

REGULAR PAPER

# The forgotten feeding ground: patterns in seasonal and depth-specific food intake of adult cod *Gadus morhua* in the western Baltic Sea

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## Abstract

This study presents the diet composition of western Baltic cod *Gadus morhua* based on 3150 stomachs sampled year-round between 2016 and 2017 using angling, gillnetting and bottom trawling, which enhanced the spatio-temporal coverage of cod habitats. Cod diet composition in shallow areas (<20 m depth) was dominated by benthic invertebrate species, mainly the common shore crab *Carcinus maenas*. Compared to historic diet data from the 1960s and 1980s (limited to depth >20 m), the contribution of herring *Clupea harengus* decreased and round goby *Neogobius melanostomus* occurred as a new prey species. Statistical modelling revealed significant relationships between diet composition, catch depth, fish length and season. Generalized additive modelling identified a negative relationship between catch depth and stomach content weight, suggesting reduced food intake in winter when cod use deeper areas for spawning and during peak summer when cod tend to avoid high water temperatures. The results of this study highlight the importance of shallow coastal areas as major feeding habitats of adult cod in the western Baltic Sea, which were previously unknown because samples were restricted to deeper trawlable areas. The results strongly suggest that historic stomach analyses overestimated the role of forage fish and underestimated the role of invertebrate prey. Eventually, this study shows the importance of a comprehensive habitat coverage for unbiased stomach sampling programmes to provide a more reliable estimation of top predator diet, a key information for food web analyses and multispecies models.

## KEYWORDS

Atlantic cod, Belt Sea, diet composition, feeding ecology, stomach content analysis, western Baltic cod

## 1 | INTRODUCTION

Fisheries management is still mostly based on single species models, although multispecies and ecosystem-based management approaches

gain more and more importance in fisheries science and are increasingly implemented. A high variety of different multispecies modelling approaches were developed in the past decades such as multispecies virtual population analyses (e.g., for the Baltic Sea: Horbowy, 1989;

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Neuenfeldt & Köster, 2000), multivariate autoregressive models (e.g., for the Baltic Sea: Lindegren *et al.*, 2010), dynamic models (e.g., for the Baltic Sea: Heikinheimo, 2011), physiological structured models (e.g., for the Baltic Sea: Van Leeuwen *et al.*, 2008), Ecosim with Ecopath models (e.g., for the Baltic Sea: Harvey *et al.*, 2003; Tomczak *et al.*, 2012) or spatially disaggregated models (e.g., for the Baltic Sea: Lindegren *et al.*, 2014). One major aspect in all these approaches is the linkage between species of different trophic levels in an ecosystem based on predator–prey interactions.

Such information is traditionally derived from stomach databases. Nonetheless, these models and even new modelling approaches are often based on predator–prey interactions derived from historic stomach sampling projects, such as from the “year of the stomach” in 1991 in the North Sea (e.g., Stäbler *et al.*, 2019). Despite recent changes in many coastal marine ecosystems (e.g., Byrnes *et al.*, 2007; Norkko *et al.*, 2007; Sala *et al.*, 2004), efforts for new stomach sampling projects are scarce. Therefore, the reliability and quality of many model outputs may be limited by diet data that are potentially outdated and biased because of incomplete historical sampling designs.

Unlike the North Sea, in the Baltic Sea stomach sampling has been conducted on a relatively regular basis, at least with regard to the commercially most important demersal fish species, Atlantic cod *Gadus morhua* (e.g., Arntz, 1974, 1977; Casini *et al.*, 2016; Dziaduch, 2011; Hüsey *et al.*, 1997; Pachur & Horbowy, 2013; Schulz, 1987, 1988, 1989a, 1989b; Weber & Damm, 1991; Zarkeschwari, 1977). Cod is considered the apex predator in the Baltic Sea, and major efforts were invested to improve the understanding of its trophic role. In the Baltic Sea, two cod stocks are distinguished, which display differences in genotype, phenotype and life-history traits (Berner & Vaske, 1985; Bleil & Oeberst, 2005; Hüsey *et al.*, 2016; Nielsen *et al.*, 2003; Paul *et al.*, 2013; Sick, 1965; Weist *et al.*, 2019). Western Baltic cod (WBC) is generally distributed in the shallower basins in the more saline west (i.e., in the Belt Sea, in the Sound and in the Arkona Sea), whereas the eastern Baltic cod (EBC) mainly uses the deeper basins in the less saline east such as the Bornholm and the Gdansk basin. The main distributional areas of the two cod stocks differ remarkably in oceanographic conditions and also in prey availability and composition. In the past decades the diet studies mainly focused on the role of EBC in the eastern Baltic food web (e.g., Casini *et al.*, 2016; Dziaduch, 2011; Hüsey *et al.*, 1997; Kulatska *et al.*, 2019; Pachur & Horbowy, 2013). These studies revealed that currently EBC relies strongly on Clupeid prey species such as herring *Clupea harengus* and sprat *Sprattus sprattus*, whereas benthic invertebrates such as the isopod *Saduria entomon* play only a minor, although from a nutrient perspective likely important, role in the overall food intake of EBC (Casini *et al.*, 2016; Neuenfeldt *et al.*, 2019; Røjbek *et al.*, 2014).

The only available studies focusing on the feeding ecology of cod in the western Baltic Sea (WBS) originated from stomach samplings between the 1960s and 1980s (Arntz, 1974, 1977; Schulz, 1987, 1988, 1989a, 1989b; Weber & Damm, 1991; Zarkeschwari, 1977). These data are most likely not representing the current ecological situation because of substantial changes in the hydrographic conditions and ecological status of the Baltic Sea in the past decades (Mohrholz

*et al.*, 2015; Möllmann *et al.*, 2009). Concurrent to these ecological changes, prey availability of cod has changed since the 1980s. For example, western Baltic spring spawning herring *C. harengus*, which was one of the main prey species of WBC in the historic diet studies (Schulz, 1987, 1988, 1989a, 1989b; Weber & Damm, 1991), showed a steady decrease in spawning stock biomass since the 1990s (ICES, 2019b, 2019c). Thus, herring might be less available as prey for WBC. Moreover, the establishment of new invasive species in the WBS, such as the round goby *Neogobius melanostomus* (unpubl. data cited in Corkum *et al.*, 2004; Hempel, 2017; Oesterwind *et al.*, 2017), may provide new feeding opportunities for WBC similar to recent observations for EBC (Pachur & Horbowy, 2013).

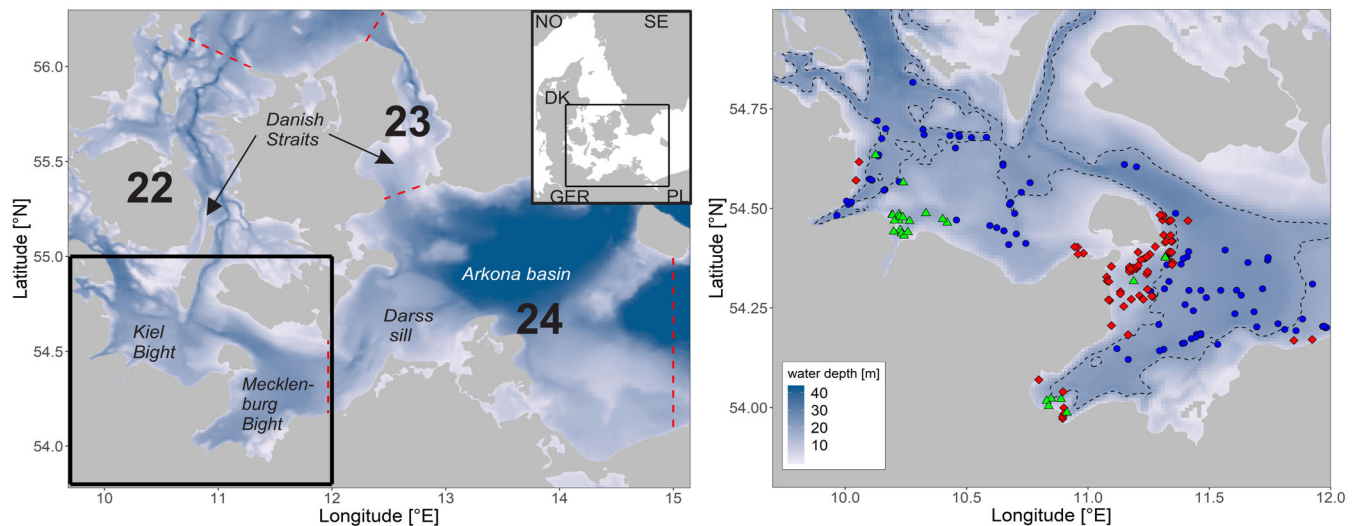
In addition to the likely changed food supply, historical cod diet studies in the WBS have been biased spatially because shallower regions (<20 m depth) were heavily underrepresented in the stomach sampling programmes, despite the fact that they account for 60% of the total WBS (i.e., of the ICES subdivisions [SD] 22, 23 and 24) (ICES, 2017) (Figure 1). Furthermore, only scientific trawl surveys and standardized otter trawl gear were used to sample stomachs. Shallower areas are often characterized by hard bottom structures, such as gravel, cobbles, boulders and rocky reef structures, posing a high risk of damaging otter trawl gear, and therefore are usually not covered by towed-gear sampling. Therefore, scientific trawling and related stomach sampling were and still are severely limited to known trawlable sites, that is, mostly soft bottom structures in depth >20 m. Nonetheless, adult cod in the WBS make intensive use of shallow-water habitats (<20 m depth) (Funk *et al.*, 2020), leading to the hypothesis that shallow-water areas have been overlooked, although they are likely playing an important role for food acquisition of WBC.

