3.5 Diet of cod

3.5.1 Coastal area

Figure 10 shows the diet composition of cod for each quarter in the coastal area. Overall, the proportion of invertebrates decreases with length. Amphipoda are the dominant prey for cod between 6-20 cm and make up to 45% of the diet in numbers, but afterwards the proportion decreases with length, in both Q2 and Q4. “Other invertebrates” consist mainly of “other Isopoda” (Figure A 4). The diet composition of cod > 20 cm differs largely between the quarters. In Q2, Saduria is the most important prey in number for cod over 21 cm and constitutes up to 45% of the diet of Lc 31-40 cm. In Q4, Caridea are the most dominant single prey in numbers for cod > 20 cm. Fish become generally more important with increasing cod size and Gobiidae are the most important fish prey in Q2 and Ammodiytidae in Q4. Considering the weight, the decrease of invertebrates with cod size is stronger. In Q2, Polychaeta are the most important prey for the Lc 6-20 cm in weight and Saduria is even more relevant in weight with a proportion of 50%. In Q4, Ammodytidae become the most important prey for cod between 31-40 cm in Q4 and make up to 60% of the weight in the diet of cod between 31-40 cm. Ammodytidae occur only rarely in Q2. “Other Pisces” consist mainly of Gasterosteidae (Figure A 4).

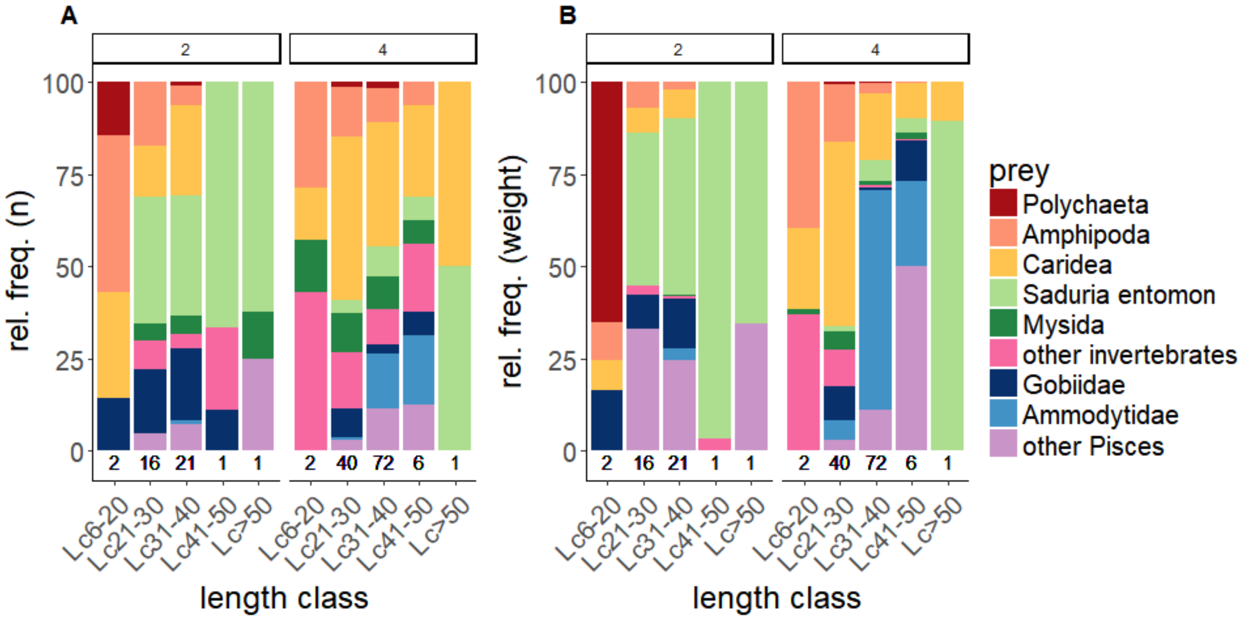

Figure 10: Diet composition of cod caught in the coastal area for each length class and quarter. Panel A shows the relative frequency in numbers, panel B the relative frequency in weight. Black numbers under the bars show the number of samples in the length class.

3.5.2 Offshore areas

Figure 11 shows the diet composition of cod for each quarter in the offshore areas. Overall, the importance of invertebrates decreases with length, while the importance of fish prey increases. In SD 25, invertebrate preys are dominant for cod between 6-40 cm, but the proportion decreases with length. Polychaeta are an important prey for cod between 6-30 cm in both quarters. In Q1 Mysida and in Q4 Cumacea and Saduria are the dominant invertebrate preys. While Cumacea are more important for cod under 20 cm, Saduria is more important for cod between 20-40 cm. Fish preys make up for around or more than 75% of the diet for cod over 41 cm in both quarters. Sprat is the dominant fish prey in number. Gadiformes occur mostly in Q1 in the diet of cod over 50 cm. In weight, fish preys reach more than 50% of the diet in all Lcs over 20 cm. Sprat, herring and Gadiformes increase in importance in weight, while “other Pisces” does not. “Other Pisces” consist mainly of “unidentified Pisces” (Figure A 6).

In SDs 26-28 the diet composition differs largely between the quarters. Overall invertebrate prey decrease, while fish preys increase with size. However, in Q1 Polychaeta are the most important invertebrate prey in numbers and fish preys become dominant already at low cod size classes. Gobiidae make up 25% of the diet of cod between 6-20 cm. Fish preys increase for cod over 20 cm from 50% to 100% of the diet in larger cod. Sprat are the dominant fish preys for cod between 21-50 cm, while herring and Gadiformes become the main fish preys for cod over 50 cm. On the other hand, in Q4, Mysida are the most important prey in numbers for cod between 6-50 cm. Fish preys increase for cod over 30 cm from 50% to 95% of the diet. Sprat are the dominant fish preys in number and weight. “Other Pisces” consist mainly of unidentified Pisces and unidentified Clupeidae (Figure A 8).

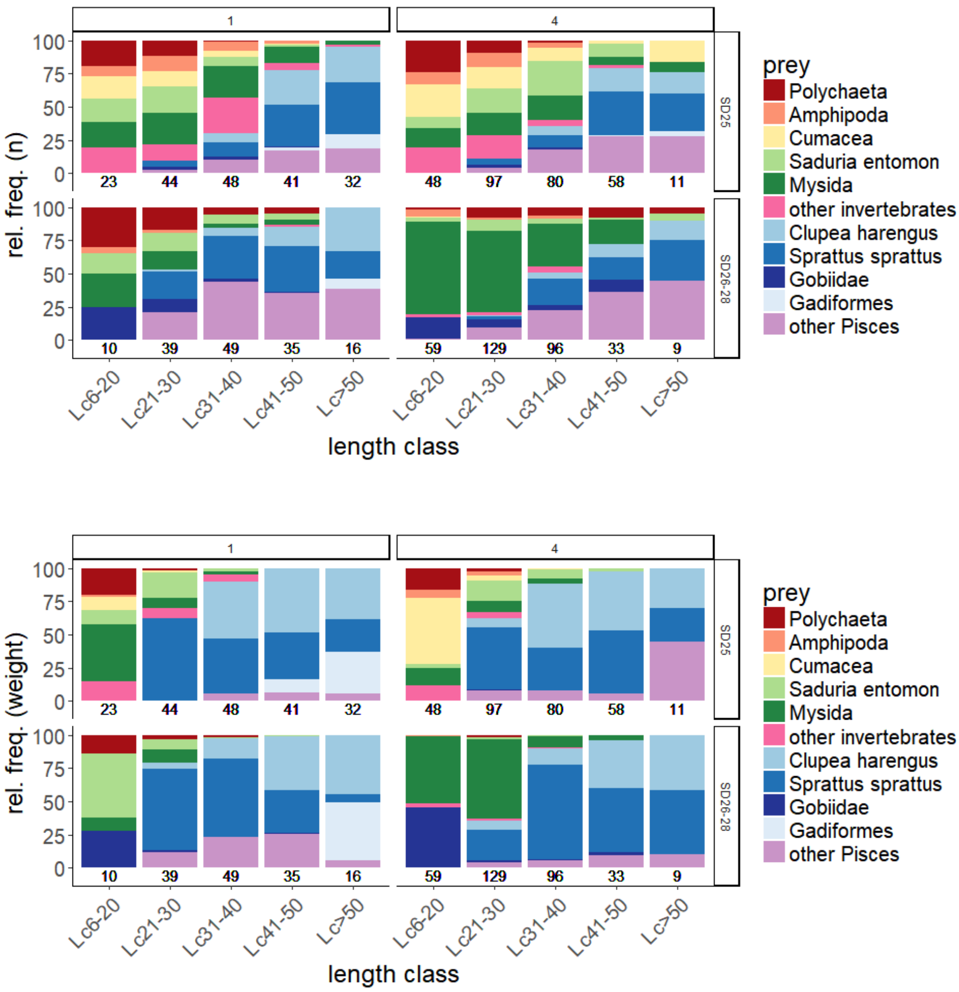

Figure 11: Diet composition of cod caught in both offshore areas for each length class and quarter. Panel A shows the relative frequency in numbers, panel B the relative frequency in weight. Black numbers under the bars show the number of samples in the length class.

3.6 Diet of flounder

3.6.1 Coastal area

Figure 12 shows the diet composition of flounder for each quarter in the coastal area. The diet composition seems to differ largely between the quarters. In Q2 Saduria seems to be the most important prey in numbers for flounder. In weight *Limecola balthica* is more important. In Q4, *Mytilus sp.* is the most dominant prey in numbers and weight for flounder between 8-20 cm and make up to 60% of the diet in weight. Amphipoda and “other invertebrates” (Figure A 5) are only important for flounder between 8-20 cm and decrease in importance with size. For flounder between 21-30 cm *Mya arenaria* is dominant in weight and constitute 50% of the diet.

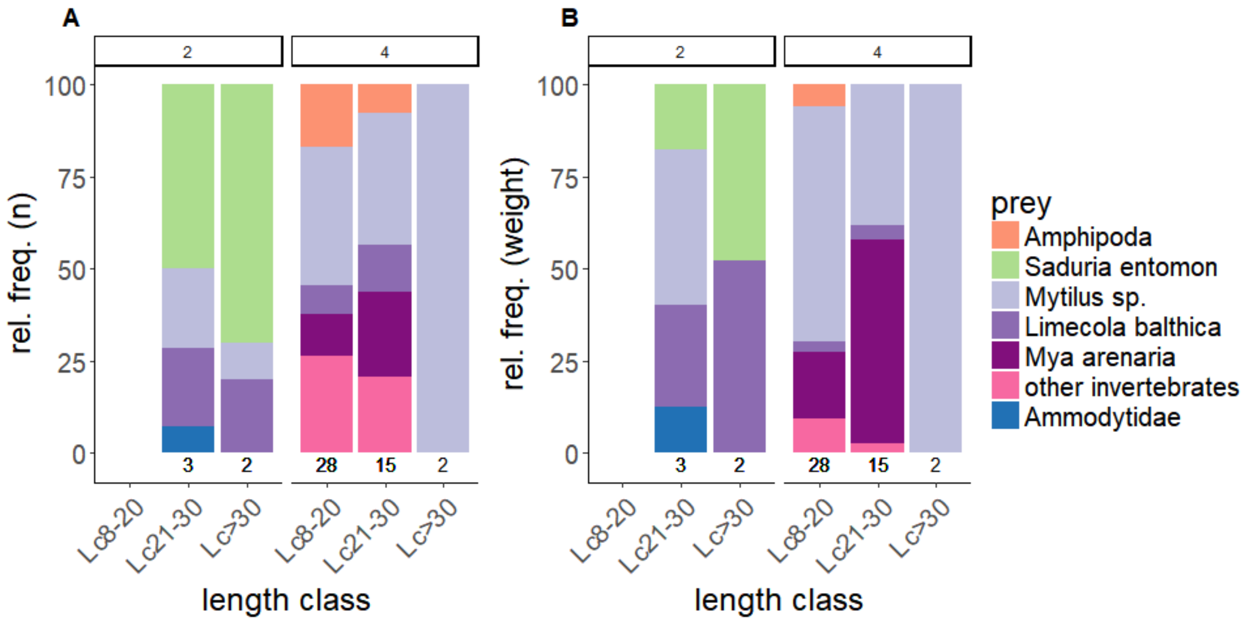

Figure 12: Diet composition of flounder caught in the coastal area for each length class and quarter. Panel A shows the relative frequency in numbers, panel B the relative frequency in weight. Black numbers under the bars show the number of samples in the length class.