In this study, the authors present a comprehensive analysis of the contemporary feeding ecology of adult cod in the WBS based on year-round stomach samplings from February 2016 to December 2017. To enhance spatial and temporal coverage of the sampling, cod stomachs were collected using a variety of fishing gears (i.e., gillnets, otter trawl gear and fishing rods) and data sources (i.e., commercial samples, scientific surveys and recreational fisheries). This multi-source data set was used to analyse seasonal patterns in length- and depth-specific food intake and diet composition. Finally, the authors assessed the potential bias that can arise in the stomach data if shallow-water habitats are not considered, as has often been the case in previous stomach sampling programmes.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

The study area was located in the Kiel Bight and the Mecklenburg Bight (Figure 1), the two major basins of the Belt Sea, ICES SD22. The Belt Sea is a stratified, brackish-water area (common salinity range: 10–25 psu) that forms together with the Sound (SD23) and the Arkona Sea (SD24) the WBS. SD22 is a relatively shallow area. Areas shallower than 20 m water depth amount to a total of 70% of SD22,



**FIGURE 1** Bathymetric map of the western Baltic Sea (WBS) (a) and of the study area (b). Numbers in the overview map indicate the three ICES subdivisions (SDs) in WBS, the Belt Sea (SD 22), the Sound (SD 23) and the Arkona Sea (SD 24). Dashed red lines indicate SD borders. The black rectangle indicates the position of the sampling area in the WBS. Coloured symbols display stomach sampling locations per fishing gear (red diamonds – gillnetting, blue circles – trawling, green triangles – angling). Dashed black lines indicate 20 m depth contour line

and areas shallower than 10 m still cover 29% (Figure 1; ICES, 2017). The Belt Sea is microtidal (tidal range: c. 10 cm) and characterized by wind-induced fluctuations in hydrography (Leppäranta & Myrberg, 2009; Snoeijs-Leijonmalm & Andrén, 2017), mainly because of changes in inflow of more saline bottom water from the north (Kattegat) and surface outflow from the east (central Baltic Sea) through the Danish Straits and the Darss sill (Figure 1a). SD22 is the distributional core area of the WBC *G. morhua* stock, and mixing with EBC *G. morhua callarias* is considered negligible (ICES, 2019a), although recent findings of McQueen *et al.* (2019) suggest that some EBC may be resident in the Belt Sea.

## 2.2 | Stomach sampling

A total of 3350 cod stomachs were collected on 76 fishing trips in the Belt Sea (Figure 1) between February 2016 and December 2017. The authors used stomach samples from scientific surveys and commercial fishing (gillnetting and trawling), and recreational fishing (angling) to maximize depth, habitat and seasonal coverage (Figure 1). A detailed description of the sampling methods and the processing of the samples is given in the Supporting Information S1.

Cod sampling and removal in the course of the study (including all sources: commercial fishing, scientific surveys and recreational fishing) were always carried out in strict compliance with the legal framework of the German Animal Welfare Act (Deutsches Tierschutzgesetz TierSchG).

## 2.3 | Length classes

Body length of cod sampled for stomach analysis ranged between 11 cm and 107 cm. The size ranges differed strongly between sampling

methods. Because individuals <31 cm (*i.e.*, smaller than the minimum conservation reference size of 35 cm) were mostly caught during the research trawl surveys, the authors decided to retain only individuals  $\geq 31$  cm ( $N = 2919$ ) for further data analysis. For the investigation of length-specific diet composition, individuals were classified into five length classes: 31–40 cm, 41–50 cm, 51–60 cm, 61–70 cm and >70 cm.

## 2.4 | Stomach content analysis

Cod stomach samples were defrosted and adherent veins were carefully removed from the outer stomach tissue. Adherent water was removed for c. 5 s with paper tissues and stomachs were weighed (accuracy: 0.001 g). Subsequently, stomachs were opened and the contents and mucus were thoroughly removed before the empty stomachs were weighed.

Stomach content weights (SCW) were derived from the differences between full ( $W_{FS}$ ) and empty ( $W_{ES}$ ) stomach weights. Prey organisms were identified to species level (mostly fish and decapods), order level (*e.g.*, for Peracarida), class level (*e.g.*, for Echinodermata and Mollusca) or only to phylum level (*e.g.*, for Annelida). If the digestion of the prey was already progressed very far to allow identification to the levels described earlier, items were allocated to the categories unidentified fish, unidentified crustaceans or unidentified invertebrates.

For each prey item, the mass ( $W_{Prey}$ ) was determined (accuracy: 0.001 g). The weight of mucus was determined by calculating the difference of mass of SCW and the sum of  $W_{Prey}$ . The authors tested for bias caused by gear-effects by statistically comparing SCW (Supporting Information S2). No significant differences could be detected. Therefore, gear effects were considered negligible. Hence, all stomach samples were treated equally in subsequent data analysis.

## 2.5 | Standardization of prey weights

Larger predators are able to eat larger and heavier prey organisms or simply a larger total amount than smaller individuals. By calculating the mean diet composition of a length class, an unintended bias may occur. The authors applied a length-standardization approach of prey weights to prevent unintended higher weighting of stomach contents of larger cod in mean calculations of diet compositions per length classes. SCW of each predator of a given length in a certain length class were standardized to the length of a medium-sized predator (i.e., geometrical mean length of the fish in a given length class), while keeping the relative diet compositions constant. For this purpose, a weight-based standardization approach was used (Brenner *et al.*, 2001) and modified it to predator length. Here, a power function was used to describe the relationship between empty stomach weight and fish length ( $N = 2919$ , adjusted  $R^2 = 0.85$ ,  $a = 8.32 \times 10^{-6}$ ,  $b = 3.69$ ).

$$W_{ES} = a \times L_{Pred}^b \quad (1)$$

where  $W_{ES}$  is the weight of empty stomachs (in g),  $a$  is the coefficient,  $L_{Pred}$  is the cod total length (in cm) and  $b$  is the exponent.

Estimates for  $a$  and  $b$  as well as the geometric mean length per length class were then used for the modified standardization approach:

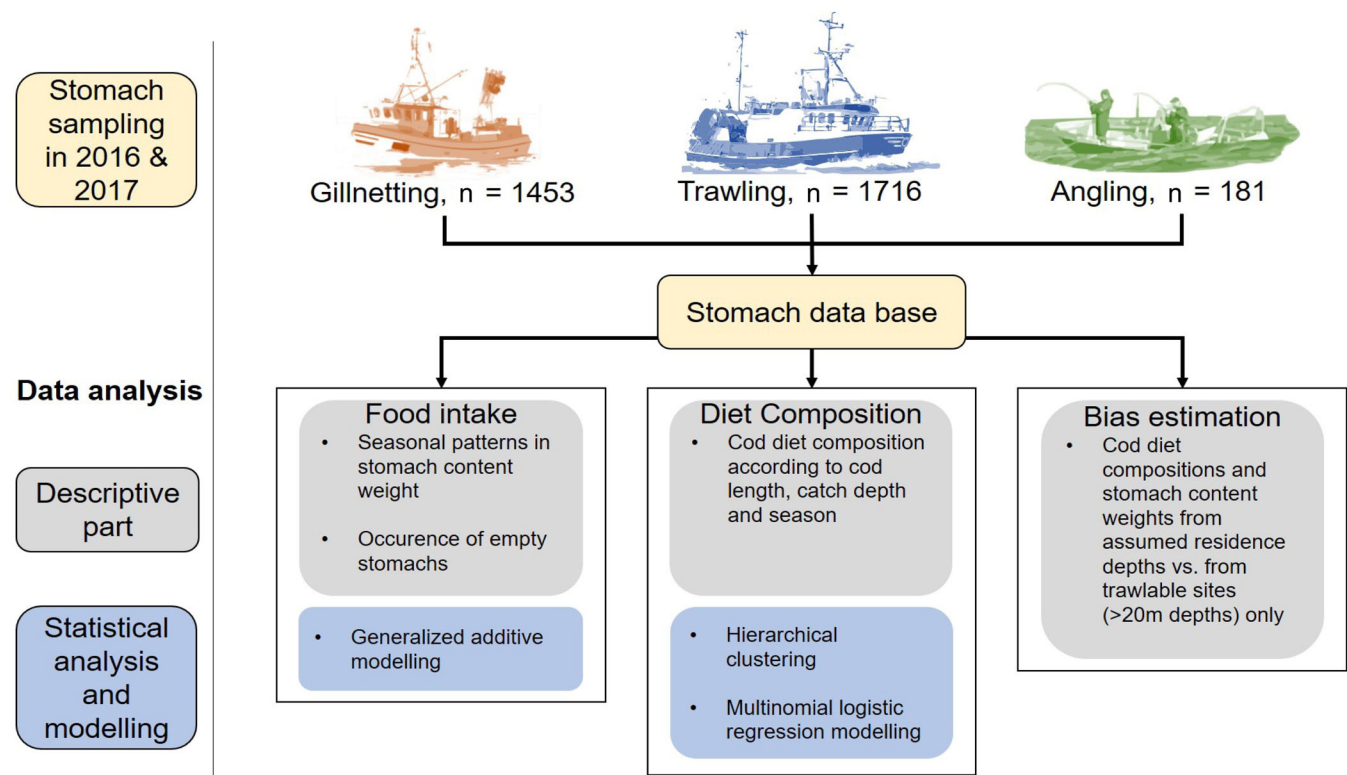
$$W_{Prey(stand)ij,k} = \frac{W_{Prey,ij,k} \times a \times GM_k^b}{a \times L_{Pred,j}^b} \quad (2)$$

where  $W_{Prey(stand)ij,k}$  is the length standardized weight of prey  $i$  observed in predator  $j$  and length class  $k$ ,  $W_{Prey,ij,k}$  is the weight of prey  $i$  observed in predator  $j$  and length class  $k$ , coefficients  $a$  and  $b$  taken from Equation (1),  $GM_k$  is the geometric mean length of length class  $k$  and  $L_{Pred,j}$  is the total length of predator  $j$ .