3.6.2 Offshore areas

Figure 13 shows the diet composition of flounder for each quarter in both offshore areas. The diet composition seems to differ more between the areas than between the quarters. Fish prey is only found in SDs 26-28 for flounder over 21 cm (Figure A 9). In SD 25 Amphipoda, *Limecola balthica*, Priapulida and “other invertebrates” make approximately 1/5 of the diet in number each for all Lcs. Priapulida are more important in Q1 and *Limecola balthica* in Q4. The proportion of *Mytilus sp.* decreases with size, while Saduria increases and make up to 40% of the diet in number of flounder over 30 cm in Q4. Considering the weight, *Limecola balthica* is the dominant prey in all Lcs and constitute up to 60% of the diet. Amphipoda, Priapulida and “other invertebrates” decrease in their proportion of the diet in weight with size. “Other invertebrates” consist mainly of Polychaeta and Cumacea (Figure A 7).

In SDs 26-28 the proportion of Saduria in number and weight, increases with length in Q1 and can make up to 95% of the diet in weight. In Q4 the proportion in number is constant over the length, while the proportion in weight increases. *Limecola balthica* is the most important prey for the Lc 8-20 cm and constitutes 60% of the diet in weight. Amphipoda are more important in Q4 with a proportion of around 20% in numbers overall Lcs.

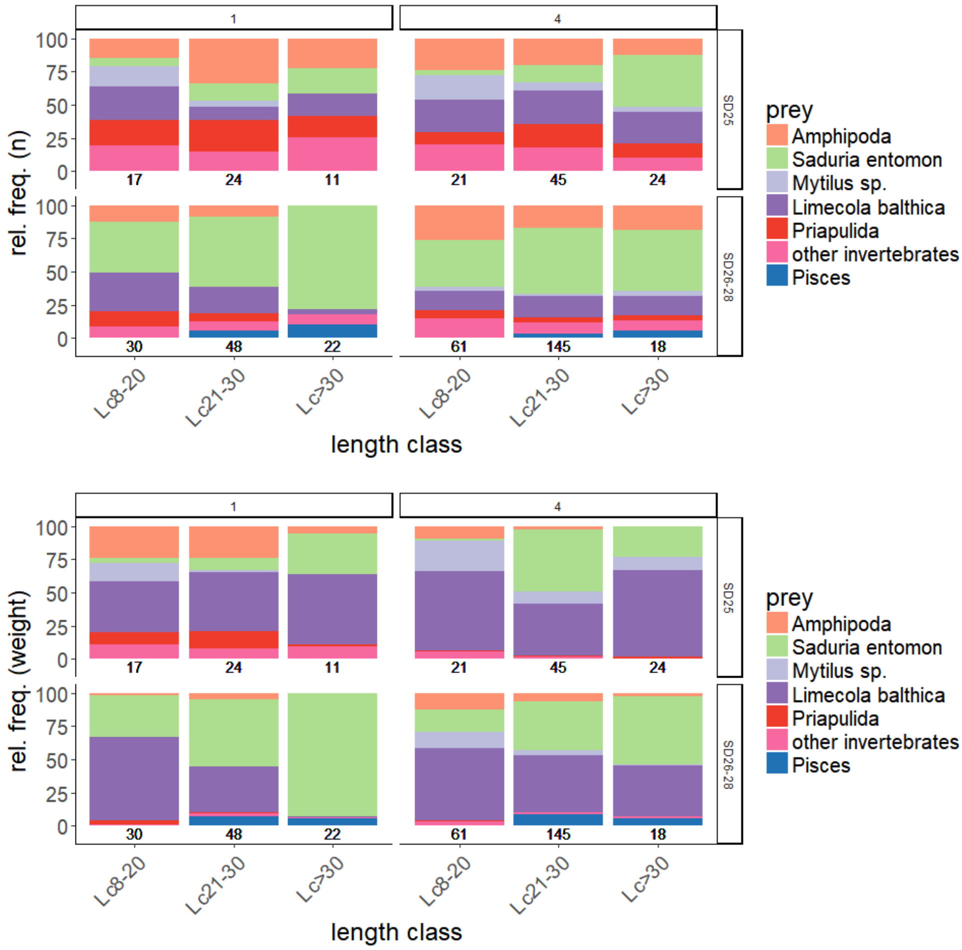

Figure 13: Diet composition of flounder caught in both offshore areas for each length class and quarter. Panel A shows the relative frequency in numbers, panel B the relative frequency in weight. Black numbers under the bars show the number of samples in the length class.

3.7 Diet overlap

3.7.1 Coastal area

The majority of the indices to determine the optimal number of clusters (8 out of 23) give 4 as optimal number of clusters for the samples from the coastal area. All three clusters with two objects (combination of Lcs and quarters) have a cophenetic distance under 0.3 (Figure 14). The first cluster consists of flounder between 8-30 cm caught in Q4, the second cluster consists of cod between 21-40 cm caught in Q2 and the third cluster consists of cod between 21-40 cm caught in Q4. The cluster with only one object, cod between 41-50 cm caught in Q4, has a cophenetic distance of 0.5 from the cluster with the other cod caught in the same quarter. The two clusters with cod caught in Q4 connect first and afterwards connect with the cod cluster from Q2. The flounder cluster has the highest cophenetic distance to the three cod clusters. The Morisita index (Figure 15) shows no significant diet overlap between cod and flounder (all $M < 0.45$). The diet overlap between the two flounder Lcs is highly significant with $M = 0.93$. Within cod, the diet overlap is also highly significant for almost all the length classes and quarters.

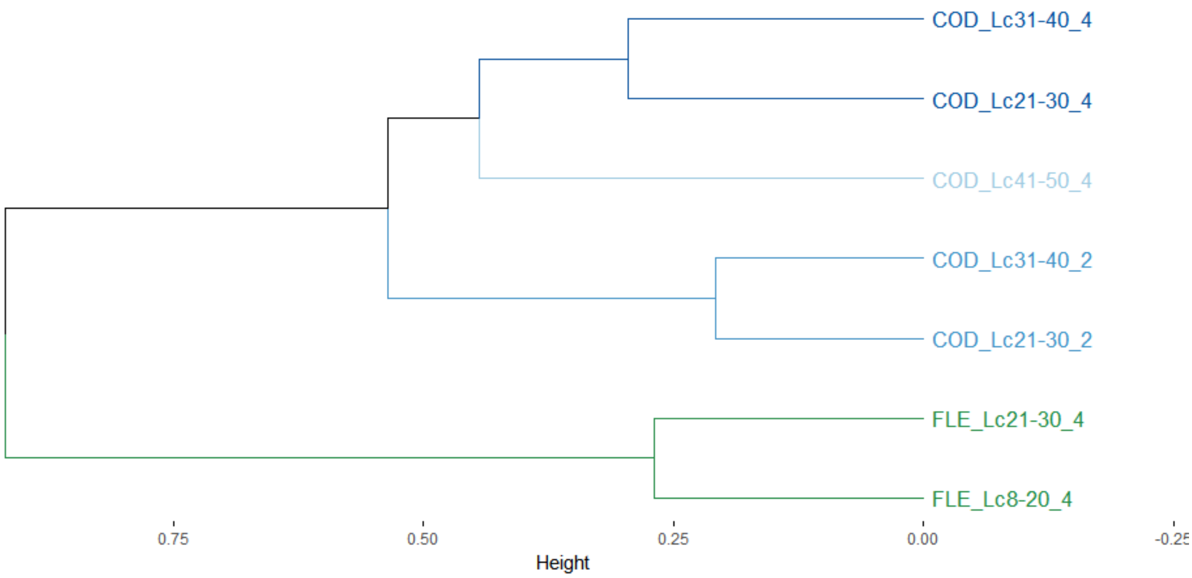

Figure 14: Dendrogram for the coastal area. Labels identify the predator, the length class and the quarter. Height reflects the cophenetic distance (dissimilarity) between the groups.

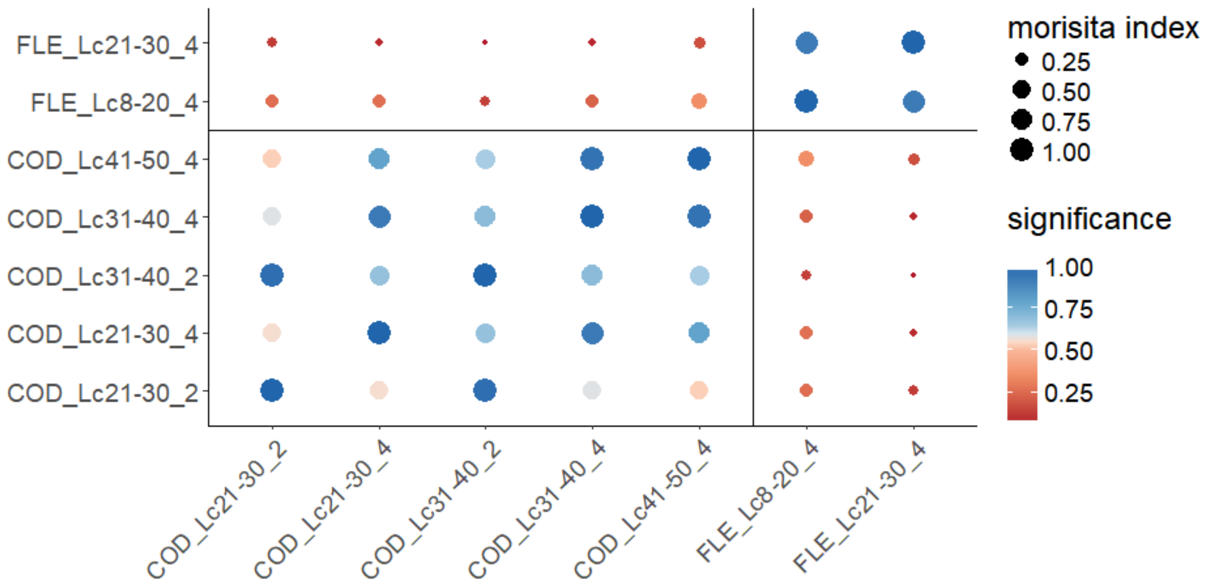

Figure 15: Diet overlap for the samples collected from the coastal area. Labels identify the predator, the length class and the quarter. The size of the points reflects the Morisita index and the color the significance of the overlap. Bluish color indicates a significant overlap with a Morisita index greater than or equal to 0.6, reddish color indicates a non-significant overlap with a Morisita index smaller than 0.6.