## 2.6 | Amounts of food intake

A first indicator of food intake is the proportion of empty stomachs. The authors compared the proportion of empty stomachs per length classes and per month to identify the factors related to their higher occurrence.

Generalized additive modelling (GAM) was applied to investigate the variations in food intake, measured by SCW (Figure 2). In general, SCW showed a distribution skewed towards lower values. Therefore, the authors chose to use log-transformed SCW as the response variable for their statistical modelling approach. The authors tested for length- and depth-specific effects using body length and depth stratum as explanatory variables. The continuous variable temperature at depth accounted for the seasonal effects. Water temperature data were taken from the MARNET temperature measurement system provided from the Bundesamt für Seeschifffahrt und Hydrographie and recorded at the measuring positions at Kiel Lighthouse, Darss sill and Fehmarn Belt buoy (BSH; <https://www.bsh.de>). Daily mean water



**FIGURE 2** Schematic diagram of the workflow of the study.  $N$  displays the number of stomachs sampled per sampling method



temperatures for every 5 m depth stratum were calculated over all three measuring positions and allocated to cod samples. In the GAM, nonlinearity is represented by smoothing terms (Hastie & Tibshirani, 1986). Model selection was conducted through a backward selection procedure using AIC (Akaike, 1974). The authors selected the more complex model only if the  $AIC + 2 \leq AIC$  of the less complex model. Performance and assumptions (normality and homogeneity of residuals) of all set-up models were checked by carefully reviewing model validation plots. The authors also tested for different interaction terms between the explanatory variables starting with a model including three interaction terms that is between all three explanatory variables. (GAM incl. 3 int.) going to a GAM not including any interaction term (GAM without int.). Model selection via AIC revealed the GAM incl. 3 int. the best model ( $AIC_{GAM \text{ incl. 3 int.}} = 9040.27$ ;  $AIC_{GAM \text{ without int.}} = 9190.87$ ). Nonetheless, because of a limited number of data, the predictions of the model including interaction terms were found to be highly influenced by a few extreme values leading to high-nonlinearity in interaction terms, which make no biological sense, whereas the additional explained variance was only marginal (adjusted  $R^2_{GAM \text{ incl. 3 int.}} = 44.8\%$  and adjusted  $R^2_{GAM \text{ without int.}} = 41.6\%$ ). Therefore, the authors decided to discard interactions between variables in the GAM (see also Section 4.3). After choosing the model without interaction terms as their final model, the authors selected the optimal effective degrees of freedom (edfs) for the smoothing terms on depth stratum, water temperature at depth stratum and body length variables using a set validation approach (James *et al.*, 2013). In the different model runs,  $k$  was set to values between 3 and 6 for each of the smoothing terms. Model performances of the different model runs were always cross-checked by carefully reviewing validation plots (*i.e.*, models with a smaller or higher  $k$  were preferred only if they did not show significantly worse model performance and did not violate assumptions such as normality and homogeneity of residuals). R code for all set-up GAM models will be shared on request. The finally selected GAM for log-transformed SCW ( $g$ ) was described by:

$$\text{Log}(\text{SCW}(g)_i) = \beta_0 + s(T [^\circ\text{C}]_i, k=3) + s(D[m]_i, k=3) + s(L [cm]_i, k=3) + \varepsilon_i \quad (3)$$

where  $\beta_0$  is the intercept,  $s$  is the smoothing term,  $k$  is the effective degrees of freedom +1,  $T$  is the temperature at catch depth,  $D$  is the catch depth,  $L$  is the body length and  $\varepsilon_i$  is the error term.

## 2.7 | Relative diet compositions

The authors discarded the empty stomachs ( $N = 467$ , 16%) from further diet composition analysis and calculated mean weights per prey type, predator length class and 5 m depth stratum using SCW. They first calculated monthly means and subsequently used these to calculate quarterly means to avoid unintended weightings resulting from unbalanced sample numbers between months. The authors used quarterly intervals (1: January to March, 2: April to June, 3: July to

September, 4: October to December) as a proxy for seasonality, reflecting winter, spring, summer and autumn, respectively.

The authors allocated all organisms observed in the stomachs into 11 main prey groups: Annelida, the common shore crab *Carcinus maenas*, Clupeiformes, Echinodermata, Mollusca, Peracarida, Pleuronectiformes, other invertebrata, other fish (defined as all non-Clupeiformes species and non-Pleuronectiformes species and including also unidentified fish; Supporting Information S1), other crustaceans (including unidentified crustaceans) and other prey. For the statistical analysis [clustering (Section 2.8) and multinomial logistic regression (Section 2.8)], stomachs containing at least one of the main prey groups listed earlier were only used ( $N = 2275$ ).

## 2.8 | Diet clusters and relationships with depth, length and season

To capture the variations in diet composition within depth stratum, season and length classes, all samples in a cluster analysis were considered (Figure 2). Ward's hierarchical agglomerative clustering (Murtagh & Legendre, 2014) was applied based on Euclidean distances of relative diet compositions between all stomach samples to identify patterns in cod diet compositions. The appropriate number of diet clusters was selected by estimating the “elbow” of a scree plot displaying calculated cluster distances (cluster height) against the corresponding numbers of clusters. (Screeplot and cluster dendrogram are given in the Supporting Information S5.)

Seasonal, depth-specific and length-specific effects determining the membership to diet clusters were analysed using multinomial logistic regression modelling (Figure 2). The identified diet cluster membership for every stomach was used as a categorical polytomous response variable. The authors used depth stratum and predator length as continuous explanatory variables accounting for depth- and length-specific effects on the diet composition. They accounted for seasonal effects by implementing quarter as a factor variable. A number of models including different interaction terms among explanatory variables were tested. Model selection was conducted through a backward selection procedure using AIC as described for the GAM modelling earlier. In the multinomial logistic regression modelling the first diet cluster (later termed as “other fish cluster”; Section 3.4) was used as a reference category. The final model included body length, depth stratum and quarter as explanatory variables and interaction terms between the explanatory variables.

$$\ln\left(\frac{\pi_i}{\pi_{\text{ref.}}}\right) = \alpha_i + \beta_{1i}x_1 + \dots + \beta_{ni}x_n \quad (4)$$

where  $\pi_{\text{ref.}}$  is the probability of membership in reference cluster,  $\pi_i$  is the probability of membership in cluster  $i$ ,  $\alpha_i$  is the intercept for cluster  $i$ ,  $\beta_{1i} \dots \beta_{ni}$  are the coefficients for variables 1 to  $n$  and  $x_1 \dots x_n$  are the variables 1 to  $n$ .

For validating the goodness of the fit of the chosen multinomial logistic regression model, McFadden's Pseudo  $R^2$  was calculated (McFadden, 1974):

$$R^2_{\text{McFadden}} = 1 - \frac{\log(L_c)}{\log(L_{\text{null}})} \quad (5)$$

where  $L_c$  is the maximized likelihood of the finally chosen multinomial logistic regression and  $L_{\text{null}}$  is the maximized likelihood of the null model.

## 2.9 | Potential bias from limited depth coverage

The authors quantified the potential bias in estimating cod feeding ecology if relying only on limited depth-coverage (Figure 2). The authors compared contemporary quarterly diet compositions and SCW of cod sampled in depth >20 m, which reflect the traditional trawlable sites covered in previous diet investigations of Belt Sea cod (Arntz, 1977; Weber & Damm, 1991) with those from cod sampled at their preferred habitat sites, estimated by their assumed residence

**TABLE 1** Median catch depth for targeted cod fishery per quarter selected by gillnet fishers in the Belt Sea and allocated 5 m depth strata

Quarter	Quarterly median depth (m)	Allocated 5 m depth strata (m)
1	19	16–20
2	10	6–10
3	8.25	6–10
4	6	6–10

Note: Data derived from Funk *et al.* (2020).

depths (ARDs) (Table 1). For the estimation of the ARDs, the authors used information on the monthly selected fishing depths of local gill-net fishers for targeted cod fishery in the Baltic Sea taken from Funk *et al.* (2020).