3.7.2 Offshore area SD 25

The majority of the indices to determine the optimal number of clusters (14 out of 24) give 3 as optimal number of clusters for the samples of the offshore area in SD 25. Figure 16 shows the three different clusters. The first cluster consists of cod over 40 cm caught in both quarters, the second cluster consists of all flounder Lcs in both quarters and the third cluster consists of cod between 6-40 cm caught in both quarters. The first two clusters have a cophenetic distance below 0.5 and the third a cophenetic distance of 0.55. The flounder cluster connects with the small and medium size cod cluster, consisting of cod between 6-40 cm. The cluster with the big cod has the highest cophenetic distance to the other clusters. The Morisita index (Figure 17) shows that, cod Lcs over 40 cm have the highest diet overlap (M above 0.85). Cod between 6-40 cm have also a significant diet overlap (M above 0.83), as well as all flounder Lcs (M above 0.8). A significant diet overlap between cod and flounder is found for cod between 6-30 cm and flounder over 20 cm, in general, the Morisita index lies around 0.6. The highest overlap is found between flounder Lc >30 cm caught in Q1 and cod Lc 21-30 cm caught in Q4 (M = 0.76).

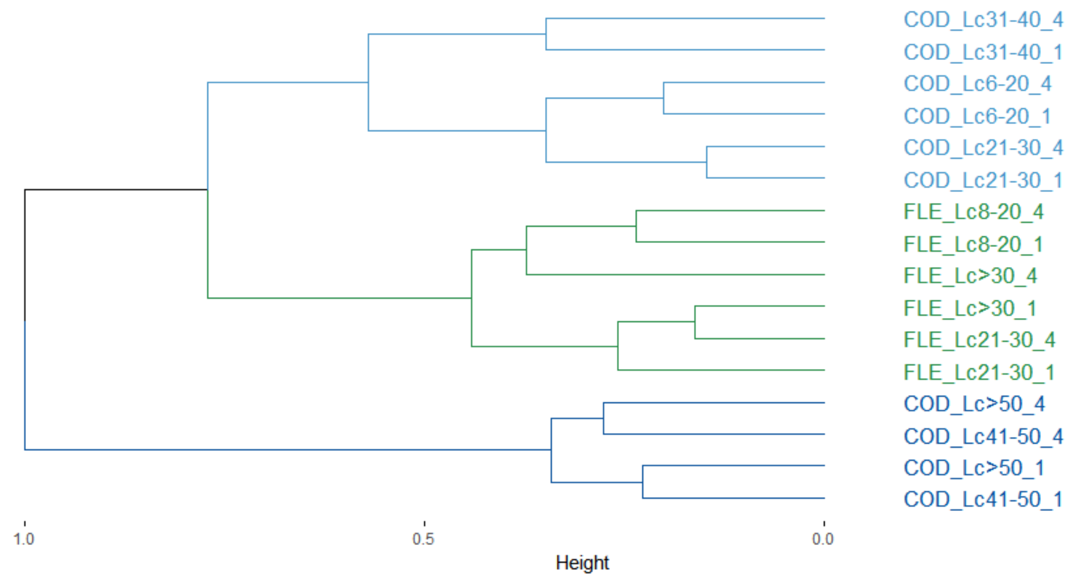

Figure 16: Dendrogram for the offshore area in SD 25. Labels identify the predator, the length class and the quarter. Height reflects the cophenetic distance (dissimilarity) between the groups.

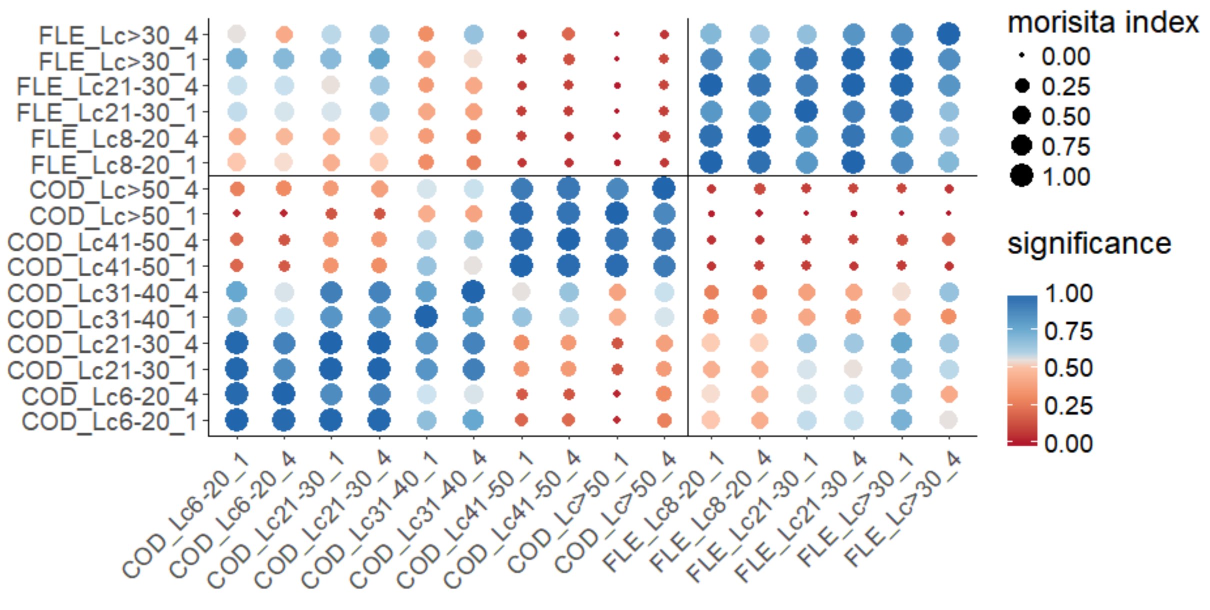

Figure 17: Diet overlap for the samples collected from the offshore area in SD 25. Labels identify the predator, the length class and the quarter. The size of the points reflects the Morisita index and the color the significance of the overlap. Bluish color indicates a significant overlap with a Morisita index greater than or equal to 0.6, reddish color indicates a non-significant overlap with a Morisita index smaller than 0.6.

3.7.3 Offshore area SDs 26-28

The majority of the indices to determine the optimal number of clusters (7 out of 24) give 3 as optimal number of clusters for the samples from the offshore area in SDs 26-28. Figure 18 shows the three different clusters. The first cluster consists of cod over 30 cm caught in both quarters and the cod Lc 21-30 cm caught in Q1, the second cluster consists of the other cod between 6-30 cm and the third cluster consists of all flounder Lcs in both quarters. Every cluster has a cophenetic distance of around 0.55. The flounder cluster connects with the small cod cluster, consisting of cod between 6-30 cm. The cluster with the big cod has the highest cophenetic distance to the other clusters. The Morisita index (Figure 19) shows that, the diet overlap between the flounder Lcs in both quarters are highly significant with a Morisita index generally above 0.8. Furthermore, the diet overlap for cod over 20 cm in both quarters is significant, with the exception of the Lc 21-30 from Q4. In addition, cod between 6-20 cm have a significant diet overlap to the Lc 21-30 cm. No significant diet overlap between cod and flounder is found (all M < 0.4).

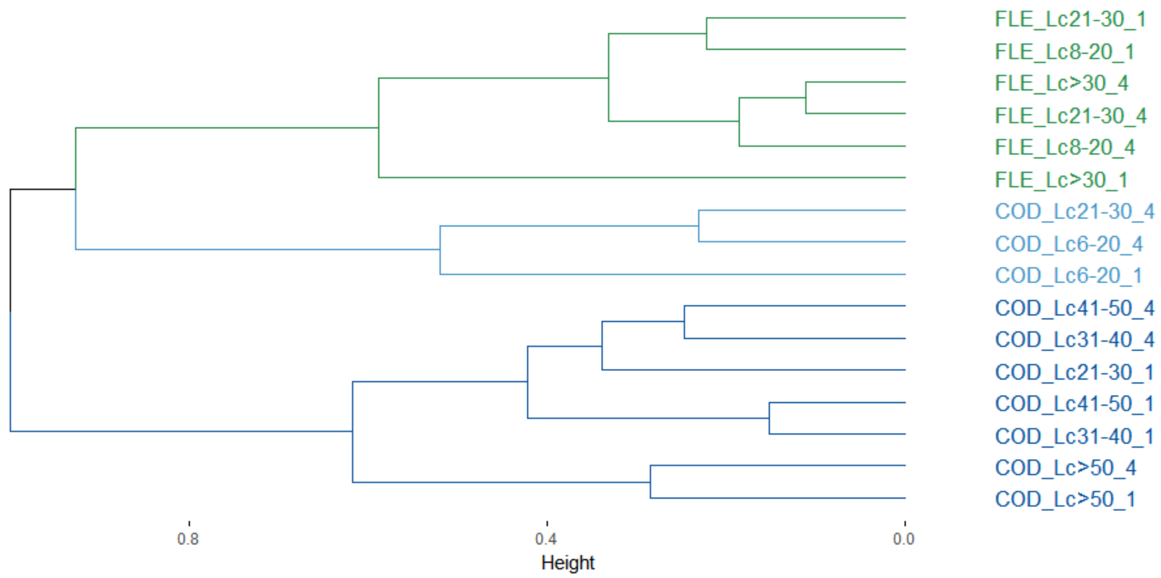

Figure 18: Dendrogram for the offshore area in SDs 26-28. Labels identify the predator, the length class and the quarter. Height reflects the cophenetic distance (dissimilarity) between the groups.

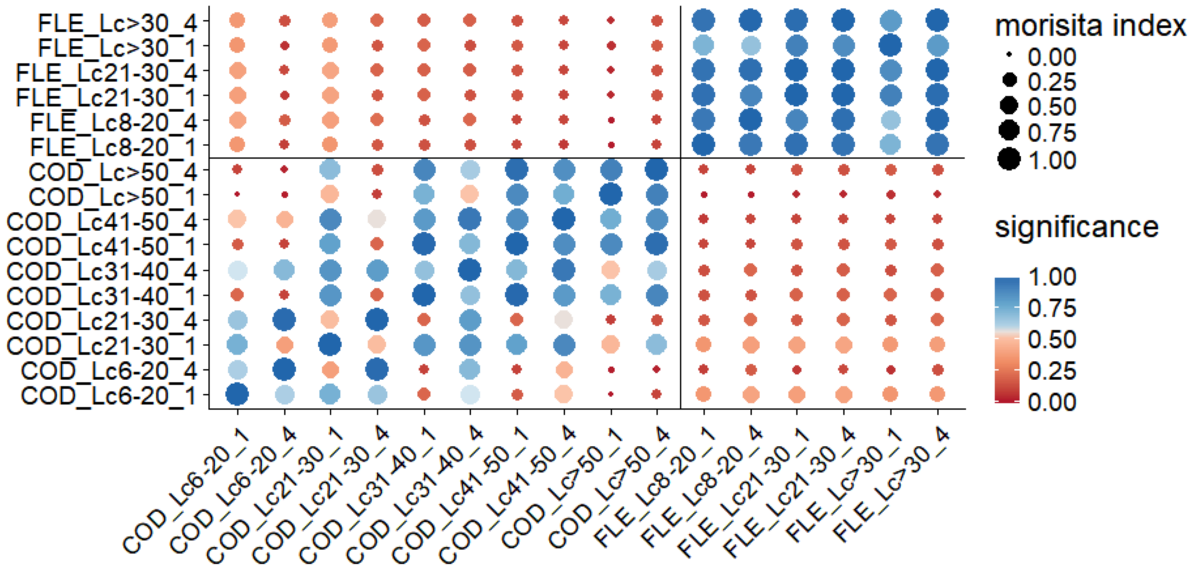

Figure 20: Diet overlap for the samples collected from the offshore area in SDs 26-28. Labels identify the predator, the length class and the quarter. The size of the points reflects the Morisita index and the color the significance of the overlap. Bluish color indicates a significant overlap with a Morisita index greater than or equal to 0.6, reddish color indicates a non-significant overlap with a Morisita index smaller than 0.6.

4 Discussion

This study presents the diet of cod and flounder in three areas of the central Baltic Sea with particular focus on different predator sizes and quarters. In addition, the diet overlap between these demersal predators was estimated for each area. The diet overlap was estimated separately for each area, because an overlap between two different areas would not represent a real competition between predators, assuming that the fish do not perform significant movements across areas. On the contrary, I estimated the diet overlap between quarters because a competition for food can be time-delayed. For example, predation on small prey individuals in spring (Q1 or Q2 in my study) can influence the availability of larger prey individuals later in the year (Q4 in my study).

To compare the diet of cod and flounder according to the Lcs, it is important that each Lc is represented by a relative equal amount of fish per length within each class. In this study, this requirement is fulfilled for most of the Lcs, accept from the smalles and biggest Lcs. However, as commonly observed in length frequency distributions, small and big fish occur less frequently than the fish in the central part of the distribution. This leads, in this study, to some biased Lcs, which are dominated by fish at the boarder of the length range. For example, the cod Lc 6-20 cm and the flounder Lc 8-20 cm from the offshore area in Q4 are dominated by fish close to 20 cm.

4.1 Coastal area

The diet of cod in the coastal area seems to differ largely between the quarters. In Q2 *Saduria entomon* and in Q4 Caridea are the most important prey. The large share of Saduria in the diet of cod in Q2 in the coastal area (30%) is also shown by Dziaduch (2011) for cod caught in February on the Polish coast at depths between 20-33 m. The higher share of Saduria in the deeper part of the coastal area (sampled in Q2) can be explained with the depth preference of Saduria. It is also known that Saduria migrates to coastal areas during winter, which can also explain the higher shares in cod diet in Q2, where Saduria starts to migrate back to deeper waters and are therefore more available due to the increased movements (Haahtela, 1990). Also, the fish preys found in my study differ from mainly Gobiidae in Q2 to mainly Ammodytidae in Q4. As in this study, Pachur and Horbowy (2013) found that Ammodytidae had a higher contribution in the diet of cod in November than in February in the coastal zones (15-20 m) in the southern Baltic Sea. This big difference between the quarters is also seen in the cluster analysis, where each cod cluster only consists of one quarter but different Lcs, and in the high Morisita values within each quarter, while the Morisita index between the quarters are lower. For the central Baltic Sea, no studies in literature are available to compare the diet of cod at depths shallower than 15m. However, the ontogenetic shift in the diet of cod between 21-50 cm from the coastal area in Q4, with a change in diet from small Crustacean (e.g. Amphipoda) to larger Crustacean (mainly Caridea), is also shown by Funk (2017) for cod <35 cm caught in the western Baltic Sea at depths shallower than 17 m. In addition, the high proportions (over 50%) of benthic prey in the coastal area have also been shown for cod in the western Baltic Sea, caught at depths shallower than 17 m (Funk, 2017). However, the share of fish preys from the Lc 41-50 cm in Q4 is so high that this length class differs from the smaller cod from the same quarter in the cluster analysis. The size class between 40-50 cm is at the end of the transition period during which cod switch from benthic to fish preys (Huwer *et al.*, 2014) and therefore it is reasonable to find this Lc in a different cluster, even if the diet overlap with most of the small cod Lcs is still significant. The change to a more fish based diet leads to a generally higher percentage of empty stomachs, which is also shown by Huwer *et al.* (2014). In conclusion, the diet of cod in the coastal area differs between the quarters but is still very similar as shown by a significant Morisita index between nearly all analysed Lcs. This similarity is mainly due to Crustacean preys, which could lead to a high competition for cod between 21-50 cm. However, when comparing the two quarters from the coastal area, it has to be considered that the differences I record can also be due to an underlying difference in depth. The samples from Q2, taken during the INSPIRE project, have depths around 15 m and deeper. Instead, the samples from Q4, sampled during commercial fishing trips, are mostly shallower than 10 m. Moreover, it is important to consider that the number of analysed cod is very small for most of the Lcs in this area.

Flounder diet, as in the case of cod, seems to differ largely between the two quarters. While in Q2 Saduria is the dominant prey, as it is for cod, this is not the case in Q4. This difference could be again due to the underlying difference in the sampled depth. In Q4 the proportion of Amphipoda and other invertebrates, mainly Gastropoda of the genus Hydrobia (Figure A 4), decreases from the Lc 8-20 cm to the Lc 21-30 cm. The same decrease has been found by Karlson *et al.* (2007) in the Gulf of

Gdansk for flounder between 10-25 cm caught at depths between 3-13 m, which indicates a preference of small flounder for Amphipoda and Hydrobia. As for cod, a decrease in small invertebrate prey leads to a higher percentage of empty stomachs. *Mya arenaria* does not occur in considerable amounts in the other available diet studies (Karlson *et al.*, 2007; Järv *et al.*, 2011; Borg, Westerbom and Lehtonen, 2014). The proportion of *Mytilus sp.* differs largely between the studies performed at comparable depth ranges and length, but in different months. In the Gulf of Gdansk (3-13 m, sampled in June - September) Mytilus occurs in proportions of only 10-20% (Karlson *et al.*, 2007), in the Muuga Bay (<20 m, sampled in July - October) in proportions of around 92% (Järv *et al.*, 2011), and Borg, Westerbom and Lehtonen (2014) found similar proportions to the current study (44%) in the Archipelago Sea of the norther Baltic Sea (4-13 m, sampled in June). For flounder between 8-30 cm, the interspecific competition is even higher than for cod with nearly the same diet composition in Q4 for both Lcs, which can also be seen in the highly significant Morisita index. However, as in the case of cod, the low number of analysed flounder in this area could affect these results, and therefore attention should be paid when trying to generalize these findings.

In the coastal area, no diet overlap between cod and flounder is found in my study, which is mostly due to the high proportion of Bivalves in the investigated flounder Lcs. However, cod under 20 cm seems not to predate on fish preys and prefers small Crustacean like flounder, which could lead to a higher overlap and competition, especially for Amphipoda. Also, the high shares of Saduria in Q2 in both predators could lead to a higher overlap, which could not be investigated due to the small amount of flounder.

4.2 Offshore areas

The ontogenetic shift in the diet of cod in the offshore areas, with a decrease of the proportion of invertebrates and an increase of fish preys with cod size, is in line with the literature. Huwer *et al.* (2014) show also a decrease in importance of "benthic prey other than Saduria" with the size of cod in the central and eastern Baltic Sea. The same decrease can also be found in the western Baltic Sea (Funk, 2017). This indicates that small cod in offshore areas prefer small Crustacean, as in coastal areas. Conversely, for bigger cod, invertebrates are not as important as in coastal areas, which could be due to lower availability of benthic preys or a higher availability of fish preys or due to a preference for fish preys. This ontogenetic diet shift causes the separation of cod in two different clusters: one cluster includes cod (6-40 cm in SD 25 and 6-30 cm in SDs 26-28), whose diet is dominated by invertebrates, while the other cod cluster (>40 cm in SD 25 and >30 cm in SDs 26-28) includes cod

whose diet is dominated by fish prey. A size-delayed increase in importance of sprat and herring, is found in both offshore areas in this study. This shift from sprat to herring, as most important prey, has also been shown for the whole central and eastern Baltic Sea (Huwer *et al.*, 2014). Pachur and Horbowy (2013) also mention that sprat is the most important prey in weight for cod between 30-50 cm in the Polish zone of the southern Baltic Sea and that afterwards the proportion of herring increases. Another size dependent diet shift of cod is the occurrence of cannibalism, which starts to occur for cod in the Lc >40 cm. In literature cod cannibalism has increased in recent years (ICES, 2016a; Köster *et al.*, 2017) and has been shown in considerable amounts for cod over 60 cm (Pachur and Horbowy, 2013; ICES, 2015b). In my study cannibalism occurs mainly in Q1, which is in accordance with Pachur and Horbowy (2013) that found higher rates of cannibalism in February than in November explainable with the different availability of young (0 or 1 year) cod. The measurable cod prey from this study, were from Q1 of 2016 samples and range between 21-29 cm, which would correspond to 1-2 years old cod (ICES, 2015a).
The diet of cod in the two offshore areas differs in the importance of Mysida and Cumacea as invertebrate preys and in the higher proportion of fish preys in SDs 26-28 than in SD 25 during Q1. In SD 25, Cumacea are the most important invertebrate prey over all Lcs in Q4 and occur frequently also in Q1. In SDs 26-28, Cumacea does not occur in the diet, instead Mysida are by far the most important invertebrate prey, especially in Q4. (Dziaduch, 2011) show also a higher proportion of *Mysis mixta* in the Gdansk Basin (SD 26) than in the Bornholm Basin and the Polish coast (both SD 25) and a reverse picture for Cumacea. This difference is probably explained by the distribution of Mysida, which occur only rarely in the Bornholm Basin (SD 25) (Salemaa, Vuorinen and Valipakka, 1990). In SDs 26-28 cod start to feed extensively on fish from a smaller size (already at the Lc 21-30) compared to in SD 25, as also shown by the groups identified by the cluster analyses. The higher share of fish prey, especially sprat, in Q1 in SDs 26-28 compared to SD 25 is also found by Pachur and Horbowy (2013). This can be explained by the distribution of sprat, which occur in higher abundances in SD 26 compared to SD 25 (ICES, 2016b). The two offshore areas differ also in the amount of empty stomachs. In SD 25 the percentage of empty stomachs is lower and constant over the Lcs, while in SDs 26-28 the percentage is higher and varies with size. Previous observations from the Bornholm Basin (SD 25), have reported percentages of empty stomach varied between 0 and 40 % in the past 40 years (ICES, 2014), therefore the percentages of empty stomach around 25% in the offshore area of SD 25 found in my study lie within this range. The increasing proportion of empty stomachs with cod size over all Lcs in Q4 and for cod over 30 cm in Q1 in the offshore area in SDs 26-28 are also found by Huwer *et al.* (2014) for the whole central and eastern Baltic Sea. The increasing proportion of empty stomachs with cod size, can be explained with the

change from continous invertebrate feeding to intermittent fish feeding. The reason why the percentage of empty stomachs in SDs 26-28 in Q1 for cod under 30 cm is extremely high (up to 60%) is not clear. It could be tentatively explained by a low availability of small crustacean, which would also explain the higher importance of Polychaeta and the earlier increase of fish preys in this area compared to all other areas and quarters.