## 2.10 | Software used

All calculations and computations were run within the statistical software and programming environment R (R Development Core Team, 2017) using the packages, *nnet* (Venables & Ripley, 2002), *mgcv* (Wood, 2011), *plyr* (Wickham, 2011), *reshape2* (Wickham, 2007), *ggplot2* (Wickham, 2009), *cowplot* (Wilke, 2017), *visreg* (Breheny & Burchett, 2017) and *mapdata* (Brownrigg, 2018).

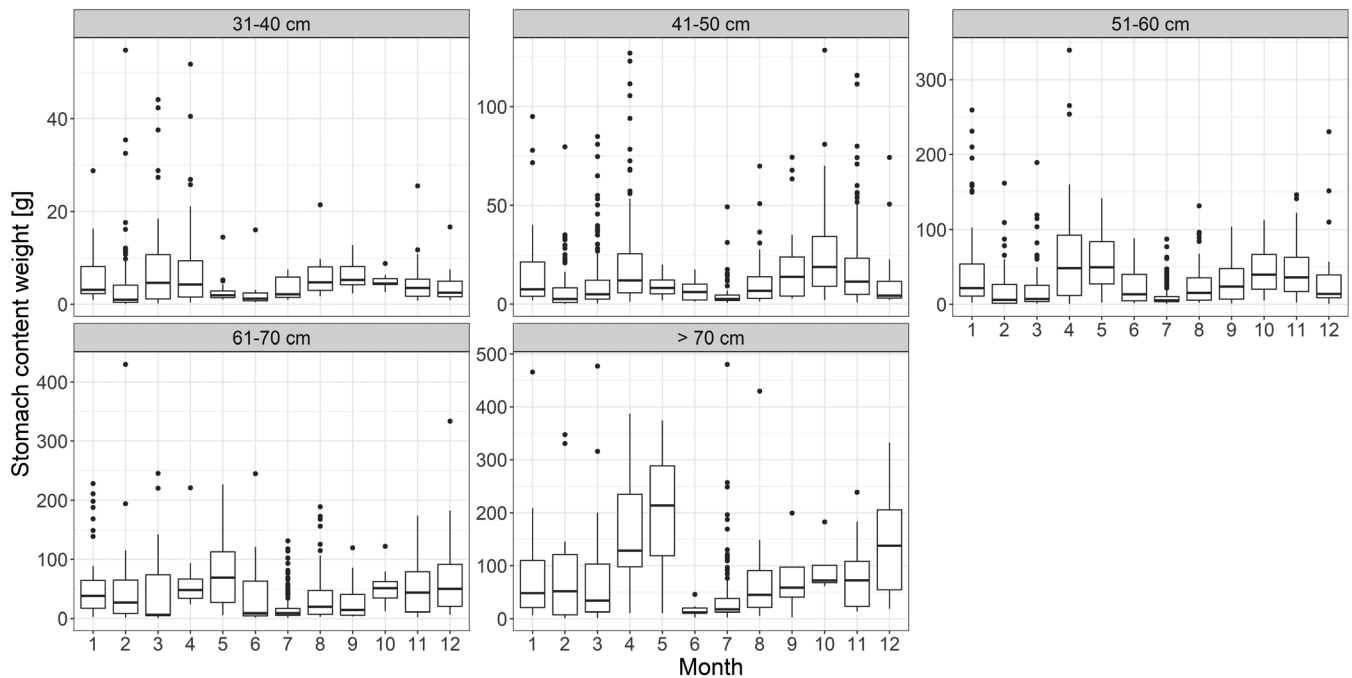
## 3 | RESULTS

### 3.1 | Stomach content weight and empty stomachs

The proportion of empty stomachs varied among the length classes between 14% (length class 51–60 cm) and 27% (length class >70 cm) (Table 2). Monthly variations in the share of empty stomachs were found within all predator length classes. Except for the smallest length class (*i.e.*, 31–40 cm), all cod showed higher shares of empty stomachs in summer months (*i.e.*, between June and August). The highest share of empty stomachs was observed in July for cod >70 cm with 52%. Moreover, high proportions of empty stomachs were observed in February, ranging among length classes between 14% and 27%, except for the largest length class, where only 6% of empty stomachs occurred (Table 2).

**TABLE 2** Number of *Gadus morhua* stomach samples (N) and relative abundance of empty stomachs (in %) per length class and month sampled between February 2016 and December 2017 in the Belt Sea (SD22)

Month	Length class									
	31–40 cm		41–50 cm		51–60 cm		61–70 cm		>70 cm	
	N	Empty (%)	N	Empty (%)	N	Empty (%)	N	Empty (%)	N	Empty (%)
January	30	3	28	7	57	12	44	5	22	5
February	158	27	145	26	66	24	28	14	16	6
March	60	5	172	12	63	6	19	5	39	15
April	36	11	102	9	62	10	11	0	5	20
May	18	17	13	23	50	8	26	12	10	10
June	8	13	23	4	33	6	43	28	6	17
July	7	14	81	23	147	22	165	34	120	52
August	8	0	31	23	93	19	96	22	30	13
September	7	0	23	17	37	14	24	21	4	0
October	7	14	69	0	46	2	10	10	4	0
November	37	5	235	3	75	8	49	10	12	8
December	13	15	12	25	23	17	44	11	17	0
Sum	389	16	934	12	752	14	559	21	285	27



**FIGURE 3** Stomach content weights (SCW) (g) (including mucus) of *Gadus morhua* per predator length class (panels) and month. Boxplots show medians with first and third quartiles (hinges) of the observed SCW from the Belt Sea (SD 22). SCW were length-standardized within each length class. Whiskers range from the upper/lower hinge to the largest value, but no further than  $1.5 \times \text{IQR}$  (interquartile range) from the hinge, respectively. Black dots represent outliers that are SCW above  $1.5 \times \text{IQR}$  from the upper hinge. Note different scale on y-axis

The length-standardized SCW over both sampling years varied within all length classes (Figure 3). During the summer period, between June and July, lowest median SCW were found within all predator length classes, except for the smallest length class (i.e., 31–40 cm). Furthermore, an M-shaped pattern in the median SCW of all length classes <61 cm was observed, displaying two periods with greater stomach contents: one during spring (i.e., April and May) and one during autumn (i.e., October and November). Cod  $\geq 61$  cm also showed higher median SCW in spring and autumn; nonetheless, the median SCW in December showed higher values compared to November (Figure 3).

### 3.2 | Variations in the stomach content weight of adult cod

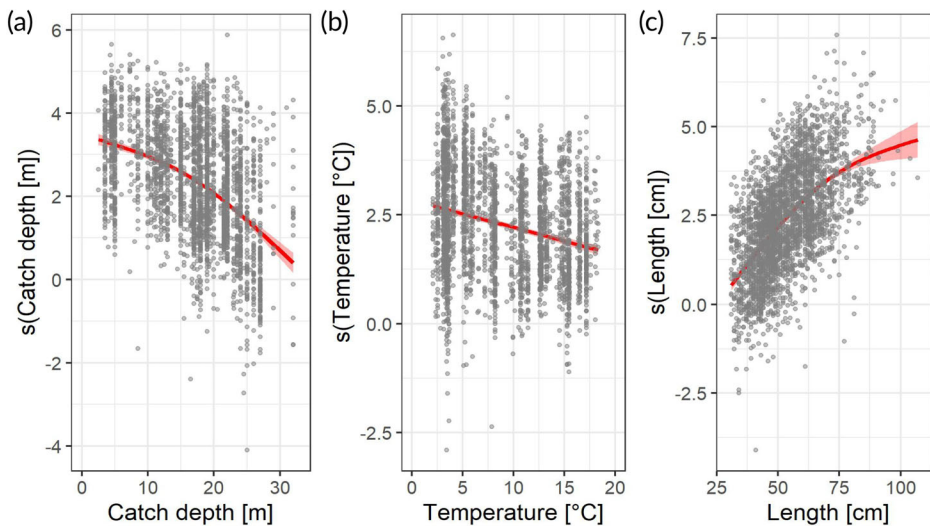
The GAM using depth stratum, water temperature at depth stratum and body length as explanatory variables explained 40% of the variance of the log-transformed SCW. Depth stratum and water temperature showed negative relationships with SCW (Figure 4a and b). In contrast, body length showed a positive relationship with SCW (Figure 4c). Although the effect of water temperature was linear, the shape of the depth stratum and length effect curves resembled an exponential function (Figure 4a and c). All smoothing terms were highly significant ( $P < 0.001$ , Supporting Information S3.1).