The diet of flounder is highly constant over the Lcs and quarters in both offshore areas, resulting in a single cluster with all Lcs and quarters. In addition, the Morisita index displays high similarity in the diet of flounder with values above 0.8. No study in literature is available to compare with my results the diet of flounder at depths over 30 m. However, as for cod, a decrease in the proportion of small invertebrates can be seen with size. In contrast to that, the importance of Saduria increases with size. The higher proportions of Saduria in SDs 26-28 compared to in SD 25 can also be explained by the distribution of this isopod, which is known to occur more abundantly in the Bothnian, Aland, Archipelago Seas, in the Gulf of Finland, and decrease south-westwards (Haahtela, 1990). However, this decreasing importance of Saduria in flounder diet between SDs 26-28 to SD 25 is not found in the diet of cod. Although it is reported from the analysis of a comprehensive cod stomach data set (ICES, 2015b). While the diet composition is relatively constant over Lcs and between the quarters, the percentage of empty stomachs lies around 40% without a clear trend over the Lcs and quarters.

In the offshore area in SDs 26-28 no diet overlap between cod and flounder is found due to the high proportions of fish prey in all cod Lcs. In SD 25 instead, a diet overlap between cod and flounder is detected. The diet overlap is significant for cod between 6-30 cm and for flounder over 20 cm in both quarters. These cod Lcs are characterized by very small proportions of fish and a 20% proportion of Saduria, similarly to the diet of the same Lcs of flounder. The diet overlap of other cod and flounder Lcs have als high Morisita values (above 0.5), when compared with the interspecies diet overlap such as between large and small cod. The diet of all these Lcs show that the competition between cod and flounder is mostly for Saduria and it is stronger when cod have a small proportion of fish in the diet.

4.3 Coastal against offshore areas

The main difference between the diet of cod in coastal and offshore areas, is the importance of fish as prey. While in the coastal area fish preys reach proportions of the diet in weight over 50% only for cod above 31 cm, in the offshore area these proportions are achieved for cod over 21 cm. Moreover, the fish species in the diet change from demersal fish in the coastal area, Gobiidea or Ammodytidea, to pelagic fish in the offshore areas, sprat and herring. Pachur and Horbowy (2013) show also a decrease in the proportion of Gobiidea and Ammodytidea with increasing depth and a higher proportion of sprat and herring at depth deeper than 40 m. On the other hand, the importance of invertebrate prey declines faster in the offshore areas, which is in line with the decreasing proportion of Amphipoda and *Crangon crangon* at increasing depth (Pachur and Horbowy, 2013). Another difference between coastal and offshore areas in the diet of cod is the composition of invertebrate preys. The dominant Amphipoda and Caridea in the coastal area are replaced by Cumacea and Mysida as dominant prey in the offshore areas. Funk (2017) shows the same change of the composition of invertebrate preys for cod in the western Baltic between the depth strata 0-17 m and 17-30 m. The change in fish and invertebrate composition between coastal and offshore areas is likely due to the distribution of the prey species. The changes between coastal and offshore waters lead, in general, to higher percentages of empty cod stomachs in offshore waters. This is in accordance with Funk (2017), which shows higher percentages of empty stomach in the deeper waters of the western Baltic Sea.

For flounder, Mytilus is much less important in offshore areas in comparison to the coastal area and *Mya arenaria* disappears completely in the diet of offshore flounder. Therefore, Saduria and *Limecola balthica* are much more important offshore. The decrease of Mytilus and *Mya arenaria* and increase of *Limecola balthica* and Saduria can be explained by their depth distribution. Saduria occurs mainly at depths between 50-85 m (Haahtela, 1990), *Limecola balthica* occurs at depths up to 86 m, while Mytilus and *Mya arenaria* occur at depth <20 m and <30 m, respectively (Gogina *et al.*, 2016). In contrast to cod, for flounder the proportion of Amphipoda does not change so much between the coastal and the offshore areas. The percentage of empty flounder stomach seems to show a similar pattern as for cod with higher percentages of empty stomachs in offshore areas.

When comparing the coastal and the offshore areas, we have to keep in mind, that the samples were collected in two different years. Coastal samples come from 2015 and offshore samples from 2015 and mainly 2016. So an underlying year effect could lead to the changes between coastal and offshore areas. A year effect was not observed in the offshore area.

In this study the cod and flounder were caught using different fishing methods. To be sure that these different methods have no effect on the diet itself, the effect of the sample type on the stomach content was investigated. Due to the potential longer time fish spend in a gillnet, the stomach content could be more digested than in the trawl samples. This would result in higher percentages of the digestion stages 1 or 2 in both predators. The results do not show a clear pattern between gillnet and trawl. Higher percentages for both predators caught with gillnet was not observed, on the contrary, for cod, the percentage of digestion stage 2 is higher in trawl samples. Due to the ongoing digestion while the fish are in the gillnet, the stomachs could also be further emptied resulting in lower stomach content or a higher percentage of empty stomachs in the gillnet samples. The SFI (stomach content weight as % of predator weight) does not show lower values for the gillnet samples and also the percentage of empty stomachs is not systematically different between the two sample gears. Also, the percentages of empty stomach are not higher in gillnet samples than in trawl samples. In conclusion, these are good indications that samples from both sampling types can be compared. Funk (2017) supports this conclusion with his findings in the western Baltic Sea. He only found an influence on SFI of the gillnet sample method in summer, when the water temperatures are high and therefore the digestion is faster, and when the soaking times were 48 hours. Both factors do not apply to this study, due to low water temperatures in the winter and a soaking time of less than 24 hours.

Another underlying effect, which could influence the diet of cod and flounder, is the maturity stage, as it has been shown that the diet of fish can change during spawning (Lall and Tibbetts, 2009). The results of the maturity stage show that the majority of analysed cod and flounder in this study are in pre- (Q1 and Q2) or post-spawning (Q4) phases and therefore no underlying trend in diet changes due to different behaviour while spawning is expected.

It is also important to consider that the proportions of some prey species in the stomachs are potentially biased because of different digestion times. For example, it is known that Crustacean are digested more slowly in comparison to fish preys and that Polychaeta are the fastest to be digested (Temming and Herrmann, 2003). Therefore, the relative contribution of crustaceans could have been overestimated, and that of fish underestimated, in the diet of both predators.

In addition, an extrapolation of the study results to other areas should be done with caution, because the diet can vary strongly between areas, as seen in the comparison to other studies and in my results of the cod diet. This is likely due to spatial differences in prey availability influencing the diet composition (Borg, Westerbom and Lehtonen, 2014; Gogina *et al.*, 2016).

4.4 Summary and conclusions

The diet of cod investigated in this study is in line with the general knowledge of the diet of the EBC. In all areas an ontogenetic shift is found with a decrease of benthic prey and an increase of fish preys with size. Polychaeta seems to be an important prey for small cod (6-20 cm) in all areas.

In the coastal area, the share of benthic preys is high (>50% in numbers) over all Lcs. In the offshore areas, conversely, the share of benthic prey decline with fish size.

ICES (2014) show higher cod condition in coastal areas, which might be explained by the higher shares of benthic prey in the diet of cod in the coastal areas. Furthermore, higher percentages (up to 60%) of empty stomach are found for cod in the offshore areas, which could be tentatively explained by a low availability of small crustacean. High percentages of empty stomach have been proposed as an indication of low feeding success (Dziaduch, 2011). Small cod cannot totally compensate for a shortage of benthic prey by increasing predation on fish prey, and this leads to low feeding levels causing growth limitation or starvation (ICES, 2018). This growth deficit can be carried throughout the whole life history of cod (ICES, 2015b) and can therefore be one reason explaining the currently bad state of the EBC.

For the first time, the diet of flounder is investigated in large areas of the Baltic Sea. Overall, the diet of flounder is much more consistent than the diet of cod in relation to predator size and between areas and quarters, which pictures a specialist feeder with a smaller niche width (Järv *et al.*, 2011) compared to cod. Bivalves are the most important prey species, Mytilus sp. and *Mya arenaria* in the coastal area and *Limecola balthica* in the offshore area, as well as Amphipoda and Saduria. The importance of Amphipoda decreases with size, while the importance of Saduria increases.

As seen in the results, Amphipoda and Saduria are important preys for both cod and flounder, but also other prey occur in both predators. Similarity in diet and significant diet overlap were especially found in the offshore area of SD 25 between cod < 30 cm and flounder > 20 cm. This diet similarity is mainly based on high shares of benthic prey (mainly Saduria) in both predators, and occurs when the fish preys share of cod is small. In the offshore area in SDs 26-28 no diet overlap was found, due to the higher shares of fish preys in the diet of cod, which could be explained by a higher availability and smaller sizes of sprat and herring (ICES, 2016b).

The competition for benthic prey found in my study could explain the negative relationship between the population biomass of EBC and flounder stocks using long-term data (Orio *et al.*, 2017b); when one species is present in high abundances could be able to outcompete the other. Also, Persson (1981) 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 preys between cod and flatfishes and that the increase of cod abundance in the 1930s were facilitated by a decrease of this competition. Competition between Gadoids and flatfishes have also been shown for example in the Georges Bank (Link *et al.*, 2015). In the Baltic Sea, the competition between cod and flounder for benthic prey could potentially have increased with the increased extension of hypoxic and anoxic areas in the eastern Baltic Sea (Carstensen *et al.*, 2014). Increasing hypoxia decreases the suitable habitat for cod (ICES, 2016a) and probably also for flounder, therefore it can lead to a higher overlap of cod and flounder in the normoxic areas, where then the feeding competition may increase. Moreover, hypoxia has been shown to directly decrease the availability of benthic prey for cod (ICES, 2014; Casini *et al.*, 2016) due to the benthic animals moving away from oxygen-poor areas or by degradation of benthic communities (Villnäs *et al.*, 2012). The combination of food competition and increasing hypoxia can lead to a shortage of benthic prey with potentiall detrimental effects on cod condition (ICES, 2015b), individual growth (Svedäng and Hornborg, 2014) and maximum length (Orio *et al.*, 2017b). Degredation of benthic habitats is expected to have a larger effect on small cod, which are mostly dependent on benthic preys and are not able yet to feed on pelagic fish like larger cod (ICES, 2018). Another important aspect relates to the nutritional quality of different preys. For instance, the high content of essential fetty acids typical for benthic invertebrates cannot be easily compensated by the availability of other preys and it can present an important limiting factor leading to lower maternal condition and have a negative impact on the reproductive success (ICES, 2018).

In the Baltic Sea, the multispecies assessment and management advice have been focused on the pelagic interactions between cod, sprat and herring, by virtue of their well-known ecology. However, the fish interactions occurring in the benthic habitat are poorly known and this study contributes to shed first light. The results of this study contribute to fill the knowledge gap on the food interactions between two dominant demersal fish species, cod and flounder, in the eastern Baltic Sea. The results of this study can provide fundamental information for futher progresses of multispecies and food-web models and can therefore present an important step forward towards improved Ecosystem-based fisheries management.

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Acknowledgements

First, I want to thank Mikael Ovegård, Anna von Wirth, Magnus Andersson, Baldvin Thorvaldsson, Fredrik Landfors, Fredrik Nilsson and Peter Johannesson for the collection of stomach samples during the BITS Surveys, Anna-Li Jonsson, Anna Lingman, Peter Johannesson and Fredrik Franzen together with the commercial fishers (Olle Viberg and Sven-Ove Nordin), and the SLU student Erik Dalman for the collection of the gillnet samples and Joanna Pawlak and Marzena Pachur at the National Marine Fisheries Research Institute, Gdynia, Poland for the taxonomic identification of the stomachs' content. Without your effort, this study would not have been possible!

My special thanks go to Michele Casini and Alessandro Orio for a great supervision. Your help with the analysis and during the writing progress was amazing! I learned a lot from both of you and you were always there to answer my question. I hope for future collaborations.

Also, I want to thank Christian Möllmann, for giving me the opportunity to write my Master Thesis here at the SLU in Lysekil and organize the formalities with the University of Hamburg. Furthermore, I want to thank Valerio Bartolino for my examination and his useful comments.

Appendix

4.5 Effect of sample gear

Figure A 1 shows the percentage of each digestion stage for cod and flounder separately for the two sample gears. The digestion stage 1, which indicates partial digestion of the prey, is the most common digestion stage with up to 80% records. Digestion stage 2 has higher values for cod caught with trawl and for flounder caught with gillnet. Stage 0 occurs rarely.

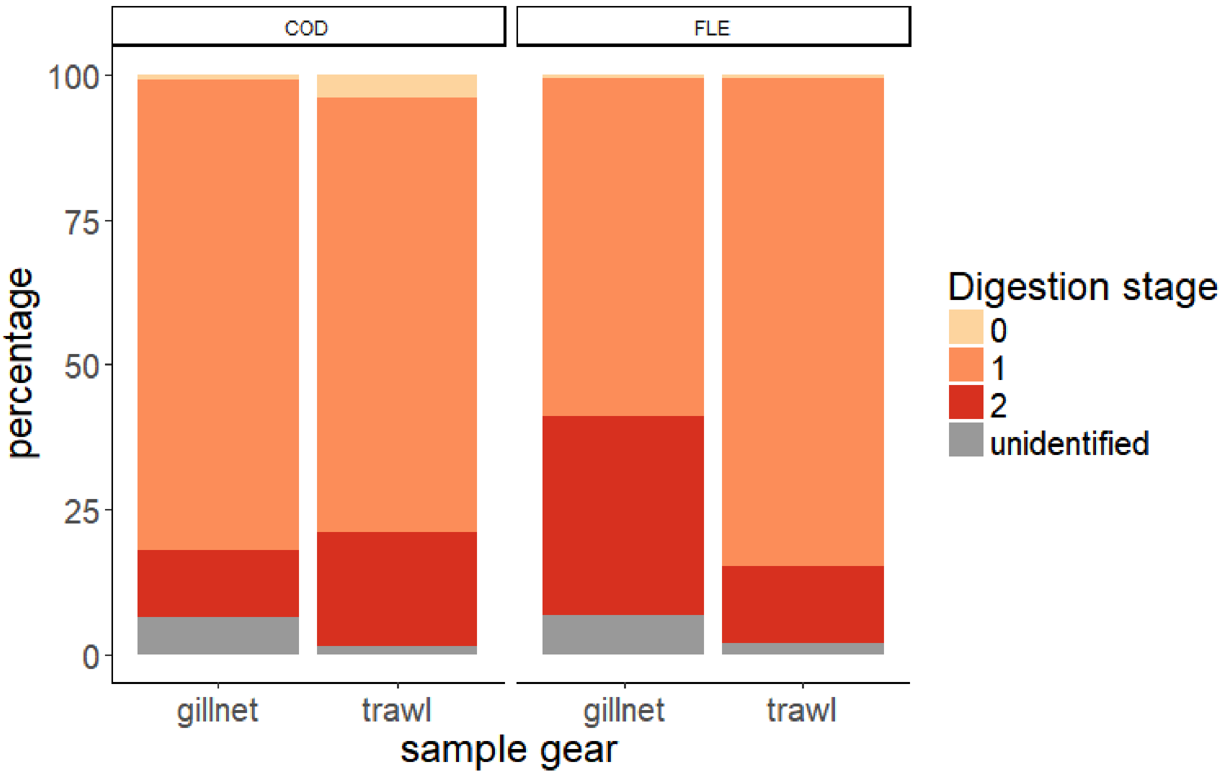

Figure A 1: Percentages of each digestion stage separately for each predator and sample gear.

The stomach content weight as percentage of the predator weight (stomach fullness index, SFI) is shown in Figure A 2 for all predator length class. In general the median SFI is, for both predators, under 5%. The SFI for cod seems to be equal for both sample gears, except for the Lc 41-50 cm, where the SFI is higher for trawl samples. For flounder, the fish in the Lc 8-20 cm seem to have similar SFI between sample gears. The Lc 21-30 cm fish collected by gillnet seem to have a higher SFI compared to the trawl samples. In the Lc > 30cm, the fish collected by trawl have a higher SFI.

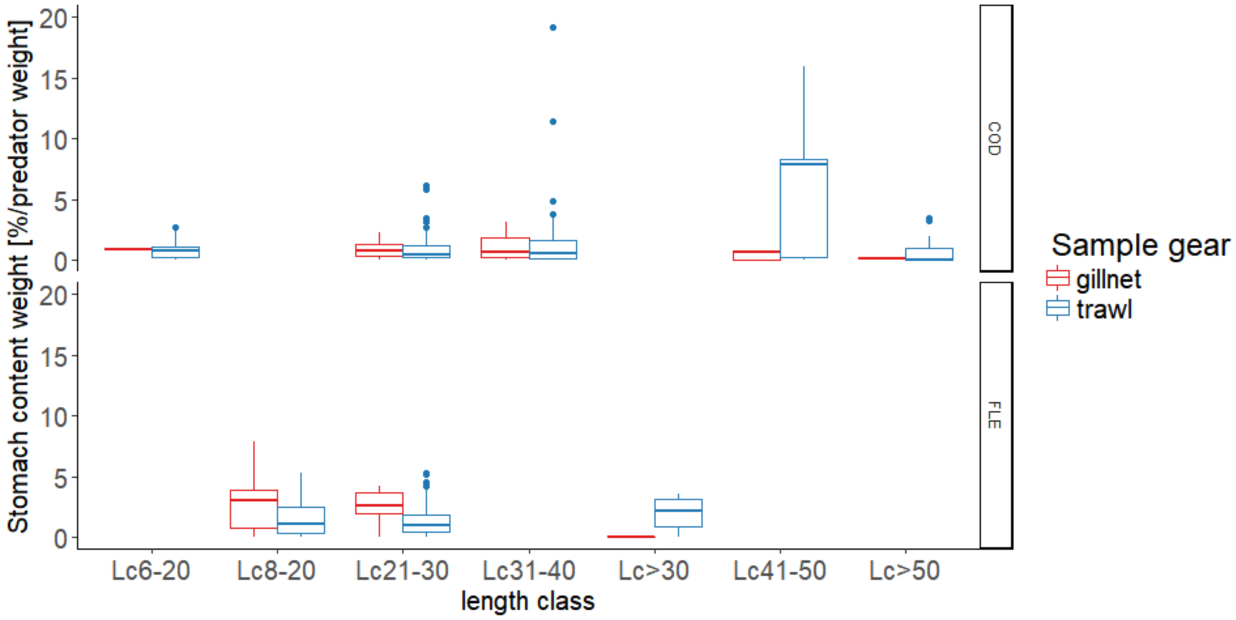

Figure A 2: Stomach content as percent of the body weight from fish, which were caught in quarter 4 of 2015 for each sample type separately. The Boxplot visualizes the median, the 25% and 75% quantile as boxes and the whiskers. Outlier are shown as dots.

For cod the percentage of empty stomachs in every Lcs was higher in the trawl than in the gillnet samples. Also, the Lc with the highest percentage of empty stomachs (Lc 41-50 cm) is the same for both trawl and gillnet samples. For flounder there is no clear trend. In the Lc 0-20 cm the percentage of empty stomachs is higher in the trawl samples. For the next Lc (21-30 cm) the percentage of empty stomachs from the trawl samples is nearly double the one of the gillnet samples. For the largest flounder Lc, the percentage of empty stomachs is nearly equal between sample gears (Figure A 3).

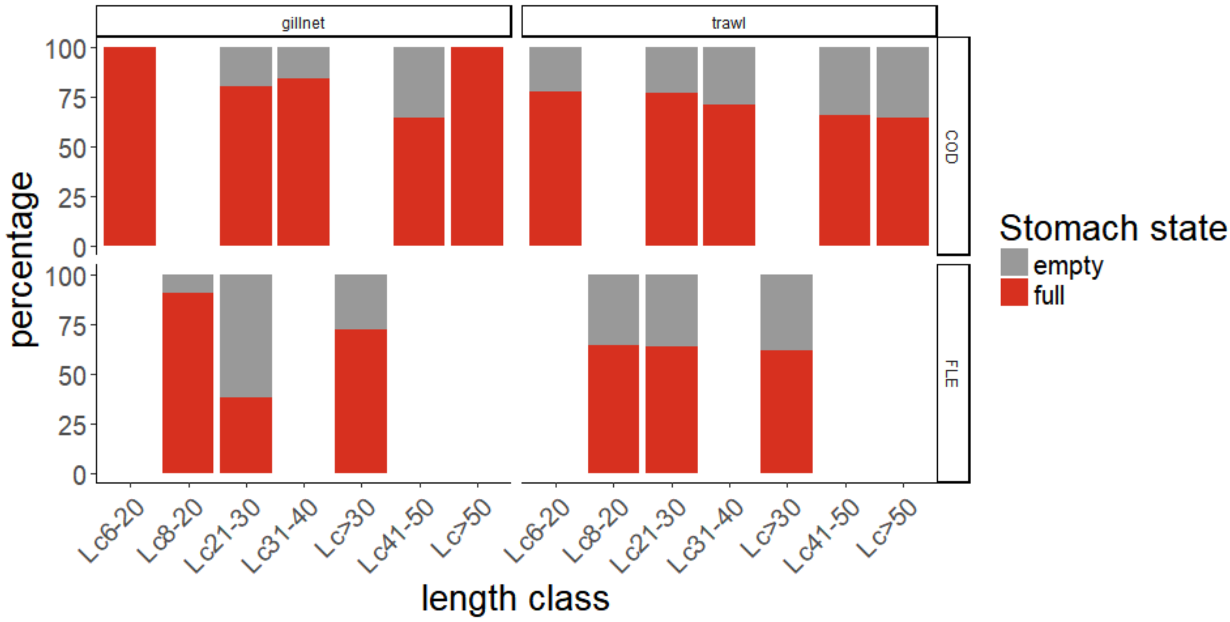

Figure A 3: Percentage of full and empty stomachs for each predator length class and sample gear.

4.6 Composition of other Prey

The composition of the prey categories “other invertebrates” and “other Pisces” differ between the predators and areas.

4.6.1 Coastal area

For cod in the coastal area (Figure A 4) the category “other Pisces” (Figure A 4 A) consists mainly of Gasterosteidae and unidentified Pisces, the category “other invertebrates” (Figure A 4 B) consists mainly of other Isopoda, which are Isopoda of the genus Idotea.