### 3.3 | Diet composition

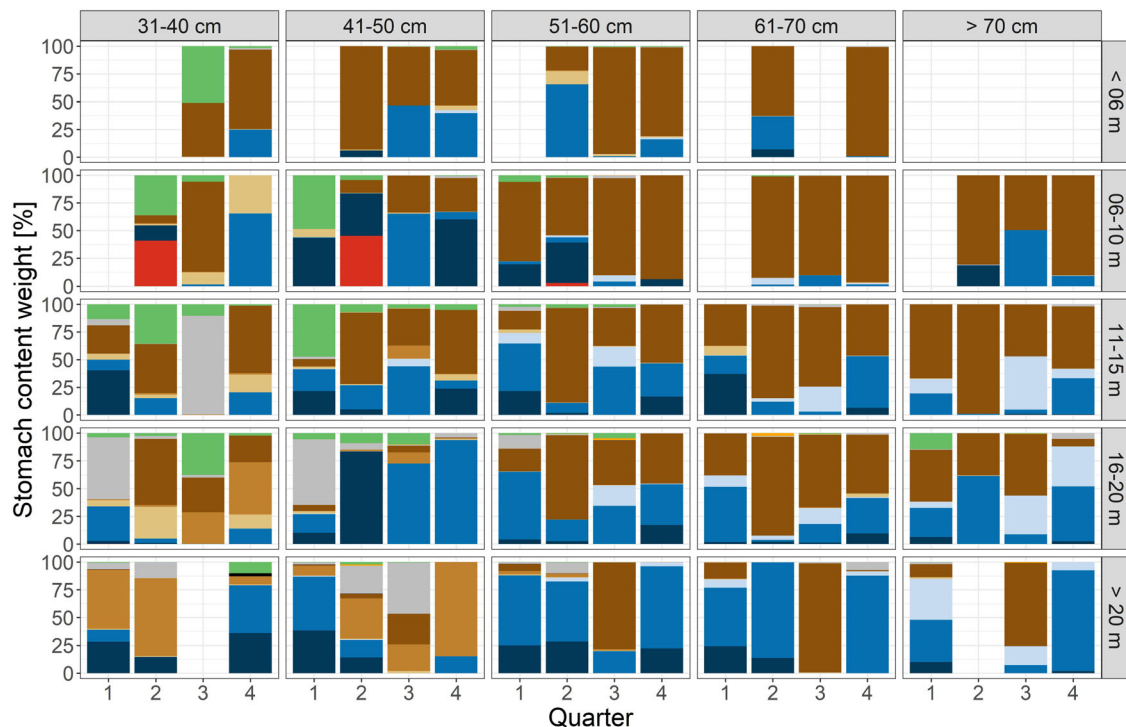
The common shore crab *C. maenas* was the main food item in all size classes (Figure 5). The proportion of common shore crabs generally decreased with increasing depth. Only in the third quarter *C. maenas* occurred also in stomachs from the deepest depth strata (up to 98% of the total SCW in length class 61–70 cm). Overall, the proportion of common shore crab increased with predator length with a maximum occurrence in the largest size class caught in medium depths (i.e., 11–15 m) in the second quarter (up to 99% of the total SCW) (Figure 5). Lowest proportions of *C. maenas* were observed in the first quarter (Figure 5).

Fish were also observed frequently in the cod stomachs. In total, 36 different prey fish species from 11 different orders were found in the stomachs. The proportions of fish prey increased with depths in stomachs of all predator sizes, and highest proportions were found in the deepest areas. Cod within the length class 41–50 cm contained higher proportions of fish in their diets compared to the smallest length class (>31–40 cm). Nonetheless, a general increase in the share of fish prey with body length was not observed (Figure 5).

The diet fraction of other fish consisted mainly of species of the orders Gobiiformes (including the invasive round goby *N. melanostomus*), Labriformes (e.g., *Ctenolabrus rupestris*) and Gadiformes (e.g., cod and four-bearded rockling *Enchelyopus cimbrius*) and to a lesser extent of species of the orders Beloniformes (e.g., *Belone belone*), Carangiformes (e.g., *Trachurus trachurus*), Perciformes (e.g., *Myoxocephalus scorpius* and *Pholis gunnellus*), Syngnathiformes



**FIGURE 4** Effect curves (red lines) and confidence intervals (red shading) of the explanatory variables at catch depth (a), water temperature at catch depth (b) and length of cod (c) used in the finally chosen generalized additive modelling. Partial residuals are displayed as grey dots



**FIGURE 5** Relative diet composition (by stomach content weight) of cod *Gadus morhua* from SD22 according to length class, depth stratum and quarter. Empty bar corresponds to depth and quarter with no sample of a given length class (■) Annelida (■) Echinodermata (■) Mollusca (■) Other invertebrata (■) *Carcinus maenas* (■) Peracarida (■) Other crustacea (■) Pleuronectiformes (■) Other fish (■) Clupeiformes (■) Other Prey

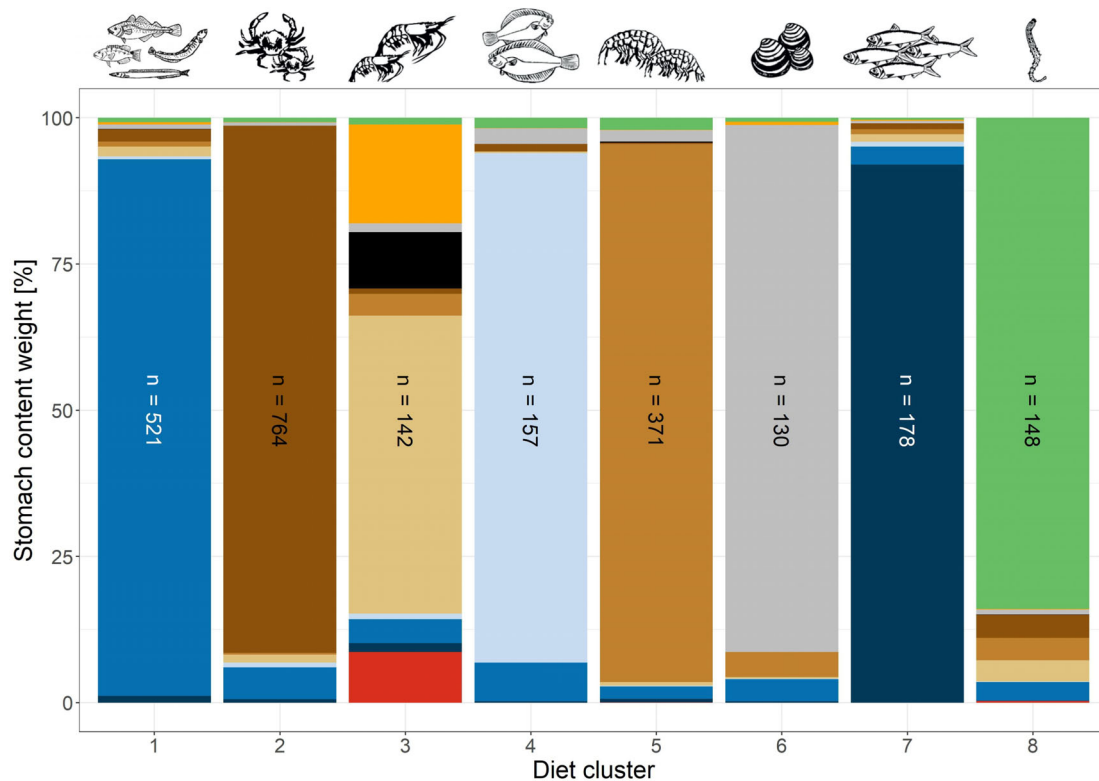
(e.g., *Sygnathus rostellatus*) and Uranoscopiformes (e.g., *Hyperoplus lanceolatus*) (Supporting Information Figure S4.1).

Other fish prey was observed in the diet of all length classes, and in all quarters (Figure 5 and Supporting Information Figure S4.1). Cod cannibalism was observed in 5% of all cod stomachs and within all length classes and depth strata. Largest proportions of cod in cod stomachs (with up to 100% of the prey fish composition) were found in the largest cod individuals (>70 cm) in the depth stratum 6–10 m in the third quarter and in length class 41–50 cm in the deepest depth

stratum ( $\geq 21$  m) in the fourth quarter (Supporting Information Figure S4.2).

The invasive round goby occurred in stomachs of all length classes of cod and in all depths and quarters. Highest proportions of round gobies in stomachs of cod  $\geq 51$  cm (over 50% of the total diet composition) were found in the fourth quarter in the deepest depth stratum ( $\geq 21$  m) of the study area (Supporting Information Figure S4.2). The diet fraction of flatfish increased with increasing body length, maximally amounting to 91% of the prey fish





**FIGURE 6** Relative prey group composition of identified diet clusters of *Gadus morhua* from SD22 (1 – other fish, 2 – common shore crab, 3 – other crustacea, 4 – Pleuronectiformes, 5 – Peracarida, 6 – Mollusca, 7 – Clupeiformes and 8 – Annelida). N displays the number of stomachs allocated to the diet cluster. Symbols above bars schematically represent the dominant prey group per cluster (■) Annelida (■) Echinodermata (■) Mollusca (■) Other invertebrata (■) *Carcinus maenas* (■) Peracarida (■) Other crustacea (■) Pleuronectiformes (■) Other fish (■) Clupeiformes (■) Other Prey

composition, and 48% of the total stomach content (i.e., for >70 cm in the third quarter). In contrast, in cod <51 cm flatfishes occurred only rarely with maximally 7% of the total stomach content (Figure 5 and Supporting Information Figure S4.1).