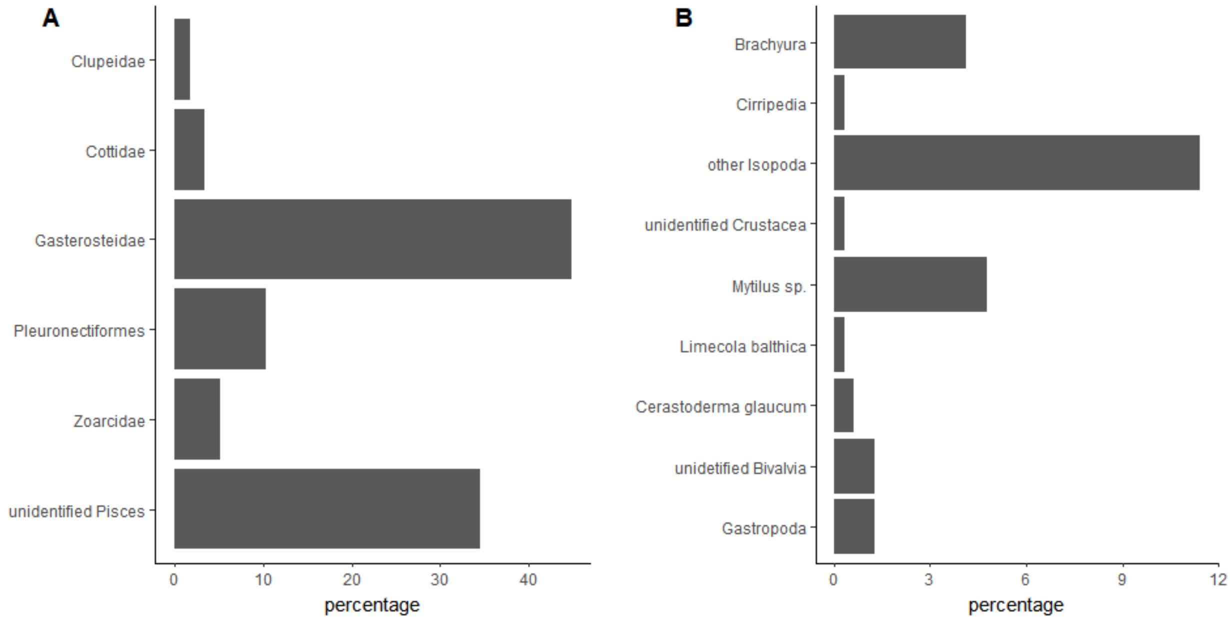

Figure A 4: Percentage of other Pisces (panel A) and other invertebrates (panel B) in the diet of cod from the coastal area.

For flounder in the coastal area (Figure A 5) the category “other invertebrates” consists mainly of Gastropoda of the genus Hydrobia and of other Isopoda of the genus Idotea.

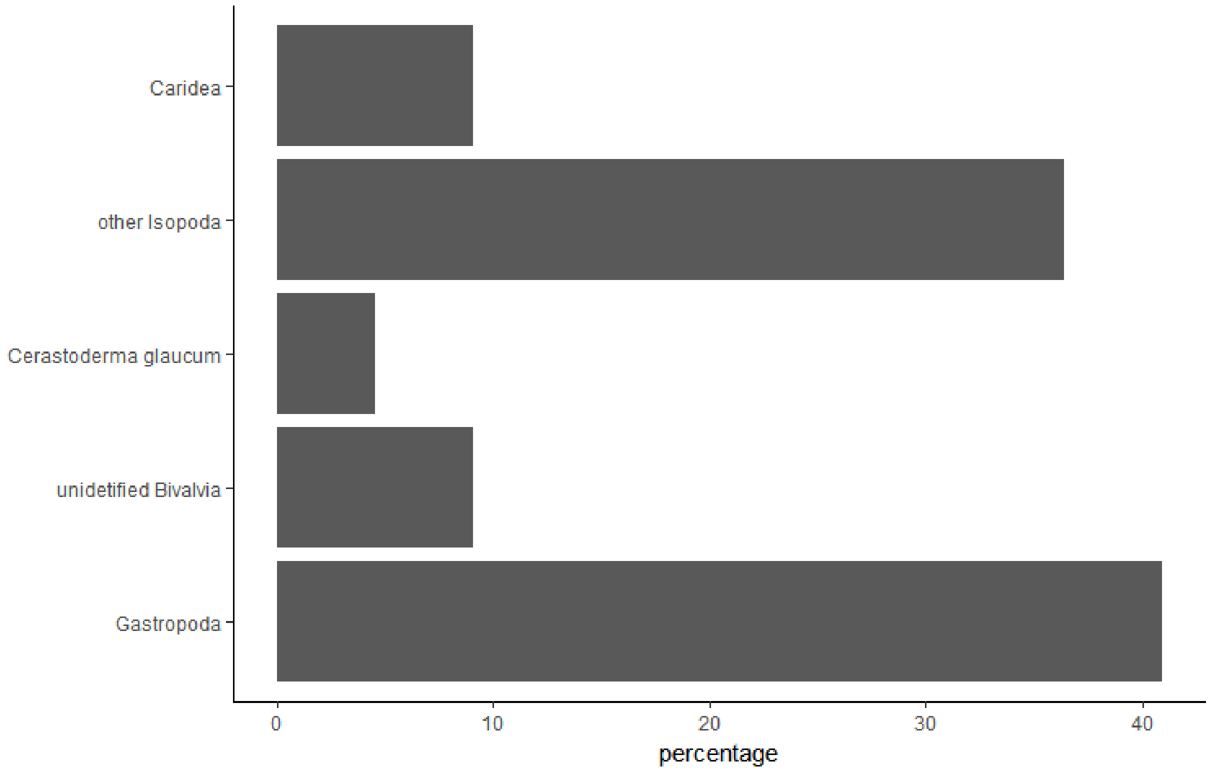

Figure A 5: Percentage of other invertebrates in the diet of flounder from the coastal area.

4.6.2 Offshore area SD 25

For cod in the offshore area in SD 25 (Figure A 6) the category "other Pisces" (Figure A 6 A) consists mainly unidentified Pisces, the category "other invertebrates" (Figure A 6 B) consists mainly of Pripulida.

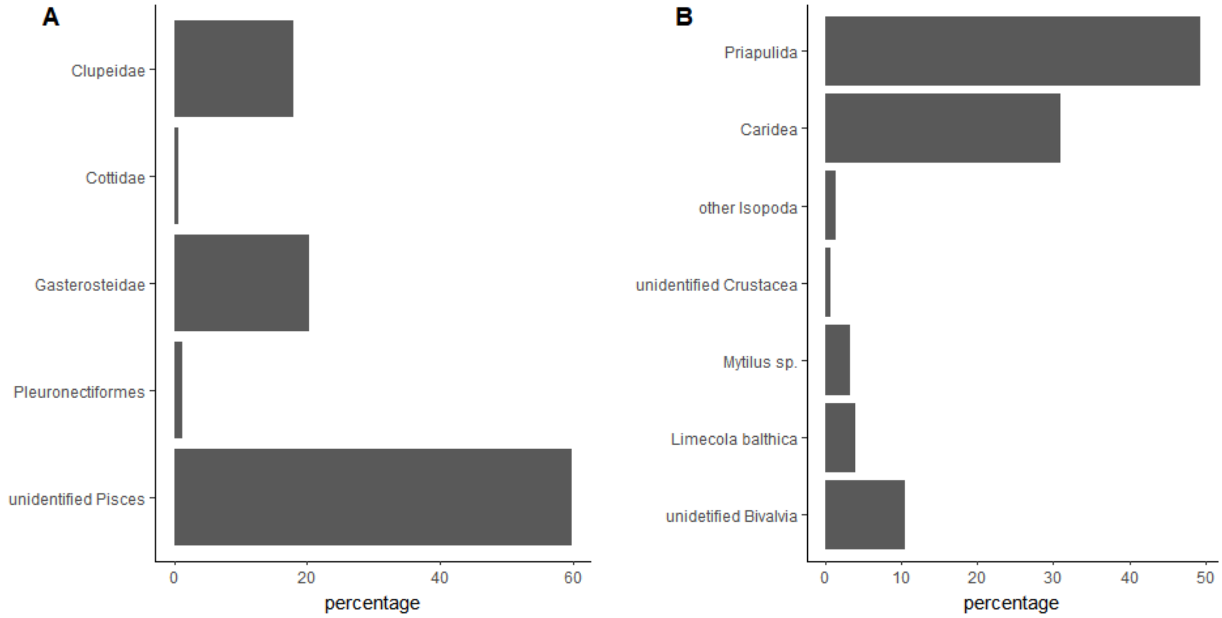

Figure A 6: Percentage of other Pisces (panel A) and other invertebrates (panel B) in the diet of cod from the offshore area in SD 25.

For flounder in the offshore area in SD 25 (Figure A 7) the category "other invertebrates" consists mainly of Polychaeta and of Cumacea.

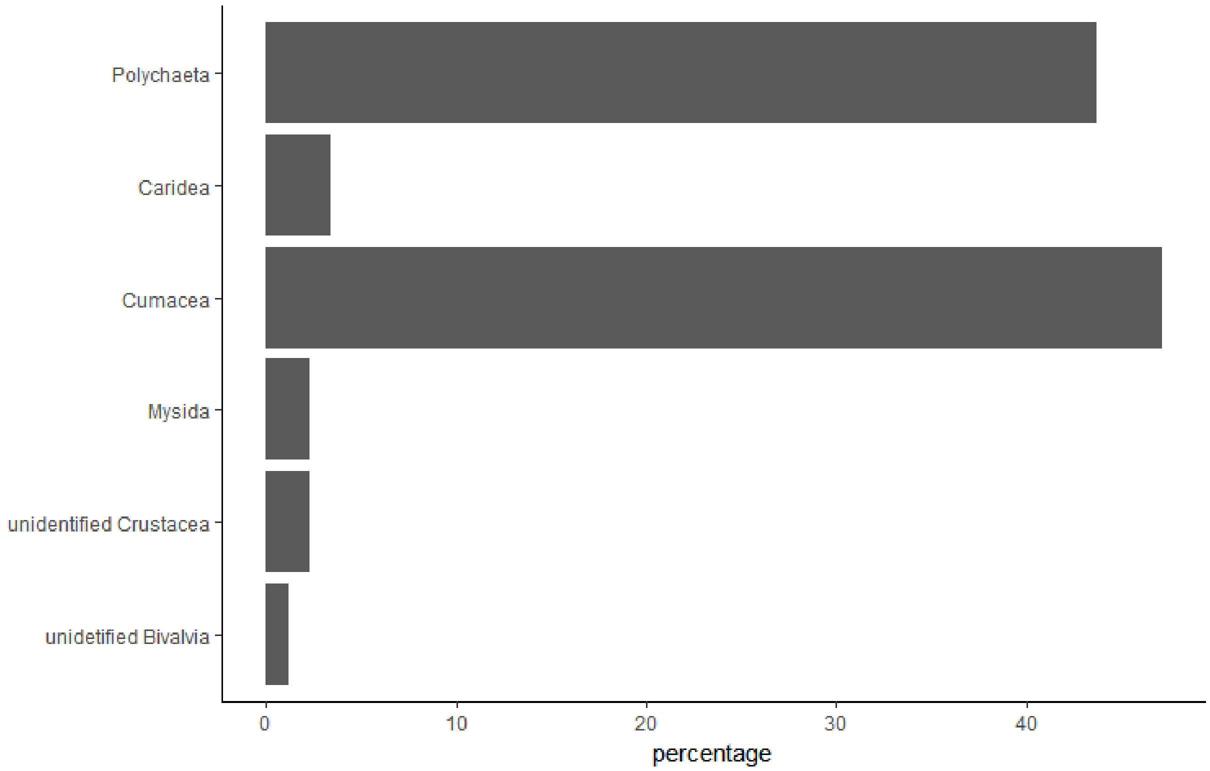

Figure A 7: Percentage of other invertebrates in the diet of flounder from the offshore area in SD 25.

4.6.3 Offshore area SDs 26-28

For cod in the offshore area in SDs 26-28 (Figure A 8) the category “other Pisces” (Figure A 8 A) consists mainly unidentified Pisces and unidentified Clupeidea, the category “other invertebrates” (Figure A 8 B) consists mainly of Caridea.

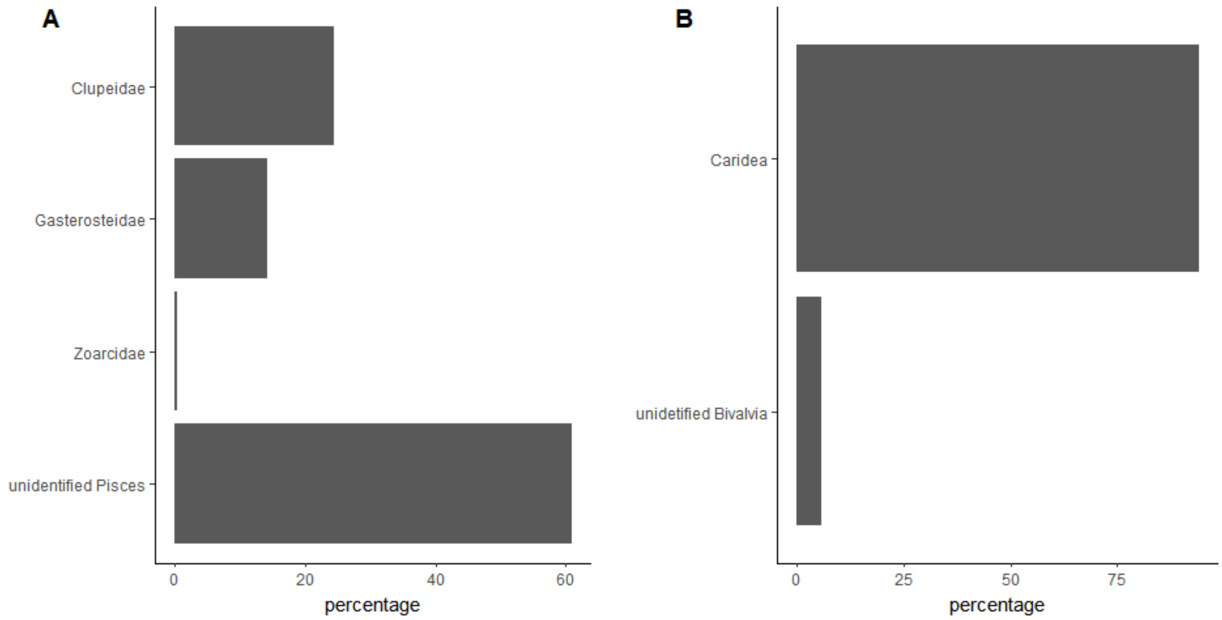

Figure A 8: Percentage of other Pisces (panel A) and other invertebrates (panel B) in the diet of cod from the offshore area in SDs 26-28.

For flounder in the offshore area in SDs 26-28 (Figure A 9) the category “other invertebrates” consists mainly of Polychaeta and of Polychaeta (Figure A 9 A) and Mysida, the categors “Pisces” (Figure A 9 B) consists mainly of unidentified Pisces.

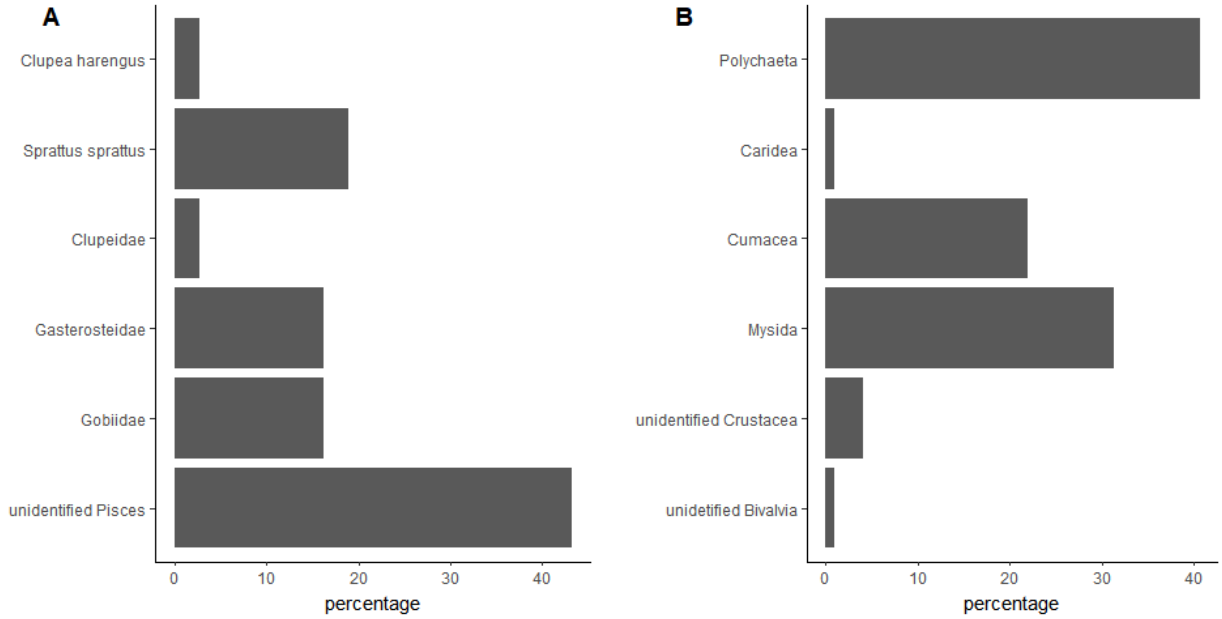

Figure A 9: Percentage of Pisces (panel A) and other invertebrates (panel B) in the diet of flounder from the offshore area in SDs 26-28.

4.7 Prey groups

Table A 1: Table show every prey found in the stomach analysis,how it is grouped and how it is shown in the diet analysis from cod and flounder.

Prey	Prey group	Cod diet	Flounder diet
Polychaeta	Polychaeta	Polychaeta	Polychaeta
Phyllodocida	Polychaeta	Polychaeta	Polychaeta
Hediste diversicolor	Polychaeta	Polychaeta	Polychaeta
Bylgides sarsi	Polychaeta	Polychaeta	Polychaeta
Scoloplos armiger	Polychaeta	Polychaeta	Polychaeta
Priapulida	Priapulida	other invertebrates	Priapulida
Halicryptus sp.	Priapulida	other invertebrates	Priapulida
Halicryptus spinulosus	Priapulida	other invertebrates	Priapulida
Priapulus caudatus	Priapulida	other invertebrates	Priapulida
Crustacea	unidentified Crustacea	other invertebrates	other invertebrates
Carcinus maenas	Brachyura	other invertebrates	other invertebrates
Caridea	Caridea	Caridea (offshore = other invertebrates)	other invertebrates
Crangon crangon	Caridea	Caridea (offshore = other invertebrates)	other invertebrates
Palaemonidae	Caridea	Caridea (offshore = other invertebrates)	other invertebrates
Palaemon sp.	Caridea	Caridea (offshore = other invertebrates)	other invertebrates
Palaemon elegans	Caridea	Caridea (offshore = other invertebrates)	other invertebrates
Saduria entomon	*Saduria entomon*	*Saduria entomon*	*Saduria entomon*
Idotea sp.	other Isopoda	other Isopoda	other Isopoda
Idotea balthica	other Isopoda	other Isopoda	other Isopoda
Amphipoda	Amphipoda	Amphipoda	Amphipoda
Corophium volutator	Amphipoda	Amphipoda	Amphipoda
Gammarus sp.	Amphipoda	Amphipoda	Amphipoda
Monoporeia affinis	Amphipoda	Amphipoda	Amphipoda
Pontoporeia femorata	Amphipoda	Amphipoda	Amphipoda
Cumacea	Cumacea	Cumacea	other invertebrates
Diastylis rathkei	Cumacea	Cumacea	other invertebrates
Mysida	Mysida	Mysida	other invertebrates
Mysidae	Mysida	Mysida	other invertebrates
Mysis mixta	Mysida	Mysida	other invertebrates

Neomysis integer	Mysida	Mysida	other invertebrates
Praunus flexuosus	Mysida	Mysida	other invertebrates
Bivalvia	unidetified Bivalvia	other invertebrates	other invertebrates
Mytilus sp.	*Mytilus sp.*	other invertebrates	*Mytilus sp.*
Limecola balthica	*Limecola balthica*	other invertebrates	*Limecola balthica*
Mya arenaria	*Mya arenaria*	other invertebrates	*Mya arenaria*
Cerastoderma glaucum	*Cerastoderma glaucum*	other invertebrates	other invertebrates
Gastropoda	Gastropoda	other invertebrates	other invertebrates
Hydrobia sp.	Gastropoda	other invertebrates	other invertebrates
Pisces	unidentified Pisces	other Pisces	Pisces
Scales	unidentified Pisces	other Pisces	Pisces
Clupeidae	Clupeidae	other Pisces	Pisces
Clupea harengus	*Clupea harengus*	*Clupea harengus*	Pisces
Sprattus sprattus	*Sprattus sprattus*	*Sprattus sprattus*	Pisces
Gadidae	Gadiformes	Gadiformes (coastal = other Pisces)	Pisces
Gadus morhua	Gadiformes	Gadiformes (coastal = other Pisces)	Pisces
Enchelyopus cimbrius	Gadiformes	Gadiformes (coastal = other Pisces)	Pisces
Pleuronectiformes	Pleuronectiformes	other Pisces	Pisces
Pleuronectidae	Pleuronectiformes	other Pisces	Pisces
Platichthys flesus	Pleuronectiformes	other Pisces	Pisces
Scophthalmus maximus	Pleuronectiformes	other Pisces	Pisces
Gobiidae	Gobiidae	Gobiidae	Pisces
Neogobius melanostomus	Gobiidae	Gobiidae	Pisces
Gobius niger	Gobiidae	Gobiidae	Pisces
Cottidae	Cottidae	other Pisces	Pisces
Myoxocephalus quadricornis	Cottidae	other Pisces	Pisces
Gasterosteidae	Gasterosteidae	other Pisces	Pisces
Gasterosteus aculeatus	Gasterosteidae	other Pisces	Pisces
Pungitius pungitius	Gasterosteidae	other Pisces	Pisces
Spinachia spinachia	Gasterosteidae	other Pisces	Pisces

Zoarces viviparus	Zoarcidae	other Pisces	Pisces
Ammodytidae	Ammodytidae	Ammodytidae (offshore = other Pisces)	Ammodytidae (off-shore = Pisces)
Ammodytes tobianus	Ammodytidae	Ammodytidae (offshore = other Pisces)	Ammodytidae (off-shore = Pisces)
Hyperoplus lanceo-latus	Ammodytidae	Ammodytidae (offshore = other Pisces)	Ammodytidae (off-shore = Pisces)
Remains	remains	excluded	excluded
digestive tract	remains	excluded	excluded
Stone	non food	excluded	excluded
Sand	non food	excluded	excluded
litter	non food	excluded	excluded
Waste	non food	excluded	excluded
Wood	non food	excluded	excluded
Algae	non food	excluded	excluded
Carbon	non food	excluded	excluded