Other important fish prey were species of the order Clupeiformes (Figure 5 and Supporting Information Figure S4.1). This group consisted mainly of sprat *S. sprattus* and herring *C. harengus* and occurred mostly in diets of cod <61 cm. Higher proportions of sprat were mostly observed in stomachs of cod caught deeper than 10 m, whereas herring was a major food item of cod caught in shallower areas (i.e., <16 m depth), especially in the second quarter (Supporting Information Figure S4.2).

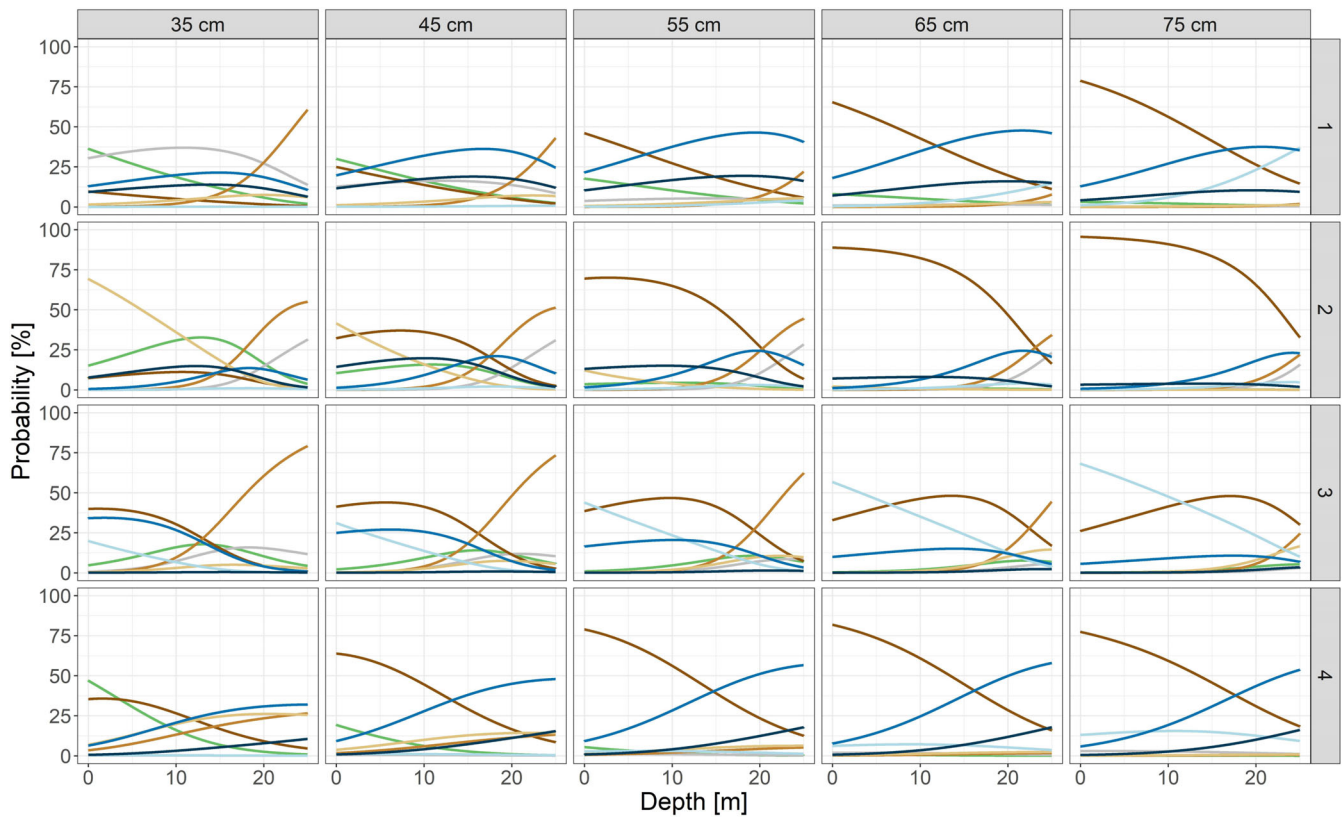
### 3.4 | Diet clusters

Hierarchical clustering of all individual cod diet compositions identified eight diet composition clusters (Figure 6). All clusters were dominated by one prey group used to identify the clusters: 1 – other fish, 2 – *C. maenas*, 3 – other crustacea, 4 – Pleuronectiformes, 5 – Peracarida, 6 – Mollusca, 7 – Clupeiformes and 8 – Annelida (Figure 6). The highest numbers of cod stomach samples were allocated to the diet cluster dominated by *C. maenas* ( $N = 764$  or 32%), followed by the diet cluster dominated by other fish ( $N = 521$  or 22%). A fewer

number of stomachs were allocated to the diet cluster dominated by Mollusca ( $N = 130$  or 5%) (Figure 6).

### 3.5 | Relationship of diet clusters with depth stratum, predator length and season

The multinomial log-linear model displayed a significantly better performance compared to the null model (McFadden's pseudo  $R^2 = 0.2$ ), suggesting that fish length, depth stratum and season have a major influence on the diet composition of adult cod (Figure 7). The Supporting Information Table S6.1 contains a list with all 84 model coefficient estimates. Smaller cod generally showed a great variability in diet cluster membership, whereas larger cod >65 cm belonged mostly to the clusters of other fish and *C. maenas* (Figure 7). The probabilities for the common shore crab cluster was greatest in shallower areas and decreased with increasing depth stratum. In contrast, the probability for other cluster membership increased with increasing depth stratum. For cod <50 cm, an increased probability for the Peracarida cluster with increasing depth stratum was predicted. In addition, seasonal effects were detected, for example, for large cod >70 cm, which showed an increased probability for the Pleuronectiformes cluster in shallower waters <15 m depth in the third quarter (Figure 7).



**FIGURE 7** Statistical model of diet cluster membership of adult *Gadus morhua* from SD22. Plots show the partial effects of catch depth (depth), quarters (quarters 1–4 are shown vertically below each other) and predator length (fixed predator lengths from 35 to 75 cm are shown from left to right) on the probability (%) of diet cluster membership (—) Annelida (—) *Carcinus maenas* (—) Other crustacea (—) Other fish (—) Mollusca (—) Peracarida (—) Pleuronectiformes (—) Clupeiformes

### 3.6 | Diet from depth >20 m vs. diet at ARDs

Comparisons of the diet compositions of cod calculated for the ARDs displayed several striking differences to those calculated for the trawlable sites (depth stratum >20 m). Diet compositions of cod in all length classes were characterized by higher proportions of fish prey at trawlable sites, except for the third quarter (Figure 8). Inversely, the diet compositions at assumed residence were always characterized by higher proportions of benthic invertebrates. The most striking differences emerged for the second quarter, where particularly higher shares of common shore crab in the diet at the assumed favoured residence depth (6–10 m) compared to those from the >20 m depth stratum were observed. For example, for the length class 61–70 cm in the second quarter, common shore crab accounting for more than 90% of the total diet composition at the ARDs was observed, whereas it was absent from the diets of individuals caught in depths at the depth stratum >20 m.

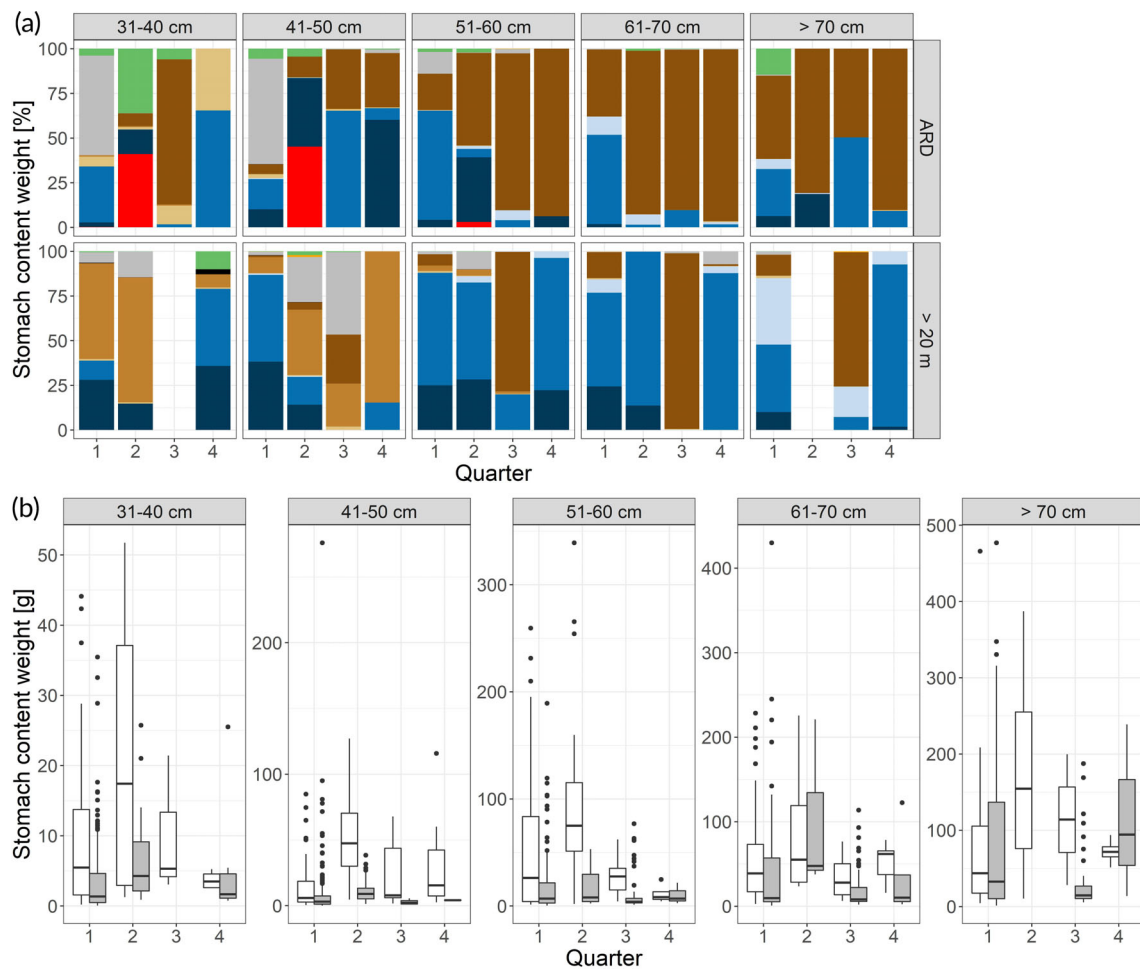
The comparison of SCW revealed also strong differences between cod sampled at assumed favoured residence depths and those sampled at trawlable sites (Figure 8). The authors consistently observed higher median SCW in the samples at the ARDs, except for two cases (i.e., the fourth quarter for length class >70 cm and the first quarter for length class 41–50 cm). These differences were most pronounced in the second and the third quarters, e.g., in the third quarter

for length class >70 cm, the median SCW was eight times higher at the ARD than at depth >20 m.

## 4 | DISCUSSION

### 4.1 | Feeding grounds of Belt Sea cod

The importance of shallow-water areas as feeding habitats of cod in the Belt Sea is emphasized by the observed depth-specific patterns in SCW. The statistical modelling results suggested that body length, water temperature and depth stratum affect SCW of adult cod. Increasing catch depth showed a clear negative effect on SCW, underlining the great importance of shallow-water areas for the quantitative food intake of cod in the Belt Sea. The shallow-water phases in spring and autumn coincide with the periods of post- and pre-spawning periods of WBC (Bleil *et al.*, 2009), presumably to refill exhausted energy reserves after spawning (spring) and to build up energy reserves for the next spawning season (autumn) (Funk *et al.*, 2020). The intensive use of shallow-water areas may reflect a higher prey availability and accessibility in these areas during spring and autumn. The observed lower SCW at the deeper habitats might be explained by a lower feeding activity and/or food scarcity. Deeper areas are



**FIGURE 8** Comparison of relative diet composition (a) and stomach content weights (SCW) (b) per predator length class and quarter between samples from assumed residence depth (ARD) stratum (quarter 1: 16–20 m; quarters 2–4: 6–10 m) and samples from depth stratum >20 m in the Belt Sea. Colours of boxplots indicate depth strata (white – ARD stratum; grey – stratum >20 m). SCW were length-standardized within each length class. Whiskers range from the upper/lower hinge to the largest value, but no further than  $1.5 \times \text{IQR}$  (interquartile range) from the hinge, respectively. Black dots represent outliers that are SCW above  $1.5 \times \text{IQR}$  from the upper hinge (■) Annelida (■) Echinodermata (■) Mollusca (■) Other invertebrata (■) *Carcinus maenas* (■) Peracarida (■) Other crustacea (■) Pleuronectiformes (■) Other fish (■) Clupeiformes (■) Other Prey

used by adult cod mostly during winter and summer (Funk *et al.*, 2020). In winter during spawning time (Bleil *et al.*, 2009), WBC move to the deeper, more saline areas that provide suitable conditions for egg buoyancy (Nissling & Westin, 1997; Petereit *et al.*, 2014). In contrast, the movement towards deeper areas in summer is most likely an avoidance response towards high water temperatures in shallower areas (Freitas *et al.*, 2016; Funk *et al.*, 2020).

In winter food intake might be reduced because of a combination of low temperatures, reduced gastric evacuation and spawning activity. Lower ambient temperatures result in lower metabolic costs (Saunders, 1963) and energy requirements of cod and – because of slowed gastric evacuation – most likely also in fewer feeding events. Slow gastric evacuation should lead to a fuller stomach at the same feeding rate, but the observed SCW were actually lower than those during other seasons, suggesting that feeding was greatly reduced during this period. In fact, feeding experiments with spawning cod showed depressed feeding activity regardless of water temperature

(Fordham & Trippel, 1999). Therefore, lower SCW in winter are most likely related to temperature- and spawning-induced depression in feeding activity in cod.

In summer, when water temperatures are highest, local gillnet fishers report a period with a general decreased activity of cod (Funk *et al.*, 2020; pers. comm. with local gillnet fishers). These periods of low movement activity during peak summer may also go along with a reduced feeding activity because of temperature stress, which might explain the low SCW in peak summer months (*i.e.*, from late June to the end of August). During the peak summer months, the authors also observed highest proportions of completely empty stomachs in depth >20 m, pointing towards an overall depressed feeding activity at greater water depths in summer, regardless of the fact that only these areas presumably provide appropriate ambient water temperatures for cod at this time. Low SCW in summer in the areas deeper than 20 m might be related to limited food availability. Mobile epibenthos organisms, such as the common shore crab, tend to remain in

shallower coastal waters from spring to late autumn (Pihl & Rosenberg, 1982), leading to a limited food supply at deeper habitats. Thus, especially during the peak summer period in July and August, there is a trade-off between prey availability and physiological temperature tolerance limits in the shallow coastal zone (Funk *et al.*, 2020). The assumption of food limitation at water depth >20 m in summer is further supported by observations of local gillnet fishers (pers. comm. with local gillnet fishers), who temporarily reported high abundances of cod in shallow waters after strong wind events during the peak summer period (Funk *et al.*, 2020). Strong wind pulses can lead to local disturbances of the thermal stratification and temporary temperature drops in coastal shallow-water areas (local upwelling) resulting in local changes in cod behaviour. Similar changes in distribution in relation to summer upwelling events were also described for cod in a south Norwegian Fjord, and it was hypothesized that cod quickly take advantage of windows of opportunity to enter the shallow-water habitats to feed (Freitas *et al.*, 2015, 2016). The argument of food scarcity and size-indiscriminate feeding (Ursin & Arntz, 1985) in the deeper areas of the Belt Sea in summer is further substantiated by the observation that cod >60 cm fed on the small peracarid species *Diastylis rathkei* in areas >20 m water depth in the third quarter.

## 4.2 | Changes in diet composition

The common shore crab is a major food item for all length classes, but the importance decreased with water depth. The authors also observed seasonal differences in the proportion of *C. maenas* with lowest shares of common shore crabs in the first quarter, similar to a study on cod diet in the Skagerrak region (Hop *et al.*, 1992). Reduced proportions during winter with lowest annual water temperatures in shallower waters might be explained by a reduced activity of *C. maenas* at low water temperature condition (Dries & Adelung, 1982), which presumably makes them more difficult for cod to detect. The common shore crab was already part of the diet in historic analyses of stomachs from waters deeper than 20 m (Arntz, 1977; Schulz, 1987, 1988). Nonetheless, the share of *C. maenas* in the samples of this study from depth >20 m was greater, and the overall dietary importance of the common shore crab including all depth strata was outstanding. In the 1980s, *C. maenas* occurred in maximum 6% of the stomach contents of body length  $\geq 65$  cm (Schulz, 1988), whereas proportions of more than 90% of common shore crabs for some length classes were observed in this study. Long-term, depth-specific trends of *C. maenas* abundance in the Belt Sea are unknown. Nonetheless, the relatively high shares of *C. maenas* in the diet might be related to a density-dependent increase in *C. maenas* availability for cod. The low stock status of WBC might have resulted in a lower predatory pressure on the common shore crab population in the area and thus a higher food supply for the remaining cod.

In the 1960s, benthic invertebrates were also identified as important food source for adult cod caught during scientific trawl surveys in

depth >20 m in the Kiel Bight (Arntz, 1977). High proportions of the mussel species *Arctica islandica* dominated the stomach contents, and a high proportion of polychaeta and crustaceans were observed (Arntz, 1977). Stomach samplings in 1980s revealed that benthic invertebrates were only a minor food source (Weber & Damm, 1991). The authors of this study observed highest proportions of *A. islandica* in stomach samples from the second and the third quarters, which coincided with the observations of Arntz (1977) who observed highest frequencies after spawning time and in early summer. Unlike Arntz (1977), the authors of this study observed higher proportions of *A. islandica* for cod in length classes <51 cm only, whereas Molluscs in general played a minor role in the diet of larger cod. Arntz (1974) observed that cod ingest mussels previously damaged by otter boards and hypothesized that fluctuations in the amount of *A. islandica* consumed by cod might also be related to differences in trawl activity in the study area.

Clupeids, especially herring, were the main prey organisms of cod in the 1980s (Schulz, 1988; Weber & Damm, 1991), which accounted for high proportions in the diet in all four quarters. In contrast, clupeids were only a minor part of the diet in 2016 and 2017. Herring might be less available as prey for cod now compared to the 1980s because of a decrease in the biomass of spring spawning western Baltic herring in the study area since the past two decades (ICES, 2019b, 2019c). Therefore, the higher shares of benthic invertebrates and other fish species in the contemporary diet composition of cod in areas deeper than 20 m could reflect a compensatory feeding behaviour to account for a lack of herring compared to the 1980s when herring was more abundant.

This study presents the first observation of round goby as a prey item for cod in the Belt Sea. Round goby is an invasive species in the Baltic Sea and was first recorded in the southern Baltic Sea in 1990 (Skora & Stolarski, 1993) and some years later in adjacent waters of the Belt Sea at the River Trave and in the Kiel Canal (Hempel, 2017). Round goby was also observed as a new prey species of cod in the southern Baltic Sea (Almqvist *et al.*, 2010; Pachur & Horbowy, 2013). Higher proportions of round gobies were found especially in the first and fourth quarters in depth  $\geq 16$  m, whereas they occurred in shallower areas mainly between the second and the beginning of the fourth quarters. This might reflect a seasonal vertical movement pattern of round gobies from shallower to deeper areas with decreasing water temperatures (Christoffersen *et al.*, 2019; Sapota & Skóra, 2005), similar to the native sand goby *Pomatoschistus minutus* (Arntz, 1974). Round gobies are a relatively easy prey in areas with little shelter (Almqvist *et al.*, 2010). Compared to native goby species, the round goby can reach larger maximum lengths (190–250 mm; Sapota, 2012), making them an attractive prey species even for larger adult cod.

In previous studies, WBC was reported to shift diet from benthic invertebrate prey towards fish prey with increasing length (Arntz, 1977; Bagge, 1979; Schulz, 1988; Weber & Damm, 1991). For example, Weber and Damm (1991) observed high shares of benthic invertebrates accounting for more than 50% of the total diet only for cod <40 cm. In the diet of cod >70 cm, they observed lesser proportion of benthic invertebrates (between 2% and 21%). The data of this

study confirm an ontogenetic shift from benthic invertebrate to fish prey only when also focusing on the diet composition of samples from areas >20 m depth. A supposed diet shift in the areas deeper than 20 m water depth was most pronounced in the first quarter, when the proportion of invertebrates in cod <40 cm was highest (61%), whereas for larger length classes the diet was dominated by fish prey (84–88% of the total diet). An exception was the third quarter when high proportions (at least 76%) of benthic invertebrates were observed in the diet of all length classes.

Nonetheless, unlike the historic and recent picture emerging from samples of areas deeper than 20 m water depth, a focus on shallower areas, such as the ARD, did not support an ontogenetic feeding shift from invertebrates towards fish with increasing length. In contrast, overall a dietary shift towards higher proportions of *C. maenas* with increasing body length was observed. For cod >50 cm, the common shore crab was the main prey organism in ARD. The depth-specific patterns in the diet composition of cod in the Belt Sea suggest that previous investigations based on samples from water deeper than >20 m could provide only an incomplete picture of the real diet composition. The authors showed that omitting shallow-water areas from the stomach sampling leads to a significant underestimation of the role of benthic invertebrates, especially of the common shore crab, whereas the role of fish as prey for adult cod is overestimated.

#### 4.3 | Limitations of the study

Differences in prey-specific gastric evacuation rates of crustacean species may lead to the fact that invertebrates with chitinous exoskeletons such as *C. maenas* remain longer in the stomachs than for example fish prey (Andersen *et al.*, 2016; dos Santos & Jobling, 1995; Temming & Herrmann, 2003). Therefore, the relative composition of stomach contents described here is not the actual prey composition of cod in terms of food intake. In actual food intake, the portion of slowly digestible prey is lower than in the stomach contents. This overestimation might be even more pronounced in the third quarter, when high ambient temperatures lead to an increased gastric evacuation rate. The authors estimated the possible bias of diet composition in terms of food intake using prey-specific differences in gastric evacuation rates (Supporting Information Figure S7.1). The results confirmed the general picture of significant depth-specific differences in prey composition of SCW (Figure 5). The proportions of the common shore crab are smaller in terms of food intake than those directly observed from SCW, but in both cases the common shore crab is one of the main prey organisms of cod (especially in the shallow areas). Therefore, the bias related to differences in gastric evacuation rates does not jeopardize the conclusions of this study.

The use of different gear types and methods significantly improved spatio-temporal coverage of this study, but it also complicates the standardization and weighting of the results. For example, the authors could not use catch-per-unit-effort values to calculate representative diet compositions for a length class over the whole study area. The use of capture methods other than trawling in

stomach sampling programmes is often debated (Bromley, 1994; Hayward *et al.*, 1989; Iyabo, 2014). The comparison based on the data set of this study (see Supporting Information S2 for further discussion) suggests that cod stomach data obtained from different fishing gears are comparable in terms of food quantity. Nonetheless, the comparison and statistical analyses of this study concerning the gear effects are limited by the low number of samples available. Evaluating the gear effect on diet composition may require a thorough experimental set-up using different fishing methods at the same day and location, as well as shorter soaking times and more frequent hauling intervals for gillnets over 24 h.

It can be assumed that different habitats, even within one depth level, have different attractiveness for different species. Therefore, the prey availability and thus diet composition might be strongly related to the habitat at the sampling station. The authors have not considered habitat-specific differences as they often had no further information about the fishing locations except for the depth. Nonetheless, it can be assumed that most of the samples collected outside the spawning season at depths between 5 and 20 m were fished on (vegetated) hard ground habitats (characterized by cobbles, boulders or rocky reef structures), as these are the preferred fishing habitats of local fishers at these depths (Funk *et al.*, 2020). Samples from deeper sites (>20 m) can be considered to originate almost all from muddy bottoms, whereas those from shallower areas (<5 m) originate most likely from habitats with seagrass meadows or sandy bottoms (Funk *et al.*, 2020). Therefore, it is assumed that the habitats and thus also the prey availability within one depth stratum were comparable. Nevertheless, the inclusion of a habitat variable could provide further insights into the food intake of cod and, therefore, should be considered in future research.

Furthermore, there are shortcomings concerning the unequal number of samples per depth, season and length influencing the analyses of this study. For example, the authors used monthly mean diet compositions to counteract unbalanced numbers of samples when calculating quarterly diet composition of cod. Nonetheless, in some cases, when there were only few samples available in a month, these samples got an unintended higher weighting. Moreover, there might be several interactions between length, depth and temperature or other confounding factors affecting the food intake of cod. Nonetheless, the data set with uneven sampling and low number of samplings in shallow areas limits the investigation of more complex patterns. The statistical analyses presented here give a first impression on the overall effects of these variables on the food intake (GAM) and diet composition (clustering and multinomial logistic regression model) of cod in the study area. The uneven sampling results in uneven uncertainties and more samplings in low sampled areas may also influence and reshape some of the identified relationships with high uncertainties.

#### 4.4 | Conclusions

Unlike the historic perception of Belt Sea cod as a year-round fish predator (Weber & Damm, 1991), contemporary data of this study



highlight that cod in this area mainly relies on benthic invertebrates such as *C. maenas* captured in shallow-water areas. Moreover, monthly sampling of this study revealed strong seasonal, length- and depth-specific patterns in habitat and food use. These new findings have important implication for food web and ecosystem models. Especially the predatory impact of cod on herring might be largely overestimated in current multispecies models.

The use of different gear types and methods significantly improved spatio-temporal coverage of this study, but it also complicates the standardization and weighting of the results. For example, the authors could not use catch-per-unit-effort values to calculate representative diet compositions for a length class over the whole study area. To use this kind of multi-source data to calculate diet compositions or consumption rates on population levels, sound knowledge on the spatio-temporal distribution of the investigated species will be needed.

The results of this study suggest that it is very likely that previous investigations on food intake and diet composition based on trawl data from habitats >20 m depth were biased. The authors attempted to provide a first impression of the potential bias by presenting the differences in SCW and in the diet composition, when samples are taken either from preferred habitat sites or from trawlable sites >20 m depth only (as previously performed in historic diet investigations). The results of this study showed that diet composition and food intake of cod largely differ, when only samples from depth >20 m are considered. SCW were remarkably higher in ARDs, which strongly points towards an underestimation of true consumption rates in this area when relying on samples from the deep areas only. Furthermore, higher proportions of fish in diet of cod sampled in depth >20 m indicate that a limited sampling design may lead to a general overestimation of the importance of fish as prey for cod in the region especially if cod is relying on shallow-water areas during periods of major food intake. In turn the importance of invertebrates such as the common shore crab is most likely underestimated in studies relying on a limited depth coverage.

Consequently, to ensure a thorough picture of the food web interactions, planning stomach sampling programmes of demersal fish stocks should consider the full spatio-temporal dynamics of the target species.

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## AUTHOR CONTRIBUTIONS

S.F. was responsible for the stomach analysis and analysis of the data and wrote the first version of the manuscript. R.F. and C.M. were involved in the statistical analysis. U.K. and A.T. helped to develop the study design. U.K. helped to coordinate the stomach sampling and provided personal contacts to local fishers involved in the stomach sampling. R.F., U.K., C.M. and A.T. critically revised subsequent versions of the manuscript.

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